EXHIBIT 1

1   FEBRUARY 13, 2009

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14   Climatic Limits of the Light Brown Apple Moth in Arizona-California:

15   Comments on its Eradication

16

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23

24   **Running Title:** Climatic limits of light brown apple moth

25

26   **ABSTRACT:** The highly polyphagous light brown apple moth (LBAM) (*Epiphyas*

27   *postvittana* (Walk.): Tortricidae) is indigenous to Australia and was first found in

28   California in 2007. It has since been found in 14 coastal counties in Northern California

29   and the Los Angeles basin, but nowhere has it reached outbreak status. The USDA

30   projects that the geographic range of LBAM will include much of Arizona and California

31   and the southern half of the U.S., which together with economic estimates of potential

32   crop losses have been the rationale for an eradication program in California.

33   We report a weather-driven physiologically based demographic model to predict the

34   likely distribution and relative abundance of LBAM using the detailed biology reported

35   by W. Danthanarayana and colleagues, and weather data from 151 locations in California

36   and Arizona for the period 1995 to 2006. The predictions of our model differ markedly

37   from those of a USDA model for California and Arizona in that LBAM appears likely to

38   be limited to near coastal regions of California and with low levels of favorability in the

39   northern Central Valley. The model also predicts LBAM populations at five locations in

40   SE Australia where it is known to occur.

41   We question whether eradication is justified or feasible, and suggest that larger gains

42   would accrue from investment in improved quarantine, biological control, and analytical

43   tools for evaluating the pest status of exotic species and the management strategies and

44   tactics that might best be used for these invaders that in some cases may include

45   eradication.

46

47   **KEY WORDS**: invasive species, distribution, GIS, model, population dynamics.

48 The light brown apple moth (LBAM, *Epiphyas postvittana* (Walk.): Tortricidae) is

49 indigenous to Australia where it is considered a pest of pome fruit crops and grape, but it

50 has been recorded from more than 75 plant species across family lines (Danthanarayana

51 1975, Geier and Briese 1981). This pest was accidentally introduced into England,

52 Hawaii, New Caledonia and New Zealand, and was first found in the San Francisco Bay

53 area by University of California Emeritus Professor Jerry Powell during March 2007

54 (CDFA 2007). LBAM has been found in 14 coastal and near coastal counties in Northern

55 California and in the Los Angeles basin suggesting it has been in California for some

56 time. The pest has not reached outbreak status at any location in California.

57   The United States Department of Agriculture (USDA) posits the potential

58 distribution of LBAM to include all areas having sufficient thermal units for the

59 completion of three generations (i.e. California and the Southern half of the United

60 States) with estimated losses of $134 million per annum (Fowler 2007).[1] In response, the

61 USDA placed quarantine on California produce in affected counties as well as all counties

62 in Hawaii (Federal Quarantine Order of May 2, 2007). In late 2007, the California

63 Department of Agriculture (CDFA) began an eradication program using pheromones,

64 sprays and other techniques. However, the pheromone spray program engendered

65 considerable public protest concerning claimed public health effects, the lack of hard

66 evidence that LBAM is a serious pest, and the proposed expenditure of nearly 100

67 million dollars for the program in California alone. Because of public outcry, an

68 eradication program based on the sterile insect technology (SIT) was substituted.

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[1] www.aphis.usda.gov/plant_health/plant_pest_info/lba_moth/downloads/lbameconomicanalysis.pdf

69   Here, we analyze the potential range and relative abundance of LBAM in Arizona

70   and California to assess its potential pest status, and make comment on the proposed SIT

71   eradication effort from the point of view of probable success.

72

73   **Biology of Light Brown Apple Moth**

74   Danthanarayana (1975) reviewed the sparse literature on the biology of LBAM prior to

75   1975 (Dumbleton 1932, 1939, Evans 1937, Geier 1965, Lawrence and Bartell 1972,

76   Bartell and Lawrence 1973, MacLellan 1973). In a series of papers, Danthanarayana

77   (1975, 1976a, b, c, 1990, Danthanarayana et al. 1995, Gu and Danthanarayana 1990,

78   1992) carefully outlined the biology of LBAM, and this body of work is the basis for our

79   analysis. The developmental biology of *E. postvittana* is summarized below and in Figs.

80   1 and 2.

81   This highly polyphagous moth does not have a diapause period and feeds on

82   numerous plant species across family lines; the lower threshold for development of all

83   stages was estimated as 7.5°C (Danthanarayana 1975), but reanalysis of the data for eggs

84   and larvae yields a non linear relationship with a slightly lower threshold of 6.8°C (Fig.

85   1) . The mean duration of the egg stage is 5.7 days at 28°C (116.9 degree days

86   (dd>6.8°C)) with no eggs hatching above 31.3°C. Larval and pupal developmental times

87   are 335.5 and 142.0 dd>6.8°C respectively with an upper threshold for development of

88   larvae and pupae of approximately 31.5°C. The generation time is 594.2dd. Fifty-

89   percent of eggs are laid by age 645.6dd; mean fecundity is approximately 384 but varies

90   considerably (0-1492) with females size, longevity, larval food and temperature. The

91   optimum temperature for oviposition is near 20°C. At constant temperatures of 20 and

92   25°C, > 50% and 80% of the eggs are laid by the fourth and the seventh day after

93   emergence respectively with peak oviposition occurring in 2-3 days old adult females.

