A simple method for estimating instantaneous levels of endoparasitism of *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae) by Hymenoptera in the field

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Although endoparasitoids are widely used for biological control of *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae) throughout the world, current methods do not allow for easy estimation of parasitism levels. I investigated the potential of using ratios of parasitoid cocoons to infestations to develop a simple and practical method of estimating parasitism levels in the field. Crop infestations by the pest and densities of its endoparasitoids' cocoons were recorded at weekly intervals over six consecutive years on unsprayed cabbage. In order to establish if there was a relationship between parasitism levels and ratios of parasitoid cocoons to infestations, samples of host larvae and pupae were collected every week during scouting for rearing in the laboratory. The majority of parasitoid cocoons belonged to the larval endoparasitoid *Cotesia vestalis* (Haliday) (Hymenoptera: Braconidae), which was the major mortality factor of *P. xylostella*. Total parasitism levels were positively related to ratios of parasitoid cocoons to infestations. Crop infestation by *P. xylostella* was low during periods of high parasitism (≥50 %) than during low parasitism (<50 %), and 50 % parasitism corresponded with 20 % ratio of parasitoid cocoons to infestations. This study shows that ratios of parasitoid cocoons to infestations can be used to estimate background parasitism levels.

Key words: diamondback moth, infestations, natural mortality, parasitoid cocoons, decision-making, integrated insect pest management.

INTRODUCTION

One of the biggest challenges for integrated insect pest management is the integration of biological and chemical control methods. This is because, in many crop systems, there are no specifics on ratios of biological control agents to hosts required to provide sufficiently high levels of biological control that would exceed the cost of insecticide application (Giles *et al*. 2003; Weinzierl 2009). This is especially true where population densities of natural enemies cannot be readily determined. Not only is it impossible to determine absolute densities of adult parasitoids in the field (Gauld & Janzen 2004; Fraser *et al*. 2007), it is an additional challenge to estimate parasitism levels when immature parasitoids develop inside the body of their hosts. Immature stages ectoparasitoids are visible on the body of their hosts and thus it is easy to determine parasitism levels on conclusion of each scouting event (Babendreier *et al*. 2005), but it takes much longer to verify that hosts are parasitized by immature endoparasitoids, which develop inside their host's body (Naranjo 2001). Methods currently used to estimate parasitism levels by endoparasitoids include: 1) rearing samples of host stages that are vulnerable to parasitoid attack to the point where either parasitoids or adult hosts emerge (van Driesche *et al*. 1991; Waage & Cherry 1992); 2) dissecting representative samples of hosts (Naranjo 2001); and 3) application of PCR-based identification techniques (Ashafaq *et al*. 2004; Greenstone 2006). Not only are these methods expensive in terms of the additional resources required, as well as time and labour, but they are also too specialized to be performed by growers.

The diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae), is a worldwide pest of *Brassica* crops against which all biological control efforts using parasitoids utilize endoparasitoids (Talekar & Shelton 1993; Sarfraz *et al*. 2005). Despite overwhelming evidence from different parts of the world that parasitoids play an important role in curtailing its populations (Talekar & Shelton 1993; Saucke *et al*. 2000; Kfir & Thomas 2001; Macharia *et al*. 2005; Sarfraz *et al*.

2005; Nofemela 2010), effective integration of endoparasitoids with chemical control has not been achieved. Instead, there is a persistent and widespread decimation of its parasitoid populations due to indiscriminate application of insecticides by growers (Talekar & Shelton 1993; Sarfraz *et al*. 2005; Upanisakorn *et al*. 2011) largely due to a lack of simple and practical methods of estimating levels of parasitism in the field. For example, the method widely used to estimate rates of parasitism of *P. xylostella* by rearing samples of its immature stages (Liu *et al*. 2000; Martínez-Castillo *et al*. 2002; Guilloux *et al*. 2003; Gichini *et al*. 2008; Nofemela 2010) allows only for a retrospective estimation of parasitism levels, and thus relationship between parasitism levels and infestations, as it may take two weeks or more to establish the fate of these samples, during which time the pest population density in the field can change substantially. Thus, growers cannot easily determine if the impact of parasitoids is sufficiently large to suppress the pest population density adequately.

