

# Limits to the potential distribution of light brown apple moth in Arizona–California based on climate suitability and host plant availability

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**Abstract** The highly polyphagous light brown apple moth (LBAM) (*Epiphyas postvittana* (Walk.): Tortricidae) is indigenous to Australia and was first found in California in 2006. It is currently found in 15 coastal counties in California, but nowhere has it reached outbreak status. The USDA projects the geographic range of LBAM will include much of Arizona and California and the southern half of the US, which together with economic estimates of potential crop losses have been used as the rationale for an eradication program in California. We report a temperature-driven demographic model to predict the likely distribution and relative abundance of LBAM

using the detailed biology reported by Danthanarayana and colleagues, and climate data from 151 locations in California and Arizona for the period 1995–2006. The predictions of our model suggest that the near coastal regions of California are most favorable for LBAM, the northern Central Valley of California being less favorable, and the desert regions of Arizona and California being unfavorable. The model also predicts that LBAM populations can develop at two of the hottest locations in SE Australia where it has long been known to occur. This reassessment of the potential distribution of LBAM in California and Arizona suggests that its likely ecological and economic impacts would be less than previously assessed by USDA and that its current pest status warrants re-evaluation.

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## Introduction

The light brown apple moth (LBAM, *Epiphyas postvittana* (Walk.): Tortricidae) is indigenous to Australia where it is considered a pest of pome fruits and grape, but it has been recorded from a broad range of host plant species including crops, ornamentals and herbaceous weeds (Danthanarayana 1975; Geier and Briese 1981; Suckling and Brockerhoff 2010). This

pest was accidentally introduced into England, Hawaii, New Caledonia and New Zealand, and was first found in the San Francisco Bay area by University of California Emeritus Professor Jerry Powell in 2006 (Brown 2007). LBAM is currently found in 15 coastal and near coastal counties in California suggesting it has been present in the state for several years. To date the pest has not reached outbreak status at any location in California.

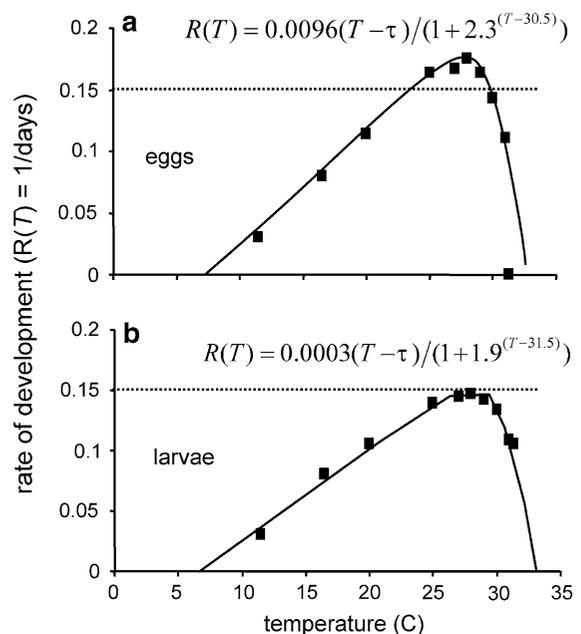
The United States Department of Agriculture (USDA) posits that the potential distribution of LBAM includes all areas having sufficient thermal units for the completion of three generations (i.e., California and the Southern half of the United States) with estimated losses of \$118 million per annum from apple, grape, orange and pear production (Fowler et al. 2009). In response to this perceived threat, the USDA considers LBAM to be an actionable quarantine pest, and has placed quarantine on California produce in affected counties as well as all counties in Hawaii (Federal Quarantine Order of May 2, 2007). In late 2007, the California Department of Agriculture (CDFA) began an eradication program using pheromones, sprays and other techniques. The pheromone spray program engendered considerable public protest concerning claimed public health effects, the lack of hard evidence that LBAM is a serious pest and the proposed expenditure of nearly 100 million dollars for the program in California alone. Because of public outcry, an eradication program based on the sterile insect technology (SIT) has now been proposed.

The potential ecological and economic impact of invasive species can be influenced by many factors (Parker et al. 1999; Levine et al. 2003; Buckley 2008), but for invasive arthropod pests, climate and temperature in particular have played a central role in the assessment of risk (e.g., Fowler et al. 2009; Migeon et al. 2009; Sutherst and Bourne 2009). A variety of climate matching models have been used to predict the potential distribution of invaders (Coetzee et al. 2009; Rodda et al. 2009; Sutherst and Bourne 2009), but there have been few attempts to include biotic interactions in addition to abiotic drivers into such models (e.g., Gutierrez and Baumgärtner 1984; Gutierrez et al. 2008). Here, we analyze the potential distribution of LBAM in Arizona and California using a temperature-driven demographic model to provide a more quantitative and realistic approach for assessment of the risk of this invasive pest.

