



Review in Advance first posted online
on September 27, 2012. (Changes may
still occur before final publication
online and in print.)

Diamondback Moth Ecology and Management: Problems, Progress and Prospects

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Annu. Rev. Entomol. 2013. 58:517–41

The *Annual Review of Entomology* is online at
ento.annualreviews.org

This article's doi:
10.1146/annurev-ento-120811-153605

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0066-4170/13/0107-0517\$20.00

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Keywords

Plutella xylostella, integrated pest management, biological control, *host plant relationships*, *insecticide resistance*, *Bt-Brassica* crops

Abstract

Agricultural intensification and greater production of *Brassica* vegetable and oilseed crops over the past two decades have increased the pest status of the diamondback moth (DBM), *Plutella xylostella* L., and it is now estimated to cost the world economy US\$4–5 billion annually. Our understanding of some fundamental aspects of DBM biology and ecology, particularly host plant relationships, tritrophic interactions, and migration, has improved considerably but knowledge of other aspects, e.g., its global distribution and relative abundance, remains surprisingly limited. Biological control still focuses almost exclusively on a few species of hymenopteran parasitoids. Although these can be remarkably effective, insecticides continue to form the basis of management; their inappropriate use disrupts parasitoids and has resulted in field resistance to all available products. Improved ecological understanding and the availability of a series of highly effective selective insecticides throughout the 1990s provided the basis for sustainable and economically viable integrated pest management (IPM) approaches. However, repeated reversion to scheduled insecticide applications has resulted in resistance to these and more recently introduced compounds and the breakdown of IPM programs. Proven technologies for the sustainable management of DBM currently exist, but overcoming the barriers to their sustained adoption remains an enormous challenge.

INTRODUCTION

Twenty years have passed since Talekar & Shelton (168) published their landmark review of the diamondback moth (DBM), *Plutella xylostella* L. (Lepidoptera: Plutellidae), and we now know considerably more about many aspects of its biology (34, 147, 155, 161), ecology (125, 129), and genetics (12). Despite these advances, DBM has retained its status as the most destructive member of the different insect pest complexes that attack *Brassica* vegetable crops in various parts of the world (34, 147, 155, 161, 165, 167), and it is increasingly considered a significant, if sporadic, threat to canola production (45).

Between 1993 and 2009 the global area of *Brassica* vegetable crops increased by 39%, and in 2009 an estimated 3.4 million hectares were grown worldwide (38). Concomitant with this change was an intensification of farming practices, with cabbage yields increasing by 27%, and *Brassica* vegetables now contribute more than US\$26 billion to the world economy (38). Over the same period, the area of oilseed rape planted increased by 59%, and in 2009 more than 31 million hectares were cultivated worldwide (38), often in regions where the crop was not previously grown. These changes have resulted in considerable modifications to many local landscapes (45) and provide revised challenges for DBM management (143).

Talekar & Shelton (168) stressed the importance of the proceedings of the international workshops on DBM held in 1985 and 1990 (165, 167). An additional four workshops convened between 1996 and 2011 and each published valuable proceedings on contemporary DBM research (34, 147, 155, 161). In consideration of this body of work, of the many publications in the academic literature, and of the changes that have occurred in *Brassica* crop production since 1993, it is timely to review our knowledge of DBM ecology and management and to set it in the current context.

DBM DISTRIBUTION, CURRENT MANAGEMENT, AND ECONOMIC COSTS

Despite the pest status of DBM and assertions that it has the most extensive distribution of all Lepidoptera (168), current understanding of its global distribution and relative abundance is limited (187). The original distribution map (25) is a composite of incomplete distribution records, and this has recently been superseded by a version that simply records countries where DBM has been reported (16).

Zalucki & Furlong (187) developed and validated a bioclimatic model for DBM that predicts its core distribution, where it persists year-round, as well as regions where it can be a seasonal pest (**Figure 1**). The model also predicts the variable seasonal phenologies exhibited by DBM across its vast range (189), illustrating the population-limiting effects of high rainfall and extreme temperatures (82) that can preclude year-round persistence (55, 58). Further, it identifies regions that are seasonally suitable for DBM population growth, where pest outbreaks can be promoted following DBM influxes (31).

Despite the considerable effort to develop integrated approaches to DBM management (39, 51), the vast majority of *Brassica* crops are treated prophylactically with insecticides (51). This practice is most acute in tropical countries, where nonselective products, which are often mixed, are typically applied 1 to 2 times per week (5, 51, 96); however, excessive use of insecticides against DBM is not restricted to the developing world or the tropics (95). Such practices promote the selection for insecticide resistance (81), destroy natural enemies (44), and contaminate the environment. They are also expensive, and a recent study (189) estimated that annual DBM control in *Brassica* vegetable crops alone costs US\$1.4 billion worldwide, rising to US\$2.7 billion if yield losses are included and to \$4–5 billion if DBM losses and control costs to the worldwide canola industry are added.