Cotesia vestalis (Haliday) (Hymenoptera: Braconidae) (Shaw 2003) and *Diadegma semiclausum* (Hellén) (Hymenoptera: Ichneumonidae) (Azidah *et al*. 2000) are the most important parasitoids of *P. xylostella* in many parts of the world (Talekar & Shelton 1993; Sarfraz *et al*. 2005). Both species are solitary and spin easily distinguishable cocoons on the plant surface on completion of their larval development (Ullyett 1947; Broodryk 1971). Since each parasitoid cocoon represents a dead host, the higher the proportion of intact parasitoid cocoons to infestations on a weekly basis, the higher the likelihood that the majority of host larvae contain immature endoparasitoids at different stages of development. Thus, ratios of parasitoid cocoons to infestations have a potential to estimate background parasitism levels reliably during scouting events (Giles *et al*. 2003).

Cotesia vestalis is the dominant parasitoid of *P. xylostella* in South Africa, often accounting for >80 % of total parasitism (Waladde *et al*. 2001; Mosiane *et al*. 2003; Smith 2004; Nofemela & Kfir 2005). This study provides evidence that ratios of *C. vestalis* cocoons to infestations can be used to reliably estimate background parasitism levels in the field.

MATERIAL AND METHODS

The study was conducted at a research farm in Brits (25°59′S 27°76′E, altitude 1082 m), North West Province of South Africa. It is a high plateau inland region characterized by a temperate climate and summer rainfall (Rutherford *et al*. 2006). Long-term annual precipitation is 600–700 mm, and mean maximum and minimum temperatures are 35.3 °C (January) and –3.3 °C (June) (Rutherford *et al*. 2006).

Cabbage, *Brassica oleracea* var. *capitata* (L.) (Brassicaceae), is one of the major crops grown under irrigation on farms in the vicinity of the study site. Growers transplant cabbage seedlings on several hectares, usually 25 000 cabbages/ha, every week during summer and autumn, but a few hectares are planted during winter and spring. It appears that the major reason for transplanting fewer cabbages during cool seasons is influenced by the slower developmental rate of the crop, which affects produce flow rate from the farm. Since immature *Brassica* plants were always present at a landscape level around the study site at any given time, the cabbage fields are assumed to be connected (*i.e*. a metapopulation] due to free movement of *P. xylostella* and its parasitoids between farms (Vandermeer & Carvajal 2001; Desouhant *et al*. 2003).

Between 2000 and 2500 cabbage seedlings were transplanted three consecutive times per year (February 2002–January 2008) at a plant spacing of 0.5 m within rows and 1.0 m between rows. Standard agronomic practices that included ploughing, irrigation, fertilization and weeding were followed in each crop, but without the application of insecticides. For each crop, monitoring of *P. xylostella* infestations (*i.e*. larvae and pupae) and its parasitoids was initiated two weeks after cabbage transplants. In subsequent plantings, a new crop was prepared next to the old one five weeks before harvest of the current crop, and two weeks later scouting on the older plot was terminated and begun on the new plot. This practice ensured that investigations were continually conducted on crops of reasonably good quality. Therefore, until it was completely harvested and remaining plants ploughed under, the older crop served as a reservoir for *P. xylostella* and its parasitoids at a local scale. One experimental plot was monitored at any given time and a total of 18 plots were monitored during the study period.

At weekly intervals, leaves of 30 randomly selected plants in each plot were thoroughly inspected and numbers of *P. xylostella* larvae,

pupae, and cocoons of its parasitoids found on each plant were recorded. Since no egg parasitoid species have been recorded from *P. xylostella* in South Africa (Kfir 1997), rates of parasitism were determined from samples of host larvae and pupae, and cocoons of its parasitoids. However, first and second instar larvae were not sampled for all known *P. xylostella* egg-larval and larval parasitoids complete their larval development once the hosts have reached the fourth instar. Thus, parasitism of *P. xylostella* eggs and larvae accumulates over the larval instars (Nofemela & Kfir 2005). Furthermore, sampling of host instars that are too young to be parasitized is inappropriate, as it tends to grossly underestimate parasitism levels (van Driesche *et al*. 1991). Depending on the number of cabbages that were transplanted and the season, the number of sampled plants during summer (December–February) and autumn (March–May) accounted for 14.4 % to 18 % of the plant population, and 19.2 % to 24 % of plant population during winter (June–August) and spring (September–November). Thus, sampling hardly influenced population densities of the pest and its parasitoids.

