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Invasion Biology, Ecology, and Management of the Light Brown Apple Moth (Tortricidae)

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Epiphyas postvittana, pest management, invasive species, eradication

Abstract

Epiphyas postvittana (Walker) (Lepidoptera: Tortricidae), the light brown apple moth (LBAM), is an important leafroller pest with an exceptionally wide host range that includes many horticultural crops and other woody and herbaceous plants. LBAM is native to southeastern Australia but has invaded Western Australia, New Zealand, Hawaii, much of England, and in 2007, it was confirmed as established in California. The discovery of this pest in California has led to a major detection and regulatory effort because of concerns about economic and environmental impacts. Its recent discovery in Sweden is also of note. LBAM has often been intercepted on imports of fruit and other plant parts, and it has the potential to become a successful invader in temperate and subtropical regions worldwide. The importance of the insect has prompted development of classical biological control programs together with a wide variety of other management interventions that can be used in integrated pest management or integrated pest eradication.

Light brown apple moth (LBAM):*Epiphyas postvittana***Integrated pest management (IPM):**

the use of a range of mortality and management factors for suppression

Integrated pest eradication (IPE):

the use of a range of compatible technologies to achieve the eradication of an unwanted organism

INTRODUCTION

Epiphyas postvittana (Walker), the light brown apple moth (LBAM) (Lepidoptera: Tortricidae), is an important horticultural and agricultural pest both in its native and introduced ranges. LBAM is well studied because it has been the target of a major research effort into almost every available insect control methodology and it has been widely used as a model organism. Aspects of LBAM biology and control have been reviewed (34, 55, 121, 146). The objective of this review is to re-examine current knowledge and options in line with future management needs. This review is particularly timely, as LBAM was confirmed to be present in California in 2007. We review and synthesize knowledge from the native and invaded regions in Australasia/Oceania, Europe, and North America. We discuss the synthesis of tactics into integrated pest management (IPM) and integrated pest eradication (IPE) and compare the tools available in an evolving social context.

LBAM larvae feed on leaves and the surface of fruit typically by webbing a leaf to a fruit to create a protected shelter (77). This causes unsightly blemishes on fruit and can lead to secondary disease development, causing rots in crops such as grapes (3). As a pest insect, LBAM is best known from tree fruits, including apples, pears, citrus, peaches, nectarines, apricots, vines, berryfruit, and to a lesser extent from forestry, vegetable, and flower crops (146). The economic importance of the insect in Australia and New Zealand is greatest on apples, pears, and grapes. It is a Class A pest on the U.S. federal register (although this is being actively petitioned for delisting) and presents market access barriers for export to many countries (142). Larval damage depends on population levels, which vary enormously across the landscape in New Zealand and are much lower in the presence of certain generalist biological control agents (37, 137) that are climatically limited (86). The zero tolerance of live larvae in exports significantly raises the requirement for control, compared with the damage done by larvae to nonexport

crops. Pest management interventions in most crops in New Zealand need to consider other leafrollers (146).

BIOLOGY

Host Range and Development

The host range of LBAM is exceptionally wide, with Australian records from 123 genera in 55 families (31, 55). This included 22 native genera and 101 exotic genera, indicative of how introduced crop and ornamental plants and accidental introductions provided LBAM with the opportunity to greatly increase its host range. Its natural hosts in its native region are thought to be evergreen acacia species, although its greater developmental rate indicates that it may have evolved on herbaceous plants (36). With additional hosts in its expanding adventive range, LBAM has been recorded from over 500 host plant species in 363 genera from 121 families across the vascular plants. This mostly includes dicotyledonous plants, with numerous monocotyledonous plants, conifers, and even ferns (**Figure 1**). The prevalence of Rosales, Fabales, Vitales and Saxifragales may be partly related to observer bias towards economically important crop plants.

Adult male and female moth behavior is affected by sex pheromone (9, 11), wind speed and direction (112), plant odorant (123), and plant surface cues (46). A potential host must be located either by adult female moths or by larvae (neonates or later instars), and the quality of the host is likely to be expressed in larval developmental parameters and in terms of increased risk of parasitism or predation. Host location and oviposition choice in LBAM are likely to be mediated by antennal olfactory receptor neurons (46, 67). Female LBAM attraction to fermenting food baits (39, 112) indicates that long-range orientation to volatile compounds occurs. Certain plant odorants were electrophysiologically active and mediated oviposition in LBAM (123), and receptors for some of these compounds have been identified (68). Smooth surface textures, ridges, and upper

surfaces are preferred by female moths for oviposition (50). Oviposition site was affected mainly by plant stimuli (46), but little is known of female moth behavior after eclosion in the field, although dispersal was predominantly upwind at dusk through a two-year-old apple orchard under a prevailing wind (112). No difference in female moth preference was reported for 15 hosts over 11 nonhosts, whereas larval preferences for these plants in bioassays were negatively correlated with female choice (47).

Data on developmental rates exist for only a few host plants. The weight of females and the finite rate of increase were consistently higher on plantain (*Plantago lanceolata*) and dock (*Rumex crispus*) than on apple (*Malus pumilla*) and were lowest on clover (*Trifolium repens*) (36). Fecundity was greater by a factor of 1.5–2.5 on plantain and dock than on apple and clover and reached means of up to 560 eggs per female (36), although during an earlier study fecundity of LBAM fed clover and plantain were about equal (31). Maximum fecundity recorded (1492 eggs) was from plantain (34). The highest population growth rate was at 25°C on most host plants, and the mean generation time differed little between LBAM reared on these different plants (36). A study in New Zealand (140) differed, in which larval development times were shorter on dock than on poplar (*Populus nigra*), apple (*Malus domestica*), gorse (*Ulex europaeus*), and blackberry (*Rubus fruticosus*), and pupal weights for LBAM on apple varieties were among the highest. Such differences between studies may reflect variation between LBAM populations as well as plant provenances. Detoxication enzyme levels in feeding larvae can be expressed

