Forest Ecology and Management 255 (2008) 3515–3523

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Full length article

Thermal requirements, field mortality and population phenology modelling of *Paropsis atomaria* Olivier, an emergent pest in subtropical hardwood plantations

Helen F. Nahrung [a,b,*], Mark K. Schutze [a], Anthony R. Clarke [a], Michael P. Duffy [a], Elizabeth A. Dunlop [a,c], Simon A. Lawson [b]

[a] School of Natural Resource Sciences, Queensland University of Technology, GPO Box 2434, Brisbane, Queensland 4001, Australia
[b] Horticulture and Forestry Science, Department of Primary Industries & Fisheries, Gate 3, 80 Meiers Road, Indooroopilly, Queensland 4068, Australia
[c] Environmental Operations Division, Environmental Protection Agency, GPO Box 2771, Brisbane, Queensland 4001, Australia

ARTICLE INFO

Article history:
Received 12 November 2007
Received in revised form 14 February 2008
Accepted 21 February 2008

Keywords:
Eucalypt
DYMEX™
Voltinism
Seasonal plasticity

ABSTRACT

Paropsis atomaria is a recently emerged pest of eucalypt plantations in subtropical Australia. Its broad host range of at least 20 eucalypt species and wide geographical distribution provides it the potential to become a serious forestry pest both within Australia and, if accidentally introduced, overseas. Although populations of *P. atomaria* are genetically similar throughout its range, population dynamics differ between regions. Here, we determine temperature-dependent developmental requirements using beetles sourced from temperate and subtropical zones by calculating lower temperature thresholds, temperature-induced mortality, and day-degree requirements. We combine these data with field mortality estimates of immature life stages to produce a cohort-based model, ParopSys, using DYMEX™ that accurately predicts the timing, duration, and relative abundance of life stages in the field and number of generations in a spring–autumn (September–May) field season. Voltinism was identified as a seasonally plastic trait dependent upon environmental conditions, with two generations observed and predicted in the Australian Capital Territory, and up to four in Queensland. Lower temperature thresholds for development ranged between 4 and 9 °C, and overall development rates did not differ according to beetle origin. Total immature development time (egg–adult) was approximately 769.2 ± S.E. 127.8 DD above a lower temperature threshold of 6.4 ± S.E. 2.6 °C. ParopSys provides a basic tool enabling forest managers to use the number of generations and seasonal fluctuations in abundance of damaging life stages to estimate the pest risk of *P. atomaria* prior to plantation establishment, and predict the occurrence and duration of damaging life stages in the field. Additionally, by using local climatic data the pest potential of *P. atomaria* can be estimated to predict the risk of it establishing if accidentally introduced overseas. Improvements to ParopSys' capability and complexity can be made as more biological data become available.

1. Introduction

Commercial hardwood production forests are a recent initiative in subtropical Australia, with large-scale eucalypt planting recently exceeding 90,000 ha (Parsons et al., 2006). The concomitant emergence of insect pests associated with plantations, and the growth and economic losses they cause, are among the most serious problems faced by plantation managers (Ohmart, 1990). For example, paropsine chrysomelid beetles cause significant defoliation that can affect the growth rate, height, volume, and possibly pulpwood quality of trees (Candy et al., 1992; Elek, 1997; Elliott et al., 1998), and are major pests in the commercial eucalypt-growing regions of Australia (de Little, 1989; Simmul and de Little, 1999), South Africa (Tribe, 2000) and New Zealand (Withers, 2001).

Paropsis atomaria Olivier (Coleoptera: Chrysomelidae) is one such paropsine pest of eucalypts. This species has four larval instars and long-lived adults that all feed on the new growth of trees, removing apical leaves and resulting in a characteristic broom-topped appearance to trees (Cumpston, 1939; Carne,

* Corresponding author at: Horticulture and Forestry Science, Department of Primary Industries & Fisheries, Gate 3, 80 Meiers Road, Indooroopilly, Queensland 4068, Australia. Tel.: +61 7 3896 9781; fax: +61 7 3896 9567.
E-mail address: helen.nahrung@dpi.qld.gov.au (H.F. Nahrung).

0378-1127/$ – see front matter.
doi:10.1016/j.foreco.2008.02.033

1966a). *P. atomaria* is the most abundant paropsine beetle in plantations of *Eucalyptus cloeziana* (F. Muell.) (Nahrung, 2006), and other eucalypt species (Lawson, personal observation), and as such poses a risk to hardwood productivity in New South Wales (NSW) and Queensland (Qld) (Stone, 1993; Lawson and King, 2002; Schutze et al., 2006). Although initially not considered a major problem in commercial eucalypt plantations (see Wylie and Peters, 1993; Elliott et al., 1998; Strauss, 2001), *P. atomaria* is now a documented pest of *E. grandis* (Hill ex Maiden), *E. cloeziana* and *E. pilularis* Smith in Qld and NSW, and of *E. camaldulensis* Dehnh., *E. dunnii* Maiden and *E. pilularis* Smith in NSW (Simmul and de Little, 1999), and is associated with *Corymbia citriodora* subsp. *variegata* (F. Muell.) A.R. Bean and M.W. McDonald in Queensland (Nahrung, 2006), and several eucalypt species in Victoria (Collett, 2001) and South Australia (Philips, 1996). Its pest potential is further evidenced by its specific inclusion as a containment hazard in the United States (Eisler, 1999; Kliejunas et al., 2003) and as a regulated pest in New Zealand for eucalypt-associated imports from Australia (MAF, 2003).

P. atomaria represents a single genetic species (Schutze et al., 2006) throughout its geographical distribution from South Australia and Victoria to northern Qld, and it has a broad host range of around 20 eucalypt species (CABInternational, 2005). Published research on *P. atomaria* originates predominantly from the Australian Capital Territory (ACT), and although we can now reliably use these data in relation to subtropical populations because populations are genetically similar (Schutze et al., 2006), climatic variation between regions may result in significant differences in population dynamics. For example, in the ACT, *P. atomaria* is bivoltine (Carne, 1966a), but in South-East Qld (SEQ) it can undergo up to four generations each year (Nahrung, 2006; Duffy, 2007).

Understanding the life history and population dynamics of pests is paramount to achieving their long-term management (Cox, 1994; Nylin, 2001), while seasonal predictability of the appearance and duration of susceptible life stages is essential for effective application of control measures. Further, the requirements for accurate forest health reporting (Stone and Coops, 2004), certification of forests for sustainability (Stone and Coops, 2004; Govender, 2002), and the contentiousness of pesticide use (Jenkin and Tomkins, 2006), mean that effective targeted management strategies are important. Here we present underpinning research and a population phenology model, ParopSys, to help deliver such targeted management for *P. atomaria*.

Laboratory trials were used to determine thermal requirements of immature stages of *P. atomaria* and these results were integrated with estimations of field mortality through the DYMEX™ modelling programme (Maywald et al., 2004), which has been used to produce predictive models for other hardwood forestry pests, including gumleaf skeletoniser (Farr, 2002) and autumn gum moth (Steinbauer et al., 2004). Lower temperature thresholds, development rates, and mortality were calculated using beetles originating from temperate and subtropical regions of Australia. Phenological sampling (not used in model construction) was conducted to assess the model's ability to predict voltinism, life stage peaks and durations.