The field-collected samples were maintained in the insectary of the ARC-Plant Protection Research Institute, Rietondale campus in Pretoria, at 25 ± 1 °C, 65 ± 5 % RH, and L16:D8 photoperiod. The larvae were provided with sections of fresh cabbage leaves and held individually in Petri dishes. The leaves were replaced every second day until all of the larvae pupated or parasitoid cocoons formed. The samples of *P. xylostella* pupae and parasitoid cocoons were confined individually in ventilated glass vials (2.5 × 10 cm). All emergent parasitoids were identified and their incidence determined. Parasitism was calculated as the percentage of emergent parasitoids out of total samples of *P. xylostella* larvae and pupae. Thus, the impact of primary parasitoids on *P. xylostella* population density was determined from parasitism of corresponding infestation levels. However, samples that died of unknown causes were excluded from calculations.

Data analysis

One-way analysis of variance (ANOVA) was used to compare the incidence of the parasitoid species (%). Prior to ANOVA, the data were square-root transformed and where significant differences were detected, the means were compared using Fisher's LSD test. Using mean values obtained over six consecutive years for each variable, linear regression analyses were performed to determine the relationship between total parasitism levels (%) and ratios of parasitoid cocoons to infestations. The data for ratios of parasitoid cocoons to infestations and parasitism levels were square-root transformed prior to performing linear regressions. All statistical analyses were performed on Statistica (2012), and treatment effects were considered significant at $P < 0.05$.

RESULTS AND DISCUSSION

Cabbage infestations by *P. xylostella* larvae and pupae were low during November–August, fluctuating between (mean ± S.D.) 0.1 ± 0.12 and 2.2 ± 2.61 *P. xylostella* per plant per week, and were high during September–October peaking at 10.6 ± 9.59 *P. xylostella* per plant (Fig. 1). Field samples of *P. xylostella* larvae and pupae yielded five species of indigenous primary parasitic Hymenoptera: *C. vestalis*; *Oomyzus sokolowskii* (Kurdjumov) (Eulophidae), a larval-pupal parasitoid; *Apanteles halfordi* (Ullyett) (Braconidae), a larval parasitoid; *Diadromus collaris* (Gravenhorst) (Ichneumonidae), a pupal parasitoid; and *Diadegma mollipla* (Holmgren) (Ichneumonidae), a larval-pupal parasitoid. The incidences of the primary parasitoids were significantly different ($F_{4,1128} = 235.73$, $P < 0.001$) with *C. vestalis* causing highest host mortality (42.05 ± 33.10 %) followed by *O. sokolowskii* (9.02 ± 16.75 %), whereas the incidences of *D. collaris* (2.25 ± 5.07 %), *A. halfordi* (1.33 ± 6.26 %) and *D. mollipla* (0.22 ± 1.81 %) were not significantly different. *Cotesia vestalis*, *O. sokolowskii* and *D. collaris* were active throughout the year, whereas incidence of *A. halfordi* and *D. mollipla* was sporadic. These results are in agreement with previous studies in South Africa (Waladde *et al*. 2001; Mosiane *et al*. 2003; Smith 2004; Nofemela & Kfir 2005).

Total parasitism levels were high during late October–May, and low during June–early October (Fig. 1). Although the period of high parasitism (≥50 %) generally coincided with low infestations, infestations also were low during cold winter months (June–August). As a consequence of low parasitism during winter, *P. xylostella* infestations increased substantially during September–early October (Fig. 1). However, parasitism levels soon

