Diamondback moth: Messages from a land down under

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ABSTRACT

Research on diamondback moth, Plutella xylostella (L.) now has an extensive history and has produced a wealth of scientific literature on the biology and management of this major pest. The transition of research focus from basic biology through reports of insecticide resistance to integrated pest management programs and development of tools for genetic investigations can be tracked over 20 years in the proceedings of the international workshops on the management of diamondback moth and other crucifer pests. Progress towards understanding the agroecology of P. xylostella (the interaction of the pest and its natural enemies with the natural and crop production landscapes) has been made, with gains in many areas such as movement, insect-plant interactions, biological control and others. The role of simulation modelling in further understanding the exploitation of resources by P. xylostella and other Brassica insect pests will gain in importance as the need to understand the implications of climate change becomes a reality. The challenge of ensuring the true integration of tactics deployed for pest management still exists as development of resistance to new insecticides re-emphasizes the vulnerability of single tactic strategies. There also remains a desperate need to help smallholders in tropical and sub-tropical areas to produce Brassica crops free from pest damage and from insecticide residues by providing a knowledge base and tools for integrated crop management—much is already known but needs to be made accessible to the farmers of the world.

INTRODUCTION

Diamondback moth, Plutella xylostella (L.) (Lepidoptera: Plutellidae) rose to prominence as a major pest of Brassica vegetables in the mid 1980s. Shelton (2004) suggests that control failures derive from one or more of the following: (a) insecticide resistance, (b) changing agronomic practices, (c) lack of effective biological control. Worldwide, there have been outbreaks of P. xylostella following the breakdown of efficacy of the synthetic pyrethroid insecticides due to the development of insecticide resistance, and associated with the disruption of the natural enemy complex, particularly Diadegma semicalausum (Hellén) (Hymenoptera: Ichneumonidae) or Cotesia vestalis (Haliday) (＝plutellae) (Kurdjumov) (Hymenoptera: Braconidae) (Shaw 2003), by these compounds. The overwhelming conclusion from the recent history of P. xylostella is that an integrated approach to pest management is essential for long-term success.
Table 1  Papers by subject from International DBM Workshops 1985-2001

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The International Workshops on the Management of Diamondback Moth and Other Crucifer Pests have provided an excellent series of snapshots of the research activities in the last 20 years. A brief analysis of the subject matter of the papers in the first 4 Workshops shows that at least half of the papers were related to biological control, insecticide resistance and integrated pest management strategies (Table 1). A major function of these Workshops has been to build relationships between international researchers and to ensure that research information is disseminated widely. The availability of many of these papers on the Internet is a major step forward in ensuring the material remains accessible. Entomologists working with *P. xylostella* will benefit greatly from re-reading many of these papers frequently. There remains a continuing need to maintain this knowledge network. An even more important challenge for the community is to ensure that smallholder farmers the world over benefit from the existing knowledge base.

Much of the international research effort has been aimed at alleviating problems of individual farmers, particularly smallholders in tropical countries where *P. xylostella* has been so destructive. The pioneering work introducing *D. semiclausum* into highland tropical areas, with concurrent training of farmers to understand and manage these parasitoids, in Taiwan province (Talekar et al. 1992), Malaysia (Ooi 1992), Philippines (Poelking 1992), Indonesia (Sastrosiwojo and Sastrodihardjo 1986), and Kenya (Nyambo and Löhr 2005) has been of enormous value. Other important areas of work have included the deployment of insecticide groups with novel modes of action (including *Bacillus thuringiensis* Berliner), detection and monitoring of insecticide resistance levels. In developing IPM systems, other control strategies including insect pathogens, mating disruption using synthetic male sex pheromone, breeding resistant *Brassica* vegetables, estimation of economic thresholds and development of robust sampling strategies underpinned the drive to reduce the dependence on broad-spectrum insecticides (Talekar and Shelton 1993).

Ninety-three research scientists and industry representatives from 23 countries gathered in Melbourne in November 2001 for the 4th International Workshop on the Management of Diamondback Moth and Other Crucifer Pests. At the same time, the rapidly expanding oilseed rape (canola) industry in Western Australia was experiencing its third successive season of major *P. xylostella* outbreaks. These dramatic Australian problems highlighted the importance of movement to the understanding of the population dynamics of *P. xylostella*. The Workshop focused shifted from problems at an individual farm level to thinking about *P.
xylostella on a landscape scale. These movement ideas ranged from important issues of trivial flight—moths and their parasitoids moving within and between adjoining fields—to natural migrations or displacements through trade across hundreds or thousands of kilometres. Intimately linked with movement is a need to understand the genetic structure of *P. xylostella* populations, which impacts on regional management of insecticide resistance, particularly for *Bacillus thuringiensis* and spinosad. Molecular biology is providing the tools to gain deeper insights into gene flow, host plant interactions, resistance mechanisms and transgenic plants.

With the advent of new insecticides in the late 1990s and onwards, *P. xylostella* has been challenged with several novel and unique modes of action. The promise of the new chemistries including spinosad, emamectin benzoate and fipronil was a feature of the Third Workshop in 1996 in Kuala Lumpur. At the Fourth Workshop in Melbourne, Sparks (2004) highlighted the limited number of new modes of action that were on the horizon for management of *P. xylostella* and emphasized the need to conserve those that are currently effective. Unfortunately, Mau and Guscukuma-Minuto (2004) and Zhao *et al.* (2002) announced the first report of resistance to spinosad that had developed rapidly under extensive spray pressure in Hawaii. Since the Workshop, resistance has also developed to fipronil (Sayyed *et al.* 2004) and to indoxacarb (Sayyed and Wright 2006; Zhao *et al.* 2006) and emamectin benzoate (Zhao *et al.* 2006) in some populations of *P. xylostella* in the field.

The challenge issued to the Melbourne delegates in the keynote address by Tony Shelton was

> “Developing sound management strategies for *Plutella xylostella* will require an understanding of the ecology of the landscape in which *P. xylostella* and its natural enemies interact with the rest of this agroecosystem.” (Shelton 2004).

