EFFECTS OF SELECTED CULTIVATED CRUCIFERS IN KENYA ON FECUNDITY, DEVELOPMENT AND PARASITISM OF DIAMONDBACK MOTH, *Plutella xylostella* L., (Lepidoptera: Plutellidae) BY PARASITOID *Diadegma semiclausum* Hellen (Hymenoptera: Ichneumonidae)

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A thesis submitted to Graduate School in partial fulfillment of the requirements for the award of the degree of Master of Science in Agronomy (Crop Protection) of Egerton University.

EGERTON UNIVERSITY

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DECLARATION AND RECOMMENDATION

Declaration

This thesis is my original work and has not been presented for the award of a degree in any other university.

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Recommendation

This thesis has been presented with our approval as supervisors.

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DEDICATION

To my wife and children for their patience and to my mother for her continued support.

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ABSTRACT

Crucifers form an important component of the livelihood of small-scale farmers in East Africa but diamondback moth (DBM) pest constrains their production. Attempts to control the pest by use of host plant resistance (HPR) have been modest especially in cultivars expressing a whitish appearance (normal wax bloom). Conversely, crucifers characterized by their shiny dark green leaves (Glossy) have shown some resistance to DBM. As a consequence, several seed companies claim resistance attributes in their novel cultivars. Thus, this work sought to investigate the effect of some *Brassica oleracea* cultivars grown in Kenya on fecundity, development and parasitism of DBM. The performance of DBM was compared on seven cultivars in both laboratory and greenhouse trials. Laboratory investigations were conducted on oviposition preference (choice, no-choice) and survivorship of DBM on the test cultivars and on the basis of these data, life tables were constructed. Egg to adult survival, plant damage as well as cultivar effect on parasitism by *Diadegma semiclausum* were studied in a plastic house. Leaf wax quantity and structure of the adaxial leaf surfaces were evaluated via scanning electron microscopy (SEM). While DBM did not discriminate any of the test cultivars for oviposition in the choice test, more eggs were laid on the cultivars “Collard Georgia” and “Green Challenger” in the no-choice test. Besides, the pest tended to oviposit a higher percent of its eggs away from the plant while probing on “Green Challenger” in both the choice and no - choice tests. Larval period was more than a day longer on “Riana” “Green Challenger” and “Thousand Head” than on “Gloria” and “Collard Georgia” in the laboratory trial, and larval survival on “Green Challenger” was greatly reduced. Pupal weight of DBM raised on “Green Challenger” (4.3 mg) in the laboratory was significantly lower ($P<0.05$) than on all cultivars except “Copenhagen Market” (4.6 mg). Consequently there was a significantly lower ($P<0.05$) fecundity by DBM raised on “Green Challenger” and “Copenhagen Market” than on the rest of the cultivars. Presence of parasitoid caused a higher death of DBM larvae on “Thousand Head” than on “Blue Dynasty” in the greenhouse. Consequently, more percent parasitoids emerged on larvae reared on “Blue Dynasty” than on the former. The net reproductive rate and the intrinsic rate of population increase were lower on “Green Challenger” and higher on “Thousand Headed”, “Blue Dynasty” and “Riana”. In addition, the cultivars “Green Challenger” and

“Thousand Headed” had the highest (4263 ± 312.3 nm) and lowest (1560 ± 140.6 nm) spaces between their wax crystals respectively. Conversely, the former had the least density of wax crystals. Thus the pest resistance attributes between cultivars tested display only subtle differences, which can, nevertheless, be harnessed in integrated pest control schemes against diamondback moth.

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CHAPTER ONE

INTRODUCTION

1.1 Importance of crucifers

Crucifers, both wild and cultivated, are found in the East and Southern Africa region (ESA). The main cultivated species include head cabbage (*Brassica oleracea* L. var *capitata* L.), rape (*Brassica carinata* L. and *B. napus* L.), or leafy cabbage, kale "Thousand Headed" (*B. oleracea* L. var. *acephala*), Chinese cabbage (*B. chinensis* L.), cauliflower (*B. oleracea* L. var. *botrytis* Alsmeer) and broccoli (*B. oleracea* L. var. *italica*) (Nyambo and Pekke, 1995). In Kenya, cabbage may be eaten raw in salads or cooked and is a source of vitamins for the producers and other consumers in the marketing system. Kale on the other hand is considered a valuable relish in many homesteads, providing necessary dietary vitamins and minerals in a maize based diet. Both cabbage and kale crops are a source of income for the producers in rural and peri-urban areas and all players in the marketing chain. In this regard, these crops serve twin purposes of providing employment and helping alleviate poverty, an important component of the United Nations Millennium Development Goals (MDGs).

In the period 1999-2002, consumption of cabbage in the country was estimated at 25g/person/day (Macharia *et al.,* 2005). Subsequently, FAO (2003) reported that an estimated 18,000 ha of land was under cabbage in Kenya with a yield of 15 tons/ha and estimated a total production of 270 000 metric tons.

1.2 Production constraints

The production of crucifers in the ESA region is often constrained by a wide range of insect and disease pests. The diamondback moth (DBM), *Plutella xylostella* (L.), aphids, *Brevicoryne brassicae* L., *Lipaphis erysimi* (Kaltenbach) and *Myzus persicae* (Sulzer), the webworm, *Crocodinolomia binotalis* Zeller, the sawfly, *Athalia* sp. and cutworms, *Agrotis* spp, are the major insect pests (Varela *et al*. 2003). However, DBM was identified as the key pest of these crucifer crops in Eastern and southern Africa in a workshop conducted in 1995 (Nyambo and Pekke, 1995). This pest may cause a complete loss of the crop (Madumadu *et al.,* 1991, Kibata, 1996) especially in the dry

season in spite of pesticide application (Herren and Lohr, 2001). In the same workshop, the pest status of cabbage aphid, *B. brassicae* was identified as an emerging threat to Brassica crops in East Africa since its attack is associated with the transmission of the tulip mosaic virus disease, which can be devastating to the crop. Other pests limiting production include diseases such as black rot, *Xanthomonas campestris* pv *campestris* (Pammell) Dawson and downy mildew, *Peronospora parasitica* (Pers.) Fr.

Diamondback moth is reported to be one of the most difficult vegetable pests to control worldwide (Talekar and Shelton, 1993). Crucifer plants are normally attacked as early as seedling stage, through to crop maturity and severity depends on location and season (Ramachandran *et al.*, 2000). While early attacked cabbages may suffer a 100% loss due to failure to form heads, heavy perforation in later stages may render them unmarketable (ICIPE, 1997).

Synthetic pesticides have dominated the attempts to control *P. xylostella* in most parts of the world in the last 50 years (Talekar and Shelton, 1993; Verkerk and Wright 1996). However, continued rate of pesticide resistance in the ESA region and in the tropics as a whole has induced farmers to use insecticide cocktails at dosages and frequencies much higher than the recommended levels (Dennill and Pretorius, 1995; Kibata, 1996; Macharia *et al.*, 2005). In Kenya alone, insecticides like organophosphates, carbamates, and pyrethroids are no longer giving effective control of DBM compared to new products such as growth regulators, phenyl pyrazoles and *Bt-aizawaii* based products (Kibata, 1996). Macharia *et al*. (2005) also demonstrated that Karate 1.75EC (lambda cyhalothrin), the most commonly used synthetic pyrethroids, was not only ineffective against the DBM pest but also brought negative economic returns to the users. As a consequence of pesticide overuse, negative impacts have been realized (Ayalew, 2003) and this has aroused the interest in alternative pest control methods, placing more emphasis on biological control, host plant resistance (HPR), cultural control and other non-polluting methods (Lim *et al.*, 1986).

Biological control of DBM involving indigenous parasitoids on one hand and entomopathogens associated with the pest on the other has yielded very low and insignificant parasitism rates in East Africa. For example, Oduor *et al*. (1996) observed that parasitoids *Diadegma mollipla* (Holmgren) (Hymenoptera: Ichneumonidae) and

Oomyzus sokolowskii (Kurdjumov) (Hymenoptera, Eulophidae) could only afford paltry parasitism rates of below 15%. Entomopathogens on the other hand, notably *Zoophthora* sp, granulosis virus and unidentified bacterial disease were recorded in Kenya and Tanzania but their impact on DBM was well below 2% (Oduor *et al*., 1996; Cherry *et al*., 2004a).

1.3 Statement of the problem

Diamondback moth is one major constraint to the production of crucifers in the East African region. While early attacked cabbages may realize up to 100% losses from the pest due to failure to form heads, heavy attack in later stages may make the crop unmarketable. DBM attack is even more enhanced on the dry season cabbage crop, which it destroys and thus prompting low supply of the crop to the market. This threatens the livelihood of small-scale farmers who depend on the crop both for food and for sale and perhaps to the attainment of millennium development goals.

Indigenous parasitoids in East Africa can only afford paltry parasitism rates but pesticide use is an additional expense, may result in insecticide resistance, poses danger to the environment and may be very ineffective. Biological control of DBM pest involving an exotic parasitoid is on going in the east African region but its impact on a wide scale is yet to be realized and is on its own not effective.

In spite of the problem, studies on resistance mechanisms against diamondback moth by cultivated crucifers grown in Kenya have received little attention. Host plant resistance as a pest control strategy is arguably environmentally benign and does not come with additional costs to production. The influence of various cultivated crucifers on suitability of the DBM for parasitism by the parasitoid and its subsequent development is not clear. This information may be important in part, for the successful establishment of the parasitoid and for sustainability of this pest control approach. Integrated pest management schemes demand some level of compatibility between various integral components in order to be successful.

1.4 Justification of the study

Cultivated crucifers are an important component of the livelihood of small-scale farmers in Kenya and even the whole of East Africa (Seif and Löhr, 1998). One major constraint to the production of the crops in the region is pest incidence, particularly diamondback moth (Madumadu *et al*., 1991, Kibata, 1996). These crucifers are grown year round in the tropics and sub tropics hence all life stages of DBM pest can be present at any time (Talekar and Shelton, 1993). Worse still, several generations (in excess of 20) can be realized per year (Vickers *et al.,* 2004). Unfortunately, most pesticides employed for DBM control are either ineffective or pose serious danger to man and his environment hence the need to seek alternative control options like host plant resistance and biological control.

The importance of resistant host plants as a component of integrated pest management for the control of *P. xylostella* has been emphasized (Verkerk and Wright, (1994a). This stems in part from the evidence that different crucifer cultivars are variedly susceptible to DBM (Lin *et al.,* 1984; Verkerk and Wright, 1994b). Groot and Dicke, (2002) have argued that environmentally benign pest control demands employment of biological control measures in combination with host plant resistance. Conversely, the two control strategies are neither always compatible nor synergistic as assumed and it is suggested that efforts should aim at bridging them (Cortesero and Lewis, 2000).

On the other hand, the DBM indigenous natural enemy fauna (parasitoids) in East Africa include *D. mollipla*, *Apanteles* sp. and *O. sokolowskii*. However, these parasitoids do not exert any meaningful control of the pest (Oduor *et al*., 1996). Cultivation of crucifers that show resistance to diamondback moth is a good component of integrated pest management against the pest (Facknath, 1997). Studies on the suitability of different cultivated crucifer hosts for the survival and development of diamondback moth and its natural enemies in Kenya is lacking. This study is, however, key to formulating an intervention strategy against the pest (Cortesero and Lewis, 2000).

Both bitrophic (plant – pest) and tritrophic (plant – pest – parasitoid) studies involving crucifers with normal wax attributes have generally received little attention as compared to the glossy type (Dickson *et al.*, 1986; Eckenrode *et al*., 1986; Eigenbrode *et al*., 1990, 1991; Eigenbrode and Shelton, 1990; Verkerk and Wright, 1996; Eigenbrode

and pillai, 1998; Verkerk *et al.,* 1998). Shiny dark green leaves normally characterize the glossy mutants in *B. oleracea*. Thus glossiness appearance is due to the lack of a whitish bloom associated with the normal plants (Anstey and Moore, 1949; Tarumoto, 2005).

In Kenya, bitrophic studies on the influence of commercial cultivars on the development of DBM have equally received little attention. Such studies are not only important as tools for breeders in their endeavour to develop resistant lines (Hamilton *et al.,* 2005) but also as basis for understanding the role played by these crucifers in the third trophic level (Schuler and van Emden, 2000). Besides, the use of resistant cultivars in pest management is crucial when they can easily complement biological, chemical and cultural pest control measures (Megallona, 1986; Cortesero and Lewis, 2000).

This work was therefore an attempt to address three main areas namely, the role of different cultivars in plant resistance (wax attributes) to DBM pest, bitrophic interactions involving different cultivars and the DBM pest and finally, tritrophic interactions between the cultivars, DBM pest and an exotic parasitoid.

1.5 Objectives

1.5.1 Broad objective

To study the effect of selected cultivated crucifers on the biology (life table statistics) of DBM and parasitism by *Diadegma semiclausum*

1.5.2 Specific objectives

1. Compare oviposition preference of DBM on selected cultivated crucifers (cabbage and kales)
2. Determine the effect of different crucifer host plants on larval and pupal survival and development of DBM
3. Compare adult longevity and reproduction potential of DBM offspring reared on different cultivated crucifers
4. Assess the effect of different crucifer hosts on DBM larval parasitism by *D. semiclausum*
5. Compare the leaf surface ultrastructure of different cultivated crucifers

1.6 Hypotheses (Null)

1. Egg laying behaviour of DBM is similar in selected cultivated crucifers in Kenya
2. Different cultivated crucifer host plants in Kenya have no effect on DBM larval and pupal survival and development
3. Adult longevity and fecundity of DBM offspring is similar on different crucifer cultivar
4. Parasitism of DBM is independent of the variety of crucifer cultivars in Kenya
5. The ultrastructure of leaf surfaces is similar in the different cultivated crucifers and has no effect on egg laying, development and parasitism of DBM

1.7 Limitations of the study

Due to limited time, studies focused on the influence of host plants on the herbivore and one natural enemy. For the same reason, chemical analysis of the epicuticular wax constituents in the cultivars could not be studied. Studies involving other natural enemies as well as the wax chemistry of the varieties can be done later.

CHAPTER TWO
LITERATURE REVIEW

2.1 Diamondback moth origin, distribution and economic status

The diamondback moth (DBM), *Plutella xylostella* L. (Lepidoptera: Plutellidae) is deemed the most destructive insect pest of crucifers the world over (Talekar and Shelton, 1993). This destruction is more realized in the tropical countries (Lim, 1992) because all life stages of the moth can be present at any time in the tropics (Talekar and Shelton, 1993). The insect may have originated in Europe (Carter, 1984), Southern Africa (Kfir, 1998) or China (Liu *et al.,* 2000) but now occurs wherever crucifers are grown and is distributed in over 100 countries and territories in the world (Talekar and Shelton, 1993). *P. xylostella* is considered to be the most widely distributed of all Lepidoptera (Shelton, 2004).

Pest status of DBM the world over is major in the absence of effective natural enemies, especially parasitoids (Lim *et al*., 1986). The genetic elasticity of this pest has enabled it to develop resistance to almost every insecticide applied in the field (Mota-Sanchez, *et al*., 2002). To overcome this resistance, farmers in Asia (Talekar and Shelton, 1993) and Kenya (Kibata, 1996; Macharia *et al.,* 2005) have resorted to increased doses and application frequency of pesticides and to pesticide cocktails. In some areas, over 60% of the market value of the cabbage crop is spent for the purchase of pesticides (Carl, 1992). Continuous use of pesticides increases the magnitude of DBM problem by reducing the associated natural enemies (Talekar and Shelton, 1993; Noda *et al*., 2000; Kfir and Thomas, 2001; Ohara *et al*., 2003) that might otherwise check their population. Consequently the cost of DBM control has been estimated at US$ 1 billion world wide for insecticides alone. The environment and cabbage consumers are equally at risk of excess pesticide use (Ayalew, 2003).

The diamondback moth is thought to feed on members of the crucifer family only (Talekar and Shelton, 1993). The cultivated host range of the insect are cabbage (*Brassica oleracea* L. var *capitata* L.) cauliflower (*B. oleracea* L. var *botrytis* L.); broccoli (*B. oleracea* L. var *italica* Plenck); radish (*Raphanus sativus* L.); turnip (*B. rapa* L. var *pekinensis* Lour), Brussels sprout (*B. oleracea* L. var *gemmifera* Zenker); chinese

cabbage (*B. rapa* L. *pekinensis* Lour), kohlrabi (*B. oleracea* L. var *gongylodes* L.), pakchoi (B. rapa L.), watercress (*Nasturtium officinal* L.) and "Thousand Headed" (*B. oleracea* L. var *alboglabra* Bailey) (Talekar and Shelton, 1993).