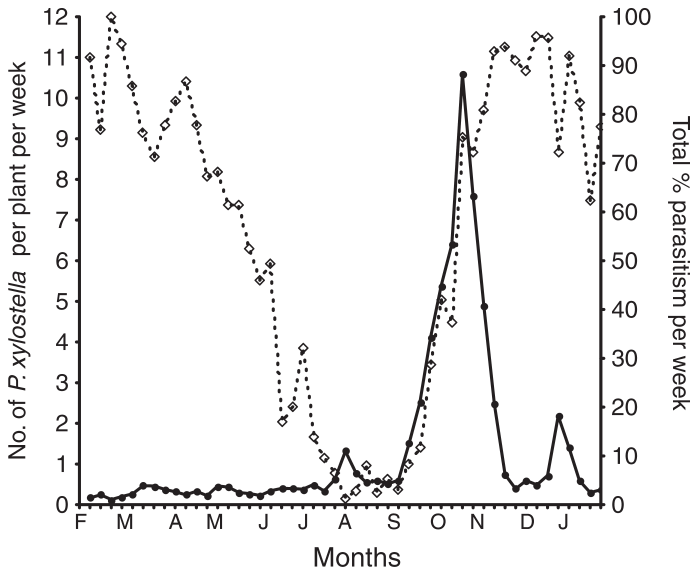

Fig. 1. The influence of mean total parasitism (dotted line) on mean incidence of *Plutella xylostella* larvae and pupae (solid line) over the course of a year. The points represent means over six years.

increased to high levels leading to a sharp decline in the pest density, and subsequently the infestations were regulated largely below one *P. xylostella* per plant per week during November–May (Fig. 1). Since infestation level below one *P. xylostella* per plant per week is considered too low to negatively affect cabbage yield and crop quality (Ayalew 2011) and the proportion of plants infested generally increases with infestation levels, it is recommended to growers not to apply insecticides when infestations are below one *P. xylostella* per plant due low risk to their crop.

Since high parasitism levels are a result of female parasitoid density maintained above a critical threshold level in the system (DeBach & Rosen 1991; van Driesche & Bellows 1996; Hawkins & Cornell 1999), a higher ratio of parasitoid to host density restrains the pest from attaining high infestation levels. As *C. vestalis* is the most dominant parasitoid of *P. xylostella* in South Africa, it is logical to assume that most of parasitoid cocoons in the field belong to it. A linear regression analysis of parasitism of *P. xylostella* against non-zero ratios of parasitoid cocoons to *P. xylostella* infestations showed a significant positive relationship (r^2 = 0.667, $F_{1,50}$ = 100.11, $P < 0.001$; Fig. 2). Thus, *P. xylostella* parasitism levels increased with the ratios of parasitoid cocoons to infestations. Fig. 1 shows that parasitism levels of ≥50 % are sufficiently high to suppress the pest population below one *P. xylostella* per plant, whereas Fig. 2 shows that a 20 % ratio of *C. vestalis* to cocoons is equivalent to 50 % parasitism of *P. xylostella*.

The major stumbling block to effective management of *P. xylostella* populations remains the lack of practical guidelines for integrating biological and chemical control methods. This challenge is now more apparent than ever in southeast Asia, where the gains obtained from parasitoid introductions in the 1980s are being reversed by indiscriminate application of insecticides by growers (Sivapragasam 2004; Upanisakorn *et al*. 2011) which has led to *P. xylostella* populations in that region to develop multiple- and cross-resistance to a wide range of insecticides (Zhao *et al*. 2006). In southeast Asia, *D. semiclausum* and *C. vestalis*, are dominant parasitoids of *P. xylostella* in the highlands and lowlands, respectively (Talekar & Shelton 1993; Verkerk & Wright 1997), while *Diadegma insulare* (Cresson) (Ichneumonidae) and *Microplitis plutellae* Muesbeck (Braconidae) are important in North America (Xu *et al*. 2001; Martínez-Castillo *et al*. 2002). Since all of these parasitoid species form easily distinguishable cocoons on the plant surface on completion of larval development, the method suggested here of estimating parasitism levels from ratios of parasitoid cocoons to infestations is simple and practical enough to be implemented at farm level in several parts of the world.