This paper highlights progress in some of these areas as well as some of the challenges remaining.

**MOVEMENT**

Knowledge of long range movement patterns and rates of dispersal of *P. xylostella* among areas of cultivated and wild host plants is important for managing *P. xylostella* locally and at the landscape scale.

**Migration**

*Plutella xylostella* has long been considered a migratory species in the Northern Hemisphere and is known to move across Europe (Chu 1986) and invade Britain in large numbers in some years (MacKenzie 1958; French and White 1960; Shaw 1960; French 1967). Honda (1992) studied the effect of low temperature (0°C) on survival of *P. xylostella* in order to identify regions in Japan where overwintering cannot occur. Pheromone trapping revealed an influx of moths into these areas in spring. Honda (1992) concluded that areas of northern Japan, in which *P. xylostella* cannot overwinter, are reinfested each spring by migrant moths which travel on southerly low pressure systems from southern Japan and possibly northeastern China and the Korean Peninsula for distances of up to 1 500 kilometres. Similar recolonisation of areas in southern Canada appears to occur with migration of *P. xylostella* from southern parts of the Americas each spring (Smith and Sears 1982; Dodsall *et al.* 2004, 2006). Goodwin and Danthanaryaana (1984) used suction traps to measure aerial density of male and female moths. Using a range of data, they were able to identify a potential major migration of *P. xylostella* in southern Victoria in spring 1973. Their suction trap data also identified a significant association in moth activity with moon phase. Do these variations in moth activity during a month result in variation in oviposition levels on sequentially planted vegetable *Brassica* crops?

Biological studies in Japan have also begun to unravel biological characteristics relating to migratory
urge and capability in *P. xylostella* (Shirai 1993). Of particular interest has been the examination of the influence that rearing *P. xylostella* on non-crop brassicaceae species has on subsequent migratory urge (Begum *et al.* 1996, Muhamad *et al.* 1994). The role of non-crop hosts remains to be fully understood. Frequently laboratory trials and field observations show some of these species to be very attractive to *P. xylostella* moths but, in non-crop habitats, polyphagous predators such as ants can frequently reduce *P. xylostella* populations greatly (Goodwin 1976).

While all wild Brassicaceae are potential hosts for *P. xylostella*, there is evidence that some species are better hosts than others with respect to development time, adult body size and fecundity of *P. xylostella* (Begum *et al.* 1996; Idris and Grafius 1996). Adult body size is positively correlated with flight duration (Shirai 1993; Begum *et al.* 1996). Shirai (1993), however, concluded that temperature experienced during the larval stage is the major factor influencing forewing length in *P. xylostella*. Moths emerging in winter and spring in southern Japan have longer forewings and a higher flight capacity than those emerging in summer (Shirai 1991). Harcourt (1986) measured a decrease in the fecundity of *P. xylostella* that was correlated with the decline in crude protein content that occurred as the host plant matured. Campos *et al.* (2004) studied the effect of age of host plant on body size, longevity and fecundity of *P. xylostella* and found that reproductive timing was influenced by the age of the plant material consumed by the larvae. Feeding by larvae on mature and senescing foliage caused an increase in the time taken by moths to lay 90% of their eggs and induced other phenotypic traits such as smaller body size and increased longevity which are often correlated with propensity to migrate (Campos *et al.* 2004). In Brazil, seasonal influxes of *P. xylostella* appeared to be related to external factors affecting source populations rather than suitability of local conditions for development (Campos *et al.* 2006).

In an insect that lacks a diapause stage, migration as an adaptive trait is a mechanism by which the species can utilise ephemeral host plants that show patchy seasonal distribution. The ecological studies described here suggest that *P. xylostella* is an actively dispersing species and when environmental conditions dictate, such as when host plants degrade, the species moves large distances to colonise particular regions when climatic conditions are favourable for migration. Conversely, in a Brassica vegetable production region where host plants are abundant, movement of moths may only occur over short distances (Mo *et al.* 2003, 2004).

In both Australia and Canada, large areas of canola are grown in areas marginal for *P. xylostella* development. In Canada, the limiting factor is the cold winters which require *P. xylostella* to re-colonize cropping areas each year in spring. In Australia, the hot, dry summers in the broadacre cropping areas are the limiting factor since potential overwintering alternative hosts are seldom present. A related problem in both systems is the difficulty in re-colonisation of the canola crops by parasitoids of *P. xylostella*.

Dodsall *et al.* (2004, 2006) provided further evidence that *P. xylostella* essentially cannot overwinter in Canada. They demonstrated likely migration patterns using trajectory analyses and suggested that it was possible for moths to move from Mexico to Canada. Low-level jet streams in the continental USA have been linked with movement of cereal and potato aphids (Rose *et al.* 1975; Irwin and Thresh 1988; Zha *et al.* 2006). Chapman *et al.* (2002) used vertical radar techniques and trajectory analysis to look at large-scale movements of *P. xylostella* in Europe and have established that long-distance migration from continental Europe is the source of the populations of *P. xylostella* that become established in the UK in late spring. Models incorporating trajectory analysis have been used extensively in Australia (Drake *et al.* 2001) for a range of species, including Heliothis spp. (Dillon *et al.* 1996; Rochester *et al.* 1996; Rochester and Zalucki 1998; Rochester 1999; Gregg *et al.* 2001), mosquitoes (Ritchie and Rochester 2001) and locusts (Deveson and Hunter 2002; Hunter 2004).
While these trajectory models can predict potential migration events, we still need to understand how these insects interact with climate. In Japan, *P. xylostella* has become less abundant since the mid 1990s while two noctuids, *Helicoverpa armigera* and *Trichoplusia ni* have become more important pests of *Brassica* vegetables (Kiritani 2006). One suggestion is that global warming may be involved in the change of pest status (Kiritani 2006). Furthermore, there are some recent examples of potential changes in the geographic range of *P. xylostella*. The establishment of *P. xylostella* on Marion Island, South Africa (Chown and Avenant 1992) is the only documented case of a recent immigrant establishing on a subantarctic island (Greenslade et al. 1999). A single *P. xylostella* moth was also recorded on the sub-Antarctic island of South Georgia in 2003 (Convey 2005). Although no Lepidoptera are known to be resident on the island, *P. xylostella* may have potential to establish there, as terrestrial microclimatic conditions are similar to those of Marion Island (Convey 2005). As well, dispersing plumes of *P. xylostella* originating from western Russia arrived in the high Arctic Svalbard in July 2000 and landed in a concentrated band along the west coast (Hodkinson et al. 2002). These recent forays into uncolonised environments suggest that as the global climate changes, *P. xylostella* may be swift to colonise new areas at high latitudes.