94   Body weight of both male and female moths at emergence increases with increasing

95   temperature to 25°C. Danthanarayana (1976a-c) provides information on the diel and

96   lunar periodicities, seasonal variation in flight activity and the influence of food and

97   temperature on flight performance in the field. Flight duration increases with

98   temperature in the range 15 to 28°C, with males being stronger fliers than females, and

99   the longest flights occurring on day four. Females may mate multiple times beginning

100   within 24h of emergence with nearly all being mated within 4 days with the average

101   number of matings being 2, though by day 11 some may mate five times (Gu and

102   Danthanarayana 1990). The flight biology was not included in the model and we assume

103   a 1:1 sex ratio and that all of the females are mated.

$$R(T) = 0.0096(T - \tau)/(1 + 2.3^{(T-30.5)})$$

$$R(T) = 0.0003(T - \tau)/(1 + 1.9^{(T-31.5)})$$
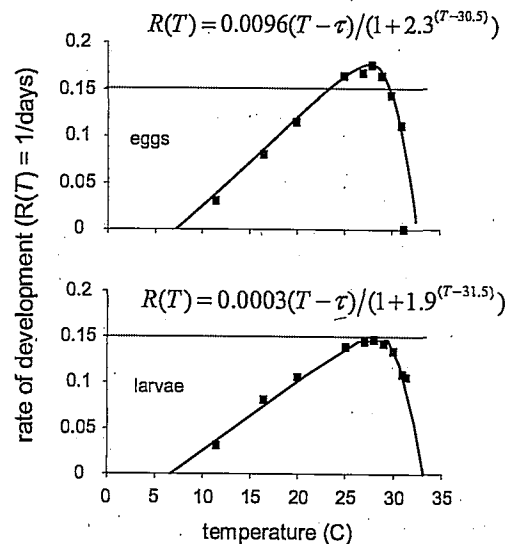
104

105   Figure1. The effect of temperature (T) on the developmental rates of LBAM eggs and
106   larvae (data from Danthanarayana 1975).
107

108   The data in Danthanarayana (1975) were also used to estimate the effects of the

109   complete range of temperatures on per capita fecundity (Fig. 2a-c), and the lethal effects

110   of extreme average temperature (Fig. 2d). The effect of temperature (T) and age (x) on

111   per capita daily fecundity is modeled as the product of the function for maximum

112   fecundity ($E(x, T_{opt})$) at the optimum temperature ($T_{opt} = 20°C$, Fig. 2a) and a scalar for

113   the effects of temperature above and below the optimum (ϕ_T, Fig. 2b) yielding

114    $E(x,T) = \phi_T(T) \cdot E(x,T_{opt})$ (Fig. 2c). The rightward displacement of the fecundity

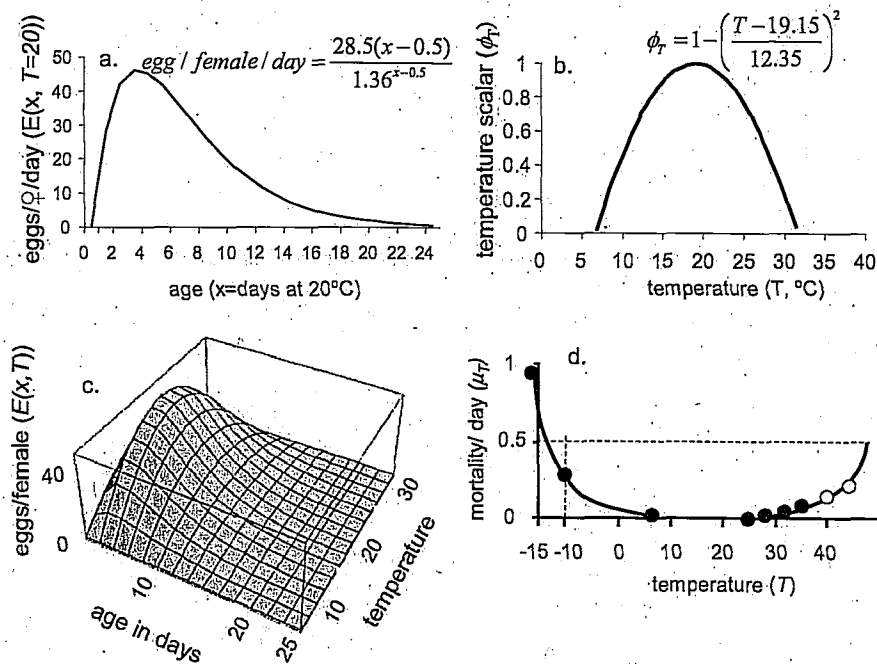115   function from the y-axis (Figs. 2a, c) reflects the short pre-oviposition period.

116

Sources of Mortality

117

118   **Extremes of Temperature.** The rate of daily mortality due to low temperatures is

119   computed as a function of dd below the developmental threshold (6.8°C) (μ_T; eqn.1i; Fig.

120   2d). Such data for LBAM are sparse, and we used ongoing data on the lethal effects for

121   larvae from Buergi and Mills (unpublished) showing that 30% of larvae die within one

122   day at -10°C and all larvae died within one day at -16°C. Eqn. 1i integrates time and

123   temperature (Gutierrez et al.2005; see Fig. 2d) and was used to model the daily over-

124   wintering mortality rate.

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

125

126   The function for daily mortality rate at high average temperatures (eqn.1ii) was

127   estimated from data in Danthanarayana (1975, i.e. figure 11) showing the percent

128   survivorship from egg hatch to adult emergence at several temperatures (T). The percent

129   mortalities at the four highest temperatures estimated from the figure were converted to

6

130   daily mortality rates by dividing by the egg to adult period (477.5dd), multiplying by the

131    $dd > 6.8°C$ at each temperature, and dividing by 100. The mortality rate increases roughly

132   linearly with <u>average</u> daily temperature above 28°C to 45°C hence a shallow exponential

133   function was fit to the data (eqn. 1ii, Fig 2d). Mean daily temperatures above 45°C are

134   unlikely to be encountered in the field, but if they do occur, the mortality rate is expected

135   to increase sharply.

a. $egg \, / \, female \, / \, day = \dfrac{28.5(x-0.5)}{1.36^{x-0.5}}$

b. $\phi_T = 1 - \left(\dfrac{T - 19.15}{12.35}\right)^2$

c.

d.

136

137   Figure 2. The effects of age and daily average temperature (T) on fecundity: (a.) per
138   capita daily fecundity on female age (x) at 20°C, (b.) a scalar ($0 \le \phi_T \le 1$) of the effects of
139   average temperature on fecundity, (c.) the combined effects of subfigures a, b (data from
140   Danthanarayana 1975), and the effects of extreme temperature (d.) on the mortality rate
141   per day ($0 \le \mu_T \le 1$). Note that the symbol (●) represents data and ○ represents linear
142   extrapolations.
143

144   **Mortality.** Field life table studies summarized by Danthanarayana (1983) for Victoria,

145   Australia give sound estimates of factors affecting LBAM life stage mortality. Total

146   generation mortality reported by Danthanarayana (1983) was approximately 98-99.5%

147   with egg mortality being a key factor during spring and autumn, and egg mortality and

148   first instar dispersal mortality being key factors during summer. He found that predation

149   of eggs and 1st instar larvae by generalist predators acted in density independent manner

150   but increased with hot dry weather nearly eliminating summer generations. High rates of

151   mortality were also observed by Geier and Briese (1980) in Australia.

