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Natural History, Ecology, and Management of Diamondback Moth (Lepidoptera: Plutellidae), With Emphasis on the United States

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ABSTRACT. Diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), has become the most destructive insect pest of cruciferous vegetables (*Brassica oleracea* L.) worldwide, and is a continuing problem especially in the southern United States. Because of inconsistencies in individual control methods, inefficiencies and time demands of scouting, and the lack of clear thresholds, current management practices emphasize the prophylactic use of insecticides. Numerous other methods are available for the management of *P. xylostella* including host plant resistance, biological controls, cultural controls, behavioral management, and judicious use of insecticides. Past experience has shown that alone, none of these strategies will work sufficiently and insecticide misuse and resistance issues will likely continue. However, when used together, these tactics can complement each other and lead to a more sustainable system. Recent research focused on the molecular genetics and genomics of *P. xylostella* has dramatically increased our understanding of specific mechanisms controlling *P. xylostella* physiology and its interactions with plants. This has the potential to revolutionize the way we manage this pest. Here we summarize the natural history and ecology of diamondback moth and present options for its sampling and management. Additionally, we highlight recent research that may lead to a more integrated approach to managing this pest and the suite of other insect pests of *Brassica* crops.

Key Words: diamondback moth, *Plutella xylostella*, *Brassica oleracea*

Introduction

Diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), has become the most destructive insect pest of *Brassica* vegetables (*Brassica oleracea* L.) worldwide, with annual management costs estimated in the billions of dollars (Talekar 1992, Talekar and Shelton 1993, Shelton 2004, Grzywacz et al. 2010, Zalucki et al. 2012). The absence of effective natural enemies and insecticide resistance are believed to be the major causes of *P. xylostella* outbreaks in most parts of the world (Lim 1986, Talekar and Shelton 1993). The importance of this insect is evidenced by the formation of the International Working Group on Diamondback Moth, as well as it being one of the few insects to have had a regular series of international conferences on its biology and management. This series began in 1985, with a seventh conference scheduled for 2015 in India. Here we summarize the natural history and ecology of *P. xylostella*, and present options for its management, with special emphasis on the United States.

Distribution and Hosts

P. xylostella is not native to the United States and is believed to have originated in either the Mediterranean region or southern Africa (Talekar and Shelton 1993, Kfir 1998). The assessment of its origin being in southern Africa is based on the diversity of parasitoids attacking *P. xylostella* as well as the large number of indigenous *Brassica* species present in that area (Kfir 1998). Today, it can be found wherever crucifers are grown and is believed to be the most universally distributed of all Lepidoptera (Talekar and Shelton 1993). *P. xylostella* was first observed in North America in Illinois in 1854, but quickly spread across the continent (Capinera 2001). It is a perennial problem in the southern part of the United States, which includes some of the nation's leading *Brassica* vegetables such as collards and cabbage (NASS 2010, Furlong et al. 2012). In these warmer climates, *P. xylostella* overwinters as an adult. Although adults are weak fliers, they are known to move over long distances and reinvade areas annually. Movement also occurs when eggs, larvae, and pupae are moved on transplants from southeastern states to northern states (Shelton et al. 1996). Furthermore, these migrating insects are often resistant to many insecticides used by northern growers.

Larvae are specialists, feeding only on plants in the Brassicaceae, and although it has been reported that strains have adapted to pea, *Pisum sativum* L. (Löhr and Gathu 2002), it is unclear whether they will survive long-term in the field on peas. The Brassicaceae contains ≈350 genera and >3,000 species of herbaceous plants. Originating in Europe and eastern Asia, it is a cool-season plant family that includes numerous cultivated crops. Plant chemicals common in this family, glucosinolates, are used by *P. xylostella* as egg-laying stimulants (Nayar and Thorsteinson 1963, Hillyer and Thorsteinson 1971). Virtually all cruciferous vegetables are attacked by *P. xylostella* including all varieties of *B. oleracea* as well as mustard, *Brassica* spp.; radish, *Raphanus sativus* (L.); turnip, *Brassica rapa* (L.); Chinese cabbage, *B. rapa* variety *pekinensis*; and watercress, *Nasturtium officinale* (W.T. Aiton) (Capinera 2001). *P. xylostella* also feeds on many cruciferous weeds common throughout the United States, including yellow rocket, *Barbarea vulgaris* (Aiton); shepherdspurse, *Capsella bursa-pastoris* (L.); pepperweed, *Lepidium* spp.; and wild mustards, *Brassica* spp. These weeds serve as important alternate hosts, especially in spring before cruciferous vegetable crops are planted (Talekar and Shelton 1993).