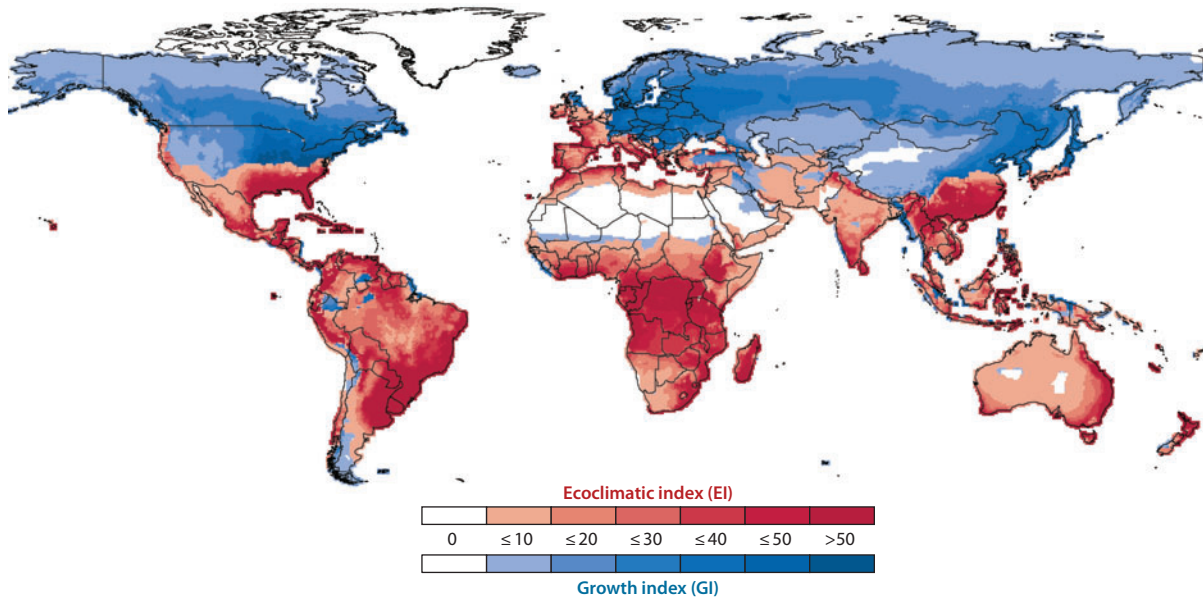


Figure 1

Predicted worldwide distribution of diamondback moth (DBM) based on a validated bioclimatic model (187). Areas shaded in red show regions of the world where the Ecoclimatic Index (EI) is positive and DBM can persist year-round; red shading demarcates the core distribution of DBM. Areas shaded in blue show regions of the world where the EI is zero but where the annual growth index (GI) is positive; in these regions DBM cannot persist year-round but it can become a seasonal pest following influxes of moths from elsewhere.

DBM BIOLOGY AND ECOLOGY: ADVANCES SINCE 1993

Natural Enemies of DBM

A wide range of natural enemies, including parasitoids, arthropod predators, viruses, microsporidia, pathogenic fungi, and bacteria, attack DBM. Considerable basic and applied research has focused on these organisms over the past two decades, particularly on classical biological control programs utilizing hymenopteran parasitoids (129).

Hymenopteran parasitoids. Classical biological control for DBM began in 1936 when the larval-pupal parasitoid *Diadegma semiclausum* (Hellén) (Hymenoptera: Ichneumonidae) and the pupal parasitoid *Diadromus collaris* (Gravenhorst) (Hymenoptera: Ichneumonidae) were successfully introduced into New Zealand from the United Kingdom (168), leading to further introductions of both species from New Zealand into Indonesia (180), Australia (186), and Malaysia (104). Following importation of *D. semiclausum* from Indonesia, the parasitoid was established in Taiwan (169), providing stock material for subsequent successful introductions into the Philippines (177), India (21), Laos, Vietnam, China (166), and Kenya (89). In 2005, *D. semiclausum* from Malaysia successfully established in the highland regions of Thailand (174). Hence, the provenance of the *D. semiclausum* populations that have established throughout Asia, Australasia, and parts of Africa is clear and well documented and all ultimately originate from the United Kingdom. Similarly, the larval parasitoid *Cotesia vestalis* (= *plutellae*) Haliday (Hymenoptera: Braconidae) has been the subject of more than 20 classical biological control introductions, and many of them have been successful (28, 166). In addition, this parasitoid appears to have a wider natural distribution than

D. semiclausum, and it has been recorded to attack DBM in many regions [e.g., Malaysia (104), Taiwan (166), Vietnam (166), China (87), and Japan (3)] with no records of introductions. The larval-pupal parasitoid *Oomyzus sokolowskii* Kurdjumov (Hymenoptera: Eulophidae) has also been recorded in countries with no records of introduction [e.g., Australia (46), Japan (166), South Africa (71), and North Korea (39)]; however it has been deliberately introduced into China and Taiwan (166). Similarly, the DBM pupal parasitoids *D. collaris* and *Diadromus subtilicornis* (Gravenhorst) (Hymenoptera: Ichneumonidae) have widespread natural distributions (28). Since the initial release of *D. collaris* in New Zealand, it has been introduced into many countries (28), but *D. subtilicornis* has never been introduced for biological control (28).

The success of classical biological control programs is often reduced or precluded by the widespread use of broad-spectrum insecticides and/or introductions of species into unfavorable climates (166). Generally, as long as broad-spectrum insecticide use is curtailed, *D. semiclausum* and *D. collaris* establish in cooler, temperate climates, such as highland regions of the tropics, and *C. vestalis* and *O. sokolowskii* perform better in warmer climates, including lowland areas of the tropics (34, 147, 155, 161, 165, 167).

Although the indigenous and introduced parasitic Hymenoptera fauna attacking DBM in many parts of the world are well documented (28), there has been considerable misidentification of specimens and pre-1950 data are often unreliable. Recently, the status of *Diadegma* species attacking DBM has been clarified (6), but recognition of *C. vestalis* Haliday as the senior synonym of *C. plutellae* Kurdjumov (145) is taking time to penetrate the literature. There is evidence for distinct biological differences between some populations of *C. vestalis*, but the existence of cryptic species is not suspected (120). Molecular methods that can reliably identify hosts and immature parasitoids (172) and separate biologically distinct but morphologically identical populations (181), which may have arisen owing to founder effects and/or changes in introduced populations following establishment, provide tools that can improve the success of future biological control programs.

Worldwide, the parasitoid complex that attacks DBM is approximately equal to 60 species (28), considerably fewer than previously suggested (168). However, only around a dozen species are frequently recovered; their taxonomic status and verified distributions are summarized in **Table 1**. Although egg parasitoids have been recorded to attack DBM in many regions of the world (e.g., 83, 87), they appear to be underrepresented in the literature (28). Whether this is due to biology, sampling in agricultural areas where pesticide use is high, or an artifact of survey and collection methods warrants investigation.

Arthropod predators. The focus on parasitoids has meant that other natural enemies, especially predatory arthropods, have received far less attention, although the difficulty of ecologically evaluating predators is likely to have contributed to the limited understanding of their role in suppressing DBM populations (47). In comprehensive life table studies, Harcourt (55) made no mention of mortality due to predators and concluded that rainfall, parasitism by *Diadegma insulare* (Cresson), and reduced female fecundity were the key factors affecting DBM populations in Ontario, Canada. This finding is somewhat surprising given that more recent studies have demonstrated that predators can significantly affect DBM populations in *Brassica*-crop agroecosystems in the United States (101), Australia (43, 44), China (86), and North Korea (39). In Australia, as in Ontario, neonate larvae suffered greatest mortality but much of this could be attributed to arthropod predation (43, 44), indicating that resource partitioning between predators and the major parasitoid, *D. semiclausum*, which attacks larger larvae, can minimize intraguild predation. Harvey & Eubanks (56) showed that field populations of *Solenopsis invicta* could be manipulated to suppress DBM populations, but other experimental field studies of DBM predation are rare; most studies utilize predatory species with no proven field efficacy against DBM in laboratory or



field cage experiments, or feed predators DBM in the laboratory (47). Despite the relative paucity of data when compared to that for parasitoids, predators can be important agents of mortality in DBM populations (39, 43, 44) and the adoption of pest management practices that conserve them can increase pest mortality dramatically (39, 44). Currently, the impact of endemic predator complexes on DBM populations in many *Brassica* agroecosystems is unknown, but it is likely that they represent an underutilized natural resource and further research is required.