Zalucki and Furlong (2005, 2006) and Zalucki and van Klinken (2006) described the use of CLIMEX, an inferential bioclimatic modelling program to make predictions using a species’ geographical distribution, abundance across its range, seasonal phenology and laboratory rearing data. Zalucki and Rochester (1999) used CLIMEX to estimate the effect of climate on the distribution and abundance of *Danaus plexippus* (L.) in Australia and North America. A preliminary model for *P. xylostella* has been outlined (Zalucki and Furlong 2006) and should be further developed. There are exciting opportunities to develop a model for *P. xylostella* on canola that would apply in such different areas as Canada and Australia. It is also important that area pest management approaches utilise the increasingly powerful and accessible weather modelling systems and satellite imagery that are now available.

**Population Structure**

Knowledge of the genetic structure of populations of insects can give an insight into gene flow, short and long range movement patterns, source populations for outbreaks and rates of dispersal among areas of cultivated and wild host plants, factors which have important implications for population management. Techniques used to examine population structure in *P. xylostella* to date comprise enzyme electrophoresis, studies of biological/life history variation, use of mitochondrial DNA markers and screening with microsatellite loci. Noran and Tang (1996) presented a study of population structure of *P. xylostella* in Malaysia between lowland and highland areas using the electrophoretic separation of allozymes. Previous and subsequent studies in the literature using the same technique have mostly found little evidence of population differentiation. For example, both Caprio and Tabashnik (1992), in an Hawaiian study, and Kim et al. (1999), using two populations from farms approximately 50 kilometres apart in Korea, found little genetic differentiation in four allozyme loci. Also Laude et al. (1992) used four allozyme loci to screen four populations of *P. xylostella* from one island in the Philippines and found little evidence of population differentiation.

Genetic differences between populations using allozyme electrophoresis and differences in oviposition parameters have been detected by Pichon et al. (2004, 2006) in some populations of *P. xylostella* from around the world. Butcher et al. (2004) assessed the potential of microsatellite markers and Amplified Fragment Length Polymorphisms (AFLP) for examining population structure in *P. xylostella*. In a study of the population structure of *P. xylostella* in Australia, Endersby et al. (2006) used microsatellite markers to demonstrate that a panmictic population occurred throughout southern Australia. Further microsatellite markers have now been isolated from *P. xylostella* by Esselink et al. (2006) for studies of population
structure in Europe.

Another technique to study population structure involves sequencing regions of the mitochondrial genome. Little variation in sequence was observed among populations of <i>P. xylostella</i> from Hawaii, continental USA and the Philippines using a portion of the mitochondrial cytochrome oxidase I (COI) gene as a genetic marker (Chang et al. 1997), though use of long-term laboratory populations and very small sample sizes may have left variation undetected. A more extensive study of the mitochondrial COI gene in Korean <i>P. xylostella</i> (Kim et al. 2003) revealed high haplotype diversity, but little genetic differentiation of populations throughout the country. A similar study in China (Li et al. 2006) suggested that dispersal over long distances was a major factor in the demography of <i>P. xylostella</i>. In Australian populations of <i>P. xylostella</i>, preliminary studies of mtDNA showed low haplotype diversity at the COI locus (Saw et al. 2006).

In general, the greatest levels of population differentiation in <i>P. xylostella</i> appear to be found between populations that are separated almost on a continental scale, with little evidence of very fine scale population structure. Genetic analysis of populations of <i>P. xylostella</i> is still at an early stage. The validity of interpretations of population data will depend on careful consideration of the choice of marker, spatial scale at which to operate, sampling regime and methods of analysis.

Kirk et al. (2004) made numerous international collections of <i>P. xylostella</i> and some of its parasitoids for studies of compatibility between populations of both the pest and its parasitoids. They found two population groups of <i>C. vestalis</i> that would not interbreed, as well as incompatibility between <i>Oomyzus sokolowskii</i> populations from Romania and Pakistan. Similar work has been continued since the Melbourne Workshop on morphological and genetic differentiation of <i>C. vestalis</i> (Rinçon et al. 2006).

Local Movement

A new theory about colonization of Brassica vegetables by insects, described as the “appropriate/inappropriate landings” hypothesis (Finch and Collier 2000, Finch 2004), considered visual stimuli to be the most important factor in the colonization of crops and looked at how diverse backgrounds can disrupt host plant selection. Bukovinsky et al. (2005) examined pre- and post-alighting mechanisms in the responses to patch size by specialist herbivores. They found that species with a pre-alighting recognition behaviour based on olfactory cues (<i>P. xylostella</i>) or visual cues (<i>P. rapae</i>) could recognise a preferred host plant in flight. In addition, differences in vegetation background were shown to influence patch responses of <i>P. xylostella</i> leading to differences in pest density (Bukovinsky et al. 2005).