It is likely that olfactory/gustatory and tactile/visual stimuli attract DBM to crucifers (Shelton, 2004; Badenes-Perez *et al.,* 2004). Glucosinolates (sinigrin, sinalbin, and glucocheirolin) that are inherent in most crucifers stimulate feeding in DBM larvae. Two glycosides (3-butenyl and 2-phenyl ethyl) in high concentrations, however, mediate the performance of the insect (Nayar and Thorsteinson 1963). Intact glucosinolates have minimal biological activity (Ratzka *et al.,* 2002), but the myrosinase-glucosinase complex in injured crucifers produce breakdown products, which may be toxic to crucifer specialist insects, including DBM (Li *et al.,* 2000; Vogel *et al.,* 2004). Ratzka *et al*. (2002) showed that the breakdown products from the plant defense mechanism are, however, disarmed by glucosinolate sulfatase (GS) enzyme in the gut of crucifer specialists, including DBM.

Oviposition by the insects is stimulated specifically by sulfur-containing glycosides or its metabolites found on crucifers (Reed, 1989). The oviposition rate can therefore be reduced based on the nutritional status of that plant (Verkerk and Wright, 1994a) and more special seems to be sulphur nutrition (Marazzi, 2003). In addition, oviposition stimulants, sinigrin and alkanes have a synergistic effect on the egg laying behaviour of the moth (Spencer *et al.,* 1999). Comparatively, glucobrassicin influences oviposition more than Cardenolides, sinigrin and glucoiberin, which are all oviposition stimulants (Renwick *et al.,* 1992)

2.2 General life cycle

The diamondback moth is multivoltine with four generations (in temperate regions) to over twenty generations (in tropical regions) in a year (Harcourt, 1986; Vickers *et al.,* 2004). Each generation undergoes four life stages, which are egg, 4-larval instars, pupa and adult (Talekar and Shelton, 1993). The adult moths are small grayish brown moths approximately 8 mm in length. The forewings have three pale triangular markings along the hind margin that form the characteristic diamond pattern on the back when the wings are folded (Koenig *et al.,* 1993). Harcourt (1954) observed that the adults were active

from dusk into the night. Most of the adults emerge in the first 8 hours of photophase, copulate at dusk of the same day and lay eggs soon after mating. The number of copulations ranges from one to four. The oviposition period lasts between 3-19 days (Harcourt, 1954). Each female can lay over 200 eggs as influenced by photoperiod, temperature and age or condition of larval food (Harcourt, 1957). The eggs are laid preferentially on the upper and lower leaf surfaces (ratio 3:2) and mainly on rough rather than on smooth leaf surfaces (Talekar *et al.*, 1994; Justus *et al.*, 2000). Isolated studies indicate oviposition preference for the bottom of the leaf because of the sheltered nature of the leaf bottom (Charleston and Kfir, 2000) and the variation in leaf wax characters between the top and leaf bottoms (Andrahennadi and Gillott, 1998). Very few eggs are laid on stems and leaf petioles (Gupta and Thorsteinson, 1960; AVRDC, 1987; Talekar *et al.*, 1994). The eggs are laid singly, or in groups of 2 to 8 and are flat, oval-shaped and shiny yellow when first laid (Ho, 1965). The egg darkens before hatching and the young larvae are visibly coiled beneath the chorion (Harcourt, 1957).

Eggs hatch to 1st instar larvae between 3 to 6 days depending on temperature (Talekar and Shelton, 1993). Upon hatching the larvae whose heads are black in colour burrow into and feed on spongy mesophyll tissue. The duration of the feeding is 3, 4 and 5 days in hot, rainy and cold seasons respectively (Chelliah and Srinivasan, 1986). The 2nd, 3rd and 4th instar larvae feed on the lower leaf surface and usually consume all tissue except the epidermis and its wax layer. The feeding style creates windows on the surface of the leaf (Talekar and Shelton, 1993). The third and fourth instar larvae have green and brown colored heads consecutively. Total larval period ranges from 6 to 30 days depending on temperature and host plant (Salinas, 1986).

Upon completion of feeding, mature caterpillars form a gauzy, loosely spun cocoon for pupation. The pupal colour, initially yellowish green, changes to brown then to dark brown by the time of adult emergence (Talekar and Shelton, 1993). The pupal period under Canadian field conditions required between 7.8-9.8 days (Harcourt, 1957). Thus the time taken to complete the life cycle of DBM varies from 25 days (under favourable condition) to 110 days under unfavourable condition (Ko and Fang, 1979). Isolated reports of a faster developmental time of 9- 10 days have also been reported (Ko and

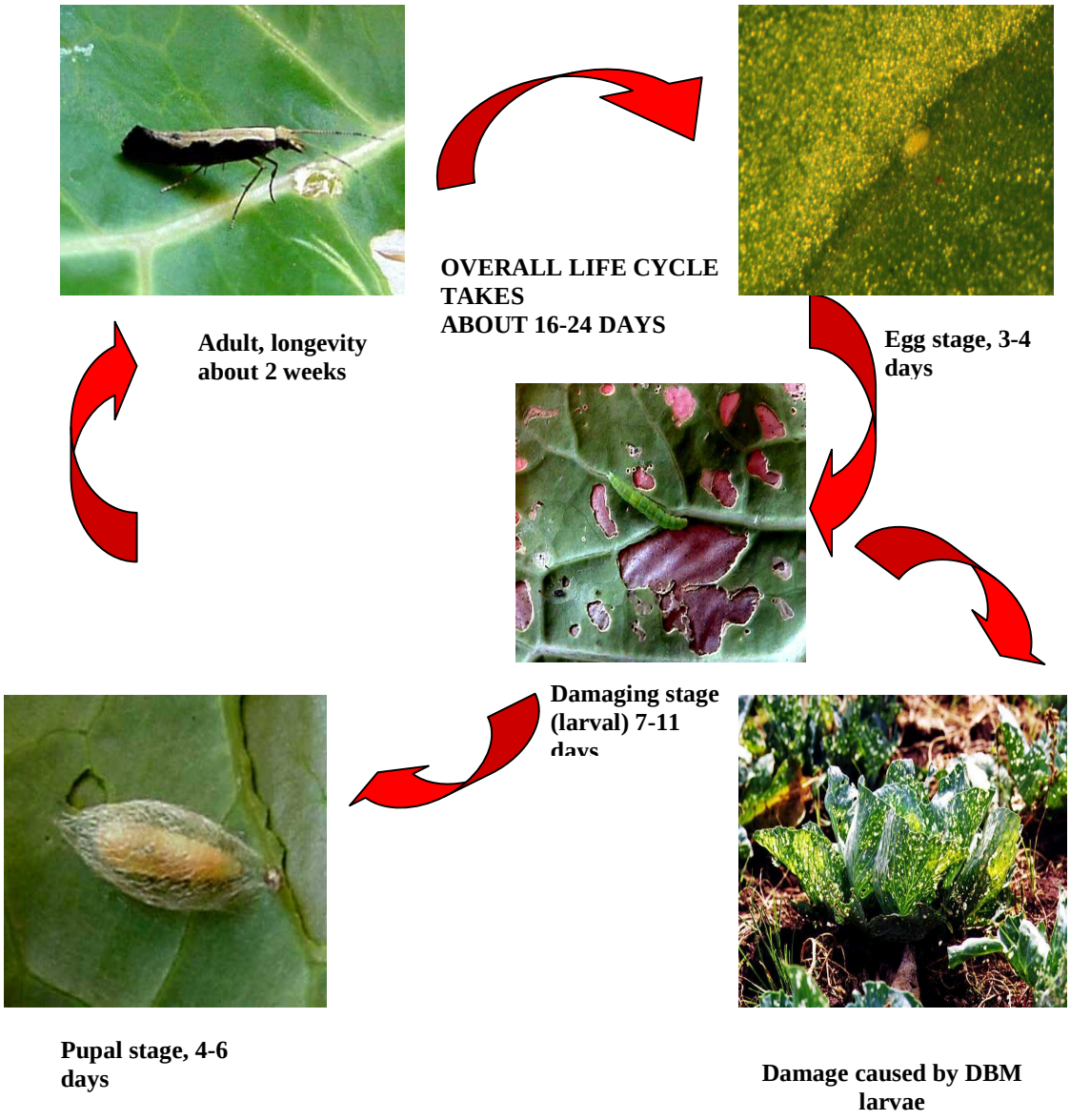

Plate 1. Life cycle of DBM (at ~25°C), showing the damaging stage

Fang, 1979). The DBM successfully develops at constant temperatures of 8-32° C and also under alternating temperatures of 4° C and 38° C (Liu *et al.*, 2002).

2.3 Ecology of DBM

The diamondback moth is a cosmopolitan pest. It is found everywhere in the world where its hosts grow (Shelton, 2004). Adults occur on the host or on other plants adjacent to the crop where they feed on flower nectar while the eggs, larva and pupae occur on the host plant. The ability of DBM adults to migrate and disperse over long distance enhances its distribution.

Reports by Chapman *et al*. (2002) indicate that DBM can remain in a continuous flight for several days and cover distances of 1500 km at 400-500 km per night. Presence or absence of wind mediates DBM migration (Honda, 1992). All life stages of the moth can be present at any time in the tropics and subtropics. This is because crucifers are grown in these areas throughout the year (Talekar and Shelton, 1993). In the temperate regions, crucifers are not grown year round but the ability of DBM to overwinter explains their perennial occurrence (Dosdall *et al.*, 2004). Reports by Shelton and Wyman (1992) show that long-distance transport of seedlings infested with DBM can be a major source for DBM population buildup in temperate areas. However, cold temperatures and high rainfall intensities in the temperate areas enhance larval mortalities of *P. xylostella.* The latter drowns and dislodges the larvae from the plants (Harcourt, 1957).

2.4 Control measures against DBM

Several control measures against DBM ranging from cultural control to use of pheromones and growth regulators have been tried with varied levels of success (Talekar and Shelton, 1993; Robert et al., 1996). The various management options are highlighted below:

2.4.1 Cultural control

Resource poor smallholder crucifer farmers have practiced cultural control measures against *P. xylostella* over time. However, interest in this control option has arisen even in commercial crucifer production as a consequence of repeated insecticide failures to

control DBM (Talekar and Shelton, 1993). This method includes practices such as intercropping, overhead irrigation, crop rotation, observed time of planting and use of physical barriers (Lim *et al*., 1986; Nakahara *et al.*, 1986).

(a) Irrigation and time of planting

Infestations by DBM on crucifers are normally lower during wetter periods than in drier periods. Control is achieved through drowning or washing away of larvae from the host plant (Talekar and Shelton, 1993). Overhead sprinkler irrigation on the other hand is reported to disrupt adult flights of DBM as well as their mating and oviposition. Studies indicate that sprinkler irrigation causes DBM eggs and larvae to be dislodged, washed off the plant and to get drowned (Nakahara *et al.*, 1986; Talekar and Shelton, 1993). Rainfall attributes that include size of rain droplets (SRD), duration of precipitation (DP) and rainfall amounts (RA) have an effect on the population dynamics of DBM. Kobori and Amano (2003) suggested that an SRD of 2.5 mm, DP of 1 hour and RA of 17.3 mm were significant to wash off both the eggs and larvae of DBM. However, complete removal of DBM could not be achieved even with extended DP. Moreover, the fate of the washed off larvae was not clear.

(b) Intercropping

Intercropping involves planting two or more crop species together. There is some evidence of decreased DBM numbers when garlic inter-rows are planted in cabbages (Facknath, 1997). Buranday and Raros (1973) indicate a deleterious effect on pest population when tomatoes are planted as inter-rows in cabbages. Subsequent studies have shown that certain principles in tomato leaf extract adversely affect oviposition of DBM on cabbage and Chinese cabbage (AVRDC, 1985). Other crops, which include dill, safflower, oat, coriander and carrot (Facknath, 1997) as well as beans and onions (Said and Itulya, 2003) have also recorded reduced incidence of DBM when planted as intercrops with cabbage. The latter workers speculated that the volatile sulphur compound, allyl-propyl-disulfide in onions might have interfered with host attraction to the pest and subsequent oviposition. Most farmers in developing countries, however,

practice such intercrops for purposes of crop diversification against other natural factors and not for pest control (Ayalew, 2003)

(c) Trap crops

In many cases, trap cropping involves the planting of species, which are less important economically but preferred by the pest, within a commercial field. The use of a trap crop preferred for oviposition by the pest but deleterious to their survival has been suggested by Shelton and Nault (2004). A success story of such trap crop is the use of a glabrous Brassica, *Barbarea vulgaris* var. *arcuata* L. that acts as a dead end trap crop. (Agerbirk, *et al.,* 2001, 2003). Dead end trap crops serve as a sink for the pests, preventing their movement to the main crop later in the season (Badenes-Perez *et al.*, 2004). In South Africa, work done by Charleston and Kfir (2000) suggest that Indian mustard has a good potential as a trap crop since *P. xylostella* prefers it for oviposition but larval survival on it is low. However, the trap crop must be available throughout the growing period to offer an effective control against the pest.

While consistency in success is a major tenet of pest management systems, this has been lacking in trap crop pest control options involving diamondback moth. Consequently, the risk of economic loss to the grower is enhanced (Shelton and Badenes-Perez, 2006). In addition, planting a trap crop with no commercial value must bring large benefits in pest reduction to justify the losses caused by the costs of planting and revenue foregone from the area it occupies. This has probably been the reason why in spite of all the research conducted, there are no documented cases of its adoption.

(d) Crop rotation

Suppression of DBM population has been substantial in a rotational system involving crucifers, cucurbits and beans. For example cabbage-peas-turnip and cabbage-squash or cucumber rotational systems have been effective against DBM (Vu, 1988). A crucifer free period in a rotational system deprives DBM population of food, forcing them to subsist on alternative hosts. However, successes of such rotational systems have not been evaluated under high DBM population levels and it is not clear under what conditions these successes can be realized (Megallona, 1986). Besides, crop rotation as a control

option is not common in the tropics where crucifers are grown year-round on small land parcels by smallholder farmers (Talekar and Shelton, 1993). Recent research conducted in Kenya indicates that DBM is ubiquitous in East Africa as it can be found on a large number of wild crucifers, which are common in highland production areas, and also exist, albeit at lower numbers, in semi-arid, mid- and low altitudes (Gathu *et al*. 2007, in press), providing a ready source for infestation even after long cabbage-free periods.

(e) Physical methods (**Nets and traps)**

Planting of crucifers under fine mesh netting houses has given good results against diamondback moth in Taiwan. However, insect damage to the vegetables in the net houses is still common (Talekar *et al.,* 2003). Yellow sticky vinyl chloride plate traps have also been used successfully to capture the DBM moths (Lim *et al*., 1986). Vattanatangum, (1988) observed that blue light traps are capable of capturing large number of adult *P. xylostella*.

2.4.2 Biological control

Many biological control measures have been employed against DBM. These include the use of microbial organisms, parasitoids and predators (Talekar and Shelton, 1993). Resistance to insecticides by DBM has necessitated the use of such bio-control options. Besides, pesticide residues in harvestable products can be avoided through biocontrol measures (Carl, 1992; Talekar and Shelton, 1993). As a sole method of control, however, biological control is seldom sufficient (Hokkanen, 1997). As a consequence, this method should be supplemented with other control options such as host plant resistance (Cortesero and Lewis, 2000). Parasitoids are the most studied biological control measure and their success stories have been reviewed extensively (Talekar and Shelton, 1993; Löhr and Kfir, 2002; Sarfraz *et al.,* 2005). The various bio-control measures are reviewed below:

(a) Microbial organisms

Various microbial pest control agents (MPCA) have been tried against *P. xylostella* as alternatives to broad-spectrum insecticide. These entomopathogens include bacteria,

fungi, nematodes, viruses and protozoa (Sarfraz *et al.,* 2005). Many workers have reported evidence of viruses attacking DBM. The main ones are a granulosis virus (GV) (Wakisaka *et al.,* 1992) and a nuclear polyhedrosis virus (NPV) (Kadir *et al.,* 1999) that are both reported to attack DBM larvae. While Wilding (1986) showed promising levels of pathogenicity by the GVs, Farrar and Ridway (1999) reported a moderate to low potency by NPVs on DBM. A Kenyan isolate of *P. xylostella* granulovirus PxGV (Nya-01) recorded high infection rates both on Kenyan DBM strain (Grzywacz *et al.,* 2004) and DBM strain from Benin (Cherry *et al.,* 2004b). There is evidence of less foliage consumption by *P. xylostella* larvae that are infected with PxGV (Lu *et al.,* 2004).

