

Understanding Heliothine (Lepidoptera: Heliothinae) Pests: What is a Host Plant?

Author(s): John Paul Cunningham and Myron P. Zalucki

Source: Journal of Economic Entomology, 107(3):881-896. 2014.

Published By: Entomological Society of America

URL: <http://www.bioone.org/doi/full/10.1603/EC14036>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Understanding Heliothine (Lepidoptera: Heliothinae) Pests: What is a Host Plant?

JOHN PAUL CUNNINGHAM¹ AND MYRON P. ZALUCKI^{2,3}

J. Econ. Entomol. 107(3): 881–896 (2014); DOI: <http://dx.doi.org/10.1603/EC14036>

ABSTRACT Heliothine moths (Lepidoptera: Heliothinae) include some of the world's most devastating pest species. Whereas the majority of nonpest heliothinae specialize on a single plant family, genus, or species, pest species are highly polyphagous, with populations often escalating in size as they move from one crop species to another. Here, we examine the current literature on heliothine host-selection behavior with the aim of providing a knowledge base for research scientists and pest managers. We review the host relations of pest heliothines, with a particular focus on *Helicoverpa armigera* (Hübner), the most economically damaging of all heliothine species. We then consider the important question of what constitutes a host plant in these moths, and some of the problems that arise when trying to determine host plant status from empirical studies on host use. The top six host plant families in the two main Australian pest species (*H. armigera* and *Helicoverpa punctigera* Wallengren) are the same and the top three (Asteraceae, Fabaceae, and Malvaceae) are ranked the same (in terms of the number of host species on which eggs or larvae have been identified), suggesting that these species may use similar cues to identify their hosts. In contrast, for the two key pest heliothines in the Americas, the Fabaceae contains $\approx 1/3$ of hosts for both. For *Helicoverpa zea* (Boddie), the remaining hosts are more evenly distributed, with Solanaceae next, followed by Poaceae, Asteraceae, Malvaceae, and Rosaceae. For *Heliothis virescens* (F.), the next highest five families are Malvaceae, Asteraceae, Solanaceae, Convolvulaceae, and Scrophulariaceae. Again there is considerable overlap in host use at generic and even species level. *H. armigera* is the most widely distributed and recorded from 68 plant families worldwide, but only 14 families are recorded as containing a host in all geographic areas. A few crop hosts are used throughout the range as expected, but in some cases there are anomalies, perhaps because host plant relation studies are not comparable. Studies on the attraction of heliothines to plant odors are examined in the context of our current understanding of insect olfaction, with the aim of better understanding the connection between odor perception and host choice. Finally, we discuss research into sustainable management of pest heliothines using knowledge of heliothine behavior and ecology. A coordinated international research effort is needed to advance our knowledge on host relations in widely distributed polyphagous species instead of the localized, piecemeal approaches to understanding these insects that has been the norm to date.

KEY WORDS polyphagy, host relation, volatile, pest management

Heliothines are a group of noctuid moths whose larvae feed predominantly on flowers and plant reproductive structures, giving these insects a variety of common names, such as bollworm, budworm, earworm, pod borer, and flower caterpillar (Zalucki et al. 1986). Worldwide there are some 365 species in the subfamily (Cho et al. 2008). In North America, 148 heliothine species in 14 genera have been described (Hardwick 1996, Knudson et al. 2003), with host plants recorded for 92 of these species; based on these records, we estimate 55% have been recorded as having been found on a single host species, 83% from a single genus, and 96% from a single plant family (predominantly

Asteraceae—74%; see also Mitter et al. 1993). These figures suggest a high degree of host specialization in most heliothines, as is common in phytophagous insects (Jermy 1984).

Although only a few heliothines are considered to be polyphagous, some of these species are widely known and studied, and are some of the world's most important agricultural pests. These pest species appear to be in a single "Heliothis" clade, suggesting the trait was inherited from a common ancestor (Cho et al. 2008). *Heliothis virescens* (F.) and *Helicoverpa zea* (Boddie) are the main heliothine pests in North and South America (Bergvinson 2005) where these moths have been recorded from 235 plant species in 36 families, with a large overlap in host plant use for the two species (see compilation by Kogan et al. 1989). Tobacco budworm (*He. virescens*) infests >19 crops, while the corn earworm, *H. zea*, infests at least 30

¹ School of Earth, Environmental and Biological Sciences, Queensland University of Technology, Brisbane 4001, Australia.

² School of Biological Sciences, The University of Queensland, Brisbane 4072, Australia.

³ Corresponding author, e-mail: M.Zalucki@uq.edu.au.

(Blanco et al. 2007). These moths are important pests of crops, such as maize, cotton, soybean, tomato, tobacco, alfalfa; horticultural crops such as beans, sweet corn, and tomato; as well as floriculture crops such as chrysanthemum. As the name implies, the tobacco budworm shows a preference for laying eggs on the Solanaceae (e.g., tobacco and tomato), while *H. zea* (the corn earworm) prefers hosts in the Poaceae (maize, sorghum; Bergvinson 2005). However, a wide range of crops can support these pests, as we show in the following analysis of host use. In addition to these major pest species, other heliothines have been recorded from more than one plant family in North America—*Heliothis borealis* (Hampson) (four families), *Heliothis oregonica* (Hy. Edwards) (three families), *Schinia tertii* (Grote) (two families), and *Schinia olivacea* Smith (two families)—but none are regarded as pests.

Helicoverpa armigera (Hübner) is widespread throughout Europe, Africa, Asia, and Australia, where it causes extensive damage to a wide range of crops (Zalucki et al. 1986, Sharma 2005). More recently the species has spread to South America (Czepak et al. 2013, Specht et al. 2013, Tay et al. 2013), with devastating effects in the broad acre cropping systems in Brazil (C. Czepak, personal communication). Certainly the presence of a diverse indigenous heliothine fauna and similar polyphagous pests has not prevented its establishment and spread. The area in the new world at risk of *H. armigera* invasion extends well beyond Brazil as suggested by Zalucki and Furlong (2005) using a simple CLIMEX model. The species has the potential to spread into the southern United States, with seasonal migration much further north (D. J. Kriticos, unpublished data).

In Australia, the two important heliothine pests are *H. armigera* and an endemic species, *Helicoverpa punctigera* Wallengren. Both *H. armigera* and *H. punctigera* are highly polyphagous, having been recorded from 35 and 49 families respectively in Australia (Zalucki et al. 1986, 1994). Crop hosts affected by these pest species include tobacco, cotton, tomato, sunflower, sorghum, pigeon pea, and chickpea. Of the remaining 37 Australian heliothine species, hosts have been recorded for only 12 (Matthews 1999); eight of these appear restricted to a single plant family (six on Poaceae and two on Fabaceae). Australian heliothines other than *H. armigera* and *H. punctigera* recorded from more than one plant family are *Heliothis punctifera* Walker (eight families), *Helicoverpa assulta* (Guenée) (five families), and *Australothlis rubrescens* (Walker) (four families). Of these polyphagous species, only *H. assulta* is a pest on plants in the Solanaceae (peppers, tobacco, tomato) and Alliaceae (onions) in some parts of its range (Africa, Asia, and Australasia; Xia et al. 2009); polyphagy per se is not a prerequisite for being considered a pest.

The variation in the breadth of host use in heliothines, in terms of the size and diversity of the host range and the individual plant species that are used as hosts, raises a number of important questions regarding what limits host range in heliothine species. How important are larval traits (development and survival on hosts),

compared with adult traits (host finding and recognition)? Are there common attributes of host species that serve as definitive host cues? Are there differences in the way host cues are perceived in specialist and generalist species? Are there particular behavioral traits present in polyphagous heliothine species that have enabled them to successfully use agro-ecosystems?

Determining the extent and nature of polyphagy is essential for understanding the behavioral- and evolutionary ecology of heliothines (Cho et al. 2008), and in the design and implementation of effective pest management strategies (Jallow et al. 2004). Here, we use published studies on polyphagous heliothines to further our understanding of what constitutes a “host plant.” We begin by carrying out a simple analysis of host plant use in the four major pest species, to investigate whether particular plant species, or families, are favored as hosts. We then review information on host preferences, and evidence for innate (genetic) and acquired (learned) differences in these preferences within species, exploring additional physiological determinants of host plant use. Focusing on olfaction in *H. armigera*, we investigate how current knowledge of sensory biology can help our understanding of host choice and polyphagy. We conclude by considering how an in-depth knowledge of the nature of polyphagy might be applied to pest management of some of the world’s most economically important species.

Host Plant Use by Polyphagous Heliothines

What Constitutes a Host? Before presenting an analysis of host use in polyphagous heliothines, we must first consider how well host plant relations have been defined (Ward 1988). A host plant should be one that supports the development of larvae and contributes to the number of reproducing adults in the population. For this to occur (in most Lepidoptera), the plant would have to be found and laid upon by adult insects in the field, and a proportion of the immatures would have to successfully complete development to become reproductive adults. More selective definitions for a host plant reflect the degree to which the plant contributes to the insects’ fitness (e.g., Jaenike 1990). Walter and Benfield (1994) suggest that the regularity with which the plant species is used as a host in the field, and the relative abundance of eggs or larvae found on it, should also be considered. Attraction to a plant (or its odor) in laboratory studies is thus not necessary an indicator of a host, as the insect may use the plants for other purposes, may reject it on alighting, or may deposit eggs that do not develop through to adult insects. In heliothines, adult moths are attracted to flowers for nectar feeding, and these species may not support larvae. Gregg (1993) found that the most common pollen on the proboscis of *H. armigera* and *H. punctigera* was from eucalypts, and Del Socorro et al. (2010a) found that these plants were among the most attractive in an olfactometer, even though they do not support larvae. In laboratory (greenhouse) studies, female *H. armigera* have been observed laying on flowering nonhosts such as *Cuphea*

and *Lantana* species (J.P. Cunningham, unpublished data; Manjunath et al. 1989), and in cage studies will lay eggs on netting and plastic-ware.

Oviposition on nonhosts may also occur in the field. Most records for host plant use by heliothines are based on incidental collections of immature stages from plants, followed by subsequent rearing on diet for identification (Zalucki et al. 1986). These records assume that adult insects choose only to lay on plants that will support the development of their larvae and that the presence of a larva on a plant implies that it is capable of using that plant species to complete its development to pupation or adulthood, which is not necessarily the case. Because few plant species have been tested for the presence of eggs and larval survival through to adulthood (in particular for noncrop hosts), a large amount of subjectivity is still inherent in current records of host plants. In general, plants on which eggs, but not larvae, have been found in the field should not be considered host plants [e.g., our unpublished records for *H. armigera* on milkweed, *Asclepias curassavica* (L.)]. When larval stages are occasionally found on a particular species in the field, the decision to class this species as a host is largely subjective, and depends on the frequency with which the event is observed (see Zalucki et al. 1994); larvae are known to move between plants, particularly in later instars (Cunningham et al. 2001, 2011). Such is the case, for example, with *H. armigera* on *Lantana camara* L., for which occasional oviposition and early instar presence has been documented (Manjunath et al. 1989). Here we do not consider *L. camara* under the definition of host plant for *H. armigera* in Australia, and Manjunath et al. (1989) lists it as a doubtful record in India.

Larval survival to adulthood is undoubtedly a key criterion in the identification of a host plant species. In any insect species, suitability of host material for immature development and survival has a strong effect on fitness, and in polyphagous heliothines, such as *H. armigera*, suitability varies considerably among host plants (e.g., Hmimina 1988, Firempong and Zalucki 1990a, Jallow and Zalucki 2003, Fatma and Pathak 2011). Laboratory-based studies assessing juvenile survival on particular plants are commonly used to determine the extent to which different plants may serve as hosts in nature, but there are a number of problems associated with this technique. In *H. armigera*, leaf material or a combination of leaf and reproductive structures is often (e.g., Ruan and Wu 2001, Liu et al. 2004), but not always, used (e.g., Kakimoto et al. 2003) rather than the more relevant flowers or reproductive structure (see e.g., Liu et al. 2010). Survival and development on intact plants tends to be poorer than on cut leaf material, even in the absence of predation (e.g., Kyi et al. 1991, Yang et al. 2008). Thus, these studies may give little indication of larval performance in nature. Under field conditions, survival on crop hosts (which have been given the most attention) is generally poor and highly variable (Titmarsh 1992, Van den Berg and Cock 1993, Fatma and Pathak 2011). Although some of this mortality is owing

to predation and climate, host plant factors are also indicated (Kyi et al. 1991, Zalucki et al. 2002).