152   California has a Mediterranean climate similar to that of SE Australia, and LBAM

153   does not reach outbreak levels in either region. In California, the egg and larval stages

154   are attacked by a suite of generalist predators and parasitoids (N. J. Mills, unpublished),

155   but field life tables of mortality are currently not available. We take a composite

156   approach to incorporating this mortality to reflects the level of LBAM observe in infested

157   areas of California. We use a functional response model (eq. 2) where mortality (μ_c)

158   increases with temperature ($\Delta t = dd > 6.8°C$) and prey density ($N_{eggs} + N_{Larvae}$) but at a

159   decreasing rate. The coefficient 0.0025 is the proportion of eggs and larvae that can be

160   attacked per dd and was chosen to produce the observed level of inverse density

161   dependent mortality rate.

162    $$0 \leq \mu_c = 1 - e^{-0.0025(N_{eggs} + N_{larvae})\Delta t} < 1 \qquad (2)$$

163

164   **Host Plant Effects.**

165   Host plant availability affects LBAM dynamics, and in our study we examine two

166   scenarios: (1.) effects of temperature assuming non limiting host plant availability

167   characteristic of irrigated or perennial evergreen host plants, and (2.) the effects of

168   prolonged late spring to early fall dry periods and winter ground frost characteristic of

169   Mediterranean climates that restrict the growth of most annual plants exploited by LBAM

170   in Australia and California. For the latter scenario, we use the well studied drought

171   tolerant Mediterranean yellow starthistle (*Centaurea solstitialis* L.; YST) as a surrogate

8

172   annual species to gain insights into the effect of rainfall on annual host plant distribution

173   and its potential influence on LBAM's distribution and relative abundance. Including the

174   plant in the simulation requires daily max-min temperatures as well as daily data on solar

175   radiation, precipitation, relative humidity and runs of wind.

176

177   **Model Overview**

178   The biology of LBAM is embedded in an Erlang distributed maturation time

179   demographic model that simulates the dynamics of an age structured population

180   (Vansickle 1977, DiCola et al. 1999, p 523-524). The general model for the ith age class

181   of a population is:

182 $$\frac{dN_i}{dt} = \frac{k\,\Delta x}{\Delta}[N_{i-1}(t) - N_i(t)] - \mu_i(t)N_i(t).$$ (3)

183   N_i is the density of the ith age class, dt is the change in time (dd/day computed using the

184   non linear model), k is the number of age classes, Δ is the expected mean developmental

185   time, Δx is a daily increment of age, and $\mu_i(t)$ includes the proportional net loss rate of

186   births as modified by temperature and age (Fig. 2c), the death rate due to low and high

187   temperatures (μ_T, eqn. 1) and composite predation (μ_c, eqn. 2).

188   All life stages can be included in one dynamics model with eggs produced by the

189   adult age classes entering the first age cohort ($N_1(t)$) as $x_0(t)$ and exiting at maximum age

190   as $y(t)$ (Fig. 3a). The flow rates ($r_i(t)$) between age classes depends on the numbers in the

191   previous age class (Fig. 3a) and dd/day. The distribution of final maturation times (Fig.

192   3b) is determined by the number of age classes, the mean maturation time Δ and the

193   variance of maturation times (var) ($k = \Delta^2 / var$). The larger the value of k, the narrower

194   is the Erlang distribution of developmental times. The variance of developmental times

195   reported by Danthanarayana (1975) was large and a value of $k = 15$ was selected to reflect

196   this biology.

197   For convenience, separate models are used for the egg, larvae, pupae and adults

198   stages ($S_{i=egg, \text{ } larval, \text{ } pupa, \text{ } adult}$) each having stage-specific characteristics (e.g. Δ_t, k_t, ...) with

199   the outflow of the last age class of a stage ($y_i(t)$) entering the first age class of the next

200   stage ($x_{i+1, \text{ } 0}(t)$), and all eggs produced by the adult stage entering the first age class of

201   eggs as $x_0(t)$ (Fig. 3c). The model parameters are reported in Table 1.
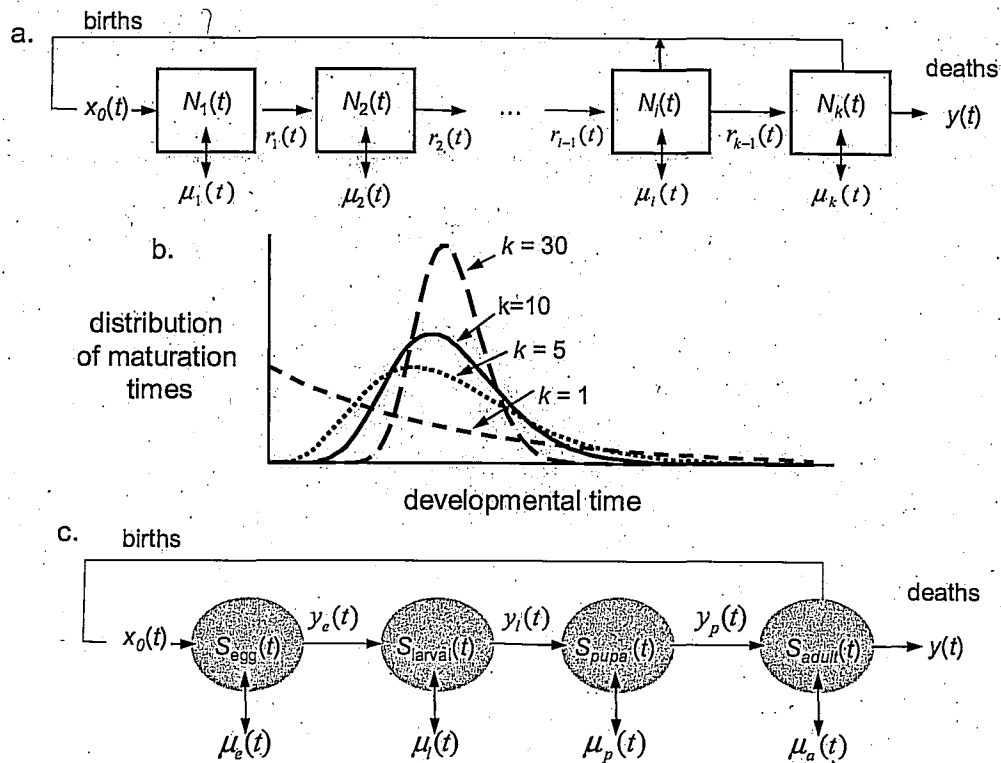
Figure 3. The distributed maturation time model: (a.) all life stages combined in one
model, (b.) the frequency distribution of maturations times with k numbers of age classes,
and (c.) separate models for each life stage each having the between age class flow
biology depicted in (3a.).