Pest Status and Damage

Crop damage is caused by larval feeding or the presence of larvae contaminating produce. Although they are small relative to other lepidopteran pests, larval densities can reach levels that result in total destruction of leaves, leading to tremendous economic losses. For example, a single outbreak in California led to losses in excess of US$6 million (Sances 1997, Shelton et al. 2000). In addition, for crops such as broccoli, the presence of larvae in florets can result in the total rejection of shipments (Capinera 2001). Globally, a conservative estimate of the total costs associated with management of *P. xylostella* was US$4–5 billion annually (Zalucki et al. 2012). Production of *Brassica* spp. in the United States over the past 20 yr has averaged ≈1.7 million tons per year, making up ≈4% of the global production, with an estimated management cost for *P. xylostella* around US$150–200 million (Zalucki et al. 2012, The Food and Agriculture Organization Corporate Statistical Database [FAOSTAT] 2013).

Damage occurs when first-instar larvae mine leaf tissue, while later instars consume leaf tissue from the underside of leaves, chewing irregular patches, and often leave the top epidermal layer and leaf veins with a window-like appearance (Fig. 1). Collards are grown primarily in the southeastern states and are particularly vulnerable to serious economic losses because *P. xylostella* has a strong preference for this crop (Harcourt 1957, Mitchell et al. 2000). Unlike most other *Brassica* vegetables, collard leaves, which *P. xylostella* larvae feed on, are the marketable portion of the crop.

Life History

P. xylostella development occurs between 8 and 32°C, with the highest survival at 14°C, taking 41 d to complete one generation (Liu et al. 2002). At the northern extremes of its range, *P. xylostella* has three to four generations per year, with fecundity being highest in the earliest generations and decreasing as the season progresses. In warmer areas, such as the southeastern United States, *P. xylostella* can breed continuously with as many as 15 generations per year (Capinera 2001).

Adult. Adults are slender, grayish-brown moths ≈6 mm in length with pronounced antennae (Fig. 2). Moths are marked with a broad, cream or light-brown band along the back that is sometimes constricted to form one or more light-colored diamonds (especially in males), which is the basis for the common name of this insect. Adult moths can live as long as 8 wk, with an average life span of 2 wk. Adults can be found resting on foliage during the day, becoming more active just before dusk when most mating and oviposition occurs (Harcourt 1957). A single female will lay eggs for ≈10 d and can deposit as many as 350 eggs, averaging around 150 (Harcourt 1957).

Egg. *P. xylostella* eggs are oval, flattened, ≈0.44 mm in length by 0.26 mm in width, and yellow or pale green (Fig. 3). Eggs are deposited singly or in clusters of two to eight usually in depressions on the surface of foliage, with ≈60% of the eggs on the upper surface (Lasota and Kok 1989). Egg incubation in the field is highly temperature dependent, ranging from 2 to 20 d and averaging around 6 d (Harcourt 1957, Liu et al. 2002).

Larva. The larval stage of *P. xylostella* includes four instars and generally requires 5–7 d for each stadium, with a total larval development time of 20–28 d (Harcourt 1957, Liu et al. 2002). First instars are ≈1.7 mm in length and are colorless to pale white with a dark head capsule (Fig. 4). After eclosion, larvae move to the undersides of leaves, chew through the epidermis, and mine the spongy mesophyll tissue. Subsequent instars are green, reaching a maximum length of 11.2 mm. The body bears a few short hairs marked by the presence of small white patches and tapers at both ends with a pair of prolegs protruding from the posterior end, forming a "V" shape (Fig. 5). When disturbed, larvae will often wriggle violently backwards, eventually spinning down on a strand of silk (Capinera 2001).

Pupa. Prepupal larvae construct a loose silk cocoon, usually formed on the lower or outer leaves of the host plant (Fig. 6). After a few days of quiescence, pupation occurs inside the cocoon. Pupae change from yellow to brown as they develop, are ≈7–9 mm in length, and require 5–15 d to complete development (Capinera 2001).