Many studies use insects that have been in laboratory cultures for long periods (e.g., Dhandapani and Balasubramanian 1980), and such assays must be treated with caution, because of potential inbreeding and selection effects (such as the selection for females that show little discrimination for oviposition sites, and larvae that develop best on artificial diets). There are, however, notable exceptions (e.g., Gu and Walter 1999). Differences in preference among individuals may also be important; Jallow and Zalucki (2003) and Gu et al. (2001) included between female family effects in studies of larval performance on a limited number of substrates and found some evidence for differences in performance among families, suggesting genetic variation in these traits. Finding genetic variations among individuals has of course been the main stay of tracking down resistance mechanisms to insecticides as well as providing pointers to what may limit host plant use (Heckel 1993; Ahn et al. 2011a,b; Celorio-Mancera et al. 2012; Joussem et al. 2012).

How then should host range be determined? What they are capable of eating, where they survive well, or where they cause significant damage? Collecting all stages of development of an insect species, on a plant species, in the field, on a regular basis, is perhaps the most reliable estimate for host plant status (Zalucki et al. 1994). However, even such relatively comprehensive studies on host use are limited by geographical and temporal constraints of the study, and by variation in host use that may occur as a result of host abundance (for example lack of oviposition on a lesser preferred host when a more preferable host is available; see Blanco et al. 2007).

Analysis of the Published Host Records. With all the above caveats in defining a host plant in mind, and accepting that host lists for polyphagous heliothines may be inflated (assuming the sampling has been extensive), an analysis of the published literature is still useful in identifying trends in host use by particular heliothine species, which may warrant further, more detailed study. The top six host plant families in the two main Australian pest species (Table 1) are the same for both species, and the top three (Asteraceae, Fabaceae, and Malvaceae) are ranked the same (in terms of the number of host species on which eggs or larvae have been identified). The Asteraceae, as in most heliothines, figure prominently. There is considerable overlap in host use at generic and even species level (Table 1), particularly in the Fabaceae, Malvaceae, and Solanaceae, suggesting that *H. armigera* and *H. punctigera* may use similar cues to identify their hosts.

Table 2 displays host use records, at a family level, for the two major pest heliothines in the Americas. Because the top six families for each of these species differ, eight families are shown. In contrast to their Australian relatives, the Fabaceae contains $\approx 1/3$ of hosts for both, and the remaining rank order of host families differ to some extent. For *H. zea*, the remaining hosts are more evenly distributed, with Solanaceae next, followed by Poaceae, Asteraceae, Malvaceae,

Table 1. Number of host plants recorded and % of total species records for the top six plant families used by *H. armigera* and *H. punctigera* in Australia

Family	<i>H. armigera</i>		<i>H. punctigera</i>		Both species %	
	No. hosts	%	No. hosts	%	Genera	Species
Asteraceae	33	25	75	28	46	27
Fabaceae	27	21	42	16	72	41
Malvaceae	11	8	18	7	88	38
Brassicaceae	7	5	16	6	33	15
Solanaceae	10	8	14	5	100	60
Poaceae	9	7	8	3	56	42

Percentage genera and species in each of these families used by both moth species are also shown.

H. armigera = 35 families, 130 species; *H. punctigera* = 46 families, 264 species.

Sources: Zalucki et al. (1986, 1994); Matthews (1999).

and Rosaceae (Table 2). For *He. virescens*, the next highest five families are Malvaceae, Asteraceae, Solanaceae, Convolvulaceae, and Scrophulariaceae. Again there is considerable overlap in host use at generic and even species level (Table 2), particularly in the Convolvulaceae, Scrophulariaceae, Fabaceae, Malvaceae, and Solanaceae.

Host use for *H. armigera* in countries outside Australia has received less attention, with the exception of India (Manjunath et al. 1989). Published records for *H. armigera* host use in China (Liu 1934, Xu et al. 1958, Bai et al. 1997), Europe (Torres-Vila et al. 2002, Buès et al. 2005), and Africa (Coaker 1959, Evans 1964, Topper 1987), go little beyond cataloguing the species status as a pest of major crops. In Table 3, we look at trends in worldwide host use in *H. armigera* (plants for which it is recorded in at least two continents). *H. armigera* is recorded from 68 plant families worldwide (Supp Table 1 [online only]), but only 14 families are recorded as containing a host in all geographic areas (Table 3).

As expected, host records for *H. armigera* focus predominantly on agricultural crops (Table 3) and a few

Table 2. Number of host plants recorded and % of total species records in the top eight plant families used by *H. zea* and *He. virescens* in North America

Family	<i>H. zea</i>		<i>He. virescens</i>		Both species %	
	No. hosts	%	No. hosts	%	Genera	Species
Fabaceae	41	33	55	31	35	25
Malvaceae	8	6	24	13	45	23
Asteraceae	8	6	19	11	16	13
Solanaceae	14	11	19	11	38	21
Convolvulaceae	3	2	9	5	67	27
Scrophulariaceae	2	2	6	3	40	33
Rosaceae	5	4	2	1	0	0
Poaceae	9	7	1	1	20	11

Percentage genera and species in each of these families used by both moth species are also shown.

H. zea = 29 families, 123 species; *He. virescens* = 27 families, 179 species.

Sources: Kogan et al. (1989), Hardwick (1996), Blanco et al. (2007).

“weeds” (*Sonchus oleraceus* L., *Sphaeranthus indicus* L., *Aeschynomene indica* L., and *Ricinus communis* L.). Gu and Walter (1999) have suggested *S. oleraceus* or sowthistle may be a primary or ancestral host plant based on oviposition trials of *H. armigera* collected from different hosts within the one locality, and larval feeding preference and performance assays. They found variation among females in preference for sowthistle over cotton, and a positive correlation between adult and offspring preference for this plant (Gu et al. 2001).

Host Plant Preferences. Ovipositing polyphagous moths do not respond to all host plants equally, leading to differences in relative preferences for hosts emerging when females are given a choice of plants on which to lay. In general, preference—differential oviposition on a plant when given a choice (Singer 1986)—is assessed on the basis of egg counts on substrates in choice tests using either individuals (Jallow and Zalucki 1995, 1996; Gu and Walter 1999; Jallow et al. 2001) or, less satisfactorily, groups of moths (Firempong and Zalucki 1990a, Ramnath et al. 1992). Although preferences based on observations in the field are possible (Walter and Benfield 1994, Benda et al., 2011), effects of host abundance and moth experience on host preferences (e.g., learning effects, below) are hard to disentangle.

In *H. armigera*, it has long been known that host preferences are strongly biased toward flowering stages (Parsons 1940). In Australia, relative oviposition preferences for *H. armigera* (based on cage trials) show consistency in rank between populations: groups of *H. armigera* from different populations in eastern Australia ranked flowering tobacco, maize, and sunflower as the most preferred host plants for oviposition, followed by soybean, cotton, and lucerne. The least preferred plants in these trials were cabbage, pigweed, and linseed (Firempong and Zalucki 1990a). In postlighting tests, which use tethered moths to look more specifically at acceptance of a host plant after alighting, Jallow and Zalucki (1995, 1996) found similar results in ranking. Certain females, however, demonstrated differences in rank among host species (Jallow and Zalucki 1995, 1996; Gu and Walter 1999).

A common assumption is that relative preferences of ovipositing females should match the suitability of the different host plants for juvenile development and survival. Although this has been shown in some insect species, it is frequently not the case (Ballabeni et al. 2001, Mayhew 2001, Scheirs and De Bruyn 2002, Gripenberg et al. 2010), including in *H. armigera* (Jallow and Zalucki 2003). Where survival and preference are not correlated, other ecological and environmental determinants may influence insect fitness and the evolution of host choice, such as host plant habitat (West and Cunningham 2002), predators and parasitoids associated with host plants (Bjorkman and Larsson 1991, Ballabeni et al. 2001), and the availability of adult and larval feeding sites (Scheirs and De Bruyn 2002, Liu et al. 2010, 2012).

Often ignored is that larval behavior may ameliorate “poor” adult host selection (Gamberale-Stille et al. 2013). Neonate *H. armigera* larvae show fine scale

Table 3. Host plant families (and Order) used by *H. armigera* in three or more countries for which host use data have been published (Australia, China, India, Uganda, Sudan, Spain, and France)

Family	Order	No. of genera	Commonly used species in at least two continents
Asteraceae	Asterales	50	<i>Helianthus annuus</i> , <i>Carthamus tinctorius</i> , <i>Sonchus oleraceus</i> , <i>Sphaeranthus indicus</i>
Iridaceae	Asterales		<i>Gladiolus</i> sp.
Caryophyllaceae	Asterales		<i>Dianthus caryophyllus</i>
Fabaceae	Leguminales	42	<i>Arachis hypogaea</i> , <i>Phaseolus vulgaris</i> , <i>Glycine max</i> , <i>Medicago sativa</i> , <i>Aeschynomene indica</i> , <i>Cajanus cajan</i> , <i>Cicer arietinum</i> , <i>Lablab purpureus</i> , <i>Lathyrus odoratus</i> , <i>Pisum sativum</i> , <i>Vigna radiata</i> , <i>Vigna unguiculata</i>
Poaceae	Graminales	14	<i>Sorghum bicolor</i> , <i>Zea mays</i> , <i>Triticum aestivum</i> , <i>Avena sativa</i> , <i>Oryza sativa</i>
Cucurbitaceae	Cucurbitales	10	<i>Citrullus lanatus</i> , <i>Cucumis sativus</i> , <i>Cucurbita maxima</i>
Malvaceae	Malvales	10	<i>Gossypium hirsutum</i> , <i>Abelmoschus esculentus</i>
Amaranthaceae	Caryophyllales	7	<i>Amaranthus</i> sp.
Solanaceae	Solanales	7	<i>Capsicum annum</i> , <i>Nicotiana tabacum</i> , <i>Lycopersicon esculentum</i> , <i>Solanum tuberosum</i>
Convolvulaceae	Solanales		<i>Ipomoea batata</i>
Euphorbiaceae	Malpighiales	6	<i>Ricinus communis</i>
Chenopodiaceae	Chenopodiales	5	<i>Beta vulgaris</i> , <i>Spinacia oleracea</i>
Rosaceae	Rosales	5	<i>Fragaria</i> sp.
Apiaceae	Umbellales	4	No common use species
Brassicaceae	Brassicales	4	<i>Brassica oleracea</i>
Lamiaceae	Lamiales	4	<i>Mentha spicata</i>
Scrophulariaceae	Personales	4	<i>Antirrhinum majus</i>
Cannabaceae	Urticales	1	<i>Cannabis sativa</i>
Pedaliaceae	Bignoniales	1	<i>Sesamum indicum</i>
Rubiaceae	Rubiales	1	<i>Coffea arabica</i>
Ruraceae	Rutales	1	<i>Citrus limon</i>
Alliaceae	Liliales	1	<i>Allium cepa</i>

Arranged by the number of host genera recorded by plant Order. Species used in at least two continents also shown (see Supp Table 1 [online only]).

Sources: Liu (1934); Xu et al. (1958); Coaker (1959); Evans (1964); Zalucki et al. (1986, 1994); Topper (1987); Manjunath et al. (1989); Bai et al. (1997); Torres-Vila et al. (2002); Buès et al. (2005).

discrimination within plants, avoiding induced leaves as well as moving between plants (Perkins et al. 2013). Large larvae can move extensively among plants (Cunningham et al. 2001, 2011).

Genetic Differences in Oviposition Preference. Genetic variation in *H. armigera* host use across different host families has been shown in Australia (Jallow and Zalucki 1995, 1996; Gu et al. 2001), but not in within host species comparisons (Cotter and Edwards 2006). Assessing the contribution of genetic differences between populations and among females within a population in host location, preference, and use is an important precondition for understanding the nature of polyphagy.

Firempong and Zalucki (1990a) and Jallow and Zalucki (1996) investigated variation in oviposition preference between geographic populations of *H. armigera* in eastern Australia. Despite some differences among individual females within populations, host preferences did not differ significantly between populations, regardless of the differences in host availability between geographic localities. Similarly Gu and Walter (1999) found no effect of collection source (different hosts) within one locality on adult host selection. Daly and Gregg (1985) found little genetic variation among populations of *H. armigera* in eastern Australia. They attributed this to gene flow between populations, which may partly account for the absence of major variation in host plant preference at this level. Endersby et al. (2007) also found panmixis. However, Scott et al. (2005) suggested genetic structure at various scales in some years (but see Weeks et al. 2010),

and Behere et al. (2013) suggest local genetic structure and significant differentiation between cotton growing and other areas in India in some years.