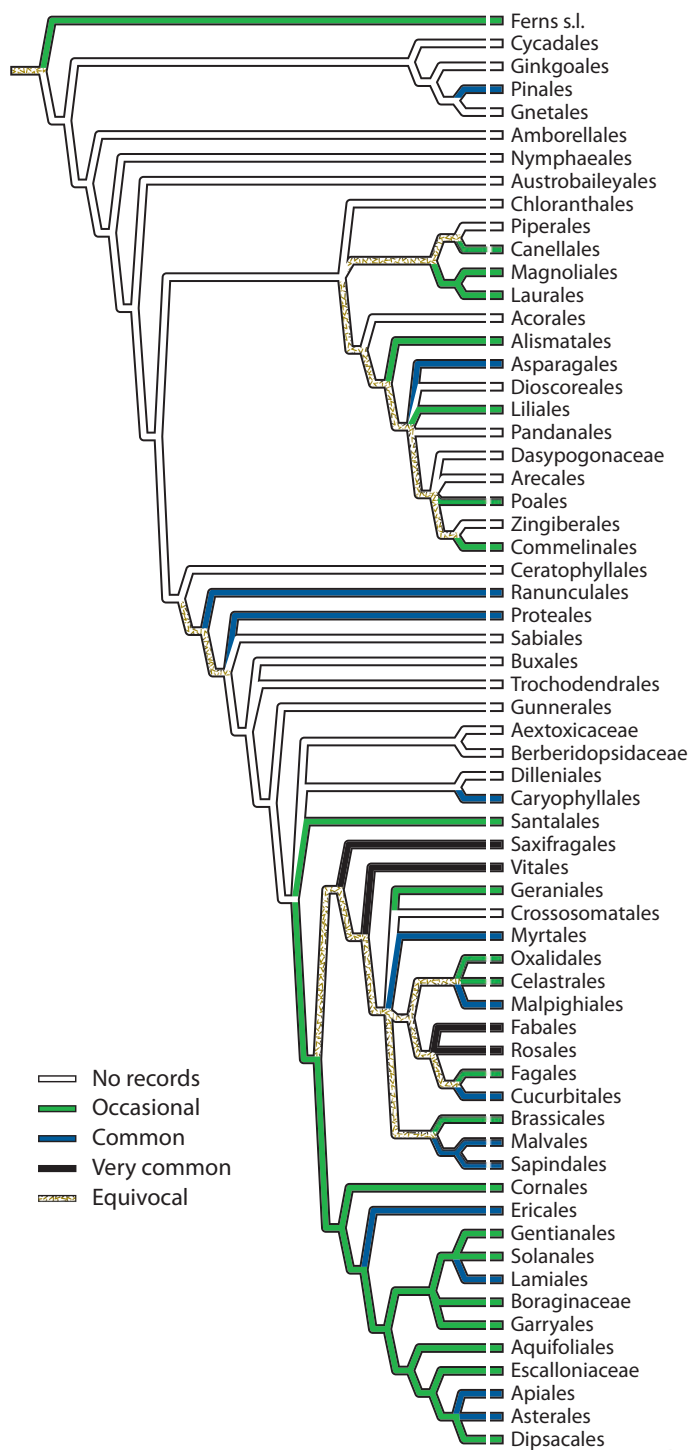


Figure 1
Cladogram of host record frequency for light brown apple moth (*Epiphyas postvittana*) from Australia, New Zealand, Hawaii, the United Kingdom, and California (23) [cladogram according to APG II 2003 (1)].



differentially on different hosts (92). Wearing et al. (145) ranked 18 apple cultivars for partial resistance to larvae and, together with field trials of 38 cultivars, found several with potentially useful LBAM resistance.

Phenology and Population Monitoring and Modeling

In Australia and New Zealand, LBAM can have two to four generations per year depending on the climate (146). In New Zealand, populations typically increase and generations broaden over time during the growing season (114). Monitoring larval populations and adult males with pheromone traps (11) showed two generations per year in Otago (at 45°S) and Canterbury (43°S) (26, 83), whereas three generations were evident in the warmer Hawke's Bay (~39°S) (114) and in the Riverina region, New South Wales, Australia (~35°S) (80). However, LBAM is thought to have up to 4.4–4.7 generations per year in orange orchards in Australia's Riverina region (84). Two generations per year are seen in Britain, with a possible third during some years (53).

Under controlled temperature conditions, the lower developmental threshold for all stages was estimated to be around 7.5°C and the rate of development increased linearly with increasing temperature to about 28°C, above which the rate declined (31). Egg hatch and development of larvae declined sharply above 30°C. A later study confirmed that population growth was zero at ~7°C and above ~31°C, and peak intrinsic rates of increase occurred between 20 and 25°C (36). However, there are few publications about modeling LBAM phenology (80), possibly because spreadsheet models have sufficed for practical purposes in Australia (147, 148), although a fuller population model was developed (132). More refined temperature thresholds as well as information about cold and heat tolerance would be useful for modeling potential distribution, and this could come from pheromone-trap-based climate and distribution limit studies.

Population Genetics and Life-History Traits

Several days after emergence and mating, females lay discrete batches of eggs (~35 eggs per batch), averaging totals of 100–300 eggs per female and, for some females, up to nearly 1500 eggs (34). Neonate larvae emerge after 1–2 weeks and disperse before settling and spinning a shelter on the underside of a leaf. Larvae have five (male) or six (female) instars and later move to feeding sites in a nest located in a leaf fold or between a leaf and the surface of a fruit. Pupation occurs either in or near the last nest. The life cycle has no diapause and development continues when ambient temperatures are above ~7°C. Some aspects of the life history of LBAM are remarkably variable across populations and locations (56, 58, 61). Significant heritabilities were documented for development time, adult body weight, and the number of eggs laid during the first 5 days (61). The study also determined that much phenotypic variation is explained by genotype and environment interactions, and that there is considerable phenotypic plasticity in the life-history traits of LBAM. This plasticity appears to be an important factor in LBAM's ability to adapt to a wide range of climatic and habitat conditions. Heritability of expression of the detoxication enzyme glutathione-S-transferase was also demonstrated (109), probably related to adaptability to a wide range of host plant compounds.