## Biology of light brown apple moth

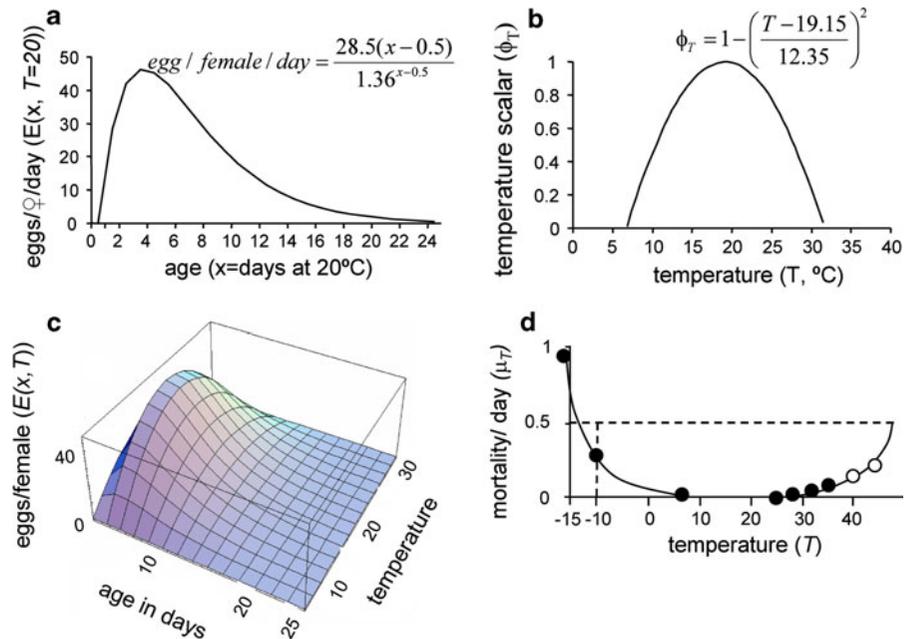
Danthanarayana (1975) reviewed the sparse literature on the biology of LBAM prior to 1975 (Dumbleton 1932, 1939; Evans 1937; Geier 1965; Lawrence and Bartell 1972; Bartell and Lawrence 1973; MacLellan 1973). In a series of papers, Danthanarayana (1975, 1976a, b, c), Danthanarayana et al. (1995), Gu and Danthanarayana (1990a, b, 1992) described the biology of LBAM, and this body of work is the basis for our analysis. The developmental biology of *E. postvittana* is summarized below and in Figs. 1 and 2.

Light brown apple moth does not have a diapause period and feeds on numerous plant species across family lines; the lower threshold for development of all stages was estimated as 7.5°C (Danthanarayana 1975), but reanalysis of the data for eggs and larvae yields a non linear relationship with a slightly lower threshold of 6.8°C (Fig. 1). The mean duration of the egg stage is 5.7 days at 28°C (120.8 degree days;  $dd_{>6.8^{\circ}\text{C}}$ ) with no eggs hatching above 31.3°C. Larval and pupal developmental times are 335 and 142 dd, respectively with an upper threshold for development for larvae and pupae of approximately 31.5°C. The generation time is 594 dd. Fifty-percent of eggs are laid by 646 dd; mean



**Fig. 1** The effect of temperature ( $T$ ) on the developmental rates of LBAM eggs (a) and larvae (b) (data from Danthanarayana 1975)

**Fig. 2** The effects of LBAM adult age and daily average temperature ( $T$ ) on fecundity: **a** per capita daily fecundity on female age ( $x$ ) at 20°C, **b** a scalar ( $0 \leq \phi_T \leq 1$ ) of the effects of average temperature on fecundity, **c** the combined effects of subfigures **a**, **b** (data from Danthanarayana 1975), and the effects of extreme temperature **d** on the mortality rate per day ( $0 \leq \mu_T \leq 1$ ). Note that the symbol (filled circle) represents data and (open circle) represents linear extrapolations



fecundity is approximately 384 but varies considerably (0–1492) with female size, larval food and temperature (Danthanarayana et al. 1995; Gu and Danthanarayana 1990a, b, 1992), but only temperature is used in the model. The optimum temperature for oviposition is near 20°C. At constant temperatures of 20 and 25°C, >50 and 80% of the eggs are laid by the fourth and the seventh day after emergence respectively with peak oviposition occurring when adult females are 2–3 days old. Body weight of both male and female moths at emergence increases with increasing temperature up to 25°C. Danthanarayana (1976a, b, c) provides information on the diel and lunar periodicities, seasonal variation in flight activity and the influence of food and temperature on flight performance in the field. Flight duration increases with temperature in the range 15–28°C, with males being stronger fliers than females with the longest flights occurring on day four. Mating in females begins within 24 h of emergence with nearly all being mated within 4 days. The average number of matings is 2, although by day 11 some females may mate as many as five times (Gu and Danthanarayana 1990a, b, 1992). Geier et al. (1978) found that a small proportion of LBAM females produce predominantly female progeny resulting in the proportion of males in field samples to range from 0.43 to 0.45. Based on LBAM's biology, theoretical considerations suggest that this value is near the

theoretical optimum assuring that nearly all females are mated (see Geier et al. 1978). The resulting sex ratio in our model is 1.1 ♀:0.9 ♂.

Data from Danthanarayana (1975) were used to estimate the effects of adult age and temperature on per capita fecundity (Fig. 2a–c). The data are illustrated in days for ease of interpretation, but all calculations in the model are made in physiological time units. The effect of temperature ( $T$ ) and age ( $x$ ) on per capita daily fecundity is modeled as the product of the function for maximum fecundity ( $E(x, T_{opt})$ ) at the optimum temperature ( $T_{opt} = 20^\circ\text{C}$ , Fig. 2a) and a scalar function of the effects of temperature above and below the optimum ( $\phi_T$ , Fig. 2b) yielding  $E(x, T) = \phi_T(T) \cdot E(x, T_{opt})$  (Fig. 2c). The rightward displacement of the fecundity function from the y-axis (Fig. 2a, c) reflects the short pre-oviposition period.

#### Sources of mortality

Three sources of LBAM mortality are included in the model: (1) Intrinsic mortality in the favorable range between 6.8 and 28°C is accounted for by the differing progression of the population members with temperature through the distributed maturation time model, (2) mortality due to extremes of temperatures, and (3) mortality due to the combined action of

natural enemies and other factors. Only mortality sources (2) and (3) require further explanation.

