

# CAN MATRIX MODELS GUIDE THE SELECTION OF PARASITOIDS FOR BIOLOGICAL CONTROL INTRODUCTIONS?: LBAM IN CALIFORNIA AS A CASE STUDY

**N. Mills**

*Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3114, U.S.A., nmills@nature.berkeley.edu*

## ABSTRACT.

The light brown apple moth (LBAM, *Epiphyas postvittana*) invaded California from S.E. Australia in 2007 and has become established in two coastal regions around San Francisco and Santa Cruz. As LBAM is not considered a key pest in Australian crops, due to the activity of its natural enemies, one of the management options for this new invader in California is classical biological control. From a series of studies in Australia much is known of the life history and population ecology of LBAM, and as is typical for Lepidoptera, LBAM supports a species rich parasitoid community. In an effort to maximize the success of this project and to guide the selection of parasitoid species for host range testing and potential introduction into California, we make use of a stage-structured matrix model to analyze the life cycle of LBAM for vulnerabilities to parasitism. This approach has been used in biological weed control to guide classical introductions, but has been neglected as a tool for the selection of parasitoids to use against new invasive insect pests. Prospective analysis of a matrix model for LBAM suggests that the mid larval and pupal stages are the most vulnerable stages of the life cycle, and thus parasitoids impacting these life stages have been prioritized for host range testing and potential introduction. Matrix models are likely to serve as a valuable tool to guide the selection of parasitoids for other invasive insect pests that support a species rich parasitoid community in their region of origin.

## INTRODUCTION.

California agriculture is a \$32 billion industry and one of the state's leading sources of revenue and employment. In March 2007, the confirmation of the light brown apple moth (LBAM) *Epiphyas postvittana* (Walker) (Lep.: Tortricidae) in California posed a new threat to the California agricultural industry with the potential to cause millions of dollars in damage to agricultural, specialty and ornamental crops (Varela *et al.* 2008). LBAM originates from SE Australia, has been recorded from more than 250 plant species including fruit, ornamentals, vegetables and weeds, and has become a well-known pest in New Zealand where it is a pest of fruit crops such as apples and grapes (Wearing *et al.* 1991). In California, LBAM has subsequently been found in 12 counties in the San Francisco Bay Area and the Monterey Bay Area. The Animal Plant Health Inspection Service arm of the United States Department of Agriculture issued a Federal Domestic Quarantine order in May 2007, with restrictions on interstate shipment of plant material, and the California Department of Food and Agriculture (CDFA) has issued a State Interior Quarantine order restricting intrastate shipment of plant material from counties where light brown apple moth is known to occur.

The current response to this new invasion is to eradicate LBAM from California and a variety of approaches that include sterile insect technology, pheromone technology, augmentative releases of *Trichogramma* egg parasitoids, and foliar sprays of Bt and/or spinosad are being considered (CDFA 2008). As a more long term management option for LBAM, classical biological control is also being considered, should eradication not be feasible or possible. A recent review of the parasitoids reared from LBAM collected from agricultural crops in Australia by Paull & Austin (2006) provides an excellent starting point for consideration of which species might be suitable for introduction into California for this purpose. Two of the most important criteria for selection of natural enemies for introduction in biological control programs are host specificity and potential impact (Sheppard *et al.* 2003; Goolsby *et al.* 2005; McClay & Balciunus 2005; Mills 2005). While much attention has been focused on host specificity, there has been far less consideration of potential impact for introductions of parasitoids for biological control of insect pests, and it is this component of the selection process that I will focus on here in the context of parasitoid introductions from Australia for biological control of LBAM in California.