Management History

Sampling and Thresholds. *P. xylostella* populations are usually monitored by visual counts of larvae or damage on plants. Although pheromone lures and traps are available, they only provide information on the presence of *P. xylostella* adults and provide little information about larval densities (Miluch et al. 2013). The use of sex pheromones and mating disruption for control are discussed in greater detail in the control section of this article. Thresholds vary by crop and

Fig. 1. Feeding damage of diamondback moth on collard leaves.

Fig. 2. Adult diamondback moth.

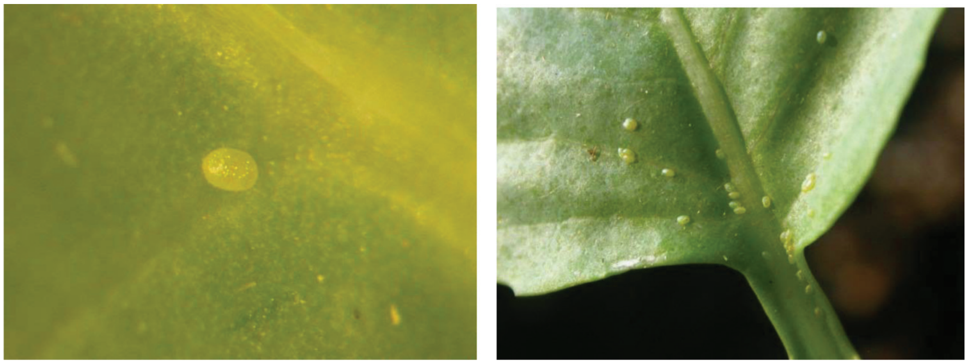

Fig. 3. Diamondback moth eggs on a collard leaf.

Fig. 4. Diamondback moth larvae and feeding damage.

Fig. 5. Diamondback moth larvae (note the protruding prolegs from the posterior end, forming a "V").

state, with the lowest thresholds being in southeastern states where pressure is most intense. In some states, treatment is recommended if populations exceed 0.3 larva per plant (Kirby and Slosser 1984). In Florida and Georgia, treatment is recommended when one or more leaf-feeding holes are found per plant (Capinera 2001). In Virginia, scouting should be done at least once per week, and treatment for cabbage is recommended if >20% of plants have at least one larvae before heading, and if >5% of plants have at least one larva from heading to harvest (Cordero and Kuhar 2009). At more northern latitudes, early treatments are only recommended if >50% of the plants are infested with more than five larvae (Hollingsworth 2014). Harcourt (1961) recommended a minimum sample size of 40–50 plants for reliable estimates of larval densities and 150 plants for egg densities in cabbage. Even with the development of resistance to numerous classes of insecticides, calendar-based sprays are still very common. However, when fields are monitored and thresholds are used, fewer insecticide applications are needed and crop yields remain high (Capinera 2001). The inefficiencies and time demands of scouting and the lack of clear thresholds have likely been partially responsible for the reliance on synthetic pesticides as the primary control method.

Fig. 6. Diamondback moth pupal cocoon.

Cultural Control

Crop Rotation. Because *P. xylostella* has a narrow host range (crucifers only), crop rotation can reduce population levels and subsequent damage. Mandatory crucifer-free periods for a region have been undertaken as a control strategy for *P. xylostella* in Mexico and Australia (Sayyed et al. 2002). However, this tactic is often not feasible in commercial vegetable-producing areas because of demand, the high price, or both, for crucifer vegetables. The management of individual fields may minimize pest damage; however, the greatest potential for improving control through cultural practices is incorporating these changes on larger temporal and spatial scales (Hoy et al. 2007).

Intercropping. Vegetation diversity, including intercropping, can result in significant reductions in pest densities (Risch et al. 1983, Andow 1991, Landis et al. 2000). Intercropping cabbage with tomatoes, garlic, dill, or clover has been shown to reduce the density of *P. xylostella* (Buranday and Raros 1975, Dover 1986, Talekar et al. 1986, Asman et al. 2001). However, large-scale experiments to test the repellency of these plants in the field have yielded inconsistent results (Latheef and Irwin 1979, Ivey and Johnson 1998).