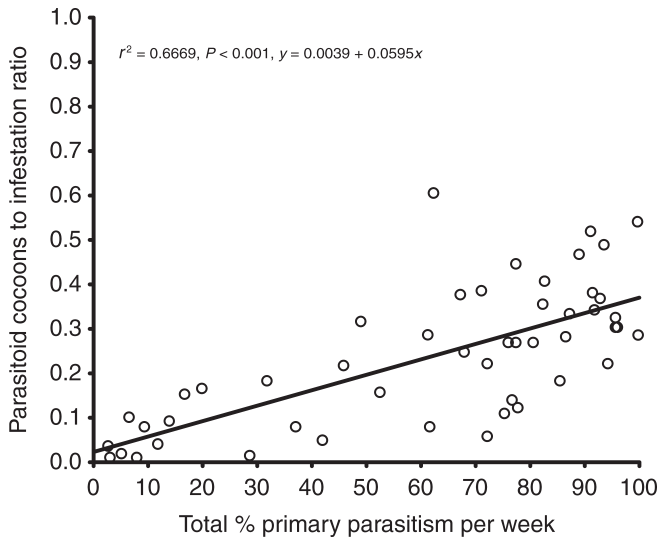

Fig. 2. The relationship between mean total parasitism of *Plutella xylostella* larvae and pupae and ratios of *Cotesia vestalis* cocoons to infestations. Points in the graph correspond to averages per week over six years.

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REFERENCES

ASHAFAQ, M., BRAUN, L., HEGEDUS, D. & ERLANDSON, M. 2004. Estimating parasitism levels in *Lygus* spp. (Hemiptera: Miridae) field populations using standard and molecular techniques. *Biocontrol Science Technology* **14**: 731–735.

AYALEW, G. 2011. Effect of the insect growth regulator novaluron on diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), and its indigenous parasitoids. *Crop Protection* **30**: 1087–1090.

AZIDAH, A.A., FITTON, M.G. & QUICKE, D.L.J. 2000. Identification of the *Diadegma* species (Hymenoptera: Ichneumonidae, Campopleginae) attacking the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Bulletin of Entomological Research* **90**: 375–389.

BABENDREIER, D., BIGLER, F. & KUHLMANN, U. 2005. Methods used to assess non-target effects of invertebrate biological control agents of arthropod pests. *BioControl* **50**: 821–870.

BROODRYK, S.W. 1971. The biology of *Diadegma stellenboschense* (Cameron) (Hymenoptera: Ichneumonidae), a parasitoid of potato tuber moth. *Journal of the Entomological Society of Southern Africa* **34**: 413–423.

DEBACH, P. & ROSEN, D. 1991. *Biological Control by Natural Enemies*. Cambridge University Press, Cambridge, U.K.

DESOUHANT, E., DRIESSEN, G., LAPCHIN, L., WIELAARD, S. & BERNSTEIN, C. 2003. Dispersal between host populations in field conditions: navigation rules in the parasitoid *Venturia canescens*. *Ecological Entomology* **28**: 257–267.

FRASER, S.E.M., DYTHAM, C. & MAYHEW, P.J. 2007. Determinants of parasitoid abundance and diversity in woodland habitats. *Journal of Applied Ecology* **44**: 352–361.

GAULD, I.D. & JANZEN, D.H. 2004. The systematics and biology of the Costa Rican species of parasitic wasps in the *Thyreodon* genus-group (Hymenoptera: Ichneumonidae). *Zoological Journal of the Linnean Society* **141**: 297–351.

GICHINI, G., LÖHR, B., ROSSBACH, A., NYAMBO, B. & GATHU, R. 2008. Can low release numbers lead to establishment and spread of an exotic parasitoid: the case of the diamondback moth parasitoid, *Diadegma semiclausum* (Hellén), in East Africa. *Crop Protection* **27**: 906–914.

GILES, K.L., JONES, D.B., ROYER, T.A., ELLIOTT, N.C. & KINLER, S.D. 2003. Development of a sampling plan in winter wheat that estimates cereal aphid parasitism levels and predicts population suppression. *Journal of Economic Entomology* **96**: 975–982.

GUILLOUX, T., MONNERAT, R., CASTELO-BRANCO,

M., KIRK, A. & BORDAT, D. 2003. Population dynamics of *Plutella xylostella* (Lep., Yponomeutidae) and its parasitoids in the region of Brasilia. *Journal of Applied Entomology* **127**: 288–292.