Entomopathogenic fungi that have been isolated from DBM include *Paecilomyces farinosus* (Holm ex Gray) Brown and Smith, *Pandora* spp., *Zoophthora radicans* (Brefeld) Batko, *Beauveria bassiana* (Balsamo) Vuillemin, *Fusarium* spp, *Conidiobolus* spp and *Scopulariopsis* spp (Vandenberg *et al.,* 1998; Cherry *et al.,* 2004a; Kirk *et al.,* 2004). Fungal entomopathogens can kill the DBM larvae in a matter of days through a series of steps starting from conidial contact. The fungal conidium gets into contact with insect cuticle, germinates and penetrates through it and develops mycelia that eventually kill the insect (Glare and O′Callaghan, 2000; Inglis *et al.,* 2001). Vandenberg *et al*. (1998) reported that a spray suspension of *B. bassiana* spores in either oil or water significantly reduced larval population of DBM.

Works of Goolaub (1995) show that a formulation of *Bacillus thuringiensis* (*Bt*) strain GC 91 provides protection against DBM similar to that of thiocarbamate insecticide. Success stories of *Bt* have been reported in South Africa where formulations of *Bt kurstaki* and *Bt aizawaii* strains are extensively used to manage diamondback moth (Nel *et al.,* 1999). However, there are reports of *P. xylostella* developing resistance to *Bt* in some parts of the world (Heckel *et al.,* 1999; Ferré and van Rie, 2002; Tabashnik *et al*., 1993, Sayyed *et al.,* 2004).

Entomopathogenic nematodes (EPN) in the families Steinernematidae and Heterorhabditidae can significantly reduce *P. xylostella* larval populations on cabbages through their infective juveniles (IJ). They are therefore a valuable alternative control measure to manage DBM populations (Schroer *et al.,* 2005) especially when their desiccation can be minimized. *Steinernema carpocapsae* (Weiser) is desiccation tolerant,

hence well adapted for foliage application against DBM larvae (Bauer *et al.*, 1995). The death of the insect host by the infective juveniles of *S. carpocapsae* is achieved through their role as vectors of a pathogenic bacterial symbiont in the family Enterobacteriaceae. The bacterium, *Xenorhabdus nematophila*, which is a gram-negative bacterium, secretes a high molecular weight protein that is lethal to *P. xylostella* larvae (Mahar *et al.*, 2006). The application of toxic metabolites of the bacteria is suggested to be more commercially and environmentally acceptable against DBM than the use of free cell suspension (Ensign *et al.*, 2002)

(b) Parasitoids and predators

Parasitoids play an important role in population dynamics of DBM (Lim *et al.*, 1986; Waterhouse and Norris, 1987). Lim *et al.*, (1986) indicated that a few countries in developing world use parasitoid introductions to control DBM but success of such efforts are thwarted by the use of synthetic insecticides. Over 135 parasitoid species are reported to attack various stages of diamondback moth on a worldwide scale (Delvare, 2004). However, larval parasitoids, particularly the genus *Diadegma* (Ichneumonidae) and *Cotesia* (Braconidae) are the most predominant and offer the greatest control potential (Talekar and Shelton, 1993). Release and successful establishment of the larval parasitoid *Diadegma semiclausum* (Hellen) (Hymenoptera: Ichneumoidae) can reduce crop losses due to DBM (Saucke *et al.*, 2000). Momanyi *et al*. (2006) showed a drastic reduction of diamondback moth survival on Thousand Headed within the first year of *D. semiclausum* release in Kenya. Other successful parasitoids include egg parasitoids *Trichogramma* spp. (Hymenoptera: Trichogrammatidae), the larval parasitoid *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae), the larval-pupal parasitoid *O. sokolowskii* and pupal parasitoid *Diadromus collaris* (Gravenhorst) (Hymenoptera: Ichneumoidae) (Talekar and Shelton, 1993). Several species of hyperparasitoids of DBM have been reported (Kfir, 1998; Liu *et al.*, 2000). The presence of these hyperparasitoids limits the efficiency of primary parasitoids to control the pest (Mustafa, 1992).

Predators, which include spiders, Pentatomid bugs, *Phytoseiulus* mites and wasps, can cause mortality of prey under heavy build up (Ooi, 1992). Nemoto *et al.*, (1985) attributed increase in the number of DBM to reduced number of predators. Sivapragasam

et al. (1988) also implied that predators could cause unknown mortalities in the life tables of DBM. However, apart from the qualitative assessment of the contributions predators can make, no quantitative study of their contribution is available.

The genus *Diadegma* is perhaps one of the most efficient and widespread parasitoids of Diamondback moth worldwide. One species, *D. semiclausum* is not only an important larval parasitoid of *P. xylostella* (Waterhouse and Norris, 1987; Talekar and Shelton, 1993) but also specializes on it (Wang and Keller, 2002). It is a black wasp 5-7mm in length with a distinct long ovipositor on females (Azidah *et al*, 2000). Each female can lay a peak of 362 eggs (Ooi, 1981) or 700 eggs (Koening *et al*., 1993) depending on food quality and female longevity (Abbas, 1988). The parasitoid is a solitary koinobiont, that is, only one egg is laid per host and the latter continues to develop at least for a while after parasitisation (Yang *et al*, 1993). Some incidences of super parasitism (host parasitised twice by the conspecifics) have been observed and this yields more females than males (Koening *et al.,* 1993; Wang, 2002). Super parasitism is also thought to confer an adaptive advantage to the parasitoid by reducing high search costs and overcoming host defenses (Wang, 2002).

Although all host larval instars can be parasitised, *D. semiclausum* prefers mainly the second and third instars (Talekar and Yang, 1991; Koening *et al*., 1993). The laid eggs incubate for two days before hatching to 1st intar larvae. The developmental period goes up to the 5th larval instar and this period is temperature dependent ranging between 11-28 days at 35°C and 15° respectively with an optimum temperature of 23°C. This optimum temperature also results in a sex ratio of 1:1. The last larval instar feeds into the pre-pupal content of its host thereby killing it as it develops its own cocoon inside the one for the host.

The emerging parasitoid adults feed on brassicae flower nectar, mates and then start laying eggs a day later. Females live longer (73 days) than males (40 days) (Ooi, 1992). Female longevity of 3 months has also been recorded under laboratory conditions (Koening *et al*, 1993). The latter workers also observed that the females can parasitise between 35-50 hosts per day but this reduces their lifespan to only three weeks in the field.

D. semiclausum thrives well in cooler highlands where the temperature range is optimum for its development (Saucke *et al.,* 2000). It maximizes host attack by applying a high degree of aggregation on patches with high host densities (Wang *et al.,* 2004). Variation in the composition of volatile odour blends between and within crucifers either DBM infested or not, enables discrimination by this parasitoid (Bukovinszky *et. al*, 2005, Rossbach *et al*., 2006). The parasitoid is also well adapted to the defensive behaviour of its host and very effective at detecting and parasitizing *P. xylostella* larvae (Wang and Keller, 2002).

Due to its effectiveness, *D. semiclausum* was among the earliest parasitoids introduced from England to New Zealand, Australia and other Asian-Pacific countries for the control of DBM (Hardy, 1938; Waterhouse and Norris, 1987; Thomas and Ferguson, 1989). Similar introductions were made in Indonesia in 1980s (Sastrosiswojo and Sastrodihardjo, 1986), the highlands of Taiwan (AVRDC, 1988) and in the highlands of Philippines in 1989 (Poelking 1992). The parasitoid in all introductions realized appreciable parasitism of up to 70% in addition to substantial savings in the cost of controlling the pest (Talekar, 1992). In Kenya this parasitoid was introduced in 2001 from Taiwan (Macharia *et al.*, 2005). It realized a reduction of DBM survival by a margin of 75% on the release sites within the first year of release (Momanyi *et al*., 2006).

2.4.3 Insecticides

The mainstay of diamondback moth (DBM) control over time has been the use of synthetic insecticides. In developing countries, the reasons advanced for this option are ready availability of insecticides at reasonable cost and lack of other proven alternatives (Talekar and Shelton, 1993). On the other hand, insecticide use in developed countries is normally incorporated in integrated pest management programmes (Theunissen and Ouden, 1987). Failures of this control option have been attributed to lack of rainfall, absence of a crucifer free period, free movement of infested transplants and development of resistance by DBM (Talekar and Shelton, 1993; Furlong and Wright*.*, 1994; Heckel *et al.,* 1999). Development of resistance has been attributed to intensive insecticide usage. This has been fuelled by high fecundity and reproduction potential of DBM, rapid turnover of its generations, continuous use of pesticides and the fact that little damage is

tolerated on marketable products (Magaro and Edelson, 1990; Talekar and Shelton, 1993).

In light of the above, DBM was the first crop insect pest reported to be resistant to DDT in Java, Indonesia (Ankersmit, 1953). Now the pest has developed resistance to almost every insecticide applied in the field including novel ones like spinosins and avermectins (Sayyed *et al*., 2004), neonicotinoids (Ninsin, 2004), pyrazoles and oxadiazines (Mohan and Gujar, 2003).

Mechanisms of resistance by DBM to insecticides include lowered nerve sensitivity, reduced cuticular penetration as well as alteration of target site(s) and detoxification of these insecticides. The enzymes involved in this detoxification process are microsomal oxidases, glutathione-S-transferases, hydrolases and reductases (Sun, 1992; Ferre and van Rie, 2002; Sarfraz, 2004).

Biopesticide extracts of *Azadractin indica* A. Juss (neem), *Lantana camara* L. (Lantana), *Melia azaderach* L. (Chinaberry) and *Chenopodium* sp. have also been used against diamondback moth. The mode of action of these extracts is one or a combination of insecticidal, antifeedant, growth regulator, repellant and oviposition deterrent (Facknath, 1997). The use of a neem seed kernel extract, NeemAzal, in field trials recorded good results against DBM (Saucke *et al.*, 2000).) Botanical pesticides (Schmutterer, 1995; 1997) and specifically neem extracts (Akol *et al.*, 2002) pose no serious danger to the survival of the parasitoid *Diadegma mollipla*. This potential can be harnessed in combination with other biological control methods to develop an integrated pest management system. However, the use of neem that is mixed with other compounds may increase side effects on beneficial organisms (Schmutterer, 1997).

Plate 2. *Diadegma semiclausum* parasitoid

2.4.4 Host plant resistance (HPR)

Host plant resistance as a control measure aims at preventing pest organisms from developing populations above the damage threshold (Dicke, 1996). Intrinsic resistance of crucifers to DBM is either vertical (under the control of a single or few genes) or horizontal (polygenic) (Eigenbrode *et al.,* 1990; Talekar and Shelton, 1993; Verkerk and Wright, 1996). Survival of diamondback moth larvae on shiny (glossy) wax crucifer genotypes is lower than on whitish appearance of normal cultivated cultivars (normal bloom) (Dickson and Eckenrode 1980; Eigenbrode *et al.,* 1991). The form of non-preference as well as tolerance and antibiosis by glossy genotypes is attributed to their reduced wax load and low density of crystalline wax structures (Eigenbrode and Espelie 1995; Justus *et al.,* 2000). This is a form of vertical resistance where the glossy character is inherited as a single recessive gene (Dickson and Eckenrode, 1975).

Studies on the mechanism of resistance in glossy genotypes imply a rejection of the plants by first instars, which results in protracted searching behaviour and reduced feeding. These behavioural differences may lead to increased larval mortality on glossy plants due to starvation and desiccation and the situation is more enhanced as the plant ages. Horizontally oriented epicuticular wax platelets on the glossy genotypes have also been associated with greater dispersal rates, reduced establishment of feeding sites, and higher mortality of first instars (Eigenbrode and Shelton, 1990). A bioassay study on the wax morphology of normal bloom and glossy crucifer genotypes, incidentally, shows no difference between the two. The behavioural difference of DBM on the genotypes may be due to the difference in allellochemicals in the waxes (Eigenbrode and Pillai, 1998).

Other studies have shown that glossy type cabbages are preferred for oviposition (Lin *et al.,* 1984) but are resistant to establishment by the 1st instar larvae in the field (Eckenrode *et al.,* 1986). Conversely, poor resistance to DBM has been observed on a glossy kale with allelic genes for glossiness (Stoner, 1990). This finding suggests the existence of variability for resistance even on glossy cultivars. While non-glossy crucifer selections have shown resistance to DBM in previous works, this resistance is far below that of derivatives of PI 234599, a plant introduction with a glossy trait through a mutation of the wax-expressing gene.

Evidence exists on reduced larval feeding (survival) in normal bloom cultivars (Verkerk and Wright, 1996). This is due to a reduction in the intrinsic rate of pest population increase and a longer duration of host availability for parasitoids and predators to attack them (Feeny, 1976). The resistance exhibited by the normal bloom genotypes is additive and dominant (Dickson *et al.*, 1986).

2.4.5 Integrated pest management (IPM)

This is the judicious and compatible use of two or more possible control measures against a pest with a view to keeping the pest population below a level causing economic loss. These control measures include biological, cultural, genetic, physical/mechanical and chemical (Facknath, 1997), the latter measure largely employed only as a last resort. Integrated pest management aims at reducing synthetic pesticide use in order to minimize their deleterious effects on environment and natural enemies (Ayalew, 2003) arising from their over-use. It also employs efforts to manipulate the habitat of an agro-ecosystem to aid in pest management (Shelton and Badenes-Perez, 2006). Finally, it seeks to integrate host plant resistance and biological control options (Cortesero and Lewis, 2000).

Several success reports through IPM have been realized against DBM. Yaseen (1975) showed a reduced DBM damage when a combination of *C. plutellae* and *O. sokolowskii* parasitoids was introduced onto crucifers in Zambia. The use of parasitoids together with safer pesticides, which have little or no harm to the parasitoids, has been successfully practiced in Asian countries (Talekar and Shelton, 1993). Application of an EPN, *S. carpocapsae*, together with a *Bt* product (Dipel) is reported to have recorded a 58% control of the pest in Hayek farms in Hawaii (Bauer *et al.*, 1998).

2.5 Life tables

Before a biological control approach can be taken against a pest in a given region, a thorough understanding of the population dynamics of the pest species in the region is important. The construction of life tables offers an opportunity to assess the mortality factor(s) acting on different life stages of the pest (Harcourt 1969). Deevey (1947) defined a life table as an organized presentation of the number of individuals of a

generation or stage surviving to a fixed point in the life cycle together with their specific mortality factors.

Host plant resistance as a pest control strategy, may rely on life table studies to identify host patches with attributes that confer or synergize mortalities on the pest. Attempts have been made to develop such life tables for DBM in various parts of the world (Sivapragasam *et al.,* 1988; Wakisaka *et al.,* 1992; Salas *et al.,* 1993; Syed and Abro, 2003). However, the applicability of life table studies across regions with a different suite of ecological conditions may be biased. Messenger (1964) argued that life-table statistics might restrict the understanding of a populations' growth potential to prevailing climatic and food conditions, factors that are varied within and between regions. In addition, the genetic elasticity of DBM pest furnished with novel behavioural tendencies (Sarfraz *et al.,* 2005) demands a constant observation of its population dynamics if control measures directed at it are to co-evolve with the pest.

Knowledge regarding interactions between mortality factors in a life table is normally limited (Aeschlimann, 1979). This may limit the capacity of life-tables as a tool to make key generalizations (Toepfer and Kuhlmann, 2006). Nonetheless, analysis of life table data provides a rational and predictive basis for pest control: enabling prognosis of the effects of changes in cultural or other control practices (Southwood, 1978)

CHAPTER THREE
MATERIALS AND METHODS

3.1 Study Site

All trials were conducted at Duduville Campus of the International Center of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya (S 01° 13′ 15″; E 036° 53′ 45″, altitude 1608 m.a.s.l), (S 01° 13′ 14.4″; E 036° 53′ 44.6″, alt 1609m,) and (S 01° 13′ 17.2; E 036° 53′ 45.7″, alt 1617m). The experiments were carried out both inside and outside the greenhouse and in the laboratory at mean relative humidity and temperature of 54% and 25°C respectively.

