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# Worldwide Host Plants of the Highly Polyphagous, Invasive *Epiphyas postvittana* (Lepidoptera: Tortricidae)

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**ABSTRACT** The light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), is a highly successful biological invader. It was accidentally introduced to several countries including New Zealand, Hawaii, England, and California. Light brown apple moth attacks a wide range of crop plants and other woody and herbaceous plants, but a more comprehensive analysis of its host range is needed for risk assessments, to evaluate the likely economic and environmental impacts, and to enable targeting of particular plant species for detection surveys and treatments. We reviewed and synthesized the host range and host selection behavior of light brown apple moth by using information from Australia and invaded countries. The host range of light brown apple moth is determined by the behavior of both adult females and larvae. Females use visual, chemical and physical cues to choose host plants. Larvae are capable of limited active dispersal by walking and longer range dispersal by ballooning on silken strands; therefore, larvae also may need to select host plants. We review larval performance indicators across a range of plants. Based on our review, there are at least 545 plant species in 363 genera from 121 families that have been reported as hosts of light brown apple moth. Some plants were reported only once and need verification. Nevertheless, many host plant species and their wide phylogenetic range (from ferns to higher dicotyledons) indicates that light brown apple moth is one of the most polyphagous insects known. This information and our categorization of frequency of host use are valuable for incursion response and pest management activities.

**KEY WORDS** host specificity, host range, invasive species, pest risk analysis, Tortricidae

Light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), is an economically important insect pest both in its native region in Australia and in several countries it has invaded (Danthanarayana 1983, Wearing et al. 1991). Light brown apple moth is most problematic on horticultural crops, but it also attacks a wide range of vegetables, ornamental plants, forest trees, and noncrop plants (Wearing et al. 1991). The association with commodities that are traded globally, and its unusually wide host range, have contributed to successful invasion of parts of Australia, New Zealand, Hawaii, the United Kingdom, Ireland, and California (Suckling and Brockerhoff 2010). The recent detection of light

brown apple moth in California has raised concerns about its impacts on the important horticultural and agricultural sectors in California and elsewhere in North America, as well as potential effects on native plants and natural ecosystems. Light brown apple moth larvae web together leaves or leaves and fruit to form a protected shelter from which they feed on leaves and the surface of fruit (Lo et al. 2000). This also can lead to secondary disease development causing rots in crops such as grapes (*Vitis* spp.) (Bailey et al. 1997). 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, and presents market access barriers for export to many countries (Varela et al. 2008). The zero tolerance for live larvae in exports significantly raises control requirements, beyond the need for control of damage from larval feeding on nonexport crops (DeLate et al. 2008). Knowledge of the host plants that are likely to be attacked is critical for risk assessment, incursion response, and pest management. Therefore, a thorough understanding is required to evaluate the likely impacts of light brown apple moth on different crops and other plants and to enable efficient targeting of particular plant species for detection and delimitation surveys and treatments.

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The host selection process can be viewed as a sequence of stages, including host location and acceptance, feeding and development, survival, and reproduction (Bernays and Graham 1988, Harris and McEvoy 1995, Aluja and Mangan 2008). Potential host plants must be located either by adult females (for oviposition) or by larvae (dispersal of neonates or later instars). Typically, a host plant must be capable of stimulating adult oviposition and larval feeding, although larval stimulation is sufficient when larval colonization occurs. Host location and oviposition choice involve complex behavioral and sensory mechanisms that are likely to be mediated by visual cues, olfactory cues (e.g., plant volatiles perceived by antennal olfactory receptor neurons), and by physical characteristics (Renwick and Chew 1994). Several other complex and interacting factors must be considered to define insect host range, including mechanisms of plant resistance to insect feeding (Karban and Baldwin 1997), and nutritional requirements for growth and development through to adulthood and reproduction (Slansky 1993). Furthermore, variation among plant species in predation and parasitism may influence the success of an insect (Bernays and Graham 1988). Not every plant on which a particular phytophagous insect is found is necessarily a suitable host. For example, some plants chosen for oviposition may not ensure sufficient larval growth, survival, or potential fecundity. All the stages from host location to survival and reproduction of offspring can be considered individually or collectively to determine the suitability of a particular plant. Many measures of 'host quality' related to the various stages can be derived, including colonization, oviposition and feeding preferences, larval development and growth, development rate, density, larval or adult survival, rates of predation and parasitism, potential fecundity, and population growth (Awmack and Leather 2002). Host specificity by ovipositing females also was defined as the length of time over which a female refuses all hosts except one (Thompson and Pellmyr 1991).

Previous compilations of light brown apple moth's host plants based on field records have listed >250 host records from New Zealand alone (Thomas 1989; Dugdale and Crosby 1995) although some of these 'hosts' may not actually be accepted for oviposition or prove adequate for larval development. However, field records can give some indication of host range and interactions with other factors such as habitat type and effects of competitors and natural enemies. It is also possible to observe how direct and indirect host factors are expressed in landscape-level and regional differences in light brown apple moth populations (Suckling et al. 1998). For example, although light brown apple moth is now less problematic in parts of New Zealand where it is under partial control by biological control agents, light brown apple moth populations are thriving in Canterbury where biological control by key parasitoids is apparently limited due to seasonally unfavorable temperatures (Munro 1998). Roadside hedges of gorse (*Ulex europaeus* L.) support light brown apple moth populations across the Can-

terbury Plains, but the highest populations are observed in pine plantation forests where light brown apple moth occurs on Monterey pine (*Pinus radiata* D. Don) and understorey shrubs including blackberry (*Rubus* sp.), gorse, Scotch broom [*Cytisus scoparius* (L.) Link], which are all good hosts that support almost year-round feeding opportunities (Suckling et al. 1998).

