



Evolutionary Ecology of Diamondback Moth, *Plutella xylostella* (L.) and *Diadegma insulare* (Cresson) in North America: A Review

Sadia Munir^{1*}, Lloyd M. Dosdall¹ and John T. O'Donovan²

¹Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Alberta, T6G 2P5, Canada.

²Lacombe Research Centre, Agriculture and Agri-Food Canada, 6000 C and E Trail, Lacombe, AB, T4L 1W1, Canada.

Authors' contributions

This work was carried out in collaboration between all authors. Author SM managed the literature searches and wrote the first draft of the manuscript. Author LMD supervised and critically reviewed the manuscript and author JTO helped in editing and final revision of manuscript. All authors read and approved the final manuscript.

Article Information

DOI: 10.9734/ARRB/2015/11834

Editor(s):

(1) George Perry, Dean and Professor of Biology, University of Texas at San Antonio, USA.

Reviewers:

(1) Anonymous, Osmania University, India.

(2) Anonymous, Southwest University, China.

(3) Isabel Bertolaccini, Department of Plant Production, Facultad de Ciencias Agrarias (U.N.L.), Kreder 2805, (3080) Esperanza (Santa Fe), Argentina.

Complete Peer review History: <http://www.sciencedomain.org/review-history.php?iid=668&id=32&aid=6211>

Review Article

Received 5th June 2014
Accepted 7th July 2014
Published 24th September 2014

ABSTRACT

The diamondback moth (DBM), *Plutella xylostella* (L.), is recognized as a widely distributed destructive insect pest of Brassicaceae. The frequency and severity of *P. xylostella* outbreaks has increased in recent years, due to climate changes, high production of host plants (vegetable and oilseed Brassica crops), genetic flexibility of the pest that enables it to develop resistance to almost all known insecticides and establish quickly and easily in new environment. All life stages of *P. xylostella* are attacked by natural enemies but *Diadegma insulare* (Cresson) is one of the principal, effective and efficient larval parasitoids in North America. In this review, we synthesize published information on the primary aspects of *P. xylostella* origin, dispersal, migration, biology, and host plants and mainly focus on evolutionary ecology of bitrophic and tritrophic interactions among *P. xylostella*, its host plants and natural enemies.

*Corresponding author: Email: smunir@ualberta.ca;

Keywords: Evolution; ecology; Diamondback moth; host plant; *Diadegma insulare*.

1. INTRODUCTION

Plutella xylostella is not only the most destructive pest of brassicaceous crops throughout the world but is also among the most difficult to manage [1,2]. It was first introduced from Europe to North America (Illinois), in 1854. *Plutella xylostella* now occurs throughout North America, wherever its host plants are cultivated [3]. Its management result in a US\$4-5 billion annual cost to the world economy [4]. A few review articles on *P. xylostella* host-plant interactions, management and ecology have been published but a focus on detailed evolutionary ecology of tritrophic interactions among *P. xylostella*, its host plants and its principle parasitoid are lacking. The main objective of this review paper is to address the gaps in the knowledge and understanding of *P. xylostella* and *D. insulare* evolutionary ecology and tritrophic interactions. It is believed that the information presented here will encourage researchers to work on important aspects of *P. xylostella* and its natural enemies and help designing appropriate management strategies involving complete and in depth awareness of tritrophic interactions in a particular agro-ecosystem.

2. DISTRIBUTION AND ORIGIN OF *P. xylostella*

Plutella xylostella is believed to be the most widely distributed species of Lepidoptera, occurring universally wherever *Brassicaceae* are grown [1]. Six economically important species of the Genus *Plutella* (Schrank) have been recorded worldwide but only *P. xylostella* is cosmopolitan in distribution [5]. It has been recorded throughout tropical and temperate zones, as far north as Iceland (60°N) and as far south as New Zealand (45°S) [6]. The geographical origin of *P. xylostella* is uncertain. Some have speculated its origin in Europe [7], the Mediterranean area [8] or China [9]. It is also assumed to have evolved in South Africa, based on the diversity of endemic Brassica plants and its indigenous diverse parasitoid fauna [5]. North American populations are most probably of European origin and were introduced about 150 years ago [7]. Recently, some climatic models have been developed to predict *P. xylostella* distribution and seasonal phenology in areas of its occasional occurrence. However, the abundance and distribution of the *P. xylostella*

population in an area is regulated by climate, availability and quality of host plants and the presence of its natural enemies [10].

3. BIOLOGY

The biology of *P. xylostella* has been studied extensively in both laboratory and natural conditions in relation to ecological factors. However, its biological and developmental parameters vary due to differences in host plant species, temperature, and geographical population distribution [11]. The moth is multivoltine and can produce four to 20 generations per year in temperate and tropical regions, respectively [12,13]. In North America, it can produce three to five generations per year [14]. At constant temperature, development can occur from 8-32°C and under fluctuating temperature from 4 to 38°C [15]. *Plutella xylostella* development has been studied by Bahar et al. [16] at different constant (7,22,30°C) and fluctuating temperatures (0-14,15-29°C, and 23-37°C). The development was very slow at lowest constant (7°C) and fluctuating temperatures (0-14°C) while fast development of *P. xylostella* was recorded at highest constant (30°C) and fluctuating temperatures (23-30°C).

Plutella xylostella has four life stages: egg, larva, pupa and adult. Oviposition mainly occurs at night in the first 24 to 48 hours of mating and then declines gradually. Egg laying reaches zero in 10 days after adult emergence [11]. Each female can lay more than 200 eggs either singly or in small clusters [17,18]. Oviposition is greatly influenced by host plant species. For instance, oviposition on brassicaceous host plant (*Brassica napus* L.) is reported to be higher than non-brassicaceous hosts (*Cleome hassleriana* Chod. and *Tropaeolum majus* L.) [19].

Eggs are oval and pale to strong yellow in color [11]. Egg hatching occurs in 4-8 days [14]. Larvae are pale yellow in color having a dark head in early instars, and are light to dark green colored in later instars. The larva has V-shaped anal legs. First-instar larvae are leaf miners, feeding in the spongy mesophyll tissue of leaves. Other larval instars feed on all tissues of leaves, buds, flowers, stems, and siliques [11,20]. The average development time from first to fourth instar is reported as 4.0, 3.6, 3.4, and 4.2 days respectively, under Canadian field conditions; pupation takes place over 7.8 to 9.8 days [14].

The adult moth is slender and greyish [21]. The mean longevity of females is significantly reduced relative to males [11]. Development and survival vary greatly depending on quality of food, quantity of adult feeding, difference in host plant cultivar and sources of carbohydrate [22,11].

4. DISPERSAL AND MIGRATION

Migration may evolve as a mechanism that permits individuals to avoid probable failures in survival [23]. Insects may develop migratory characteristics when their habitat deteriorates [24]. *Plutella xylostella* possesses a high migratory ability to disperse over long distances in a very short time. This can explain why it gets easily established in novel environments and newly planted Brassica crops [7,25,26]. *Plutella xylostella* does not diapause; therefore long-distance immigration through aerial currents is a major process affecting population outbreaks [27,28]. *Plutella xylostella* migration and population seasonality is well documented [1]. Similar seasonal migrations have been reported in Japan's south western islands [29], in the United Kingdom [7,30], New Zealand, South Africa, and southern parts of Chile and Argentina [1], and Australia [31]. In both eastern and western Canada, *P. xylostella* re-establishes each year from annual adult population immigrations from the southern U.S.A. and Mexico [32,27,33]. *Plutella xylostella* adults have the ability to travel about 1500 km. Therefore, its densities can vary considerably from year to year [32,27,34,33]. *Plutella xylostella* cannot survive severe winters. Dodsall [35] reported its survival under mild winter conditions in western Canada. However, successful overwintering in northern latitudes in large numbers is considered to be an unusual phenomenon [36]. Hence, it is assumed that migration is the most important cause of population seasonality in *P. xylostella*. It is a regular ecological event that occurs at approximately the same time of the year and a characteristic of the vast majority of insect populations [28]. Campos et al. [37] noted that low nutritional quality and short temporal persistence of mature host plants, reduced body size, prolonged longevity and delayed sexual maturation of moths due to unfavorable environmental conditions. This will increase the chances of reaching new reproductive sites. Moths having such characteristics have greater fitness and are active migrants, when the resources are limited and habitat deteriorated.

5. EVOLUTIONARY ECOLOGY OF INTERACTIONS AMONG *P. xylostella* AND ITS HOST PLANTS

Plutella xylostella has a wide ecological host range. The genetic and phenotypic flexibility of *P. xylostella*, and its ability to modify traits of its life history according to environmental conditions during development enables the pest to survive throughout the year in areas where environmental conditions are favorable and host plants are easily available, in the absence of other ecological and evolutionary pressures [28,37]. The moth feeds almost exclusively on plants of the family *Brassicaceae*, particularly the genus *Brassica*, which are widely distributed geographically, and include 338 genera and 3709 species [38] (Table 1).