Trap Cropping. Trap crops are highly attractive plant stands grown to attract, retain, or intercept pests to reduce or eliminate damage in the cash crop (Shelton and Badenes-Perez 2006). This strategy has shown some success in reducing injury of several species of pests that attack cruciferous crops including *P. xylostella* (Ludwig and Kok 1998, Shelton and Nault 2004, Shelton and Badenes-Perez 2006, Wallingford et al. 2013). Several trap crops have been recommended for management of *P. xylostella,* including collards and Indian mustard (*Brassica juncea* (L.)). Because collards are more attractive to *P. xylostella* than other crucifer vegetables (Harcourt 1957, Mitchell et al. 1997a), planting collards in field peripheries can help to manage *P. xylostella* in crops such as cabbage or broccoli. Mitchell et al. (2000) showed that densities of *P. xylostella* never exceeded the action threshold of 0.3 larva per plant in cabbage fields surrounded by collards, but did exceed threshold in three of nine cabbage monocltures. Moreover, the number of insecticide applications was greatly reduced in cabbage surrounded by collards, with no reduction in marketable yield. In addition, Badenes-Perez et al. (2004) found that oviposition by *P. xylostella* was up to 300 times greater in collard trap crops than cabbage. While there is plenty of evidence suggesting a collard trap crop may reduce pests in cash crops, other studies have demonstrated inconsistent results (Shelton and Nault 2004, Musser et al. 2005).

Resistant Varieties. Crucifer crops differ in their susceptibility to attack by *P. xylostella*. Mustards, turnips, and kohlrabi are among the most resistant (Radcliffe and Chapman 1966, Capinera 2001). Variations in plant morphological characteristics including leaf wax content, leaf color, or head compactness and plant biochemical compounds such as glucosinolates may be involved in these differences in resistance and have been widely studied in recent years (Stoner 1997; Ulmer et al. 2001, 2002; Agrawal and Kurashige 2003; Poelman et al. 2008). The presence and structure of leaf waxes and their associated chemicals is a major component of resistance, eliciting nonacceptance behavior of *P. xylostella* neonate larvae, resulting in their failure to establish (Eigenbrode and Shelton 1990). These varieties contain shiny green or glossy leaves due to a genetic mutation, causing larvae to spend more time searching and less time feeding. This may also enhance predation because of the increased searching, and because of the improved mobility of predators (Eigenbrode and Trumble 1994, Eigenbrode et al. 1995).

In addition to traditional breeding programs, resistant varieties produced through biotechnology have been shown to be a powerful tool in integrated pest management programs for *P. xylostella*. For example, several *Brassica* species have been developed to express the Cry1 insecticidal protein of the soil bacterium, *Bacillus thuringiensis* (Shelton 2012). These plants show tremendous potential with high levels of resistance to *P. xylostella* and other lepidopteran pests. However, given the current negative public perception of genetically modified organisms and the difficulty in bringing them to market, biotechnology is not likely to be a viable option anytime in the near future (Shelton 2012).

Mating Disruption. Among the various control alternatives, the use of pheromones has attracted interest because of their specificity and low toxicity to nontarget organisms. Sex pheromone-mediated mating disruption involves dispensing high quantities of insect sex pheromone over large areas to decrease the likelihood that males will find females and mate (Cardé 1990, Jones 1998, Miller et al. 2006, Baker 2008). Since the first use of mating disruption in the 1970s to control pink bollworm, *Pectinophora gossypiella* (Saunders), the use of sex pheromones in IPM programs has grown steadily, with numerous successes in the United States and other countries (Baker 2008).

The female sex pheromone of *P. xylostella* has been identified, synthesized, and is commercially available (Chisholm et al. 1979). While several studies have used these products as part of integrated control programs, results have been inconsistent (Talekar and Shelton 1993, Mitchell et al. 1997b, Schroeder et al. 2000). Nevertheless, the commercial product CheckMate (Suterra LLC, Bend, OR) remains available to growers. Although pheromones have become well established in some integrated pest management programs, there are several limitations to these tools, the most limiting of which is cost (Baker 2008).