3.2 Materials

3.2.1 Plants (Cabbages and Kales)

A total of seven crucifer cultivars from different seed companies were used in the experiment. This involved five cabbage cultivars, “Blue Dynasty”, “Gloria”, “Green Challenger” “Riana” and “Copenhagen Market” (all *B. oleracea* L.) together with two leafy ones, Collard Georgias, “Collard Georgia” and kale “Thousand Headed” (*B. oleracea* L. var. *acephala*). All the cultivars used in the trial were obtained from three seed companies namely East African Seed, Simlaw Seed Company and Royal Sluis. Two cultivars, “Gloria” and “Collard Georgia” were obtained from East African Seed Company while “Copenhagen Market”, “Thousand Headed” and “Riana” were from Simlaw Seed Company. The remaining cultivars “Green Challenger” and “Blue Dynasty were both from Royal Sluis. “Blue Dynasty” cultivar was recruited into the experiment for its glossiness and assumed resistance, while “Gloria” represented a normal bloom susceptible cultivar. The crucifer plants were raised in seedling trays (Plate 3) in the plastic greenhouse and transplanted after four weeks (Plate 4) into 15 cm diameter planting pots with a volume of 2000 ml. The growth medium was a mixture of garden compost, red soil and sand (2: 1: 1). No fertilizer was added. The transplants were placed on tables outside the greenhouse to enable them receive normal ultraviolet radiation, as UV radiation appears to affect the resistance to DBM by Brassica (Lin *et al*., 1983) and

Plate 3. Crucifer seeds germinating on seedling trays in the greenhouse

Plate 4. Four week old crucifer seedlings ready for transplanting

Plate 5. Six- weeks old crucifer seedlings in 15 cm diameter pots ready for trials

the formation of leaf surface waxes (Tevini and Steinmuller, 1987; Barnes *et al,* 1996; Kakani *et al.,* 2003). These transplants were ready for use after six weeks (Plate 5).

3.2.2 Diamondback moth laboratory cultures

A cabbage strain of *P. xylostella* that was initially obtained from a vegetable growing area of Limuru, Central Province, Kenya and maintained on cabbage plants in the laboratory was used in all experiments. Diamondback moth (DBM) larvae were reared from eggs of uniform age produced in a perspex cage (20x20x25cm, Plate 6d) with an opening of 11cm diameter on two opposite sides. One opening was covered with a removable lid for egg and moth manipulation while the other was screened for ventilation.

Pupae were placed inside the cage and kept until the adults emerged. Over 100 adults were used for the experiments. These adults were fed on 10% sugar solution soaked in cotton wool and kept until they died. Four or five strips of aluminum foil (3x15cm) were soaked in cabbage extract, dried, crumpled then suspended from the top of the cage as substrate for egg laying. Crumpling the strips makes them irregular hence providing tactile stimuli for egg laying (Shelton,, 2004). The strips were replaced daily to obtain eggs of equal age. The harvested strips with eggs were ready for use after two days when they were placed on plants in larvae rearing cages. Emerging larvae were allowed to settle on the host naturally.

The DBM cultures obtained were sustained on food plants, potted cabbage “Gloria” in the rearing room. The cultures were maintained at a temperature of 23±3°C. The plants were replaced at irregular times to supply fresh food. The process of pupation and adult emergence took place in the room while the emerging adults were transferred to the oviposition cage daily by use of an aspirator.

3.3. Bioassays

3.3.1 Effect of crucifer cultivars on oviposition of *Plutella xylostella* in the laboratory

Both choice and no choice oviposition preference experiments were conducted in the laboratory using leaves from the test plants. The leaves were placed in plastic vials (one

per vial) filled with water to avoid wilting of the leaves. Each vial was sealed with cotton wool at the top to avoid drowning of the moths. In the choice tests, one excised leaf from each of the seven test plant cultivars was placed in a random arrangement in a 70x105x57cm perspex cage (Plate 6b). Spacing in the cage was 20cm between and 15cm within the leaves to avoid the leaves from touching each other. Fifteen pairs of newly emerged diamondback moth were then introduced into the cage. The leaves were removed after 48 hours and all the eggs per leaf counted. Eggs were counted under a binocular microscope using a tally counter. The experiment was replicated 15 times.

For the no choice tests, excised leaves were obtained from each of the seven test plants and placed in vials as described above. Vials were then placed individually in 70x105x57 cm perspex cages with cloth sleeves on the sides for introducing leaves and adult moths. Newly emerged adult moths (ten pairs) from the cabbage culture were released into each cage and artificial food, 10% sugar solution soaked in cotton wool, provided in the cage. The leaves were removed after 48 hours and all the eggs on the upper, lower epidermis, petiole and on the walls of the vial counted. The experiment was replicated 15 times.

3.3.2 Effect of crucifer cultivars on oviposition, number of larvae surviving to pupae and damage by *Plutella xylostella* in the greenhouse

Test plants from the seven cultivars were raised as described in 3.2.1 above. From these plants, three of each of the seven test cultivars were obtained, and together the 21 plants arranged in a completely randomized design on tables in a screen house along with 100 mated moths. The plants were spaced at 30 cm between and 25 cm within rows in a 215 x 105 x 95 cm cage (Plate 7). The moths were fed on 10% sugar solution in open petri dishes. Eggs were counted after 48 hours and all the DBM moths removed from the cage. Larvae (and later pupae) were counted twice weekly starting 12 days after oviposition until the end of the third week. In the last larval reading, larval feeding damage were scored on a scale of 0-5 based on the area of the leaf damaged (0=No damage at all; 1=Less than 0.1 damage on leaves; 2=Damage lies between 0.1 and 0.25 of the leaf area; 3= Leaf area damage of 0.25 and less than 0.5; 4=Leaf area damage of 0.5; Leaf area damage of more than 0.5) (Wemin and Wesis, 2004; Ayalew, 2006). Averages were derived from the egg counts and the three larval and pupal counts. The

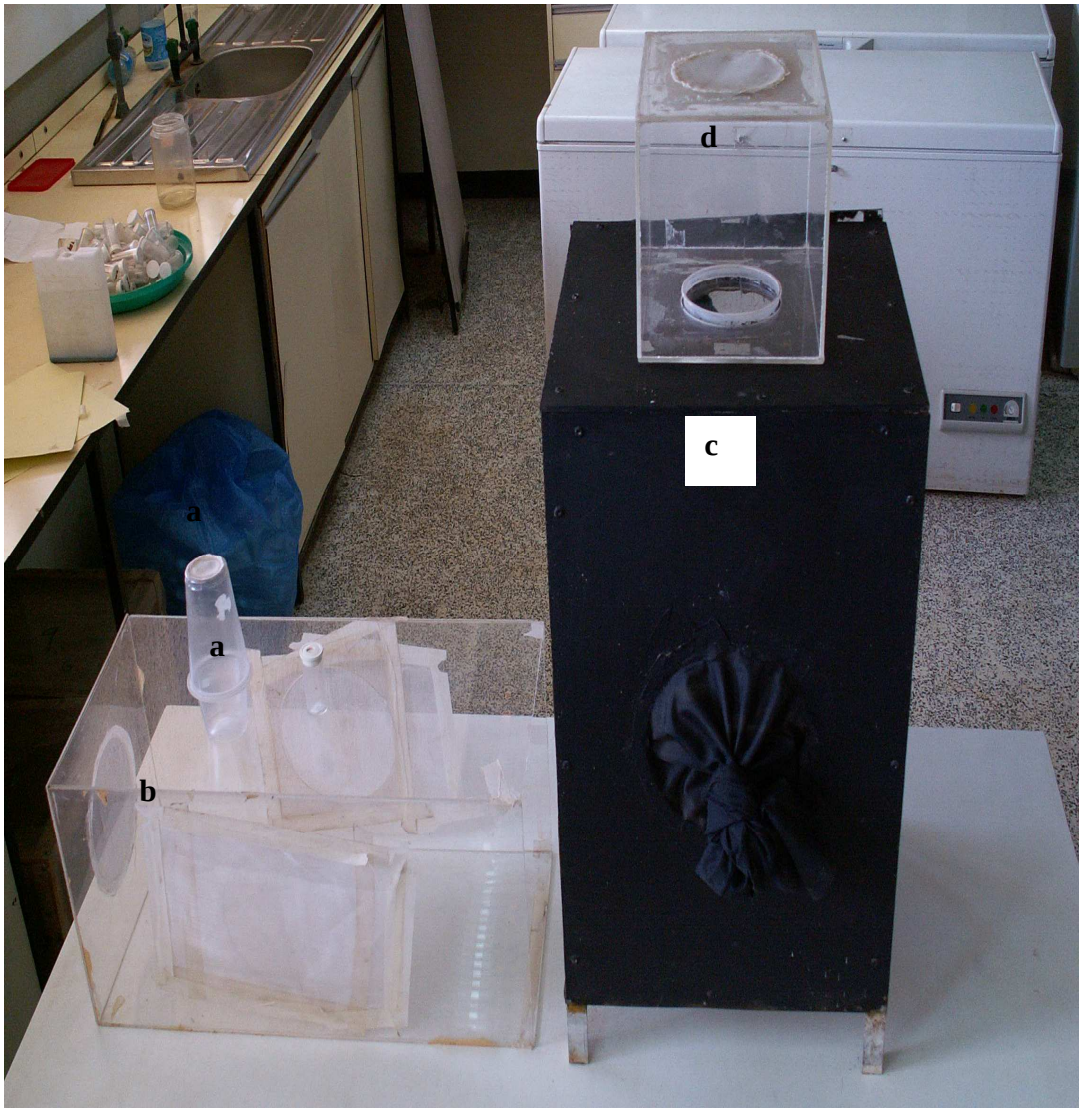

Plate 6. Cage set up for oviposition tests (**a** and **b**) and for rearing of *Plutella xylostella* (**c and d**)

Plate 7. Cages set up in the greenhouse for oviposition and larval development tests of *Plutella xylostella*

experiment was replicated in four cages. A record of temperature and humidity in the green house was taken daily using a data logger.

3.3.3 Effect of crucifer cultivars on larval survival and development of *Plutella xylostella* in the laboratory

Seven hundred diamondback moth eggs of the same age laid on aluminum foils were obtained from the cabbage culture, incubated at 26°C and left to hatch to 1st instar larvae. Neonate larvae were picked at random using a fine camel brush and individually placed in marked plastic vials (2.5x6cm). Leaf discs from each test plants (6 th leaf stage) were introduced into the vials and a piece of tissue paper placed inside to absorb extra moisture and keep the leaf fresh. The vials were incubated at 25±1°C, 60-80ọ RH, 12:12 (L: D) and the number of surviving larvae recorded daily. The leaves were replaced with fresh ones after every two days until the larvae pupated or died. The experiment was replicated 100 times for each cultivar.

The parameters measured were the number of surviving larvae (all instars) and the total larval period. All larvae that pupated were removed and the pupae weighed within 24 hours of pupation using an analytical balance (Mettler AM 100, Mettler Instrument Ltd, Switzerland). Records were also made of pupal duration, date of adult emergence and the sex of adults.

3.3.4 Effect of the crucifer cultivars on larvae of *Plutella xylostella* surviving to pupae in the greenhouse

Seedlings of the 7-crucifer cultivars were established as described in the oviposition test (3.3.2) above and placed on tables in a DBM free greenhouse. The seven cultivars at 6 th leaf stage were placed in a completely randomized design on tables in a screen house at a spacing of 30 cm between and 25 cm within cultivar inside a 215 x 105 x 95 cm cage. The test plants were manually infested with 1st instar larvae of DBM (30 larvae per plant) from DBM rearing room. Larvae (and later) pupae were counted after seven days and subsequently after ten and thirteen days on all the cultivars. Mean counts of larvae and pupae were converted to percent larval survival. The set up was replicated five times.

Records of temperature and humidity in the green house were taken daily using a data logger.

3.3.5 Effect of the crucifer cultivars on adult longevity and reproductive potential of *Plutella xylostella*

Both studies were done on adults obtained from the larval survival and development experiment 3.3.3 above. The newly emerged females and males emanating from pupae of known weights and from the same plant were paired and allowed to mate for 24 hours. From each test plant an excised leaf was obtained and placed in plastic vials as described in section 3.3.3. The vials were each placed in a 5 x 6.5 x 7cm clear conical plastic container. This set up was covered with an inverted transparent plastic container (5 x 6.8 x 12cm) with the bottom covered with a muslin cloth for ventilation (Plate 6a). A pair of adult moth was released in the plastic container with a leaf of the cultivar it had been reared on and the moths fed on 10% sugar solution soaked in cotton wool. The leaves were replaced with fresh ones after every 48 hours and the number of eggs on the upper and lower leaf surfaces and on the wall of the container recorded. This procedure was repeated after every 48 hours till the female was dead and all records of egg distribution; the date of the death of males and females was also taken. The experiment was replicated 15 times.

3.4 Construction of Life table

Data obtained from section 3.3.2 was used to generate the life table parameters. The realized mortality, fertility, sex ratio as well as longevity figures for each cohort were used to construct age specific life tables.

The fertility life-table studies involved repeated counting of individuals in a single cohort in two generations as described above. Data on the development of a cohort was represented according to Maia *et al.* (2002). It included the following columns in a sequence: identification of the group (Cultivar) as alphanumeric variable, female identification as a numeric variable, female age expressed in time units (days), number of eggs laid per female at each age, proportion of females in the population as a numeric variable (0-1) and immature stage survivorship also as a numeric variable (0-1).

Accordingly, population parameter estimates for all the groups were compared as described by the author. Given that the population under study is a closed one and is subjected to age specific schedules of fertility and mortality it was assumed to have an exponential growth represented by the model (Southwood, 1978)

$$N_t = No \times e^{rm} \times t$$

Where, Nt is the population size at time t, No is the initial population size and rm is the intrinsic rate of natural increase. The latter parameter can be approximated from

$$\sum e^{-rm} x.lx.mx = 1$$

The multiplication factor of the initial population per unit time is the finite rate of increase (λ) and can be obtained from

$$\lambda - e^{rm} = \text{anti log } e^{rm} = \frac{Nt+1}{Nt}$$

The net reproductive rate is the mean net contribution per female to the next generation expressed as female offspring per female in a unit time. To calculate this, the probability at birth of being alive at age x, that is lx is obtained. The latter value is multiplied with the mean number of female offspring produced in a unit of time by a female of age x, that is mx. The sum of these products is the net reproductive rate, (Ro). Thus

$$Ro = \sum lxmx$$

Doubling time (Dt) is the time required by a population to double and is represented by

$$Dt = \frac{Ln(2)}{rm}$$

Mean Generation time is the mean length of a generation and starts from the birth of individuals of a generation to the birth of those in the subsequent generation. It is calculated from

$$T = \frac{\log e\, Ro}{rm}$$

The true population parameters (obtained without re-sampling) were obtained through iterative method (Southwood, 1978) using algorithms described in SAS program developed by Maia *et al*. (2002). This method provides a functional link of the main population parameters rm and Ro. Subsequently, the jackknife method (Meyer *et al*., 1986; Wermelinger *et al*., 1991) was used to estimate the uncertainties associated with the population estimators. The jackknife re-sampling method allows for the generation of the standard error and confidence interval using pseudo-values rj of rm which have a normal (Gaussian) distribution (Hogg and Chen, 1988). Re-sampling is achieved by excluding one individual *j* from the initial population *n* in successive samplings and the new values used to estimate the new population parameters.

3.5 Effect of crucifer cultivars on larval parasitism of *Plutella xylostella* by *Diadegma semiclausum* in the greenhouse

This test was done to measure the effect of the different cultivars on parasitism by *D. semiclausum*. Potted plants obtained from the varietal test plants were placed at a spacing of 30 cm by 25 cm on tables in the plastic greenhouse in a completely randomized design. Using a camel hairbrush, thirty of the 2nd instar DBM larvae (Liu *et al*., 2000) from the cabbage culture were introduced into the respective plants. Ten three-day-old, mated *D. semiclausum* were then released in the cage for 2 days at temperatures of 23±3°C after which all the parasitoids were removed. All larvae were then left to feed on their respective host plants, collected after 5 days and then reared in plastic boxes in the laboratory. In these boxes, the larvae were fed on leaves of their respective plant cultivar until pupation. This experiment was replicated 4 times. The number of normally pupating

DBM and their corresponding pupal weights, number of *D. semiclausum* cocoons and those that did not complete development as well as sex ratios of both the pest and the parasitoid were recorded.