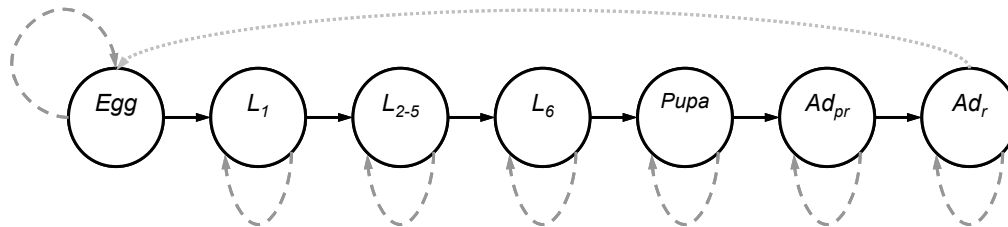
There are a number of different ways in which the potential impact of an exotic parasitoid of an invasive insect pest might be evaluated, and although used more extensively in biological weed control, there are very few specific examples from the biological control of insect pests. Approaches that have been used include estimation of rates of parasitism in the region of origin prior to collection (Mills 2005), estimation of rates of parasitism in cages in quarantine (Goolsby *et al.* 2005), tactical modeling as pioneered by Godfray & Waage (1991), and the use of matrix models to identify the most vulnerable stages in the life cycle of the pest (Mills 2005). One of the most promising of these approaches that has been used more broadly and effectively in biological weed control (McEvoy & Coombs 1999; Raghu *et al.* 2006), is the evaluation of vulnerabilities in the life cycle and it is this approach that will be explored further in the context of selecting Australian parasitoids that are most likely to impact populations of LBAM in California.

#### PARAMETERIZING A STAGE-STRUCTURED MATRIX MODEL FOR LBAM.

Benton & Grant (1999) provide a valuable introduction to the application of matrix models in applied ecology, including biological control, and Caswell (2001) provides a detailed guide to their use. Life cycle stages included in the matrix model are egg, 1<sup>st</sup> instar larva ( $L_1$ ), 2<sup>nd</sup>-5<sup>th</sup> instar larva ( $L_{2-5}$ ), 6<sup>th</sup> instar larva ( $L_6$ ) and pupa to match life table data provided by Danthanarayana (1983), and prereproductive ( $Ad_{pr}$ ) and reproductive ( $Ad_r$ ) adult females to effectively capture the onset of reproduction in this species (Fig. 1). The projection matrix developed for LBAM (Table 1) consists of a set of upper diagonal elements ( $P_i$ ) representing the probability of stasis in which an individual survives and remains within the same life stage, and a set of lower diagonal elements ( $G_i$ ) representing the probability of transition in which an individual survives and moves on to the next life stage. These probabilities are dependent upon the survival ( $\sigma_i$ ) and development ( $\gamma_i$ ) rates of each life stage ( $i$ ) in relation to the time step of the projection (1 day), such that  $P_i = \sigma_i(1 - \gamma_i)$  and  $G_i = \sigma_i\gamma_i$ .

The model was parameterized for California populations of LBAM using data available from studies carried out in Australia. Daily survival rate for each juvenile life

stage was estimated as the mean survivorship from the 16 life tables in Danthanarayana (1983) from the La Trobe University site near Melbourne in Australia excluding mortality due to parasitism, as these parasitoids are not present in



**Fig. 1.** The life cycle diagram for LBAM showing the successive life stages with connectors representing the probability of stasis ( $P_i$ , dashed gray arrows), the probability of transition to the next life stage ( $G_i$ , solid black arrows), and recruitment from the reproductive adult stage to the egg stage ( $F$ , dotted gray arrow).

California. Mean survivorship was converted to daily survival rate, assuming a constant rate of mortality through the life stage, using the expression  $\sigma_i = s^{1/d}$  where  $s$  is mean life stage survivorship and  $d$  is mean life stage duration. Life stage durations were taken from data provided by Danthanarayana *et al.* (1995) for a constant temperature of 19.9°C, with the duration of the complete larval stage broken down into the three larval instar ranges used in the model from personal observations of the duration of 1<sup>st</sup> and 6<sup>th</sup> instar larvae.