There is a long history of studies into herbivore abundance in diversified plantings (Pimentel 1961; Root 1973; Andow 1991) with many studies in Brassica crops (Smith 1976; Andow et al. 1981; Bach and Tabashnik 1992; Schellhorn and Sork 1997; Hooks and Johnson 2002, 2006). To date, results, particularly with <i>P. xylostella</i>, have been variable and need to be examined carefully on a crop-by-crop basis. Hooks and Johnson (2006) studied <i>Pieris rapae</i>, <i>Trichoplusia ni</i> and <i>H. undalis</i> in broccoli grown either as a monoculture or interplanted with either chili pepper, <i>Capsicum annuum</i>, or sweet yellow clover, <i>Melilotus officinalis</i>. They found natural enemies (spiders, parasitoids and entomopathogens) to be the most significant factor influencing the abundance of <i>P. rapae</i>, and that these natural enemies were more effective in the mixed plantings than in the monoculture. However, the results were not considered good enough to allow them to make recommendations for commercial growers in Hawaii. In tropical areas in Asia and Africa, where crop size is small and intercropping is widely practised, there is considerable scope to ensure that the interplanting is optimised in terms of potential interactions.

Sivapragasam et al. (1988) and Shirai and Nakamura (1994) pioneered mark-recapture techniques for <i>P. xylostella</i> to measure dispersal movement of male moths in Brassica vegetables. In Australia, further
studies of short distance movement, both between- and within-field, of *P. xylostella* (Mo et al. 2003, 2004) and natural enemies (Schellhorn et al. 2004) have been conducted. Schellhorn and Silberbauer (2003) and Schellhorn et al. (2004) used fluorescent dyes to mark insects in the field, a relatively simple technique that is less expensive than marking with rubidium and also avoids the use of laboratory-adapted insects in field release-recapture studies. The study looked at movement of *P. xylostella* and its parasitoid, *Diadegma semiclausum*, in sequentially sown broccoli after a crop was harvested, and revealed greater disturbance and dispersal of the parasitoid, relative to *P. xylostella* (Schellhorn and Silberbauer 2003). These field movement studies are essential if the promise of habitat manipulation as a pest management tool is to be fulfilled. There is a pressing need for these types of studies to be undertaken in the multi-cropping situations commonly found in the tropics.

In New Zealand, Lavandero et al. (2005) used rubidium to mark *D. semiclausum* in order to measure movement between nectar resources and the crop. Although their results suggested that the parasitoids can move 80 m in a short period, parasitism rates were lower in a non-flower treated plot separated from a flower treated plot by just 60 m. Lavandero et al. (2005) suggested that parasitoid mobility alone will not give a complete indication of the spatial arrangement to follow to produce enhanced parasitism rates. They noted that there was a clear difference between how far a parasitoid can move and how far apart floral subsidies should be deployed. Improved knowledge of the movement patterns and the nectar preferences of the key natural enemies of *Brassica* pests is needed before pest managers can confidently utilise habitat diversity and the supply of appropriate floral resources to promote conservation biological control as a viable pest management tactic (Gurr et al. 2004).

**INSECT-PLANT INTERACTIONS**

The close association of *Brassica* specialist insects with the specific leaf chemistries has been the subject of much research (Renwick 2002; Sarfraz et al. 2006).

Potent oviposition stimulants for *P. xylostella* were identified in chloroform extracts of cabbage leaves (Hughes et al. 1997). Further studies (Renwick et al. 2006) used mass spectrometry to identify two major volatile compounds as the isothiocyanates, iberin (3-methylsulfinylpropyl isothiocyanate) and sulforaphane (4-methylsulfinyl-3-butenyl isothiocyanate). In recent years, sulforaphane has been identified as a potent cancer-preventing compound (Zhang et al. 1992) and also has the potential to treat *Helicobacter pylori*-induced gastritis (Fahey et al. 2002). These results are encouraging scientists to increase the sulforaphane content of broccoli and to promote the health benefits of this vegetable (Halkier and Gershenzon 2006). It will be important that entomologists work closely with plant breeders to ensure that the high-health broccoli lines are not also highly attractive to *P. xylostella*.

The unravelling of the mechanism by which *P. xylostella* is able to defuse the myrosinase defence of brassicaceous plants (Ratzka et al. 2002; Vogel et al. 2004) has been a major advance. A glucosinolate sulfatase (GSS) was found in the gut of *P. xylostella* that largely prevented the formation of toxic hydrolysis products arising from the glucosinolate-myrosinase defence system. This opens up the possibility of targeting GSS as a potential tactic for pest management. Subsequent work with *P. rapae* (Wittstock et al. 2004) showed a different mechanism to overcome the glucosinolate-myrosinase defence. They found that the nitrile-specifier protein activity in the gut redirected glucosinolate hydrolysis toward nitrile formation, circumventing the generation of the toxic isothiocyanates.

The functional genomics research on *Arabidopsis* has led to progress in molecular engineering of glucosinolates (Halkier and Gershenzon 2006). The advances also provide a wonderful opportunity to
elucidate the host/insect interactions at a molecular level (Jenks et al. 2002). The ability to transform Arabidopsis relatively easily could allow the molecular basis for these stimulants to be understood more completely and ultimately exploited effectively. Barker et al. (2004, 2007) provided biological data of P. xylostella on A. thaliana that will underpin such work.

Trap Cropping

The need to understand oviposition stimulation is central to the exploitation of trap crops, which have been advocated for a number of years as a management tool for both P. xylostella (Mitchell et al. 1997, 2000) and the caddisfly, Crocidolomia pavonana (Srinivasan and Krishna Moorthy 1991; Muniappan and Marutani 1992; Muniappan et al. 1997, 2004). The large body of recent work on trap cropping has been reviewed fully by Shelton and Badenes-Perez (2006), while Sarfraz et al. (2006) cover aspects of trap cropping in their review of P. xylostella/host plant interactions. Generally results have been inconsistent and have usually involved planting a more susceptible crop such as mustard or collards in order to attract moths away from less susceptible crops such as cabbage.

At the fourth DBM Workshop, Shelton (2004) and Keller (2004) drew attention to the great potential of the brassicaceae weed, Barbarea vulgaris ssp. arcuata, as a dead-end trap crop—a plant which was much more attractive to P. xylostella for oviposition but on which larval survival was very low (Idris and Geftius 1996). Similar findings have been reported with the interaction of flea beetle Phyllostreta cruciferae and B. vulgaris in Europe (Nelson 1997). There are now resistant and susceptible races of the flea beetle which are observed (single gene resistance).