3.6 Scanning electron microscopy (SEM) study of the leaf surfaces of the crucifer cultivars

Two samples of the second and the fifth leaf of all cultivars were obtained at the six-leaf stage just before plants were used in the trials. Leaf blades were cut into 5 mm transverse thin sections with a sharp razor blade. The samples were fixed for 1 week using 2.5% glutaraldehyde in 0.05M PO_4, 5.0% sucrose buffer with a PH of 7.4. The samples were then air-dried for a week and the dried specimens (1x3 mm) mounted on metal discs with silver conductive cement then coated with carbon and gold in a vacuum evaporator using JFC- 1100E ION Sputter. The adaxial rectangular surfaces of the coated samples were examined at X2000 magnification using a scanning electron microscope (JEOL JSM- T330A) at 15 kV accelerating voltage. The crystal shapes, their diameters, inter-crystal spaces as well as crystallite densities on the different cultivars were then examined and printed.

3.7 Statistical analysis

Natural logarithmic transformation was applied to the data on oviposition preference (Laboratory), larval survival in the greenhouse, adult longevity and reproduction potential and leaf surface waxes to improve homoscedasticity and normality of data for each cultivar. Arcsine square root transformation was performed on the percent parasitism, percent larvae dead and percent adult emergence.

The effect of cultivar on oviposition preference (Number of eggs laid), larval and pupal survival and development measured as the number of larvae, pupa and adult moths in the laboratory was analyzed using procedure Means and GLM in Statistical Analytical Software (SAS) (SAS, 1999). Where significant differences were realized, the mean number of eggs laid as well as larval and pupal survival and development on each cultivar were separated using Student – Newman – Keuls test (SNK).

The effect of cultivar on adult longevity and reproductive potential was analyzed using procedure univariate in SAS and means separated using SNK. The life table parameters were analyzed using algorithms developed by Maia *et al*. (2002).

Linear regression between intrinsic rate of population increase and generation time was analyzed using least squares method in SAS (SAS, 1999). Similar method was used to analyze the linear regression between intrinsic rate of population increase and fecundity as well as longevity and pupal weight. Effect of cultivars on parasitism of *P. xylostella* by *D. semiclausum* in the greenhouse was analysed using procedure Means and GLM and so was the test on characteristics of leaf surface waxes of seven commercial crucifer cultivars.

CHAPTER FOUR
RESULTS

4.1 Effect of crucifer cultivars on oviposition of *Plutella xylostella* in the laboratory

The number of eggs laid on the seven test cultivars ranged from 21.3 ± 4.2 to 45.7 ± 10.3 in the choice experiment (Fig. 1) and from 1.4 ± 0.5 to 20.3 ± 4.3 in the no choice experiment (Fig. 2). Although DBM consistently laid more eggs on "Collard Georgia" as compared to the other crucifers in both the choice and no choice tests, there was no significant difference elicited by the cultivars in egg laying in the former test.

However, most of these eggs were not laid on the leaf but anywhere in the container: on the vial, the cotton wool covering the top of the vial and the container itself. The number of off-target eggs showed disparity between cultivars. For example, it was significantly lower ($F_{6, 77} = 5.63$; $P < 0.05$) on kale "Thousand Headed" and "Collard Georgia" in the choice test (Fig 1) and on "Collard Georgia" and "Green Challenger" in the no-choice test ($F_{6, 98} = 4.54$; $P < 0.05$, Fig. 1).

Analysis of variance carried out on the percent off-target eggs reveals that "Green Challenger" elicited a significantly higher ($F_{6, 98} = 4.12$; $P < 0.05$) percent off target egg laying by the pest than was "Riana", "Blue Dynasty" and "Thousand Headed" in the no choice test. The cultivars "Thousand Headed" and "Collard Georgia" elicited a significantly lower ($F_{6, 77} = 5.63$; $P < 0.05$) percent off-target laying in the choice test (Fig. 4.1).

4.2 Effect of crucifer cultivars on oviposition, larvae to pupae and pupae to adult development of *Plutella xylostella* in the greenhouse and on damage indices

In the greenhouse, oviposition by the DBM pest was significantly higher ($P < 0.05$) on "Blue Dynasty" than was on "Gloria" but similar to the rest of the cultivars under study, (Table 2)

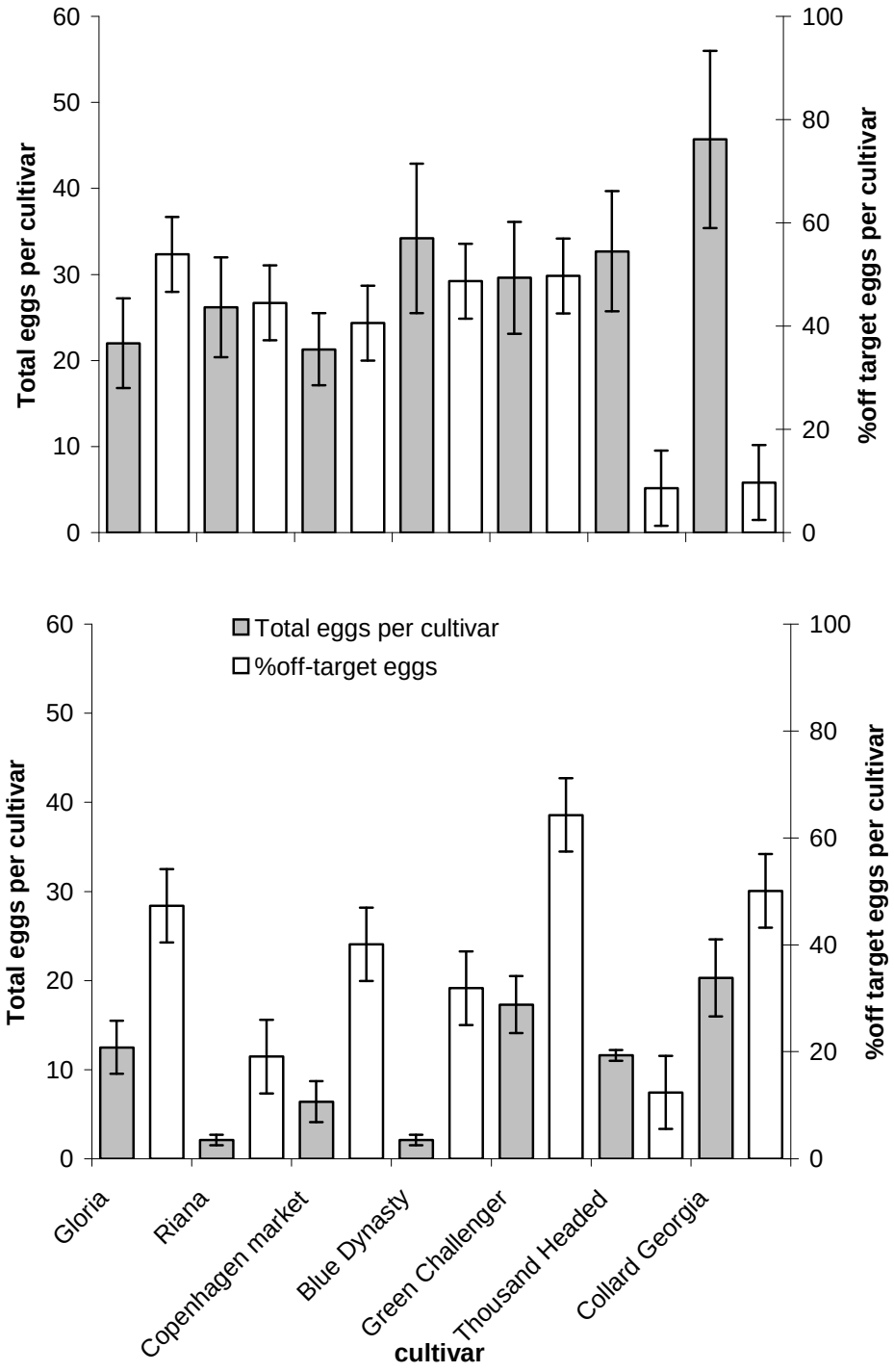

Figure 4.1. Eggs laid in 48 hours in choice (top) and no choice (bottom) experiments on commercial leafy and head crucifer cultivars

Consequently, larval survival of diamondback moth larvae to pupae then to adult showed significant difference between cultivars (Table 1). Survival was significantly higher on the cultivar "Green Challenger" ($F_{6, 28} = 5.18$; $P < 0.05$) followed by "Blue Dynasty" and "Collard Georgia". Interestingly, larvae on "Green Challenger" appeared thin, pale in colour and emaciated. On the other hand, survival of the pest on the cultivar "Riana" was significantly ($F_{6, 28} = 5.18$; $P < 0.05$) the lowest in the greenhouse, which follows the relatively low number of eggs that they developed from (Table 2).

No difference was observed on either the number of pupae or damage scores between the cultivars. While DBM larval survival records on "Green Challenger" "Collard Georgia" and "Gloria" were above the number of eggs that were noted to be oviposited on these cultivars, the other test cultivars showed survivorship within the number of eggs laid on them.

4.3 Effect of crucifer cultivars on larval and pupal survival and development of *Plutella xylostella* in the laboratory

The mean larval period ranged from 9.2 ± 0.29 to 10.7 ± 0.2 days between cultivars (Table 1). Diamondback moth raised on "Riana", "Green Challenger" and "Thousand headed" cultivars had the most prolonged larval period that was significantly different ($F_{6, 200} = 6.47$; $P < 0.05$) from "Gloria" and "Collard Georgia". However, there was no significant difference) in larval period in the other test cultivars. . Consequently, the lowest percent pupation was observed on "Green Challenger" (31%) and the highest on "Blue Dynasty" (73%).

Highest pupal weight was observed on DBM raised on "Collard Georgia" and was significantly different ($F_{6, 166} = 9.13$; $P < 0.05$) from all other tested cultivars. The lowest weight was recorded on "Green Challenger" and "Copenhagen market" although there was no significant difference ($P > 0.05$) between these two cultivars. to In addition, DBM on "Gloria" and "Green Challenger" had the highest pupal development time, which was significantly different ($F_{6, 513} = 15.61$; $P < 0.05$) from all the cultivars except "Thousand Headed" and "Riana.

The percent DBM developing to adult was in the range of 29-69 between cultivars and was lowest and highest on "Green Challenger" and "Blue Dynasty" respectively.

Table 1. Effect of crucifer cultivars on larvae to pupae and pupae to adult development of *Plutella xylostella* in the laboratory

Crucifer cultivar	Larval period days ($\bar{x}$ ±SE)	Pupal period (days) $\bar{x}$ ±SE	Pupal weight (mg) $\bar{x}$ ±SE	%pupation	%Adult emergence
Gloria	9.3±0.31^{b}	5.3±0.13^{a}	4.75±0.10^{bc}	49	45
Riana	10.7±0.20^{a}	5.1±0.10^{ab}	4.80±0.08^{bc}	69	65
Copenhagen Market	9.8±0.33^{ab}	4.8±0.08^{b}	4.57±0.09^{cd}	52	46
Blue Dynasty	9.8±0.16^{ab}	4.9±0.08^{b}	4.88±0.08^{bc}	73	69
Green Challenger	10.5±0.43^{a}	5.3±0.12^{a}	4.34±0.13^{d}	31	29
Thousand Head	10.6±0.31a	5.1±0.08^{ab}	4.97±0.08^{b}	65	59
Collard Georgia	9.2±0.29^{b}	3.1±0.32^{b}	5.91±0.16^{a}	55	50

Means ± SE followed by the same letter in a column are not significantly different, ($P > 0.05$, SNK).

Table 2. Effect of crucifer cultivars on oviposition, larvae to pupae and pupae to adult development of *Plutella xylostella* in the greenhouse and on damage scores

Crucifer cultivar	Mean no. of eggs $\bar{x}$ ±SE	Mean no. of larvae $\bar{x}$ ±SE	Mean no. of Pupa $\bar{x}$ ±SE	Damage score $\bar{x}$ ±SE
Blue Dynasty	40.8±10.2^{a} (3.60±0.22)	36.9±4.9^{ab} (3.57±0.13	12.8±2.42^{a} (2.43±0.27)	2.6±0.51^{a} (0.86±0.24)
Green Challenger	28.8±5.8^{ab} (3.30±0.17)	48.9±7.7^{a} (3.84±0.17)	20.4±3.98^{a} (2.95±0.18)	3.2±0.37^{a} (1.13±0.13)
Collard Georgia	23.2±5.9^{ab} (3.04±0.21)	35.4±7.85^{ab} (3.46±0.24)	12.6±3.3^{a} (2.78±0.33)	3.8±0.58^{a} (1.28±0.17)
Riana	17.4±5.5^{ab} (2.64±0.34)	17.2±1.38^{b} (2.83±0.08)	7.6±1.29^{a} (1.95±0.22)	1.8±0.58^{a} (0.42±0.28)
Thousand Headed	25.6±5.8^{ab} (3.11±0.26)	19.5±5.16^{b} (2.85±0.24)	12.6±3.3^{a} (2.33±0.36)	2.4±0.75^{a} (0.68±0.31)
Gloria	12.2±3.2^{b} (2.15±0.54	21.5±4.69^{b} (2.98±0.20)	9.2±2.71^{a} (2.04±0.30)	2.8±0.58^{a} (0.96±0.18)
Copenhagen Market	22.6±1.5^{ab} (3.11±0.06)	18.0±2.65^{b} (2.85±0.14)	9.8±3.4^{a} (2.09±0.29)	3.6±0.4^{a} (1.26±0.10)

Means ± SE followed by the same letter in a column are no significantly different, ($P > 0.05$, SNK). Figures in parenthesis are transformed means.

4.4 Life table construction

All the life table parameters under study showed significant disparity between the various cultivars with the exception of the generation time (T) and the finite rate of increase (λ) (Table 3). The net reproductive rate (Ro) was in the range of 19.4 ± 2.2 to 60.6 ± 3.0. It was significantly higher ($P < 0.05$) on DBM pest reared on "Thousand Head", "Blue Dynasty" and "Riana" than on "Copenhagen Market" and "Green Challenger" but similar to those reared on "Collard Georgia" and "Gloria". In addition, the Ro of DBM on "Green Challenger" was significantly lower than that on "Copenhagen Market" but the latter was similar to "Collard Georgia" and "Gloria".

On the other hand, the intrinsic rate of increase (r_m) was significantly lower ($P < 0.05$) when DBM pest was raised on "Green Challenger" than on the other test cultivars except "Riana" and "Collard Georgia". As a consequence, the lowest doubling time was observed on DBM raised on "Green Challenger" and this was significantly different ($P < 0.05$) from the other cultivars but similar to "Gloria".

4.5 Effect of crucifer cultivars on adult longevity and fecundity of *Plutella xylostella* in the laboratory

Pupal weights of diamondback moth reared on different cultivars in the laboratory differed significantly between the cultivars (Table 4). Lower weights ($F_{6, 145}=5.26$; $P < 0.05$) were observed on both "Green Challenger" and "Copenhagen Market" than the rest of the test cultivars all of which were significantly similar.

Adult female longevity, on the other hand, ranged from 13.3 ± 0.87 to 17.8 ± 0.85 days and was significantly lower ($F_{6, 145}=3.48$; $P < 0.05$) on "Thousand Headed" and "Collard Georgia" than the other test cultivars except "Blue Dynasty and Green Challenger".

In addition, fecundity of adults ranged from 138.4 ± 15.9 to 192.6 ± 18.1 eggs between the cultivars. DBM was significantly ($F_{6, 145} = 2.25$; $P < 0.05$) less fecund on both "Copenhagen Market" and "Green Challenger" than on the rest of the test cultivars all of which showed no significant divergences.