Cultural controls play a major role in *P. xylostella* management programs, with the most important being rotations, resistant varieties, and trap crops. When combined with other methods such as biological control, cultural controls can lead to significant reductions in *P. xylostella* populations. However, these practices can make crops more susceptible to attack from other pests or do not yield as well, leading to an overall decrease in grower revenues. Moving forward, these practices must be aimed at achieving multiple benefits while at the same time maintaining high levels of yield and quality. Recent molecular advances (covered in a later section) have provided a tremendous amount of information that will help achieve those goals.

Biological Control

All life stages of *P. xylostella* are attacked by natural enemies, including parasitoids, predators, and pathogens that can reduce densities below damaging levels. In fact, pest outbreaks are often attributed to lack of effective natural enemies in a specific region or disruption of these natural enemies, usually by pesticides (Talekar and Shelton 1993).

Parasitoids. Hymenopteran parasitoids play an essential role in the control of *P. xylostella* (Harcourt 1960, Pimentel 1961, Talekar and Shelton 1993). Goodwin (1979) reported >90 species of parasitoids attacking *P. xylostella* worldwide. Lim (1986) reported six species of parasitoids attacking eggs, 38 attacking larvae, and 13 attacking pupae of *P. xylostella*. Egg parasitoids belonging to the genus, *Trichogramma*, are usually present, but overall parasitism is relatively low and does little for control of *P. xylostella* (Talekar and Shelton 1993). Larval parasitoids are the most predominant and most effective. Worldwide, the most efficacious larval parasitoids of *P. xylostella* belong to the genera, *Diadegma* and *Cotesia* (=*Apanteles*; Lim 1986). In North America, *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) (Fig. 7) and *Microplites plutellae* (Muesebeck) (Hymenoptera: Braconidae) are the dominant species of parasitoids attacking *P. xylostella*, particularly in the northern United States (Pimentel 1961, Harcourt 1963, Putnam 1968, Oatman and Platner 1969, Kok 2004). *D. insulare* emerges from the host after it has spun its cocoon, and then spins its own cocoon within (Fig. 8), whereas *M. plutellae* emerges from the active host larva and spins a brown cocoon, less conspicuous than that of *D. insulare* (Pimentel 1961; Fig. 9). From different regions of North America, researchers have reported parasitism rates of *D. insulare* ranging from 35 to 80% (Harcourt 1960, 1963; Oatman and Platner 1969; Mitchell et al. 1997a; Xu et al. 2001a). *Oomyzus sokolowskii* (Kurdjumov) (Hymenoptera: Eulophidae) is another important gregarious larval–pupal parasitoid of *P. xylostella* that is well adapted to the high-temperature conditions that are typical of the southeastern United States (Latheef and Irwin 1983, Fitton and Walker 1992, Talekar and Hu 1996; Fig. 10). Both *M. plutellae* and *D. insulare* provided high rates of mortality of *P. xylostella* with late-season parasitism rates as high as 80%, but both of these parasitoids are highly sensitive to insecticides (Xu et al. 2001a,b; Cordero et al. 2007). Therefore, careful selection of insecticides is essential to maintain natural biological control of *P. xylostella*.

Predators. Although numerous studies have investigated the role of parasitism in controlling *P. xylostella*, much less is known about the role predators play in regulating populations. Ullyet (1947) reported that predatory arthropods including various staphylinids, vespids, syrphids, chrysopids, hemerobiids, anthocorids, and spiders are an important source of *P. xylostella* larval mortality. Additional research using small laboratory tests indicate that carabid beetles can provide mortality as high as 95% (Suenaga and Hamamura 1998). Muckenfuss and Shepard (1994) acknowledged that not much is known about the impact of predators on *P. xylostella* populations, but they estimated that predators kill an average of 90% of *P. xylostella* first instars. To develop and implement sound integrated pest management programs, a better understanding of the role predators play in population regulation is necessary.

Pathogens. Several entomopathogens, including viruses, fungi, and nematodes, show promise as biological pesticides for *P. xylostella*, but few commercial products have yet to be registered outside China (Sun and Peng 2007). The bacterium, *Bacillus thuringiensis* subsp. *kurstaki* (Berl.) is the most widely used pathogen for control of *P. xylostella*, and has been used as a foliar spray for decades. It is used similar to conventional insecticides and now resistance is becoming a problem. Kadir et al. (1999) indicate that granulosis virus was highly infective against *P. xylostella* and that it could be developed as a selective microbial pesticide. The nuclear polyhedrosis virus of alfalfa looper, *Autographa californica* and closely related genomic variants are also infective to *P. xylostella* and may have potential as control agents (Farrar and Ridgway 1999).