An integration of knowledge of the host range of light brown apple moth is long overdue, although components of it have been reported previously (Danthanarayana 1975, Thomas 1989). This review synthesizes knowledge of host plant records, preferences for female oviposition and larval feeding from the native range (eastern Australia) and across the invaded regions in Australasia, Hawaii, Europe, and North America. The objectives are to 1) to discuss measures of suitability of hosts; 2) compare or contrast female and larval host plant choice affecting host suitability; 3) compile a list of recorded host plants for this species; and 4) superimpose the host range of light brown apple moth on the most recent plant classification proposed by the Angiosperm Phylogeny Group (APGIII 2009).

## Materials and Methods

**Measures of Host Plant Use for Oviposition and Larval Feeding.** We conducted a literature review of measures of host plant suitability relevant to light brown apple moth. Information from published studies on the ecology and physiology of host location and host quality for light brown apple moth was compiled based on retrievals from Thomson Reuters' Web of Knowledge, cross-references in published papers, and unpublished reports from credible sources such as government research organizations. Findings were evaluated and summarized, contrasting factors affecting female oviposition and larval host plant acceptance.

**Host Lists From Native and Invaded Ranges of Light Brown Apple Moth.** We compiled a list of recorded host plants of light brown apple moth from both published and credible unpublished sources. All plant names were verified, and spelling errors and incorrect plant names were corrected according to Mabberley (2008). Name changes and synonyms were considered and multiple occurrences of species under different names were removed. To obtain the tally of host species, we disregarded records of genera that were not identified to species if another record from an identified species in the same genus occurred, to avoid potential double-counting. Hybrids (crosses) between species or subspecies also were disregarded if another record of a parent species also was listed.

Where possible, we recorded information about the relative host quality of different plants. Foster and Howard (1999), writing about light brown apple moth, defined the host plant of an insect as one on which immature stages have been found and reared through to adulthood, whereas nonhosts were defined by an absence of records of the insect on a plant. Although

this definition does not distinguish between adult female choice and suitability for larval development and survival, it does give reliable information on host suitability. However, most information about light brown apple moth's host range comes from simple observations in the field; that is, records of light brown apple moth on different plants. The most important studies and databases providing host plant records for light brown apple moth are listed below.

Not all hosts are equal in biotic potential, and some may in fact be observations of accidental presence of larvae on unsuitable plants. Chapman (1973) suggested that host plants among tortricids attacking apple (worldwide) could be divided into categories of primary, secondary, accidental, and incidental. According to the definition of Chapman (1973), primary hosts are those that are consistently sought for oviposition and where the resultant larvae complete their development on it in an apparently normal manner. Secondary hosts are those where a plant is used in a limited way and largely because of its proximity to the insect's primary hosts. Infestations in this class may arise either from eggs or from dispersal of airborne first-instar larvae. An accidental host is one of marginal suitability resulting from accidental use by wind-dispersed larvae or accidental oviposition on an unsuitable host (see below). An incidental host is one which is only occasionally used, resulting, for example, from migration of older larvae. These definitions were independent of a plant's origin in terms of ancient or novel insect-host relationship.

Unfortunately, our knowledge is insufficient to assign many plant species according to the classifications of Chapman (1973). However, his definitions seem to align reasonably well with the terms used by Wearing (1999) for the results of a survey of several leafroller species in New Zealand. This work was able to build upon unpublished efforts of W. P. Thomas (unpublished; see below). The Wearing (1999) and Thomas (unpublished) categories of "host quality" across a range of available plants were very common, common, and occasional host use. We adopted this classification because of the lack of other, more robust information for the majority of plants. This classification enabled us to combine host information from a wide range of sources by using a consistent framework.

We have used primarily the following sources to characterize and quantify patterns of host plant use by light brown apple moth. Many of these are based on field observations where the roles of female oviposition choice, larval feeding preferences and other factors cannot be separated. Published studies are summarized only briefly but we give detailed information about unpublished studies.

Danthanarayana (1975) published the first comprehensive list of host records for light brown apple moth. He listed 73 plant species from 27 families as recorded "hosts" of which 61 species were from a wide range of literature sources from Australia, New Zealand, England, and Hawaii, and a further 12 species were new records from Victoria, Australia. These host records were compiled from sources where the relative roles

of oviposition choice, larval feeding preferences, development, and survival were not systematically recorded.

The review by Geier and Briese (1981) of light brown apple moth's ecology and pest characteristics includes a substantially expanded list of host plants in Australia. They listed 123 plant genera from 55 families; however, individual species were not specified. Whereas other host lists focus primarily on economically important crop plants, the list by Geier and Briese (1981) includes 22 native Australian plant genera.