Plutella xylostella is commonly considered a specialist on *Brassicaceae*. However, evidence of its occasional occurrence on sugar snap peas (*Pisum sativum* L., Fabaceae) in Kenya [70], Taiwan and the Philippines [55,64], the chenopodiaceous vegetable *Salsola kali* L. (prickly saltwort, Russian thistle) in Russia [71], and okra in Ghana [72] have been recorded. Genetic analysis indicated an incomplete evolutionary host range expansion and ability to complete development on the novel host plant (snap peas) by *P. xylostella* strain [67,68,70]. It has also been documented by Dodsall et al. [34] that an introduction of a novel crop into an area can increase insect pest problems, including *P. xylostella* infestations.

Plutella xylostella is often studied in its relationship with its host plant's specific chemistry. The plants of the family *Brassicaceae* are characterized by the presence of sulphur-containing secondary metabolites known as glucosinolates that play a key role in plant defense against herbivores [73]. Some glucosinolate hydrolysis products like isothiocyanates are highly toxic to insect herbivores, but those insects specialized in feeding on plants with these secondary compounds have a mechanism to overcome this toxicity [74,75]. Very little is known about the mechanisms evolved by herbivores to overcome these defensive plant compounds [73]. There is some evidence of temporal association between the diversification of the host plants and insect herbivores [75]. However, the origin of an evolutionary novel defense mechanism and diversification of *Brassicales* (90-85 mya) were most probably followed by co-evolution of insect

herbivores and their host plants [76,77]. In *Brassicaceae*, the glucosinolates co-occur with myrosinases and are together known as “mustard oil bomb” [78]. These two compounds are compartmentalized in plants but come together upon plant tissue damage and release toxic isothiocyanates. The larvae of *P. xylostella* have evolved a defensive mechanism to detoxify glucosinolate (mustard oil bomb) and its toxic hydrolysis products by an enzyme glucosinolate sulfatase present in their gut. The enzyme actively prevents the formation of toxic hydrolysis products by converting glucosinolates to desulfoglucosinolates rather than more toxic nitrile and isothiocyanates. This mechanism enables *P. xylostella* herbivory on wide range of Brassica plants [54,74].

Plutella xylostella adults rely on morphological and chemical cues (glucosinolates like sinigrin, sinalbin and glucocheirolin) for host plant location, recognition, oviposition, stimulation and feeding initiation [79,80,74]. The performance of *P. xylostella* varies on cultivars of the same plant species with different glucosinolate contents and profiles; for example, high performance of larvae has occurred in plant species with intermediate glucosinolate content [81] or with low myrosinase content [82]. Similarly, higher densities of *P. xylostella* larvae are reported to be associated with plant cultivars having higher glucosinolate contents [83]. High concentrations of allyl isothiocyanates are reported to be toxic for larvae and adults [82]. In fact, glucosinolates are not the only plant compounds that stimulate oviposition and feeding activity; other aspects of host plant nutritional quality, such as host plant volatiles, morphology and chemistry or a combination of these also play an important role [48,75].

Some plant compounds like saponins, present on the leaf surface of some *Barbarea* spp., act as deterrents for larval development but attractants for oviposition. The presence of these compounds supports their ecological role in host recognition and stimulation of oviposition for the diamondback moth [84]. *Plutella xylostella* adults can also respond differently to different host plant volatiles emitted as a result of insect damage. Females rely on these volatile cues to recognize acceptable hosts for its progeny survival, fitness and to reduce competition for food [85]. Reddy & Guerrero [86] reported three cabbage green leaf volatiles that are highly attractive to *P. xylostella* females.

Brassicaceae host plant species and cultivars vary considerably in their level of susceptibility for *P. xylostella*. Sarfraz et al. [40] proposed that *Sinapis alba* L. and *Brassica rapa* L. are highly preferred for oviposition. The developmental time, longevity, body weight, and other parameters are greatly affected by host plant species; e.g., larval and pupal developmental times of females are faster on *Brassica juncea* (L.) Czern. and *S. alba* than on several other *Brassicaceae*.

Accumulating evidence indicates that host plant morphological characteristics like leaf color, size, and their position on the plant, epicuticular waxes, trichome density, chemosensory stimulation and abiotic factors affect *P. xylostella* oviposition, development and herbivory [79,80]. For instance, *P. xylostella* females prefer glossy cultivars (i.e., low surface wax) over waxy cultivars (normal wax bloom) for oviposition; though larval survival is reduced on glossy cultivars [48]. Some studies reported oviposition preference of *P. xylostella* on lower leaf surfaces of host plants [11,87,88], while some reported a higher oviposition preference on the upper surfaces of crucifer leaves [14,1]. Similarly, number of eggs laid and trichome density were positively correlated [17,89]. A recent study showed a positive correlation between *P. xylostella* oviposition choice and larval survival on undamaged host plants [90]. Variations in the host plant nutritional quality can affect the pest directly. Usually sulphur-deficient plants are less attractive but plants grown under a high fertilizer regime are more attractive for *P. xylostella* oviposition [91,92].

The preferences and performance of *P. xylostella* vary significantly among brassicaceous wild and cultivated species. *Sinapis alba* is a most preferred host followed by *B. rapa*, *B. juncea*, and *Brassica napus* L. among the cultivated species [36], while *Sinapis arvensis* L. followed by *Erysimum cheiranthoides* L. and *Capsella bursa-pastoris* (L.) are preferred wild brassicaceous hosts [59]. One of the main reasons for variation in development and fecundity of *P. xylostella* on different plant species or different cultivars of the same species is due to the differences in plant quality, reflected either in insect nutrient requirements or phagostimulation of *P. xylostella* [93].

Table 1. Host plants of *Plutella xylostella*

Cultivar/Species	Common name	Plant type	Ref. No
<i>Brassica carinata</i> L.	Ethiopian mustard	Vegetable, Oilseed	[39,40,41]
<i>Brassica juncea</i> L.	Indian mustard, brown mustard	Vegetable, Trap crop, Oilseed	[42,43,40,44]
<i>Brassica napus</i> L.	Canola, Canadian turnip, rutabaga	Vegetable, Oilseed	[45,42,40,41,46,47]
<i>Brassica nigra</i> L.	Black mustard	Vegetable, Spice	[45]
<i>Brassica oleracea</i> L. var. acephala	Collard, flowering kale	Vegetable	[45, 48, 49]
<i>Brassica oleracea</i> L. var. alboglabra	Kale	Vegetable	[1]
<i>Brassica oleracea</i> L. var. botrytis	Cauliflower	Vegetable	[45,50,46]
<i>Brassica oleracea</i> L. var. sabauda	Savoy cabbage	Vegetable	[51]
<i>Brassica oleracea</i> L. var. capitata	Cabbage	Vegetable	[52,45,46,47]
<i>Brassica oleracea</i> L. var. gemmifera	Brussels sprouts	Vegetable	[1]
<i>Brassica oleracea</i> L. var. gongylodes	Kohlrabi	Vegetable	[50,46]
<i>Brassica oleracea</i> L. var. italica	Broccoli	Vegetable	[45,50]
<i>Brassica rapa</i> L. var. pakchoi	Pak choi	Vegetable	[1]
<i>Brassica rapa</i> L. var. pekinensis	Chinese cabbage	Vegetable	[17,53,47]
<i>Brassica rapa</i> L.	Canola	Oilseed	[40]
<i>Raphanus sativus</i> L.	Radish, bier radish	Vegetable	[52]
<i>Sinapis alba</i> L. (<i>Brassica hirta</i> Moench)	White mustard, yellow mustard	Vegetable, spice	[42,40,41]
Wild Cruciferous			
<i>Arabidopsis thaliana</i> (L.) Heynh	Thalecress, mouse-earcress		[54]
<i>Barbarea vulgaris</i> (L.) R. Br.	Yellow rocket, rocketcress		[45,55,48]
<i>Berteroa incana</i> (L.) DC.	Hoary alyssum		[45]
<i>Capsella bursa-pastoris</i> L.	Shepherd's purse, mother's-heart		[45,56]
<i>Cardamine flexuosa</i> With.	Flexuous bittercress		[57]
<i>Descurainia sophia</i> L.	Flixweed		[1]
<i>Erysimum cheiranthoides</i> L.	Wormseed mustard, treacle mustard		[58,45,56,59]
<i>Erucastrum arabicum</i> (Fisch. & Mey.)	-		[60]
<i>Lepidium campestre</i> (L.) R. Br.	Field pepperweed		[45]
<i>Lepidium virginicum</i> L.	Virginia pepperweed, peppergrass		[61]
<i>Raphanus raphanistrum</i> L.	Wild radish, wild rape, wild turnip		[45,49]
<i>Rorippa indica</i> (L.) Hiern	Indian marshcress		[57,61]
<i>Rorippa islandica</i> (Oeder) Barba`s	Marsh yellowcress		[57]
<i>Rorippa micrantha</i> (Roth.)	-		[49]

Cultivar/Species	Common name	Plant type	Ref. No
Jonsell			
<i>Rorippa nudiuscula</i> (E.Mey. ex Sond.) Thell.	-		[49]
<i>Sinapis arvensis</i> L. (<i>Brassica kaber</i> (DC) Wheeler)	Wild mustard, crunch weed		[45,59,56]
<i>Sisymbrium altissimum</i> L.	Tumbling mustard, tall hedge mustard		[1]
<i>Thlaspi arvense</i> L.	Stinkweed, pennycress, French weed		[45]
Non-cruciferous			
<i>Tropaeolum majus</i> L.	Nasturtium, Indian cress	Flowering ornamental plant	[58]
Cleome species	Spider plant	Flowering plant	[62]
<i>Pisum sativum</i> L.	Peas	Pulse	[63,64,65,66,67,68]
<i>Hibiscus esculentus</i> L.	Okra, Lady fingers	Vegetable	[69]

6. NATURAL ENEMIES OF *P. xylostella*

All stages of *P. xylostella* are attacked by various parasitoids and predators (Table 2).