Behavior of Larvae

Neonate larvae emerge and search for a settlement site; they may disperse by ballooning on silken thread depending on weather conditions. Like other surface-feeding tortricids (12), LBAM larvae are thigmotactic and spin silken shelters between convenient surfaces from which they venture out to feed nearby. The silken thread is also used for escape from parasitoids (113). Several factors likely determine how larvae utilize hosts such as apple trees

during the year and how this affects crop damage. Physical and physiological changes to the fruit are likely to be important. The extent of physical contact between adjacent surfaces is likely to influence the selection of a shelter site. As the season progresses, leaf-to-fruit niches offer increasingly preferred physical properties with increasing fruit size (77, 120). LBAM larvae also respond to plant volatiles, including those given off by apple leaves and ripening fruit (64, 120). Maturing fruit may therefore become increasingly attractive as well as having greater surface area. Increases in larval size and abundance can also increase the extent of fruit damage toward harvest (77).

Pheromones: Role, Biosynthesis, and Detection

The sex pheromone plays a pivotal role in the life cycle (mate location) and has been targeted for intervention. The early choice of LBAM as a model by pheromone researchers (8, 9), with the powerful multidisciplinary assemblage of electrophysiology (92, 97, 98), chemistry (11), and behavior (8), has led to significant new management options. The pheromone, first delivered in behavioral experiments as diluted female equivalents, elicits a hierarchical series of behaviors in male LBAM (9, 11) (Figure 2a). The median concentration required for antennal elevation or behavioral activation (wing fanning) was lower than that for subsequent orientation or copulatory movements (9), as in other species (95). Bellas et al. (11) found peak male catch at a 95:5 blend of (*E*)-11-tetradecenyl acetate (*E*11-14:Ac) and (*E,E*)-9,11-tetradecen-1-yl acetate (*E,E*-9,11-14:Ac). Male behavioral response to sex pheromone was saturated by pre-exposure (5, 7), especially if pulsed (7) or at a higher concentration (6). Flight tunnels have enabled the expression of a wider range of behaviors, including factors affecting flight and landing (48, 51, 100). *Z*-11-tetradecenyl acetate is a strong behavioral antagonist (48, 51, 100, 106). Pheromone titer is mediated by a pheromone biosynthesis-activating neuropeptide (52).

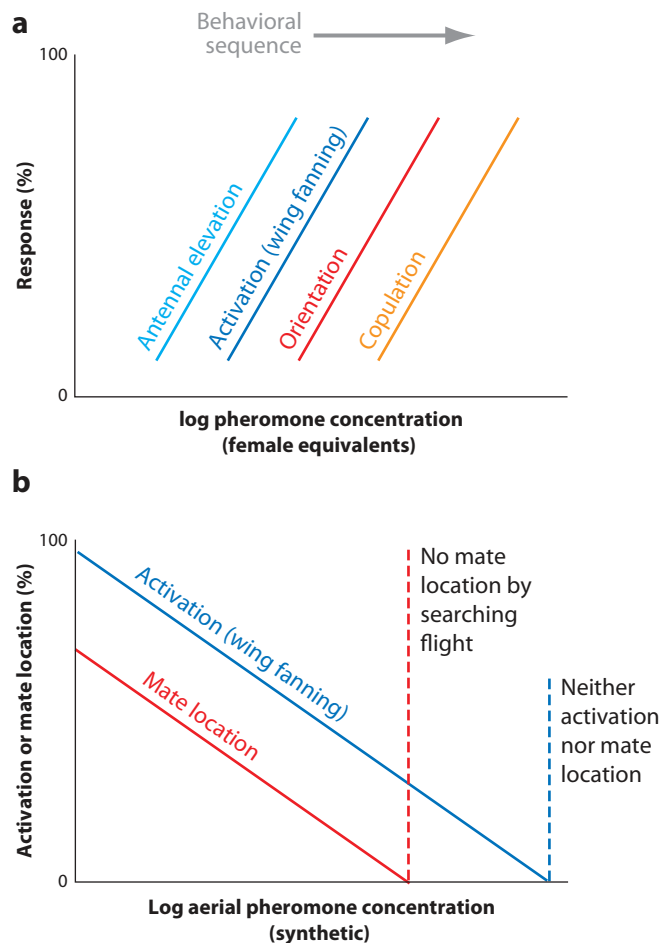


Figure 2

Light brown apple moth (*Epiphyas postvittana*) dose responses to pheromones. (a) The natural behavioral hierarchy leading to mating requires increasing concentration of pheromone for each stage (9). (b) For management, mate location was prevented at lower atmospheric concentrations of pheromone, compared with prevention of activation (118).

After mating, pheromone production usually ceases (45, 49). Males can mate more than once (lifetime mean of 6.6), but this is rare in females (45). Three pheromone binding proteins present within sensilla trichoidea in LBAM antennae (69) include one that binds *E*11-14:Ac (89). Discrimination between the two components evident at the olfactory receptor neuron (98, 99) probably occurs at pheromone receptors that have yet to be identified.

ECOLOGY

Dispersal and Distribution

Active dispersal after mating occurs primarily by flight (55). Release-recapture experiments have shown that males are capable of flight for at least 600 m, and females for at least 300 m, although the majority of recaptures occurred within 100 m (112, 126). Reinvasion distances of wild insects were similar (112). The flight duration of mated tethered LBAM females was longer than that of unmated females (35). Flights occur primarily 1–5 h after sunset, with a small flight at sunrise (32). Smaller LBAM adults have a lower wing loading, which is suggested to allow longer flights (32). Because the size of adult LBAM is correlated with food quality, this may be an adaptive trait that enhances the ability to disperse from less suitable habitats (33). There is a genetic basis for differences in flight capacity between populations (60). There is also a strong relationship between ambient temperature and flight duration, with the longest flights occurring at ~25°C and only short flights occurring at 10 and 30°C (35). Flight duration peaked at 60% relative humidity in approximately five-day-old moths. Males appear to be much more dispersive, as they fly on average two to four times as long as females. Besides active dispersal, LBAM has spread and invaded new territories primarily with human assistance via trade in plants, foliage, and fruit (see Invasion History and Impact, below).