**Table 1.** The projection matrix for LBAM with diagonal elements representing the probability of survival and remaining in the same life stage (upper element) and the probability of survival and transitioning to the next life stage (lower element), and the upper right hand element representing the daily per capita realized production of female eggs. Values derived from Danthanarayana (1975, 1983), Danthanarayana *et al.* (1995) and Robison *et al.* (1998) as indicated in the text.

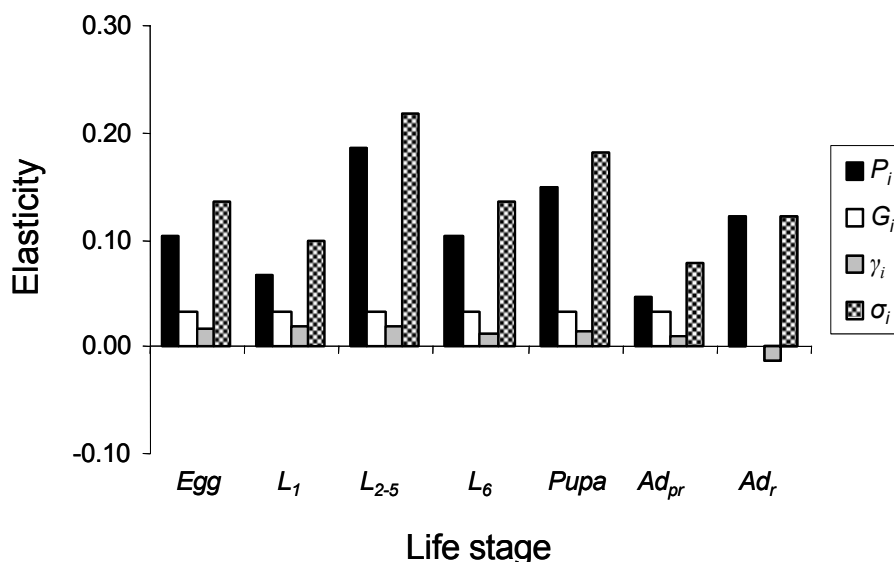
	Egg	$L_1$	$L_{2-5}$	$L_6$	Pupa	$Ad_{pr}$	$Ad_r$
Egg	0.815	–	–	–	–	–	12.125
$L_1$	0.118	0.718	–	–	–	–	–
$L_{2-5}$	–	0.144	0.910	–	–	–	–
$L_6$	–	–	0.066	0.813	–	–	–
Pupa	–	–	–	0.163	0.878	–	–
$Ad_{pr}$	–	–	–	–	0.103	0.625	–
$Ad_r$	–	–	–	–	–	0.313	0.844

The mean longevity of the prereproductive and reproductive periods of adult female life and the progeny sex ratio were taken from Danthanarayana (1975), while

data on female fecundity in the laboratory at 19.9°C was obtained from Danthanarayana *et al.* (1995). The daily survival rate of adult females was estimated, after Caswell (2001) as  $1 - (1/\text{mean longevity})$ , and their daily realized fecundity was estimated as  $F = \text{sex ratio} * (\text{lab fecundity}/\text{reproductive period}) * \text{proportion realized}$ . While loss of potential fecundity is often not included in life table data, such as that from Danthanarayana (1983) for LBAM, the fecundity realized under field conditions is often only a proportion of that measured under laboratory conditions (Price *et al.* 1990). The proportion of the laboratory fecundity realized was estimated from data provided by Robison *et al.* (1998) for another archipine tortricid *Choristoneura fumiferana*.

PROSPECTIVE ANALYSIS OF THE LBAM MATRIX MODEL: LIFE CYCLE VULNERABILITIES.