An unpublished national survey of the leafroller species attacking fruit crops in New Zealand was undertaken by Entomology Division of the New Zealand Department of Scientific and Industrial Research, during three seasons (1974–1975, 1975–1976, and 1976–1977), in collaboration with officers of the Advisory Services Division of the New Zealand Ministry of Agriculture and Fisheries. The results of this survey formed the basis of a report (Wearing 1994) and a web-based compendium (Wearing 1999). These surveys were biased toward economically important plants but, nevertheless, provided a large data set of the incidence of light brown apple moth (and 16 other Lepidoptera and their parasitoids) on many economically important or valued plants, albeit without quantitative assessments of host use. Because the methods used for this survey have not been published elsewhere, we provide more information here. Foliage and fruits damaged by leafroller larvae were collected from the most important crops and associated shelter trees and shrubs in each fruit-growing region (i.e., Northland, Auckland, Waikato, Bay of Plenty, Taranaki, Gisborne, Hawke's Bay, Horowhenua, Nelson, Canterbury, and Central Otago). This was done three times in each season to ensure that the different generations of leafrollers were sampled. Sampling was timed and was concentrated on commercial crops because the objective was to determine the leafroller pest problems under commercial growing conditions. The important crops that were regularly sampled were species of apple, apricot, avocado, blackberry, boysenberry, citrus, grape, kiwifruit, peach, plum, raspberry, and strawberry. Other samples were obtained from species of brambles, feijoa, loquat, and various nut crops. However, the inclusion of shelter and other host plants was done to provide information on leafroller pest species in the environment surrounding orchards. All larvae were dispatched to Mt. Albert Research Centre, Auckland, New Zealand, where a team of scientists and technicians reared the larvae on artificial diet and identified them to species. In addition, parasitoids of the larvae were reared and identified by E. W. Valentine. Diseased larvae were supplied to the Pathology Section for the possible identification of pathogens. These last two steps provided data on the associations between pest species, crops, parasitoids, and pathogens. Identification of larvae was undertaken by John S. Dugdale. Insect rearing was done primarily by F. A. Gunson, with advice from



P. Singh. Many other staff of Entomology Division and the Advisory Services Division collected samples.

Other light brown apple moth host records from New Zealand were obtained from the catalog of New Zealand insects and their host plants by Spiller and Wise (1982), records held by the New Zealand Arthropod Collection (NZAC 2003), and the Plant Pest Information Network database of the New Zealand Ministry of Agriculture and Forestry which was accessed in 2007 (MAF PPIN 2007). Further records were obtained from the Forest Health Database, administered by Scion/New Zealand Forest Research Institute (Scion/NZFRI 2007), which originate from forest health surveys conducted in New Zealand's planted forests as well as natural and urban areas.

Host records from California have been kept since the detection of light brown apple moth in the San Francisco Bay area in 2007. Plants on which light brown apple moth has been found have been compiled by the local USDA office, initially in Watsonville, CA, based on samples supplied from nurseries and collections by field staff as part of the quarantine program (USDA 2008). The light brown apple moth program concentrated its regulatory activities on commercially produced nursery plants as these had been determined to have the greatest risk of artificially moving the pest. All nurseries were inspected that were located within light brown apple moth quarantine boundaries (i.e., within 2.4 km [1.5 miles] from a positive detection of at least two males, an egg mass or a gravid female). All plants with the potential to move from a property were inspected, primarily focusing on potted nursery stock, as well as flowers, foliage and other plant matter produced for the cut flower industry. Plant inspections were conducted year-round, whereby production nurseries were inspected at two week intervals, and retail-only sites were inspected monthly. Light brown apple moth program staff, university farm advisers and County Agricultural Commissioners conducted additional surveys of commercial field and tree crops, and native vegetation. All suspect light brown apple moth life stages found during these inspections were sent to the California Department of Food and Agriculture Plant Pest Diagnostics Center where they were identified by trained specialists by using a combination of morphological and genetic characters (Gilligan and Epstein 2009). Records from California listed in Supp Table 1 [online only] show the number of times different host plants were found with larvae or egg masses present.

Numerous other lists of the host plants of light brown apple moth have been compiled elsewhere. Most of these contain primarily secondary records from other publications and databases, whereby the original sources are not always mentioned. We added records from the following compilations: The Plant Protection and Quarantine (PPQ) program of the Animal and Plant Health Inspection Service (APHIS), U.S. Department of Agriculture, compiled information on numerous insect pests that were not present in the United States. The information compiled for light brown apple moth included numerous host records

from a variety of sources (USDA-APHIS-PPQ 1984). A subsequent host list was compiled for APHIS by Venette et al. (2003) as part of a risk assessment for light brown apple moth. The CABI Crop Protection Compendium (CABI 2002), the 'HOSTS Database of the World's Lepidopteran Hostplants' (Robinson et al. 2001), and several other sources mentioned herein also contain compilations of light brown apple moth host records.