Natural Enemies

The sources of mortality from natural enemies are many and varied (34, 42, 90). Additional records of numerous natural enemies attacking LBAM exist from New Zealand and other countries outside its natural range prior to classical biological control introductions (39, 137, 146). According to life tables for Australian orchards (34), predation and parasitism of eggs were important mortality factors, although the egg parasitoid *Trichogramma funiculatum* was absent in the eggs of the winter generation. Predation of larvae and pupae was also significant,

mainly from various spiders and the earwig *Forficula auricularia*, as well as several carabid, ladybird, and rove beetles; reduviid and mirid bugs; chrysopids; and syrphids; among others (34, 55, 79). Larval and pupal parasitism of final instars and pupae reached as high as 20% and 18%, respectively (34). The most common larval and pupal parasitoids in Australia were the bethylid *Gonozius jacintae*; the braconid *Dolichogenidea tasmanica*; the ichneumonids *Australoglypta latrobei*, *Exochus* sp., and *Xanthopimpla rhopaloceros*; the chalcid *Brachymeria rubripes*; and the tachinid *Voriella uniseta*. A recent review (90) of LBAM parasitoids in Australia provided a key for 25 species, including five hyperparasitoids. Some species appear to be common over much of LBAM's range (e.g., *D. tasmanica* and *X. rhopaloceros*), but others are less common and more geographically restricted. A nucleopolyhedrosis virus (NPV) is relatively common, but it is not an important mortality factor (34, 57). The development of 50-fold NPV resistance following a colony crash due to the virus (19) is an example of selection in a closed population but shows adaptability in the moth.

In New Zealand, LBAM is also attacked by numerous predators and several parasitoids recruited from native leafrollers (137, 146). The earliest comprehensive survey in New Zealand documented *Trichogramma minutum*, six larval parasitoids, and two pupal parasitoids from LBAM (39). Although this was done before any planned biocontrol releases had taken place, the Australian *Dolichogenidea* (= *Apanteles*) *tasmanica* was already present in New Zealand, probably introduced along with its host (40), and *Gonozius* sp. (a larval parasitoid) also may have been already established from Australia at that time (137). Several hyperparasitoids have been recorded from LBAM parasitoids in New Zealand but they appear to be rare (146). Geographical variation in parasitoid guild components occurred in New Zealand (114). There are few records of LBAM parasitoids from Hawaii, but *Trichogramma minutum*, *Chalcis obscurata*, and *Perisierola emigrata* were cited by Dumbleton (39). In England, several hymenopterous and dipterous parasitoids were

recorded from LBAM, with parasitism rates higher than 25% (4). Although no published records are yet available about parasitoids attacking LBAM in California, there are reports of considerable parasitism by existing native leafroller parasitoids (96).

INVASION HISTORY AND IMPACT

Timeline and Characteristics of Invasions

The spread of LBAM beyond its native region in southeast Australia was facilitated by its wide host range and its association with many fruit and other crops and plant propagation materials, some widely exported from Australia. The first recorded interception in New Zealand is a specimen in the Canterbury Museum in Christchurch labeled “reared from Tasmanian apples.” Meyrick’s collections between 1879 and 1886 did not reveal any LBAM, but in the 1890s LBAM was becoming widespread across the North and South Islands (38) (possibly because of multiple independent introductions). LBAM is now one of the most common Microlepidoptera in cultivated and disturbed land across New Zealand, where it appears to out-compete native leafroller species (146). Some of the highest populations occur in gorse scrub and plantation forests (20), but LBAM has not been documented from intact, inland native forest areas. The establishment of LBAM in Hawaii is surprising given its native distribution in Australia. In Hawaii, LBAM appears to be present mainly in zones above 950 m on the islands of Kauai, Oahu, Molokai, Lanai, Maui, and Hawaii, but has been found as low as 85 m and as high as 2267 m on the island of Hawaii (Big Island) (B.R. Kumashiro, personal communication). Its successful colonization across the archipelago from about 1900 to 1925 and its widespread occurrence (150) are remarkable given the apparently suboptimal conditions at lower elevations. There is limited published information about its habitat preferences and abundance in Hawaii.

In the United Kingdom, LBAM was first recorded breeding in Cornwall in 1936, and for several decades it was rarely found in abundance beyond coastal Cornwall and Devon (91). In the 1990s, LBAM appears to have spread rapidly, possibly with nursery stock. According to long-term records from a light trap in Surrey, LBAM suddenly became the most common moth in this area (91). In the last 20 years it has spread through much of England and Wales. The adult moth can now be found throughout the year and it can be caught every night from May to September. However, LBAM appears to occur primarily in milder urban areas and less in the countryside. The discovery of a male LBAM in 1997 in southeast Ireland in County Wexford appears to have been interpreted as an establishment (17). In Western Australia, where a close relative, *Epiphyas pulla*, is present, breeding populations of LBAM were discovered in 1968 (58). Several publications cite the presence of LBAM in New Caledonia (4, 31), but this could not be verified (C. Mille, personal communication). Border interceptions of LBAM on imported fruit, nursery stock, and other plant material have been reported in California, Hawaii, and other countries such as Japan (143). The most recent detection was in Sweden (133). With the globalization of trade in such plant materials, assisted by LBAM’s wide host range, it is likely to spread further. The scale of trade in California of LBAM hosts is simply immense, which could exacerbate spread.

Finds of two moths in Berkeley occurred in July and November 2006 (by retired University of California Professor Jerry Powell). Upon deployment of more than 30,000 traps in 2007, it was determined using Jackson traps (small delta traps designed for fruit flies) that LBAM was present over an area ranging from Marin County to Monterey County, spanning more than 150 km along the coast and up to 40 km inland. Further, occasional moths were detected as far south as Los Angeles (<http://www.cdfa.ca.gov/>), although the contiguous area was limited to the San Francisco-Monterrey Bay areas. Based on evidence of

USDA: U.S. Department of Agriculture

Dichloro-diphenyl-trichloroethane

(DDT): an organochlorine insecticide

Dichloro-diphenyl-dichloroethane

(DDD): an organochlorine insecticide, similar to DDT

LBAM's greatest abundance within the infested area, the original establishment of LBAM may have occurred either in San Francisco or near Santa Cruz, which are strong foci compared to the vast majority of the catches reported. Import of and trade in plant nursery stock could well be an important part of the history of establishment there, as in the United Kingdom and New Zealand. There has been speculation that LBAM has been present in California for 30–50 years (73). However, moth surveys without detection over the last 10–20 years in the San Francisco and Monterey Bay areas suggest that LBAM's establishment occurred much more recently (J. Powell, personal communication). A program initiated in 2007 with the goal of containment and/or eradication has faced an expanding and backfilling population (<http://www.cdfa.ca.gov/>).