To be able to ask the question: ‘If parasitism reduced the survival rate of a particular stage in the life cycle of LBAM what effect would it have on population growth rate?’ we use prospective analyses of the LBAM matrix model. One approach is to evaluate the impact of a very small proportional change in value for each matrix element, or their component vital rates, on population growth rate ( $\lambda$ ). Referred to as the elasticity of  $\lambda$  to the matrix element or vital rate, elasticity analysis has been widely used. Benton & Grant (1999) point out that considerable caution must be used in extrapolating the results of elasticity analysis to the impact of larger changes in vital rates on population growth rates due to inherent nonlinearities and the unequal durations of life stages represented in stage-structured models. Nonetheless, de Kroon *et al.* (2000) and Caswell (2001) indicate that in practice elasticity analysis does a good job of predicting the effects of large perturbations in vital rates. Thus as a first step toward prospective analysis of the likely impact of



**Fig. 2.** Prospective analysis to show the elasticity of  $\lambda$  to the stasis ( $P_i$ ) and transition ( $G_i$ ) elements of the matrix model for LBAM, and their subcomponent vital rates of development rate ( $\gamma_i$ ) and survival rate ( $\sigma_i$ ) for each life stage.

adding parasitism at different life cycle stages to the population growth rate of LBAM we use elasticity analysis, both for the stasis and transition elements of the matrix, and for their component vital rates (Fig. 2). In addition, the elasticity of  $\lambda$  to daily realized fecundity ( $F$ ) is 0.032 (not shown in Fig. 2). The larger the elasticity, the greater its impact on the population growth rate of LBAM. Thus it can be seen for all life stages that the probability of stasis has a greater influence than the probability of transition, and that this is due to the greater influence of the component survival rates compared to development rates. Looking for vulnerabilities (the largest elasticities) in the life cycle of LBAM, we can also clearly see that changes in survival rate of the mid larval stage ( $L_{2-5}$ ) and the pupal stage have the greatest impact on population growth rate.

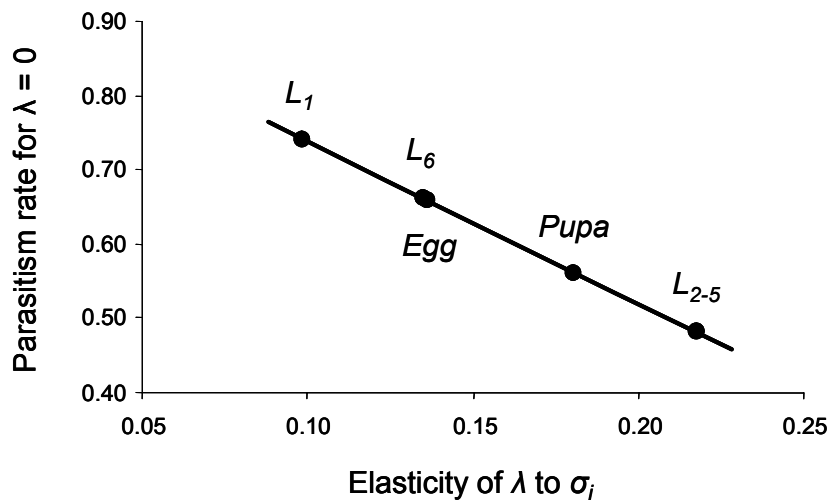
As a second step toward prospective analysis of the likely impact of adding parasitism at different life cycle stages, we can also examine the extent to which survival rate would need to be reduced at a particular life cycle stage to suppress population growth (i.e., to reduce  $\lambda$  to 1). This approach has been used previously by Lin & Ives (2003) and Mills (2005) to further verify the life cycle vulnerabilities identified through elasticity analysis. The daily survival rate from added parasitism ( $\sigma_p$ ) can be incorporated into the matrix model elements as  $\sigma_{p_i} * P_i$  and  $\sigma_{p_i} * G_i$  where for each life stage  $i$ ,  $p_i$  is the level of parasitism contributed by an introduced parasitoid at that life stage and  $\sigma_{p_i} = (1 - p_i)^{1/d_i}$ . By incorporating parasitism into individual life stages (egg through pupa) while keeping other life stages free from parasitism, we can determine the rate of parasitism required to generate zero population growth for LBAM. These rates of parasitism thus provide a further indication of the relative vulnerability of the different life cycle stages of LBAM to the impact of introduced parasitoids acting at different stages in the life cycle.