2. Materials and methods

2.1. Thermal requirements and thresholds for immature *P. atomaria* life stages

Although Carne (1966a) reported development rates of an ACT population of *P. atomaria* at 5–6 constant temperatures (7.2–29.4 °C), we conducted our own development trials for this study. We considered that inherent inaccuracies in reading from the development time curves presented and subjectively determining the linear portion of Carne's results may cumulatively render DD estimates unreliable. Further, the question of local adaptation and isolation-by-distance (see Schutze et al., 2006) and differences in voltinism (Nahrung, 2006) between temperate and subtropical populations may also mean that results from the ACT do not apply to subtropical populations. We therefore conducted a new series of constant temperature-development trials using *P. atomaria* collected from the ACT and Queensland. These experiments also formed part of a larger study (see Schutze and Clarke, 2008) examining the species status, causes of intraspecific body size variation, and host plant utilisation of *P. atomaria* throughout its geographical range.

P. atomaria were collected from two field sites (ACT (Canberra) 35°18′51″S, 149°09′16″E and Qld (Lowmead) 24°29′22″S, 151°42′14″E) in December 2004 and January 2005, and 50–100 beetles from each site were maintained in separate outdoor colonies on *E. tereticornis* Smith foliage.

Egg batches were collected daily from rearing colonies, placed in Petri dishes (one egg batch per dish), and maintained at one of four trial temperatures: 16, 2, 24 and 27 °C. Between 9 and 13 replicate egg batches were used for each temperature/population origin treatment, with egg development time recorded as the number of days from egg batch laying to larval eclosion.

For larval development trials, larvae hatched from egg batches in each colony were divided between temperature treatments to control for possible maternal effects. Twenty neonate larvae (which had been allowed to feed on their egg chorion) were placed in each replicate container (Petri dish: 10–13 replicates per population), together with foliage and moistened filter paper. Temperatures used were the same as for the egg development trials. Larvae were supplied daily with fresh *E. pilularis* leaves taken from potted or plantation trees. To control for possible diet effects, on any 1 day all leaves supplied to larvae came from one source, with individual shoots randomised before being placed in rearing containers.

Replicates were checked daily and instar changes noted: instar duration was calculated based on when 50% of surviving individuals had moulted into the next stage. Once greater than 50% of larvae in any one replicate reached Liii, all larvae were transferred to larger containers for the remainder of larval development. When individuals reached the pre-pupal stage (characterised by cessation of activity and longitudinal compression, see Cumpston, 1939; Carne, 1966a), they were removed from rearing containers and placed in clean Petri dishes until adult eclosion. Between 10 and 13 replicates were conducted for each population (ACT and Qld) and treatment temperature, but not all replicates survived through to adult eclosion, especially Qld individuals reared at 27 °C (due to increased mortality during development).

Six immature developmental stages were used in DD and T_0 calculations (egg, Li, Lii, Liii, Liv, pre-pupa + pupa), and development time for each stage was considered as the number of days until 50% of the surviving cohort reached the subsequent stage. Pre-pupal and pupal stages were combined at the outset because they are non-feeding, difficult to sample in the field, and ecologically inactive. Data were analysed using mean development rate (the reciprocal of development time) for each developmental stage for each treatment temperature. A linear regression model was fitted to the development rate for each of the six immature life stages described above, yielding for each an equation in the form $y = a + bx$, where y is the rate of development (1/days), x is temperature, a is the intercept and b is the slope. An analysis of covariance (ANCOVA) was conducted for each developmental stage to determine whether development rate differed between

population origin. Total immature development time did not differ between ACT and Qld populations except at 16 °C (Schutze and Clarke, 2008); nor was there any difference in development rate for each immature stage separately (see Section 3) so mean development data for each site were pooled for DD and T_0 calculations. Because early instars (Li and Lii) are difficult to differentiate in the field (Duffy, 2007), they were combined into an additional developmental stage to enable model development and validation, and permit application of field-based mortality estimates. The lower temperature thresholds (T_0) for development were estimated by solving the regression equation for development rate = 0 (x-intercept, i.e. the temperature below which no development occurs), and the number of DD required for each life stage was estimated by $1/b$ for each immature life stage (as in Nahrung et al., 2004). Standard errors for T_0 and DD estimates were calculated using the methods of Campbell et al. (1974).

2.2. Mortality of immature life stages

2.2.1. Laboratory estimates

Using data from the development rate experiments outlined above, mortality was compared between beetle origin (ACT and Qld) and treatment temperature, following arcsine-square-root transformation of mortality rates, using a two-way ANOVA, with post hoc differences between temperature treatments identified using Fishers LSD test. Stage-specific mortality as a function of temperature was also determined, and compared using a two-way ANOVA (temperature × development stage). Overall laboratory egg–Li mortality data were estimated using the average hatch rate of unparasitised field-collected egg batches reported by Duffy (2007) and Duffy et al. (in press).

2.2.2. Field estimates

To compare laboratory mortality estimates and mortality in the presence of natural enemies (see Nahrung et al., in press), field surveys counting the number of eggs, early instar larvae (Li + Lii), Liii, and Liv were conducted at 2-weekly intervals between September 2004 and April 2005 at two *E. cloeziana* plantation sites as follows: *Site I* 26°04′30.72″S, 152°44′8.88″E. Mean average daily temperature was 22.48 ± 0.19 °C, maximum mean 28.75 °C and minimum mean 13.75 °C; and *Site II* 26°11′20.4″S, 152°29′40.2″E. Mean average daily temperature was 22.66 ± 0.20 °C, maximum mean 29.5 °C and minimum mean 13.75 °C.

Eight sections across each plantation were representatively selected on each census date (different sections and trees each time), and three branches from each of six trees within each section were visually searched for *P. atomaria* life stages. The number of egg batches and larvae of each instar on these 144 branches was counted and used to determine the average number of every life stage present per branch throughout the field season. The population difference between egg and final instar larvae was calculated to estimate overall field mortality rates of immature stages. Mortality between each developmental stage was estimated using the total of all life stages recorded during the season at each site. Proportional mortality was calculated using the difference between the number of individuals in successional stages, and between egg and final instar larvae for overall immature mortality. An average egg batch size of 76 eggs per batch (Duffy, 2007) was used to estimate subsequent mortality rates.

2.3. Population modelling

2.3.1. Model description and overview

The model, ParopSys, describes the life cycle processes and population dynamics of *P. atomaria* in relation to climate. ParopSys was created using DYMEX™ V2 (Maywald et al., 2004). The life cycle processes for ParopSys were modelled on a daily time step for 236 days, representing the phase of the *P. atomaria* life cycle when the beetles are active on foliage (i.e. flying, feeding and mating) during the months of September–May (Duffy, 2007). The first time step (Day 1) begins on the 21st of September (when beetles were first observed in the field) and concludes on the 15th May (after which no adults were observed in the field, Duffy, 2007). Immigration and emigration are not explicitly considered, as they are assumed to be equal with no net effect on the numbers of eggs.