### Extremes of temperature

Data on the lethal effects of low temperature on LBAM are sparse, and hence we used estimates from an ongoing study by Buerger and Mills (unpublished observations) showing that 30% of larvae die within 1 day at  $-10^{\circ}\text{C}$  and all larvae died within 1 day at  $-16^{\circ}\text{C}$ . We computed the daily mortality rate from low temperatures as the integral of time and temperature below the developmental threshold ( $\mu_T$ ; Eq. 1i; Fig. 2d; Gutierrez et al. 2005), and used it to model the daily over-wintering mortality rate.

$$\begin{aligned} &\text{if } T_{\min} < 6.8^{\circ}\text{C}, 0.01 < \mu_T = 1 \\ &\quad - 0.015 \exp(0.323dd_{<6.8^{\circ}\text{C}}) < 1 \quad \text{i} \\ &\text{if } T_{\max} > 28^{\circ}\text{C}, 0.01 < \mu_T = 1 \quad (1) \\ &\quad - 0.125 \exp(0.025dd_{>28^{\circ}\text{C}}) < 1 \quad \text{ii} \\ &\text{else } \mu_T = 0 \end{aligned}$$

The daily mortality rate at high average temperatures (Eq. 1ii) was estimated from data in figure 11 in Danthanarayana (1975) showing the percent survivorship from egg hatch to adult emergence at several temperatures ( $T$ ). The daily proportional mortality was computed from the percent mortality at the four highest temperatures shown in the figure by dividing by the egg to adult period (477.5  $dd$ ), multiplying by the  $dd_{>6.8^{\circ}\text{C}}$  at each temperature ( $T$ ), and dividing by 100. The mortality rate increases with average daily temperature above 28–45°C (Eq. 1ii, Fig. 2d). Mean daily temperatures above 45°C are unlikely to be encountered in the field.

### Other mortality

Field life table studies summarized by Danthanarayana (1983) in Victoria, Australia estimate the action of various mortality factors affecting LBAM life stages. Total generation mortality was approximately 98–99.5% with egg mortality being a key factor during spring and autumn, and egg mortality and losses of first instar during dispersal being key factors during summer. Predation of eggs and first instar larvae by generalist predators acting in a density independent manner increased with hot dry weather

and nearly eliminated summer generations. Similar high rates of mortality were also observed by Geier and Briese (1980) including widespread nuclear polyhedrosis virus infection (Geier and Briese 1979).

Despite having been present in California for several years, LBAM has failed to reach outbreak levels, even though it has invaded a Mediterranean climate similar to that of SE Australia. Recent field observations in California have also shown that the egg and larval stages of LBAM are attacked by a suite of generalist predators and parasitoids (NJ Mills, unpublished observations). In the absence of field life tables for LBAM in California, we take a composite approach to incorporating this mortality in a manner that reflects the population levels of LBAM observed in the invaded areas. We develop a functional response model (Eq. 2) wherein the daily proportional mortality ( $\mu_c$ ) increases with both temperature ( $\Delta t = dd_{>6.8^{\circ}\text{C}}$ ) and prey density ( $N_{\text{eggs}} + N_{\text{larvae}}$ ) at a decreasing rate. The coefficient 0.0025 in Eq. 2 is the proportion of eggs and larvae attacked  $dd^{-1}$ , and was chosen iteratively to produce the low population levels that are currently observed in the field.

$$0 \leq \mu_c = 1 - e^{-0.0025(N_{\text{eggs}} + N_{\text{larvae}})\Delta t} < 1 \quad (2)$$

### Rainfall

Rainfall can have an important indirect effect on LBAM dynamics through host plant availability. Outside of irrigated crops, herbaceous weedy plants are important hosts for LBAM, and as it is an insect with no winter diapause these are often the only host plants available for the period from late summer through spring (Geier and Briese 1981). To examine the effect of rainfall on annual host plant distribution and consequently the potential distribution of LBAM, we use the well-studied drought tolerant Mediterranean yellow starthistle (*Centaurea solstitialis* L.; YST) as a surrogate annual plant species (see Gutierrez et al. 2005).

### Model overview

The biology of LBAM is embedded in an Erlang distributed maturation time demographic model that

simulates the dynamics of an age structured population (Vansickle 1977; DiCola et al. 1999, p. 523–524). The general model for the  $i$ th age class of a population is:

$$\frac{dN_i}{dt} = \frac{k\Delta x}{\Delta} [N_{i-1}(t) - N_i(t)] - \mu_i(t)N_i(t). \quad (3)$$

$N_i$  is the abundance of the  $i$ th age class,  $dt$  is the change in time ( $dd/day$  computed using the non linear model),  $k$  is the number of age classes,  $\Delta$  is the expected mean developmental time,  $\Delta x$  is a daily increment of age, and  $\mu_i(t)$  includes the proportional net loss rate of births as modified by temperature and age (Fig. 2c), the death rate due to extremes of temperature ( $\mu_T$ , Eq. 1) and to composite mortality effects ( $\mu_c$ , Eq. 2).

All life stages can be included in one dynamics model with eggs produced by the adult age classes entering the first age cohort ( $N_1(t)$ ) as  $x_0(t)$  and the survivors exiting at maximum age as  $y(t)$  (Fig. 3a). The flow rates ( $r_i(t)$ ) between age classes depends on the numbers in the previous age class (Fig. 3a) and  $dt$ . The distribution of final maturation times (Fig. 3b) is determined by the number of age classes, the mean maturation time  $\Delta$  and the variance of maturation