Pathogens. DBM is attacked by a range of pathogens and, with the exception of the bacterium *Bacillus thuringiensis*, which has revolutionized DBM management (129), the most important are fungi, viruses, and nematodes. The most well-studied fungal pathogens of DBM include

Table 1 Major primary parasitoids of DBM and their confirmed worldwide distributions

Species [original genus] {synonyms}	Origin	Confirmed distribution records ^a
Primary larval parasitoids		
<i>Diadegma semiclausum</i> (Hellén) [<i>Angita</i>] { <i>Angitia cerophaga</i> Gravenhorst; <i>Diadegma eucerphaga</i> Hortsmann; <i>Diadegma xylostellae</i> Kusigemati}	Palearctic	Europe: United Kingdom, France, Austria, Netherlands, Serbia, Romania, Bulgaria, Turkey, Finland, Russia; Asia: Uzbekistan, Nepal, Iran, Taiwan, Indonesia, Malaysia, Thailand, China, India; Africa: Egypt, Kenya; Australia and Oceania: Australia, New Zealand, Papua New Guinea
<i>Diadegma fenestrata</i> (Holmgren) [<i>Limmeria</i>] { <i>Diadegma varuna</i> Gupta; <i>Diadegma niponica</i> Kusigemati}	Palearctic	Europe: United Kingdom, France, Germany, Romania, Greece, Poland, Finland, Russia; Asia: Japan, India
<i>Diadegma mollipla</i> (Holmgren) [<i>Limmeria</i>]	Afrotropic	Africa: Eritrea, Kenya, Malawi, Tanzania, South Africa, Réunion Island, Mauritius
<i>Diadegma insulare</i> (Cresson) [<i>Mesoleptus</i>] { <i>Limmeria polynesialis</i> Cameron}	Nearctic/Neotropic	North America: Canada, United States, Mexico; South America: Honduras, Venezuela; Caribbean: Puerto Rico, Cuba, Jamaica, Dominican Republic
<i>Diadegma leontinae</i> (Brèthes) [<i>Limmerium</i>]	Neotropic	South America: Brazil, Uruguay, Argentina, Chile
<i>Diadegma novaezealandiae</i> Azidah, Fitton & Quicke	Australasia	Australia and Oceania: New Zealand
<i>Diadegma rapi</i> (Cameron) [<i>Bosminia</i>]	Australasia	Australia and Oceania: Australia
<i>Cotesia vestalis</i> Haliday [Apanteles] { <i>Cotesia plutellae</i> (Kurdjumov)}	Palearctic	Europe: France, Austria, Finland, Serbia, Bulgaria, Russia, Ukraine, Turkey; Asia: Japan, Sri Lanka, China, Taiwan, Vietnam, Indonesia, Malaysia, Philippines, Thailand, Myanmar, India, Pakistan; Africa: Cape Verde Islands, Benin, Senegal, South Africa, Réunion Island; North America: United States; South America: Venezuela, Brazil; Caribbean: Martinique, Barbados, Leeward Islands, St. Kitts, St. Lucia, Trinidad, Guadeloupe; Australia and Oceania: Australia ^b , Hawaii, Fiji ^c
<i>Microplitis plutellae</i> Muesbeck	Nearctic	North America: Canada, United States; Asia: Laos
<i>Apanteles balfordii</i> Ulyett { <i>Apanteles eriophyes</i> Nixon}	Afrotropic	Africa: South Africa
<i>Apanteles picotrichosus</i> Blanchrad	Neotropic	South America: Argentina, Brazil, Venezuela

(Continued)



Table 1 (Continued)

Species [original genus] {synonyms}	Origin	Confirmed distribution records ^a
<i>Oomyzus sokolowskii</i> (Kurdjumov) [<i>Tetrastichus</i>]	Palaearctic	Europe: France, Switzerland, Italy, Hungary, Romania, Russia; Asia: Pakistan, India, Sri Lanka, Japan, China, <i>North Korea</i> ; Africa: Egypt, Cape Verde Islands, Senegal, Benin, Kenya, South Africa; North America: Canada, United States; South America: Brazil, Chile; Caribbean: Jamaica, Dominican Republic, Barbados, Trinidad, Martinique; Australia and Oceania: <i>Australia, Fiji</i> ^c
Primary pupal parasitoids		
<i>Diadromus collaris</i> (Gravenhorst) [<i>Ischnus</i>]	Palaearctic	Europe: United Kingdom, Netherlands, Germany, France, Austria, Serbia, Romania, Bulgaria, Turkey; Asia: India, Japan, China, Malaysia, <i>North Korea</i> ; Africa: South Africa; Australia and Oceania: Australia, New Zealand, Fiji ^c , Cook Islands
<i>Diadromus subtilicornis</i> (Gravenhorst) [Ichneumon]	Holarctic	Europe: Germany, Poland, Serbia, Romania, Finland, Russia; Asia: Japan; North America: Canada; Caribbean: Dominican Republic

^aConfirmed distribution records compiled from References 28, 34, 147, 148, 166. Sources: regular font, Delvare (28); *italic font*, field records published since Delvare (28); underlined font, records published since Delvare (28) where the parasitoid was established in a country following a classical biological control program and identity was not in doubt.

^bRecent studies (45) indicate that *C. vestalis* is not widely distributed in Australia and is only encountered extremely rarely.

^cExtensive surveys in Fiji showed that *Cotesia vestalis* and *Oomyzus sokolowskii* are regularly recovered from diamondback moth hosts but indicate that *Diadromus collaris* is not established (5).