Several entomopathogenic fungi, including *Beauveria bassiana* (Bassi), *Metarhizium anisopliae* (Mechinikov), and *Paecilomyces fumosoroseus* (Wize), have been evaluated as insect biocontrol agents in *Brassica* systems. Most of these fungi have been evaluated for use as direct replacements for synthetic insecticides rather than as inoculative agents for classical biological control (Grzywacz et al. 2010). Although the use of fungi to control *P. xylostella* continues to be a focus

Fig. 7. *D. insulare* adult and pupa.

Fig. 8. Diamondback moth pupa and a *D. insulare* pupa.

Fig. 9. *M. plutellae* pupae.

Fig. 10. *O. sokolowskii* adult.

of numerous research projects, to date its use remains unrealistic and large-scale practical uses remain to be determined (Furlong and Pell 1997, Lacey et al. 2001, Vickers et al. 2004, Grzywacz et al. 2010). Nevertheless, several fungi are now commercially available, but use of these products in integrated pest management programs for *P. xylostella* has not been widely adopted (Furlong et al. 2012).

The use of entomopathogenic nematodes has also been evaluated for their efficacy in controlling *P. xylostella* (Baur et al. 1997, Mason and Wright 1997). *Steinernema carpocapsae* (Weiser) has been the most effective nematode tested against *P. xylostella*, causing up to 100% mortality of larvae after 6 h of exposure and 40% mortality of pupae (Ratnasinghe and Hague 1998). A foliar application of infective juveniles of *S. carpocapsae* caused 98% mortality of *P. xylostella* larvae in the field (Lello et al. 1996). Although the use of entomopathogens has potential, their limitations (e.g., short shelf life, slow action, and low host specificity) have inhibited adoption into IPM programs for *P. xylostella* (Cherry et al. 2004, Grzywacz et al. 2010). More work is needed to reach a point where entomopathogens are ready for wide-scale adoption into IPM programs.

Chemical Control

Historically, insecticide applications in *Bassica* spp. have been dictated by the presence of early season pests, including root maggots, *Delia* spp., and flea beetles, *Phyllotreta* spp., that has led to the prophylactic use of conventional insecticides to control later season pests such as *P. xylostella*. General insecticide use patterns vary widely over time and space, but have been greatly influenced by the development of insecticide resistance and new insecticides becoming available. Given this heavy reliance on synthetic chemicals, *P. xylostella* has developed resistance to almost every class of insecticide (Shelton and Wyman 1990, Talekar and Shelton 1993, Shelton et al. 1993a, Shelton et al. 2000). It was one of the first agricultural pests in the world to develop resistance to DDT (Ankersmith 1953, Johnson 1953), and later to the microbial insecticide *Bacillus thuringiensis* (Kirsch and Schmutterer 1988, Tabashnik et al. 1990, Shelton et al. 1993b). The arthropod pesticide resistance database [APRD] 2012 reported that *P. xylostella* has developed resistance to >80 active ingredients in populations from >20 countries. In addition, some populations have evolved resistance to the anthranilic diamide, chlorantraniliprole (Wang and Wu 2012).

Populations of *P. xylostella* from North America are reported to be >100-fold resistant to pyrethroids and some carbamates, and >200-fold to *B. thuringiensis* (Shelton and Wyman 1990), but these resistance levels vary by region (Cordero and Kuhar 2007). Shelton et al. (1993b) found up to 461-fold resistance to *B. thuringiensis* subsp. *kurstaki*. Additional research has shown that populations of *P. xylostella* from five different states were susceptible to various insecticides and developed high levels of resistance in just a few years (Zhao et al. 2006). While populations vary widely in their susceptibility to particular compounds, *P. xylostella* has a remarkable ability to rapidly develop resistance.

Crucifer producers in much of the world, including the United States, have been on a "pesticide treadmill," employing new insecticide chemistries followed quickly by resistance development. Although environmental and human safety concerns have influenced the registration status of some insecticides around the world, and effective nonchemical strategies have been identified, chemical control still remains one of the most widely used strategies for preventing crop damage. As novel insecticides become available, it is important that we use them judiciously, combining them with all other available tools for *P. xylostella* management to prevent the continued development of insecticide resistance.