**Phylogenetic Analysis of Host Plants.** We used the revised and updated classification of land plant families proposed by Chase and Reveal (2009) and the Angiosperm Phylogeny Group (APGIII 2009) as a framework to trace occurrence of light brown apple moth on its host plants, based on our corrected host list (see above). The APGIII system is based upon a synthesis of phylogenetic studies and provides the most recent and comprehensive assessment of ordinal and familial relationships. For our purposes, polytomies in the APGIII phylogeny were interpreted as regions of ambiguous resolution rather than multiple speciation events. Four character states were recognized that described the host range of light brown apple moth occurrence: very common, common, and occasional host use as well as no record of host use of a given taxon. MacClade 4.08 (Maddison and Maddison 2004) was then used to trace the distribution of these character states on the APGIII phylogeny. The character state changes were unordered. Ambiguities in the character reconstruction were shown with a horizontal stripe pattern on the phylogeny branch.

## Results and Discussion

**Female Host Plant Choice.** The main stages of female moth host plant choice involve searching, orientation, and encounter as the first phase of the behavioral sequence, followed by landing, contact evaluation, and acceptance or rejection (Renwick and Chew 1994). The host finding and acceptance sequence depends on a wide variety of sensory cues, including visual and chemical cues. Contact perception of both physical and chemical characteristics of the leaf or other plant surface ultimately determines suitability for oviposition. Sensory receptors are present on the tarsi, antennae, proboscis, and ovipositor of moths, but final acceptance or rejection of an oviposition site depends on central nervous system processing of the information provided by balancing the various sensory inputs received, modified by physiological state, genotype and learning (Renwick and Chew 1994). There are many challenging aspects to determining the true host preferences of insects, because experimental designs frequently struggle to simulate the experiences of insects in nature (Thompson and Pellmyr 1991).

For light brown apple moth, much is known about the behavioral and sensory mechanisms relating to host location and host "quality." Long-range orientation to volatile compounds has been observed previously (Dumbleton 1932, Suckling et al. 1994), and the behavior of adult female light brown apple moth is

demonstrably affected by wind speed and direction (Suckling et al. 1994). Certain specific plant odorants elicited electroantennogram responses and mediated oviposition (Suckling et al. 1996), whereas fresh host plants elicited stronger electroantennogram recordings than a similar mass of nonhosts. The highest electrophysiological and behavioral response was to an oviposition repellent mixture of geraniol and neral called citral (Suckling et al. 1996). Receptors for some of these compounds have been identified (Jordan et al. 2009).

In addition to the volatile plant compounds potentially involved in host recognition, other chemicals can provide information to ovipositing females on the relative quality of a particular species or individual (Thompson and Pellmyr 1991). Foster and Howard (1998) reported that leaf surface texture (i.e., a raised midvein fine structure) and some nonpolar leaf extracts stimulated oviposition in light brown apple moth, and they concluded that the widespread occurrence of these stimuli could account for the polyphagous host range (obviously together with larval survival). Smooth surface textures and ridges, especially on upper surfaces, are preferred oviposition sites (Foster et al. 1997). Foster and Howard (1999) found larval preferences for 15 hosts and 11 nonhosts to be negatively correlated with female choice. The difficulties in direct observation of wild night-active insects and in detecting egg masses in the landscape have limited progress in the elucidation of these processes in the field. It is far easier to determine host suitability for larvae, because damage to foliage is typically clearly visible.

**Larval Host Plant Preferences and Development.** Species in the Archipini tribe of Tortricidae, including *E. postvittana*, lay egg masses but do not feed colonially. This creates pressure for the young larvae to desert the hatching site with most dispersing to a suitable place to feed nearby (Chapman 1973). Others disperse by spinning a strand of silk, either nearby on the host or down to the ground cover (Green 1984). Some disperse considerable distances with the aid of air currents, although this is probably risky as some larvae may not land on a host plant (Chapman 1973). Otherwise, larval mobility is limited but can occur to some extent, probably also for evasion of predation. However, this implies that female oviposition site selection still largely determines where a caterpillar will develop, as larvae must actively relocate if an ovipositing female has chosen an unsuitable host plant or when conditions become adverse (Menken et al. 2010). However, for a polyphagous species such as light brown apple moth, this is somewhat less important than for a monophagous or oligophagous species, in which appropriate host plant choice by ovipositing females is more critical.

Evolution of host range in the Lepidoptera has led to the large radiation of phytophagous insects, which is probably related to innovations resulting from the diversification of feeding niches (Menken et al. 2010). External (i.e., exposed) feeding by larvae is common in the Tortricoidea, although concealed habits such as

leaf rolling are common and some tortricids even have completely concealed internal feeding (Horak 1998). Light brown apple moth larvae predominantly display external but protected, somewhat sheltered feeding on commercial fruits, such as apple (Lo et al. 2000). Physical niches of leaf-leaf or leaf-fruitlet were equally attractive and more so than combinations with any plastic surrogates (Suckling and Ioriatti 1996). Apple odors also were attractive when released from wax. Harris et al. (1999) reported that several chemicals in leaf extracts mediated larval walking behavior.