Both offspring–parent regression analysis and Kendall's coefficient of concordance (measuring agreement in plant ranking between parent and offspring) indicated that differences in observed oviposition preference among females can have a genetic basis (Jallow and Zalucki 1996). These heritability estimates are consistent with those reported by Firempong (1987), whose estimates were based on the regression of mean preference for F_1 females against that of their parents, but they are lower than estimates recorded by Gu et al. (2001) using *S. oleraceus* and *G. hirsutum*. Although only the postalighting components of oviposition behavior of *H. armigera* were addressed by Jallow and Zalucki (1996), it is conceivable that genetic variation exists in prealighting components of host selection (Sheck and Gould 1995).

The availability of genetically very closely related species in the "Heliothis/ Helicoverpa" clade that differ markedly in host relations; the highly polyphagous or generalist *He. virescens* and *H. armigera* and their closely related respective host specialist *Heliothis subflexa* (Guenée) and *H. assulta*; has led to comparative studies addressing the genetics of oviposition, host preference, larval feeding, and adaptation (Oppenheim and Hooper 2009). Comparative studies of adult oviposition choice, larval host plant choice, and larval performance in *H. armigera* and *H. assulta* (Wang et al. 2004; Tang et al. 2006; Liu et al. 2010, 2012) and in *He. virescens* and *He. subflexa* (Sheck and Gould 1993,

1995; Oppenheim and Hooper 2009) provide means of identifying the genes involved in switching from polyphagy to host specialization. The basis of host utilization and resistance in larvae has certainly gained from recent genetic and molecular approaches. For example, the genetic basis of resistance to insecticides (Heckel et al. 1998, Gahan et al. 2001, Jousset et al. 2012) and *Bacillus thuringiensis* (Gahan et al. 2010), proteomics of the midgut (Pauchet et al. 2008) and salivary gland (Celorio-Mancera et al. 2011a), transcriptional responses to plant secondary compounds such as gossypol (Celorio-Mancera et al. 2011b) and to different host plants (Celorio-Mancera et al. 2012), detoxification of plant secondary compounds such as capsaicin (Ahn et al. 2011), and gene families involved in detoxification and defense (Ahn et al. 2011, Courtiade et al. 2011) have been in part elucidated. There is a much stronger genetic effect on larval weight gain (e.g., Cotter and Edwards 2006). Genes for oviposition behavior have been more elusive, possible because adult behavior is more phenotypically plastic, including the effects of learning and other ontogenetic influences.

Learning. Host selection behavior in many polyphagous lepidopteran species has been shown to change with experience (Papaj and Prokopy 1989) and heliothines are no exception. Cunningham et al. (1998a) presented the first detailed evidence of learning in pre-alighting (host selection) and postalighting (host acceptance) behavior in *H. armigera*. Under laboratory and glasshouse conditions, female moths exposed to a particular host (tobacco or tomato) accepted that host for oviposition (in pre- and postalighting tests) more frequently than female moths experienced on other hosts, or moths with no experience.

If learning is common in polyphagous Lepidoptera, might this trait enable these insects to use a greater host range? Cunningham and West (2008) constructed a model to predict which environments might be most favorable to learning. Their results showed that the relative advantages of learning are maximized when within-generation variability is minimized (an ovipositing female is likely to encounter only a single host plant species) and between-generation variability is maximized (different host plant species are most common in different generations). These conditions are approached in many agro-ecosystems; ovipositing females frequently encounter abundant patches of a single host plant species, as a result of crop monoculture and through environmental factors (e.g., climate or soil quality), which favor the growth of certain crops in particular regions. In general, a particular crop species will be present for longer than the adult lifespan (e.g., Wardhaugh et al. 1980, Nyambo 1988, Sequeira 2001), whereas between insect generations, ovipositing females will frequently encounter different crop species through crop rotation and seasonal variations in agriculture or long-range movement of adult insects (migration). Similarly, the abundance of wild (noncrop) hosts of this insect are patchy in their distribution, forming large stands of particular species (Walter and Benfield 1994, Zalucki et al. 1994).

Learning may be of particular advantage to polyphagous lepidopteran species if neurological constraints (that is, the total amount of information on suitability of different oviposition sites that can be processed by the insect nervous system) limit the amount of information that can be processed for host plant suitability (Bernays 2001, Egan and Funk 2006, Cunningham 2012). We still know little about the precise way in which chemical information on host suitability is coded within the insect nervous system (Cunningham 2012), but generalists have been shown to sacrifice some information on host suitability as a result of increased host range (Janz and Nylin 1997, Janz 2003, Egan and Funk 2006). Such constraints may lead to a higher relative advantage of learning with increasing host range, or with hosts that span many plant taxa, as with heliothines such as *H. armigera*, *H. punctigera*, *H. zea*, and *He. virescens*.

If learning were advantageous to polyphagous insects, would we expect to find this trait widespread in the oviposition behavior of agricultural pests? Studies on oviposition in *Drosophila melanogaster* Meigen have shown that environments that favor learning, will select for "good learners" (increased effects of behavioral conditioning), providing evidence that learning is a trait under selection by the environment (Mery and Kawecki 2002). Learning has been shown in a number of polyphagous and oligophagous Lepidoptera, such as *Trichoplusia ni* (Hübner) (cabbage looper), *Plutella xylostella* (L.) (diamondback moth), and *Pieris brassicae* (L.) (cabbage white butterfly; Traynier 1984; Landolt and Molina 1996; Cunningham et al. 1998b, 1999; Landolt 2001; Monks and Kelly 2003; Liu et al. 2005; Skiri et al. 2005; Zhang et al. 2007). As yet, learning has not been studied in nonpest heliothines. The absence of learning has, however, been suggested in the oviposition behavior of three (nonpest) lepidopteran species—the checkerspot butterfly, *Euphydryas editha* (Boisduval) (Parmesan et al. 1995), the eastern black swallowtail *Papilio polyxenes* F. (Heinz and Feeny 2005), and *Heliconius* butterflies, *Heliconius erato* (L.) (Kerpel and Moreira 2005). Further evidence for the absence of learning may be lacking owing to difficulties in conclusively proving negative results and in publication biases against negative results (Jennions and Møller 2002).

Although there is no direct empirical field evidence of the influence of learning on oviposition behavior in *H. armigera*, studies indicate that oviposition preferences may be influenced by host abundance (see Pyke et al. 1987, Shanower and Romeis 1999). If learning in oviposition behavior is exhibited by *H. armigera* in the field, then more abundant hosts should receive proportionally more eggs than less abundant hosts, irrespective of "innate" relative preferences displayed in laboratory or glasshouse bioassays (Cunningham et al. 1998a). Recent large-scale landscape studies of *Helicoverpa* populations in Australia assessing the effect of surrounding fields on eggs in central focal fields suggest that such plants do receive more eggs for highly ranked hosts: Sorghum received more eggs the more Bt cotton there was around compared with sorghum

surrounded by sorghum. This was not the case for Bt cotton (N. Schellhorn, Unpublished data).

Other Physiological Determinants of Host-Plant Use by Adults. The physiological state of an insect can affect host-selection behavior. An insect's "motivation" to oviposit is controlled by internal factors that increasingly influence the expression of certain behaviors as time elapses since last oviposition (Barton-Browne 1993). Jallow and Zalucki (1998) demonstrated that the number of mature eggs produced by a mature *H. armigera* female influenced host-plant specificity and the propensity to oviposit. Female moths were less discriminating against cowpea (a low-ranked host) relative to maize (a high-ranked host) as egg load increased. Similarly, increased egg load led to a greater propensity to oviposit on both cowpea and maize. In the laboratory, *Helicoverpa* moths will oviposit on unsuitable surfaces such as glass, fabric, or plastic containers (and if left unmated will lay unfertilized eggs) even if collected directly from the field, which may reflect a capacity to void eggs under high egg loads, regardless of substrate suitability.

In the field, less preferred host species are likely to receive more eggs in the absence of preferred species as egg loads of females increase, as time elapses since eclosion, or both. Consequently, large-scale planting of a less attractive host variety might not necessary receive fewer eggs than a susceptible variety. Other factors that determine the actual use of a host by *H. armigera* in the field may include long-distance cues used in detecting host patches (Drake 1991), differential predation rates (Evans 1985), plant height (Firempong and Zalucki 1990b), presence of larval feeding damage or frass (Firempong and Zalucki 1991), and sources of nectar (Adjei-Mafo and Wilson 1983a,b).

Attraction to Host Odors. As with most phytophagous moth species, adult heliothines are strongly attracted to host plant odors. Laboratory experiments, predominantly using flight tunnels, have established that adult male and female moths show a characteristic upwind flight response (positive anaemotaxis) in the presence of host odors and their individual volatile constituents (Tingle and Mitchell 1992; Hartlieb 1996; Hull et al. 2004; Cunningham et al. 2006; Gregg et al. 2010a,b). De Moraes et al. (2001) demonstrated that complex odor blends, based on volatiles released by damaged tobacco plants, deterred ovipositing *He. virescens* females when compared with untreated control plants. Mozuraitis et al. (2002) have demonstrated attraction and oviposition preference of *He. virescens* for the sesquiterpene, germacrene-D. In *H. armigera*, females showed a positive oviposition response toward a blend containing 3-nitrobenzyl alcohol and minor amounts of 3-nitrobenzaldehyde, and a negative (deterrent) response to a blend containing 3-nitrobenzyl alcohol and small amounts of docosane and trimethyldecane (Srinivasan et al. 2006). A possible complication in many behavioral studies on heliothines is the separation of oviposition responses from nectar-feeding responses, particularly as male and female moths show similar responses to most compounds (Rajapakse et al. 2006, Del Socorro et al. 2010a).

Table 4. Electrophysiological response to plant volatiles in *H. armigera* adult females as demonstrated by electroantennogram (a,b,c,e) and olfactory receptor neuron (d,f) studies

Volatile compound	Reference			
Terpenoids				
α -pinene	a	b	c	e
β -pinene	a	e		
β -myrcene	a	b	d	e
dihydromyrcene	d			
β -ocimene	a	b	d	e
limonene	a	b	c	
linalool	a	b	d	f
α -farnesene	d			
(+)-3-carene	f			
verbenol	f			
borneol	f			
4,8-dimethyl-1,2-E-7-nonatriene	e			
β -caryophyllene	a	c		
1,8-cineol	a			
β -phellandrene	a			
Fatty acid-derived alcohols and esters				
<i>z</i> -3-hexen-1-ol	a			
<i>e</i> -2-hexen-1-ol	a			
<i>e</i> -3-hexen-1-ol	a			
1-hexanol	c			
hexan-3-ol	a			
hexan-1-ol	a			
hexan-2-ol	a			
<i>z</i> -3-hexenyl acetate	b	e		
<i>e</i> -2-hexenyl acetate	a			
butan-1-ol	a			
pentan-1-ol	a			
heptan-1-ol	a			
octan-1-ol	a			
<i>e</i> -2-hexenal	a			
<i>z</i> -3-hexenyl-2-methylbutyrate	b			
Aromatic alcohols, aldehydes, and esters				
benzaldehyde	a	c	e	
vinylbenzaldehyde	f			
phenylacetaldehyde	a	c		
2-phenylethanol	a			
vinyl-benzaldehyde	f			
2-phenylethanol	a			
benzyl alcohol	a			
methyl-benzoate	f			
methyl-salicylate	a			

References: a, Burguiere et al. (2001); b, Rajapakse et al. (2006); c, Cribb et al. (2007); d, Strandén et al. (2003); e, Yan et al. (2004); f, Rostelien et al. (2005).

Electrophysiological studies on *H. armigera* have identified plant volatiles that are detected by the insect's antennae (see Table 4). All of these volatiles are common to wide range of plants, terpenes and aromatic compounds in particular being ubiquitous floral volatiles (Pichersky and Gershenzon 2002, Dudareva et al. 2004). Predictable volatile indicators of a host plant species ("key volatiles") are therefore unlikely in this and other polyphagous species. Specialist heliothines might conceivably narrow their olfactory detection by the antenna, although a study by Strandén et al. (2003) comparing olfactory neuron responses to volatiles in *H. armigera* and *He. virescens* with the more specialist *H. assulta*, showed no decrease in the range of responses in *H. assulta* when compared with the two polyphagous species.