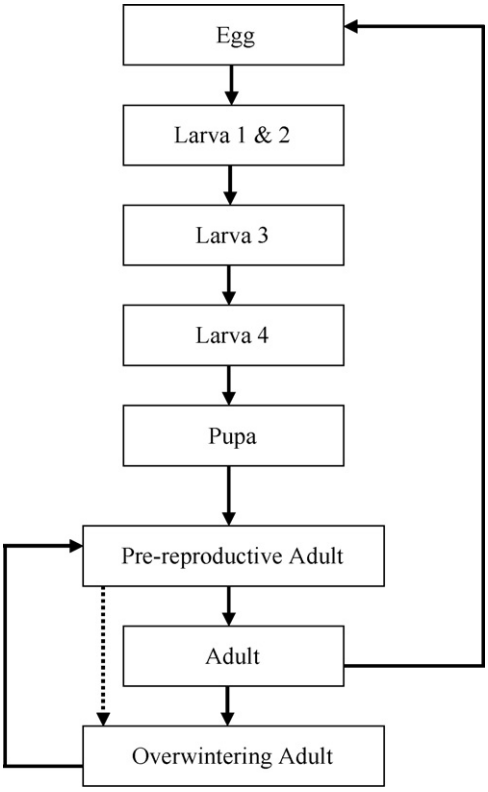

Fig. 1. Schematic diagram of the life cycle of ***Paropsis atomaria*** used in the DYMEX™ model.

ParopSys identifies eight discrete life stages in the *P. atomaria* life cycle: egg, early instar larvae (1st and 2nd instar), 3rd instar larvae, 4th instar larvae, pupae (pre-pupae and pupae), pre-reproductive adults, overwintering adults, and sexually mature adults (reproductive) (Fig. 1). A series of functions describe the lifecycle processes, including development and mortality rates for each life stage, as well as the transfer of individuals from one life stage to the next, and adult fecundity and rates of reproduction. Field and laboratory data presented within this paper were used wherever possible to derive life cycle functions. Where this data set was insufficient, data published in Carne (1966a) or unpublished laboratory estimates were used. Relationships of *P. atomaria* to environmental factors other than temperature were not explicitly considered.

2.3.2. Egg and larval development

The thermal thresholds and functions for rates of egg and larval development used in ParopSys are presented in Table 1. T_0 were entered as the threshold temperature, above which a linear relationship between temperature and development time occurred. High temperature-induced reduction in development rate was not considered in this model.

2.3.3. Mortality

Table 2 shows the average estimated mortality of each immature *P. atomaria* life stage experienced under field conditions.

Table 1
Developmental thresholds (T_0), thermal requirements (DD) and proportion of development time for immature life stages of *Paropsis atomaria*

Immature stage	Regression equation[a]	R^2, *P*-value	$T_0 \pm$ S.E. (°C)	DD ± S.E.	Proportion of immature life cycle[b]
Egg	$y = 0.008x - 0.0713$	0.98, <0.001	8.9 ± 0.7	125.0 ± 7.0	0.20
Li	$y = 0.0115x - 0.0607$	0.887, <0.001	5.3 ± 2.4	87.0 ± 12.7	
Lii	$y = 0.0156x - 0.0862$	0.884, <0.001	5.6 ± 2.4	64.1 ± 9.5	
Li + Lii	$y = 0.0066x - 0.0358$	0.887, <0.001	5.4 ± 2.9	166.7 ± 26.8	0.21
Liii	$y = 0.0145x - 0.0876$	0.927, <0.001	6.0 ± 1.8	69.0 ± 7.9	0.09
Liv	$y = 0.0037x - 0.0147$	0.703, 0.01	4.0 ± 6.9	270.3 ± 72.2	0.11
pp + p	$y = 0.0051x - 0.041$	0.964, <0.001	8.0 ± 1.1	196.1 ± 15.5	0.40

[a] Temperature range 16–27 °C. Linear regression model $y = a + bx$ where y is the rate of development (1/days), x is temperature, a is the intercept and b is the slope.
[b] At an average spring/summer temperature of 23 °C.

However, Table 2 does not quantify field mortality of pupae and adult beetles. Mortality experienced in laboratory trials was used instead, with a correction for increased mortality that would be experienced in the field by these stages. This was derived by calculating the average mean difference between field and laboratory mortality data for the egg through to 4th larval instar stages, and multiplying the pupal and adult lab mortality rates by this average value. In the model, pupae experience a 0.08 mortality rate on exit, while adult mortality and longevity was modelled using a constant mortality parameter of 0.006 per day (mortality associated with field predation and other biotic and abiotic factors) combined with mortality due to age. Beetles were assumed to live for 85.6 days based on mean longevity of adult beetles (average of Carne, 1966a,b; Nahrung, unpublished data). Rates for each possible cause of mortality in the field were not quantified explicitly. Therefore, in ParopSys, *P. atomaria* cohorts experience a combined total mortality on exit from each life stage.

2.3.4. Stage transfer

Stage transfer of egg and larval stages in ParopSys was determined by analysing the relationship between accumulated degree days and the proportion of individuals developing into each life stage at each temperature. The resulting pattern of transfer is predominantly linear (Maywald et al., 2004; our results not shown) and hence ParopSys uses a linear-above-threshold transfer function to determine transfer rate (i.e. the daily proportion of individuals in a cohort moving into a new stage). This function results in a spread of individuals transferring between stages whereby transfer commences at the lower heat threshold (accumulated degree days) and is completed at the upper heat threshold. Pre-pupal and pupal stages were considered together for the purposes of development rate estimation and therefore also in the model. As with the larval stages, development and transfer from the fourth larval instar used a linear above threshold function (Table 1).

2.3.5. Pre-reproductive adult development and fecundity

Development rates for pre-reproductive adult beetles (pre-oviposition period) were derived from Carne (1966a). Newly emerged adults undergo a period of maturation before being capable of oviposition, modelled as a linear above threshold function in the model (development rate = 0.0018, T_0 = 2.7 °C). Potential reproductive capacity of 640 eggs per female (Carne, 1966a) was used to describe fecundity. Because DYMEX™ does not specifically model sex ratios, a mean fecundity of 320 eggs per beetle was applied in the model based on the observed 1:1 operational sex ratio of this beetle (Duffy, 2007). A pulse function was used to describe the temporal distribution of egg laying, with batches of 32.5 eggs per adult being laid every 7 days (Carne, 1966a).

Table 2
Estimated mortality (proportion of eggs and larvae lost) at each immature life stage of *Paropsis atomaria* in the field at two sites (Li = first instar, Lii = second instar, Liii = third instar, Liv = fourth instar)

Life stage	Site I	Site II	Average ± S.E.
Egg to Li + Lii	0.81	0.68	0.75 ± 0.1
Li + Lii to Liii	0.60	0.74	0.67 ± 0.1
Liii to Liv	0.38	0.04	0.21 ± 0.2
All larvae (Li to Liv)	0.75	0.75	0.75 ± 0
Egg to Liv	0.95	0.92	0.94 ± 0.02

2.3.6. Overwintering adults

Carne (1966a) reported that *P. atomaria* overwintering in ACT populations is triggered by daylength and terminated in response to temperature, but he did not provide specific data that we could use in our model. Furthermore, the translation to SEQ populations may not be accurate. Arbitrary days of the year were therefore used in ParopSys to initiate (27th April) and terminate (21st September) overwintering. These dates coincide with changes in beetle activity observed in the field (Duffy, 2007). Adults are the only life stage that overwinter, and the model assumes that all pre-reproductive individuals present will overwinter between the 27th of April and the 21st September, with half (Nahrung, unpublished data) surviving to reproduce. In the model lifecycle, surviving over-wintered adults resume activity as pre-reproductive adults and thus undergo a pre-oviposition period before eggs are produced (Carne, 1966a) (Fig. 1).