Zoophthora radicans, *Beauveria bassiana*, *Metarhizium anisopliae*, and *Isaria farinosa* (= *Paecilomyces farinosus*) (129), and significant work has been conducted on their pathogenicity, biology, and ecology (41, 42, 129). Natural epizootics of *Z. radicans* can cause DBM populations to crash; the biology and ecology of the pathogen are well understood (41, 42) and practical methods for its dissemination have been developed (40, 179). However, much of the work on entomopathogenic fungi remains experimental, and although some products are available for field use, they do not yet form part of adopted IPM programs. Similarly, granulosis, nucleopolyhedrosis, and cyroviruses have been isolated from DBM (51). Although the granulosis virus *PlxyGV* has performed well in experimental trials, commercial products are not available outside China and viruses do not form part of any current IPM program (51). Finally, entomopathogenic nematodes (*Steinernema* sp. and *Heterorhabditis* sp.) have been investigated for microbial control of DBM and ultra-low-volume application techniques have been promising in trials (94); however, open field use is constrained by susceptibility to UV and high relative humidity requirements (51).

DBM–Host Plant Interactions

The economic importance of DBM is defined by its pest status on crops belonging to the family Brassicaceae, especially the genus *Brassica* (1). Not all plants exploited are crops and many of the noncrop and weedy species utilized (67, 125) are often considered important refugia for DBM and associated parasitoids when crop hosts are scarce (46, 67).

Glucosinolates. Glucosinolates are nonvolatile compounds (59, 171) that dominate interactions between DBM and its Brassicaceae hosts, although other secondary plant compounds play important roles (118, 175). Approximately 30 aliphatic, aromatic, and indole glucosinolates have been

isolated in the genus *Brassica* (59, 171); the complement within plants is affected by environmental conditions and varies among tissues, ontogenetic stages, species, and cultivars within species (59). Glucosinolates have limited biological activity, but when plant tissue is damaged they come into contact with myrosinase, resulting in the rapid production of toxic hydrolysis products. These products include the isothiocyanates, which have broad-spectrum toxicity to insects, including DBM (80). However, their production in DBM is circumvented by a glucosinolate sulfatase in the gut lumen that removes sulfur from glucosinolate molecules, thereby preventing myrosinase hydrolysis and inhibiting the formation of toxic products (114). Consequently, DBM can consume glucosinolates with no or little effect on larval performance (80, 103) provided myrosinase activity is not elevated (80); both aliphatic and indole glucosinolates actually promote feeding in DBM larvae (103).

Isothiocyanates are powerful attractants and oviposition stimulants (119) while intact glucosinolates are potent postlighting DBM oviposition stimulants (66); recent research indicates that nonvolatile indole glucosinolates are particularly important in this regard (164). Surface waxes are also important for DBM oviposition and synergistic interactions with cabbage homogenates, and the aliphatic glucosinolate sinigrin promotes DBM oviposition (160). Owing to the nonvolatile nature of sinigrin, it has been suggested that spontaneous degradation of the glucosinolate and then adsorption of the allyl isothiocyanate released to the wax are the likely mechanisms for this effect (119). However, in at least some *Barbarea* species, glucosinolates may be present in the surface waxes of leaves (7), providing a possible explanation for the attractiveness of these plants for DBM oviposition (146). Total glucosinolate levels in plants can increase in response to feeding by DBM or by exogenous application of defense response elicitors, which leads to changes in the ratios of aliphatic, aromatic, and indole compounds (171). To date no distinct patterns have emerged and induced changes to the glucosinolate profile, if they occur, are heavily dependent on plant species (171).

Inducible host plant responses: effects on DBM oviposition and performance. Contrasting constitutive defenses between host plants can result in considerable differences in the performance of DBM (110, 126, 191, 192). Herbivory or the application of defense response elicitors can induce changes in the glucosinolate (49, 171) and volatile profiles (48, 74) of DBM host plants that can manifest both as modified patterns of oviposition between (91, 151) and within (153) plants and as additional, but variable, effects on DBM performance (60, 192). Despite considerable attention in recent years, understanding of the relationships between constitutive and induced defenses remains a challenge due to their complexity (191) and the confounding effects of herbivory on experimental systems (192). The complexity of induced defenses increases further when their role in indirect defenses are considered (48, 74), and there is even evidence that ovipositing DBM can discriminate between plants harboring parasitized conspecific hosts (24).

Non-Brassicaceae host plant associations. DBM oviposition on non-host plants can be induced by experience (190) and is associated with hosts outside the Brassicaceae (125). Still, the reported host shift of a Kenyan DBM population onto *Pisum sativum* L. (Fabaceae) in 1999 (90) caused considerable interest. Genetic analysis of the DBM population showed that the alleles enabling survival on *P. sativum* were not fixed (57), indicating the significant genetic plasticity of DBM and an incomplete host shift.

Tritrophic interactions. *Cotesia vestalis* and *D. semiclausum* are attracted to volatiles emitted from DBM-infested host plants (15, 111) but show distinct preferences for infested *Brassica rapa* and *Brassica oleracea* plants, respectively (84, 178). *B. oleracea* and *B. rapa* plants emit volatile blends



that include green leaf volatiles, isothiocyanates, nitriles, dimethyl trisulfide, and terpenes (48, 74), and DBM feeding induces qualitative, but not quantitative, changes in the volatile profiles of each plant species, which result in increased attraction of *C. vestalis* (48, 74). Feeding induces greater production of certain volatiles and the changed profiles are indicative of current infestation status (74) and the density of infesting DBM larvae (48); they also stimulate postlighting foraging of parasitoids (173). Despite these advances, much about the roles of different volatile blend components and the plant signaling pathways (157) that mediate attraction of DBM natural enemies to infested plants remains poorly understood. For example, Reddy et al. (117) reported that green leaf volatiles are attractive to *C. vestalis*, whereas Shiojiri et al. (150) suggested that they are not attractants but that they may play roles in postlighting arrestment of the parasitoid and Kugimiya et al. (74) and Ibrahim et al. (60) reported conflicting results regarding the attraction of *C. vestalis* to limonene. Similarly, methyl salicylate appears to have negative effects on *D. semiclausum* orientation to plants (156), but it is produced in large quantities by DBM-infested *B. oleracea* (48) that are attractive to *D. semiclausum* (15). Clearly, blends of volatiles, rather than single compounds, mediate the responses of DBM parasitoids and this requires further investigation.

The nutritional status of host plants can significantly affect DBM oviposition preferences, and sulfur fertilizers (8, 93) and treatments that increase foliar nitrogen (162) promote egg laying. Although sulfur improved DBM larval performance on *Brassica napus* (93), the effects of different fertilizer treatments on larval performance in other crops are less clear (163). Similarly, the performance of *D. insulare* was affected by DBM host plant (127) and fertilizer regimes (128), and elevated foliar nitrogen resulted in improved *D. insulare* performance (128).