Recognition of host odors may instead require information pertaining to the unique blend of volatiles emitted by each plant species (Bruce et al. 2005).

Support for this blend recognition hypothesis has come from both behavioral and neurological studies. The insect antennal lobe (AL) receives incoming information from the antennae, and is widely recognized as the primary center for odor processing in insects. It is within this structure that combinations of volatiles detected by the antennae are represented as blend-specific excitation patterns (Joerges et al. 1997; Galizia and Menzel 2000; Vosshall et al. 2000; Carlsson et al. 2002, 2005; Lofaldi et al. 2010). Outgoing information (from the AL) to the higher centers of the insect brain is not simply a summation of the input effects (i.e., of independent volatile effects from the antennae), and host volatiles show synergistic effects when presented together, both in the AL, and in the resultant attraction of the insect in behavioral assays (Tasin et al. 2006, Piñero et al. 2008, Riffell et al. 2009).

Integrating this knowledge of odor processing into our understanding of host-selection behavior in polyphagous insects brings a crucial question to the fore: is the AL processing mechanism capable of recognizing multiple host plants, and if so, how is this achieved? Cunningham (2012) has suggested a theory for host selection and the evolution of host choice based on the workings of the olfactory mechanism, rather than solely on what we observe from host choice experiments. This theory has its basis in an earlier neural constraints theory (Janz and Nylin 1997, Bernays 2001), and predicts that owing to AL processing limitations, highly polyphagous insects may only be able to generally classify plants into categories such as good, poor, and nonhosts. Under this AL processing theory, preference hierarchies seen in behavioral experiments need not necessarily correlate with offspring fitness and nonhost species may be “mistakenly” accepted as hosts (as seen in heliothines), while still making evolutionary sense. Furthermore, the theory predicts that the complex circuitry of the AL might restrict polyphagous insect’s adaptation toward (or away from) individual host species. This may help explain the lack of any evidence for evolutionary change in host preference in *H. armigera* against transgenic Bt cotton, even though this nonhost variety now dominates the environment in Australian cotton-growing regions (Zalucki et al. 2012).

Could key volatiles still play a role in host selection in polyphagous insects? Theoretically, this would be expected if they acted as predictable signals for host quality. Evidence in support of this has been elegantly demonstrated in a recent study on *D. melanogaster* (Stensmyr et al. 2012), where the presence of a volatile (geosmin) in an odor blend, overrides any attraction to host odors. Geosmin is produced by molds, fungi, and bacteria, and the presence of these microorganisms makes fruit unsuitable for *Drosophila* oviposition; thus, the volatile is a good predictor of poor host quality across all host fruit species. Antennal lobe studies have shown that, unlike many plant volatiles, geosmin forms a functionally segregated pathway to the higher centers of the insect brain in *D. melanogaster*, offering further support that the volatile has a

specific (deterrent) role in determining host choice (Stensmyr et al. 2012).

Attraction to Visual Cues. Heliothine moth species show strong preferences for flowering hosts for both nectar feeding and oviposition, and yet the role of visual cues in host attraction has received little attention. Visual cues have been shown to be important in instigating nectar foraging behavior in *Manduca sexta* (L.) (Raguso and Willis 2005), with moths failing to respond to either odor sources or visual cues when provided in isolation. Moreover, decoupling of these two sensory cues revealed that the stimulation with odors before foraging enhanced responsiveness to odorless visual cues, and that moths were more responsive when both cues emanated from a single source (Goyret et al. 2007). Interaction between visual and olfactory cues may be important in evoking oviposition responses and thus should be borne in mind when assessing responses to olfactory cues in isolation.

Application of Host Plant Studies for Management of Pest Heliothines

Large-scale insecticide resistance in *H. armigera* has led to a number of crop protection strategies that rely on our knowledge of the host-selection process. Such management strategies presently in use or under investigation include behavioral manipulation methods e.g., use of trap crops and synthetic analogues of natural stimuli (Foster and Harris 1997; Gregg et al. 1998, 2010a,b; Agelopoulos et al. 1999; Del Socorro et al. 2010a,b), cultural control and conventional host plant resistance (Fitt 2000).

Intra-Specific Variation in Relation to Use of Trap Crops. Trap crops are host plant species grown in small patches to divert pests away from a major crop where they can be destroyed (Cook et al. 2007). Trap cropping relies on insects displaying relative preferences for oviposition; and assumes that most females in the pest population will rank the trap crop higher than the crop being protected. Chickpeas, maize, and sorghum have been suggested as possible trap crop options for *H. armigera* (Murray and Titmarsh 1990).

To date, trap cropping has not been successfully shown to reduce *H. armigera* infestations in the field (but see Grundy et al. 2006), and a number of factors may be responsible: 1) ovipositing females may not remain within the trap crop for long enough, may not lay enough of their eggs within these patches to significantly affect egg distribution in field crops, or both; 2) flowering and fruiting stages of the trap crop (the most attractive stage to ovipositing moths) may fail to coincide with (or continue for the duration of) susceptible stages of the main crop; 3) learning effects (experience) are known to evoke positive pre- and postlighting discrimination behavior in *H. armigera* (Cunningham et al. 1998a). As insects are likely to experience the most abundant host (the crop) before reaching the trap crop, learning effects may reduce the relative attractiveness of the trap crop species (Cunningham et al. 1999).

Behavioral Manipulation With Host Plant Volatiles. The use of insect pheromones for controlling some insect pests has been successful (Witzgall et al. 2010), but pheromone technologies may not necessarily translate to similar strategies using plant volatiles. The success of these olfaction-based control measures depends on the strength of the insect response to (or away from) the odor used relative to other odors that have a similar function within the environment. Plant odors and insect pheromones are both blends of volatiles, but the context in which they appear within the environment differs significantly: whereas pheromones are highly specific blends of volatiles released from a point source (the insect), plant odors are variable blends of volatiles (Effmert et al. 2005, Dudareva et al. 2006) released in relatively large quantities and often over a wide area (especially in the cropping environment). Additionally, attraction to plant volatiles may vary as a result of the insects' physiological state (Jallow and Zalucki 1998), or previous experience (Cunningham et al. 1999).

Current or tentative pest management strategies using the use of plant odors include—1) “Lure and kill” technologies to attract females to poisonous baits away from valuable crops, thus reducing the number of reproductive females (Agelopoulos et al. 1999, Del Socorro et al. 2010b); 2) Using odors to repel or deter females from finding or using resources (Foster and Harris 1997, Gregg et al. 1998); 3) Combined “Push-pull” strategies that modify the pattern of egg laying using a combination of deterrents and attractant odors or plants (Pyke et al. 1987, Agelopoulos et al. 1999, Cook et al. 2007); 4) developing cultivars that have reduced attractiveness to ovipositing females (Pickett et al. 1997, McCallum et al. 2012); and 5) monitor and forecasting populations (Witzgall et al. 2010).

Use of Resistant Plant Genotypes. The successful development of insect-resistant cultivars depends heavily on the nature of host-selection behavior in the pest insect, and whether (and how quickly) it will adapt to using these new plants (Kennedy et al. 1987). In the management of *H. armigera* in cotton, resistant plant genotypes such as okra leaf, glabrous, and frego bract rely heavily on behavioral nonpreference for oviposition (e.g., Jallow et al. 1999). Resistance to such varieties may be quickly acquired if they are widely cultivated and alternative susceptible hosts are not available. Increased egg load (Jallow and Zalucki 1998) may cause female moths to become less discriminating, and learning effects (Cunningham et al. 1999) could increase the apparent preference toward more “resistant” genotypes. Resistance will be less likely if the “nonpreferred” genotype is widely cultivated within a region and carries both antixenosis and antibiosis resistant factors (e.g., transgenic Bt cotton; Fitt and Wilson 2000). How rapidly any adaptation takes place will depend on many factors, including the availability of alternative host crops, the proportion of the resistant variety planted in the agro-ecosystem, the resistance management strategies put in place for the transgenic plant, the prevalence and effective gene flow among *Helicoverpa* “populations” (Zalucki

et al. 2012), and the degree of adaptability of the insect sensory system (Cunningham 2012).

Current resistance management strategies that hope to protect the longevity of crops that express Bt toxins at high levels for target pests are based on simple population genetic models (e.g., Tabashnik 1994) and more complex models (e.g., Jongsma et al. 2010). These models predict that “refuges,” effectively analogous to trap crops and therefore sources of homozygous Bt susceptible moths, would substantially decrease the rate at which populations evolve physiological resistance to these transgenic crops. The prediction is based on relative differences in population densities from different sources, a sink crop expressing toxin at a high enough level to kill any individuals that are heterozygous for resistance genes, extensive movement of moths in the landscape with random mating resulting in very few crosses between rare homozygous resistant individuals, should these arise from Bt-crops. However, these models do not directly incorporate information on oviposition behavior and host preferences of the target insects; rather, they assume that adults do not shift their oviposition behavior in response to the introduction of Bt-crops into the landscape, and oviposit randomly with respect to the target crop, or maintain their previous preferences. When shifting host preferences are incorporated into a model (see Jongsma et al. 2010), the resulting prediction is a preference shift in favor of alternative hosts. If moths were to avoid laying eggs on sink crops, then physiological resistance should be slower to evolve, as a smaller fraction of the population will be subject to selection (Jongsma et al. 2010).

The strategy of growing nontransgenic (susceptible) crops alongside transgenic varieties has been widely used in the management of resistance toward novel toxic genes in cotton (Zalucki et al. 2012). In Australia, the most commonly used refuge crop is pigeon pea, one of the key *H. armigera* hosts (Table 3). The effectiveness of this strategy rests on the assumption that individuals (possible resistant and susceptible ones) in an area overlap phenologically, move around, effectively mix, and mate at random (Dillon et al. 1998). Although effective population size in *Helicoverpa* is most likely larger than an individual crop field (Rochester et al. 2002), the propensity of females to prefer the more abundant host through learning effects (Cunningham et al. 1999) may lead to non-random distribution with respect to natal hosts. The selection effects on behavior of a “host” that is now a sink at a landscape scale have not been fully investigated (see below in Evolutionary Change in Host Utilization).

Evolutionary Change in Host Utilization. Heritable individual variation in host plant oviposition preference provides the basis for host range expansion, “host shift” (Tabashnik et al. 1981), and host races formation (Jaenike 1981). Host races have obvious implications: different moth populations will have different host preferences. Failure to recognize distinct populations can reduce the effectiveness of management strategies (Via 1990).

Both genetic and nongenetic variation (learning, physiological state, or both) contribute to variation in host preference within Australian *H. armigera* populations (see Host Plant Preferences). This variability suggests there is the potential for evolutionary change in host utilization in *H. armigera*, i.e., host range expansion and host shift leading to race formation. Several factors preclude or at least make difficult the likelihood of host-specific individuals or race formation in this moth species. First, there is behavioral variation for host plant selection among individual female moths in host plant preference for oviposition. This in addition to the wide host range of individual females and larvae permits populations to exploit potential host plants in both optimal and less optimal environments. Furthermore, irrespective of the order of plant preference ranking, all individual females within a population will accept all host plant species at some stage (Jallow and Zalucki 1995, 1996; Gu and Walter 1999). The combined consequences of these factors are that similar selective pressures will be acting more or less on all individuals. In insects purported to be showing host race formation (Singer et al. 1988), 1) host plant usage differs among allopatric populations and 2) there is a significant genetic divergence between sympatric populations using different host plant species. Neither of these factors appear to apply to *H. armigera* in Australia at least (Jallow et al. 2004).

The inherent variability and unpredictability of the host system being exploited may preclude long-term association between *H. armigera* and its host plants in one area. Most hosts, whether cultivated or uncultivated, support only one generation (Wardhaugh et al. 1980, Fitt 1989). This short-term association between *H. armigera* and its host plants in combination with the long-range migration in this genus (Gregg et al. 1995) and lack of genetic variation between populations (Daly and Gregg 1985, Endersby et al. 2007) reduces the possibility of non interbreeding sympatric or allopatric populations, thus minimizing the probability of host race formation.