2.3.7. Meteorological data

Meteorological data used in ParopSys were obtained from the Silo Data drill website (http://www.nrw.qld.gov.au/silo/datadrill/). This is spatially interpolated data and may not equate exactly with localised conditions. A circadian temperature model was used to drive temperature related functions in ParopSys. This enables hourly calculations of the average temperature to be derived, which are based on the interpolation of the daily maximum and minimum temperatures using a composite sine and exponential function.

2.3.8. Model initialisation

For all sites, the model was run for the period from 21st September 2005 to 15th May 2006. It was assumed that only adults survive over winter, so the lifecycle module was initialised with 0.5 pre-reproductive adults per day for 10 days from the start date. Pre-reproductive adults were used to initialise the model instead of reproductive adults because overwintering adults need to feed for a period of time before reproduction (Carne, 1966a,b; see above).

2.4. Field validation

2.4.1. South-East Queensland

To provide data to validate ParopSys, a third plantation, Site III, 26°05′97.2″S, 152°43′7.54″E, was sampled during the 2005/2006 season. Mean average daily temperature was 23.00 ± 0.19 °C, with

a maximum mean of 29.75 °C and minimum mean of 14.25 °C. Samples as in Section 2.2.2 were taken every 2 weeks between October 2005 and April 2006 to provide phenological data that were then used to check the accuracy of the model in predicting the onset, duration and peaks of each developmental stage in the field, and to predict the number of beetle generations.

2.4.2. Temperate vs. subtropical conditions

To test the model's validity over a range of environmental conditions that occur in the extremely wide natural distribution of *P. atomaria* and for the populations where developmental data were compared in this study, the model was run over the same time period (September 2005–May 2006) using climatic data for Canberra (temperate South Eastern Australia) and Lowmead (subtropical central Qld).

3. Results

*3.1. Thermal requirements and thresholds for immature **P. atomaria** life stages*

Development rates did not differ according to source of beetle origin for any developmental stage (ANCOVA, $F_{1,5} = 0$–0.62, $P = 0.47$–0.99), suggesting that the differences in voltinism reported between them (compare Carne, 1966a,b; Nahrung, 2006) is probably a seasonally plastic trait dependent upon field conditions. Data from ACT and Qld populations were therefore combined to produce developmental thresholds (T_0) and DD requirements for ParopSys (Table 1).

Total immature development time (egg–adult) was approximately 769.2 ± S.E. 127.8 DD above T_0 6.4 ± S.E. 2.6 °C: about 49 days at the average field temperature of 23 °C. As a proportion of total development time under average field conditions, the longest stage durations were for fourth instar larvae and pre-pupae + pupae (Table 1), while the shortest was Lii and Liii.

Overall Li–adult mortality in the laboratory was higher from Qld-sourced *P. atomaria* (two-way ANOVA, $F_{1,72} = 4.4$, $P = 0.04$) with ACT larvae exhibiting greater survival at 20 and 27 °C than those from Qld; survival at 16 and 24 °C did not differ according to origin. Overall Li–adult mortality (Fig. 2) increased with temperature (two-way ANOVA, $F_{3,72} = 13.9$, $P < 0.001$), best described ($R^2 = 0.98$) by the polynomial function $y = -0.028x^2 + 0.28x + 0.17$. The interaction between beetle origin and temperature on overall immature mortality was almost significant (two-way ANOVA, $F_{3,72} = 2.8$, $P = 0.05$). Nevertheless, to obtain stage-specific mortality as a function of temperature for ParopSys, we combined data from ACT and Qld populations.

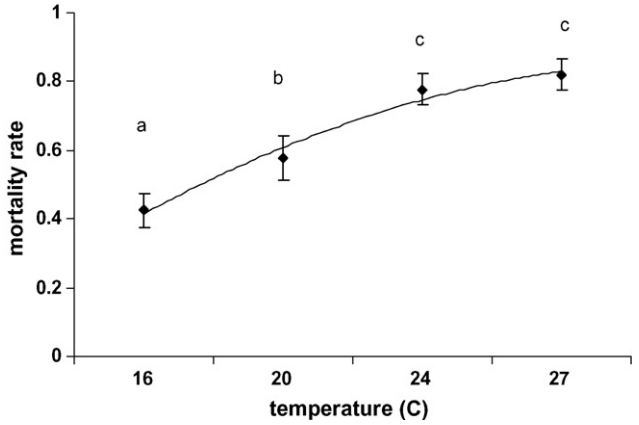

Fig. 2. Mean ± S.E. mortality rate between Li and adult ***Paropsis atomaria*** at four constant temperatures in the laboratory. Different letters denote means that differ significantly.

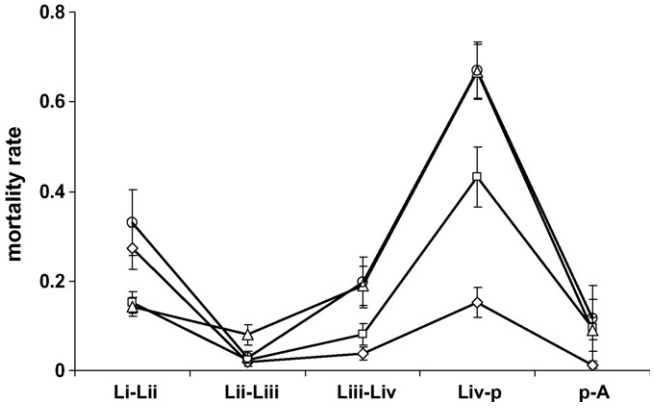

Fig. 3. Stage-specific average ± S.E. mortality of immature ***Paropsis atomaria*** at four temperatures: 16 °C (diamonds), 20 °C (squares), 24 °C (triangles) and 27 °C (circles).

Stage-specific transfer mortality differed according to developmental stage and temperature (two-way ANOVA, stage: $F_{3,361} = 63.1$, $P < 0.001$; temperature: $F_{4,361} = 14.2$, $P < 0.001$; Fig. 3), but with a significant interaction between factors (stage × temperature: $F_{12,361} = 5.03$, $P < 0.001$). Mortality at temperatures 24 °C and above did not differ significantly (Fishers LSD post hoc test).

3.2. Field mortality of immature life stages

Less than 8% of eggs survived to become fourth instar larvae (Table 2). The highest mortality occurred between egg and early instar larvae (first and second instars) at Site I, and between early instar larvae and third instar larvae at Sites II and III. These data do not reflect loss from larval parasitoids which generally emerge from fourth instar larvae or pre-pupae, and nor is loss from Liv onwards determined.

3.3. Population modelling and field validation

3.3.1. South-East Queensland

To validate the model's predictive capability, we compared field-derived phenological data obtained from Site III for September 2005–May 2006 and predictions made by ParopSys (Fig. 4). The model shows a very good fit with the field data in terms of number of generations, timing of generational peaks, and the relative sizes and shapes of each peak. Three *P. atomaria* generations were observed during the active beetle season at Site III and the model was accurate in predicting the same number of generations. Timing of each peak in the model differed somewhat from the field data, but was mostly within the margin associated with fortnightly collection of field data (Fig. 4). Relative sizes of each population peak were very well predicted by the model for all life stages, with the greatest variation occurring in the timing and size of the first generation for both eggs and total larvae. The size and timing of the final, highest population peak was very close to that of the observed field data for all life stages (Fig. 4).