Using this second approach to prospective analysis of the LBAM matrix model, we see that there is a very good match between the rates of parasitism required for zero population growth at each life stage and the corresponding elasticities of  $\lambda$  to survival rates (Fig. 3). Those life stages with the greatest elasticity of  $\lambda$  to survival rate require the lowest rates of parasitism to suppress population growth and again highlight the mid larval ( $L_{2-5}$ ) and pupal stages as being most vulnerable. The negative relationship is perfectly linear giving us further confidence that we have correctly identified these two life stages as most vulnerable to introduced parasitoids in the life cycle of LBAM.

### CONCLUSIONS: A STRATEGY TO PRIORITIZE PARASITOID INTRODUCTIONS.

In a recent review, Paull & Austin (2006) reviewed what is known of the parasitoids reared from LBAM collected from a variety of agricultural crops in Australia. A schematic form of this information (Fig. 4) summarizes the species present in the parasitoid community, together with basic details of the parasitoid guilds to which they belong (*sensu* Mills 1994). With such a wide range of parasitoids to select from this clearly poses a considerable problem with regard to host specificity screening. However, using the prospective analyses of the matrix model for LBAM as a guide to likely impact, we can see from the schematic summary (Fig. 4) that there is only a single parasitoid species, *Dolichogenidea tasmanica* (Cameron) (Hym.: Braconidae), that can influence the survival rate of the mid larval stage ( $L_{2-5}$ ), although there are

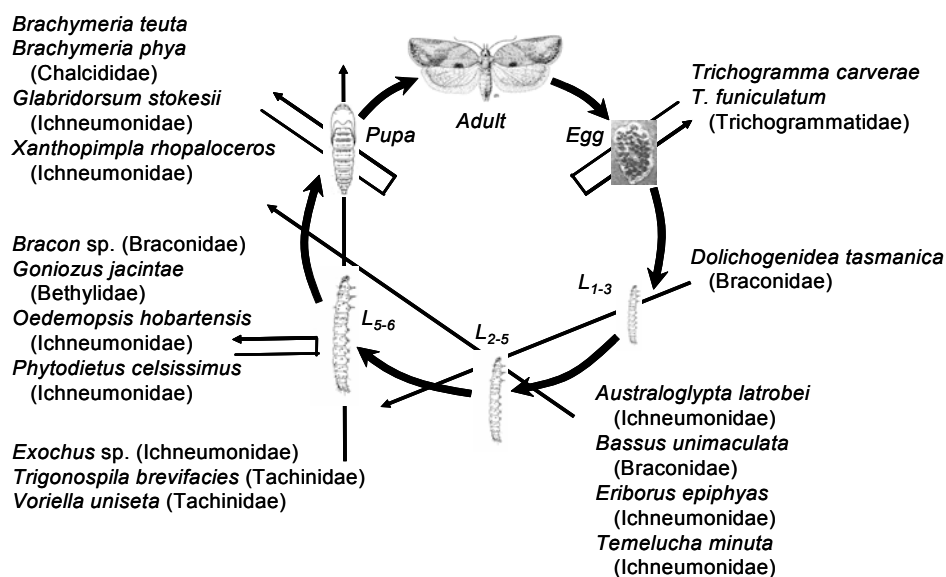
still 7 parasitoid species that could influence the survival rate of the pupal stage (those attacking the late larval stage as well as those attacking the pupal stage).



**Fig. 3.** A comparison of two approaches to prospective analysis of the LBAM matrix model: the relationship between rate of parasitism required to suppress population growth rate and the elasticity of population growth rate to survival rate for each life stage.