Japanese and European researchers have isolated saponins from B. vulgaris, which are highly correlated with the observed effect on larval survival of P. xylostella (Shinoda et al. 2002; Agerlirke et al. 2003). Equally, it will be important to identify the very powerful oviposition stimulants in B. vulgaris. As yet, the compounds responsible for high levels of oviposition and the types of isothiocyanates released from this plant have yet to be determined (Renwick et al. 2006). Another challenge is to see whether other brassicaceae plants display similar traits. A first step would be to screen a wide range of species for the saponins affecting larval survival. This could extend the dead-end trap crop concept for other target species, such as C. pavonana and Hellula undalis, which are important pest species for tropical smallholders.

Host Range Expansion

The host range expansion of P. xylostella to sugar snap peas (Pisum sativum) in Kenya (Löhr and Gathu 2002; Löhr and Rossbach 2004) jolted the paradigm of P. xylostella as a specialist herbivore on brassicaceae plants. Until the event in Kenya, there had been very few instances of P. xylostella being recorded feeding on plants from outside the Brassicaceae; however Gupta and Thorsteinson (1960) described experiments where P. xylostella was reared successfully for several generations on Fabaceae. In addition, Robinson and Sattler (2001) have reported some host plant races of P. xylostella on Capparaceae in Hawaii. Host plant shifts to some other plant families have occasionally been noted when P. xylostella occurs at extremely high densities after mass immigration (Shaw 1960). The Kenyan pea strain of P. xylostella could survive equally well on pea as on kale or cabbage (Löhr and Rossbach 2004, Rossbach et al. 2006) and arose during an outbreak situation in which numbers of P. xylostella on the Brassica host were extremely high (Löhr and Gathu 2002). Pupae of cabbage-feeding P. xylostella were significantly heavier than pupae of pea-feeding P. xylostella, and the endemic African parasitoid, Diadegma mollipia, preferred to parasitize those feeding on peas (Rossbach et al. 2006).
Resistant Cultivars

There has been considerable interest in developing resistant cultivars of vegetable *Brassica* crops (Dickson et al. 1986; Eckenrode et al. 1986; Eigenbrode and Shelton 1992; Stoner 1992). The glossy leaf trait found in PI234599, a dark, glossy-leaved, long-season cauliflower from Australia, was found to be resistant in the field to the lepidopterous complex. However, the role of leaf surface waxes in host plant resistance is complex. Visual, chemical and tactile factors associated with leaf waxes may each play a role in oviposition attraction of *P. xylostella* (Justus et al. 2000) and wax morphological factors have a profound impact on natural enemy interactions (Eigenbrode et al. 1995, 1996).

Although commercially acceptable vegetable cultivars proved difficult to obtain, the glossy trait could prove useful in oilseed rape particularly in Australia where serious attack of crops by *P. xylostella* is sporadic and broadacre spraying is difficult, expensive and likely to disrupt beneficial insects. Ulmer et al. (2002) observed an increase in dispersal of first instar larvae of *P. xylostella* on lines of glossy *B. rapa* which is likely to lead to increased mortality in the field. However, Ramachandran et al. (1998) found little effect of glossy varieties of *B. napus* on feeding of *P. xylostella* and instead found a new type of resistance in a non-glossy line of *B. oleracea* (PI 171538). Cultivars of oilseed rape with reduced wax bloom can be more susceptible to damage by flea beetles (*Phyllotreta* spp.) so the trait will only be of use in regions where flea beetles are of minor importance (Eigenbrode et al. 2000).

The potential benefits of pest-resistant transgenic *Brassica* vegetables in terms of massive reduction in pesticide applications continue to excite researchers who are seeking sustainable vegetable *Brassica* production in tropical and sub-tropical areas. However, many hurdles remain before commercial deployment. Apart from resistance problems and the fundamental issue of consumer acceptance, an important area to consider is the tritrophic effects on the ecological system. Schuler et al. (2004a, 2004b, 2005) investigated the impact of Bt-transformed oilseed rape on *P. xylostella*, other pests and their natural enemies. Apart from death of *C. vestalis* larvae due to the premature death of their hosts that fed on Bt plants (Schuler et al. 2004b), negligible adverse effects were observed on the tritrophic system. Development, evaluation and safety screening of Bt *Brassica* vegetables for control of *P. xylostella* is currently underway through CIMBAA (Collaboration on Insect Management for Brassicas in Asia and Africa), a public/private partnership (Russell et al. 2006).

*Bacillus thuringiensis* (Bt) is of great value as an insecticide for use in ecologically sound pest management (Tabashnik et al. 1997) and in situations where *P. xylostella* is resistant to conventional insecticides (Shelton et al. 1993). Development of resistance in field populations of *P. xylostella* (Tabashnik et al. 1990; Shelton et al. 1993; Iqbal et al. 1996) has prompted an extensive effort of research into resistance mechanisms (Tabashnik et al. 1997; Wright et al. 1997; Ballester et al. 1999; Heckel et al. 1999; Sayyed et al. 2000, Baxter et al. 2005). At the Fourth Workshop, Heckel et al. (2004) discussed the concept of identifying the genetic basis of resistance mechanisms to Bt in *P. xylostella* so that specific detection methods could be designed. Such research has continued since the Workshop and has revealed that Mode 1 resistance to Bt does not have the same genetic basis in all Lepidoptera (Baxter et al. 2005).

== BIOLOGICAL CONTROL ==

A clearer understanding of how *P. xylostella* populations are regulated in the field is vital. Until we can predict outcomes with more certainty, pest management will continue to be underpinned by use of pesticides by farmers who are typically more risk-averse than the average entomologist. The International Symposium on
Improving Biocontrol of *Plutella xylostella* was held in Montpellier in October 2003 (Kirk and Bordat 2004) with the aim of exploring how biological control of *P. xylostella* could be improved globally. Sarfraz *et al.* (2005) have recently reviewed the role of biological control of *P. xylostella*, building on the more general review of the bionomics of *P. xylostella* by Talekar and Shelton (1993).