Delvare [114] reported over 135 parasitoid species worldwide. Among these, the most common ones include six species of egg parasitoids, 38 larval, and 13 pupal parasitoids [115]. Egg parasitoids (genera *Trichogramma* and *Trichogrammatoidea*) (Hymenoptera: *Trichogrammatidae*) contribute little to natural control generally because of their nonhost-specific nature [116]. In addition, to utilize them in biological control initiatives requires frequent inundated releases [1]. Larval parasitoids are predominant and have maximum control potential. The most effective *P. xylostella* larval parasitoids belong to hymenopteran genera *Microplitis* (*Braconidae*), *Cotesia* (*Braconidae*), and *Diadegma* (*Ichneumonidae*) [115,1]. A few prepupal and pupal parasitoids of the genus *Diadromus* (*Ichneumonidae*) also provide significant control [7,1,117,104,2]. Occasionally some species of *Pteromalus* (Hymenoptera: *Pteromalidae*) species parasitize *P. xylostella* pupae [100].

On a worldwide scale, large numbers of *P. xylostella* parasitoid species have been reported but some of them were misidentified [118,95]. Thompson [119] catalogued 48 species of parasitoids associated with *P. xylostella*, while Goodwin [120] reported over 90 such parasitoid species. Similarly, Mustata [121] listed 25 parasitoid species from Moldavia (Romania). Ten species of *Diadegma* that attack *P. xylostella* are recognized by Fitton & Walker [122]. Moreover, seven *Diadegma* species are revised by Azidah

et al. [95]. Kirk et al. [104] reported 27 parasitoid species mainly of the hymenopteran genera *Diadegma*, *Cotesia* and *Oomyzus* on 115 populations of *P. xylostella* collected in 32 countries. The majority of these parasitoid species are known to come from Europe where *P. xylostella* is believed by some to have originated.

In different geographical areas of the world, various parasitoid species are responsible for suppressing *P. xylostella* populations. For instance, *Diadegma* spp. and *Diadromus* spp. predominate in Europe [7], New Zealand [123] and South Africa [124]. *Diadegma semiclausum* (Helle'n), *Diadegma rapi* (Cameron) and *Diadromus collaris* (Grav.) are collectively responsible for 93% parasitism in Victoria, Australia [120]. *Diadegma semiclausum* has been reported to keep the *P. xylostella* population below economic threshold levels in certain areas of Europe, Africa, Asia [1], Malaysia, Taiwan, Philippines, Indonesia, Thailand, Zambia, New Zealand and Australia [125,96]. The most abundant parasitoids in east Africa are *Diadegma mollipla* (Holmgren) and *Oomyzus sokolowskii* (Kurdjumov) [126]. In Ethiopia, *Diadegma* spp. and *Cotesia plutellae* (Kurdj.) are key parasitoid species [39]. *Cotesia plutellae* and *O. sokolowskii* are considered the most promising biological control agents in China [113]. In the relatively hotter lowlands of many Asia-Pacific regions, *C. plutellae* is the dominant and most effective larval parasitoid of *P. xylostella* [1]. In the Eastern Cape (South Africa), four species viz., *D. mollipla*, *C. plutellae*, *D. collaris* and *O. sokolowskii*, are recorded as main parasitoids of *P. xylostella* [127]. Similarly, seven species are observed in Brasilia but only

two species, *D. leonitinae* (Brethe's) and *Apanteles piceotrichosus* (Blanchard) are dominant [128]. In general, few parasitoid species are responsible for a high level of parasitism in an area. Lim [125] noted that the ability to function as biological control agents varies between species, and usually depends on their direct relationships with their host, environment and interspecific interactions.

Table 2. Example of some common natural enemies of *Plutella xylostella*

Natural Enemies	Host stage attacked	Ref. No
A-Parasitoid		
<i>Trichogrammatoidea bactrae</i> (Nagaraja)	Egg	[94]
<i>Trichogramma pretiosum</i> (Riley)		
<i>Trichogrammatidae</i> spp.		
<i>Diadegma insulare</i> (Cresson)	Larva	[95]
<i>D. fenestrata</i> (Holmgren)		
<i>D. mollipla</i> (Holmgren)		
<i>D. varuna</i> Gupta		
<i>D. leontinae</i> (Brèthes)		
<i>D. rapi</i> (Cameron)		
<i>D. semiclausum</i> (Hellén)	Larva	[96]
<i>Apanteles ippeus</i> (Nixon)		
<i>Cotesia plutellae</i> (Kurdjumov)	Larva	[97]
<i>Microplitis plutellae</i> Muesbeck	Larva	[25]
<i>Oomyzus sokolowskii</i> (Kurdjumov)	Larva-Pupa	[98]
<i>Tatrstichus ayyari</i> (Rohwen)	Pupa	[99]
<i>Brachymeria phyta</i> (Walker)	Pupa	[96]
<i>Diadromus collaris</i> (Gravenhorst)	Pre-pupa, Pupa	
<i>D. subtilicornis</i> (Gravenhorst)	Pre-pupa, Pupa	[25]
<i>Pteromalus</i> spp.	Pupa	[100]
B-Pathogen		
<i>Bacillus thuringiensis</i> Berliner	Larva	[101]
<i>Zoophthora radicans</i> (Brefeld) Batko,	Larva	[102,
<i>Beauveria bassiana</i> (Balsamo) Vuillemin,		103, 104]
<i>Metarhizium anisopliae</i> (Metsch.) Sorokin		
<i>Paecilomyces farinosus</i> (Holm ex Gray)		
<i>Nomuraea rileyi</i> (Farlow) Sampson		
<i>Fusarium</i> spp.		
<i>Pandora</i> spp.		
<i>Erynia</i> spp.		
<i>Conidiobolus</i> spp.		
<i>Scopulariopsis</i> spp.		
Granuloviruses (GVs)	Larva	[105,106]
Nucleopolyhedrovirus NPVs		
Cypovirus CPVs		
<i>Steinernema carpocapsae</i> (Weiser)	Larva	[107]
<i>Heterorhabditis</i> sp.		[108]
<i>Nosema bombycis</i> (Negali)		[109]
<i>Vairimorpha</i> sp.		[110]
C-Predator		
Lycosids	Mostly Larva	[111,112]
Linyphiids		
Syrphids	Egg, Larva	[112]
Staphylinids		
Reduviids		
Nabids		
Carabids		
<i>Coccinella</i> spp.	Egg-Larva	[113]

Among parasitoids that attack *P. xylostella*, only a few solitary larval parasitoid species in the Ichneumonid genus *Diadegma*, solitary pupal parasitoids in the genus *Diadromus*, solitary larval parasitoids in the braconid genera *Microplitis* and *Cotesia*, and the gregarious larval-pupal parasitoid in the eulophid genus *Oomyzus* are considered to be predominant [2].

6.1 Evolutionary Ecology of *Diadegma insulare*: A Key Larval Parasitoid of *P. xylostella*

The genus *Diadegma* Froster (*Hymenoptera: Ichneumonidae: Campopleginae*) represents a large group of koinobiont endoparasitoids of Lepidoptera with 201 species known to occur worldwide [129]. Several *Diadegma* species, such as *D. fenestrata* (Holmgren), *D. insulare* (Cresson), *D. leontinae*, *D. mollipla*, *D. rapi*, and *D. semiclausum*, are reported to attack *P. xylostella* [95,130]. There is a wide geographical variation in predominance of *Diadegma* species, with the majority (131 species) having a Palearctic and a few (33 species) have a Nearctic distribution [1].