Current Management: the Need for a True Integrated Approach

Integrated management programs for *P. xylostella* will never be a one-size-fits-all approach. However, as more programs are initiated globally, we must learn from the successes and failures of these programs. It is difficult to identify clear successes given the heavy reliance on insecticides, but one thing is clear: any program that relies on a single management component is destined to fail (Talekar and Shelton 1993, Shelton 2004).

Several large organizations have worked to implement IPM programs all over the world. The foundation of most of these programs is the introduction of parasitoids and promoting the use of softer chemistries when insecticides are needed. While all of the previously mentioned management tactics work to varying degrees, due to inconsistencies in pest suppression and the continued availability of cheap broad-spectrum insecticides, most IPM programs have failed to become widely adopted, and insecticides remain the main control tactic (Talekar and Shelton 1993, Rauf et al. 2004, Wright 2004, Mazlan and Mumford 2005, Grzywacz et al. 2010, Srinivasan et al. 2011).

Another confounding issue in the management of *P. xylostella* is that it is part of a large complex of hard-to-manage pests attacking *Brassica* spp. Therefore, it is not necessarily the presence of *P. xylostella* that initiates treatments. Often the primary motivation for the prophylactic use of insecticides is the presence of other pests (Grzywacz et al. 2010). Moving forward, IPM programs must focus on not just *P. xylostella* but the entire *Brassica* pest complex. The design of these programs must incorporate an understanding of the limitations of growers, thereby implementing strategies that recognize their need to manage *P. xylostella* but also numerous other pests.

As new information becomes available and new programs are developed, growers must include multiple tactics implemented over wide areas that work synergistically to suppress multiple pests. Otherwise, these programs will continue to fail. Growers need a truly integrated approach that incorporates host plant resistance, biological controls, cultural controls, behavioral management, and judicious use of insecticides. When used alone, none of these strategies will work sufficiently and pesticide misuse and resistance issues will continue. When used together, however, these tactics can complement each other and lead to improved pest suppression, reduced insecticide resistance, and a more sustainable pest management program.

The Future of *P. xylostella* IPM

Research focused on the molecular genetics and genomics of *P. xylostella* has dramatically increased in recent years, providing tremendous amounts of information on the specific mechanisms controlling *P. xylostella* physiology and its interactions with plants. This new information has the potential to revolutionize the way we approach management of this pest. There is now a large and rapidly accumulating body of knowledge on *P. xylostella* physiology and pesticide resistance, including chemosensory proteins (Gong et al. 2010), proteinase activities in the midgut (Shi et al. 2013), pheromones and their receptors (Lee et al. 2011, Sun et al. 2013), sodium channel genes, cytochrome P450 genes (Bautista et al. 2009, Endersby et al. 2011), and bacterial symbionts (Xia et al. 2013). In addition, these approaches have provided a more thorough understanding of the molecular mechanisms behind the detoxification of glucosinolates and insecticides by *P. xylostella* (Liu et al. 2000, You et al. 2013). These basic studies may provide new insights into novel effective management tools to control adults and larvae.

Larval target strategies focus on insect genes associated with nervous systems and insecticide resistance, but also those that convert plant host material to repellent plants by targeting plant-derived protease inhibitors. For example, Bautista et al. (2009) used RNA interference (RNAi) to knock out the cytochrome P450 gene, CYP6BG1, which was overexpressed in fourth instars of permethrin-resistant strains of *P. xylostella*, leading to significant reductions in larval resistance to permethrin. A similar RNAi design was used by Gong et al. (2013) targeting acetylcholine esterase genes, which are essential in neurotransmission, leading to significant mortality of *P. xylostella* larvae under laboratory and field conditions. Insect proteinase hydrolyzes ingested protein into peptides that play important biochemical roles in insect growth and development. Zhang et al. (2012) constructed transgenic cabbage-expressing potato proteinase inhibitor II gene, which limited the ability of *P. xylostella* to breakdown plant proteins, resulting in stunted larval development and increased larval mortality.