Apple trees are an excellent host for light brown apple moth, despite that the herbivore and plant did not evolve sympatrically (Suckling et al. 2001). Still, the number of tortricids using apple as a host (ancient or novel) is fairly extensive (Chapman 1973); so, the suitability of this host for light brown apple moth is perhaps not surprising. Irrigation and fertilization of orchards induces a flush of suitable shoot growth. This, together with the relative plant species richness of orchards with many excellent hosts, offering continuously changing niches among the ground cover and wind shelter species such as poplars (*Populus* spp.) and willows (*Salix* spp.) (Suckling et al. 1998), undoubtedly provides the opportunity for colonization of the orchard environment and rapid population development.

Plantain (*Plantago lanceolata* L.), curled dock (*Rumex crispus* L.), and capeweed [*Arctotheca calendula* (L.) Levyns] are important herbaceous hosts in Australia, despite that all are considered exotic there. In a study in apple and pear orchards in Victoria, Australia, Danthanarayana (1983) searched for light brown apple moth on all plants present and subsequently reared individuals from the plant species with eggs, larvae, or both present, including apple, pear, plantain, dock, amaranth, bushy starwort (*Aster subulatus* Shinn.), and several others. The ability to colonize and develop on a range of plants allows the use of alternate hosts when conditions on one host plant become unfavorable (Danthanarayana 1983). For example, because apple and many other fruit trees are deciduous, they are unsuitable for larval feeding of the winter generation, after leaf fall has occurred. By contrast, herbaceous plants may be available during winter whereas they may be more affected by summer drought and less available (Danthanarayana 1983). However, these plants vary in terms of "food preference" of light brown apple moth larvae. The order of preference (under laboratory conditions, from highest to lowest) is dock (*R. crispus*), clover (*Trifolium repens* L.), apple (*Malus domestica* Borkh.), silver wattle (*Acacia dealbata* Link), plantain (*P. lanceolata*), bushy starwort (*A. subulatus*), goosefoot (*Chenopodium album* L.), amaranth (*Amaranthus patulus* L.), capeweed, and pear (*Pyrus communis* L.) (Danthanarayana 1983). Although it seems that light brown apple moth's natural hosts are evergreen acacia trees, its better performance on herbaceous rather than woody plants suggests that it primarily evolved in association with the former (Clark 1970, Danthanarayana et al. 1995).

**Table 1.** Most commonly recorded host plants of light brown apple moth in New Zealand based on observations in orchards, agricultural land, and other environments (from Wearing 1999)

Genus and species	Common name	Family	Order
<i>Acacia</i> spp. (including <i>Racosperma</i> spp.)	Acacias and wattles	Fabaceae	Fabales
<i>Achillea millefolium</i> L.	Yarrow	Asteraceae	Asterales
<i>Carmichaelia</i> species <sup>a</sup>	New Zealand brooms	Fabaceae	Fabales
<i>Cassia</i> spp.	Sennas	Fabaceae	Fabales
<i>Chaenomeles speciosa</i> (Sweet) Nak.	Chinese quince	Rosaceae	Rosales
<i>Clianthus puniceus</i> (G. Don) Sol. ex Lindl. <sup>a</sup>	Glory-pea	Fabaceae	Fabales
<i>Cotoneaster</i> spp.	Cotoneaster or milkflower	Rosaceae	Rosales
<i>Crataegus</i> spp.	Hawthorns	Rosaceae	Rosales
<i>Cydonia</i> spp.	Quinces	Rosaceae	Rosales
<i>Cytisus</i> spp., <i>Genista</i> spp.	Brooms	Fabaceae	Fabales
<i>Duchesnea indica</i> (Andr.) Focke	Mock strawberry	Rosaceae	Rosales
<i>Fragaria moschata</i> Duchesne	Strawberry	Rosaceae	Rosales
<i>Hardenbergia violacea</i> (Schneev.) Stearn	Coral pea	Fabaceae	Fabales
<i>Kerria japonica</i> (L.) DC.	Japanese kerria	Rosaceae	Rosales
<i>Laburnum anagyroides</i> Medik.	Golden chain	Fabaceae	Fabales
<i>Lotus</i> spp.	Trefoils	Fabaceae	Fabales
<i>Lupinus</i> species	Lupins	Fabaceae	Fabales
<i>Malus</i> spp.	Apple, crab apple	Rosaceae	Rosales
<i>Medicago sativa</i> L., <i>M. lupulina</i> L.	Alfalfa or lucerne, medick	Fabaceae	Fabales
<i>Melilotus albus</i> Medik.	Sweet clover	Fabaceae	Fabales
<i>Parthenocissus inserta</i> (A. Kern.) C. Fritsch	Virginia creeper	Vitaceae	Vitales
<i>Phaseolus vulgaris</i> L.	Common bean	Fabaceae	Fabales
<i>Photinia glabra</i> (Thunb.) Franch. & Sav.	Japanese photinia	Rosaceae	Rosales
<i>Pisum sativum</i> L.	Pea	Fabaceae	Fabales
<i>Plantago</i> species	Plantains	Plantaginaceae	Lamiales
<i>Populus</i> spp.	Poplars	Salicaceae	Malpighiales
<i>Prunus</i> spp.	Almond, apricot, cherry, plum, peach, other <i>Prunus</i> spp.	Rosaceae	Rosales
<i>Pyracantha angustifolia</i> (Franch.) C. K. Schneid.	Firethorn	Rosaceae	Rosales
<i>Pyrus communis</i> L., other <i>Pyrus</i> spp.	Pears	Rosaceae	Rosales
<i>Rhaphiolepis umbellata</i> Makino	Japanese hawthorn	Rosaceae	Rosales
<i>Ribes</i> spp.	Currants, gooseberry	Grossulariaceae	Saxifragales
<i>Rosa</i> species	Roses	Rosaceae	Rosales
<i>Rubus fruticosus</i> aggregate, <i>R. idaeus</i> L.	Blackberry, raspberry	Rosaceae	Rosales
<i>Rubus parvus</i> Buchanan <sup>a</sup>	Creeping lawyer	Rosaceae	Rosales
<i>Spiraea</i> sp. ( <i>Spiraea x arguta</i> )	Meadowsweet, bridal wreath	Rosaceae	Rosales
<i>Trifolium</i> spp. and other clovers	Various clovers	Fabaceae	Fabales
<i>Ulex europaeus</i> L.	Gorse	Fabaceae	Fabales
<i>Vicia faba</i> L., other <i>Vicia</i> spp.	Broad bean, other beans	Fabaceae	Fabales
<i>Vitis vinifera</i> L., <i>Vitis</i> spp.	Grapevines	Vitaceae	Vitales
<i>Wisteria sinensis</i> (Sims) DC., <i>Wisteria</i> spp.	Chinese wisteria, wisteria	Fabaceae	Fabales