Diadegma insulare (Cresson) (*Hymenoptera: Ichneumonidae*) is native to the Neotropics [95], and is a key parasitoid of *P. xylostella* in North America [131,132,133]. *Diadegma insulare* is also one of three major hymenopterans parasitoids of *P. xylostella* in Canada; the other two include a larval parasitoid *Microplitis plutellae* (Mues.), and a prepupal and pupal parasitoid, *Diadromus subtilicornis* (Grav.) [12,25,27]. The *D. insulare* origin in western Canada is unknown, but it likely migrates northward in spring along with its hosts rather than overwintering [134].

Diadegma insulare, a solitary endoparasitoid, feeds within the *P. xylostella* larva [12]. The number of generations per year corresponds to the number of generations of its host as one host larva supports only one parasitoid larva [135]. It can parasitize all four larval instars of *P. xylostella* [136]. The specific larval instars parasitized by *D. insulare* can affect the sex ratio of offspring. More males than females are produced when second instars are parasitized, but when third and fourth instars are parasitized the progeny comprise a greater proportion of females than males [137,138]. The parasitoid emerges as a mature larva from the pre-pupa of its host, and spins its own cocoon within that of the host where it can easily be distinguished

[139,136]. On average, adult *D. insulare* live for 26 days and lay 814 eggs per female at 23°C [140]. Adults require a continuous nectar source for survival and longevity and as a result they prefer habitats with abundant food sources [141]; such habitats appear to enhance *D. insulare* fecundity and longevity [142]. For instance, sites with flowering plants like alyssum, *Lobularia maritime* (L.) Desv. (*Brassicaceae*) [143], or with borders of flowering buckwheat, *Fagopyrum esculentum* Moench (*Polygonaceae*) in cabbage fields enhance *D. insulare* populations [142]. The number of *P. xylostella* larvae parasitized by a single *D. insulare* female may vary from zero to 150, depending upon the food source [144]. Unlike its host, *D. insulare* developmental biology has not been studied extensively. However, in a recent study longer development time was recorded at constant and lower temperatures. High pupal mortality of *D. insulare* was also observed at higher temperature, and this may explain the greater effectiveness of this parasitoid in cooler regions [16].

Resource variation and their spatiotemporal distribution has a significant impact on the physiology of herbivore pests, which in turn mediates pest-parasitoid interactions, as well as the effectiveness, survival, development, size, longevity, and fecundity of parasitoids [145,146,147]. The density and distribution of a parasitoid's population is correlated with the density and distribution of its herbivore's host plant. For instance, field populations of *D. insulare* are often clustered, with distributions that correlate with their herbivore host populations and host plants having high sulphur content [148,19,36].

Parasitoid life history traits are influenced by the choice made by its herbivore host via mediated host plant quality [149,150]. The nutritional quality of plants consumed by the herbivore host of *D. insulare* affects the sex ratio of the parasitoid; more female parasitoids emerged from *P. xylostella* larvae on well-fertilized plants [137]. Similarly, the performance of *D. insulare* is improved when *P. xylostella* larvae are reared on highly fertilized plants [92,36]. Survival, parasitism, and development time of *D. insulare* varied considerably among the plant genotypes utilized by its *P. xylostella* host [41]. Percentage parasitism of *D. insulare* is higher and development time shorter on cultivated crucifers than on wild species [45]. Sarfraz et al. [41] reported that *S. alba* supports high *P. xylostella* parasitism levels and parasitoid survival, and

relatively rapid parasitoid development as compared to *B. napus* L. cv. Q2.

The role of plants in the ecology and biology of parasitoids is clearly evident in their effect of parasitoid host selection. Plant-associated visual cues are important in the process of host location by parasitoids [151]. Similarly, plants respond to herbivore damage by emitting complex mixtures of volatile compounds that attract natural enemies. Many field experiments suggested that parasitoids respond directly to both herbivores and their host plant volatile cues [152,153]. In these studies, *D. insulare* was assumed to be attracted to plant tissue damaged by *P. xylostella* larvae [133].

When the herbivore host of a parasitoid feeds on a narrow range of plants, with similarities in secondary chemistry, better discrimination for the parasitoid is possible. However, the choice to recognize a broad range of plants in many families as harbouring potential host larvae may reduce the ability of parasitoids to recognize and respond to qualitative differences among plants [152].

Different efficiencies of parasitoids are often correlated with the level of specificity of both host and parasitoids [150]. Host-specialist parasitoids are supposed to have greater efficiencies in searching hosts and have specialized adaptations to overcome host defense than generalist species that display relatively plastic foraging behaviours [154]. For instance, the host searching and parasitizing strategies employed by the specialist *D. semiclasum* are better adapted than those strategies employed by generalist parasitoids [154]. Moreover, *D. insulare* is an efficient host searcher and shows very flexible behavior by sitting motionless near the silken thread, waiting for the suspended *P. xylostella* larva to climb up and then attacking it again. Sometimes, it may follow down the suspended larva by its silken thread and attempt quickly to parasitize it [2].

Many studies indicate that parasitoids often experience high levels of mortality. Therefore, selection of hosts should favor developmental strategies that maximize progeny survival. It is also proposed that rapid development time at the cost of size may be preferred in parasitoids whose hosts confront high risks of predation [155,156]. This indirectly suggests that parasitoids have evolved under selection pressures exerted by risks of predation [157].

The mortality risks appear to be high for koinobionts (that cause the host temporary or nonlethal paralysis), through hyperparasitism and multiparasitism [158,159,160] as they are competitively inferior to idiobionts (cause permanent paralysis or death) [161,162]. Nonetheless, *D. insulare* has a significant ability to avoid multiparasitism and super parasitism [140].

7. CONCLUSION

In conclusion, understanding the evolutionary ecology of a pest, its host plants, and its parasitoid and their tritrophic interactions is very complex and variable. It requires detailed studies of pest and parasitoid behaviors, their life histories, factors affecting their development, and pest-parasitoid interactions in various agro ecosystems. For any effective management strategy whether it involves habitat management, biological control or integration of different control measures, up to date knowledge of pest and parasitoid behavior, population dynamics and also cautious evolutionary interpretation of tritrophic relationship in a particular agro ecosystem is crucial.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

1. Talekar NS, Shelton AM. Biology, ecology, and management of the diamondback moth. *Ann Rev Entomol.* 1993;38:275-301.
2. Sarfraz M, Keddie AB, Dossdall LM. Biological control of the diamondback moth, *Plutella xylostella*: A review. *Biocontrol Sci Tech.* 2005;15:763-789.
3. Anonymous. Canola council of Canada. Canola encyclopaedia. Diamondback moth. Accessed 15 May 2014. Available: <http://www.canolacouncil.org/canola-encyclopedia/insects/diamondback-moth/>
4. Furlong MJ, Wright DS, Dossdall LM. Diamondback moth ecology and management: Problems, progress, and prospect. *Ann Rev Entomol.* 2013;(58):517-541.
5. Kfir R. Origin of the diamondback moth (*Lepidoptera: Plutellidae*). *Ann Entomol Soc Am.* 1998;91:164-167.