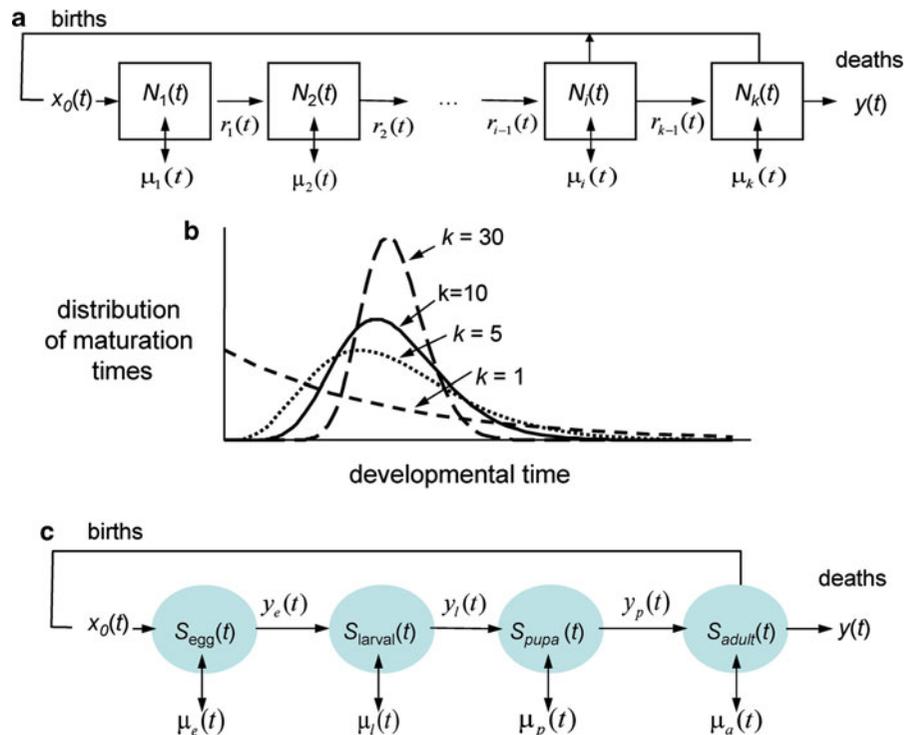
times (var) ( $k = \Delta^2/\text{var}$ ). The larger the value of  $k$ , the narrower is the Erlang distribution of developmental times. The variance of developmental times reported by Danthanarayana (1975) was large and a value of  $k = 15$  was selected to reflect this biology.

For convenience, separate models are used for the egg, larvae, pupae and adults stages ( $S_{i=\text{egg, larval, pupa, adult}}$ ) each having stage-specific characteristics (e.g.  $\Delta_i, k_i, \dots$ ) with the outflow of the last age class of a stage ( $y_i(t)$ ) entering the first age class of the next stage ( $x_{i+1,0}(t)$ ), and all eggs produced by the adult stage entering the first age class of eggs as  $x_0(t)$  (Fig. 3c). The model parameters are reported in Table 1.

### Simulation and GIS

Daily weather data (maximum and minimum temperatures, solar radiation, precipitation, RH and runs of wind) for the period 1 January 1995 to 15 November 2006 from 151 locations across California and Arizona (Fig. 4a) were used in across year simulations. An initial population density of 50 first instar larvae  $m^{-2}$  was assumed at all locations in California and Arizona and the simulations were run

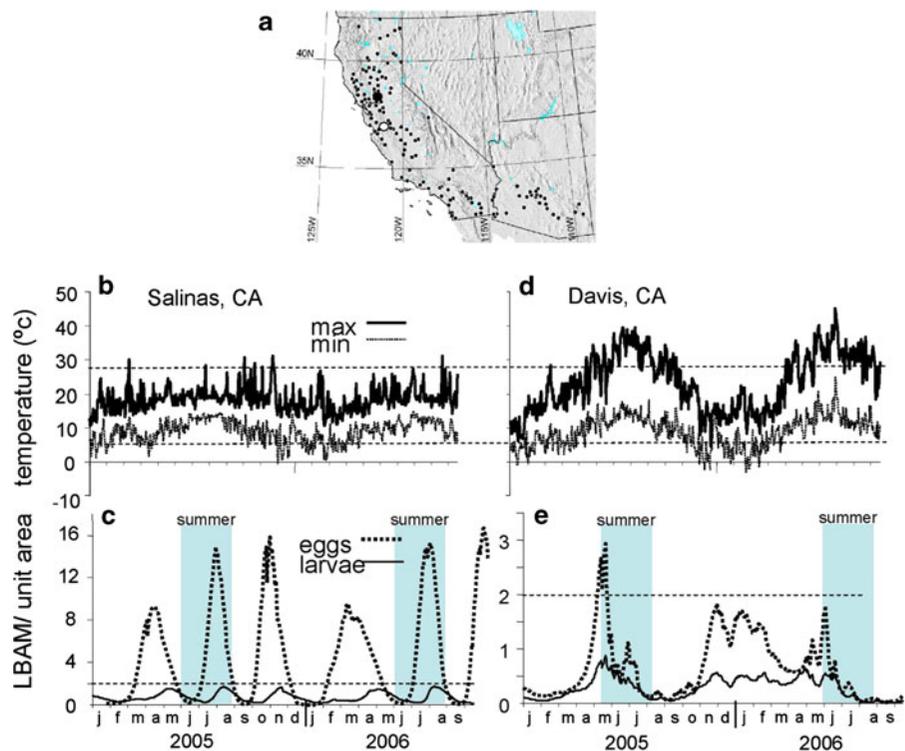
**Fig. 3** The distributed maturation time model: **a** all life stages, **b** the frequency distribution of maturation times with different numbers of age classes ( $k$ ) and **c** separate models for each life stage each having flow biology depicted in **a**



**Table 1** Biological parameters for the light brown apple moth

Process	Parameter/eqn	Light brown apple moth
Thermal threshold (in °C)	$\tau$	6.8°C
Daily degree days	$\Delta dd(t)$	
	$335.3 \times (0.0003(T - \tau)/(1 + 1.9^{(T-31.5)}))$	
Duration of life stages in degree days at 20°C	$dd$	Egg (120.8) Larvae (335.5) Pupa (142.0) Adult (290.4)
Maximum age ( $x$ ) per capita fecundity/ day at age $x$ and temperature $T$	$a$ $b$	28.50 1.36
$F(x, T) = \phi(T) \cdot a(x - 0.5)/b^{x-0.5}$		
$\phi(T) = 1 - \left[ \frac{(T - T_{\min} - T_{\text{mid}})}{T_{\text{mid}}} \right]^2$	$T_{\min}$ $T_{\text{max}}$ $T_{\text{mid}}$	6.8°C 31.50°C 19.15°C
Sex ratio		1.1♀:0.9♂
Delay parameter	$k$	15

**Fig. 4** Weather stations used in the regional study (**a**), and maximum and minimum temperatures and simulation dynamics of LBAM egg and larval dynamics at Salinas (**b, c**) and Davis, California (**d, e**) during 1/1/2005 and 15/10/2006. The lower (6.8°C) and upper (28°C) thresholds below and above which temperature mortality accrues are shown as *dashed lines* in sub figs. **b** and **d**. The location of Salinas (*open circle*) and Davis (*filled circle*) are illustrated in **a**



continuously over the 1995–2006 period. Data from the first year of simulation were not included in the analysis to allow populations to adjust to the effects of site-specific weather.