<sup>a</sup> Indicates New Zealand native species.

Danthanarayana et al. (1995) conducted laboratory studies to determine the effects on fecundity of a range of larval host plants at temperatures ranging from 10 to 32°C. Developmental times were shorter and fecundity was greater by a factor of 1.5–2.5 on plantain and dock than on apple and clover (*T. repens*) (Danthanarayana et al. 1995). This order of preference differed from the results of the previous study (Danthanarayana 1983) in which *T. repens* and apple were preferable to light brown apple moth larvae. The results of Danthanarayana et al. (1995) are perhaps more reliable because that study was more systematic, well replicated and undertaken in controlled conditions. According to Danthanarayana et al. (1995) fecundity reached means of up to 560 eggs per female. During the earlier study, mean fecundity ranged from 209 to 455 eggs per female (Danthanarayana 1983). The maximum fecundity observed for a single moth (1,492 eggs) was recorded from one that was reared on plantain. In New Zealand, Thomas (1965) recorded a maximum mean fecundity of 736 on plum ( $n = 7$ , for Nelson colony), 615 on apple ( $n = 6$ ), and 535 on

clover ( $n = 4$ ). In New Zealand, important perennial “weed” hosts include gorse and Scotch broom, and it has been commonly recorded on annual weeds (*Rumex obtusifolius* L. and *Plantago* spp.), shelter and amenity trees (especially species of *Salix* and *Populus* spp.) (Suckling et al. 1998). Also, in New Zealand, Tomkins et al. (1989) found that larval developmental times were shortest on dock, followed by poplar (*Populus nigra* L.), apple, gorse, and blackberry (*Rubus fruticosus* L.). Pupal weights were among the highest on several apple varieties. Light brown apple moth has readily colonized the native leguminous tree *Acacia koa* A.Gray in Hawaii, along with gorse and other species, and there are numerous new host records from California (see below).

Wearing et al. (2003) ranked 18 apple cultivars for partial resistance to light brown apple moth larvae, based on larval period and pupal weight, and together with field trials of 38 cultivars found several with potentially useful light brown apple moth resistance. Such differences between studies may reflect variation between light brown apple moth populations as

**Table 2.** Most common host plants of light brown apple moth in California (i.e., species with at least five records), based on USDA (2008)

Genus and species	Common name	Family	Order
<i>Alstroemeria</i> sp.	Peruvian lily	Alstroemeriaceae	Liliales
<i>Arctostaphylos</i> spp.	Manzanita	Ericaceae	Ericales
<i>Boronia</i> sp.	Boronia	Rutaceae	Sapindales
<i>Callistemon</i> sp.	Bottlebrush	Myrtaceae	Myrtales
<i>Calluna vulgaris</i> (L.) Hull	Heather	Ericaceae	Ericales
<i>Ceanothus</i> sp.	Ceanothus	Rhamnaceae	Rosales
<i>Citrus x limon</i> (L.) Burm.f.	Lemon	Rutaceae	Sapindales
<i>Crowea</i> sp.	Waxflower	Rutaceae	Sapindales
<i>Dodonaea viscosa</i> Jacq.	Purple hopseed, akeake	Sapindaceae	Sapindales
<i>Euonymus</i> sp.	Spindle trees	Celastraceae	Celastrales
<i>Fragaria</i> sp.	Strawberry	Rosaceae	Rosales
<i>Fuchsia</i> sp.	Fuchsia	Onagraceae	Myrtales
<i>Hebe</i> sp.	Hebe	Plantaginaceae	Lamiales
<i>Hydrangea</i> sp.	Hydrangeas	Hydrangeaceae	Cornales
<i>Laurus nobilis</i> L.	Sweet bay	Canellaceae	Canellales
<i>Leucadendron</i> sp.	Leucadendron	Proteaceae	Proteales
<i>Malus</i> sp.	Apple	Rosaceae	Rosales
<i>Myrica californica</i> Cham. & Schltdl.	California wax myrtle	Myricaceae	Fagales
<i>Olea europaea</i> L., <i>Olea</i> sp.	Olive	Oleaceae	Lamiales
<i>Penstemon</i> sp.	Penstemon	Scrophulariaceae	Lamiales
<i>Photinia x fraseri</i>	Red tip photinia	Rosaceae	Rosales
<i>Pittosporum</i> spp.	Pittosporum	Pittosporaceae	Apiales
<i>Prunus</i> spp.	Stone fruits	Rosaceae	Rosales
<i>Rhamnus</i> sp.	Rhamnus	Rhamnaceae	Rosales
<i>Ribes viburnifolium</i> Gray	Island gooseberry	Grossulariaceae	Saxifragales
<i>Rosa</i> sp.	Rose	Rosaceae	Rosales
<i>Rubus</i> sp.	Blackberry	Rosaceae	Rosales
<i>Salvia</i> spp. <sup>a</sup>	Sage	Lamiaceae	Lamiales
<i>Tibouchina urvilleana</i> (DC.) Cogn.	Princess flower	Melastomataceae	Myrtales
<i>Vaccinium</i> sp.	Blueberry	Ericaceae	Ericales