3.3.2. Temperate vs. subtropical conditions

Results of the simulations comparing temperate and subtropical populations are shown in Fig. 5. ParopSys correctly predicted bivoltinism in Canberra (see Carne, 1966a) and that *P. atomaria* would have had four generations during the season at Lowmead. The model initialised both locations with the same number of pre-reproductive adults but peak adult populations were around 10-fold higher at Lowmead than at Canberra. The model predicts one more generation per year at Lowmead compared to Site III in SEQ.

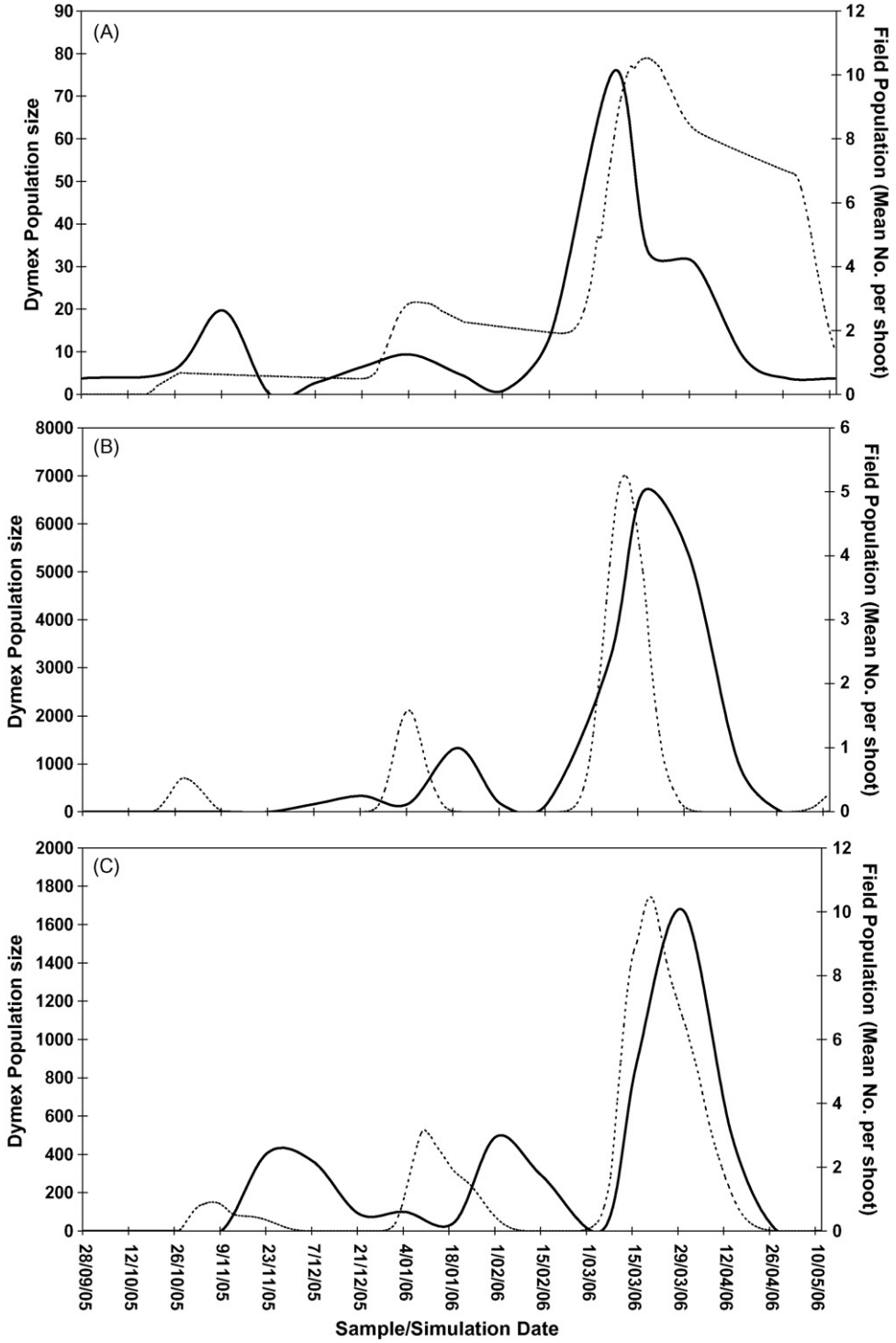

Fig. 4. Field validation of ParopSys model between 28 September 2005 and 10 May 2006 for Site III, South-East Queensland: (A) adults, (B) eggs and (C) total larvae. Solid lines represent field phenological data collected fortnightly (right ***y***-axis); dotted lines represent DYMEX™ model data using Data Drill meteorological data for Site III (left ***y***-axis). DYMEX™ population numbers are dependent on numbers initialised and so relate relatively to field data (numbers per shoot).

4. Discussion

4.1. Development and mortality

Our temperature-development results coincide with those originally calculated by Carne (1966a) for ACT beetles, and they are also consistent across populations sourced from within relative extremes of *P. atomaria*'s geographical distribution. Such low variation in development rates between populations over spatial and temporal scales supports the finding that *P. atomaria* is genetically similar throughout its range (Schutze et al., 2006). Therefore, the difference in the number of *P. atomaria* generations observed between regions suggests that voltinism is a seasonally plastic trait influenced by environmental conditions such as temperature. This is supported by the high degree of accuracy provided by our model in which temperature was the only environmental variable included. We do, however, consider other factors – especially photoperiod and host plant quality –