Data from the simulation for all locations were georeferenced and written to files for mapping at elevations below 1,000 m. The open source geographic

information system (*Grass GIS*) originally developed by the United State Army Corp of Engineers was used to map the data (*Geographic Resources Analysis Support System (GRASS) Software*, ITC-irst, Trento, Italy (<http://grass.itc.it>)). Raster-based triangulation kriging on a one km grid was used to interpolate the simulation data. The cumulative larval days per year

from the simulation was used as an index of the favorability of the climate for the occurrence of LBAM at a particular location. This index should not be considered a prediction of either absolute population densities of LBAM or potential damage caused by LBAM at a particular location. Its purpose is merely to reflect the favorability of the climate for LBAM population growth.

Three simulation analyses were performed:

1. The relative abundance and phenology of LBAM under mild conditions of Salinas, CA and more extreme conditions common to Davis, CA to show the effects of temperature assuming non limiting host plant availability.
2. A regional analysis of the favorability of temperature for LBAM across all locations in California and Arizona assuming non limiting host plant availability.
3. A regional analysis of climatic favorability for LBAM using the limiting effect of rainfall on a surrogate annual plant to illustrate the potential effects of rainfall on the availability of weedy host plants for LBAM in California and Arizona.

## Results

### Simulation for Salinas and Davis, CA

Simulations of egg and larval population dynamics using observed maximum and minimum temperatures

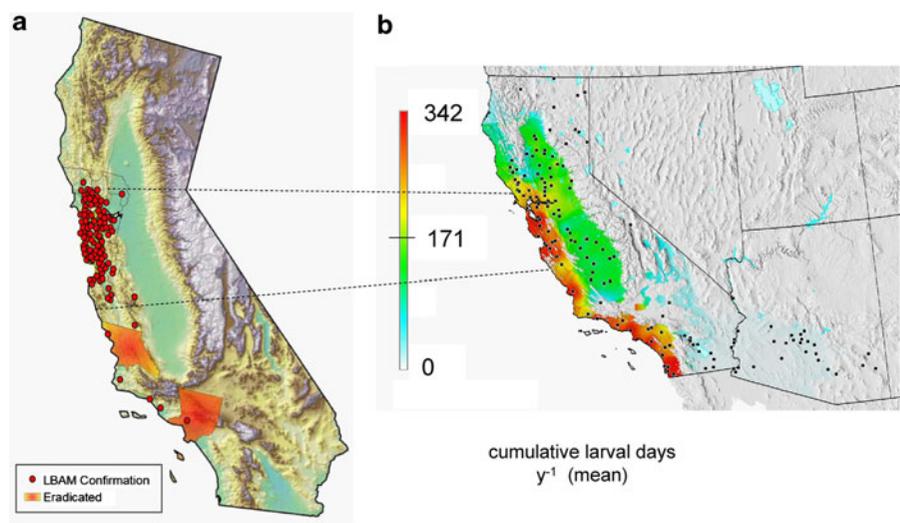
at Salinas, Monterey County in coastal Northern California and Davis, Yolo County in Central California (Fig. 4) were conducted for the period 1 January 2005 to 15 October 2006 to illustrate the effects of differing climatic temperatures on the relative abundance and phenology of LBAM. Temperatures in Salinas were generally mild throughout the year (Fig. 4b) allowing the development of three generations (Fig. 4c). In contrast, temperatures at Davis were colder during winter though rarely freezing, while summers were often very hot (Fig. 4d). The resulting generations at Davis are less distinct (Fig. 4e) with extremes of temperature reducing fecundity and increasing mortality and restricting population growth to the milder times of the year. Consequently the relative abundance of egg and larval populations at Salinas were predicted to be six and two fold greater, respectively than those at Davis.

Regional analysis: influence of temperature with non-limiting host plants

A map of the locations where LBAM adults have been caught in pheromone traps was reported in Fowler et al. (2009) (Fig. 5a). The moth catches are concentrated in the San Francisco and Monterey Bay areas, but some catches have occurred in coastal regions of southern California.

Mean larval-days year<sup>-1</sup> for the period 1996–2006 is used as an index of LBAM favorability with respect to temperature for regional mapping (Fig. 5b). The

**Fig. 5** GIS mapping of average simulated light brown apple moth populations (larval days during 1996–2005) in Arizona and California: **a** locations where the moth has been recovered in north-central California (from Fowler et al. 2009) and **b** the simulated average distribution below 750 m



simulation shows good correspondence between the predicted distribution of LBAM and the recorded trap catches in California, especially in the San Francisco and Monterey Bay areas. The model also suggests that the potential distribution of LBAM could extend southward along the coastal into Southern California (Fig. 5b, areas of red–orange–yellow), and eastward from San Francisco Bay into parts of the Central Valley (e.g., Davis) where areas of intermediate favorability (yellow) are created by the moderating influence of easterly ocean breezes during summer. These areas of intermediate to high favorability include some important apple, pear and grape growing regions of California. In contrast, most of the Central Valley shows low to intermediate favorability (green), while the desert valleys of Southern California and the deserts of Arizona are predicted largely unfavorable because of very high summer temperatures that reduce fecundity and increase mortality (very light blue to absence of color).