One effective way of testing our understanding of the pest system is to construct a simulation model. Liu *et al.* (2002) published an extremely detailed study of temperature development of *P. xylostella* that will be a foundation for future simulation work. Mohandas and Zaczkowski (2004) revisited the plethora of temperature development studies on *P. xylostella* and outlined some of the problems in using them. In Australia, there is a lack of data on high temperature mortality in the field. The work of Hoy *et al.* (1989), looking at movement patterns of *T. ni* larvae within the cabbage plant, also needs to be investigated for *P. xylostella*, particularly in high temperature situations. Typically the effect of temperature is the easiest to model, with mortality factors more difficult (but parasitism and disease are more easily quantified than predation and effects of rainfall). While life tables are laborious to undertake, they are invaluable for documenting the processes occurring in the field.

At the inaugural DBM Workshop, Harcourt (1986) reviewed his groundbreaking series of 74 life table studies conducted in southeastern Ontario between 1960 and 1970. These painstaking studies provide an invaluable data resource for future generations of entomologists as the basis for developing robust simulation models. There have been other life table studies of *P. xylostella* reported from other parts of the world such as Australia (Goodwin 1976), Japan (Wakisaka *et al.* 1992), Thailand (Keinmeesuke *et al.* 1992) and USA (Muckenfuss *et al.* 1992). Recently a series of studies in China and Australia have sought to measure the impact of various mortality factors on the mortality of *P. xylostella* in commercial fields under a range of farming practices (Furlong *et al.* 2004a, b). Exclusion trials have also been conducted in Australia to look closely at field performance of *Diadegma semicoloratum* (Wang *et al.* 2004).

For many pests, historically, the impact of parasitoids has been the main focus. While there are methodological issues to overcome (Waage and Cherry 1992), many studies have been conducted in *Brassica* pests. The influence of pathogens is also relatively easy to measure, although results can be easily confounded by handling issues and by secondary pathogens. There are a number of examples where insects can have latent infections of virus, which only manifest in disease when the insects are stressed. However, generally, the role of predation and abiotic factors are more difficult to measure and are often the label given to unexplained residual mortality in a life table study.

Over many years, entomologists have looked for meaningful tools to measure predation in the field and to identify which of the potential predatory species present in the agroecosystem are in fact important predators of a particular pest. Early work in *Brassica* pests focused on *Pieris rapae*, the cabbage white butterfly or imported cabbageworm. In New Zealand, Ashby (1974) and Ashby and Pottinger (1974) used precipitin ring tests in association with exclusion cages to estimate impact of predation on *P. rapae*. They identified an opilionid, *Philangium opilio* as the most important ground-inhabiting predator and two syrphid species (*Melanostoma fasciatum* (Macquart) and *Melangyna novaealandiae* (Macquart)) as the most important predators on the foliage. In Australia, using enzyme-linked immunosorbent assay (ELISA) with polyclonal antibodies, Kapuge *et al.* (1987) found the major predators of *P. rapae* to be two species of earwigs, *Nala lividipes* and *Labidura truncata*, a staphylinid beetle, *Thyrocoelus cyanopterus* and an eusparassid spider, *Olias diana*. Schmaedick *et al.* (2001) also developed a polyclonal ELISA to assess predation of *P. rapae*. In a series of 8 life tables, using exclusion cages, Schmaedick and Shelton (1997, 1999) found that the mortality of immature stages of *P. rapae* (mainly eggs and first instar larvae) averaged 543 but ranged from 23% to 80%. They also used monoclonal antibodies to identify potential predators. In
many field life table studies, neonate larvae are often the vulnerable life stage although often it can be difficult to assign a cause of mortality i.e. they go missing (Zalucki et al. 2002).

“Experimental and manipulative studies, as well as detailed observations of the animal, are vital if the subtle interaction of factors responsible for this high and variable mortality are to be understood. These studies are essential for an understanding of theories linking female oviposition behavior with larval survival, plant defense theory, and population dynamics, as well as modern crop resistance breeding programs” (Zalucki et al. 2002).

More recently, DNA markers have been used to improve accuracy of prey identification from predator gut contents (Symondson 2002). In Australia, detection of P. xylostella in gut contents of the nabis, Nabis kinsbergi, has been done using a PCR amplification of a 275 bp fragment of the ITS-1 region of the ribosomal gene (Ma et al. 2005). DNA markers can also be used to distinguish taxonomically indistinct specimens such as immature lycosids (Hosseini et al. 2007).

In an earlier study in Australia, Goodwin (1976) used precipitin ring tests to check for potential predators of P. xylostella in the field. The most common species giving positive reactions to the precipitin ring test were from Araneidae, Coccinellidae and Opilionesidae, while species from Syrphidae and Neuroptera gave fewer positive tests than expected, given the results of laboratory feeding trials. The test was not sensitive enough to detect egg predation, which was considered to be a very important component of predation in the field. It will be interesting to see how the predictions from precipitin tests compare to the results being obtained with more modern techniques.

These types of trials, using either DNA markers or monoclonal antibodies in an ELISA, are very instructive but need to be done in a wide range of environments as well as for the full range of pest species encountered (Sheppard and Harwood 2005).