210   **Simulation and GIS.**

211   Daily maximum and minimum temperatures for the period 1 January 1995 to 15

212   November 2006 from 151 locations across AZ-CA (Fig. 4a) were used in across year

213   simulations that assume non limiting host plant availability. An initial population density

214   of 50 first instar larvae m^{-2} was assumed at all locations in AZ-CA and the simulations

215   were run continuously during the 1995-2006 period. Data from the first year of

216   simulation were not included in the analysis to allow populations to adjust to the effects

217   of site-specific weather.

218   Data from the simulation for all locations were geo-referenced and written to files

219   for mapping at elevations below 1000m. The open source geographic information system

220   (*Grass* GIS) originally developed by the United State Army Corp of Engineers was used

221   for mapping the data (the version maintained by the Geographic Resources Analysis

222   Support System (GRASS) Software, ITC-irst, Trento, Italy (http://grass.itc.it)). Raster-

223   based triangulation kriging on a one km grid was used to interpolate the simulation data.

224   Three simulation analyses were performed:

225   (1.) The population dynamics of LBAM under mild conditions of Salinas, CA

226   and more extreme conditions common to Davis, CA to show the effects of

227   temperature assuming non limiting host plant availability.

228   (2.) Assuming non limiting host plant availability, a regional analysis of dynamics

229   across all locations in AZ-CA was made using cumulative larval days per year

230   as a metric of favorability.

231   (3.) The limiting effects of rainfall on a surrogate annual plant is used to illustrate

232   the potential effects on LBAM's distribution.

11

233 **Results**

234 **Simulation for Salinas and Davis, CA**

235 Simulations of egg and larval population dynamics and observed maximum and

236 minimum temperatures at Salinas, Monterey County in coastal Northern California

237 (symbol ○) and Davis, Yolo County in Central California (●) are shown in Fig. 4 for the

238 period 1 January 2005 to 15 October 2006 to illustrate the effects of low and high

239 temperatures on LBAM development, fecundity and mortality, and the aggregate

240 influence of composite mortality factors. Temperatures in Salinas are generally mild

241 during the period (Fig. 4b) allowing three generations exhibiting fairly regular

242 oscillations to develop (Fig. 4c). In contrast, temperatures at Davis were colder during

243 winter though rarely freezing, while summers were often very hot (Fig. 4d). The

244 resulting generations are less distinct (Fig. 4e) with extremes of temperature reducing

245 fecundity and increase mortality and restricting population growth to the milder times of

246 the year. Relative egg and larval populations at Salinas were 6 and 2 fold greater

247 respectively than those at Davis.
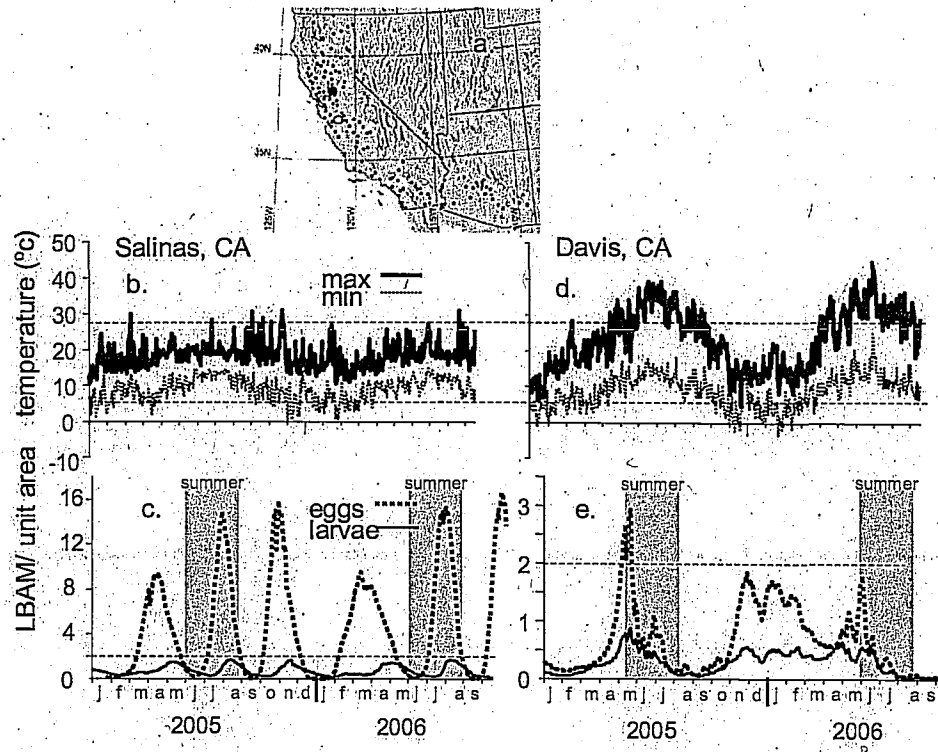
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Figure 4. Weather stations used in the regional study (a), and maximum and minimum temperatures and simulation dynamics of LBAM eggs and larvae m^{-2}y^{-1} at Salinas (b, c: o) and Davis, California (d, e; ●) during 1/1/2005-1996 and 15/10/2006. The 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 (o) and Davis (●) are illustrated in 4a.