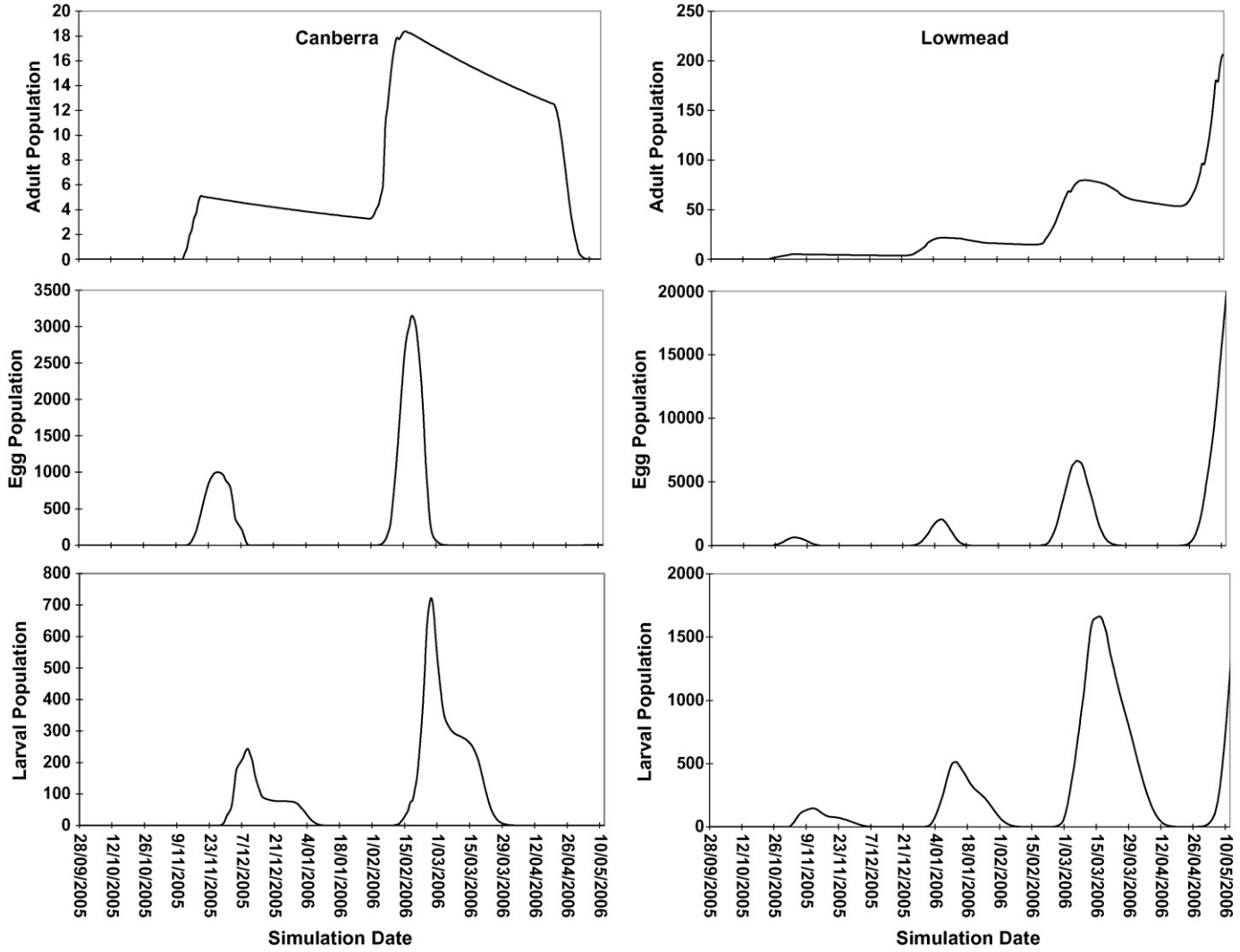

Fig. 5. DYMEX™ model predictions for adult, egg and total larval populations of ***Paropsis atomaria*** for ACT (Canberra) and Queensland (Lowmead) between 28 September 2005 and 10 May 2006. DYMEX™ population numbers are dependent on numbers initialised and so relate relatively to field data (numbers per shoot).

contribute towards determining voltinism in *P. atomaria* (see Carne, 1966a).

Photoperiod is an important factor that can indirectly influence voltinism through its role as a trigger in diapause initiation and termination. Photoperiod is considered the most influential and seasonally reliable diapause cue in insects, while temperature is considered the second most important environmental regulator (Tauber and Tauber, 1976; Tauber et al., 1986). In the paropsine *Chrysophtharta agricola* (Chapuis) (Coleoptera: Chrysomelidae), for example, whilst temperature was secondarily responsible for inducing diapause under controlled conditions, photoperiod was the dominant environmental factor (Nahrung and Allen, 2004b). Further, the interplay between photoperiod and temperature may be critical for the induction of diapause, as demonstrated for the flea beetle, *Argopistes coccinelliformis* Csiki (Coleoptera: Chrysomelidae) (Inoue, 2001). Carne (1966a) reported that newly emerged *P. atomaria* adults are responsive to photoperiodic cues for reproductive diapause: in the ACT, adults emerging from pupation in February attain reproductive maturity, whereas those that emerge after the first week of March enter diapause without reproductive development. Further work is required to elucidate diapause cues under subtropical conditions: a limitation of ParopSys is our use of an arbitrary date, rather than a specific environmental cue, for simulating the initiation of reproductive diapause. Indeed, altering the start date by 1 week to 14 September gave a better fit with field data for the timing of peaks (output not shown), suggesting that we did not accurately identify the start of the season. Nevertheless, ParopSys generates field-corroborated voltinism accurately for subtropical and temperate regions.

Host plant quality and availability is also likely to contribute to the number of generations produced in a season, whereby if host plant quality is poor, or suitable hosts are not present, oviposition may be delayed until suitable larval food sources appear (see Carne, 1966a). Host plant influence is an important factor for paropsine population dynamics (Ohmart, 1991) as for *Chrysophtharta bimaculata* (Olivier), an important paropsine pest of Tasmanian eucalypt plantations (Steinbauer et al., 1998). In this case, host plant quality (amount of flush foliage present) plays a more important role in stimulating oviposition than does host species (Steinbauer et al., 1998). Further, *P. atomaria* populations located merely 20 km apart in SEQ exhibited variable voltinism within the same field season (Nahrung, 2006; Duffy, 2007)—a result unexplainable using temperature or photoperiod data alone. Delayed oviposition by females due to poor early season host plant quality (i.e. less flush foliage) was proposed as the driving cause influencing variable voltinism in that case (Duffy, 2007). The potential importance of flush foliage in driving *P. atomaria* populations is not unexpected considering the importance of host

plant quality on successful *P. atomaria* larval establishment, with first instars suffering extremely high levels of mortality on older, tougher leaves (Ohmart et al., 1987; Larsson and Ohmart, 1988).

Early instars suffer the greatest mortality in the field despite their gregarious behaviour potentially increasing defence (Sillen-Tullberg, 1988) and feeding establishment (Nahrung et al., 2001). Early paropsine instars experience high mortality under laboratory conditions in *C. bimaculata* (Baker et al., 2002) and *C. agricola* (Nahrung et al., 2001), and our overall egg–Liv field mortality estimates for *P. atomaria* were similar to these temperate species (de Little et al., 1990; Nahrung and Allen, 2004a, respectively). Our laboratory trials revealed relatively low survival rates for fourth instar larvae, exacerbated by higher rearing temperatures, especially above 24 °C. Increased heat stress under experimental conditions may have caused high mortality at this life stage in the laboratory.

4.2. Population modelling

ParopSys is a simple DYMEX™ model based on temperature-dependent development thresholds, field- and laboratory-derived mortality data and general ecological knowledge of the beetle's behaviour. Despite this simplicity, validation against field data showed that ParopSys was accurate in predicting the number, timing, and relative size of *P. atomaria* generations. This varied somewhat with beetle stage: timing of adult population peaks most closely matched that of the field data, with larval peaks showing the greatest discrepancies with timing of egg peak heights intermediate between these (Fig. 4). The model also suggested that an early field egg peak may have been missed because field sampling did not commence until 25 October 2005. For all stages, relative peak heights for each generation closely matched that of the field data, with the largest populations occurring from early March (adults) to late March–early April (larvae). Height of this final peak for all stages was approximately threefold higher than for the earlier two peaks. This agrees with field observations of severe beetle damage at this time.

The model was also robust across climatic zones by correctly predicting bivoltinism at Canberra (ACT), and one extra generation at Lowmead (central Qld) compared to SEQ. Since 2004 forestry plantation companies in this area have reported severe *P. atomaria* defoliation of young *Eucalyptus* taxa in mid- to late-May, coinciding with peak larval and adult populations predicted by ParopSys (Lawson, unpublished data), although phenological field data for Lowmead are not currently available. The model also predicts that *P. atomaria* is likely to be a more serious pest in the subtropics, with much larger populations compared with temperate areas.