Bold entries are newly recorded plants (not listed from Australia, New Zealand, or other areas colonized by light brown apple moth).

<sup>a</sup> In addition to the most common hosts reported by USDA (2008), subsequent inspections (USDA, unpublished records) revealed that *Salvia* species were frequently infested by light brown apple moth.

well as plant provenances. It is also possible that the levels of detoxication enzymes in feeding light brown apple moth larvae may be expressed differentially on different host plants (Robertson et al. 1990).

**Host Plants of Light Brown Apple Moth and Phylogenetic Analysis.** According to our compilation the host range of light brown apple moth includes at least 545 host plant species in 363 genera from 121 families (Supp Table 1 [online only]). Earlier compilations by Danthanarayana (1975) and Geier and Briese (1980) for Australia recorded hosts from 123 genera (in 55 families). Our compilation includes all of the records of Danthanarayana (1975) but not those by Geier and Briese (1980), which were limited to plant genera and did not provide species names of host plants. However, none of the genera of Geier and Briese (1980) were omitted from our list because all those genera were included in other sources. In addition to light brown apple moth host plants reported from Australia, our list contains 424 records from New Zealand, nine from Hawaii, 40 from England, 276 from California, and numerous others where no geographic information could be ascertained.

One hundred and one host plants reported from Australia by Geier and Briese (1980) were exotic genera and only 22 genera represented native plants. This suggests that introduced crop and ornamental plants as well as accidental introductions of plants allowed light brown apple moth to increase its host range well

beyond the range of plants normally used in its natural habitat. With its expanding geographic range and the opportunity to colonize many other plants occurring under varying climatic conditions, light brown apple moth was able to increase its hosts even further. Recent surveys undertaken in California added considerably to the known host records, with many additions of plant species that had not been recorded in previous surveys in other countries. Although most host records are thought to be reliable, especially those cited by multiple sources, it is possible that some erroneous host records are included in our compilation. This could have been caused by misidentification of the caterpillar or the host plant, or by misinterpretation of accidental occurrences of light brown apple moth on plants that are actually suitable as hosts. We therefore advise caution in the use of this compilation, particularly in the case of single records.

The 1970s survey in New Zealand conducted by DSIR Entomology Division Horticulture Group (Wearing 1994) provided information that allowed the categorization of plants representing very common, common, or occasional hosts (Wearing 1999). The occasional hosts were not all confirmed as being capable of supporting larval development. The most common plants are given in Table 1 (for a complete list, see Supp Table 1 [online only]). Information on the frequency of host use by light brown apple moth from the surveys in California was used as an indica-