6. Ooi PAC. Diamondback moth in Malaysia. In: Talekar NS, Griggs TD, editors. Diamond back Moth Management: Proceedings of the first international workshop. AVRDC. Shanhua. Taiwan. 1986;25-34.
7. Hardy JE. *Plutella maculipennis* Curt., its natural and biological control in England. Bull Entomol Res. 1938;29(4):343-372.
8. Harcourt DG. The biology and ecology of the diamondback moth, *Plutella maculipennis*, Curtis, in Eastern Ontario. Cornell Univ., Ithaca, NY. PhD thesis. 1954;107.
9. Liu S, Wang XG, Guo SJ, He JH, Shi ZH. Seasonal abundance of the parasitoid complex associated with the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) in Hangzhou, China. Bull Entomol Res. 2000;90(3):221-231.
10. Zalucki MP, Furlong MJ. Predicting outbreaks of a migratory pest: An analysis of DBM distribution and abundance revisited. In: Srinivasan R, Anthony M. Shelton and Hilda LC. Proceedings: The Sixth International Workshop on Management of the Diamondback Moth and Other Crucifer Insect Pests. International Workshop on Management of the Diamondback Moth and Other Crucifer Insect Pests (6th, 2011), Nakhon Pathom, Thailand. 2011;21-25.
11. Alizadeh M, Rassouljan GR, Karimzadeh J, Hosseini-Naveh V, Farazmand H. Biological study of *Plutella xylostella* (L.) (Lep: Plutellidae) and its solitary endoparasitoid, *Cotesia vestalis* (Haliday) (Hym. Braconidae) under laboratory conditions. Pak J Bio Sci. 2011;14(24):1090-1099.
12. Harcourt DG. Population dynamics of the diamondback moth in southern Ontario. In: Talekar NS, editor. Diamondback moth and other crucifer pests. Proceedings of the First International Workshop, 11-15 March 1985. Tainan, Taiwan: Asian Vegetable Research and Development Center. 1986;3-16.
13. Vickers RA, Furlong MJ, White A, Pell JK. Initiation of fungal epizootics in diamondback moth populations within a large field cage: Proof of concept of auto-dissemination. Entomol Exp Appl. 2004;111:7-17.
14. Harcourt DG. Biology of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae), in Eastern Ontario. II. Life history, behavior, and host relationship. Can Entomol. 1957;12:554-564.
15. Liu S, Chen FZ, Zalucki MP. Development and survival of the diamondback moth (Lepidoptera: Plutellidae) at constant and alternating temperatures. Environ Entomol. 2002;31:221-231.
16. Bahar MH, Soroka JJ, Dossdall LM. Constant versus fluctuating temperatures in the interactions between *Plutella xylostella* (Lepidoptera: Plutellidae) and its larval parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). Environ Entomol. 2012;41:1653-1661.
17. Talekar NS, Liu S, Chen C, Yiin Y. Characteristics of oviposition of diamondback moth (Lepidoptera: Yponomeutidae) on cabbage. ZoolStud. 1994;33(1):72-77.
18. Justus KA, Dossdall LM, Mitchell BK. Oviposition by *Plutella xylostella* (Lepidoptera: Plutellidae) and effect of phylloplane waxiness. J Econ Entomol. 2000;93:1152-1159.
19. Sarfraz M, Dossdall LM, Keddie BA. Performance of the specialist herbivore *Plutella xylostella* (Lepidoptera: Plutellidae) on Brassicaceae and non-Brassicaceae species. Can Entomol. 2010;142:24-35.
20. Anonymous. Diamondback moth. Canada's Green Plan. 1996. Accessed 10 September 2013. Available: <http://www.agr.gov.sk.ca/docs/crops>.
21. Ooi PAC, Kelderman W. The biology of three common pests of cabbage in Cameron Highlands, Malaysia. Malay Agri J. 1979;52:85-101.
22. Winkler K, Wackers FL, Stingli A, Van Lenteren JC. *Plutella xylostella* (Diamondback moth) and its parasitoid *Diadegma semiclausum* show different gustatory and longevity responses to a range of nectar and honey dew sugars. Entomol Exp Appl. 2005;115:187-192.
23. Southwood TRE. Migration of terrestrial arthropods in relation to habitat. Biol Rev. 1962;37:171-214.
24. Harrison RG. Dispersal polymorphism in insects. Annu Rev Ecol Syst. 1980;11:95-118.
25. Braun L, Olfert O, Soroka J, Mason P, Dossdall LM. Diamondback moth biocontrol activities in Canada. In: Kirk AA, Bordat D, editors. Improving biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002.

- Montpellier, France. 2004;144-146.
26. Coulson SJ, Hodkinson ID, Webb NR, Mikkola K, Harrison JA, Pedgley DE. Aerial colonisation of high Arctic islands by invertebrates: The diamondback moth *Plutella xylostella* (Lepidoptera: Yponomeutidae) as a potential indicator species. *Divers Distrib.* 2002;8:327-334.
 27. Dosedall LM, Mason PG, Olfert O, Kaminski L, Keddie BA. The origins of infestations of diamondback moth, *Plutella xylostella* (L.), in canola in western Canada. In: Endersby NM, Ridland PM, editors. The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne. Melbourne, Australia: Department of Natural Resources and Environment. 2004;95-100.
 28. Campos WG, Schoereeder LH, DeSouza OF. Seasonality in neotropical populations of *Plutella xylostella* (Lepidoptera): Resource availability and migration. *Popul Ecol.* 2006;48:151-158.
 29. Honda K. Hibernation and migration of the diamondback moth in north Japan. In: Talekar NS, editor. Diamondback moth and other crucifer pests. Proceedings of the Second International Workshop, 10-14 December 1990. Tainan, Taiwan: Asian Vegetable Research and Development Center. 1992;43-50.
 30. Chapman JW, Reynolds DR, Smith AD, Riley JR, Pedgley DE, Woiwod IP. High altitude migration of the diamondback moth *Plutella xylostella* to the UK: A study using radar, aerial netting, and ground trapping. *Ecol Entomol.* 2002;27:641-650.
 31. Goodwin S, Danthanarayana W. Flight activity of *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae). *J Aust Entomol Soc.* 1984;23:235-240.
 32. Smith DB, Sears MK. Evidence of dispersal of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) into southern Ontario. Proceedings of the Entomological Society of Ontario. 1982;113:21-27.
 33. Hopkinson RF, Soroka JJ. Air trajectory model applied to an in-depth diagnosis of potential diamondback moth infestations on the Canadian Prairies. *Agric For Meteorol.* 2010;150:1-11.
 34. Dosedall LM, Weiss RM, Olfert O, Mason PG, Soroka JJ. 2008. Diamondback moth, *Plutella xylostella* (L.), as a pest of canola in Canada: Its historical impact on the crop and predicted effects of climate change on its pest status. In: Shelton AM, Collins HL, Zhang Y, Wu Q, editors. Proceedings of the Fifth International Workshop on the Management of Diamondback Moth and Other Crucifer Pests, Beijing, China. 2008;112-121.
 35. Dosedall LM. Evidence for successful overwintering of diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), in Alberta. *Can Entomol.* 1994;126:183-185.
 36. Dosedall LM, Soroka JJ, Olfert O. The diamondback moth in canola and mustard: Current pest status and future prospects. *Prairie Soils and Crops Journal.* 2011;4:66-76.
 37. Campos WG, Schoereeder JH, Sperber CF. Does the age of the host plant modulate migratory activity of *Plutella xylostella*? *Entomol Sci.* 2004;7:323-329.
 38. Warwick SI, Francis A, Al-Shehbaz IA. Brassicaceae: Species checklist and database on CD-Rom. *Plant Syst Evol.* 2006;259:249-258.
 39. Ayalew G, Lohr B, Baumgaertner J, Ogol CKPO. Diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) and its parasitoids in Ethiopia. In: Kirk AA, Bordat D, editors. Improving biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. 2004;140-143.
 40. Sarfraz M, Dosedall LM, Keddie BA. Resistance of some cultivated Brassicaceae to infestations by *Plutella xylostella* (Lepidoptera: Plutellidae). *J Econ Entomol.* 2007;1:215-224.
 41. Sarfraz M, Dosedall LM, Keddie BA. Host plant genotype of the herbivore *Plutella xylostella* (Lepidoptera: Plutellidae) affects the performance of its parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Biol Control.* 2008;44:42-51.
 42. Brown J, McCaffrey JP, Harmon BL, Davis JB, Brown AP, Erickson DA. Effect of late season insect infestation on yield, yield components and oil quality of *Brassica napus*, *B. rapa*, *B. juncea* and *Sinapis alba* in the Pacific Northwest region of the United States. *J Agric Sci.* 1999;132:281-288.
 43. Srinivasan K, Krishna Moorthy PN. Indian mustard as a trap crop for management of major lepidopterous pests on cabbage. *Trop Pest Manage.* 1991;37:26-32.