4.3. Future improvements

At its current state of development, ParopSys does not incorporate sophisticated environmental and life cycle parameters that could improve its predictive ability. The interaction between leaf dynamics, herbivory, and rainfall (see e.g. Stone and Bacon, 1995), as well as tree growth rates could be incorporated to provide estimates of stand productivity and losses. Although the good fit of the model with field data suggests that beetle immigration and emigration is absent or equal within seasons, any such movement could potentially be linked to plantation proximity to native vegetation acting as a beetle and natural enemy source or sink (see Strauss, 2001). Future improvements to ParopSys may also incorporate egg parasitism (Duffy et al., in press; Nahrung et al., in press; Nahrung and Duffy, 2008); basking behaviour of beetle stages that may affect development rates (e.g. Maddox, 1995); differential performance on different host species, and specific factors that determine diapause induction and termination (particularly in relation to daylength). The relationships between beetle size with geographic origin, host plant species/quality, and fecundity also deserves further investigation (see Carne, 1966a; Schutze and Clarke, 2008).

Future versions of ParopSys will incorporate 'event scenarios' where the efficacy of number and timing of control measures, such as insecticides, can be evaluated as desktop studies. The model can also be linked with tree growth models to produce cost-benefit analyses of management strategies for *P. atomaria* when impact data become available. Linking the model with GIS software may also enhance its attractiveness to plantation managers. DYMEX™ Versions 2 and 3 incorporate a Climex-type mapping function (Maywald et al., 2004) that can be used in regional and global risk modelling for plantations and a climate change function that can be used to predict how the risk of serious damage by *P. atomaria* may change with currently available global warming scenarios.

5. Conclusion

The robustness of ParopSys for predicting numbers of generations, timing of population peaks (in particular the late season population peak, where the most severe and long-term impact on tree growth rates occurs), and size of the final population peak suggest that ParopSys may be helpful to plantation managers in developing risk models for current and future plantations. The model may also assist in predicting year-to-year fluctuations in *P. atomaria* damage and thus assist managers in planning forest health surveys, monitoring, and management responses.

Acknowledgments

Our sincere thanks to Nikki Sims and Andy Hulthen (both QUT) for laboratory assistance; Jacinta Hodnett, Janet McDonald, Daniel Hancox and Rebeccah Aigner (all Departments of Primary Industries and Fisheries) for field assistance. Sincere thanks also to Gunter Maywald (CSIRO Entomology) for assistance with DYMEX™. MKS was in receipt of a QUT Postgraduate Research Award, and parts of this work were carried out under Australian Research Council Linkage Projects Program (LP0454856) in conjunction with Forestry Plantations Queensland (formerly DPI-Forestry). We gratefully acknowledge all organisations for their support.

References

Baker, S.C., Elek, J.A., Candy, S.G., 2002. A comparison of feeding efficiency, development time and survival of Tasmanian eucalyptus leaf beetle larvae *Chrysophtharta bimaculata* (Olivier) (Coleoptera: Chrysomelidae) on two hosts. Aust. J. Entomol. 41, 174–181.

CABInternational, 2005. Forestry Compendium. CAB International, Wallingford UK.

Campbell, A., Frazer, B.D., Gilbert, N., Gutierrez, A.P., Mackauer, M., 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11, 431–438.

Candy, S.G., Elliott, H.J., Bashford, R., Greener, A., 1992. Modelling the impact of defoliation by the leaf beetle, *Chrysophtharta bimaculata* (Coleoptera: Chrysomelidae), on height growth of *Eucalyptus regnans*. Forest Ecol. Manage. 54, 69–87.

Carne, P.B., 1966a. Ecological characteristics of the eucalypt-defoliating chrysomelid *Paropsis atomaria* Ol. Aust. J. Zool. 14, 647–672.

Carne, P.B., 1966b. Growth and food consumption during the larval stages of *Paropsis atomaria* (Coleoptera: Chrysomelidae). Entomol. Exp. Appl. 9, 105–112.

Collett, N., 2001. Insect Pests of Young Eucalypt Plantations. Agriculture Notes 6, December 2001. Department of Natural Resources and Environment, Heidelberg.

Cox, M.L., 1994. Diapause in the Chrysomelidae. In: Jolivet, P.H., Cox, M.L., Petitpierre, E. (Eds.), Novel Aspects of the Biology of Chrysomelidae. Kluwer Academic Publishers, Dordrecht, pp. 469–502.