We cannot exclude the potential for genetically based evolutionary change in host utilization in *H. armigera*. It is generally argued that the evolution of more specialist oviposition behavior would be faster in species that are host generalists, and potentially flip-flop between the two extremes (Janz and Nylin 2008), if host selection is labile and populations become fragmented. A population faced with an abundant novel plant may contain individual female moths that are genetically preadapted to recognize stimuli from this plant, thus initiating oviposition. The recent introduction of *H. armigera* into South America into a new host plant environment would be an opportunity to examine evolutionary change in host use. Although the species is using known economically important hosts (cotton, soybean, maize, tomatoes), eggs and larvae have been recorded from a number of novel hosts, including a new Family record, *Caryocar brasiliense* (Caryocaraceae), as well as new genera and species in existing families e.g., *Brachiaria ruziziensis* (Poaceae) and *Chamaesyce* sp. (Euphorbiaceae) (C. Czapak,

personal communication). Female moths are unlikely to develop an exclusive preference for the novel plant and lose the response to previously accepted plants, but rather will expand their host range and acquire greater polyphagy. There are few, well-documented cases of host-specific individuals or race formation in polyphagous insect species (see Pashley et al. 1987). The examples of rapid host shift that have been examined in more detail in a polyphagous heliothine species (*He. virescens*) show that the genetic potential to feed on the new plant already existed in the population before the host shift event (Schneider and Roush 1986).

The widespread replacement of conventional cotton with plants genetically modified (GM) to express various Bt toxins has effectively turned one major crop into a "sink" across whole landscapes where cotton is grown. Currently Bt cotton comprises nearly 90% of all cotton crops in Australia (Zalucki et al. 2009), as it does in other parts of the world (Wu et al. 2008). This landscape-level change began in the late 1990s, with the introduction of one-gene cotton transformations (INGARD), followed by two-gene Bollgard II in 2004. At a landscape level, cotton has effectively become a sink crop, as virtually no offspring survive from eggs laid in the crop (Rochester et al. 2002). A priori we might expect that there would be strong selection pressure on host plant preference with females that do not lay on cotton favored. Zalucki et al. (2012) assessed oviposition by female *H. armigera* collected from two cotton-growing regions when given a choice of tobacco, cotton, and cabbage. Earlier work in the 1980s and 1990s on populations from the same geographic locations indicated these hosts were on average ranked as high, mid, and low preference plants respectively. There was no change in the relative ranking of hosts by females, with most eggs being laid on tobacco, then cotton and least on cabbage as before.

Nevertheless there appear to be differences in host plant usage across the geographic range of *H. armigera* as well as similarities (Table 3), e.g., pigeon-pea appears to attract high numbers of eggs in all regions (Rajapakse et al. 2006), and differences, with cotton and Okra favored for oviposition in Japan (Jallow et al. 2001, Kakimoto et al. 2003), whereas in Australia cotton is not generally ranked high in choice assays (Zalucki et al. 2012). Sorghum in western China was virtually ignored as a host in field experiments (Lu et al. 2013) but is highly ranked by moths in Australia (Firempong and Zalucki 1990b) and elsewhere, e.g., Africa (Topper 1987). This may reflect opportunity, environmental effects on oviposition or differences in oviposition preferences representing "localized" adaptations (Jallow et al. 2004).

Until comparative studies of host selection and utilization of this polyphagous pest from across its range are undertaken under standard conditions, using a combination of laboratory and common garden experiments, any number of interpretations are possible. The problem we have highlighted above is that to date no one has been able to disentangle innate preference versus environmental (host plant experience) effects

in host plant use in this insect. This is an important question. Put simply, if host relations are in fact the “same” throughout the species range then “one size fits all” in terms of managing resistance to GM crops, for example. If in fact host relations (oviposition, larval utilization, or both) are labile then management will need to be specific to the “local” area. In addition, understanding the basis for these polyphagous insects being able to feed on such a wide range of hosts will enable improved management options, from the development of host plant resistance to managing resistance to insecticides. The biochemistry that enables these insects to handle host toxins is likely related to their ability to develop resistance to insecticides (Heckel et al. 1998, Celorio-Mancera et al. 2012).

What is a Heliothine Host? Future Research Needs

We have highlighted the difficulties of defining a host in terms of empirical work on larval survival and adult choice, and its role as a host in nature, due in part to plant variability (variety, phenology, location and so forth) and the insect variability (physiology, experience, genetic variation). Understanding the genetic and nongenetic determinants of *H. armigera*, and indeed other polyphagous pest heliothine, host use must be founded on comprehensive theoretical and empirical studies. Empirical work must move from initial laboratory tests using insect cultures to testing of multiple field-sourced populations from across the species range.

To date the field-work on host plant use in heliothines has tended to be piecemeal and geographically localized. No studies truly test host selection by adults and control for availability and host plant variety. Common garden experiments across the species range are required. These need to account for what is available in the local landscape. Such studies would require a coordinated and collaborative international effort. In addition, a comparison of host choice in controlled conditions using populations sampled from across the species range would be ideal, again using a common plant set, combined with odor responses prelighting and postalighting, as well as larval host use, preferably on intact plants. Such work could isolate differences between females in host responses if designed appropriately and potentially identify the genetic basis of both host selection and utilization by larvae. Potential new methods of behavioral control, which develop from these studies, should then be assessed for their interaction with existing integrated control strategies (e.g., natural enemy release) and considered for implementation on an area wide basis. Perhaps the ongoing threat *H. armigera* poses in the Old world and the imminent problems throughout the New may well provide the impetus for such work.

Acknowledgments

This work was in part supported by Australian Research Council discovery grant DP0988150. We thank Professor Liu Shu-sheng for translating the Chinese host records for *H. armigera*. We thank Peter Gregg (University of New Eng-

land), Gurion Ang (University of Queensland), and Tom Walsh (Commonwealth Scientific and Industrial Research Organization) for comments on the manuscript.

References Cited

- Adjei-Maafa, I. K., and L. T. Wilson. 1983a. Factors affecting the relative abundance of arthropods on nectaried and nectariless cotton. *Environ. Entomol.* 12: 349–352.
- Adjei-Maafa, I. K., and L. T. Wilson. 1983b. Association of cotton nectar production with *Helicoverpa punctigera* (Lepidoptera: Noctuidae) oviposition. *Environ. Entomol.* 12: 1166–1170.
- Agelopoulos, N. G., M. A. Birkett, A. J. Hick, A. M. Hopper, J. A. Pickett, E. M. Pow, L. E. Smart, D. W. M. Smiley, L. J. Wadhams, and C. M. Woodcock. 1999. Exploiting semiochemicals in insect control. *Pestic. Sci.* 55: 235–255.
- Ahn, S.-J., F. R. Badenes-Pérez, and D. G. Heckel. 2011a. A host-plant specialist, *Helicoverpa assulta*, is more tolerant to capsaicin from *Capsicum annuum* than other noctuid species. *J. Insect Physiol.* 57: 1212–1219.
- Ahn, S.-J., F. R. Badenes-Pérez, M. Reichelt, A. Svatos, B. Schneider, J. Gershenson, and D. G. Heckel. 2011b. Metabolic detoxification of capsaicin by UDP-glycosyltransferase in three *Helicoverpa* species. *Arch. Insect Biochem. Physiol.* 78: 104–118.
- Bai, L.-X., H.-W. Sun, Y.-W. Sun, and C.-E. Su. 1997. The host plant of the cotton bollworm, *Helicoverpa armigera* (Hübner) and their fitness. *Acta Phytophyacica Sin.* 24: 1–6.
- Ballabeni, P., M. Włodarczyk, and M. Rahier. 2001. Does enemy free space for eggs contribute to a leaf beetle's oviposition preference for a nutritionally inferior host plant? *Funct. Ecol.* 15: 318–324.
- Barton-Browne, L. 1993. Physiologically induced changes in resource-oriented behavior. *Annu. Rev. Entomol.* 38: 1–25.
- Behere, G. T., W. T. Tay, D. A. Russell, K. R. Kranthi, and P. Batterham. 2013. Population genetic structure of the cotton bollworm *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) in India as inferred from EPIC-PCR DNA markers. *PLoS ONE* 8: e53448. (doi:10.1371/journal.pone.0053448).
- Benda, N. D., C. Brownie, C. Schal, and F. Gould. 2011. Field observations of oviposition by a specialist herbivore on plant parts and plant species unsuitable as larval food. *Environ. Entomol.* 40: 1478–1486.
- Bergvinson, D. J. 2005. *Heliothis/Helicoverpa* problem in the Americas: Biology and Management, pp. 7–37. In H. C. Sharma (ed.), *Heliothis/Helicoverpa* management: emerging trends and strategies for future research. Oxford and IBH Publishing, New Delhi, India.
- Bernays, E. A. 2001. Neural limitations in phytophagous insects: Implications for diet breadth and evolution of host affiliation. *Annu. Rev. Entomol.* 46: 703–727.
- Bjorkman, C., and S. Larsson. 1991. Pine sawfly defense and variation in host plant resin acids – a trade-off with growth. *Ecol. Entomol.* 16: 283–289.
- Blanco, C. A., A. P. Terán-Vargas, J. D. López Jr., J. V. Kauffman, and X.-K. Wei. 2007. Densities of *Heliothis virescens* and *Helicoverpa zea* (Lepidoptera: Noctuidae) in three plant hosts. *Fla. Entomol.* 90: 742–750.
- Bruce, T. J., L. J. Wadhams, and C. M. Woodcock. 2005. Insect host location: a volatile situation. *Trend Plant Sci.* 10: 269–274.
- Bués, R., J. C. Bouvier, and L. Boudinhon. 2005. Insecticide resistance and mechanisms of resistance to selected