44. Soufbaf M, Fathipour Y, Karimzadeh J, Zaluck IMP. Development and age-specific mortality of diamondback moth on *brassica* host plants: Pattern and causes of mortality under laboratory conditions ecology and population biology. *Ann Entomol Soc Am.* 2010;103:574-579.
45. Idris AB, Grafius E. Effects of wild and cultivated host plants on oviposition, survival, and development of diamondback moth (*Lepidoptera: Plutellidae*) and its parasitoid *Diadegma insulare* (*Hymenoptera: Ichneumonidae*). *Environ Entomol.* 1996;25:825-833.
46. Golizadeh A, Kamali K, Fathipour Y, Abbasipour H. Life table of the diamondback moth, *Plutella xylostella* (L.) (*Lepidoptera: Plutellidae*) on five cultivated brassicaceous host plants. *J Agric Sci Tech.* 2009;11:115-124
47. Silva R, Furlong MJ. Diamondback moth oviposition: Effects of host plant and herbivory. *Entomol Exp Appl.* 2012;143:218-230.
48. Badenes-Perez FR, Shelton AM, Nault BA. Evaluating trap crops for diamondback moth, *Plutella xylostella* (*Lepidoptera: Plutellidae*). *J Econ Entomol.* 2004;97:1365-1372.
49. Gathu RK, Lohr B, Poehling HM. Development and reproductive potential of diamondback moth *Plutella xylostella* (*Lepidoptera: Plutellidae*) on cultivated and wild crucifer species in Kenya. *Intl J Trop Insect Sci.* 2008;28:19-29.
50. Reddy GVP, Tabone E, Smith MT. Mediation of host selection and oviposition behavior in the diamondback moth, *Plutella xylostella* and its predator, *Chrysoperla carnea* by chemical cues from cole crops. *Bio Control.* 2004;29:270-277.
51. Abro GH. Varietal resistance and insecticide efficacy against the diamondback moth, *Plutella xylostella* L. PhD Thesis, University of London. 1985;159.
52. Abro GH, Jayo AL, Syed TS. Ecology of diamondback moth, *Plutella xylostella* (L.) in Pakistan. Host plant preference. *Pak J Zool.* 1994;26:35-38.
53. Liu S, Jiang L. Differential parasitism of *Plutella xylostella* (*Lepidoptera: Plutellidae*) larvae by the parasitoid *Cotesia plutellae* (*Hymenoptera: Braconidae*) on two host plant species. *Bull Entomol Res.* 2003;93:65-72.
54. Ratzka A, Vogel H, Kliebenstein DJ, Mitchell-Olds T, Kroymann J. Disarming the mustard oil bomb. *Proceedings of the National Academy of Sciences USA.* 2002;99:11223-11228.
55. Shelton AM, Nault BA. Dead-end trap cropping: a technique to improve management of the diamondback moth. *Crop Prot.* 2004;23:497-503.
56. Sarfraz MR, Dossall LM, Keddie BA. Influence of the herbivore host's wild food plants on parasitism, survival and development of the parasitoid *Diadegma insulare*. *Biol Control.* 2012;62:38-44.
57. Muhamad O, Tsukuda R, Oki Y, Fujisaki K, Nakasuji F. Influences of wild crucifers on life history traits and flight ability of the diamondback moth, *Plutella xylostella* (*Lepidoptera: Yponomeutidae*). *Res Popul Ecol.* 1994;36:53-62.
58. Renwick JAA, Radke CD. Plant constituents mediating oviposition by the diamondback moth, *Plutella xylostella* (L.) (*Lepidoptera: Plutellidae*). *Phytophaga.* 1990;3:37-46.
59. Sarfraz M, Dossall LM, Keddie BA, Myers J. Larval survival, host plant preferences and developmental responses of the diamondback moth *Plutella xylostella* (*Lepidoptera: Plutellidae*) on wild brassicaceous species. *Entomol Sci.* 2011;14:20-30.
60. Ayalew G, Lohr B, Ogol CKPO, Baumgärtner J. Suitability of cultivated and wild crucifers for the development of diamondback moth, *Plutella xylostella* L. (*Lepidoptera: Plutellidae*). *J Entomol.* 2006;3:82-88.
61. Begum S, Tsukuda R, Fujisaki K, Nakasuji F. The effects of wild cruciferous host plants on morphology, reproductive performance and flight activity in the diamondback moth, *Plutella xylostella* (*Lepidoptera: Yponomeutidae*). *Res Popul Ecol.* 1996;38:257-263.
62. Sarfraz M, Dossall LM, Keddie BA. Evidence for behavioral resistance by the diamondback moth, *Plutella xylostella* (L.). *J Appl Entomol.* 2005;129:340-341.
63. Gupta PD, Thornsteinson AJ. Food plant relationships of the diamondback moth (*Plutella maculipennis* (Curt)) II. Sensory relationship of oviposition of the adult female. *Entomol Exp Appl.* 1960;3:305-314.

64. Lohr B. Diamondback moth on peas, really. *Biocontrol News and Information*. 2001;19:38-39N.
65. Lohr B, Gathu R. Evidence of adaptation of diamondback moth, *Plutella xylostella* (L.), to pea, *Pisumsativum* L. *Insect Sci Appl*. 2002;22:161-173.
66. Roszbach, Lohr B, Vidal S. Host shift to peas in the diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) and response of its parasitoid *Diadegma mollipla* (Hymenoptera: Ichneumonidae). *Bull Entomol Res*. 2006;96:413-419.
67. Henniges-Janssen K, Reineke A, Heckel DG, Groot AT. Complex inheritance of larval adaptation in *Plutella xylostella* to a novel host plant. *Heredity*. 2011;107:421-432.
68. Henniges-Janssen K, Schoepl G, Reineke A, Heckel DG, Groot AT. Oviposition of diamondback moth in the presence and absence of a novel host plant. *Bull Entomol Res*. 2011;101:99-105.
69. Gupta JC. Okra, a new host of diamondback moth. *FAO Plant Prot. Bull*. 1971;19:89-90.
70. Knolhoff LM, Heckel DG. Behavioral and genetic components of a host range expansion in the diamondback moth. In: Srinivasan R, Shelton AM, Collins HL, editors. 2011. Proceedings of the Sixth International Workshop on Management of the Diamondback Moth and Other Crucifer Insect Pests, 21-25 March 2011, Kasetsart University, Nakhon Pathom, Thailand. AVRDC – The World Vegetable Center, Publication No. 11-755. AVRDC – The World Vegetable Center, Taiwan. 2011;321.
71. Talekar NS, Yang HC, Lee ST, Chen BS, Sun LY. [compilers]. Annotated bibliography of diamondback moth. Asian Vegetable Research and Development Center, Shanhu, Taiwan; 1985.
72. Anonymous. Outbreaks and new records. *FAO Plant Prot Bull*. 1971;19:89-92.
73. Despres L, David JP, Gallet C. The evolutionary ecology of insect resistance to plant chemicals. *Trends Ecol Evol*. 2007;22:298-307.
74. Hopkins RJ, van Dam NM, van Loon JJA. Role of glucosinolates in insect-plant relationships and multitrophic interactions. *Ann Rev Entomol*. 2009;54:57-83.
75. Futuyma DJ, Agrawal AA. Macroevolution and the biological diversity of plants and herbivores. *Proceedings of the National Academy of Sciences USA*. 2009;106:18054-18061.
76. Wheat CW, Vogel H, Wittstock U, Braby MF, Underwood D. The genetic basis of a plant–insect coevolutionary key innovation. *Proceedings of the National Academy of Sciences USA*. 2007;104:20427–20431.
77. Wikstrom N, Savolainen V, Chase MW. Evolution of the angiosperms: Calibrating the family tree. *Proceedings of the Royal Society of London*. 2001;268:2211-2220.
78. Luthy B, Matile P. The mustard oil bomb: rectified analysis of the subcellular organization of myrosinases system. *Biochemie und Physiologie der Pflanzen*. 1984;179:5-12.
79. Sarfraz M, Dossall LM, Keddie BA. Diamondback moth host plant interactions: Implications for pest management. *Crop Prot*. 2006;25:625-639.
80. Renwick JAA, Haribal M, Gouinguene S, Stadler E. Isothiocyanates stimulating oviposition by the diamondback moth, *Plutella xylostella*. *J Chem Ecol*. 2006;32:755-766.
81. Siemens DH, Mitchell-Olds T. Glucosinolates and herbivory by specialists (*Coleoptera: Chrysomelidae, Lepidoptera: Plutellidae*): consequences of concentration and induced resistance. *Environ Entomol*. 1996;25:1344-1353.
82. Li Q, Eigenbrode SD, Stringam GR, Thiagarajah MR. Feeding and growth of *Plutella xylostella* and *Spodoptera eridania* on *Brassica juncea* with varying glucosinolate concentrations and myrosinase activities. *J Chem Ecol*. 2000;10:2401-2419.
83. Bidart-Bouzat MG, Kliebenstein DJ. Differential levels of insect herbivory in the field associated with genotypic variation in glucosinolates in *Arabidopsis thaliana*. *J Chem Ecol*. 2008;34:1026-1037.
84. Badenes-Perez FR, Reichelt M, Gershenzon J, Heckel DG. Phylloplane location of glucosinolates in *Barbarea* spp. (*Brassicaceae*) and misleading assessment of host suitability by a specialist herbivore. *New Phytol*. 2011;189:549-556.
85. Abuzid MN, Mohamad Roff MN, Mansour S, Idris AB. Olfactory responses of *Plutella xylostella* to Chinese mustard volatiles. The 6th International Workshop on Management of the Diamondback Moth and Other Crucifer Insect Pests. AVRDC - The World Vegetable Center. 2011;66-69.