Table 3. Jackknife estimates and respective standard errors of the population parameters

Crucifer cultivar	RO1±SE	RM1±SE	T1±SE	DT1±SE	LAM1±SE
Blue Dynasty	57.5±3.9[a]	1.1±0.05[a]	3.6±0.1[a]	0.61±0.03[b]	3.1±0.2[a]
Collard Georgia	54.8±4.2[ab]	1.0±0.05[ab]	4.0±0.2[a]	0.68±0.03[b]	2.8±0.1[a]
Copenhagen Market	41.0±3.3[b]	1.0d±0.04[a]	3.6±0.1[a]	0.68±0.03[b]	2.8±0.1[a]
Gloria"	49.4±4.7[ab]	0.9±0.05[a]	4.2±0.2[a]	0.75±0.04[ab]	2.5±0.1[a]
Green Challenger	19.4±2.2[c]	0.7±0.06[b]	4.2±0.2[a]	0.97±0.07[a]	2.0±0.1[a]
Thousand Headed	60.6±3.0[a]	1.0±0.03[a]	4.0 ±0.1[a]	0.68±0.02[b]	2.8±0.1[a]
Riana	55.0±3.3[a]	1.0±0.05[ab]	3.9±0.2[a]	0.68±0.03[b]	2.8±0.2[a]

Means followed by the same letter in a column are not significantly different, **(*P* >** 0.05, SNK**).**

Table 4. Mean pupal weights, longevity and fecundity of *Plutella xylostella* adults reared on different crucifer cultivars in the laboratory

Crucifer cultivar	Mean pupal weight ± SE	Mean adult female longevity ± SE	Mean adult fecundity± SE
Gloria	5.3±0.13[a] (1.46±0.09)	17.8±0.85[a] (2.57±0.12)	192.6±18.12[a] (4.61±0.17)
Riana	5.1±0.14[a] (1.61±0.04)	17.1±0.45[a] (2.82±0.04)	171.8±10.38[a] (5.05±0.04)
Copenhagen Market	4.8±0.16[b] (1.46±0.03)	17.7±1.13[a] (2.82±0.10)	146.6±11.62[b] (4.81±0.09)
Blue Dynasty	5.3±0.13[a] (1.66±0.03)	16.7±1.27[ab] (2.75±0.09)	169.0±11.52[a] (5.04±0.08)
Green Challenger	4.7±0.26[b] (1.46±0.09)	15.7±1.22[ab] (2.57±0.12)	138.4±15.90[b] (4.61±0.17)
Thousand Headed	5.3±0.09[a] (1.69±0.02)	14.3±0.92[b] (2.51±0.06)	171.2±8.37[a] (5.10±0.07)
Collard Georgia	5.8±0.20[a] (1.68±0.05)	13.3±0.87[b] (2.48±0.06)	192.3±14.61[a] (5.16±0.11)

Means ± SE followed by the same letter in a column are not significantly different (*P* > 0.05, SNK). Figures in parenthesis are transformed means.

Doubling time as a regresson did not significantly explain the intrinsic rate of increase in the linear model. However, 52 % of the variability in the latter could be explained by it ($Y = 2.53 – 0.34\ x$; $R^2 = 0.52$, Fig. 3). Similarly, fecundity explained 53 % of the total variability found on Rm using the regression equation $Y = 0.0016\ x + 0.2135$ ($R^2 = 0.53$, Fig. 4) but the relationship was not significant. On the contrary, when there was a significant ($F_{1, 97} = 17.97$; $P < 0.05$) linear relationship between pupal weight and fecundity using the equation $Y = -4.83 + 33.2\ x$ only 16 % of variability in the dependent variable could be explained by the regresson ($R^2 = 0.16$, Fig. 5). Pupal weight, however, had no significant influence ($F_{1, 97} = 0.16$; $P = 0.688$; $R^2 = 0.0017$) on adult longevity of DBM.

4.6 Effect of crucifer cultivars on parasitism of *Plutella xylostella* by *Diadegma semiclausum* in the greenhouse

Although DBM raised on the cultivar “Green Challenger” had the lowest pupal weight numerically and “Copenhagen Market” the highest, there was no difference between pupal weights of diamondback moth reared on the cultivars under study. Similarly, no difference was observed on percent parasitism of the pest on the study cultivars despite “Blue Dynasty” and “Thousand Headed” having the highest and the lowest percent parasitism respectively (Table 6).

However, there were more dead DBM larvae on the cultivar “Thousand Headed” which was higher than ($F6, 77 = 2.66$; $P = 0.02$) on “Blue Dynasty” but similar to the rest of the cultivars. In spite of this, an equal percent of DBM adults ($F6, 77 = 0.45$; $P > 0.05$) developed on these cultivars. Subsequently, a higher percent of *D. semiclausum* adult emergence was observed on “Blue Dynasty” which was significantly different ($F6, 77 = 2.38$; $P < 0.05$) from “Thousand Headed” but similar) to the rest of the cultivars.

4.7 Scanning electron microscopy (SEM) study of the leaf surfaces of the crucifer cultivars

There were observable differences on the amount, shapes, conspicuousness and ramifications of epicuticular wax crystals on the various test cultivars (Plate 8). The cultivar “Thousand Headed” unlike the others had a heavy presence of rods and rodlets

mixed with thin platelets of varied shape: semicircular, angular and irregular crystals. Isolated cases of rodlets connected to platelet aggregates were also observed. Ramifications on the crystals were minimal (Plate 8a).

The cultivar “Collard Georgia” was predominantly covered with irregular crystal platelets with extensive ramifications. The crystals, unlike on the other cultivars, were thinly oriented parallel to the surface. Rodlets, although minimal, were transversely ridged and protruded from the margins of both large and minute platelets. No transversely ridged rods were noted on the other test cultivars. Scanty rods existed independently (Plate 8b).

Cultivar “Green Challenger” had neither rods nor rodlets but bore large and irregularly shaped conspicuous polygon crystals that were widely spaced parallel to the surface (Plate 8c). “Riana” predominantly had dense crystalline platelets with a blend of shapes ranging from smooth circular crystals to polygon and irregular crystals. The crystals were parallel to the surface and had multiple ramifications. Scanty short rods and rodlets were mainly around the stomata and on few areas devoid of platelet aggregate (Plate 8d).

“Blue Dynasty” also had few rods and rodlets around the stomata and aggregated crystalline polygon platelets along defined paths parallel to the surface. No other test cultivar exhibited this definite pattern. The aggregates were of mixed shapes (regular and irregular) with few ramifications. While aggregation was evident on irregular platelets, the regular (angular and polygon) ones lacked it and the latter were spread on patches devoid of the former. There were wide spaces in between these aggregates (Plate 8e).

The cultivar “Gloria” had thin, isolated wax crystals of varied shapes. Most crystals had minimal ramification. Minute rods were evident around the stomata (Plate 8f). “Copenhagen Market” cultivar had most crystals showing definite shapes: rectangular, polygon and angular to circular with smooth or minimally ramified edges (Plate 8g).

There were significant differences on crystal diameters, inter-crystal spaces and crystallite densities (Table 5). Although statistically similar to “Copenhagen Market” the cultivar “Green Challenger” had significantly wider ($F_{6,\ 203} = 16.13$; $P < 0.05$) crystals while “Thousand Headed” had the narrowest. Spaces between the crystals were also significantly different ($F_{6,\ 203} = 28.32$; $P < 0.05$). Both “Blue Dynasty” and “Green

Challenger" cultivars were more widely spaced than the rest of the cultivars. "Riana" had significantly higher ($F_{6, 28} = 7.76$; $P < 0.05$) crystal density than "Green Challenger" and "Copenhagen Market.

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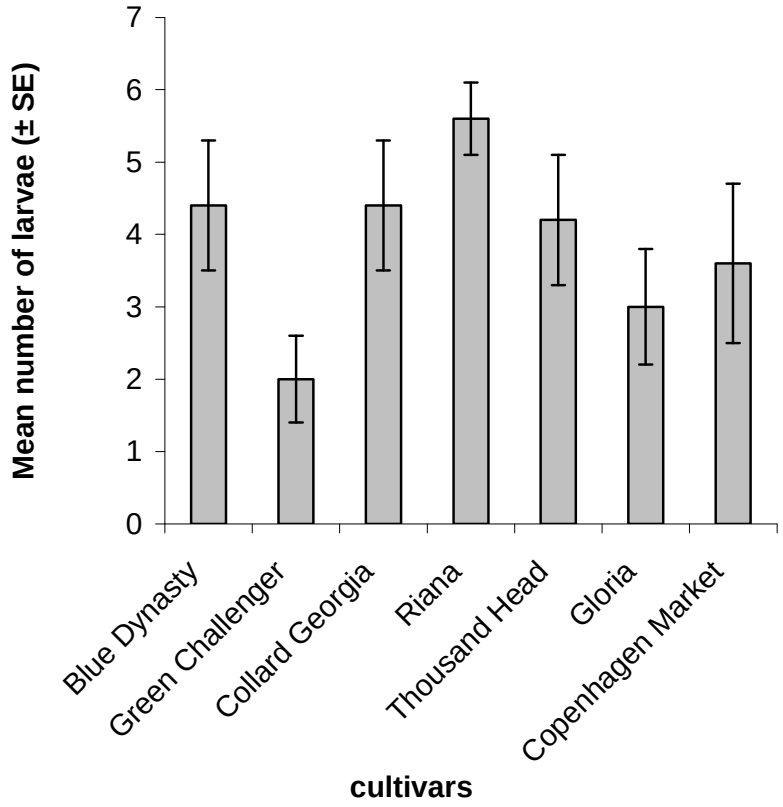

Figure 4.2. Effect of crucifer cultivars on egg to larvae development of *Plutella xylostella* in the greenhouse

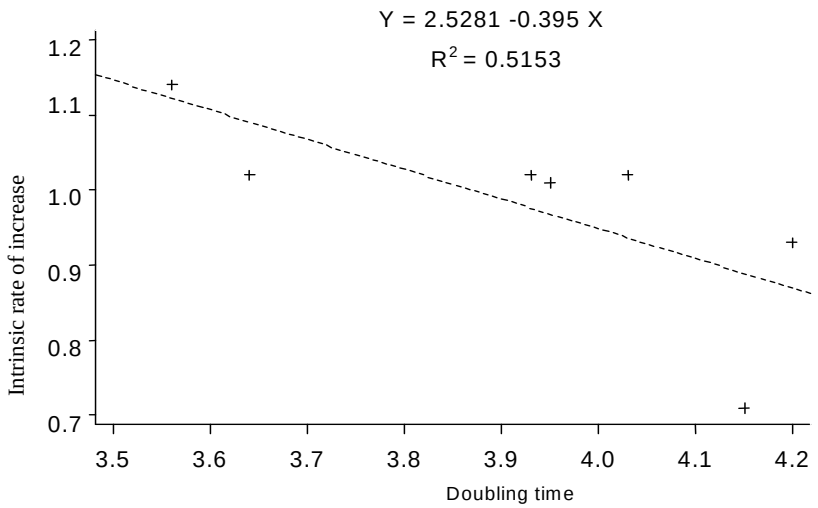

Figure 4.3. Effect of doubling time (T) on intrinsic rate of natural increase (rm) of diamondback moth in the laboratory

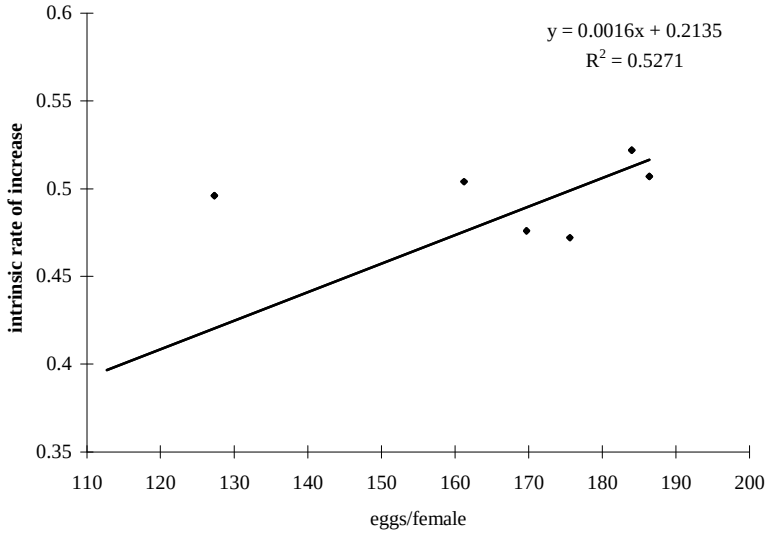

Figure 4.4. Effect of fecundity on intrinsic rate of natural increase (rm) of diamondback moth in the laboratory

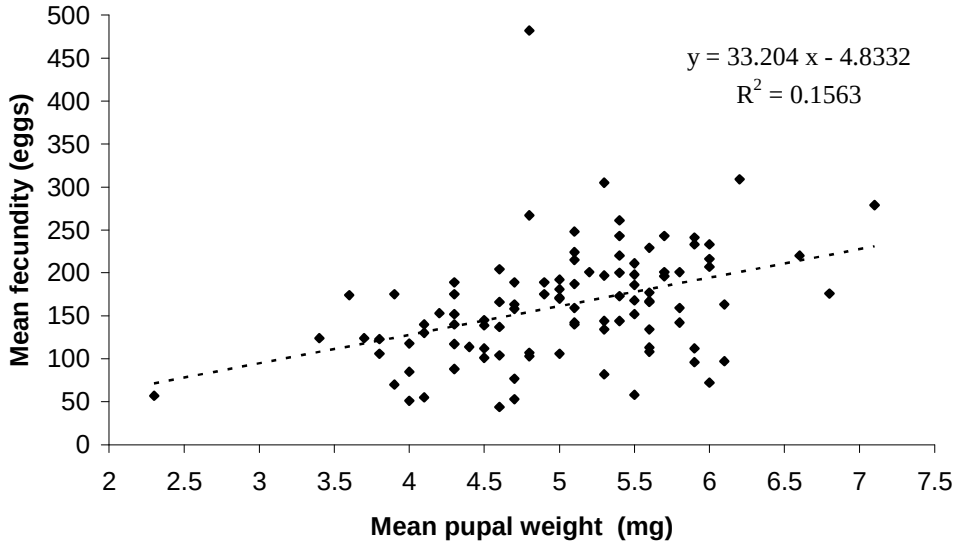

Figure 4.5. Effect of pupal weight on fecundity of diamondback moth in the laboratory

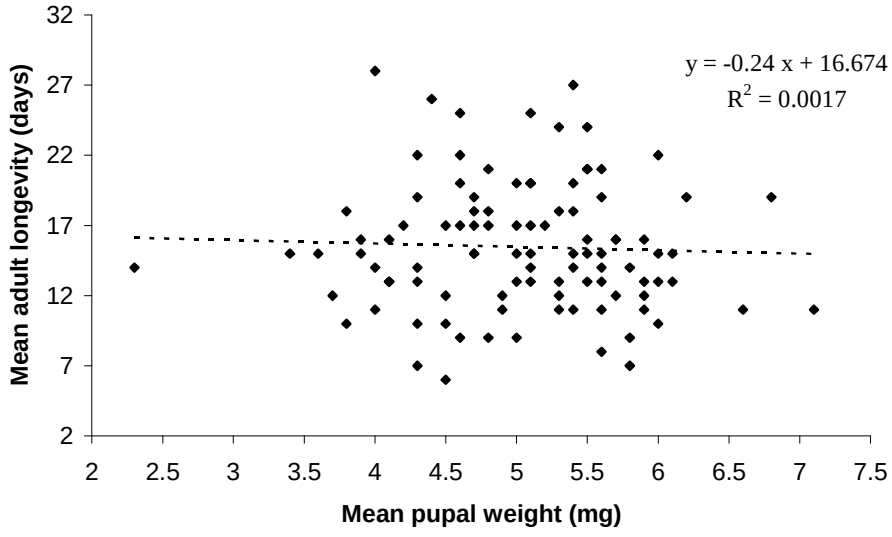

Figure 4.6. Effect of pupal weight on longevity of diamondback moth in the laboratory

Table 5. Characteristics of leaf surface waxes of seven commercial crucifer cultivars

Cultivar	Mean Crystal diameter (nm) Mean ± SE	Mean Space between crystals (nm) Mean ± SE	Mean Crystallite per 0.001mm^2 Mean ± SE	Mean Rod Length (nm) Mean ± SE
Blue Dynasty	1146.7±82.9^{dc} (6.97±0.07)	3716.7±306.0^{a} (8.10±0.10)	260.0±13.8^{ab} (5.56±0.05)	1673.3±121.7 (7.35±0.07)
Green Challenger	2096.7±171.2^{a} (7.55±0.08)	4263.3±312.3^{a} (8.28±0.08)	150.0±15.8^{c} (4.99±0.10)	
Collard Georgia	1576.7±128.3^{bc} (7.22±0.12)	1880.0±166.0^{bc} (7.44±0.08)	276.0±6.78^{ab} (5.62±0.02)	
Riana	1130.0±118.0^{d} (6.85±0.12)	1463.3±142.1^{c} (7.16±0.10)	306.0±23.2^{a} (5.71±0.08)	
Thousand Head	683.3±77.9^{e} (6.34±0.11)	1560.0±140.6^{c} (7.23±0.09)	294.0±27.3^{ab} (5.67±0.1)	
Gloria	1143.3±113.8^{d} (6.88±0.11)	2090.0±155.5^{b} (7.56±0.08)	268.0±11.1^{ab} (5.59±0.04)	
Copenhagen Market	1670.0±87.0^{ab} (7.38±0.05)	2026.7±132.2^{b} (7.55±0.07)	216.0±26.6^{b} (5.34±0.12)	

Means ± SE followed by the same letter in a column are not significantly different, ($P > 0.05$, SNK). Figures in parenthesis are transformed means.