Cumpston, M., 1939. Observations of the bionomics and morphology of seven species of the tribe Paropsini (Chrysomelidae). In: Proceedings of the Linnean Society of New South Wales, vol. 64. pp. 353–366.
de Little, D.W., 1989. Paropsine chrysomelid attack on plantations of *Eucalyptus nitens* in Tasmania. NZ J. For. Sci. 19, 223–227.
de Little, D.W., Elliott, H.J., Madden, J.L., Bashford, R., 1990. Stage-specific mortality in two field populations of immature *Chrysophtharta bimaculata* (Oliver) (Coleoptera: Chrysomelidae). J. Aust. Entomol. Soc. 29, 51–55.
Duffy, M.P., 2007. Population Phenology and Natural Enemies of *Paropsis atomaria* in South-East Queensland. MSc thesis, School of Natural Resource Sciences, Queensland University of Technology, 100 pp.
Duffy, M.P., Nahrung, H.F., Lawson, S.A., Clarke, A.R., in press. Direct and indirect effects of egg parasitism by *Neopolycystus* Girault sp. (Hymenoptera: Pteromalidae) on *Paropsis atomaria* Olivier (Coleoptera: Chrysomelidae). Aust. J. Entomol.
Eisler, R., 1999. Containment Hazard Reviews Report No. 35 Cumulative Index to Chemicals and to Common and Scientific Names of Species Listed in Containment Hazard Reviews 1 through 34. Biological Science Report USGS/BRD/BSR-1999-0002. Pauxtent Wildlife Research Center, Laurel, MD, 80 pp.
Elek, J.A., 1997. Assessing the impact of leaf beetles in eucalypt plantations and exploring options for their management. Tasforests 9, 139–154.
Elliott, H.J., Ohmart, C.P., Wylie, F.R., 1998. Insect Pests of Australian Forests: Ecology and Management. Inkata Press, Melbourne.
Farr, J.D., 2002. Biology of the gumleaf skelentoniser, *Uraba lugens* Walker (Lepidoptera: Noctuidae), in the southern jarrah forest of Western Australia. Aust. J. Entomol. 41, 60–69.
Govender, P., 2002. Management of insect pests: have the goalposts changed with certification? S. Afr. For. J. 195, 39–45.
Inoue, T., 2001. Life history of the flea beetle, *Argopistes coccinelliformis* Csiki (Coleoptera: Chrysomelidae) VII. Effects of photoperiod and temperature on induction of reproductive diapause in newly emerged adults. Appl. Entomol. Zool. 36, 53–58.
Jenkin, B.M., Tomkins, B., 2006. Chemical Pesticide usage by Australian Plantation Industries. FWPRDC Project PN06.4016. Forest and Wood Products Research and Development Corporation, Melbourne.
Kliejunas, J.T., Burdsall, H.H.J., deNitto, G.A., Eglitis, A., Haugen, D.A., Haverty, M.I., Micales, J.A., Tkacz, B.M., Powell, M.R., 2003. Pest risk assessment of the importation into the United States of unprocessed logs and chips of eighteen Eucalypt species from Australia. General Technical Report FPL-GTR-137. U.S. Department of Agriculture, Forest Service, Forest Products Laboratory, Madison, WI, 206 pp.
Larsson, J., Ohmart, C.P., 1988. Leaf age and performance of the leaf beetle *Paropsis atomaria*. Ecol. Entomol. 13, 19–24.
Lawson, S.A., King, J., 2002. Leaf Beetles (Paropsines). Queensland Forest Research Institute, Agency for Food and Fibre Sciences, DPI. DPI Note FOR0027, Brisbane.
Maddox, C.D.A., 1995. Aspects of the Biology of *Paropsisterna tigrina* (Chapuis) (Coleoptera: Chrysomelidae) the Major Pest Species of *Melaleuca alernifolia* (Cheel) (Myrtaceae). Masters thesis, Department of Entomology, The University of Queensland.
MAF, 2003. Import Health Standard: Sawn Wood from All Countries. New Zealand Ministry for Agriculture and Forestry, Forest Biosecurity, 21 pp.
Maywald, G.F., Sutherst, R.W., Kriticos, D.J., 2004. DYMEX Professional: Modelling Natural Systems, Version 2.0. Hearne Scientific Publishing, Melbourne.
Nahrung, H.F., 2006. Paropsine beetles (Coleoptera: Chrysomelidae) in South-East Queensland hardwood plantations: identifying potential pest species. Aust. For. 69, 270–274.
Nahrung, H.F., Allen, G.R., 2004a. Population dynamics of the chrysomelid leaf beetle *Chrysophtharta agricola* (Chapuis), a pest of *Eucalyptus nitens* plantations in Tasmania. Tasforests 15, 67–84.
Nahrung, H.F., Allen, G.R., 2004b. Overwintering ecology of *Chrysophtharta agricola*: mechanisms of reproductive diapause induction and termination. Aust. J. Zool. 52, 505–520.
Nahrung, H.F., Duffy, M.P., 2008. Exploring the fourth trophic level: do hyperparasitoids influence biocontrol of a forestry pest in a native system? NZ Entomol. 31, 6–12.
Nahrung, H.F., Dunstan, P.K., Allen, G.R., 2001. Larval gregariousness and neonate establishment of the eucalypt-feeding beetle *Chrysophtharta agricola* (Coleoptera: Chrysomelidae: Paropsini). Oikos 94, 358–364.
Nahrung, H.F., Allen, G.R., Patel, V.S., 2004. Day-degree development and phenology modelling of the immature stages of *Chrysophtharta agricola* (Chapuis) (Coleoptera: Chrysomelidae), a pest of eucalypt plantations. Aust. J. Entomol. 43, 177–183.
Nahrung, H.F., Duffy, M.P., Lawson, S.A., Clarke, A.R., in press. Natural enemies of *Paropsis atomaria* (Coleoptera: Chrysomelidae) in South-East Queensland eucalypt plantations. Aust. J. Entomol.
Nylin, S., 2001. Life history perspectives on pest insects: What's the use? Aust. Ecol. 26, 507–517.
Ohmart, C.P., 1990. Insect pests in intensively-managed eucalypt plantations in Australia: some thoughts on this challenge to a new era in forest management. Aust. For. 53, 7–12.
Ohmart, C.P., 1991. Role of food quality in the population dynamics of chrysomelid beetles feeding on *Eucalyptus*. Forest Ecol. Manage. 39, 35–46.
Ohmart, C.P., Thomas, J.R., Stewart, L.G., 1987. Nitrogen, leaf toughness and the population dynamics of *Paropsis atomaria* Olivier (Coleoptera: Chrysomelidae)—a hypothesis. J. Aust. Entomol. Soc. 26, 203–207.
Parsons, M., Gavran, M., Davidson, J., 2006. Australia's plantations 2006 National Report. Department of Agriculture, Fisheries and Forestry, 24 pp.
Philips, C., 1996. Insects, Diseases and Deficiencies Associated with Eucalypts in South Australia. Primary Industries South Australia, Mt Gambier.
Schutze, M.K., Clarke, A.R., 2008. Converse Bergmann cline in a *Eucalyptus* herbivore, *Paropsis atomaria* Olivier (Coleoptera: Chrysomelidae): phenotypic plasticity or local adaptation? Global Ecol. Biogeogr. 17, 424–431.
Schutze, M.K., Mather, P.B., Clarke, A.R., 2006. Species status and population structure of the Australian Eucalyptus pest *Paropsis atomaria* Olivier (Coleoptera: Chrysomelidae). Agric. Forest Entomol. 8, 323–332.
Sillen-Tullberg, B., 1988. Evolution of gregariousness in aposematic butterfly larvae: a phylogenetic analysis. Evolution 42, 293–305.
Simmul, T.L., de Little, D.W., 1999. Biology of the Paropsini (Chrysomelidae: Chrysomelinae). In: Cox, M.L. (Ed.), In Advances in Chrysomelidae Biology. Backhuys Publishers, Leiden, pp. 463–477.
Steinbauer, M.J., Clarke, A.R., Madden, J.L., 1998. Oviposition preference of a *Eucalyptus* herbivore and the importance of leaf age on interspecific host choice. Ecol. Entomol. 23, 201–206.
Steinbauer, M.J., Kriticos, D.J., Lukacs, Z., Clarke, A.R., 2004. Modelling a forest lepidopteran: phonological plasticity determines voltinism which influences population dynamics. Forest Ecol. Manage. 198, 117–131.
Stone, C., 1993. Insect problems of eucalypt plantations in Australia. Aust. For. 56, 363–369.
Stone, C., Bacon, P.E., 1995. Leaf dynamics and insect herbivory in a *Eucalyptus camaldulensis* forest under moisture stress. Aust. J. Ecol. 20, 473–481.
Stone, C., Coops, N., 2004. Assessment and monitoring of damage from insects in Australian eucalypt forests and commercial plantations. Aust. J. Entomol. 43, 283.
Strauss, S.Y., 2001. Benefits and risks of biotic exchange between *Eucalyptus* plantations and native Australian forests. Aust. Ecol. 26, 447–457.
Tauber, M.J., Tauber, C.A., 1976. Insect seasonality, diapause maintenance, termination and post-diapause development. Annu. Rev. Entomol. 21, 81–107.
Tauber, M.J., Tauber, C.A., Masaki, S., 1986. Seasonal Adaptations of Insects. Oxford University Press, New York, 411 pp.
Tribe, G.D., 2000. Ecology, distribution and natural enemies of the *Eucalyptus*-defoliating beetle *Trachymela tincticollis* (Blackburn) (Chrysomelidae: Chrysomelini: Paropsina) in southwestern Australia, with reference to its biological control in South Africa. Afr. Entomol. 8, 23–45.
Withers, T.M., 2001. Colonisation of eucalypts in New Zealand by Australian insects. Aust. Ecol. 26, 467–476.
Wylie, F.R., Peters, B.C., 1993. Insect pest problems of eucalypt plantations in Australia. 1. Queensland. Aust. For. 56, 358–362.