Despite demonstrable host plant effects on the performance and fitness of DBM (126, 158) and its parasitoids (32, 49, 127), measurable negative effects on DBM do not affect parasitism by *C. vestalis* (70) or host-parasitoid populations dynamics (69). There is still a great deal to understand about these complex interactions, and future studies utilizing nondomesticated ancestral host plants (49) will provide important insights and possible evolutionary interpretation. Currently, studies using domesticated host plants that proffer evolutionary explanations for tritrophic interactions should be treated with great caution.

Local Movement and Migration

DBM movement within crops is effected via a series of short, trivial flights within the crop canopy (97). In mark-recapture studies, male and female moths had similar dispersal characteristics and together more than 95% of individuals moved less than 110 m and more than 99% moved less than 200 m from release points within 5 to 9 days (97). Although the vast majority of individuals typically remain with the natal crop, there can be significant movement between the crop and neighboring flowering vegetation (142), and a small proportion of individuals (<1%) may move greater distances from healthy crops to colonize neighboring crop patches (97).

Longer-range movement of DBM is achieved through active migration, which explains its cosmopolitan distribution (168) (**Figure 1**) and the apparently panmictic populations that cover much of the globe (33, 79). This migratory capacity enables DBM to move from areas that allow year-round persistence into areas that are only seasonally suitable for growth and development (**Figure 1**). Regions where DBM cannot survive low winter temperatures can be invaded annually from regions where it can overwinter. A three-dimensional back-trajectory model based on wind fields originating in southern United States and northern Mexico explains the arrival of DBM to the Canadian prairies, where its overwinter survival is limited (31). In northern Japan, cold winter conditions prevent DBM from overwintering, but annual recolonization from southerly regions can occur (58). Most evidence for such migrations is indirect, but in the United Kingdom

vertical-looking radar and aerial netting has confirmed DBM migrations from continental Europe (22) and radar has also been used to successfully predict DBM migrations in Finland (78).

Although mass migration of DBM is a well-established phenomenon (22), causal factors require further investigation. Typically, migrants have smaller bodies, larger wings, and extended adult longevity compared with nonmigratory forms (19), and these characteristic phenotypic traits are exhibited by DBM reared on mature plants and wild Brassicaceae (19, 102). Photoperiod alone did not affect the development of these phenotypic traits in DBM (18), but it has yet to be studied in combination with other environmental factors. Similarly, DBM reared on optimally fertilized foliage (131) or preferred host plants (132) had larger wing areas and lived longer as adults than did DBM reared on suboptimally fertilized foliage or less preferred hosts but they also had larger bodies than insects reared on suboptimal diets. Thus, in isolation, host plant genotype and nutritional status do not appear to promote traits characteristic of migrant forms. However, Shirai (152) argues that large-bodied, long-winged adult DBM that typically develop in cooler seasons are well adapted to migration, as they have enhanced flight abilities and are more fecund. Although more is now understood about mass movements of DBM, the phenotypic characteristics of migrating individuals, the biotic and abiotic cues that promote migration, and whether populations make return migrations remain unclear.

Possible migration of DBM parasitoids has also been used to explain their confluence with the progeny of migrating DBM adults. In western Canada, *D. insulare* is the principal parasitoid of DBM but it cannot survive the harsh winter conditions (30). Its origins remain undetermined, but it most likely migrates northward along with its hosts. In Australia, migration of *D. semiclausum* has also been proposed to explain recolonization of canola cropping regions following population declines or extinctions in hot, dry summers (45). However, in northern Japan, *C. vestalis* overwinters as diapausing prepupae in regions too harsh for DBM winter survival and adults emerge in spring (3) just as migrating DBM populations arrive from southern Japan (58). Similarly in Hangzhou, China, *O. sokolowskii* and *D. collaris* are quiescent in winter (87), and winter diapause of both *C. vestalis* and *O. sokolowskii* in North Korea has been suggested to explain the remarkably consistent parasitism of DBM populations, presumably from southern China (79), that invade *Brassica* crops each year (39). It is likely that both migration and overwintering of parasitoids play a significant role but that the relative importance of each differs both spatially and temporally; this warrants further research.

DBM at the Landscape Scale

DBM uses mainly olfactory cues to locate host plants (108), and volatile plant chemical cues are more important than vision at short distances (26). Upon landing, DBM uses chemical cues to verify plant identity and to select a site for oviposition (66).

Agricultural landscapes can be extremely variable, and noncrop habitats can provide alternative prey, hosts, and nectar sources for natural enemies that can suppress herbivorous insect populations (77). The proximity to less-managed habitats can provide access to refugia for predators and parasitoids of DBM (14, 142).

Spatial distribution patterns of DBM are often patchy in both vegetable (109, 185) and canola cropping systems (130). The mechanisms driving these patterns are variable but can include host plant patch size (53), intraspecific variation in plant chemistry and morphology (73), nutrient levels of host plants (130), and feeding damage caused by other herbivores (185).

In canola cropping systems, DBM distributions were generally dissociated with high levels of nitrogen in leaf tissues (130). Although laboratory studies determined that oviposition was higher

on sulfur-sufficient than on sulfur-deficient plants (8, 93), relationships between field distributions of DBM and sulfur were inconclusive (130). Much more research is needed to better understand how DBM processes olfactory, visual, and other cues relating to host plant location and acceptance, and how these characteristics interact with its flight and dispersal characteristics, perceptive ability, and preferences for feeding and oviposition.

INSECTICIDES, RESISTANCE, AND INTEGRATED RESISTANCE MANAGEMENT STRATEGIES

Insecticide Resistance and DBM

DBM is one of several secondary crop pests that have dramatically increased in importance owing to the overuse of broad-spectrum insecticides since their introduction in the late 1940s (168). Intensive insecticide use against DBM in high-value *Brassica* crop production has led to increased selection pressure for resistance, particularly in the tropics and subtropics, where there are many generations of DBM each year, crop production can be continuous, and there are few noncrop host plants (168). For example in highland areas of Malaysia, more than 90% of farmers use synthetic insecticides against DBM; typically farmers use three to four types of insecticide during the 10- to 12-week crop cycle and applications are made 1 to 2 times per week (96).