Parasitoids

Following the insightful review of the taxonomy of parasitoids of P. xylostella by Fitton and Walker (1992), the revision of Diadegma species (Hymenoptera: Ichneumonidae) attacking P. xylostella has been completed (Azidah et al. 2000). The endemic sub-Saharan African parasitoid was shown to be the inefficient D. mollipila (Holmgren). Wagener et al. (2004, 2006) developed a PCR-based approach to distinguish important Diadegma species associated with P. xylostella. Subsequently, there has been a very successful program initiated by ICITEP to establish the specialist D. semiclaustrum into Ethiopia, Kenya, Tanzania and Uganda (Nyambo and Löh 2005). In Australia, Wang and Keller (2002, 2003, 2004, 2005) made detailed wind-tunnel observations of the behaviour acts of C. vestalis and D. semiclaustrum. Their conceptual model of the patch-leaving behavior of D. semiclaustrum was as follows:

(1) Upon arriving at an empty patch without kairomone sources, the parasitoid leaves it quickly.
(2) The parasitoid has the ability to estimate initial patch quality in relation to kairomone concentration. Upon arriving at a patch containing kairomone sources, it sets up a basic leaving tendency which is an increasing function of elapsed patch residence time.
(3) The basic leaving tendency decreases with increasing interpatch distance, host density, or clustered host distribution.
(4) Subsequent foraging experience within the patch provides the parasitoid with a more realistic assessment of and updated information on the availability of host and the degree of patch depletion. The parasitoid’s leaving tendency decreases with unsuccessful host encounters as a result of host defense, but increases with successful oviposition.
(5) The patch-leaveing tendency further increases when ovipositions occur in rapid succession or when the parasitoid is involved (Wang and Keller 2005).

Fittted and Walker (1992) suggested that *plutellae* might be a junior synonym of *vestalis* Haliday. Shaw (2003) has now confirmed that *Microgaster vestalis* Haliday is a senior synonym of *Apanteles plutellae* Kurdjumov. So, *Cotesia vestalis* (Haliday) takes precedence over *Cotesia plutellae*.

Rinçon et al. (2006) examined 5 widely-separated populations of *C. vestalis* and found that all populations were indeed the same species but there were two partially incompatible population aggregates present. They cautioned that the need to ensure population incompatibility was not going to be a problem if populations of *C. vestalis* were to be re-introduced into a country where it had previously been established but had not achieved satisfactory levels of control of *P. xylostella*. Rinçon et al. (2006) suggested that molecular diagnostics be used to check for incompatibility of strains of *C. vestalis*. Certainly, they were able to distinguish the two partially incompatible groups in their study.

A strain of *C. vestalis* from Italy was released into Australia between 1951 and 1955 (Waterhouse and Sands 2001). The literature records that *C. vestalis* is well-established in Australia and is contributing to effective biological control, together with *Diadegma semiclausum* and *Diadromus collaris* (Wilson 1960, Waterhouse 1992, Waterhouse and Sands 2001). In reality, the species is now extremely scarce in Australia and plays no significant role in regulating *P. xylostella* (Goodwin 1979, Hamilton 1979). It is likely that workers making general field observations of parasitism of *P. xylostella* in the past may have mistaken *Apanteles ippeus* Nixon (Hymenoptera: Braconidae) found commonly in Australia for *C. vestalis*, as both species spin a single white cocoon. It would be worth investigating the re-introduction of appropriate strains of *C. vestalis* to Australia. For example, the very successful South African strain of *C. vestalis* (Kfir 1997; Löhr and Kfir 2004) could be an appropriate introduction to Australia. The extreme scarcity of *C. vestalis* in Australia currently suggests that the issue of compatibility of strains would not be significant. Again, CLIMEX modelling would be a useful tool here to determine the areas of Australia that would benefit from *C. vestalis*.

Pathogens

Cherry et al. (2004) and Sarfraz et al. (2005) have comprehensively reviewed the role of pathogens for the control of *P. xylostella*. The development of a surfactant-polymer-formulation to assist in the foliar application of entomopathogenic nematodes (Schroer et al. 2005a, b, c) is an important advance that could also be used against other lepidopteran pests.

Field studies on the initiation of epizootics of *Zoophthora radicans* (Vickers et al. 2004) suggested that the auto-dissemination of fungal pathogens was a feasible strategy for control of *P. xylostella*, provided that epizootics can be established and maintained when *P. xylostella* population densities are low. Again, there is the prospect of deploying this strategy using other pathogens such as *Beauveria bassiana* as well as targeting other lepidopteran pests.

**OTHER IMPORTANT LEPIDOPTERAN PESTS**

*Crocidolomia pavoana* (Fabricius) (Lepidoptera: Cramidae) is an important cambid pest in tropical and sub-tropical *Brassica* vegetable crops in countries such as India, South East Asia, Australia (Queensland), East Africa, Papua New Guinea and the South Pacific (Nyang and Löhr 2005; Sastrosiswojo and Setiaawi 1992; Shepard and Schellhorn 1997; Waterhouse 1992). Females lay 75-300
eggs in a partially overlapping shingled mass on the undersurface of leaves close to the midrib or veins. However, egg parasitoids have only been infrequently recorded in Indonesia (Shepard and Schellhorn 1997) and Papua New Guinea (Saucke et al. 2000). The value of an effective egg parasitoid that would parasitize virtually all eggs in the mass would be immense. The early instar larvae are gregarious but older larvae disperse over the plant before they pupate in the soil. In Indonesia, only low levels of parasitism are recorded (Sastrasiswojo and Setiawati 1992; Shepard and Schellhorn 1997) with generalist parasitoids such as *Erioborus sinicus* (Holmgren) being recorded at levels around 10%. Smyth et al. (2003a) found that oviposition preference of *C. pavonana* varied with host phenology, with Stage 4 (11-12 true leaves) being the preferred cabbage stage. Studies on the larval performance of *C. pavonana* indicated that preference of phenological stages of cabbage is correlated, with stage 4 being a nutritionally superior host for their offspring (Smyth 2003b).

In a detailed survey of cabbage growing areas in Indonesia, Shepard and Schellhorn (1997) found that *P. xylostella* was generally heavily parasitized with *D. semiclauseum* (75% on average) but ironically observed “that dense *P. xylostella* populations were always indicative of frequent insecticide use by farmers and when *C. pavonana* numbers were high, fields were sprayed less frequently or not at all.”

Waterhouse (1992) noted that *C. pavonana* is only occasionally important in Western Samoa, New Caledonia and French Polynesia and so concluded that it would be worthwhile to investigate the reasons for the apparent low pest status of *C. pavonana* on these islands.