Strategies aimed at controlling adults tend to target oviposition and mating behavior as well as locating or generating efficient dead-end trap crops (Badenes-Perez et al. 2014). For example, because glucosinolates are oviposition stimuli for *P. xylostella*, transferring genes for glucosinolate production to tobacco plants stimulated oviposition of *P. xylostella* females, but newly hatched larvae failed to survive (Møldrup et al. 2012). In another study, Lee et al. (2011) used RNAi to suppress the expression of the receptor gene of pheromone biosynthesis, Plx-PBANr, on female *P. xylostella*, resulting in loss of male attractiveness. Although these tools show tremendous potential, public perception of genetically modified plants remains low, and RNAi is a relatively new technology that requires more work before this tool becomes a viable long-term option for management.

Finally, new DNA-based approaches to prey detection provide new methods to understand what role generalist predators are playing in *P. xylostella* control. The basic approach is to collect predators, grind them up, then use polymerase chain reaction (PCR) to identify pests' DNA in the stomach of predators (Harwood and Greenstone 2008). Because DNA barcoding is unique to each species, carefully designed, pest-specific PCR "primers" can yield unambiguous identification of which predators are eating *P. xylostella*, allowing land managers to target conservation efforts accordingly. These primers are now available for *P. xylostella* (Ma et al. 2005) and will provide tremendous insight into how to enhance natural control.

These are just a few of the ways in which this new information can be incorporated into biotechnology-based IPM for *P. xylostella.* This approach requires sound knowledge on pest physiology and the molecular mechanisms underlying specific phenotypes. The whole genome sequence (You et al. 2013) and tissue-specific transcriptome (Xie et al. 2012) of *P. xylostella* are now available and offer wider options for developing resistant transgenic crops and new approaches to pest management and insecticide resistance. All of this information has been incorporated into a database with tools that allow for the efficient analysis of the molecular mechanism of *P. xylostella* insecticide resistance (Jouraku et al. 2013, Tang et al. 2014).

This new genetic information can be used to develop new effective insecticides with novel modes of action, modify trap crops and crop resistance breeding programs, monitor insecticide resistance, and improve biological control and cultural management practices. By adding this new information to the arsenal of traditional IPM tactics, we can decrease reliance on synthetic broad-spectrum insecticide and take a landscape perspective to implementing regional resistance management programs that incorporate host plant resistance, biological and cultural controls, behavioral management, and when necessary highly selective insecticides to manage this pest. One caveat is that we need to understand these same mechanisms in other pests of *Brassica* crops to ensure that by improving management of one pest we are not exacerbating outbreaks of another.

Summary and Conclusions

For decades, researchers have studied various aspects of *P. xylostella*, and in recent years, our molecular and ecological understanding of this pest has greatly improved (Furlong et al. 2012). Nevertheless, there are areas where additional research will prove valuable. These include host plant interactions, including the role of plant volatiles in host plant selection; trap cropping; tri-trophic interactions of pests, plants, and natural enemies; knowledge of movement patterns of *P. xylostella* on local and regional scales as well as migratory differences among populations; the physiological mechanisms associated with resistance to different classes of insecticides; long-term experiments evaluating the role of predators in controlling *P. xylostella*; host plant-resistant lines including those expressing *Bt* proteins and other factors through genetic engineering; and finally, the efficacy and feasibility of incorporating alternative management strategies such as pathogens on a large scale. By gaining a better understanding of this pest and the population dynamics of the cruciferous crop ecosystem, we can develop sound integrated pest management programs that provide better control and reduce the development of, and possibly reverse, insecticide resistance (Zhao et al. 2006).

The successful implementation of IPM programs for *P. xylostella* hinges on practices that also improve management and decision support tools for all other pests of *Brassica* crops, especially early-season pests. Because treatment decisions often hinge on the presence of these pests, it is likely that treatments early in season lead to decreases in natural enemies and concomitant increases in *P. xylostella* abundance. By changing the focus from *P. xylostella* to the suite of *Brassica* spp. pests, we can greatly improve the overall management and production of these crops. Recent molecular advances show promise to improve specific management practices for *P. xylostella*; however, there is a need to determine the same kinds of information for the other pests of *Brassica* spp. to implement a comprehensive *Brassica* IPM program tailored to specific regions. When integrated, this information will allow us to improve management of the cropping system, reducing reliance on synthetic chemicals. Our challenge now is to develop new information and procedures to create an integrated approach to manage this system, not merely specific pests within it.

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