The regional simulation data were analyzed using a multiple linear regression (Eq. 4) to assess the relative influence of high and low extremes of temperature on the index of favorability. The dependent variable was regressed on cumulative yearly  $dd_{>6.8^{\circ}\text{C}}$ ,  $dd_{>28^{\circ}\text{C}}$  and  $dd_{<6.8^{\circ}\text{C}}$  together with their interactions and only those variables and interactions with slopes significantly different from zero ( $P < 0.01$ ) were retained in the final model:

$$\begin{aligned} \text{larval days} = & 251.09 - 0.223dd_{<6.8^{\circ}\text{C}} \\ & - 0.297dd_{>28^{\circ}\text{C}} - 0.0007dd_{<6.8^{\circ}\text{C}} \times dd_{>28^{\circ}\text{C}} \\ n = & 1490, \quad R^2 = 0.80, \quad F = 1989.2 \end{aligned} \quad (4)$$

These results show that on average,  $dd_{>28^{\circ}\text{C}}$  had a 33% greater marginal effect on the index of favorability than  $dd_{<6.8^{\circ}\text{C}}$  (i.e.  $\partial y / \partial dd_{>28^{\circ}\text{C}} > \partial y / \partial dd_{<6.8^{\circ}\text{C}}$ ).

The assumption of this analysis is that host plant availability is not limiting, but this is obviously not the case as experience from Australia shows that annual plants are an integral component of the LBAM life system (Geier and Briese 1981).

#### Regional analysis: influence of temperature and rainfall-limited host plants

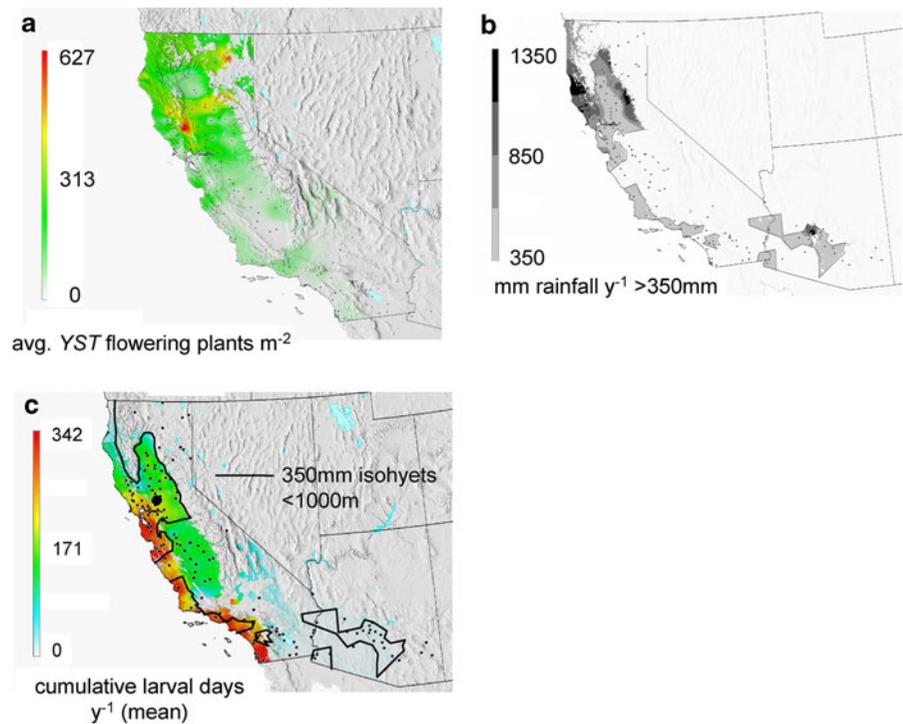
Many Mediterranean annual plants germinate during fall and early winter periods of rain and favorable temperatures. For these plants to persist without irrigation, sufficient rainfall for them to grow and

produce seed must occur. The invasive yellow starthistle (YST) is used here to illustrate the potential effect of host plant availability on the distribution of LBAM. YST occurs widely in California except in the southern half of the Central Valley and the desert regions of Arizona and California (Fig. 6a) where it is limited by low variable rainfall that on average is below the 350 mm isohyets (Fig. 6b) (see Gutierrez et al. 2005). The combined effects of temperature and limiting rainfall for annual host plants on the potential distribution of LBAM may be viewed by overlaying Fig. 6b on Fig. 5b yielding Fig. 6c. The combination of the two factors reinforces the conclusion that the potential distribution of LBAM is largely near coastal with some extension into the Sacramento Valley. Its distribution in Southern California and the deserts of Arizona is likely to be limited by both high summer temperatures and low levels of precipitation across much of the region, with temperature alone as the limiting factor in irrigated crops.

## Discussion

Exotic pests are thought to cause losses in excess of \$137 billion annually in the US (Pimentel et al. 2000), and potential losses due to light brown apple moth are estimated to be \$118 million per annum for apple, grape, orange and pear crops across the USA (Fowler et al. 2009). LBAM is not the first exotic leafroller to invade California; the Palearctic species *Acleris variegana* (Schifferrmüller) and *Cnephasia longana* (Haworth) remain confined to coastal regions after 90 and 60 years, respectively, while the Mexican species *Platynota stultana* (Walsingham) took 50 years to spread from southern California into Central California where it is considered a secondary pest of grape (Powell 1983, 1997, and personal communication). Leaf rollers are generally not considered primary pests of agricultural crops, and while many, including LBAM, have the potential to have direct impact by grazing on the surface of fruit or facilitating *Botrytis* infection within grape clusters, they remain classified as secondary pests due to their amenability to integrated pest management. The experience in New Zealand where LBAM is also an invasive pest and where climatic conditions of temperature and rainfall are conducive to LBAM population development, serves as a valuable example of how its damage can be readily managed as part of an

**Fig. 6** The added indirect effects of rainfall on LBAM distribution: **a** the simulated average distribution of yellow starthistle in California (see Gutierrez et al. 2005), **b** the distribution of average total rainfall greater than 350 mm at elevations below 1,000 m, **c** superimposing total rainfall >350 mm on the simulated distribution and abundance of LBAM based only on temperature



ongoing integrated fruit production program (Walker et al. 1999; Delate et al. 2008).