Economic and Ecological Impact in Different Countries

LBAM's impact on agriculture, horticulture, and natural and urban environments has varied among countries. In New Zealand, its direct impacts include damage to numerous kinds of fruit, other crops, and seedlings of trees and ornamental plants. In unsprayed crops, damage levels as high as 70% were formerly experienced (146). Today, biological control and selective insecticide programs with population monitoring using pheromone traps usually provide adequate control. However, even occasional finds of LBAM on exports significantly affect trade. Serious effects of trade restrictions have already occurred in California, affecting a wide range of crops and nursery stock in quarantine areas (142). An economic risk analysis for LBAM in the mainland United States, using a probabilistic modeling approach for costs to four major fruit crops (apple, grape, orange, and pear), estimates the mean annual cost to be US\$105 million (54), including costs of direct damage to crops and control (\$93 million), quarantine (\$7.5 million), and research (\$4.5 million). Additional losses are expected to occur for other crops and plant nurseries,

and because of domestic and international trade restrictions (54). The U.S. Department of Agriculture's (USDA) allocated budget for eradication, research, monitoring, and regulation in 2008 was \$74.5 million.

MANAGEMENT

Insecticides, Insecticide Resistance Management, and IPM

DDT (dichloro-diphenyl-trichloroethane) was the first synthetic insecticide introduced into Australian orchards for codling moth and LBAM (138). In New Zealand, brief orchard use of DDD (dichloro-diphenyl-dichloroethane) in the 1950s led to LBAM resistance (105). Azinphos-methyl replaced it circa 1960, but insecticide resistance occurred within 20 years in larvae (115) and adults (125). This was demonstrated at 100 ha landscape scale of mixed orchard and other habitat in the following way. Handheld pheromone lures were used to attract and sweep net male moths, which were weighed in groups and precisely dosed to discriminate phenotypes, as resistant or susceptible. In fact, the phenotypic frequency of resistance in pheromone-collected males (131) showed gene flow of the insecticide resistance trait in moths dispersing from apple orchards into wasteland population reservoirs of susceptibility within an area of 100 ha. The area was entirely surrounded by susceptible insects on wasteland (125). Elevation of degradation enzymes (nonspecific esterases, cytochrome P450s, and glutathione-S-transferases) (2) was correlated with expression and responded to threshold selection by insecticide in larvae (109). Chlorpyrifos gave adequate control despite cross resistance (124). Mating disruption was effective for resistance management (127) but not widely adopted against the cheaper organophosphates at the time. Pyrethroids were never deployed in New Zealand orchards, partly to avoid nontarget impacts on natural enemies. Tebufenozide and lufenuron (144) provided the first insecticide class change in LBAM control at an industry

scale in 40 years. The industry-wide removal of organophosphates in New Zealand apple orchards by 2001 (128) has greatly reduced the risk of insecticide resistance, and there are many different alternative controls today. Fresh fruit exporters from New Zealand responded to strong negative market signals about organophosphates by adopting alternative tactics. Pheromone trap thresholds are still used to justify interventions in integrated and organic orchards (37). Biological control of LBAM and other pests has increased substantially.

Similar increases in the availability of the above chemistries for LBAM have occurred in Australia. In the state of Victoria, Australia, LBAM was controlled reasonably well with codling moth sprays required for the higher number of generations and population pressure of that pest (147). The ornamentals industry has zero tolerance for damage and live insects and has generally used pyrethroids because they targeted more pests and had a lower mammalian toxicity and short re-entry periods, important considerations for greenhouse workers.

Organic growers can merge other tactics in IPM, including cultural controls, to provide a range of sources of mortality to limit LBAM populations beyond the level provided by natural enemies in the wider environment (114). Although the toolkit available to pest managers is determined by market standards, most tactics apart from insecticides are compatible with organic and IPM requirements and their inclusion is largely a function of safety, reliability, and cost. Reducing LBAM pest pressure by active management of groundcover plants in orchards has been achieved through grazing or other means of host removal (94). There may be potential for oversowing resistant plants into the understory (25) or into the crop (145). The combined use of pheromone-monitoring traps and rigorous spray programs has helped to increase market access in practice (37).

Biopesticides

Bacillus thuringiensis kurstaki (*Btk*) is effective in vineyards for control of LBAM in Australia

and is also used in kiwifruit (107) and, to a limited extent, in organic apples in New Zealand (37). Insecticidal efficacy appears to depend on canopy type, with some canopies open to photosynthetically active radiation but also UV degradation (e.g., apples), whereas other crops such as kiwifruit have a more shaded canopy, affording greater longevity. Harris et al. (63) found that Bt endotoxin inhibited feeding in larvae, which were capable of recovery. Combination of *Bt* with mating disruption was used to achieve low-residue apples at harvest, but two *Bt* applications prior to harvest did not enhance control (130). The NPV of LBAM (57, 78) is limited by virus supply and cost. Other microbial products have struggled for efficacy against LBAM, although spinosad is effective (37). The situation contrasts with the commercial development of granulosis virus against codling moth (74).

Trapping in IPM

Port wine pots have been used for trapping LBAM in New Zealand (41, 112, 139) and Australia (3, 24, 80), but pheromone traps are much more readily operated by growers and are far more sensitive. Calendar-based programs using broad-spectrum insecticides prevailed for many years and pest monitoring was limited (101). Bradley et al. (18) developed a threshold of pheromone trap catch inside apple orchard blocks, which was required for application of the ecdysone agonist tebufenozide by growers, as part of a wider program of integrated fruit production (128).

Degree-day accumulation was developed for phenology prediction of LBAM in Australian grapes (80, 147), although the accuracy of predictions was reduced after the first generation, probably because adults emerged from multiple host plants with different developmental rates (34, 140). Common Australian practice involves setting traps in a grid pattern consisting of three to five traps within each vineyard. Egg masses and young larvae are most abundant soon after peak moth trap catch.