GREENSTONE, M.H. 2006. Molecular methods for assessing insect parasitism. *Bulletin of Entomological Research* **96**: 1–13.

HAWKINS, B.A. & CORNELL, H.V. 1999. *Theoretical Approaches to Biological Control*. Cambridge University Press, Cambridge, U.K.

KFIR, R. & THOMAS, J. 2001. Biological control of diamondback moth on St. Helena Island with parasitoids supplied by the ARC-PPRI. *Biocontrol News and Information* **22**: 4N.

KFIR, R. 1997. Parasitoids of *Plutella xylostella* (Lep.: Plutellidae) in South Africa: an annotated list. *Entomophaga* **42**: 517–523.

LIU, S.S., WANG, X.G., GUO, S., HE, J. & SHI, Z.H. 2000. Seasonal abundance of the parasitoid complex associated with the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) in Hangzhou, China. *Bulletin of Entomological Research* **90**: 221–231.

MACHARIA, I., LÖHR, B. & DE GROOTE, H. 2005. Assessing the potential impact of biological control of *Plutella xylostella* (diamondback moth) in cabbage production in Kenya. *Crop Protection* **24**: 981–989.

MARTÍNEZ-CASTILLO, M., LEYVA, J.L., CIBRIÁN-TOVAR, J. & BUJANOS-MUÑIZ, R. 2002. Parasitoid diversity and impact on populations of the diamondback moth *Plutella xylostella* (L.) on *Brassica* crops in central México. *BioControl* **47**: 23–31.

MOSIANE, M.S., KFIR, R. & VILLET, M.H. 2003. Seasonal phenology of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), and its parasitoids on canola, *Brassica napus* (L.), Gauteng Province, South Africa. *African Entomology* **11**: 277–285.

NARANJO, S.E. 2001. Conservation and evaluation of natural enemies in IPM systems for *Bemesia tabaci*. *Crop Protection* **20**: 835–852.

NOFEMELA, R.S. & KFIR, R. 2005. The role of parasitoids in suppressing diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), populations on unsprayed cabbage in the North West Province of South Africa. *African Entomology* **13**: 71–83.

NOFEMELA, R.S. 2010. The ability of synthetic sex pheromone traps to forecast *Plutella xylostella* infestations depends on survival of immature stages. *Entomologia Experimentalis et Applicata* **136**: 281–289.

RUTHERFORD, M.C., MUCINA, L., LÖTTER, M.C., BREDENKAMP, G.J., SMIT, J.H.L., SCOTT-SHAWN, C.R., HOARE, D.B., GOODMAN, P.S., BEZUIDENHOUT, H., SCOTT, L. & ELLIS, F., POWRIE, L.W., SIEBERT, F., MOSTERT, T.H., HENNING, B.J., VENTER, C.E., CAMP, K.G.T., SIEBERT, S.J., MATTHEWS, W.S., BURROWS, J.E., DOBSON, L., VAN ROOYEN, N., SCHMIDT, E., WINTER, P.J.D., DU PREEZ, P.J., WARD, R.A., WILLIAMSON, S. & HURTER, P.J.H. 2006. Savanna Biome. In: Mucina L. & Rutherford M.C. (Eds) *The Vegetation of South Africa, Lesotho and Swaziland*. 439–464. South African National Biodiversity Institute, Pretoria.

SAUCKE, H., DORI, F. & SCHMUTTERER, H. 2000. Biological and integrated control of *Plutella xylostella* (Lep., Yponomeutidae) and *Crocidolomia pavonana* (Lep., Pyralidae) in brassica crops in Papua New Guinea. *Biocontrol Science and Technology* **10**: 595–606.

SARFRAZ, M., KEDDIE, B.A. & DOSDALL, L.M. 2005. Biological control of the diamondback moth, *Plutella xylostella*: a review. *Biocontrol Science and Technology* **15**: 763–789.

SHAW, M.R. 2003. Revised synonymy in the genus *Cotesia* (Hymenoptera: Braconidae: Micrograstrinae): the identity of *Microgaster vestalis* Haliday, 1934, as a senior synonym of *Apanteles plutellae* Kurdjumov, 1912. *Entomologist's Gazette* **54**: 187–189.