Talekar & Shelton (168) reviewed the early history of insecticide resistance in DBM, and we focus on examples of field resistance reported more recently (**Table 2**). DBM is one of the few insect species that has developed field resistance to all major classes of insecticides (**Table 2**) and is ranked second in the Arthropod Pesticide Resistance Database (APRD) for the highest number of insecticides with reported resistance in at least one population (4). In 2012, the APRD listed 82 compounds for which resistance in DBM has been reported (4). DBM was the first species to develop field resistance to *Bacillus thuringiensis* (*Bt*) Cry toxins (168), and it is one of only three insect species to have developed field resistance to Bt-based spray products (4); this resistance is also widespread (4) (**Table 2**).

Whether insecticide resistance in field populations of DBM is a primary factor in control failure is debatable, and growers can often quickly resort to a product with a different active ingredient to which resistance is not initially observable (178). Pest resurgence due to the destruction of natural enemies through the overuse of persistent broad-spectrum insecticides (39, 44) is at least as important as resistance and also increases the likelihood of crop residue problems (166, 168, 178).

Many of the newer insecticides introduced to control DBM over the past 25 to 30 years have been more selective and thus more compatible with natural enemies. They have, however, usually been introduced sequentially and in spray mixtures with less selective older compounds to which the insect population has already become resistant. This has often resulted in the rapid development of resistance to the newer insecticide and has precluded conservation of natural enemies (96, 140, 141, 178). Evidence suggests that it may only take two to three years for problematic levels of resistance to develop following the introduction of a new insecticide (195, 141, 184). Recent examples of field resistance to relatively selective compounds, such as indoxacarb, avermectins, spinosad, *Bt*-based products, benzoylureas, and chlorantraniliprole, are presented in **Table 2**. Thus, although insecticide resistance may or may not result in control failure, it has been responsible for the loss of many of the more selective insecticides that could otherwise have formed part of integrated resistance management (IRM) and, more broadly, IPM programs for DBM.



Resistance Mechanisms and Cross-Resistance and Multiple Resistance in DBM

Details of the mechanisms and genetics of resistance in field-selected DBM populations are often limited (**Table 2**). Metabolic resistance mechanisms are the most commonly detected, although altered target site resistance to pyrethroids is known (36) and it is the major mechanism for resistance to *Bt* (**Table 2**). Inheritance of resistance in field-selected populations appears to be

Table 2 Reports of diamondback moth field resistance to insecticides (1996–2012)

Insecticide class ^a	Country ^b	Mechanism ^c	Cross-resistance	Genetics ^d
Organophosphate	Australia (10, 37), China (197), Costa Rica (20), India (76, 123, 176) (65), Nicaragua (106), Pakistan (5a), Philippines (133), South Africa (144), South Korea (72)	MFO, GST, esterase (37)	None: avermectin (10)	–
Carbamate	China (196), India (123, 176), South Africa (144), South Korea (72), Taiwan (68)	–	–	–
Pyrethroid	Australia (10, 35, 37) (36), Brazil (27), China (183, 193, 197), India (29, 76, 123, 176) (65), Japan (100), Malaysia (135), New Zealand (17), Nicaragua (106), Pakistan (5a, 134), Philippines (133), South Africa (144), South Korea (75), United States (148)	MFO, GST, esterase (37), Kdr (75)	None: indoxacarb, spinosad, fipronil (134)	I-D (29) I, poly (134)
Indoxacarb	Australia (37), Brazil (124), Malaysia (137) (141), United States (194), Pakistan (5a)	MFO, GST (37), esterase (37, 141)	–	I, mono (141)
Avermectin	Brazil (27, 124), China (52, 112, 193, 196, 197), Malaysia (137) (62, 63), Pakistan (5a), Taiwan (68)	MFO/esterase (63)	None: benzoylureas (196) (63), <i>Bt</i> (62) Low: spinosad, fipronil (112)	I, poly (112)
Cyclodiene (endosulfan)	India (76, 176)	–	–	–
Phenylpyrazole	China (197), Malaysia (137), India (99), Taiwan (68)	–	Low: spinosad, indoxacarb (140)	I, mono (140)
Spinosyn	Malaysia (137), United States (11, 95, 194, 195), Pakistan (5a), Taiwan (68)	Probably not MFO or esterase (195)	None: emamectin, indoxacarb (195)	I, mono (195), R-I, mono (137)
Nereistoxin analog	China (197), India (99), Taiwan (68), Nicaragua (106)	–	–	–
Neonicotinoid (acetamiprid)	Malaysia (135)	–	Maintains pyrethroid R (135)	I, mono (135)
<i>Bt kurstaki</i> Cry1A	Central America (107), China (50, 182), India (98, 105, 176), Malaysia (62, 137), United States (88, 170), Taiwan (68), Thailand (61)	No binding to gut membrane (138)	Low: Cry1C (50, 62)	R-I, mono (138), I, mono (170)

(Continued)

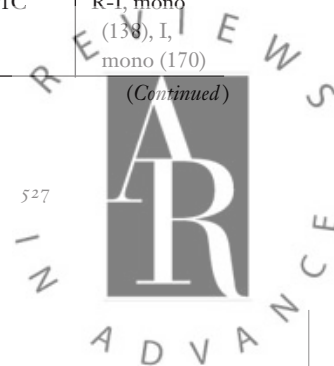


Table 2 (Continued)

Insecticide class ^a	Country ^b	Mechanism ^c	Cross-resistance	Genetics ^d
<i>Bt aizawai</i> Cry1C	Malaysia (137) (62), United States (88), Taiwan (68), Thailand (61)	–	Low: Cry1A (62)	–
Oxidative phosphorylation uncoupler	China (196), Taiwan (68)	–	–	–
Benzoylurea	Brazil (124), China (52, 193), Japan (100), Malaysia (62, 63), Nicaragua (106)	MFO/esterase (63)	None: avermectin (63)	–
Diaclhydrazine	China (196)	–	–	–
Azadirachtin	Taiwan (68)	–	–	–
Anthranilic diamides	China (81, 184)	–	–	–

^aMode of action (IRAC classification; 64) for each insecticide class: organophosphate, acetylcholinesterase (AChE) inhibitor; carbamate, AChE inhibitor; pyrethroid, Na⁺ channel inhibitor; indoxacarb, Na⁺ channel blocker; avermectin, Cl⁻ channel activator; cyclodiene, γ -aminobutyric acid (GABA) Cl⁻ channel antagonist; phenylpyrazole, GABA Cl⁻ channel antagonist; spinosyn, nicotinic acetylcholine receptor (nAChR) activator; nereistxin analog, nAChR blocker; neonicotinoid, nAChR agonist; *Bt kurstaki/aizawai*, midgut membranes; benzoylurea, chitin synthesis inhibitor; diaclhydrazine, ecdysone agonist; azadirachtin, unknown.