Regional Analysis – Temperature and non limiting host plants

A map of the eleven county San Francisco and Monterey Bay areas shows the locations where LBAM adults have been caught in pheromone traps (Fig. 5a, CDFA 2007). The moth has also been trapped in coastal Santa Barbara County in southern California during 2008.
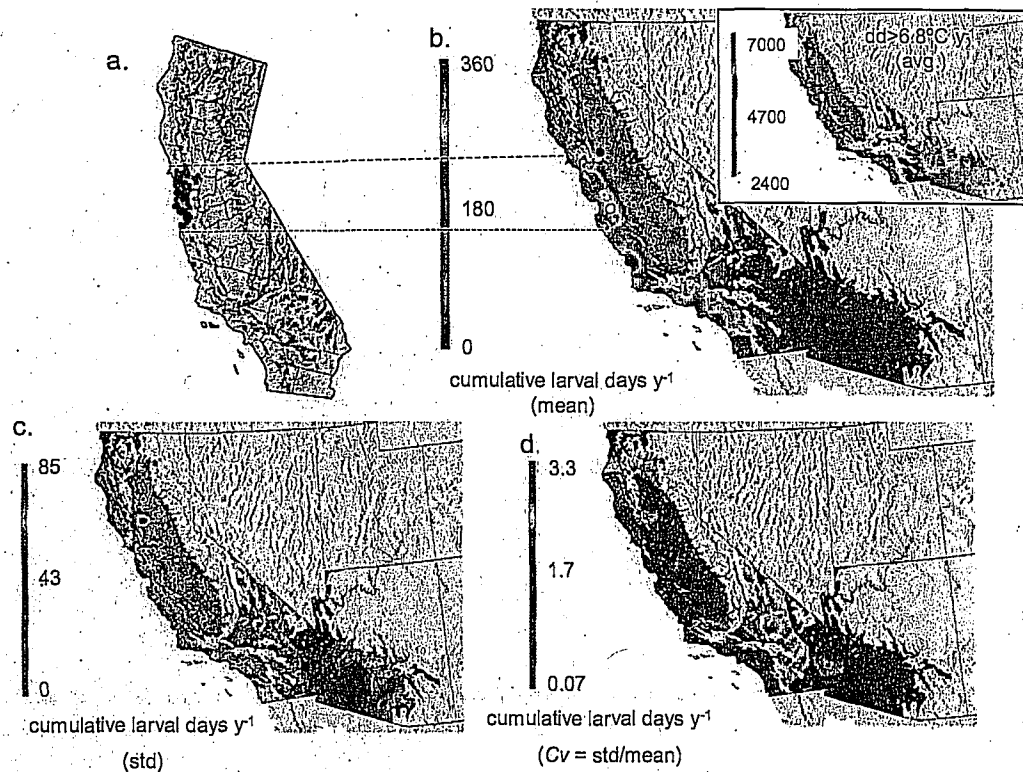
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Figure 5. GIS mapping of simulated light brown apple moth populations in Arizona and California: (a.) locations where the moth has been recovered in north-central California (from Fowler et al. 2007), (b.) average larval days m^{-1} y^{-1} with cumulative *dd* shown as an inset (Davis and Salinas, CA indicated by ●, ○ respectively), (c.) the standard deviations (*std*) of 1996 -2006 of larval days, and (d.) the coefficients of variation (*Cv* (= *std* / *mean*)). The inset in 5b shows the average *dd*>6.8°C.

Average cumulative *dd* > 6.8°C for the 151 locations across Arizona and California

for the 11 year period (1 January 1996 to 15 October 2006) is mapped in the inset in Fig.

5b. Mean larval-days for 1996-2006 is used to map regional favorability for LBAM (Fig.

5b), and shows good correspondence between the predicted distribution of LBAM and

the recorded trap catches in Northern California, especially around the San Francisco Bay

and Monterey Bay areas. The model also suggests LBAM's distribution could extend

southward along the coastal into Southern California (Fig. 5b), eastward of San Francisco

Bay where areas of intermediate favorability in the northern half of the Great Central

14

285   Valley (e.g., Davis) are created by the moderating influence of easterly ocean breezes that

286   lower high summer temperatures. These areas include the important apple, pear and grape

287   growing regions of California. In contrast, the southern half of the Great Central Valley,

288   the desert valleys of Southern California and the deserts of Arizona are largely

289   unfavorable because of very high summer temperatures (see inset in 5b) that reduce

290   fecundity and increase mortality. The standard deviations for cumulative larval days (Fig.

291   5c) are lowest in areas predicted to be unfavorable for LBAM, while the lowest

292     $Cv (= std / mean)$ (Fig. 5d) occur in the more favorable areas (i.e. higher population and

293   lower variability).

294   The regional simulation data were analyzed using a multiple linear-regression

295   (eqn. 4) to assess the relative impact of high and low temperatures. The dependent

296   variable larval-days $m^{-2}y^{-1}$ was regressed on cumulative yearly $dd_{>6.8°C}$, $dd_{>28°C}$ and

297     $dd_{<6.8°C}$. Only independent variable and interactions with slopes significantly different

298   from zero were retained in the model that in our case $p < 0.01$.

299

300
$$larval\ days = 251.09 - 0.223dd_{<6.8°C} - 0.297dd_{>28°C} - 0.0007dd_{<6.8°C} \times dd_{>28°C} \quad (4)$$
$$n = 1490, \quad R^2 = 0.80, \quad F = 1989.2$$

301

302   The results show that on average, $dd_{>28°C}$ has a 33% greater marginal effect on larval days

303   than does $dd_{<6.8°C}$ (i.e. $\partial y / \partial dd_{>28°C} > \partial y / \partial dd_{<6.8°C}$).

304   The assumption of this analysis is that host plant availability is not limiting, but this is

305   obviously not the case as experience from Australia has shown annual plants are an

306   integral component of the LBAM life system (Geier and Briese 1981).

a.

135
0

700

30
mm rainfall y⁻¹ (avg.)

b.

627

313

0

avg. *YST* flowering plants m⁻²

c.

1350

850

350
mm rainfall y⁻¹ >350mm

d.