SIVAPRAGASAM, A. 2004. *Brassica* IPM adoption: progress and constraints in south-east Asia. In: Endersby, N.M. & Ridland, P.M. (Eds) *The Management of Diamondback Moth and Other Crucifer Pests*. 11–18. Proceedings of the Fourth International Workshop. The Regional Institute Ltd, Gosford, Australia.

SMITH, T.J. 2004. The Diamondback Moth *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) and its biological bontrol in the Eastern Cape Province, South Africa. Ph.D. dissertation, Rhodes University, Grahamstown, South Africa.

STATISTICA. 2012. Statistica 10 for Windows. Statistica Enterprise System Technology, Tulsa, OK, U.S.A.

TALEKAR, N.S. & SHELTON, A.M. 1993. Biology, ecology, and management of the diamondback moth. *Annual Review of Entomology* **38**: 275–301

ULLYETT, G.C. 1947. Mortality factors in populations of *Plutella maculipennis* Curtis (Tinedae: Lep.), and their relation to the problem of control. *Entomology Memoirs* **2**: 77–202, Department of Agriculture and Forestry, Pretoria, South Africa.

UPANISAKORN, A., JEERAPONG, L., KETELAAR, J.W. & LIM, G.S. 2011. Diversity and abundance of diamondback moth in north Thailand. In: Srinivasan, R., Shelton, A.M. & Collins, H.L. (Eds) *Management of Diamondback Moth and Other Crucifer Insect Pests*. 97–102. Proceedings of the Sixth International Workshop. AVRDC – The World Vegetable Center, Publication No. 11-755, Taipei, Taiwan.

VANDERMEER, J. & CARVAJAL, R. 2001. Metapopulation dynamics and the quality of the matrix. *American Naturalist* **158**: 211–220.

VAN DRIESCHE, R.G., BELLOWS, T.S. JR., ELKINTON, J.S., GOULD, J.R. & FERRO, D.N. 1991. The meaning of percentage parasitism revisited: solutions to the problem of accurately estimating total losses from parasitism. *Environmental Entomology* **20**: 1–7.

VAN DRIESCHE, R.G. & BELLOWS, T.S. Jr. 1996. *Biological Control*. Chapman and Hall, New York.

VERKERK, R.H.J. & WRIGHT, D.J. 1997. Field-based studies with the diamondback moth tritophic system in Cameron Highlands of Malaysia: implications for pest management. *International Journal of Pest Management* **43**: 27–33.

WAAGE, J. & CHERRY, A. 1992. Quantifying the impact of parasitoids on diamondback moth. In: Talekar, N.S. (Ed.) *Diamondback Moth and Other Crucifer Pests.* 245–253. Proceedings of the Second International

Workshop. AVRDC – The World Vegetable Center, Publication No. 92-368, Taipei, Taiwan.
WALADDE, S.M., LEUTLE, M.F. & VILLET, M.H. 2001. Parasitism of *Plutella xylostella* (Lepidoptera: Plutellidae): field and laboratory observations. *South African Journal of Plant and Soil* **18**: 32–37.
WEINZIERL, R.A. 2009. Integrating pesticides with biotic and biological control for pest management. In: Radcliffe, E.B., Hutchison, W.D. & Cancelado, R.E. (Eds) *Integrated Pest Management*: *Concepts, Tactics, Strategies and Case Studies*. 179–191. Cambridge University Press, Cambridge, U.K.
XU, J. SHELTON, A.M. & CHENG, X. 2001. Comparison of *Diadegma insulare* (Hymenoptera: Ichneumonidae) and *Microplitis plutellae* (Hymenoptera: Plutellidae): field parasitism, insecticide susceptibility, and host searching. *Journal of Economic Entomology* **94**: 14–20.
ZHAO, J.Z., COLLINS, H.L., LI, Y.X., MAU, R.F.L., THOMPSON, G.D., BOYKIN, R., HERTLEIN, M., ANDALORO, J.T. & SHELTON, A.M. 2006. Monitoring of diamondback moth (Lepidoptera: Plutellidae) resistance to spinosad, indoxacarb and emamectin benzoate. *Journal of Economic Entomology* **99**: 176–181.

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