Among these later two parasitoid guilds, however, it is already known from New Zealand that the tachinids and the ichneumonid pupal parasitoids are polyphagous species (Thomas 1989; Munro 1998), leaving *Exochus* sp. (Hym.: Ichneumonidae) and the two *Brachymeria* species *B. teuta* (Walker) (Hym.: Chalcididae) and *B. phya* (Walker) (Hym.: Chalcididae) as potential candidates. Thus, as a result of using the stage-structured matrix model we have been able to prioritize those parasitoids that are most likely to have a greater impact on the population growth rate of LBAM for host range testing. We are currently testing the host range of *D. tasmanica* and will soon be carrying out similar tests with *Brachymeria teuta* as these are two of the most common parasitoids of LBAM in Australia, while both *Exochus* sp. and *B. phya* appear to be less common associates of LBAM.

Plant-feeding insects differ considerably in the species richness of their parasitoid communities, which is influenced by host abundance, taxonomy, and feeding niche (Hawkins 1994). In the context of classical biological control, when the richness of the parasitoid community is high, as is the case for many lepidopteran, symphytan and leafmining hosts, it is of particular importance to be able to prioritize the host range testing of potential candidates for introduction, not only to optimize the timeline of the project, but also to reduce the cost of the background research required. Matrix models to estimate the likely impact of parasitoids at different life cycle stages offer a very valuable tool for the optimization of such decision-making in classical biological control.



**Fig. 4.** A schematic representation of the life cycle of LBAM and the more frequently associates members of the parasitoid community, indicating timing of host attack (origin of the arrows) and host death (end of the arrows) and distinguishing between endoparasitoids (arrows passing through the circle) and ectoparasitoids (arrows remaining outside of the circle).

## REFERENCES.

- Benton, T. G., Grant, A. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology and Evolution* **14**, 467-471.
- CDFA 2008. Light brown apple moth project. [http://www.cdca.ca.gov/phpps/PDEP/lbam/lbam\\_main.html](http://www.cdca.ca.gov/phpps/PDEP/lbam/lbam_main.html) (last accessed Sept. 29 2008)
- Caswell, H. 2001. "Matrix Population Models. Construction, Analysis and Interpretation," Sinauer Associates, Sunderland.
- Danthanarayana, W. 1975. The bionomics, distribution and host range of the light brown apple moth, *Epiphyas postvittana* (Walk.) (Tortricidae). *Australian Journal of Zoology* **23**, 419-437.
- Danthanarayana, W. 1983. Population ecology of the light brown apple moth, *Epiphyas postvittana* (Lepidoptera: Tortricidae). *Journal of Animal Ecology* **52**, 1-33.
- Danthanarayana, W., Gu, H., Ashley, S. 1995. Population growth potential of *Epiphyas postvittana*, the lightbrown apple moth (Lepidoptera: Tortricidae) in relation to diet, temperature and climate. *Australian Journal of Zoology* **43**, 381-394.
- Godfray, H. C. J., Waage, J. K. 1991. Predictive modeling in biological control: the mango mealy bug (*Rastrococcus invadens*) and its parasitoids. *Journal of Applied Ecology* **28**, 434-453.