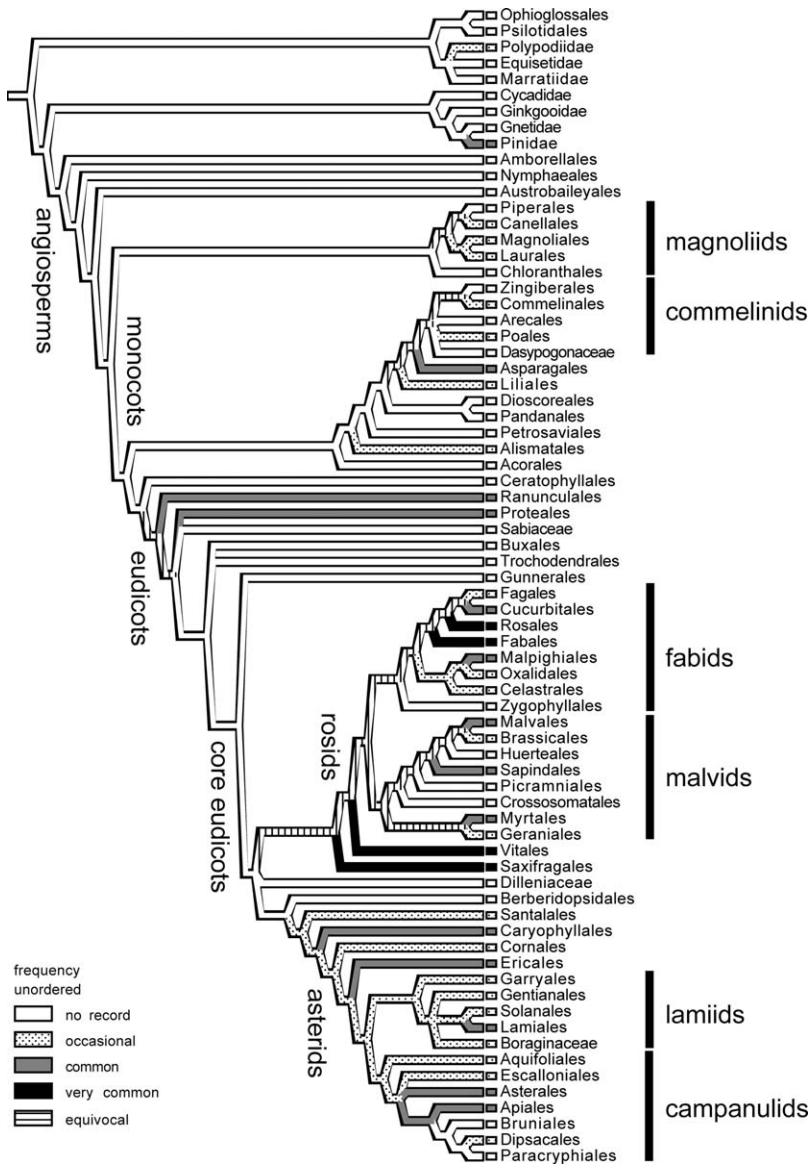


Fig. 1. Cladogram of light brown apple moth host record frequency (cladogram after APGIII 2009).

tion of which hosts were more commonly associated with light brown apple moth. The most common host plants are listed in Table 2. Several new hosts that had not been recorded previously for light brown apple moth are commonly attacked in California, for example, species of *Arctostaphylos* (manzanita), which are common and widely planted in urban areas. Note, however, that neither of these surveys were conducted as designed experiments, and records of economically important and common plants are probably overemphasized compared with less economically important and rarer plants.

The host range of light brown apple moth covers species in orders across the vascular plants (Fig. 1; Supp Table 1 [online only]), and includes at least 545

plant species (Supp Table 1 [online only]). Most records are for dicotyledonous plants but the list encompasses many monocotyledonous plants and conifers, and, remarkably, even some ferns. All orders in the rosids and asterids and approximately half of the other eudicot orders are represented among the host records (Fig. 1). As mentioned, the prevalence of Rosales, Fabales, as well as Vitales and Saxifragales may be partly related to observer bias toward economically important crop plants. Apart from the relative rarity of lower dicotyledons, monocotyledons, magnoliids, and ferns, there is no apparent phylogenetic relationship noticeable in the host range of light brown apple moth. However, one would expect that species of rosids and asterids are at a greater risk of

attack than lower orders of vascular plants. Phylogenetic relatedness to commonly used host plants is often a good indicator of insect fitness on novel hosts (Bertheau et al. 2010); however, highly polyphagous herbivores, such as light brown apple moth, may experience no loss in fitness when they develop on distantly related new hosts (Bertheau et al. 2010).

In conclusion, our compilation of host records from the native region of light brown apple moth in Australia and from the invaded territories in New Zealand, Hawaii, England, and California demonstrates that, by any standards, light brown apple moth has a very wide host range. Observations on the recent invasion in California confirm that light brown apple moth can quickly colonize new host plants that it has not experienced before. Our phylogenetic analysis of the host range indicates that there are no striking patterns of host specificity, apart from the apparent predominance of Rosales and Fabales and the comparative rarity of host records in the lower orders of vascular plants.

Host selection by light brown apple moth (and other polyphagous leafrollers) is thought to be a two-component process, undertaken by ovipositing females and young larvae. The host range and relative suitability of potential host plants is determined by multiple factors including attractiveness of plant odors to females searching for oviposition sites and the presence of further chemical and physical cues stimulating oviposition. Factors that determine larval host preferences and larval development on different plants include suitability for creating defensive shelters and feeding sites, and surface area of leaves suitably prepositioned to create a shelter (e.g., *Photinia* species are predisposed by leaf architecture to be a suitable nest offering protection and feeding). Host plant preferences for adults and for larvae seem to be largely independent of each other (Foster and Howard 1999). Poor host discrimination by ovipositing females, combined with highly dispersive larvae, could be a powerful behavioral means for expanding the host range of such polyphagous insects such as leafrollers. The initial settlement and feeding of larvae on a novel or nonhost plant (e.g., Foster and Howard 1999) could test its suitability as a host and determine whether the larvae would remain and develop. Larval dispersal ability combined with a wide host range would provide a safety mechanism to reach an alternative host if the initial plant used by the ovipositing female proved unsuitable or became unsuitable, for example, as a result of leaf drop in deciduous trees.

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