360

350mm isohyets
<1000m

180

0

cumulative larval days
y⁻¹ (mean)
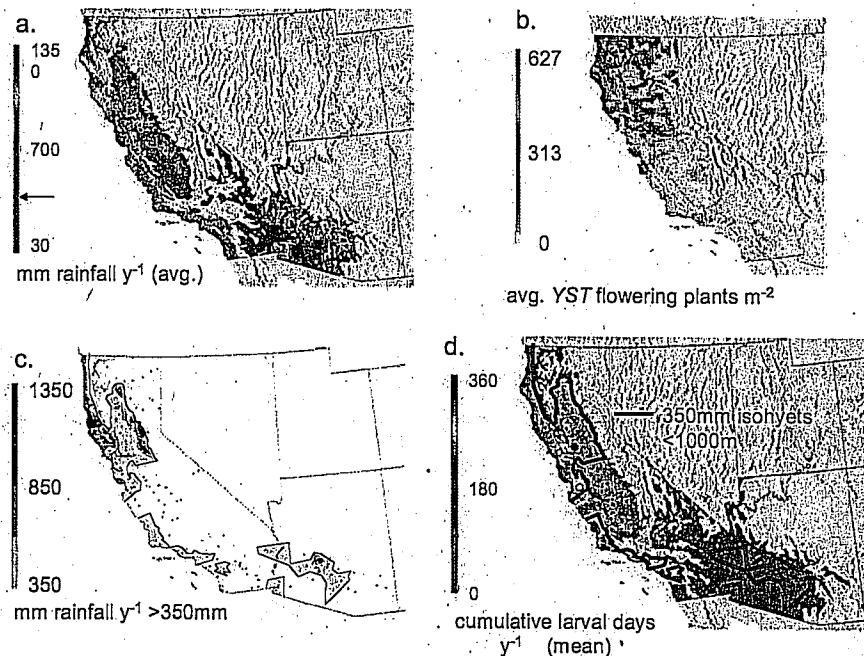
307

308 Figure 6. The added effects of rainfall on LBAM distribution: (a.) average mm rainfall
309 below 1000m elevation, (b.) the simulated distribution of yellow starthistle in California
310 (see Gutierrez et al. 2005), (c.) the distribution of total rainfall greater than 350mm at
311 elevations below 1000m, (d.) superimposing total rainfall > 350mm below 1000m on the
312 simulated distribution and abundance of LBAM based only on temperature.
313

314 **Effects of an Annual Host Plant.** Many Mediterranean annual host plants for LBAM

315 germinate in the fall and early winter during periods of rain and favorable temperatures.

316 For the annual host plats to persist out side of irrigated areas, sufficient rainfall must

317 occur for the plants to grow to maturity and produce seed. An example is the invasive

318 yellow starthistle (YST) that is largely excluded in the dry southern half of the Central

319 Valley and the desert regions of Arizona and California by low variable rainfall (Fig. 6b)

320 above 350mm isohyets (fig. 6c) (see Gutierrez et al. 2005). The combined effects of

321 limiting temperatures on LBAM and limiting rainfall may be viewed in fig. 6d by

322 overlaying fig. 6c on fig. 5b. The combination of the two factors reinforces that LBAM's

323 distribution is largely near coastal with some extension into the Sacramento Valley.

324   LBAM's distribution in Southern California and the deserts of Arizona is limited by both

325   high summer temperatures and low levels of precipitation.

326

327   **Discussion**

328   Exotic pests are thought to cause losses in excess of 137 billion dollars annually in the

329   U.S. (Pimentel et al. 2000), and losses due to LBAM are estimated to be $134 million per

330   annum across the USA (Fowler 2007). The proposed eradication of LBAM in California

331   is in the range of 100 million dollars, but thes loss estimate and the motivation for the

332   eradication are not based on solid economic or scientific grounds. To establish a scientific

333   basis, one must be able to characterize the likely geographic distribution, relative

334   abundance and damage potential of the pest. This had not occurred for LBAM.

335   LBAM is not the first exotic leafroller to invade California; the Palearctic species

336   *Acleris variegana* (Schiffermüller) and *Cnephasia longana* (Haworth) remain confined to

337   coastal regions after 90 and 60 years respectively, while the Mexican species *Platynota*

338   *stultana* (Walsingham) took 50 years to spread from southern California into Central

339   California where it is considered a secondary pest of grape (Powell 1983, 1997, and

340   personal communication). Leaf rollers are generally not considered primary pests of

341   agricultural crops, and while many, including LBAM, have the potential to have direct

342   impact by grazing on the surface of fruit or within grape clusters, they remain classified

343   as secondary pests due to their amenability to integrated pest management. The

344   experience in New Zealand where LBAM is also an invasive pest and where climatic

345   conditions of temperature and rainfall are conducive to LBAM population development,

346   serves as a valuable example of how it's damage can be readily managed as part of an

347   integrated fruit production program (Walker et al. 1999, Delate et al. 2008).

348

349   **Geographic Distribution and Relative Abundance**

350   It is well accepted that climate plays a major role in limiting the distribution and

351   abundance of species (e.g., Andrewartha and Birch 1954, Brown et al. 1996, Wellington

352   et al. 1999, Gaston 2003). In poikilotherms, extant weather influences net growth and

353   reproduction, and trophic interactions may influence the level of control by natural

354   enemies (Huffaker et al. 1971, Rochat and Gutierrez 2001).

from Fowler et al. 2007
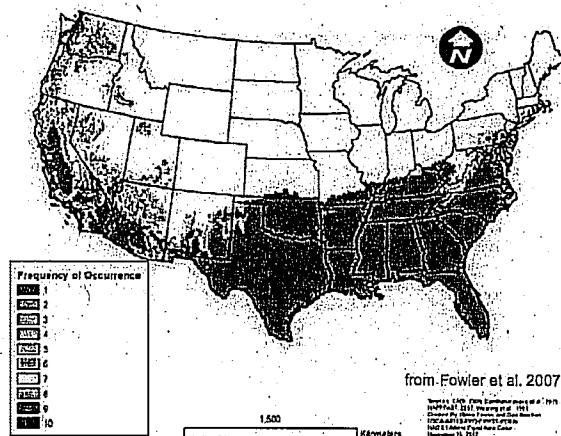
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356
357   Figure 7. The proposed USDA geographic distribution of favorableness for the
358   establishment of LBAM (from Fowler et al. 2007).
359

360   Fowler et al. (2007) used a criterion of degree day sums sufficient for the

361   development of three or more generations of LBAM to circumscribe the areas of

362   favorability in the United States (Fig. 7). Other approaches are available to characterize

363   the favorableness of climatic zones for poikilothermic species: comparisons of time series

364   plots of daily, weekly or monthly temperature, rainfall, vapor-pressure deficit, and other

365   variables from the area of origin and the invaded area. A widely used approach is

366   physiological indices to estimate the tolerance limits of species to temperature, moisture

367   and other factors (Fritzpatrick and Nix 1968, Gutierrez et al. 1972, Sutherst et al. 1991).