- strains of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in the south of France. *Crop Prot.* 24: 814–820.
- Burguiere, L., F. Marion-Poll, and A. Cork. 2001. Electrophysiological responses of female *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) to synthetic host odors. *J. Insect Physiol.* 47: 509–514.
- Carlsson, M. A., C. G. Galizia, and B. S. Hansson. 2002. Spatial representation of odors in the antennal lobe of the moth *Spodoptera littoralis* (Lepidoptera: Noctuidae). *Chem. Senses* 27: 231–244.
- Carlsson, M. A., P. Knusel, P. Verschure, and B. S. Hansson. 2005. Spatio-temporal Ca²⁺ dynamics of moth olfactory projection neurones. *Eur. J. Neurosci.* 22: 647–657.
- Celorio-Mancera, Mde L., S.-J. Ahn, H. Vogel, and D. G. Heckel. 2011a. Transcriptional responses underlying the hormetic and detrimental effects of the plant secondary metabolite gossypol on the generalist herbivore *Helicoverpa armigera*. *BMC Genomics* 12: 575.
- Celorio-Mancera, Mde L., J. Courtiade, A. Muck, D. G. Heckel, R. O. Musser, and H. Vogel. 2011b. Sialome of a generalist lepidopteran herbivore: Identification of transcripts and proteins from *Helicoverpa armigera* labial salivary glands. *PLoS ONE* 6: e26676.
- Celorio-Mancera, Mde L., D. G. Heckel, and H. Vogel. 2012. Transcriptional analysis of physiological pathways in a generalist herbivore: responses to different host plants and plant structures by the cotton bollworm, *Helicoverpa armigera*. *Entomol. Exp. Appl.* 144: 123–133.
- Cho, S., A. Mitchell, C. Mitter, J. Regier, M. Matthews, and R. Robertson. 2008. Molecular phylogenetics of heliothine moths (Lepidoptera: Noctuidae: Heliothinae), with comments on the evolution of host range and pest status. *Syst. Entomol.* 33: 581–594.
- Coaker, T. M. 1959. Investigations on *Heliothis armiger* (Hb.) in Uganda. *Bull. Entomol. Res.* 50: 487–505.
- Cook, S. M., Z. R. Khan, and J. A. Pickett. 2007. The use of push-pull strategies in integrated pest management. *Annu. Rev. Entomol.* 52: 375–400.
- Cotter, S. C., and O. R. Edwards. 2006. Quantitative genetics of preference and performance on chickpeas in the noctuid moth, *Helicoverpa armigera*. *Heredity* 96: 396–402.
- Courtiade, J., Y. Pauchet, H. Vogel, and D. G. Heckel. 2011. A comprehensive characterization of the caspase gene family in insects from the order Lepidoptera. *BMC Genomics* 12: 357.
- Cribb, B. W., C. D. Hull, C. J. Moore, J. P. Cunningham, and M. P. Zalucki. 2007. Variability in odor reception in the peripheral sensory system of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Aust. J. Entomol.* 46: 1–6.
- Cunningham, J. P. 2012. Can mechanism help explain insect host choice? *J. Evol. Biol.* 25: 244–251. (doi: <http://dx.doi.org/10.1111/j.1420-9101.2011.02435.x>).
- Cunningham, J. P., and S. A. West. 2008. How host plant variability influences the advantages to learning: A theoretical model for oviposition behavior in Lepidoptera. *J. Theor. Biol.* 251: 404–410.
- Cunningham, J. P., M.F.A. Jallow, D. J. Wright, and M. P. Zalucki. 1998a. Learning in host selection in *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Anim. Behav.* 55: 227–234.
- Cunningham, J. P., S. A. West, and D. J. Wright. 1998b. Learning in the nectar foraging behavior of *Helicoverpa armigera*. *Ecol. Entomol.* 23: 363–369.
- Cunningham, J. P., M. P. Zalucki, and S. A. West. 1999. Learning in *Helicoverpa armigera* (Lepidoptera: Noctuidae): a new look at the behavior and control of a polyphagous pest. *Bull. Entomol. Res.* 89: 201–207.
- Cunningham, J. P., S. A. West, and M. P. Zalucki. 2001. Host selection in phytophagous insects: a new explanation for learning in adults. *Oikos* 95: 537–543.
- Cunningham, J. P., C. J. Moore, M. P. Zalucki, and B. W. Cribb. 2006. Insect odor perception: Recognition of odor components by flower foraging moths. *Proc. R. Soc. Lond. Biol. Sci.* 273: 2035–2040.
- Cunningham, J. P., C. Lange, G. Walter, and M. P. Zalucki. 2011. Host selection behavior in desert caterpillars. *Entomol. Exp. Appl.* 141: 1–7.
- Czepak, C., K. C. Albernaz, L. M. Vivan, H. O. Guimarães, and T. Carvalhais. 2013. First reported occurrence of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) in Brazil. *Pesq. Agropec. Trop. Goiânia.* 43: 110–113.
- Daly, J. C., and P. C. Gregg. 1985. Genetic variation in *Heliothis* in Australia: species identification and gene flow in two pest species *H. armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera: Noctuidae). *Bull. Entomol. Res.* 75: 169–184.
- De Moraes, C. M., M. C. Mescher, and J. H. Tumlinson. 2001. Caterpillar-induced nocturnal plant volatiles repel non-specific females. *Nature* 410: 577–580.
- Del Socorro, A. P., P. C. Gregg, D. Alter, and C. J. Moore. 2010a. Development of a synthetic plant volatile-based attracticide for female noctuid moths. I. Potential sources of volatiles attractive to *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Aust. J. Entomol.* 49: 10–20.
- Del Socorro, A. P., P. C. Gregg, and A. J. Hawes. 2010b. Development of a synthetic plant volatile-based attracticide for female noctuid moths. III. Insecticides for adult *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Aust. J. Entomol.* 49: 31–39.
- Dhandapani, N., and M. Balasubramanian. 1980. Effect of different food plants on the development and reproduction of *Heliothis armigera* (Hbn). *Experientia* 36: 930–931.
- Dillon, M. L., G. P. Fitt, and M. P. Zalucki. 1998. How should refugia be placed upon the landscape? A modeling study considering pest movement and behavior, pp. 179–189. *In* M. P. Zalucki, R.A.I. Drew, and G. G. White (eds.), *Pest management – Future Challenges*. UQ Press, Brisbane, Australia.
- Drake, V. A. 1991. Methods for studying adult movement in *Helicoverpa*, pp. 109–121. *In* M. P. Zalucki (ed.), *Research techniques for the study of Heliothis: problems and prospects*. Springer Experimental Entomology Series, Springer, New York, NY.
- Dudareva, N., E. Pichersky, and J. Gershenzon. 2004. Biochemistry of plant volatiles. *Plant Physiol.* 135: 1893–1902.
- Dudareva, N., F. Negre, D. A. Nagegowda, and I. Orlova. 2006. Plant volatiles: recent advances and future perspectives. *Crit. Rev. Plant Sci.* 25: 417–440.
- Effmert, U., J. Grosse, U.S.R. Rose, F. Ehrig, R. Kagi, and B. Piechulla. 2005. Volatile composition, emission pattern, and localization of floral scent emission in *Mirabilis jalapa* (Nyctaginaceae). *Am. J. Bot.* 92: 2–12.
- Egan, S. P., and D. J. Funk. 2006. Individual advantages to ecological specialization: insights on cognitive constraints from three conspecific taxa. *Proc. R. Soc. Lond. Biol. Sci.* 273: 843–848.
- Endersby, N. M., A. A. Hoffmann, S. W. McKechnie, and A. R. Weeks. 2007. Is there genetic structure in populations of *Helicoverpa armigera* from Australia? *Entomol. Exp. Appl.* 122: 253–263.
- Evans, D. E. 1964. Status of American Bollworm on cotton at Stennar, Sudan. *Emp. Cotton Growing Rev.* 41: 202–209.
- Evans, M. L. 1985. Arthropod species in soybeans in South east Queensland. *J. Aust. Entomol. Soc.* 24: 169–177.

- Fatma, Z., and P. H. Pathak. 2011. Food plants of *Helicoverpa armigera* (Hübner) and extent of parasitism by its parasitoids *Trichogramma Chilonis* Ishii and *Campoletis chloridae* Uchida- a field study. *Int. J. Entomol.* 2: 31–39.
- Firempong, S. 1987. Some factors affecting host plant selection by *Heliothis armigera* (Hübner) (Lepidoptera: Noctuidae). Ph.D thesis, University of Queensland, Brisbane, Australia.
- Firempong, S., and M. P. Zalucki. 1990a. Host plant preferences of populations of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) from different geographic locations. *Aust. J. Zool.* 37: 665–673.
- Firempong, S., and M. P. Zalucki. 1990b. Host plant selection by *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae): role of certain plant attributes. *Aust. J. Zool.* 37: 675–683.
- Firempong, S., and M. P. Zalucki. 1991. Host plant selection by *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae): the role of some herbivore attributes. *Aust. J. Zool.* 39: 343–350.
- Fitt, G. P. 1989. The ecology of *Heliothis* species in relation to agroecosystems. *Annu. Rev. Entomol.* 34: 17–52.
- Fitt, G. P. 2000. An Australian approach to IPM in Cotton: integrating new technologies to minimise insecticide dependence. *Crop Prot.* 19: 793–800.
- Fitt, G. P., and L. J. Wilson. 2000. Genetic Engineering in IPM: Case study—Bt plants, pp108–125. In G. G. Kennedy and T. B. Sutton (eds.), *Emerging technologies in integrated pest management: Concepts, research and implementation*. APS Press. St. Paul, MN.
- Foster, S. P., and M. O. Harris. 1997. Behavioral manipulation methods for insect pest-management. *Annu. Rev. Entomol.* 42: 123–146.
- Gahan, L. J., F. Gould, and D. G. Heckel. 2001. Identification of a gene associated with Bt resistance in *Heliothis virescens*. *Science* 293: 857–860.
- Gahan, L. J., Y. Pauchet, H. Vogel, and D. G. Heckel. 2010. An ABC transporter mutation is correlated with insect resistance to *Bacillus thuringiensis* Cry1Ac Toxin. *PLoS Genetics* 6: e1001248.
- Galizia, C. G., and R. Menzel. 2000. Probing the olfactory code. *Nat. Neurosci.* 3: 853–854.
- Gamberale-Stille, G., L. Söderlind, N. Janz, and S. Nylin. 2013. Host plant choice in the comma butterfly—larval choosiness may ameliorate effects of indiscriminate oviposition. *Ins. Sci.* (doi: <http://dx.doi.org/10.1111/1744-7917.12059>).
- Goyret, J., P. M. Markwell, and R. A. Raguso. 2007. The effect of decoupling olfactory and visual stimuli on the foraging behavior of *Manduca sexta*. *J. Exp. Biol.* 210: 1398–1405.
- Gregg, P. C. 1993. Pollen as a marker for migration of *Helicoverpa armigera* and *H. punctigera* (Lepidoptera: Noctuidae) from western Queensland. *Aust. J. Ecol.* 18: 209–219.
- Gregg, P. C., G. P. Fitt, M. P. Zalucki, and D.A.H. Murray. 1995. Insect migration in an arid continent: II. *Helicoverpa* spp. in eastern Australia, pp. 151–172. In V. D. Drake, and A. G. Gatehouse (eds.), *Insect migration: tracking resources through space and time*. Cambridge University Press, Cambridge, United Kingdom.
- Gregg, P. C., A. P. Del Socorro, G. S. Henderson, N. W. Forrester, and C. J. Moore. 1998. Plant-based attractants for adult *Helicoverpa* spp, pp. 341–347. In M. P. Zalucki, R.A.I. Drew, and G. G. White (eds.), *Pest management—future challenges*. University of Qld Press, Brisbane, Australia.
- Gregg, P. C., K. A. Grieve, A. P. Del Socorro, and A. J. Hawes. 2010a. Research to realisation: the challenging path for novel pest management products in Australia. *Aust. J. Entomol.* 49: 1–9.
- Gregg, P. C., A. P. Del Socorro, and G. S. Henderson. 2010b. Development of a synthetic plant volatile-based attracticide for female noctuid moths. II. Bioassays of synthetic plant volatiles as attractants for the adults of the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Aust. J. Entomol.* 49: 21–30.
- Gripenberg, S., P. J. Mayhew, M. Parnell, and T. Roslin. 2010. A meta-analysis of preference-performance relationships in phytophagous insects. *Ecol. Lett.* 13: 383–393. (doi: [10.1111/j.1461-0248.2009.01433.x](https://doi.org/10.1111/j.1461-0248.2009.01433.x)).
- Grundy, P., S. Short, A. Hawes, M. P. Zalucki, and P. C. Gregg. 2006. Moth busting for Bt resistance management. 13th Australian Cotton Conference, Broadbeach, 7–11 August. Australian Cotton Growers Research Association Inc., Brisbane, Australia.
- Gu, H., and G. H. Walter. 1999. Is the common sowthistle (*Sonchus oleraceus*) a primary host plant of the cotton bollworm, *Helicoverpa armigera* (Lep., Noctuidae)? Oviposition and larval performance. *J. Appl. Entomol.* 123: 99–105.
- Gu, H., A. Cao, and G. H. Walter. 2001. Host selection and utilisation of *Sonchus oleraceus* (Asteraceae) by *Helicoverpa armigera* (Lepidoptera: Noctuidae): A genetic analysis. *Ann. Appl. Biol.* 138: 293–299.
- Hardwick, D. F. 1996. A monograph to the North American *Heliothinae* (Lepidoptera: Noctuidae). Center for Land and Biological Resources Research, Ottawa, Canada.
- Hartlieb, E. 1996. Olfactory conditioning in the moth *Heliothis virescens*. *Naturwissenschaften* 83: 87–88.
- Heckel, D. G. 1993. Comparative genetic linkage mapping in insects. *Annu. Rev. Entomol.* 38: 381–408.
- Heckel, D. G., L. J. Gahan, J. C. Daly, and S. Trowell. 1998. A genomic approach to understanding *Heliothis* and *Helicoverpa* resistance to chemical and biological insecticides. *Phil. Trans. R. Soc. Lond. B* 353: 1713–1722.
- Heinz, C. A., and P. Feeny. 2005. Effects of contact chemistry and host plant experience in the oviposition behavior of the eastern black swallowtail butterfly. *Anim. Behav.* 69: 107–115.
- Hmimina, M. 1988. Biotic potential of *Heliothis armigera* Hb. (Lepidoptera, Noctuidae): influence of host-plants and their distribution on the infestation of planted areas. *J. Appl. Entomol.* 106: 241–251.
- Hull, C. D., J. P. Cunningham, C. J. Moore, M. P. Zalucki, and B. W. Cribb. 2004. Discrepancy between antennal and behavioral responses for enantiomers of alpha-pinene: Electrophysiology and behavior of *Helicoverpa armigera* (Lepidoptera). *J. Chem. Ecol.* 30: 2071–2084.
- Jaenike, J. 1981. Criteria for ascertaining the existence of host races. *Am. Nat.* 117: 830–834.
- Jaenike, J. 1990. Host specialization in phytophagous insects. *Annu. Rev. Ecol. Syst.* 21: 243–274.
- Jallow, M.F.A., and M. P. Zalucki. 1995. A technique for measuring intra-specific variation in oviposition preference of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *J. Aust. Entomol. Soc.* 34: 281–288.
- Jallow, M.F.A., and M. P. Zalucki. 1996. Within - and between-population variation in host-plant preference and specificity in Australian *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Aust. J. Zool.* 44: 503–519.
- Jallow, M.F.A., and M. P. Zalucki. 1998. Age-specific fecundity of *Helicoverpa armigera* (Hübner) (Lepidoptera:

- Noctuidae) and the effects of egg load on oviposition behavior. *Aust. J. Zool.* 46: 291–299.
- Jallow, M.F.A., and M. P. Zalucki. 2003. Relationship between oviposition preference and offspring performance in Australian *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Aust. J. Entomol.* 42: 343–348.
- Jallow, M.F.A., M. P. Zalucki, and G. P. Fitt. 1999. The role of chemical cues from cotton in mediating host selection and oviposition behavior in *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Aust. J. Entomol.* 38: 359–366.
- Jallow, M.F.A., M. Matsumura, and Y. Suzuki. 2001. Oviposition preference and reproductive performance of Japanese *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Appl. Entomol. Zool.* 36: 419–426.
- Jallow, M.F.A., J. P. Cunningham, and M. P. Zalucki. 2004. Intra-specific variation for host plant use in *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae): implications for management. *Crop Prot.* 23: 955–964.
- Janz, N. 2003. The cost of polyphagy: oviposition decision time vs error rate in a butterfly. *Oikos* 100: 493–496.
- Janz, N., and S. Nylin. 1997. The role of female search behavior in determining host plant range in plant feeding insects: A test of the information processing hypothesis. *Proc. R. Soc. Lond. Biol. Sci.* 264: 701–707.
- Janz, N., and S. Nylin. 2008. The oscillation hypothesis of host-plant range and speciation, pp. 203–215. In K. J. Tilmon (ed.), *Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects*. University of California Press, Berkeley, CA.
- Jennions, M. D., and A. P. Møller. 2002. Publication bias in ecology and evolution: an empirical assessment using the 'trim and fill' method. *Biol. Rev.* 77: 211–222.
- Jermey, T. 1984. Evolution of insect/host plant relationships. *Am. Nat.* 124: 609–630.
- Joerges, J., A. Kuttner, C. G. Galizia, and R. Menzel. 1997. Representations of odors and odor mixtures visualized in the honeybee brain. *Nature* 387: 285–288.
- Jongsma, M. A., F. Gould, M. Legros, L. M. Yang, J.J.A. van Loon, and M. Dicke. 2010. Insect oviposition behavior affects the evolution of adaptation to Bt crops: consequences for refuge policies. *Evol. Ecol.* 24: 1017–1030.
- Jousson, N., S. Agnolet, S. Lorenz, S. E. Schoene, R. Ellinger, B. Schneider, and D. G. Heckel. 2012. Resistance of Australian *Helicoverpa armigera* to fenvalerate is due to the chimeric P450 enzyme CYP337B3. *Proc. Nat. Acad. Sci. U.S.A.* 109: 15206–15211.
- Kakimoto, T., K. Fujisaki, and T. Miyatake. 2003. Egg laying preference, larval dispersion, and cannibalism in *Helicoverpa armigera* (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* 96: 793–798.
- Kennedy, G. G., F. Gould, O.M.B. DePonti, and R. E. Stinner. 1987. Ecological, agricultural, genetics, and commercial considerations in the development of insect-resistant germplasm. *Environ. Entomol.* 16: 327–338.
- Kerpel, S. M., and G.R.P. Moreira. 2005. Absence of learning and local specialization on host plant selection by *Heliconius erato*. *J. Insect Behav.* 18: 433–452.
- Kogan, M., C. G. Helm, J. Kogan, and E. Brewer. 1989. Distribution and economic importance of *Heliothis virescens* and *Heliothis zea* in North, Central and South America and of their natural enemies and host plants, pp. 241–298. In E. G. King and R. D. Jackson (eds.), *Proceedings of the Workshop on Biological Control of Heliothis: Increasing the Effectiveness of Natural Enemies*. Far Eastern Regional Research Services, Office of International Cooperation and Development, US Department of Agriculture, New Delhi, India.
- Knudson, E., C. Bordelon, and M. G. Pogue. 2003. A new species of *Schinia* Hübner (Lepidoptera: Noctuidae: Heliothinae). *Zootaxa* 382: 1–7.
- Kyi, A., M. P. Zalucki, and I. J. Titmarsh. 1991. An experimental study of early stage survival of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) on cotton. *Bull. Entomol. Res.* 81: 263–271.
- Landolt, P. J. 2001. Moth experience and not plant injury affected female cabbage looper moth (Lepidoptera: Noctuidae) orientation to potato plants. *Fla. Entomol.* 84: 243–249.
- Landolt, P. J., and O. Molina. 1996. Host-finding by cabbage looper moths (Lepidoptera: Noctuidae): Learning of host odor upon contact with host foliage. *J. Insect Behav.* 9: 899–908.
- Lofaldli, B. B., P. Kvello, and H. Mustaparta. 2010. Integration of the antennal lobe glomeruli and three projection neurons in the standard brain atlas of the moth *Heliothis virescens*. *Front. Syst. Neurosci.* 4: 5.
- Liu, G.-S. 1934. The economic food plants of cotton bollworm, *Heliothis obsoleta* Fab. *Insect Plant Pathol.* 2: 708–709.
- Liu, Z.-D., D.-M. Li, P.-Y. Gong, and K.-J. Wu. 2004. Life table studies of the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), on different host plants. *Environ. Entomol.* 33: 1570–1576.
- Liu, S.-S., Y.-H. Li, Y.-Q. Liu, and M. P. Zalucki. 2005. Experience induced preference for oviposition repellents derived from a non-host plant by a specialist herbivore. *Ecol. Lett.* 8: 722–729.
- Liu, Z., J. Scheirs, and D. G. Heckel. 2010. Host Plant Flowering Increases Both Adult Oviposition Preference and Larval Performance of a Generalist Herbivore. *Environ. Entomol.* 39: 552–560.
- Liu, Z., J. Scheirs, and D. G. Heckel. 2012. Trade-offs of host use between generalist and specialist *Helicoverpa* sibling species: adult oviposition and larval performance. *Oecologia* 168: 459–469.
- Lu, Z.-Z., M. P. Zalucki, L. Perkins, D.-Y. Wang, and L.-L. Wu. 2013. Towards a resistance management strategy for *Helicoverpa armigera* in Bt-cotton in northwestern China: potential refuge crops. *J. Pest Sci.* 86: 695–703.
- Manjunath, T. M., V. S. Bhatnagar, C. S. Pawar, and S. Sithanatham. 1989. Economic importance of *Heliothis* spp. in India and an assessment of their natural enemies and host plants, pp. 197–228. In E. G. King, and R. D. Jackson (eds.), *Proceedings of the Workshop on Biological Control of Heliothis: Increasing the Effectiveness of Natural Enemies*. New Delhi, India: Far Eastern Regional Research Services, US Department of Agriculture.
- Matthews, M. 1999. *Heliothine moths of Australia*. CSIRO Publishing, Collingwood, Victoria.
- Mayhew, P. J. 2001. Herbivore host choice and optimal bad motherhood. *Trends Ecol. Evol.* 16: 165–167.
- Mery, F., and T. J. Kawecki. 2002. Experimental evolution of learning ability in fruit flies. *Proc. Nat. Acad. Sci. U.S.A.* 99: 14274–14279.
- McCallum, E. J., J. P. Cunningham, J. Lucker, M. P. Zalucki, J. J. De Voss, and J. R. Botella. 2012. Increased plant volatile production affects oviposition, but not larval development in the moth *Helicoverpa armigera*. *J. Exp. Biol.* 214: 3672–3677. doi:10.1242/jeb.059923.
- Mitter, C., R. W. Poole, and M. Matthews. 1993. Biosystematics of the Heliothinae (Lepidoptera: Noctuidae). *Annu. Rev. Entomol.* 38: 207–225.
- Monks, A., and D. Kelly. 2003. Motivation models fail to explain oviposition behavior in the diamondback moth. *Physiol. Entomol.* 28: 199–208.