86. Reddy GVP, Guerrero A. Behavioural responses of diamondback moth, *Plutella xylostella*, to green leaf volatiles of *Brassica oleracea* subsp. *capitata*. J Agric Food Chem. 2000;48:6025-6029.
87. Satpathy S, Shivalingaswamy TM, Kumar A, Rai AM, Rai M. Potentiality of Chinese cabbage (*Brassica rapa* subsp. *Pekinensis*) as a trap crop for diamondback moth (*Plutella xylostella*) management. Indian J Agric Sci. 2010;80:240-243.
88. Charleston DS, Kfir R. The possibility of using Indian mustard, *Brassica juncea*, as a trap crop for diamondback moth, *Plutella xylostella*, in South Africa. Crop Prot. 2000;19:455-460.
89. Agerbirk N, Olsen CE, Bibby BM, Frandsen HO, Brown L.D, Neilsen JK, Renwick JAA. A saponin correlated with variable resistance of *Barbarea vulgaris* to the diamondback moth, *Plutella xylostella*. J ChemEcol. 2003;29:1417-1433.
90. Zhang PJ, Lu YB, Zalucki MP, Liu SS. Relationship between adult oviposition preference and larval performance of the diamondback moth, *Plutella xylostella*. J Pest Sci. 2012;85:247-252.
91. Marazzi C, Patrian B, Studler E. Secondary metabolites of the leaf surface affected by sulfur fertilization and perceived by the diamondback moth. Chemoecology. 2004;14:81-86.
92. Sarfraz M, Dossall LM, Keddie BA. Host plant nutritional quality affects the performance of the parasitoid *Diadegma insulare*. Biol Control. 2009;51:34-41.
93. Ebrahimi N, Talebi AA, Fathipour Y, Zamani AA. Host plants effect on preference, development and reproduction of *Plutella xylostella* (L.) (*Lepidoptera: Plutellidae*) under laboratory conditions. Adv Enviro Biol. 2008;2:108-114.
94. Liu S, Li Y, Tang Z. Host resistance to an insecticide and selection at larval stage favor development of resistance in the parasitoid, *Cotesia plutellae*. In: Endersby NM, Ridland PM, editors. The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne. Melbourne, Australia: Department of Natural Resources and Environment. 2004;227-233.
95. Azidah AA, Fitton MG, Quicke DLJ. Identification of the *Diadegma* species (*Hymenoptera: Ichneumonidae*, Campopleginae) attacking the diamondback moth, *Plutella xylostella* (*Lepidoptera: Plutellidae*). Bull Entomol Res. 2000;90:375-389.
96. Furlong MJ, Zalucki MP. Parasitoid complex of diamondback moth in south-east Queensland: First records of *Oomyzus sokolowskii* (*Hymenoptera: Eulophidae*) in Australia. Aust J Entomol. 2007;46:167-75.
97. Verkerk RHJ, Wright DJ. Multitrophic interactions and management of the diamondback moth: a review. Bull Entomol Res.1996;86:205-216.
98. Shi Z, Li Q, Li X, Liu S. Interspecific competition between *Diadegma semiclausum* and *Oomyzus sokolowskii*, parasitoids of diamondback moth, *Plutella xylostella*. In: Endersby NM, Ridland PM, editors. The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne. Melbourne, Australia: Department of Natural Resources and Environment. 2004;243-248.
99. Ooi PAC, Lim GS. Introduction of exotic parasitoids to control diamondback moth in Malaysia. J Plant Prot. 1989;6:103-111.
100. Chauhan U, Sharma KC. Status of biocontrol agents of *Plutella xylostella* (L.) (*Lepidoptera: Yponomeutidae*) in hilly areas of the north-west Himalayas, India. In: Kirk AA, Bordat D, editors. Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. 2004;153-157.
101. Bauer LS. 1995. Resistance: A threat to the insecticidal crystal proteins of *Bacillus thuringiensis*. Fla Entomol. 1995;78:414-443.
102. Cherry AJ, Mercadier G, Meikle W, Castelo-Blanco M, Schroer S. The role of entomopathogens in DBM biological control. In: Kirk AA, Bordat D, editors. Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France.2004;51-70.
103. Vandenberg JD, Shelton AM, Wilsey WT, Ramos M. Assessment of *Beauveria bassiana* sprays for control of diamondback moth (*Lepidoptera: Plutellidae*) on crucifers. J Econ Entomol. 1998;91:624-630.

104. Kirk AA, Mercadier G, Bordat D, Delvare G, Pichon A, Arvanitakis L, Goude'gnon AE, Rincon C. Variability in *Plutella* and its natural enemies: Implications for biological control. In: Endersby NM, Ridland PM, editors. The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne. Melbourne, Australia: Department of Natural Resources and Environment. 2004;71-77.
105. Woodward DT, Grzywacz D, Winstanely D. Biological and molecular characterization of granuloviruses isolated from diamondback moth (*Plutella xylostella*, Plutellidae) in Kenya. In: Kirk AA, Bordat D, editors. Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. 2004;263-266.
106. Cherry AJ, Osae M, Djegui D. Relative potency, yield and transmission of a Kenyan isolate of *Plutella xylostella* granulovirus in a population of diamondback moth from Benin, West Africa. In: Kirk AA, Bordat D, editors. Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. 2004;158-162.
107. Baur ME, Kaya HK, Tabashnik BE, Chilcutt CF. Suppression of diamondback moth (*Lepidoptera: Plutellidae*) with an entomopathogenic nematode (*Rhabditida: Steinernematidae*) and *Bacillus thuringiensis* Berliner. J Econ Entomol. 1998;91:1089-1095.
108. Mason JM, Matthews GA, Wright DJ. Evaluation of spinning disc technology for the application of entomopathogenic nematodes against a foliar pest. J Invertebr Pathol. 1999;73:282-88.
109. Idris AB, Zainal-Abidin BAH, Sajap AS, Noran AM, Hussan AK. Some studies on Nosema infecting DBM in Malaysia. In: Endersby NM, Ridland PM, editors. The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne. Melbourne, Australia: Department of Natural Resources and Environment. 2004;295-303.
110. Anuradha M. Possibility on integration of bio-agent for the management of diamondback moth, *Plutella xylostella* (L.) (*Lepidoptera: Yponomeutidae*). University of Agricultural Sciences, Bangalore. PhD Thesis. 1997;117.
111. Quan X, WU L, Zhou Q, Yun Y, Peng Y, Chen J. Identification of predation by spiders on the diamondback moth *Plutella xylostella*. Bull Insectology. 2011;64:223-227.
112. Ortiz FM. Biological control of diamondback moth. The role of predators, parasitoids and insecticides. Faculty of Natural Resources and Agriculture Sciences. Department of Ecology. Uppsala. PhD Thesis; 2011. Available: http://pub.epsilon.slu.se/8073/1/miranda_f_110414.pdf
113. Gabriela LV. Interactions between *Plutella xylostella*, *Diadegma semiclausum* and some generalist predators of brassica crops. University of Adelaide, School of Agriculture, Food and Wine. PhD Thesis; 2011. Available: <http://digital.library.adelaide.edu.au/dspace/handle/2440/65487>
114. Delvare G. The taxonomic status and role of Hymenoptera in biological control of DBM, *Plutella xylostella* (L.) (*Lepidoptera: Plutellidae*). In: Kirk AA, Bordat D, editors. Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. 2004;17-49.
115. Lim GS. Biological control of diamondback moth. In: Talekar NS, editor. Diamondback moth and other crucifer pests. Proceedings of the First International Workshop, 11-15 March 1985. Tainan, Taiwan: Asian Vegetable Research and Development Center. 1986;159-171.
116. Goulet H, Huber JT. Hymenoptera of the world: An identification guide to families. Agriculture Canada Publication. 1993;668.
117. Liu S, Wang XG, Guo SJ, He JH, Shi ZH. Seasonal abundance of the parasitoid complex associated with the diamondback moth, *Plutella xylostella* (*Lepidoptera: Plutellidae*) in Hangzhou, China. Bull Entomol Res. 2000;90:221-231.
118. Noyes JS. The reliability of published host-parasitoid records: A taxonomist's view. Norwegian Journal of Agricultural Sciences. 1994;16: 59-69.
119. Thompson WR. A catalogue of the parasites and predators of insect pests. Section 1; Parasite Host Catalogue: Part 7; Parasites of *Lepidoptera* (G-M):259-185.