368   Davis et al. (1998) called these and related methods the 'climate envelope' approach, and

369   suggested that conclusions may be misleading because higher tropic levels and important

370   temporal factors and events that affect the dynamics and distributional limits of a species

371   are not included.

372   We used a weather-driven physiologically based demographic model (PBDM) to map

373   the potential geographic range and relative abundance of LBAM in Arizona and

374   California. The PBDM approach requires considerably more data but it increases

375   biological realism and strives to capture important temporal factors that affect the

376   distribution and abundance of a species (e.g., Gutierrez and Baumgärtner 1984, Gutierrez

377   et al. 1994, Gurney et al. 1996, Gutierrez 1996, Holst and Ruggle 1997, Rochat and

378   Gutierrez 2001, Gutierrez et al. 2007).

379   LBAM populations are low in both Australia and California. The developmental

380   biology of LBAM is relatively simple; it lacks a diapause stage, it is polyphagous, and

381   it's populations are suppressed by a combination of dispersal mortality, temperatures and

382   host plant availability, and in Australia native natural enemies that operate in a density

383   independent manner (Danthanarayana and colleagues). Similar factors affect LBAM in

384   California, it is also attacked by a suite of generalist native predators and parasitoids (N.

385   Mills), the effect of which was captured using a functional response model that increases

386   on temperature and LBAM density but at a decreasing rate.

387   Using only temperature, the predicted the distribution of LBAM in California is

388   largely restricted to the near coastal areas with some extension eastward into the

389   Sacramento Valley (Fig. 6). The limiting effect of rainfall on Mediterranean annual host

390   plant reinforced the greater suitability of coastal regions.
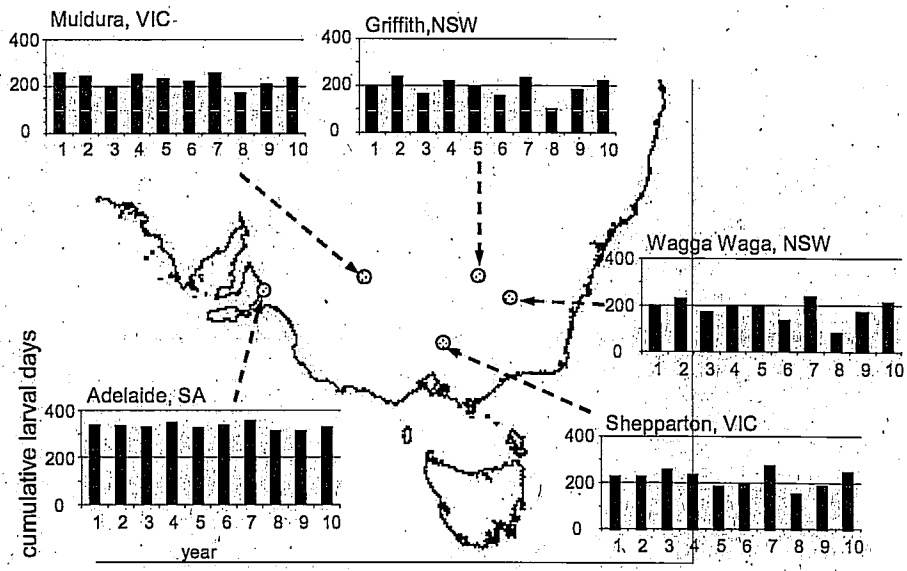
391

392   Figure 8. Annual larval-days m^{-1} y^{-1} at five locations in SE Australia for the ten year

393   period of 1/1/1998 to 1/1/2009.

394

395   Critics posit that LBAM is present in regions of Australia that are much hotter than

396   regions of California our model predicts are unfavourable. To test this, we ran using daily

397   weathers data for five locations in SE Australia (Adelaide SA, Mildura and Shepparton,

398   VIC, Griffith and Wagga Wagga NSW) for the period 1/1/1998 to 1/1/2009. LBAM is

399   reported from all of these areas, and here larval-days m^{-1} y^{-1} is used as a summary metric

400   of favorability (Figure 8). These sites are on a west to east cline of cooler to hotter

401 climates. Population levels in the milder coastal area of Adelaide were roughly twice as

402 high as those in more inland locations: Adelaide > Shepparton >Mildura > Griffith ≈

403 Wagga Wagga. Mean daily maximum temperatures at Mildura and Griffith are similar to

404 those at Davis, CA where our model predicts moderate favourability for LBAM. In

405 contrast, winter temperatures at Mildura and Griffith are lower than at Davis reducing

406 total *dd* (see Figure 4).[2]

407 Ideally, the analysis should be extended to the rest of the continental United States

408 and Australia, but a lack of funding to assemble the extensive weather data set (e.g. daily

409 max-min temperatures, solar radiation, daily precipitation, RH and daily runs of wind)

410 prohibited this.

411

412 **Eradication of LBAM in California.** Initially, a 100 million dollar program of aerial

413 applications of micro-encapsulated pheromone, twist ties utilizing LBAM-specific

414 pheromone, organically-approved insecticides (spinosad and *Bacillus thuringiensis*

415 *kurstaki*), and inundative releases of *Trichogramma* egg parasitoids were proposed for

416 eradicating LBAM.[3] The aerial application of a mating-disruption pheromone

417 engendered harsh public outcry concerning supposed health issues associated with

418 properties of the formulation, and the program was abandoned and substituted with an

419 ongoing program based on the sterile insect technology (SIT).

420 The SIT approach for LBAM eradication engenders little public opposition aside

421 from concerns over its high cost and the low likelihood of success. SIT programs have a

422 checkered record worldwide, and even supposed successful programs have been

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[2] Solar radiation data for the period 11/17/2005-12/31/2005 substituted with data for the same period during 2004.

[3] www.aphis.usda.gov/plant_health/ea/downloads/lbam-treatmentprog-02-14-08.pdf

423   questioned. For example, the eradication of the tropical screwworm *Cochliomyia*

424   *hominivorax* (Coquerel) in Florida during the 1960 -70s was challenged by Readshaw

425   (1986), as were eradication attempts for Mediterranean fruit fly (medfly, *Ceratitis*

426   *capitata* (Wiedemann)) (Carey 1991), and pink bollworm (PBW, *Pectinophora*

427   *gossypiella* Saunders) in California (Gutierrez et al. 2005).