In contrast, the USDA has classified LBAM as an actionable quarantine pest in California based on estimates of its potential geographic distribution in the United States and projected economic losses to apple, grape, orange and pear crops within this predicted distribution (Fowler et al. 2009; Fig. 7). The potential distribution predicted by Fowler et al. (2009) was modeled using NAPPFAST (North Carolina State University Animal and Plant Health Inspection Service Plant Pest Forecasting System) based on two simple criteria estimated from a 10 years daily climatology database; the frequency of degree days sufficient for the development of three or more LBAM generations, and the frequency of limiting winter temperatures below  $-16^{\circ}\text{C}$  for one full day that would preclude winter survival.

#### Potential geographic distribution and relative abundance of LBAM

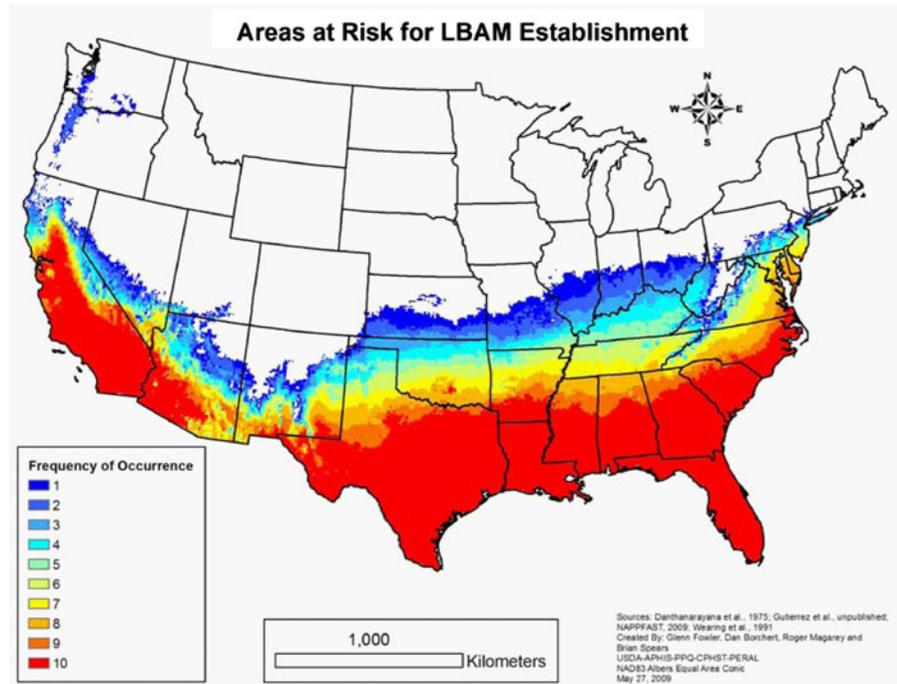
It is well accepted that climate plays a major role in limiting the distribution and abundance of species (e.g., Andrewartha and Birch 1954; Brown et al. 1996; Wellington et al. 1999; Gaston 2003). For

poikilotherms, temperature has a strong influence on growth and reproduction, and consequently is often a major determinant of geographic distribution.

Many approaches have been used to characterize the favorability of climatic zones for poikilothermic species: comparisons of time series of daily, weekly or monthly temperatures, rainfall, relative humidity, and other variables from the area of origin and the invaded area. A widely accepted approach is the use of physiological indices to estimate the tolerance limits of species to temperature, moisture and other factors (Fitzpatrick and Nix 1968; Gutierrez et al. 1974; Sutherst et al. 1991; Sutherst and Bourne 2009). Davis et al. (1998) called these and related methods the ‘climate envelope’ approach, and suggested that conclusions may be misleading because higher tropic levels and important temporal factors and events that affect the dynamics and distributional limits of a species are not included.

The weather-driven demographic model used in this study circumvents many of the criticisms raised by Davis et al. (1998), and was used here to map the potential geographic distribution of LBAM in Arizona and California. This approach requires considerably more weather data to drive the model, which increases biological realism and captures important

**Fig. 7** The proposed USDA geographic distribution of favorableness for the establishment of LBAM (from Fowler et al. 2009)



temporal factors that affect the distribution and abundance of a species (e.g., Gutierrez et al. 1994; Gurney et al. 1996; Gutierrez 1996; Holst and Ruggie 1997; Rochat and Gutierrez 2001; Gutierrez and Baumgärtner 1984, 2007).

The developmental biology of LBAM is relatively simple; it lacks an overwintering diapause, it is polyphagous, and its populations are suppressed by a combination of dispersal mortality, extremes of temperature, host plant availability, and in Australia, by native natural enemies that operate in a density independent manner (Danthanarayana and colleagues). This combination of factors is able to keep LBAM populations at a relatively low level of abundance in Australia, except occasionally in irrigated crops where natural enemies are disrupted through use on non-selective insecticides (Geier and Briese 1981). LBAM populations, although currently established in California, remain sparsely distributed and generally low. Here the species is also affected by patterns of temperature and plant availability similar to the patterns in SE Australia, and LBAM in California is also attacked by a suite of native generalist predators and parasitoids (N. J. Mills, unpublished observations).