- Goolsby, J. A., DeBarro, P. J., Kirk, A. A., Sutherst, R. W., Canas, L., Ciomperlik, M. A., Ellsworth, P. C., Gould, J. R., Hartley, D. M., Hoelmer, K. A., Naranjo, S. E., Rose, M., Roltsch, W. J., Ruiz, R. A., Pickett, C. H., Vacek, D. C. 2005. Post-release evaluation of biological control of *Bemisia tabaci* biotype “B” in the USA and the development of predictive tools to guide introductions for other countries. *Biological Control* **32**, 70-77.
- Hawkins, B. A. 1994. “Pattern and Process in Host-Parasitoid Interactions,” Cambridge University Press, Cambridge.
- de Kroon, H., van Groenendael, J., Ehrlén, J. 2000. Elasticities: a review of methods and model limitations. *Ecology*, **81**, 607–618.
- Lin, L. A., Ives, A. R. 2003. The effect of parasitoid host-size preference on host population growth rates: an example of *Aphidius colemani* and *Aphis glycines*. *Ecological Entomology* **28**, 542-550.
- McClay, A. S., Balciunas, J. K. 2005. The role of pre-release efficacy assessment in selecting classical biological control agents for weeds – applying the Anna Karenina principle. *Biological Control* **35**, 197-207.
- McEvoy, P. B., Coombs, E. M. 1999. Biological control of plant invaders: regional patterns, field experiments, and structured population models. *Ecological Applications* **9**, 387-401.
- Mills, N. J. 1994. Parasitoid guilds: defining the structure of the parasitoid communities of endopterygote insect hosts. *Environmental Entomology* **23**, 1066-1083.
- Mills, N. 2005. Selecting effective parasitoids for biological control introductions: codling moth as a case study. *Biological Control* **34**, 274-282.
- Munro, V. M. W. 1998. A retrospective analysis of the establishment and dispersal of the introduced Australian parasitoids *Xanthopimpla rhopaloceros* (Kreiger) (Hymenoptera: Ichneumonidae) and *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) within New Zealand. *Biocontrol Science and Technology* **8**, 559-571.
- Paull, C., Austin, A. D. 2006. The hymenopteran parasitoids of light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera : Tortricidae) in Australia. *Australian Journal of Entomology* **45**, 142-156.
- Price, P. W., Cobb, N., Craig, T. P., Frenandes, G. W., Itami, J. K., Mopper, S., Preszler, R. W. 1990. Insect herbivore population dynamics on trees and shrubs: new approaches relevant to latent and eruptive species and life table development. In “Insect-Plant Interactions, Volume 2” (E. A. Bernays, Ed.), pp. 1-38. CRC Press, Boca Raton.
- Raghu, S., Wilson, J. R., Dhileepan, K. 2006. Refining the process of agent selection through understanding plant demography and plant response to herbivory. *Australian Journal of Entomology* **45**, 308-316.
- Robison, D. J., Abrahamson, L. P., Raffa, K. F., White, E. H. 1998. Spruce budworm (Lepidoptera : Tortricidae) field fecundity: new insights into its estimation and use. *Forest Ecology and Management* **106**, 73-81.
- Sheppard, A. W., Heard, T. A., Briese, D. T. 2003. What is needed to improve the selection, testing and evaluation of weed biological control agents: workshop synthesis and recommendations. In “Improving the Selection, Testing and Evaluation of Weed Biological Control Agents” (H. S. Jacob and D. T. Briese, Eds.), pp. 87-98. CRC for Australian Weed Management, Glen Osmond.
- Thomas, W. P. 1989. *Epiphyas postvittana* (Walker), lightbrown apple moth (Lepidoptera: Tortricidae). In “A Review of Biological Control of Invertebrate



- Pests and Weeds in New Zealand 1874 to 1987” (P. J. Cameron, R. L. Hill, J. Bain and W. P. Thomas, Eds.), pp. 187-195. CAB International, Wallingford.
- Varela, L. G., Johnson, M. W., Strand, L., Wilen, C. A., Pickel, C. 2008. Light brown apple moth's arrival in California worries commodity groups. *California Agriculture* **62**, 57-61.
- Wearing, C. H., Thomas, W. P., Dugdale, J. S., Danthanarayana, W. 1991. Tortricid pests of pome and stone fruits, Australian and New Zealand species. *In* “Tortricid Pests, their Biology, Natural Enemies and Control” (L. P. S. van der Geest and H. H. Evenhuis, Eds.), pp. 453-472. Elsevier, Amsterdam.