Table 6. Effect of cultivars on parasitism of *Plutella xylostella* by *Diadegma semiclausum* in the greenhouse

	Mean pupal weight	Mean percent parasitism	Mean percent larvae dead	Mean percent adult emergence	
Cultivar	Mean± SE	Mean ± SE	Mean ± SE	Diamondback Moth ± SE	*Diadegma Semiclausum* ± SE
Blue Dynasty	5.69±0.15[a] (1.73±0.03)	60.4±5.6[a] (0.77±0.04)	19.7±3.8[b] (0.42±0.05)	30.8±4.3[a] (0.54±0.04)	49.4±5.7[a] (0.69±0.04)
Green Challenger	5.36±0.2[a] (1.64±0.05)	56.2±5.2[a] (0.74±0.04)	37.8±3.9[ab] (0.60±0.04)	26.9±3.[6 a] (0.51±0.03)	35.3±4.7[ab] (0.58±0.04)
Collard Georgia	5.55±0.18[a] (1.69±0.03)	50.5±5.4[a] (0.70±0.04)	35.0±4.8[ab] (0.57±0.04)	32.5±4.4 [a] (0.55±0.04)	32.5±4.0[ab] (0.56±0.04)
Riana	5.86±0.13[a] (1.76±0.02)	52.8±4.6[a] (0.72±0.03)	31.1±3.9[ab] (0.54±0.04)	31.7±2.9 [a] (0.55±0.03)	37.2±4.7[ab] (0.60±0.04)
Thousand Headed	5.70±0.15[a] (1.73±0.03)	47.6±6.0a (0.51±0.04)	45.3±5.8[a] (0.71±0.03)	26.1±3.2[a] (0.72±0.04)	27.8±5.8[b] (0.59±0.03)
Gloria	5.63±0.16[a] (1.71±0.03)	60.3±4.6[a] (0.77±0.03)	30.8±4.0[ab] (0.53±0.05)	27.1±3.3[a] (0.51±0.04)	42.1±4.4[ab] (0.64±0.03)
Copenhagen Market	6.04±0.22[a] (1.78±0.04)	56.7±4.2[a] (0.75±0.03)	26.4±5.4[ab] (0.47±0.06)	29.0±2.2[a] (0.53±0.02)	42.4±5.5[ab] (0.63±0.04)

Means ± SE followed by the same letter in a column are not significantly different. Figures in parenthesis for all columns except pupal weights are arcsine square root transformation of the mean. Figures in parenthesis for pupal weights are natural logarithmic transformations of the means ($P > 0.05$, SNK)

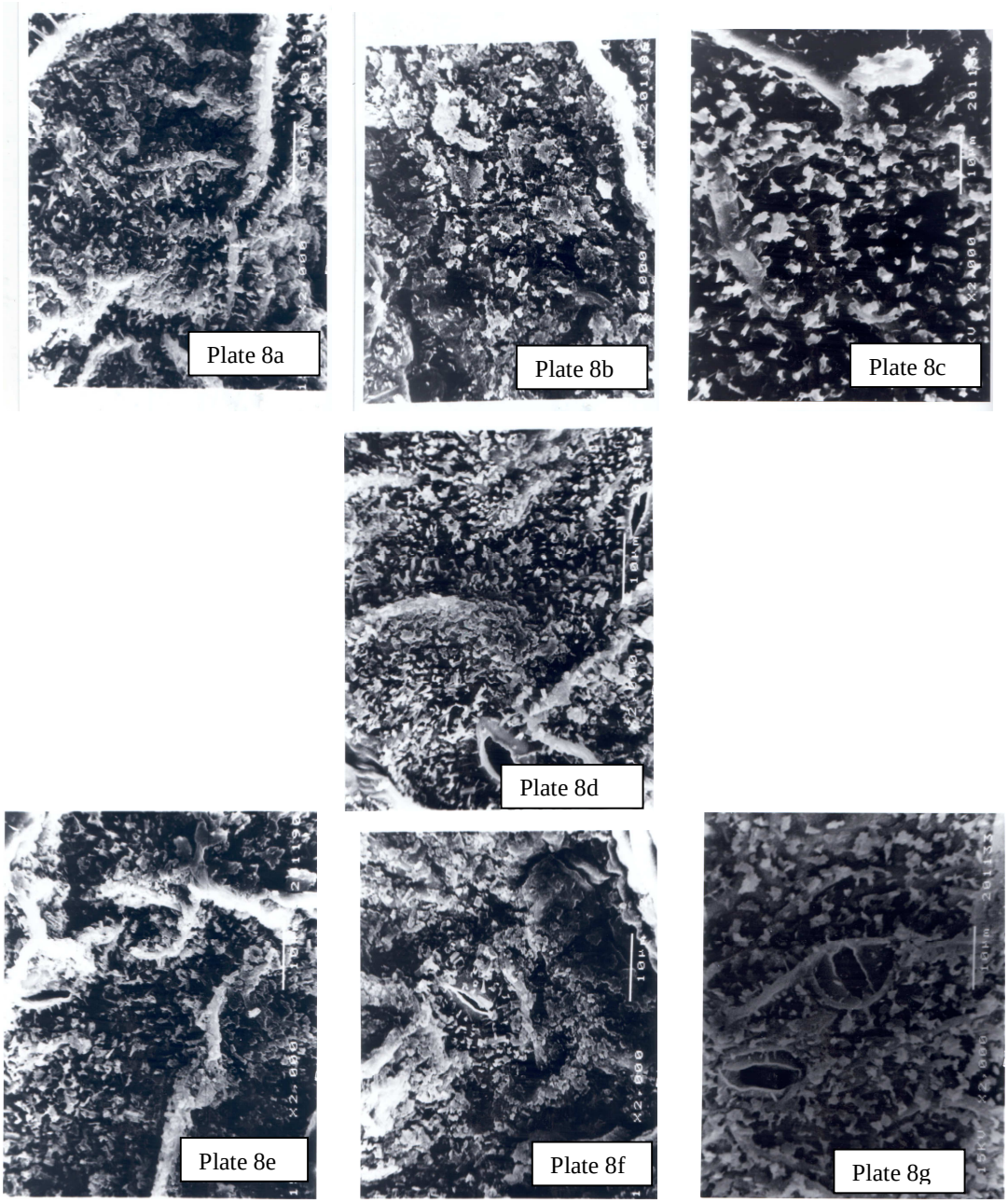

Plate 8. Scanning electron micrographs of adaxial leaf surfaces of the test cultivars

Plate 8a- Dense rods and rodlets mixed with thin platelets on Thousand Headed

Plate8b- Irregular thin polygon crystallites mixed with transversely ridged rods and rodlets on Collard Georgia

Plate 8c- large irregular platelates widely spaced but no rods on Green Challenger

Plate 8d- Dense platelet crystallites of varied shapes on Riana

Plate 8e- Aggregated crystallite polygons of mixed shapes on Blue Dynasty

Plate 8f- Thin platelet crystals of mixed shapes on Gloria

Plate 8g- Sparse crystallite platelets of varied shapes of smooth edges on Copenhagen Market

CHAPTER FIVE
DISCUSSION

5.1 Effect of crucifer cultivars on oviposition of *Plutella xylostella* in the laboratory

It is evident from the oviposition results that females did not discriminate between the cabbage cultivars for oviposition in the choice test regardless of their varied levels of wax bloom. This behavior has been noted before where diamondback moth (DBM) females did not discriminate to oviposit on normal and reduced wax bloom genotypes (Eigenbrode and Shelton, 1990, Ulmer *et al*, 2002). However, results of "Collard Georgia" and "Green Challenger" as significantly superior oviposition substrates in the no choice test may suggest either higher levels of glucobrassicin (Renwick *et al*., 1992) or the twin effect of sinigrin and alkanes (Spencer *et al*., 1999) on these cultivars. Notable also was the low oviposition on both "Blue Dynasty" and "Riana" in the no choice test as opposed to that in the choice test. Renwick and Chew (1994) observed that ovipositing female determines oviposition on a suitable host in two distinct processes. In the first process, visual and volatile chemical cues mediate host landing. However, vision was observed to be of minor importance for DBM as compared to olfaction in this regard (Couty *et al*., 2006). In the second process, females while on the plant perceive gustatory stimuli through chemoreceptors located on their tarsi, antennae, proboscis and ovipositor and are thus guided to accept or reject the host. It is likely that landing played a critical role where "Blue Dynasty" and "Riana" may have produced weaker volatile blends in the no choice test to excite sufficient oviposition stimulation. On the other hand a mixture of volatiles from all cultivars may have confused the females in accepting all cultivars in the choice test. Couty *et al*. (2006) observed that when host plants are present in a mixture, foraging DBM are likely to land on the first row of the plants alluding to the extent of the confusion due to host plant mixtures.

Of concern however, is the level of off-target eggs (laid on vials and cotton wool surrounding the vials) in the laboratory trials. Evolutionary theory demands that herbivores oviposit on patches that accord their offspring maximum survival opportunities (Thompson and Pellmyr, 1991; Barker and Maczka, 1996). The tendency of the DBM female to lay eggs on non-hosts or on hosts that confer poor larval fitness has

been a subject of some discussions (Uematsu and Sakanoshita, 1989; Charleston and Kfir, 2000). The paradox of such tendencies is not a novel one either and has been explored by many authors (Courtney, 1982; Larsson and Ekborn, 1995; Mayhew, 1997; Nylin and Janz, 2000; Graves and Shapiro, 2003; Stefanescu *et al*, 2006). Attempts to explain the tendency have yielded few reasons namely, to enable the eggs get better adhesion on surfaces devoid of waxy substances (Uematsu and Sakanoshita, 1989; Charleston and Kfir, 2000) and to avoid interacting with natural enemies that explore the herbivore host plant niches (Fox and Eisenbach, 1992). Additionally, Sarfraz *et al*. (2005) indicated that DBM in Canada have developed behavioural resistance by laying eggs on the soil stem interface ostensibly to avoid toxic pesticide spray on the foliage.

While the trade-off between escaping waxes, predation and pesticide toxicity by DBM on one hand and optimizing survival on the other is noble, this tendency may be costly. This is because the fate of the eggs and subsequently the neonate larvae on the perceived 'safe havens' is not clear in the wake of abiotic (Terry *et al.,* 1989) and biotic adversities on the foreign surfaces. Ampong *et al*. (1994) indicated that mortalities of neonates coming from eggs laid on non-hosts increases proportionally with the distance to the host. Thus, the tendency of DBM to lay off-target eggs may become an oviposition mistake if such oviposition surfaces are distant from the host plant or if the action of mortality factors is enhanced away from the host or both. It implies then that the cultivars that condition the pest to elicit more of this tendency may potentially be better at warding off the pest than the others. The un-answered question is whether these plants are evolving to produce novel anti-oviposition chemicals that warrant a behavioural site selection change in mitigation.

In this trial, cabbages had significantly more percent off-target eggs compared to Collard Georgia and "Thousand headed" in the choice experiment whereas "Green Challenger" and "Collard Georgia" had a higher percent off-target eggs in the no-choice test. Thus within cabbages the cultivar "Green Challenger" had the highest mean off-target egg count in the no-choice test and was among the highest in the choice test although this was not significantly different from the other cabbages.

5.2 Effect of crucifer cultivars on oviposition and larval survival of *Plutella xylostella* in the greenhouse and on damage indices

More eggs were oviposited on “Blue Dynasty” than was on “Gloria”. However, a higher larval load was observed on “Green Challenger” than on the other test cultivars followed by “Blue Dynasty” and “Collard Georgia”. On the other hand “Riana” had the lowest larval survival. No significant difference was observed on pupal load between cultivars.

The differences in laboratory and greenhouse results may be due to the disparity in pest stages and populations used at the start of the two experiments. While in the greenhouse trial, monitoring started from eggs, which were quite variable, the laboratory trial was conducted with a uniform number of 1st instar larvae. However the divergences in oviposition and survival values did not translate to a similar pattern in damage scores. For example DBM on “Blue Dynasty”, “Green Challenger” and “Collard Georgia” required double larval load that was on “Gloria” and “Copenhagen Market” to realize similar or comparable damage on the crop. Leaves of Collard Georgias have been observed to suffer more damage by DBM than the leaves of cabbages in a previous study (Mitchell *et al* 1997) and this may be attributed in part to thin wax crystals as observed in this study. It is also possible that the crystals contained lower levels of n-alkanoic acids that induce larvae to palpate and similarly lower levels of n-alkan-1-ol appropriate for biting. Eigenbrode and Jetter (2002) observed that there were quantitative rather than qualitative differences on epicuticular wax (wax crystals on the leaf cuticule) constituents on crucifers with different wax blooms. The mentioned EW attributes cause pest arrestment leading to reduction in walking and enhanced feeding. It is also likely that more energy expended on walking by the pest reduces available energy directed to feeding and its general development hence slow growth.

Besides, crowding of larvae as observed on “Green Challenger” due to a higher larval load, might condition individual DBM to a slower growth rate and smaller moth sizes (Myers *et al* 1997). The moths produced under such density related stresses as crowding and reduced availability of quality food also experience delayed sexual maturation (McDonald and Cole, 1991) due to poor ovarian development (Castelo Branco and Gatehouse, 1999). This may impact negatively on the reproduction rate of the subsequent

population generation. The cultivar “Green Challenger” realized the lowest net reproductive rate in laboratory life table studies devoid of crowding implying some intrinsic factors were involved.

No cultivar seemed to interfere with egg hatchability as observed on oviposition and survivorship figures in the greenhouse trial. However, higher survivorship on “Collard Georgia” and “Green Challenger” relative to the oviposited eggs confirms that indeed some eggs were laid off the plant (Soil or pot surface) hence not captured in the records. This is in agreement with the laboratory results where cultivar “Green Challenger” had high percent off-target eggs whereas “Collard Georgia” had among the highest off-target egg counts.

5.3 Effect of crucifer cultivars on larvae to pupae and pupae to adult development of *Plutella xylostella* in the laboratory and greenhouse

The larval survival and subsequently pupation of DBM especially on the cultivar “Gloria” are far below what has been reported under comparable conditions in this laboratory (Löhr and Gathu, 2002). The reason for the difference may partly be due to the manner the test plants were raised. These plants were grown in the open where they were exposed to ambient ultraviolet radiation. This radiation is known to alter the quantity and chemical composition of leaf wax deposits (Tevini and Steinmuller, 1987; Barnes *et al*, 1996; Kakani *et al.*, 2003). The other test plants are conventionally raised in the greenhouse where perhaps the level of this radiation is different and hence results in a change in food quality. Besides, resistance of glossy Brassica genotypes to establishment by 1st instar larvae is reportedly not expressed when the plants are grown in the greenhouse (Eigenbrode *et al*. 1995)

On both “Gloria” and “Collard Georgia” cultivars, DBM had a shorter larval development time, which was significantly different from “Riana”, “Green Challenger” and “Thousand Headed”. Consequently, “Blue dynasty” and “Riana” enabled a better larval survival than the other test cultivars while “Green Challenger offered the leas survival chance. The latter results were confirmed under greenhouse trial.

Feeny (1976) argued that a longer duration of host availability affords parasitoids and predators more opportunities to attack. Eigenbrode *et al*. (1990) also observed that

resistance to *P. xylostella* is primarily due to reduced larval survival. Thus “Riana”, “Green Challenger” and “Thousand Headed” would predispose the pest to predation and parasitisation due to longer larval development time than “Gloria” and “Collard Georgia” In addition, “Green Challenger” seems to induce an extra stress to the pest as observed on thin and emaciated larvae, lowered pupal weights and subsequently prolonged pupal period. As a consequence, the low larvae to pupae development of DBM on “Green Challenger” relative to the other cultivars in all laboratory and green house studies except one and in the life table studies points to the contribution of some intrinsic factors towards mortality. Out of four elaborate tests on egg to larvae and larvae to puoae development, only one green house test showed Green Challenger as superior substrate for survivorship of the DBM neonates. This could be attributed to the mix up in gustatory and volatile crucifer blends.