- Imperial Agricultural Bureau, Belleville, Ontario, Canada. 1946.
120. Goodwin S. Changes in numbers in parasitoid complex associated with the diamondback moth, *Plutella xylostella*(L.) (*Lepidoptera*) in Victoria. Aust J Zool. 1979;27:981-989.
 121. Mustata G. Role of parasitoid complex in limiting the population of diamondback moth in Moldavia, Romania. In: Talekar NS, editor. Diamondback moth and other crucifer pests. Proceedings of the Second International Workshop, 10-14 December 1990. Tainan, Taiwan. Asian Vegetable Research and Development Center. 1992;203-212.
 122. Fitton M, Walker A. Hymenopterous parasitoids associated with diamondback moth: Taxonomic dilemma. In: Talekar NS, editor. Diamondback moth and other crucifer pests. Proceedings of the Second International Workshop, 10-14 December 1990. Tainan, Taiwan. Asian Vegetable Research and Development Center. Shanhu, Taiwan. 1992;225-232.
 123. Todd DH. Incidence and parasitism of insect pests of cruciferous crops in the North Island, evaluation of data, 1955-58 seasons. New Zeal J Agr Res. 1959;2:613-622.
 124. Kfir R. Parasitoids of *Plutella xylostella* (*Lepidoptera: Plutellidae*) in South Africa: An annotated list. Entomophaga. 1997;42:517-523.
 125. Lim GS. Integrated pest management of diamondback moth. In: Talekar NS, editor. Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Tainan, Taiwan, 10-14 December 1990. Asian Vegetable Research and Development Center, Shanhu, Taiwan. 1992;565-576.
 126. Lohr B, Kfir R. Diamondback moth *Plutella xylostella* (L.) in Africa. A review with emphasis on biological control. In Improving Biocontrol of *Plutella xylostella*. In: Kirk AA, Bordat D, editors. CIRAD, Montpellier, France. 2004;71-83.
 127. Smith TJ, Villet MH. Parasitoids associated with the diamondback moth, *Plutella xylostella* (L.), in the Eastern Cape, South Africa. In: Endersby NM, Ridland PM, editors. The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne. Melbourne, Australia: Department of Natural Resources and Environment. 2004;249-253.
 128. Guilloux T, Monnerat R, Castelo-Brancho M, Kirk AA, Bordat D. Population dynamics of *Plutella xylostella* (*Lepidoptera: Yponomeutidae*) and its parasitoids in the region of Brasilia. In: Kirk AA, Bordat D, editors. Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. 2004;184-189.
 129. Yu DS, Horstmann K. A catalogue of world *Ichneumonidae* (*Hymenoptera*). Memoirs of the American Entomological Institute. 1997;58:1-1558.
 130. Wagener B, Reineke A, Lohr B, Zebitz CPW. Molecular identification of *Diadegma* species (*Ichneumonidae*) parasitizing diamondback moth, *Plutella xylostella* (*Plutellidae*) in eastern and southern Africa. In: Kirk AA, Bordat D, editors. Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. 2004;252-257.
 131. Harcourt DG. Biology of cabbage caterpillars in Eastern Ontario. Proceedings of the Entomological Society Ontario. 1963;83:61-75.
 132. Bieber KD, Hostetter DL, Kern JR. Evolution and implementation of biological control-IPM system for crucifers, 24 year case history. American Entomologist. 1994;40:103-108.
 133. Mitchell ER, Hu GY, Okine JS. Diamondback moth (*Lepidoptera: Plutellidae*) infestation and parasitism by *Diadegma insulare* (*Hymenoptera: Ichneumonidae*) in collards and adjacent cabbage fields. Florida Entomologist. 1997;80:54-62.
 134. Dossall LM, Mason PG. Key pests and parasitoids of oilseed rape or canola in North America and the importance of parasitoids in integrated management. In Biocontrol-Based Integrated Management of Oilseed Rape Pests, ed. IH Williams. Dordrecht/London: Springer. 2010;167-213.
 135. Sourakov A, Mitchell ER. Featured Creatures. USDA. 2000. Accessed 10 March 2014. Available: http://creatures.ifas.edu/wasps/diadegma_insulare.htm.
 136. Putnam LG. Experiments in the quantitative relationships between *Diadegma insularis* (*Hymenoptera:*

- Ichneumonidae*) and *Microplitis plutellae* (Hymenoptera: Braconidae) with their host *Plutella maculipennis* (Lepidoptera: Plutellidae). Can Entomol. 1968;100:11-16.
137. Fox LR, Letourneau DK, Eisenbach J, Nouhuys SV. Parasitism rates and sex ratios of a parasitoid wasp: Effects of herbivore and plant quality. Oecologia. 1990;83:414-419.
 138. Monnerat RG, Kirk AA, Bordat ED. Biology of *Diadegma* sp. (Hymenoptera: Ichneumonidae), a parasitoid of *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae), from Reunion Island. Neotrop Entomol. 2002;31:271-274.
 139. Harcourt DG. Biology of the diamondback moth, *Plutella maculipennis*(Curt.) (Lepidoptera: Plutellidae), in eastern Ontario. III. Natural enemies. Can Entomol. 1960;29:419-428.
 140. Bolter CJ, Laing JE. Competition between *Diadegma insulare* (Hymenoptera: Ichneumonidae) and *Microplitis plutellae* (Hymenoptera: Braconidae) for larvae of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). Proceedings of the Entomological Society of Ontario. 1983;14:1-10.
 141. Idris AB, Grafius E. Evidence of *Diadegma insulare* (Cresson), a parasitoid of diamondback moth, *Plutella xylostella* (L.), present in various habitats. Pak J Biol Sci. 2001;1:742-743.
 142. Lee JC, Heimpel GE. Floral resources impact longevity and oviposition rate of a parasitoid in the field. J Anim Ecol. 2008;77:565-572.
 143. Johanowicz DL, Mitchell ER Effects of sweet alyssum flowers on the longevity of the parasitoid wasps *Cotesia marginiventris* (Hymenoptera: Braconidae) and *Diadegma insulare* (Hymenoptera: Ichneumonidae). Fla Entomol. 2000;83:41-47.
 144. Grafius EJ, Idris AB. Know your friends: *Diadegma insulare*, parasite of diamondback moth. Midwest Biological Control. 1997. Accessed 10 September 2013. Available: <http://www.entomology.wisc.edu/mbcn/kyf401.html>
 145. Moon DC, Rossi AM, Stiling P. The effects of abiotically induced changes in host plant quality and morphology on a salt marsh plant hopper and its parasitoid. Ecol Entomol. 2000;25:325-331.
 146. Sumerford DV, Abrahamson WG, Weis AE. The effects of drought on the *Solidago altissima*–*Eurosta solidaginis*– natural enemy complex: Population dynamics, local extirpations, and measures of selection intensity on gall size. Oecologia. 2000;122:240-248.
 147. Teder T, Tammaru T. Cascading effects of variation in plant vigor on the relative performance of insect herbivores and their parasitoids. Ecol Entomol. 2002;27:94-104.
 148. Ulmer BJ, Dossdall LM, Gibson GAP. Spatio-temporal distribution patterns of the diamondback moth and its principal parasitoid, *Diadegma insulare*, in canola crops and the occurrence of hyperparasitism. Brassica. 2005;6:63-69.
 149. Vet LEM, Dick M. Ecology of infochemicals use by natural enemies in tritrophic contest. Ann Rev Entomol. 1992;37:141-172.
 150. GodfrayHCJ. Parasitoids. Behavioral and Evolutionary Ecology. Princeton University Press, Princeton University Press, Princeton, New Jersey; 1994.
 151. Idris AB, Grafius E. Nectar-collecting behavior of *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth, *Plutella xylostella* L. Environ Entomol. 1997;26:114-120.
 152. Fox LR, Kester KM, Eisenbach J. Direct and indirect responses of parasitoids to plants: Sex ratio, plant quality and herbivore diet breadth. Entomol Exp Appl. 1996;80:289-292.
 153. McCormick AC, Sybille BU, Gershenson J. The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. Trends Plant Sci. 2012;17:303-310.
 154. Wang XG, Keller MA. A comparison of host searching efficiency of two larval parasitoids of *Plutella xylostella*. Ecol Entomol. 2002;27:105-114.
 155. Whitfield JB. Phylogeny and evolution of host–parasitoid interactions in Hymenoptera. Ann Rev Entomol. 1998;43:129-151.
 156. Quicke DLJ, Fitton MG, Notton DG, Broad GR, Dolphin K. Phylogeny of the *Ichneumonidae* (Hymenoptera): A simultaneous molecular and morphological analysis. In Proceedings of the Fourth International Hymenopterists Conference. Canberra, Australia; 2000.
 157. Harvey JA, Strand MR. The developmental strategies of endoparasitoid wasps vary

- with host feeding ecology. *Ecology*. 2002;83:2349-2451.
158. Rosenheim JA, Kaya HK, Ehler LE, Marois JJ, Jaffee BA. Intraguild predation among biological control agents: Theory and evidence. *Biol Control*. 1995;5:303-335.
159. Rosenheim JA. Higher-order predators and the regulation of insect herbivore populations. *Ann Rev Entomol*. 1998;43:421-447.
160. Brodeur J. Host specificity and trophic relationships of hyperparasitoids. In: Hochberg ME, Ives AR, editors. *Parasitoid Population Biology*. Princeton University Press, Princeton, New Jersey, USA. 2000;163-183.
161. Shaw MR. Parasitoid host ranges. In: Hawkins BA, Sheehan W, editors. *Parasitoid community Ecology*. Oxford University Press, Oxford, UK. 1994;11-144.
162. Stiling P, Rossi AM. The window of parasitoid vulnerability to hyperparasitism: Template for parasitoid complex structure. In: Hawkins BA, Sheehan W, editors. *Parasitoid Community Ecology*. Oxford University Press, Oxford, UK. 1994;228-244.

© 2015 Munir et al.; This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Peer-review history:

The peer review history for this paper can be accessed here:
<http://www.sciencedomain.org/review-history.php?iid=668&id=32&aid=6211>