Bacillus thuringiensis kurstaki (*Btk*): a naturally occurring bacterial insecticide specific to Lepidoptera

Pheromone-Based Direct Control Tactics

Mating disruption of LBAM is improved with both components (116), although the less expensive, 70% isomerically pure *E*11-14:Ac (i.e., 30% Z11-14:Ac, an inhibitor) is effective (129, 130). Presentation of both pheromone and inhibitor together reduced takeoff (100) and catch (106). Because both pheromone and inhibitor are present at >25% in pheromone used for mating disruption, false trail following cannot be the mechanism of disruption (121).

Successful management of insecticide resistance by mating disruption was dramatically demonstrated after several years of trapping in the same orchards, peaking beforehand at 15 moths per trap per day, whereupon after one treatment of polyethylene dispensers, the population flatlined for the next year and the fruit damage disappeared with annual treatments (127). Mating disruption from mid-season supported low-insecticide residue apples following early-season insecticide use to prevent LBAM population buildup in the first generation (130). Adoption trials in Australian apples initially in Tasmania and Victoria expanded to treat grapes, and mating disruption of LBAM in citrus orchards was also recently demonstrated (85). Aerosols have also been examined for disruption (117).

Field electroantennogram recordings, which allow humans virtually to eavesdrop on the olfactory environment in a treated crop, show that the orchard air is filled with pulses or filamentous strands of different concentrations and return periods, depending on point source density and other variables (70, 108, 118, 119). Apple foliage acts as a system buffer in that it is a short-term sink and source of pheromone and inhibitor without detectable atmospheric filaments (71), but is sufficient for mating disruption for one night, or for three nights at ten times the application rate (122). Mean atmospheric concentrations of pheromone in the orchard air (ppb or ng/m³) were modeled and linked to wing fanning

bioassays (9, 118) (**Figure 2b**). On the basis of current wind and temperature, this model used crop canopy shape, tree and row spacing, vertical leaf area index, and pheromone release height and rate to estimate the vertical pheromone concentration profile. It separates an upwind well-mixed or far-field effect and a local near-field effect from dispensers, which is also seen in electroantennogram recordings of antennal responses to strong filaments in orchards, where high strength pulses can travel at least 40 m (118).

The estimated atmospheric concentration required to prevent catch to female-equivalent lures was approximately fivefold lower than the concentration required to prevent wing fanning (118) and disrupted in the reverse order (**Figure 2b**) from the normal behavioral sequence (**Figure 2a**).

Sprayable LBAM pheromone was applied aerially over 20,000 ha in California on two occasions in 2007 as part of the incursion response. The effect, if any, was short-lived but the formulation contained no sticker and would have had limited longevity on foliage, and the effects were difficult to assess. In a subsequent smaller scale, replicated trial, aerially applied microencapsulated pheromone formulations were not as effective as an amorphous mixture of waxes and oils or flakes, which gave promising results and disrupted trap catch for several weeks or months (22). Public opposition and intervention from the governor of California terminated the program (<http://www.cdffa.ca.gov/>). However, aerial applications of dis-parlure against gypsy moth continue to be developed and used in 13 eastern states (136).

Mass trapping and lure-and-kill tactics have recently been reviewed for insects (43, 44), including an account of a LBAM lure-and-kill formulation. LBAM pheromone was added to an existing gel formulation for codling moth with pheromone plus permethrin to test the concept of multiple species lure-and-kill (21), which looked at the mechanisms involved. Attractive droplets containing pheromone (300 µg) and permethrin (5%) were placed out at 500 points ha⁻¹ either caged

(i.e., pheromone, no contact) or exposed (pheromone plus insecticide) (111). False trails alone gave $\leq 50\%$ reduction in catch (caged droplets compared with controls), whereas mortality was superior ($\leq 96\%$ less catch among fully exposed droplets compared with controls). After the caged droplets were removed, catches immediately returned to control levels, unlike the plot with fully exposed droplets. However, the practicality of this approach appears to be low in urban areas. For mass trapping, a high trap density is likely to be needed for success (44, 93). Although the idea of mass trapping became popular with nongovernmental organizations in the California media, lure-and-kill (43) may be more appropriate once practical considerations are reviewed and if an acceptable street-based system can be developed for urban use, in concert with other tactics.

Biocontrol

Classical biological control introductions against LBAM have only occurred in New Zealand. Following surveys in Australia (42, 137), 19 parasitoid species and three predator species were imported to New Zealand as potential classical biological control agents, of which 10 parasitoids were eventually released between 1967 and 1972 (137). *Xanthopimpla rhopaloceros*, the ichneumonid *Glabridorsum stokesii*, and the tachinid *Trigonospila brevifacies* have become established successfully as a result of these releases, but there is some uncertainty about some of the other species (137). There was typically little quantitative follow-up because of limited resources and because the priority was placed on further new introductions. Nearly 250 specimens of *Dolichogenidea tasmanica* were released in 1969, although this species was already present in New Zealand at the time (137) and was probably introduced with its host (40). As in Australia, *D. tasmanica* has become the most abundant parasitoid of LBAM in New Zealand, with parasitism rates of up to 50%, particularly in unsprayed areas (114, 146). LBAM's parasitoid complex varies

from relatively simple (Canterbury) to more complex (e.g., Nelson) (114). Indirect evidence suggests that *T. brevifacies* and *X. rhopaloceros* have had a major impact on LBAM in North Island orchard regions but are climatically limited (86). *T. brevifacies* is of concern as the most common parasitoid of many native leafrollers in broadleaf/podocarp forests in the central North Island (87), although it has not been determined whether *T. brevifacies* reduces populations of native leafrollers or displaces any of the native parasitoids in these natural ecosystems. *D. tasmanica* also attacks native leafrollers, but it is less successful than on LBAM apparently because of the defensive behavior of larger New Zealand native leafrollers (113). There was an unequal likelihood of *D. tasmanica* attack of LBAM on different host plants. Major reductions in broad-spectrum insecticide use has greatly helped the reassertion of biological control (128). Conservation biocontrol utilizing flowering plants to provide food sources for adult parasitoids has been tested against LBAM in vineyards and orchards, but results varied (10, 13, 66). Inundative release of an egg parasitoid, *Trichogramma carverae*, has been used in Australia (59) and could be considered elsewhere. Classical biological control in California will likely depend on the discovery of host-specific parasitoids.