There is very little information about the impact of natural enemies on *C. pavonana*. Initial field life table studies of *C. pavonana* in Queensland using exclusion studies have revealed very little predation or parasitism (M. Furlong personal communication). This type of study, coupled with use of molecular or serological techniques to identify significant predatory species in the particular ecosystem, needs to be undertaken in many parts of the tropics. Only then will we have a clearer picture of predation of *C. pavonana* and *P. xylostella*.

It is important to continue to survey for more effective natural enemies. To date it has not been possible to determine the centre of origin of *C. pavonana* so an international effort to undertake a genetic analysis of populations from a number of tropical regions should result in improved targeting of exploration for natural effective enemies.

As well as *Crocidolomia*, further work is needed on the lowland pest crambid, *Hellula undalis* (F.), the cabbage webworm. Apart from Sivapragasam and Abdul Aziz (1992) and Sivapragasam and Chua (1997a, b), there are very few published papers on the biology and ecology of this pest. Parasitoids of *H. undalis* are very rare in Malaysia, which has led to the suggestion that *H. undalis* is exotic to Malaysia. Again, better knowledge of its centre of origin should assist in targeting surveys for potential natural enemies.

Female sex pheromone blends for *C. pavonana* (Usui et al. 1987) and *H. undalis* (Arai et al. 1982; Sugie et al. 2003) have been published. Sugie et al. (2003) found that a mixture of 5 mg of (E, E)-11, 13-hexadecadienal and 15-500 ng of (Z)-11-hexadecenyl showed the same attraction activity as virgin females. However, there needs to be widespread testing of these blends before they can be used reliably by farmers for monitoring male moth flights and forecasting oviposition events in the field.

In Guam, Indian mustard crops have been used as trap crops for *P. xylostella*, *C. pavonana* and *H. undalis* (Muniappan and Marutani 1992, Muniappan et al. 1997, 2004). However, as with *P. xylostella*, results have been variable. Can we identify “dead-end” trap crops as with *P. xylostella* (Shelton and Badenes-Perez 2006)? There is also the possibility of deploying pathogens or entomopathogenic nematodes as spot treatments for infestations of *C. pavonana* or *H. undalis*.

With the development of transgenic *Brassica* vegetables, using Bt transgenes to control *P. xylostella*
(Russell et al. 2006), it would be desirable for farmers if the resistance extended to all lepidopteran species affecting cabbage (e.g. *C. pavonana*, *H. undalis*, *Helicoverpa armigera*, *Spodoptera* spp. and *T. ni*).

**BOTANICAL INSECTICIDES**

The use of botanical extracts as insecticides has long been practised in agriculture (Ismam 2006). While their use is not widespread globally, there is great interest in the use of botanical insecticides in developing countries where farmers struggle to afford synthetic pesticides and the possibility of using local vegetation to provide pest management tools is highly attractive (Ismam 2006). While extensive testing has shown that extracts of many plant species are toxic to *P. xylostella* (Morrallo-Rejesus 1986; Dadang and Ohsawa 2001; Leatemia and Isman 2004), very few extracts are used widely. Neem-based insecticides have been studied in many areas and show considerable promise for control of *P. xylostella* (Saucke et al. 2000). Drawbacks to the wide scale use of botanical extracts have included the ability to produce the products consistently, in terms of both quality (Liu and Liu 2005) and quantity (Ismam 2006). Of some concern in developing countries is the use of “cocktails” of botanical extracts without consideration of the acute human toxicity of some products such as rotenone (traditionally used as a fish poison).

In recent years, a number of detailed studies of the effects of botanical extracts derived from *Azadirachta indica* and *Melia azedarach* on *P. xylostella* and its parasitoids, *C. vestalis* and *Diadromus collaris* have been undertaken (Charleston et al. 2005a, 2005b, 2006). In Kenya, Akol et al. (2002, 2003) examined the effects of two neem-based insecticides on *Diadegma mOLLIPA*. These types of studies are essential if the impacts of botanical extracts are to be understood more clearly, a pre-requisite for ensuring the potential benefits are realised.

**MAKING INFORMATION ACCESSIBLE TO SMALLHOLDER FARMERS**

Sivapragasam (2004) identified a number of problems in sustaining farmer involvement in *Brassica* IPM programs. These restraints included relentless sales pressure from pesticide salesmen, lack of continued support from change agencies, difficulties with the economic thresholds and complex monitoring protocols, and a lack of information about other pests in the system. To overcome some of these issues, Sivapragasam (2004) advocated simplifying the monitoring procedures, encouraging farmers to switch from broad-spectrum insecticides, and switching to a “bottom-up” farmer focus as illustrated in the Farmer Field School models. The empowerment of farmers through adult learning techniques has been very valuable in improving communities. The learning mottos are very similar in different areas. In a recent Farmer Field School in Timor Leste, the catch cry was:

Hau Rona Hau Haluna (I Hear, I Forget)
Hau Hare Hau Hanoine (I See, I Remember)
Hau Halo Hau Hatene (I Practise, I Understand)

There is an impressive array of facts known about *P. xylostella*. However, millions of smallholders are unable to access the current information. There is a pressing need for much of this material to be translated into a range of languages to enable extension workers and farmer trainers in developing countries to have access to a wider range of resource material. Key IPM documents that should be translated include the FAO Ecological Guide for Cabbage Integrated Pest Management (Praaterink 2000) and the CABI Discovery Learning Manual for Cabbage Pest Management (Van Mele et al. 2002).

The series of five International Workshops for Diamondback Moth and other Crucifer Pests have provided
a wonderful opportunity for scientists from many countries to exchange information and forge research networks. While the Workshops are valuable events, they can only ever attract a subset of involved scientists to attend. So, it is important to embrace new ideas and techniques from all parts of the world, and from a range of disciplines. It is also important for scientists to revisit the treasure store of prior research contained in the pre-electronic scientific literature.

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