Using only temperature, our demographic model predicts the distribution of LBAM in California to be restricted largely to near coastal areas with some

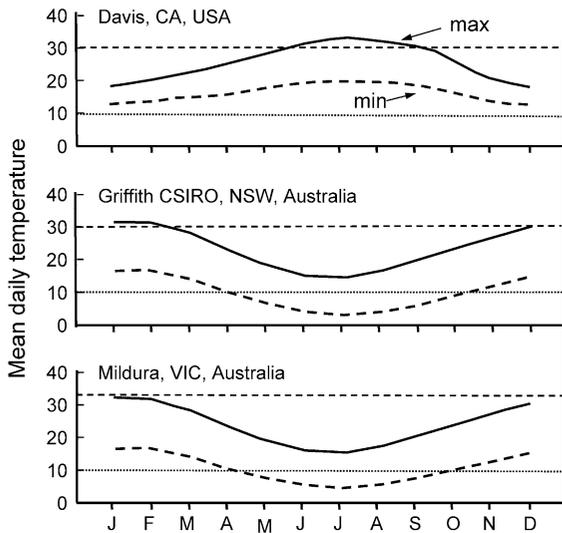
extension eastward into the northern part of the Central valley (Fig. 5b). The majority of the Central Valley shows less than intermediate favourability due to summer temperatures that exceed the tolerance of LBAM. This suggests that if populations could persist in these areas, the relative abundance of larvae would be lower than those at Davis and approximately one-third the abundance predicted in more favorable coastal areas. The limiting effect of rainfall on the potential distribution of YST, a surrogate annual host plant, reinforces the greater favorability of the coastal regions and further highlights the lack of suitable environmental conditions for LBAM in the southern half of the Central Valley (Fig. 6). These predictions of our demographic model differ markedly from those of the Fowler et al. (2009) model for Arizona and California (Figs. 5, 6 vs. 7). The differences stem primarily from the level of biological detail built into the two models, that of Fowler et al. (2009) being a simple degree-day accumulation model versus our mechanistic simulation model. Our dynamic simulation model has the advantages of incorporating biotic as well as abiotic influences, and daily temperatures rather than weekly, monthly or yearly means, and can more readily track the influence of limiting climatic conditions on LBAM populations. The disparity in

predictions of the two models also provides support to Sutherst and Maywald (2005) and Sutherst and Bourne (2009), who have highlighted both model structure, and format and choice of climate variables, in influencing predictions of species distributions.

Critics may ask why we have not validated the model by predicting the distribution of LBAM in Australia, and may posit that LBAM is present in

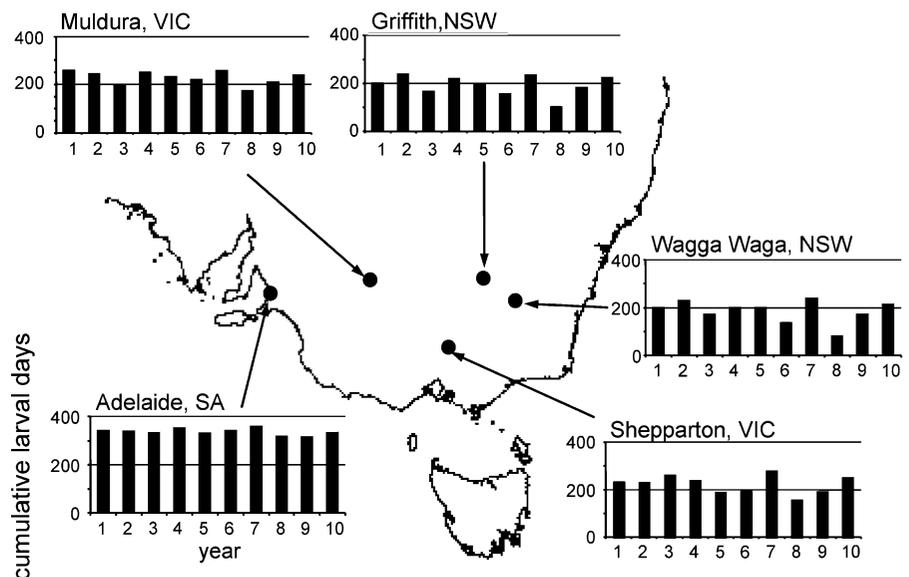
regions of Australia that are much hotter than the regions of California that our model predicts as unfavorable. In the absence of sufficient daily climate data to validate the model for the whole country, we examined daily climate data for the period 1/1/1998–1/1/2009 from five locations in SE Australia (Victoria and New South Wales) where LBAM is known to occur. Mean daily maximum summer temperatures at Mildura (VIC) and Griffith (NSW), the two hottest locations, prove similar to those at Davis, CA, while winter temperatures are lower (Fig. 8). Our model predicts moderate favourability for LBAM at the four hotter inland locations in Australia, as was the case for Davis in California, and greater favourability for the coastal location of Adelaide (Fig. 9). Lloyd et al. (1970) found LBAM infestations were most frequent (and most damaging) in the areas seemingly least favorable for its development, namely cooler southern Victoria and Tasmania. As for the comparison between Davis and Salinas in California (Fig. 4), the relative abundance of LBAM is also predicted to be approximately twice as high in Adelaide as at the inland locations in Australia (Fig. 9).

Any assessment of the pest status of an invasive species must be based on a sound understanding of its likely range of distribution in the new region, in addition to an appraisal of the potential ecological and economic impact that it could have on production and natural ecosystems. The current designation of LBAM as an actionable quarantine pest in the United



**Fig. 8** A comparison of mean daily temperatures for Davis, CA, and two locations in SE Australia (Griffith, NSW and Mildura, VIC) over a 10 years period from 1/1/1998 to 1/1/2009

**Fig. 9** Annual larval days  $m^{-1} year^{-1}$  at five locations in SE Australia for a 10 years period from 1/1/1998 to 1/1/2009



States by USDA is in part based upon the predicted distribution of Fowler et al. (2009). The strong decline in favourability from coastal to interior regions of California and its likely absence from Arizona, as predicted by our model, question the accuracy of the USDA assessment of risk to production and natural ecosystems and suggest the need for re-evaluation of the current pest status of LBAM in the United States.

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