Sterile Insect Technique

Sterile insect technique (SIT) has successfully targeted two moths on a large scale, codling moth in Canada and pink bollworm in the southwestern U.S. cotton areas, although there have also been other programs (15, 16). One of the main benefits of releasing sterile moths during an eradication is the sensitivity estimation of a trapping grid, which can be invaluable for predicting and declaring eradication and can use relatively few insects (110). Irradiation biology of LBAM was initially investigated for quarantine use. A joint Australia–New Zealand project has targeted LBAM SIT since 2005, but international efforts have increased following

Sterile insect technique (SIT): involves mass release of sterile insects to overflood wild populations

Inverse density dependency: effect on population density of factors that are most effective at low density

Allee effect: effect at low population density of natural limits to forming self-sustaining population

the decision to instigate this approach as a main tactic in California. The modular mass rearing facilities planned by USDA APHIS will require attention to quality and supporting technologies (103).

Postharvest Treatments

A range of postharvest treatments have been examined for fruit, but few have reached commercialization. Single and combination treatments, such as hot water treatment and high-temperature controlled-atmosphere storage (29) and high-temperature low-oxygen pulse followed by cold storage (30, 134) or other stresses, have been examined, although LBAM has proven more tolerant than the fruit to some treatments (75). The use of a postharvest oil and a spray oil, both of which were applied as dips, was investigated for disinfestation of citrus (135). Phosphine and controlled atmospheres have been used for cut flowers (72). Recent peony exports from New Zealand to the United States were temporarily halted after the find of a larva, but an IPM program has been rapidly developed and the market reopened in seven weeks, which was seen as a success by the USDA (14). However, this incident highlights increasing vigilance for insects such as LBAM associated with trade in plants and fresh produce. Quarantine treatments, with an inspection and treatment regime based on insecticides, were also developed for movement of nursery plant material within California.

Integrated Pest Eradication

There has been increasing recognition by governments of the need to eradicate certain unwanted organisms (88), and some authors suggest that attempts to eradicate should be made more often than is currently the case (102). The range of tactics available requires consideration, because for many pests there are few or no options for response that are likely to be successful at the stringency required for population eradication. Even when such tactics are available (Figure 3), eradication of a

self-sustaining population on a major landmass is probably the most challenging program target imaginable. This is partly because of the difficulties inherent in detecting and fully delimiting the population, as well as the effectiveness of the tactics available. Myers et al. (88) identified factors important for successful eradication: sufficient resources, clear lines of authority, target organism susceptibility to controls, prevention of reinvasion, and detection at relatively low densities.

IPE applies the principles of IPM to new incursions of invasive species, especially in the context of sensitive or high-value ecosystems, including inhabited areas where insecticides or other IPM tools may be contentious. It is a pest-specific approach rather than a crop-specific approach, often seen for IPM, and the context is usually different in some other important ways. In some settings, tactics that could normally be used in IPM cannot be used in IPE. The social acceptability of these IPM tactics in agriculture or horticulture cannot be assumed to apply in urban areas, where many new organisms arrive and special considerations for eradication technologies apply.

The integrated approach targeting different life stages with different tactics was illustrated during the eradication of the painted apple moth (*Teia anartoides*) (Lepidoptera: Lymantriidae) in urban Auckland, New Zealand. It was achieved for \$NZ65 million by using thorough weekly delimitation with female-baited traps and periodic ground searches and life stage removal, vegetation movement control, ground sprays of insecticides, as many as 40 aerial applications of *Btk* over 12,000 ha in urban Auckland, combined with small-scale use of the male-only inherited sterility technique once populations were substantially reduced (110). Such inversely density-dependent tactics are aided by the Allee effect, so that the effective target is the last individual that can find a mate in space and time (76). The limitations of operating a major eradication campaign with significant public interest (and open opposition to the methods used) signify that new tactics with greater social acceptance are needed.

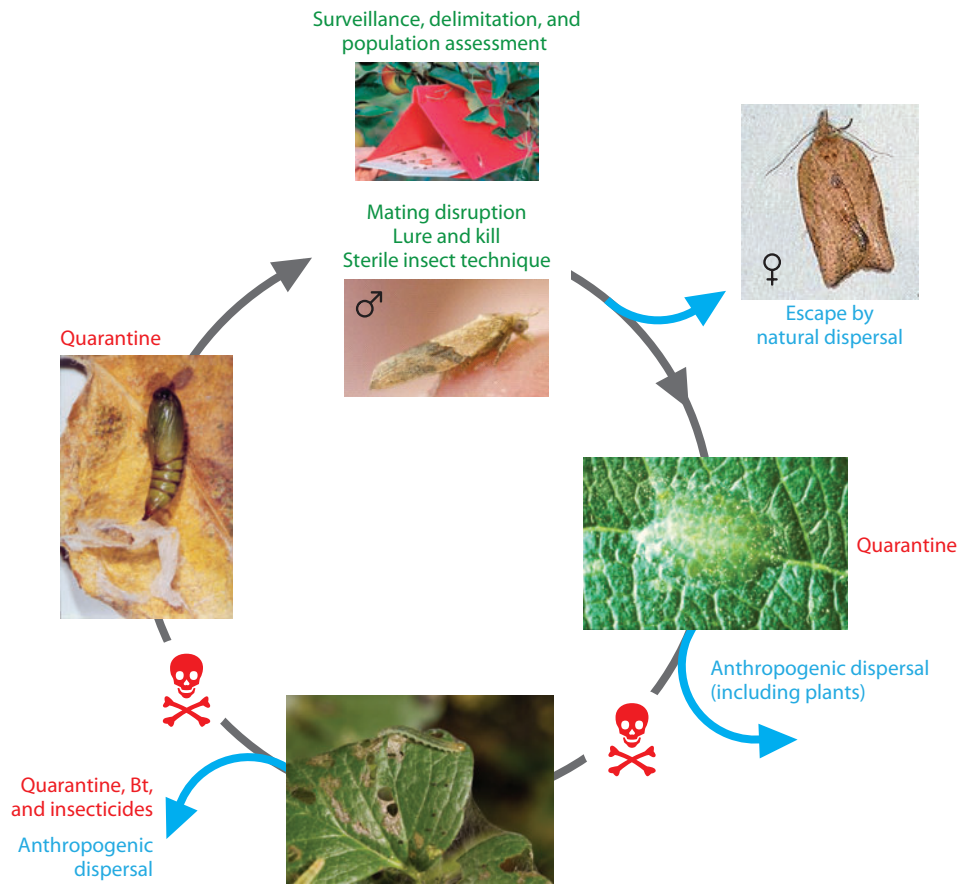


Figure 3

Life cycle of the light brown apple moth (*Epiphyas postvittana*) showing potential points of intervention (red text indicates high environmental hazard; green text indicates low environmental hazard) that could be considered during integrated pest eradication and integrated pest management to avoid pest spread (blue arrows).