^bCountry where field resistance has been documented.

^cPutative resistance mechanisms: MFO, mixed function oxidase; GST, glutathione-S-transferase; Kdr, knock-down resistance (Na⁺ channel).

^dSuggested mode of inheritance: R, recessive; I, intermediate (incompletely recessive to incompletely dominant); D, dominant. Estimated number of factors: mono, monogenic; poly, polygenic.

mostly intermediate (incompletely recessive to incompletely dominant) and monogenic (Table 2). In addition to studies on field-selected populations, studies of laboratory-selected field populations have been informative regarding resistance mechanisms and cross-resistance. With the caveat that laboratory selection for resistance may not completely mirror what happens in the field, where environmental influences can influence resistance expression (115), such studies are informative (159).

Reports of little or no cross-resistance between insecticide classes predominate in field-selected populations of DBM, although cross-resistance to other, untested classes of compounds cannot be excluded, particularly as metabolic mechanisms of resistance, which can confer broad-spectrum resistance, are common (Table 2). For example, an unexpected case of putative reciprocal cross-resistance between *Bt* Cry1Ac toxin and the pyrethroid deltamethrin has been reported in a laboratory-reselected field population of DBM from Malaysia (136). Multiple resistance, in which several different resistance mechanisms present in resistant individuals combine to give resistance to multiple classes of compounds, is a common phenomenon in insects and examples of putative multiple resistance have been reported in several DBM field populations (62, 63, 65, 112).

Insecticide Resistance Management: Theory and Implementation

Selection for resistance results in a fitness cost in the absence of the insecticide and can lead to a reversion of resistance in the absence of selection; that this occurs is the underlying assumption in resistance management (121). Various laboratory studies have examined fitness factors in field- and laboratory-selected DBM populations; whereas some studies have shown large fitness costs



(139) others have not (88), although such costs are not always easily discernible. In most laboratory studies resistance declines in the absence of reselection but it can also be stable (88, 170).

The effects of fitness costs are likely to be more critical to insect survival in the field than in the laboratory where factors such as pathogens, resource limitation, and temperature extremes increase costs of resistance, although the mechanisms behind these increases remain unknown (115). A meta-analysis of standardized fitness studies on DBM found that fitness costs were consistently high on low-quality plants but more variable on high-quality plants, suggesting that fitness modifiers moderate fitness costs only when resources are high (116). Molecular genetic studies on insecticide resistance in DBM (12, 36) will provide greater insights into the evolution and movement of insecticide resistance alleles in DBM populations and ultimately lead to improved pest management.

The factors limiting widespread introduction and sustainability of IRM programs in many regions are complex, but the need to strengthen links between research and extension is central to their success (149, 154). An IRM program to conserve selective insecticides for DBM has been implemented in the Hawaiian Archipelago (95), where resistance to spinosad evolved following continuous exposure of insect populations. The Insecticide Resistance Action Committee (IRAC)-sponsored program, which was implemented by growers and assisted by extension advisors, banned spinosad and replaced it with monthly rotations of emamectin benzoate and indoxacarb until DBM populations recovered susceptibility. In Australia, a national insecticide rotation strategy for IRM on *Brassica* crops includes six different mode-of-action insecticide groups (9), although there is concern about the widespread adoption of three recently registered diamide products, particularly a persistent systemic formulation, in place of other selective products (9).

ALTERNATIVE AND EMERGENT TECHNOLOGIES AND MANAGEMENT STRATEGIES

Transgenic *Bt-Brassica* Crops

Transgenic canola, cabbage, and cauliflower plants carrying gene(s) for *Bt* toxins have been tested successfully against DBM in field and screen-house trials (113, 122). Transformed cabbage and cauliflower lines can suppress populations of DBM and other major lepidopteran pests of *Brassica* vegetables but they have no direct effects on either *D. insulare* or a generalist predator (122). As such, they offer considerable promise for inclusion in improved IPM programs, particularly as the technology offers a possible solution to the current intractable overuse of broad-spectrum insecticides in many developing countries. However, despite these experimental successes, regulatory and liability issues have made it impossible for the transformed vegetables to be field released and product development ceased in 2010 (122).

Genetic Control Techniques

Mass release of sterile γ -irradiated DBM (168) has not proved effective for pest management. However, recent developments in genetic technologies have seen the development of autocidal biological control strategies in which mass-reared insects are homozygous for dominant lethal genetic constructs and the timing of death can be engineered (2). Such strategies for DBM have yet to be tested in the field, but recent theoretical work shows that they could make significant contributions to the dilution of insecticide resistance alleles in pest populations, particularly in the context of the high-dose refuge strategies that are fundamental to the deployment of *Bt* crops (2).

Trap Crops and the Manipulation of Host Plant Resistance

Shelton & Badenes-Perez (146) reviewed 21 studies on the use of trap crops against DBM, but in only one instance (Indian mustard as a trap crop for cabbage in India) had the technology been adopted by farmers; all other cases were unsuccessful or had been tested only in small-scale laboratory or field experiments. An interesting development has been the deployment of dead-end trap crops based on *Barbarea vulgaris* var. *arcuata*, which is preferred for oviposition but contains saponin that is lethal to neonate larvae (7). Recent work has shown that sulfur fertilization can increase glucosinolate levels of *B. vulgaris* and promote DBM oviposition on fertilized plants (8). When extracts of *Chrysanthemum morifolium* were applied to host plants, volatiles were less attractive to DBM compared with untreated plants and oviposition was reduced; however, extract-treated plants were more attractive to *C. vestalis* and promoted parasitism rates (85). Charleston et al. (23) showed that *Syringa* extracts changed the volatile profile of treated plants, making them more attractive to *C. vestalis*. Although host plant experience can significantly affect DBM oviposition preferences (190), studies such as these, which show that the behavior of DBM and its natural enemies can be manipulated simultaneously, and research investigating plant defensive chemistry provide new ways in which host plants can be manipulated and they could play an important role in the future management of DBM.

INTEGRATED PEST MANAGEMENT: CONSTRAINTS TO IMPLEMENTATION AND ADOPTION

The abject failure of single-tactic control programs is clear, and the importance of integrated strategies for the sustainable management of DBM has been central to research for decades (51, 165, 167). Fundamental to all programs is the conservation of natural enemies, frequent pest and natural enemy sampling, and threshold-directed interventions with selective insecticides, particularly *Bt* (39, 149, 154). The benefits of IPM adoption can include higher profits due to improved crop quality, higher yields, and reduced input costs and reduced exposure of farmworkers and the environment to hazardous broad-spectrum insecticides (39, 154).