428   In California, fourteen million dollars are spent annually on detection and

429   eradication of medfly, but it continues to persist in Los Angeles County (Carey 1991) and

430   is periodically found in other counties with the most recent capture being in Northern

431   California during 2007 (http://westernfarmpress.com /news/100107-dixon-medfly/). On

432   a positive note, medfly is cold intolerant, and laboratory and field studies (Messenger and

433   Flitters 1954, Israely et al. 2004) suggest its permanent geographic range is smaller than

434   proposed by Carey (1996).

435   When PBW invaded the cotton growing regions of Arizona in the early 1960's

436   and the desert valleys of Southern California in 1965, the USDA began a very large SIT

437   eradication program (Staten et al. 1992). When eradication proved infeasible, the

438   program was modified with the goal of preventing PBW from extending its range into the

439   Central Valley of California (Chu et al. 1996) at a cost of 15-20 million dollars per year.

440   A recent PBDM analysis shows PBW is limited in the Central Valley by winter

441   temperatures, but this could change with climate warming (Gutierrez et al. 2005).

442   Eradication of LBAM in California using any of the proposed technologies may

443   not be feasible because it is multi-voltine, its is cold tolerant, it lacks a diapause stage, the

444   infested area is already large, females can mate multiple time, it has a broad age-structure

445   that varies with time and place across the landscape, there is a lack of analytical tools to

446   guide and evaluate the eradication effort, and as indicated by Carey (1991) non detection

447   of the target pest does not mean eradication. Furthermore, the pest status of LBAM is of

448   secondary pest and manageable through normal IPM practices as evidenced in New

449   Zealand. As such, not only is the probability of success for eradication of LBAM from

450   California questionable, the economic and scientific justifications for its eradication are

451   lacking.

452   What is obvious is that regional management of invasive pests including

453   evaluation of eradication efforts must be based on sound knowledge of their potential

454   geographic range and relative abundance, and on realistic estimates of their potential for

455   environmental impact and losses to the public good. We suggest that the greatest benefits

456   in the area of exotic invasive pests will accrue from increased investment in prevention

457   (e.g., improved quarantine). However, once exotic pests are established, the focus should

458   be on biological control, rapid estimation of the life history parameters of the species, and

459   the development of modeling tools for assessing management strategies for evaluating

460   the efficacy of biological control efforts (e.g., for YST; Gutierrez et l. 2005) and the

461   feasibility of eradication.

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Table 1. Biological parameters for the light brown apple moth

Process	Parameter/eqn.	Light brown apple moth [1]
Thermal threshold (in °C)	τ	6.8°C
Daily degree days $335.3 \times (0.0003(T-\tau)/(1+1.9^{(T-31.5)}))$	$\Delta dd(t)$	
Duration of life stages in degree days at 20°C	dd	Egg (116.2dd) Larvae (335.5) Pupa (142.0) Adult (290.4)
Maximum age (x) per capita fecundity/day at age x and temperature T $F(x,T)=\phi(T)\cdot a(x-0.5)/b^{x-0.5}$ see above [7] $\phi(T)=1-\left[\dfrac{(T-T_{min}-T_{mid})}{T_{mid}}\right]^2$	a b T_{min} T_{max} T_{midx}	28.50 1.36 6.8°C 31.50°C 19.15°C
Sex ratio		0.5
Delay parameter	k	15

Figure Legends

595   Fig. 1. The effect of temperature (*T*) on the developmental rates of LBAM eggs and

596   larvae (data from Danthanarayana 1975).

597   Fig. 2. The effects of LBAM adult age and daily average temperature (*T*) on fecundity:

598   (a.) per capita daily fecundity on female age (*x*) at 20°C, (b.) a scalar ($0 \leq \phi_T \leq 1$) of

599   the effects of average temperature on fecundity, (c.) the combined effects of

600   subfigures a, b (data from Danthanarayana 1975), and the effects of extreme

601   temperature (d.) on the mortality rate per day ($0 \leq \mu_T \leq 1$). Note that the symbol (●)

602   represents data and ○ represents linear extrapolations.

603   Fig. 3. The distributed maturation time model: (a.) all life stages, (b.) the frequency

604   distribution of maturations times with different numbers of age classes (*k*) and (b.)

605   separate models for each life stage each having flow biology depicted in (a.).

606   Figure 4. Weather stations used in the regional study (a), and maximum and minimum

607   temperatures and simulation dynamics of LBAM egg and larval dynamics at Salinas

608   (b, c: ○) and Davis, California (d, e; ●) during 1/1/2005-1996 and 15/10/2006. The

609   lower (6.8°C) and upper (28°C) thresholds below and above which temperature

610   mortality accrues are shown as dashed lines in sub figs. b and d. The location of

611   Salinas (○) and Davis (●) are illustrated in 4a.

612   Figure 5. GIS mapping of simulated light brown apple moth populations in Arizona and

613   California: (a.) locations where the moth has been recovered in north-central

614   California (from Fowler et al. 2007), (b.) average larval days y^{-1} with cumulative *dd*

615   shown as an inset (Davis and Salinas, CA indicated by ●, ○ respectively), (c.) the

616   standard deviations (*std*) of 1996 -2006 of larval days, and (d.) the coefficients of

617   variation ($Cv (= std / mean)$). The inset in 5b shows the average dd>6.8°C.

618 Figure 6. The added effects of rainfall on LBAM distribution: (a.) average mm rainfall

619   below 1000m elevation, (b.) the simulated distribution of yellow starthistle in

620   California (see Gutierrez et al. 2005), (c.) the distribution of total rainfall greater than

621   350mm at elevations below 1000m, (d.) superimposing total rainfall > 350mm on the

622   simulated distribution and abundance of LBAM based only on temperature.

623 Fig. 7. The proposed USDA geographic distribution of favorableness for the

624   establishment of LBAM (from Fowler et al. 2007).

625 Figure 8. Annual larval days m^{-1} y^{-1} at five locations in SE Australia for a ten year period

626   of 1/1/1998 to 1/1/2009.

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