The potential tactical options for eradication or long-term pest management are more numerous and developed for LBAM than for many other pest species, and there are potential points of intervention at several different stages in the life cycle (**Figure 3**). Many, but not all, tactics are incompatible (e.g., broad-spectrum insecticides and SIT are not). Biological control is also an important component of long-term management, but there appear to be few scenarios in which biological control can contribute to eradication. The combination of SIT and inundative release of *Trichogramma* could be synergistic, which is a useful goal (16).

New Developments and Knowledge Frontiers

Advances are being reported on several frontiers. Pheromone binding proteins in LBAM have been identified (69, 89). The structure of the takeout protein has been solved by X-ray crystallography, indicating a role for proteins as ligand carriers (62). The feeding of double-stranded RNA to LBAM larvae triggered RNA interference (including reducing levels of the pheromone binding protein gene in adult antennae), but unfortunately transcript levels recovered to wild-type levels after adult emergence (141). The derivation of expressed

sequence tags from the midgut of LBAM has led to the discovery of several gene families, including a broad range of digestive proteases, lipases, and carbohydrases, as well as carboxylesterases, glutathione-S-transferases, and cytochrome P450 monooxygenases (104), potentially involved in xenobiotic degradation (2). The recent characterization of the NPV of LBAM (EpoMNPV) (65) has included sequencing of an ecdysteroid UDP-glucosyltransferase (28) and the characterization of chitinases (149). Multiple transgenic crops that express *Bt* genes have been considered for the management of LBAM (27), as have alternative approaches such as proteins with insecticidal properties coded with single genes (81, 82). However, the potential for controlling LBAM with transgenic plants or other genetically modified organisms will have to contend with regulatory obstacles and potential lack of consumer acceptance.

CONCLUSIONS

LBAM is highly polyphagous and an economic pest mainly of numerous horticultural crops, although it can be abundant on many other woody and herbaceous plants. Its pest status has historically been exacerbated by international quarantine and insecticide suppression of natural enemies. LBAM has shown characteristics of invasiveness in diverse environmental conditions in New Zealand, Hawaii, Western Australia, and the United Kingdom over several decades, and it appears this pattern is being repeated in California. Populations are largest in temperate areas with adequate rainfall or irrigation but can occur within a wide climatic range. The presence or absence of certain natural enemies can have a great impact on whether populations reach an economic threshold. Natural enemy impact varies among host plants. LBAM economic thresholds for fruit or commodities involving quarantine are much lower, and pest management interventions are likely to be more intensive, than for process crops such as wine grapes. The leafroller larval habit of webbing together leaves complicates

control with insecticides, but market access may require a zero tolerance of live larvae. The consumer demand for blemish-free fruit also drives control programs. Many alternative interventions have been examined, but selective insecticides and *Btk*, followed by pheromones, are the dominant field-control tactics in use. Insecticide resistance has evolved to several classes of products, suggesting that a range of tactics should be employed for resistance management. Mating disruption has been used to overcome resistance. Biological control agents and natural enemies including generalists (e.g., spiders) can effectively regulate populations in Australia, although in southern parts of New Zealand, higher pest populations occur in the absence of certain climate-limited biocontrol agents. Research is needed in a range of areas, but LBAM is manageable with an integrated approach.

RESEARCH NEEDS

Pest impact in new ranges such as the United Kingdom and California is not well understood; economic modeling of impacts is needed where thresholds are exceeded. Ecological limits, in terms of temperature and habitat tolerance, remain uncertain and the possible geographic distribution in North America (and Europe) is unlikely to be reached for some time. Factors affecting host range require elucidation, including peripheral and neural components, as well as neuroethological integration to explain behavior. A better understanding of host plant effects, including development rates and relative abundance as a function of host frequency or presence on the landscape, niche abundance on plants (usually shoots), and the effects of overlapping development of individuals that developed on different host plants, would improve estimates of the requirements needed for control in California. Different approaches to modeling climatic suitability have revealed conflicting results, and it should be a high priority to resolve this to enable better risk assessment and response planning. The abundance of LBAM in California is rising in many areas but overall,

a greater understanding of population ecology at low densities, together with an understanding of absolute population numbers (based on quantified sampling efficiency), will permit a more precise definition of eradication criteria needed for new and existing areas. New quarantine treatments on new crops are needed as LBAM expands its range.

Novel control tactics and combinations of tactics are urgently needed that meet the needs of people in communities yet are proven to be effective at suppressing or eradicating LBAM. Biological control agent suitability for release in California should be examined, taking into

account factors that affect success and nontarget impact of introductions elsewhere (e.g., New Zealand). SIT may expand in the future, and supporting technologies will be needed to obtain the best outcomes from the investment. SIT operational systems will need benchmarks of progress, for example, using recapture rates of steriles to model trap grid efficacy and to predict when eradication has been achieved in an area. The neurophysiological and molecular basis for olfaction of pheromones and host plant odorants or other areas may provide the basis for new tactics for pest management.

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RELATED RESOURCES

California Department of Food and Agriculture (CDFA). <http://www.cdfa.ca.gov/>
 The Pherobase. Database of Pheromones and Semiochemicals. <http://www.pherobase.com/>
 CDFA Light brown apple moth program. <http://www.cdfa.ca.gov/phpps/pdep/lbam/situationreports.html/>
 Department for Environment Food and Rural Affairs. Plants and seeds. <http://www.defra.gov.uk/plant/index.htm>
 HortNET. <http://www.hortnet.co.nz/>