Despite these clear advantages, IPM adoption typically regresses following the termination of implementation initiatives (149, 154, 188) due to lack of confidence in the technology, co-occurring pests, the time taken to sample pest populations, and the relative complexity of threshold-based decision making (149, 154). Recognition of the need to manage the wider pest complex has led to the development of weighted sequential sampling plans to guide decisions based on the overall density of the pest complex (54, 149), but adoption remains constrained. In developed countries, traditional extension practices can be effective but retention of trained personnel and conservative decision making compromise the process. Ironically, the advent of several selective insecticides (e.g., spinosad, emamectin, and indoxacarb) in the late 1990s exacerbated problems as their initial effectiveness led to overuse and the gradual, if inadvertent, abandonment of IPM by previous practitioners (149, 188). In Australia, partial adopters of an IPM strategy accrued the associated costs but did not reap the benefits of suppressed DBM populations enjoyed by complete adopters (44).

In the developing world, resource-poor farmers produce *Brassica* crops on numerous small farms. Typically, they are subject to considerable pressure to buy pesticides, have access to illegal compounds, and are supported by very weak extension agencies and networks (154). Since the late 1990s farmer field schools (FFS) have been used extensively to promote IPM in developing countries, particularly in Southeast Asia. *Brassica*-IPM FFS ideally consist of groups of approximately 20 farmers that meet weekly under the guidance of a trained facilitator to learn to

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monitor the ecology of their crops, particularly pest and natural enemy populations, and thereby make informed decisions regarding interventions. Such programs, though costly and requiring a well-developed research infrastructure, have been effective and trained farmers commonly use lower insecticide inputs than untrained neighbors do (92). However, claims that FFS initiatives are propagated by trained farmers training subsequent cohorts appear to be exaggerated (13), and other face-to-face methods and use of mass media are likely to be effective IPM extension techniques for the valuable farmer education programs promulgated by FFS.

SYNTHESIS AND CONCLUSIONS

DBM is a secondary pest of *Brassica* vegetables and associated crops that has been elevated to major pest status by current modern farming practices, particularly the widespread, and often indiscriminate, use of broad-spectrum synthetic insecticides.

The dominant role of insecticides in DBM management is reflected in their profile in the research agenda. Analysis of the papers presented at the six international workshops on DBM management that have been held since 1985 is informative (**Supplemental Figure 1**; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>) and the importance of insecticides is clear (**Supplemental Figure 1c**). The proportion of papers reporting on insecticides and IRM fell from a high of 40% in 1985 to a low of 18% in 2001; however, by 2011 it had increased to 32% due to several reports of strategies to manage resistance to selective insecticides, including the recently introduced diamide class. Similarly, the data also reflect the dominance of parasitoids in biological control research, and there is a significant negative correlation ($F_{1,5} = 8.72$; $P = 0.04$; $r^2 = 0.685$) between reported biological control research and research on insecticides (**Supplemental Figure 1b,c**). IPM strategies and their implementation consistently account for only approximately 15% of research (**Supplemental Figure 1e**), a worrying statistic considering that effective implementation is fundamental to the adoption of IPM and is the greatest current constraint to sustainable DBM management. Studies on basic biology and ecology typically represent 10–20% of research (**Supplemental Figure 1a**), and over the past decade considerable research has been conducted on *Brassica* crops engineered to express *Bt* toxins (**Supplemental Figure 1f**). This has coincided with cessation of research on other novel strategies and a decrease in research on interactions with host plants (**Supplemental Figure 1d**). Given the current constraints on field release of *Brassica* vegetable crops, adoption of this technology in the short term appears unlikely.

For many decades researchers have studied the biology and ecology of DBM, and in recent years our understanding of some fundamental aspects, particularly DBM–host plant relationships, plant–DBM–parasitoid tritrophic interactions, and migration, has improved considerably. DBM is attacked by a wide range of natural enemies, and biological control has focused primarily on larval and pupal hymenopteran parasitoids that have formed the basis of IPM programs proven to work in the short term. However, despite the sustainability of this technology, adoption is poor and programs typically regress following implementation as growers gradually return to calendar application of insecticides. This was particularly the case following the introduction of the selective insecticides indoxacarb and spinosad into DBM management in the late 1990s. Both products, like *Bt* formulations before them, eventually became the victims of their own success, as initial judicious use gave way to indiscriminate application and the rapid evolution of resistance; this cycle is currently being repeated for the recently introduced diamide insecticides. Overcoming the barriers to the sustained adoption of these proven technologies for the management of DBM remains an enormous challenge but one that must be overcome as the number of effective selective insecticides continues to dwindle.

FUTURE ISSUES

1. Mechanisms to facilitate sustained adoption of conventional IPM must be developed. The technology for sustainable management of DBM within the context of integrated *Brassica*-crop management exists, but current weak extension mechanisms fail to achieve the requisite community-level behavioral changes that are necessary for enduring adoption. In order to succeed, future initiatives will need to target broader community education programs, be developed on a regional scale, and ensure the active participation of growers, extension officers, pesticide resellers, policy makers, and scientists.
2. The deployment of *Bt-Brassica* crops offers tremendous opportunities for improved DBM management, and solutions to the current regulatory impasses are required. Sustainable adoption of the technology will depend on effective resistance mitigation strategies that will require effective community education and possibly legislation. The technology for tissue and ontogenetically specific expression of transgene products and the deployment of transgenic insects for autocidal biological control that could attenuate the evolution of resistance already exist.
3. Understanding regional movement of DBM is fundamental to effective pest management, particularly in the context of resistance management. Current comprehension of the biotic and abiotic cues that underpin migration of DBM is incomplete, and studies investigating the effects of extreme temperature and nutritional stresses are likely to provide significant insight.
4. The predatory arthropod fauna in *Brassica* agroecosystems can represent a significant natural resource for DBM management. However, despite huge investments in other aspects of biological control, predators remain poorly studied and they are likely underexploited in IPM; this should be addressed in future research.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Sue Scull for her incredible patience and for collating and formatting all the references.

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6. Resolves taxonomic confusion involving this important genus, thereby facilitating identification of different species worldwide.

12. Uses restriction-site associated DNA sequencing to construct de novo genetic linkage map from DBM backcross that segregated for resistance to spinosad.

22. Provides direct evidence for long-range flight by monitoring and intercepting aerially migrating DBM.



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