- Mozuraitis, R., M. Strandén, M. I. Ramírez, A. K. Borg-Karlson, and H. Mustaparta. 2002. (-)-Germacrene D increases attraction and oviposition by the tobacco budworm moth *Heliothis virescens*. *Chem. Senses* 27: 505–509.
- Murray, D.A.H., and I. J. Titmarsh. 1990. *Helicoverpa* dynamics on the Darling Downs, pp. 345–349. In D. Swallow (ed.), *Proceedings of the 5th Australian Cotton Conference*. ACGRA, Wee Waa, Australia.
- Nyambo, B. T. 1988. Significance of host-plant phenology in the dynamics and pest incidence of the cotton bollworm, heliothis armigera Hübner (Lepidoptera, Noctuidae), in Western Tanzania. *Crop Prot.* 7: 161–167.
- Oppenheim, S. J., and K. R. Hopper. 2009. Genetics of host range in Lepidoptera, pp. 195–217. In M. Goldsmith, and F. Marec (eds.), *Molecular biology and genetics of the lepidoptera*. CRC Press, Taylor & Francis Group, Boca Raton, FL.
- Papaj, D. R., and R. J. Prokopy. 1989. Ecological and evolutionary aspects of learning in phytophagous insects. *Annu. Rev. Entomol.* 34: 315–350.
- Parmesan, C., M. C. Singer, and I. Harris. 1995. Absence of adaptive learning from the oviposition foraging behavior of a checkerspot butterfly. *Anim. Behav.* 50: 161–175.
- Parsons, F. S. 1940. Investigations on the cotton bollworm, *Heliothis armigera*, Hübner. III. Relationships between oviposition and the flowering curves of food-plants. *Bull. Entomol. Res.* 31: 147–177.
- Pashley, D. P., S. S. Quisenberry, and T. Jamjanya. 1987. Impact of fall armyworm (Lepidoptera: Noctuidae) host strains on the evaluation of Bermuda grass resistance. *J. Econ. Entomol.* 80: 1126–1130.
- Pauchet, Y., A. Muck, A. Svatos, D. G. Heckel, and S. Preiss. 2008. Mapping the larval midgut proteome of *Helicoverpa armigera*, a generalist herbivorous insect. *J. Proteome Res.* 7: 1629–1639.
- Perkins, L. E., B. W. Cribb, P. B. Brewer, J. Hanan, M. Grant, M. de Torres, and M. P. Zalucki. 2013. Generalist insects behave in a jasmonate dependent manner on their host plants, leaving induced areas quickly and staying longer on distant parts. *Proc. R. Soc. B* 280: 20122646. (<http://dx.doi.org/10.1098/rspb.2012.2646>).
- Pichersky, E., and J. Gershenzon. 2002. The formation and function of plant volatiles: perfumes for pollinator attraction and defense. *Curr. Opin. Plant Biol.* 5: 237–243.
- Pickett, J. A., L. J. Wadhams, and C. M. Woodcock. 1997. Developing sustainable pest control from chemical ecology. *Agric. Ecosyst. Environ.* 64: 149–156.
- Piñero, J. C., C. G. Galizia, and S. Dorn. 2008. Synergistic behavioral responses of female oriental fruit moths (Lepidoptera: Tortricidae) to synthetic host plant-derived mixtures are mirrored by odor-evoked calcium activity in their antennal lobes. *J. Insects Physiol.* 54: 333–343. (doi: 10.1016/j.jinsphys.2007.10.002).
- Pye, B., M. Rice, B. Sabine, and M. P. Zalucki. 1987. The push-pull strategy: behavioral control of *Heliothis*. *Aust. Cotton Grow* 9: 7–9.
- Raguso, R. A., and M. A. Willis. 2005. Synergy between visual and olfactory cues in nectar feeding by wild hawkmoths, *Manuca sexta*. *Anim. Behav.* 69: 407–418.
- Rajapakse, C.N.K., G. H. Walter, C. J. Moore, C. D. Hull, and B. W. Cribb. 2006. Host recognition by a polyphagous lepidopteran (*Helicoverpa armigera*): primary host plants, host produced volatiles and neurosensory stimulation. *Physiol. Entomol.* 31: 270–277.
- Rammath, S., K. Chitra, and S. Uthamasamy. 1992. Behavioral response of *Helicoverpa armigera* (Hüb.) to certain host plants. *J. Insect Sci.* 5: 147–149.
- Riffell, J. A., H. Lei, T. A. Christensen, and J. G. Hildebrand. 2009. Characterization and coding of behaviorally significant odor mixtures. *Curr. Biol.* 19: 335–340. (doi: 10.1016/j.cub.2009.01.041).
- Rochester, W. A., M. P. Zalucki, A. Ward, M. Miles, and D.A.H. Murray. 2002. Testing insect movement theory: empirical analysis of pest data routinely collected from agricultural crops. *Comp. Elect. Agric.* 35: 139–149.
- Rostelien, T., M. Strandén, A. K. Borg-Karlson, and H. Mustaparta. 2005. Olfactory receptor neurons in two heliothine moth species responding selectively to aliphatic green leaf volatiles, aromatic compounds, monoterpenes and sesquiterpenes of plant origin. *Chem. Senses* 30: 443–461.
- Ruan, Y. M., and K. J. Wu. 2001. Performances of the cotton bollworm, *Helicoverpa armigera* on different food plants. *Acta Entomol. Sin.* 44: 205–212.
- Scheirs, J., and L. De Bruyn. 2002. Integrating optimal foraging and optimal oviposition theory in plant-insect research. *Oikos* 96: 187–191.
- Schneider, J. C., and R. T. Roush. 1986. Genetic differences in oviposition preference between two populations of *Heliothis virescens*, pp. 163–171. In M. D. Huettel (ed.), *Evolutionary genetics of invertebrate behavior*. Plenum, New York, NY.
- Scott, K. D., K. S. Wilkinson, N. Lawrence, C. L. Lange, L. J. Scott, M. A. Merritt, A. J. Lowe, and G. C. Graham. 2005. Gene-flow between populations of cotton bollworm *Helicoverpa armigera* (Lepidoptera: Noctuidae) is highly variable between years. *Bull. Entomol. Res.* 95: 381–392.
- Sequeira, R. 2001. Inter-seasonal population dynamics and cultural management of *Helicoverpa* spp. in a Central Queensland cropping system. *Aust. J. Exp. Agric.* 41: 249–259.
- Shanower, T. G., and J. Romeis. 1999. Insect pests of pigeonpea and their management. *Annu. Rev. Entomol.* 44: 77–96.
- Sharma, H. C. (ed.). 2005. *Heliothis/Helicoverpa management: Emerging trends and strategies for future research*. Oxford and IBH Publishing, New Delhi, India.
- Sheck, A. L., and F. Gould. 1993. The genetic basis of host range in *Heliothis virescens*-larval survival and growth. *Entomol. Exp. Appl.* 69: 157–172.
- Sheck, A. L., and F. Gould. 1995. Genetic analysis of differences in oviposition preferences of *Heliothis virescens* and *H. subflexa* (Lepidoptera: Noctuidae). *Environ. Entomol.* 24: 341–347.
- Singer, M. C. 1986. The definition and measurement of oviposition preference in plant-feeding insects, pp. 65–94. In T. A. Miller, and J. Miller (eds.), *Insect-plant interactions*. Springer, New York, NY.
- Singer, M. C., D. Ng, and C. D. Thomas. 1988. Heritability of oviposition preference and its relationship to offspring performance with a single insect population. *Evolution* 42: 977–985.
- Skiri, H. T., M. Strandén, J. C. Sandoz, R. Menzel, and H. Mustaparta. 2005. Associative learning of plant odorants activating the same or different receptor neurons in the moth *Heliothis virescens*. *J. Exp. Biol.* 208: 787–796.
- Specht, A., D. R. Sosa-Gómez, S. V. de Paula-Moraes, and S.A.C. Yano. 2013. Morphological and molecular identification of *Helicoverpa armigera* (Lepidoptera: Noctuidae) and expansion of its occurrence record in Brazil. *Pesquisa Agropecuária Brasileira* 48: 689–692.
- Srinivasan, R., S. Uthamasamy, and N. S. Talekar. 2006. Characterization of oviposition attractants of *Helicoverpa armigera* in two solanaceous plants, *Solanum viarum* and *Lycopersicon esculentum*. *Curr. Sci.* 90: 846–850.
- Stensmyr, M. C., H.K.M. Dweck, A. Farhan, I. Ibba, A. Strutz, L. Mukunda, J. Linz, V. Grabe, K. Steck, S. Lavista-Llanos,

- et al. 2012. A conserved dedicated olfactory circuit for detecting harmful microbes in drosophila. *Cell* 151: 1345–1357. (doi:10.1016/j.cell.2012.09.046).
- Stranden, M., T. Rostelien, I. Liblikas, T. J. Almaas, A. K. Borg-Karlson, and H. Mustaparta. 2003. Receptor neurons in three heliothine moths responding to floral and inducible plant volatiles. *Chemoecology* 13: 143–154.
- Tabashnik, B. E. 1994. Delaying insect adaptation to transgenic plants: seed mixtures and refugia reconsidered. *Proc. R. Soc. Lond. B Biol. Sci.* 255: 7–12.
- Tabashnik, B. E., H. Wheelock, J. D. Rainbolt, and W. B. Watt. 1981. Individual variation in the butterfly, *Colias eurytheme*. *Oecologia* 50: 225–230.
- Tang, Q.-B., J.-W. Jiang, Y.-H. Yan, J.J.A. Van Loon, and C.-Z. Wang. 2006. Genetic analysis of larval host-plant preference in two sibling species of *Helicoverpa*. *Entomol. Exp. Appl.* 118: 221–228.
- Tasin, M., A. C. Backman, M. Bengtsson, C. Ioriatti, and P. Witzgall. 2006. Essential host plant cues in the grapevine moth. *Naturwissenschaften* 93: 141–144.
- Tay, W. T., M. F. Sorial, T. K. Walsh, D. Thomazoni, P. Silvie, G. T. Behere, C. Anderson, and S. Downes. 2013. A brave new world for an Old World pest: *Helicoverpa armigera* (Lepidoptera: Noctuidae) in Brazil. *PLoS ONE* e80134.
- Tingle, F. C., and E. R. Mitchell. 1992. Attraction of *Heliothis virescens* (F) (Lepidoptera, Noctuidae) to volatiles from extracts of cotton flowers. *J. Chem. Ecol.* 18: 907–914.
- Titmarsh, I. J. 1992. Mortality of immature Lepidoptera: a case study with *Helicoverpa* species (Lepidoptera: Noctuidae) in agricultural crops on the Darling Downs. Ph.D thesis. The University of Queensland, St Lucia, Australia.
- Topper, C. P. 1987. The dynamics of the adult population of *Heliothis armigera* (Hübner) (Lepidoptera: Noctuidae) within the Sudan Gezira in relation to cropping pattern and pest control on cotton. *Bull. Entomol. Res.* 77: 525–539.
- Torres-Vila, L. M., M. C. Rodriguez-Molina, A. Lacasa-Plasencia, and P. Bielza-Lino. 2002. Insecticide resistance of *Helicoverpa armigera* to endosulfan, carbamates and organophosphates: the Spanish case. *Crop Prot.* 21: 1003–1013.
- Traynier, R.M.M. 1984. Associative learning in the ovipositional behavior of the cabbage butterfly, *Pieris rapae*. *Physiol. Entomol.* 9: 465–472.
- Via, S. 1990. Ecological genetics and host adaptation in herbivorous insects: The experimental study of evolution in natural and agricultural systems. *Annu. Rev. Entomol.* 35: 421–446.
- Van den Berg, H., and M.J.W. Cock. 1993. Stage-specific mortality of *Helicoverpa armigera* in three smallholder crops in Kenya. *J. Appl. Ecol.* 30: 640–653.
- Vosshall, L. B., A. M. Wong, and R. Axel. 2000. An olfactory sensory map in the fly brain. *Cell* 102: 147–159.
- Walter, G. H., and M. D. Benfield. 1994. Temporal host plant use in three polyphagous Heliothinae, with special reference to *Helicoverpa punctigera* (Wallengren) (Noctuidae: Lepidoptera). *Aust. J. Ecol.* 19: 458–465.
- Wang, C.-Z., J.-F. Dong, D.-L. Tang, J.-H. Zhang, W. Li, and J. Qin. 2004. Host selection of *Helicoverpa armigera* and *H. assulta* and its inheritance. *Prog. Nat. Sci.* 14: 880–884.
- Ward, L. K. 1988. The validity and interpretation of insect foodplant records. *Br. J. Entomol. Nat. Hist.* 1: 153–162.
- Wardhaugh, K. G., P. M. Room, and L. R. Greenup. 1980. The incidence of *Helicoverpa armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera: Noctuidae) on cotton and other host plants in the Namoi Valley of New South Wales. *Bull. Entomol. Res.* 70: 113–131.
- Weeks, A. R., N. M. Endersby, C. L. Lange, A. Lowe, M. P. Zalucki, and A. A. Hoffmann. 2010. Genetic variation among *Helicoverpa armigera* populations as assessed by microsatellites: a cautionary tale about accurate allele scoring. *Bull. Entomol. Res.* 100: 445–450.
- West, S. A., and J. P. Cunningham. 2002. A general model for host plant selection in phytophagous insects. *J. Theor. Biol.* 214: 499–513.
- Witzgall, P., P. Kirsch, and A. Cork. 2010. Sex pheromones and their impact on pest management. *J. Chem. Ecol.* 36: 80–100.
- Wu, K.-M., Y.-H. Lu, H.-Q. Feng, Y.-Y. Jiang, and J.-Z. Zhao. 2008. Suppression of cotton bollworm in multiple crops in China in areas with Bt toxin-containing cotton. *Science* 321: 1676–1678.
- Xia, X. M., K. Y. Wang, and H. Y. Wang. 2009. Resistance of *Helicoverpa assulta* (Guenée) (Lepidoptera: Noctuidae) to fenvalerate, phoxim and methomyl in China. *Crop Prot.* 28: 162–167.
- Xu, M.-X., G.-X. Zhang, and H.-F. Zhu. 1958. Research on Cotton bollworm. *Acta Oeconomico-Entomolo. Sin.* 1: 18–29.
- Yan, F., M. Bengtsson, P. Anderson, L. Ansebo, C. Xu, and P. Witzgall. 2004. Antennal response of cotton bollworm (*Helicoverpa armigera*) to volatiles in transgenic Bt cotton. *J. Appl. Entomol.* 128: 354–357.
- Yang, Y.-Z., M.-L. Johnson, and M. P. Zalucki. 2008. Possible effect of genetically modified cotton on foraging habits of early instar *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) larvae. *Aust. J. Entomol.* 47: 137–141.
- Zalucki, M. P., and M. J. Furlong. 2005. Forecasting *Helicoverpa* populations in Australia: a comparison of regression based models and a bio-climatic based modelling approach. *Insect Sci.* 12: 45–56.
- Zalucki, M. P., G. Daghli, S. Firempong, and P. H. Twine. 1986. The biology and ecology of *Heliothis armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera: Noctuidae) in Australia: What do we know? *Aust. J. Zool.* 34: 779–814.
- Zalucki, M. P., D.A.H. Murray, P. C. Gregg, G. P. Fitt, P. H. Twine, and C. Jones. 1994. Ecology of *Helicoverpa armigera* (Hübner) and *H. punctigera* (Wallengren) in the inland of Australia: Larval sampling and host plant relationships during winter and spring. *Aust. J. Zool.* 42: 329–346.
- Zalucki, M. P., A. R. Clarke, and S. B. Malcolm. 2002. Ecology and behavior of first instar larval Lepidoptera. *Annu. Rev. Entomol.* 47: 361–393.
- Zalucki, M. P., D. Adamson, and M. J. Furlong. 2009. The future of IPM: whither or wither? *Aust. J. Entomol.* 48: 85–96.
- Zalucki, M. P., J. P. Cunningham, S. Downes, P. Ward, C. Lange, M. Meisse, N. A. Schellhorn, J. M. Zalucki. 2012. No evidence for change in oviposition behaviour of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) after widespread adoption of transgenic insecticidal cotton. *Bull. Entomol. Res.* 102: 468–476.
- Zhang, P.-J., S.-S. Liu, H. Wang, and M. P. Zalucki. 2007. Olfactory learning induces moth oviposition on nonhost plants. *J. Chem. Ecol.* 33: 1528–1541.

Received 23 January 2014; accepted 16 March 2014.