Eigenbrode *et al*. (1990) revealed that antibiosis or non-preference on normal bloom cultivars could be caused in part by polar ethanol-extractible compounds in normal bloom cultivars. Renwick and Huang (1994) underscored the importance that a balance between chemical deterrents and attractants intrinsic to host plants posed to the general behaviour of insects. He, however, indicated that this balance could be tipped in either direction based on factors extrinsic to the host plant. Perhaps this kind of balance is varied in the test plants used in this study and may favour “Green Challenger” against the DBM pest.

5.4 Effect of crucifer cultivars on adult longevity and fecundity of DBM in the laboratory

Both food quality and amounts that are ingested by larvae influence resource allocation to reproduction by a pest in the subsequent generation (Awmack and Leather, 2002). This may explain the positive correlation between pupal weight and reproduction as observed in this trial. Besides, the pheromone that is emitted by the females and males is a function of the food quality ingested by larvae (Landolt and Phillips, 1997). In this trial, therefore, the cultivars “Thousand Headed” and “Collard Georgia” would seem to be poorer hosts for the pest than are “Riana”, “Gloria” and “Copenhagen Market” by virtue of lower longevity of adults raised from them. In addition, adult females raised on “Blue Dynasty” and “Green Challenger” lived much shorter. In spite of this, it is only

DBM reared on “Green Challenger” and “Copenhagen Market” in the laboratory whose females produced less eggs implying that female longevity may not necessarily translate to improved fecundity by DBM.

Earlier postulates indicate that egg development in DBM ovarioles starting from oocytes is subject to some internal inhibition factors (Hillyer and Thorteinson, 1971). These factors allow egg maturation to take place in the DBM adult only once some threshold level of eggs in the ovariole (30 or fewer) is attained.

The role of the tested cultivars in influencing the stringency of this inhibition is not clear. However, it may seem that some of the cultivars as “Green Challenger” and “Copenhagen Market” may have induced an increase in the pre-reproductive phase (PRP), which is the time period between adult emergence and the onset of egg production. In addition they may have lowered egg maturation rate during the reproductive phase (RP), that is, the period from onset of egg production to the end of it. The two latter scenarios would compromise reproductive success more as evidenced in the laboratory trials on the two cultivars “Green Challenger” and “Copenhagen Market” leading to low fecundity of adult pest raised on them. An elongated PRP and a lowered egg maturation rate are believed to induce abortion of the terminal oocytes in the ovarioles to pave way for the sub-terminal ones in the developmental sequence, a process that is repetitive ((Hillyer and Thorteinson, 1971). Consequently, there is low egg production due to massive abortions.

The workers also adduced that PRP and RP are mediated by sensory stimuli from host plants implying that the test cultivars may have had differential influence on egg development. However, attributes of food quality in this case are not limited to nutrition alone but may include the relative proportions of chemical attractants and repellants.

5.5 Life table construction

Two important population growth parameters, the net reproductive rate (Ro) and the intrinsic rate of population increase (Rm) have been used extensively as pointers to a depressed or increased growth of *P. xylostella* population (Sivapragasam *et al*, 1988; Wakisaka *et al.*, 1992, Salas *et al.,* 1993; Syed and Abro, 2003). The DBM on cultivar “Green Challenger” had a lower net reproductive rate compared to those on other

cultivars in the present study. Similarly, DBM on this cultivar showed a significantly lower intrinsic rate of population increase compared to the others except “Riana” and “Collard Georgia”. As a consequence, “Green Challenger” had a lower doubling time.

Although differences in life table parameters of DBM may arise due to many factors including the number of copulations (Wang *et al*., 2005) and synchrony between male and female development time (Hillyer and Thorsteinson, 1971), Environmental factors and host plant play a significant role (Wakisaka *et al.*, 1992; Shelton *et al.*, 1991).

Crucifer host plant leaves differ intra- and inter-specifically on wax load and density of crystalline wax structures. Lower levels of both wax attributes have been shown to reduce survival of DBM (Eigenbrode and Espelie 1995; Justus *et al.*, 2000). Eigenbrode and Pillai (1998) observed that waxes on glossy Crucifers have higher concentrations of four n-alkane-1-ols or a mixture of α and β amyrins compared to the non-glossy ones. The workers further indicated that these wax attributes not only decreased the number and time of neonate DBM biting the plant but also increased their walking time.

It is possible that different types and levels of allellochemicals were present in the test cultivars as evidenced in the varied shapes of wax crystals. Shapes of wax crystals are determined by their chemical composition, which may be a predominant chemical component (Jetter and Riederer, 1994, 1995) or a minor one (Meusel *et al*., 1999). This might explain the varied responses to growth, development and reproduction of the pest in the test cultivars that mainly pits “Green Challenger” against the pest. However, it may be difficult to make meaningful inference from wax shapes alone since the role of either the major or minor wax chemical component on the biology of the pest needs to be assessed further.

The relative contribution of larger inter-crystal spaces in reducing the adhesiveness of the pest to the plant cannot be ignored. This wax attribute was more conspicuous on “Green Challenger” cultivar than others and might explain in part the low levels of life table parameters Ro and r_m. Both Generation time (T) and Fecundity data had a positive influence on the intrinsic rate of population increase in a linear model implying that the two factors could be used to explain the latter. However, the relationships were not significant hence a general linear model appears inept at evaluating the role of these factors in the general population dynamics of DBM pest.

5.6 Effect of crucifer cultivars on parasitism of *Plutella xylostella* by *Diadegma semiclausum* in the greenhouse

Diamondback moth larvae on "Thousand Headed" appeared more disturbed in the presence of parasitoids as evidenced in higher percent larval mortalities. Momanyi *et al*. (2006) observed that the mere presence of parasitoid enhanced DBM mortality and attributed this to their constant disturbance by the parasitoid. This is indeed an important attribute in pest control systems involving parasitoids.

However, less parasitoid numbers were recruited in the subsequent generation in this tritrophic set up involving "Thousand Headed", DBM and *D. semiclausum*, which might reduce the sustainability of the pest control option. "Thousand Headed" is one of the cultivars on which DBM had the slowest growth rates in laboratory trial, an important aspect in host plant resistance. That it should support less parasitoid development presents a mild clash between biological control and host plant resistance.

Food stress experienced by the wondering larvae in the presence of parasitoid might have caused the mortalities of DBM larvae and subsequently, in case of parasitism, extended such stresses to the developing parasitoid. This cultivar had the least inter-crystal diameters; high crystal density of rods and rodlets and together with Riana had the lowest inter-crystal spaces.

The behaviour of DBM larvae is such that it would violently wriggle and suspend on its silken thread upon provocation. On kales it is possible that this behaviour initiated a process where either the silken thread or its suspended larvae detached from the plant thereby severing a faster link back or perhaps the thin, rod like EW crystals easily detached or broke thus severing the pest-plant link. Kimura (1987) observed that waxes detach with eggs as a result of precipitation while Markstadler *et al*. (2000) indicated that thin EW crystal threads break and can detach with even an insects leg. Whether this tritrophic experience with Kale as the host plant would slow the establishment of introduced parasitoid in predominantly kale growing areas is not clear but seems plausible.

A body of evidence exists indicating that high EW density hinders pest adhesion to its host (Stork, 1980a; Stoner, 1990; Eigenbrode *et al*, 2000) and also hinders a predator attachment to the host plant occupied by its prey (Eigenbrode and Jetter, 2002). However,

as explored by the latter author the wetting agent employed by the pest and EW chemistry additionally influence pest attachment or adhesion to host plants. A predator, *Hippodamia convergens* Gue'rin-Me'neville, is thought to employ a hydrophilic wetting agent to better its adhesion on less acidic (n-alkanoic acid) and more alcoholic (n-alkan-1-ol) substratum of EW surface of glossy crucifers (Eigenbrode and Jetter, 2002). Holloway *et al*., (1977) observed that acids had larger contact angles, were less wettable hence could not spread well on thin surfaces as opposed to water or other hydrophilic substances like alcohol. It might be fair to assume a converse mechanism for diamondback moth as a basis for discrimination against glossy genotypes. Thus, the wetting agent employed by DBM could be one that spreads well on the acidic surfaces of waxy genotypes but hydrophobic to n-alkan-1-ol since DBM prefers waxy crucifer genotypes that normally have higher acid levels.

On the other hand, the cultivar "Blue Dynasty" seemed suitable for DBM development and reproduction in greenhouse studies. However, high *D. semiclausum* numbers were recorded on it. This might imply that the odour blends emanating from its damaged parts were comparatively more attractive to the parasitoid (Bukovinszky *et al*., 2005).

5.7 Scanning electron microscopy (SEM) study of the leaf surfaces of the crucifer cultivars

All test cultivars with the exception of "Blue Dynasty" had a heterogeneous arrangement of wax crystals suggestive of diffused pores as a mechanism of their secretion (Whitecross and Armstrong, 1995). Both cultivars "Green Challenger" and "Blue Dynasty" had wider gaps between their crystals and crystal aggregates respectively than all other test cultivars (Table 6).

Markstadler *et al*. (2000) argued hypothetically that gaps between wax crystals contain air spaces, which diminish the action of suction cup that should otherwise enable insects to attach effectively on leaves and other plant parts. Wider gaps would therefore harbor more air spaces reducing the effective attachment and foraging ability of herbivores. This may explain in part the reduction of larval survival (Table 1, Table 3 and Fig 4.2) on "Green Challenger" thereby lending support to this hypothesis. However,

DBM on the cultivar “Blue Dynasty” had a fairly better survival. The aggregation of its wax crystals, which, minimizes inter-crystal spaces but maximizes gaps between aggregates seems a plausible reason. This aggregation also makes it realize a high crystal density as observed in this trial.

Subtle divergences observed on the conspicuousness of wax crystals may imply that there existed variations on the levels of single lipid classes on the various test cultivars. Gultz *et al*. (1992) observed that crystallization of waxes takes place when concentration of single lipid class is at least 40% of the total wax constituents. The waxes on the cultivar “Collard Georgia” had thin crystal platelets (reduced conspicuousness) spread on the leaf surface with no clearly defined boundaries (Plate 1b). This may suggest single lipid concentrations just above threshold levels.

Whatever the blend of inherent chemicals on its waxes, “Collard Georgia” encouraged the pest to lay a higher proportion of its eggs on the leaves rather than on foreign surfaces under choice test. The role of transversely ridged rodlets, unique to this cultivar, in enhancing this scenario is not clear. Similarly, the cultivar “Thousand Headed”, with its significantly smaller crystals elicited more egg laying on the leaf and leaf parts than on other surfaces in the no choice test. Conversely, the prominent and large crystals as found on “Green Challenger” instead elicited more oviposition on surfaces other than the leaf and other plant parts. The damage scores on the various test cultivars show no difference in damage caused by the pest on them (Table 2).

The crystallite densities obtained on our test cultivars (150-306) are below what was recorded on the normal bloom (817) and above that on glossy (88.8) cultivars used by Eigenbrode and Shelton (1990).

CHAPTER SIX
CONCLUSION AND RECOMMENDATION

6.1 Conclusion

Two cultivars “Collard Georgia” and “Thousand Headed” have shown comparatively better attraction to DBM moth for oviposition than other tested cultivars. On the other hand, most of the oviposition results in the laboratory and greenhouse have indicated that headed cabbage cultivars and more particularly “Green Challenger” condition the pest to lay a good percent of its eggs away from the plant than the leafy ones.

None of the tested cultivars in their current state (without genetic manipulations) qualifies as good candidates for either tolerance or resistance against the diamondback moth pest contrary to the claims of the seed companies involved in their manufacture. Besides, survivorship of DBM on different cultivars indicates that those cultivars with higher inter-crystal spaces realize a lower net reproductive rate as well as low intrinsic rate of population increase. The plausible reason is the divergences on pest attachment to the plant caused by this wax attribute. The subtle variances on life-table parameters of the DBM pest on the test cultivars indicate that host plant resistance attributes is displayed also on non-glossy varieties.

Fecundity of female DBM adults seem to be independent of their longevity since on the cultivars “Green Challenger” and “Blue Dynasty”, a long duration of stay still resulted in low fecundity.

The cultivar “Thousand Headed” seems to expose the DBM developing larvae to food stress and early mortalities in the presence of *D. semiclausum.* Thus more larvae die or are lost on “Thousand Headed” due to a more indirect effect of parasitoid disturbance. While this may favour pest control by reducing pest population, the other implication is that less parasitoid are recruited or required in the subsequent generation.

6.2 Recommendation

In summation, the cultivars “Collard Georgia” and “Thousand Headed” can be used as trap crops against the pest in an intercrop situation where they are not the main crops. This may help to distract the pest from laying eggs on the main cabbage crop. Moreover,

since cultivars like “Green Challenger”, “Gloria” and “Copenhagen Market” consistently condition the pest to lay eggs away from the plant, such cultural practices as earthing-up or flooding may be useful in enhancing mortalities of the pest away from the crop. In addition, the factors involved in this repulsion should be investigated and identified with the hope of exploiting this IPM component.

Exploratory study of wax ultra-structure and chemistry in other cultivars not tested in this work may be a faster and less tedious way of screening large number of test plants for host plant resistance against this pest. This study should, however, incorporate inter-crystal spaces since earlier studies have always ignored this important aspect. Consequently, it would be interesting to subject the various test cultivars to sprinkler/overhead irrigation if the differences in inter-crystal wax spaces can enhance mortalities on cultivars with higher spaces.

An IPM that involves an intercrop of either “Thousand Headed” or “Collard Georgia” in cabbage fields and an introduction of the exotic parasitoid *D. semiclausum* should be tried to enhance DBM mortalities. However, the cropping system should ensure that parasitoid introduction is efficient and sustainable to reduce costs associated with their re-introduction.

REFERENCES

Abbas, M. S. T. 1988 [*]. Biological and ecological studies on *Diadegma semiclausum* Hellen (Hymenoptera: Ichneumonidae), a larval parasite of the diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae) in Egypt. Anz. Schadlingskde., Pflanzenschutze, and Umweltschutz 61: 1-2.

Aeschlimann, J. P. 1979. Sampling methods and construction of life tables for *Sitona humeralis* populations (Col: Curculionidae) in Mediterranean climatic areas. *Journal of Applied Entomology,* 16: 405-415.

Agerbirk, N., Olsen, C. E and Nielsen, J. K. 2001. Seasonal variation in leaf glucosinolates and insect resistance in two types of *Barbarea vulgaris* ssp. *Arcuata, Phytochemistry*, 58: 91-100.

Agerbirk, N., Olsen, C. E., Bibby, B. M., Frandsen, H. O., Brown, L. D., Nielsen, J. K. and Renwick, J. A. A. 2003. A saponin correlated with variable resistance of *Barbarea vulgaris* to the Diamondback moth *Plutella xylostella*. *Journal of Chemical Ecology*, 29:1417- 1433.

Akol, A. M., Sithanantham, S., Njagi, P. G. N., Varela, A. and Mueke, J. M. 2002. Relative safety of sprays of two neem insecticides to *Diadegma mollipla* (Holmgren) a parasitoid of diamondback moth: effects on adult longevity and foraging behaviour. *Crop Protection*, 21: 853-859.

Ampong, N. Kreddy, K. V. S and Saxena, K, N. 1994[*]. *Chilo partellus* (Swinhoe) (Lep: Pyralidae) Oviposition in non hosts: a mechanism for reduced pest incidence in intercropping, *Acta Oecologia*, 15: 469-475.

Andrahennadi, R. and Gillot, C. 1998. Resistance of brassica, especially *Brassica juncea* (L.) Czern genotypes to the diamondback moth, *Plutella xylostella* (L), *Crop Protection*, 17: 85-94.

Ankersmit, G. W. 1953[*]. DDT resistance in *Plutella maculipenis* (Curt.) (Lepidoptera) in Java, Bulletin of Entomological Research 44: 421-425.

Anstey, T. H. and Moore J. F. 1949[*]. Inheritance of glossy foliage and cream petals in green sprouting broccoli. *Journal Hered*, 45: 39-41.

AVRDC. 1985. 1984. Progress Report. Asian Vegetable Research and Development Center, Shanhua, Taiwan.

AVRDC. Asian Vegetable Research and Development Center, 1988. Progress Report. Shanhua, Taiwan, 540 pp

AVRDC. Asian Vegetable Research and Development Center. 1987. Progress Report Summaries, 1986, Shanhua, Taiwan, 94 pp.

Awmack, C. S. and Leather, S. R. 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, 47: 817-844.

Ayalew, G. 2003. Population ecology of diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae) and its parasitoids in Ethiopia, PhD Thesis Kenyatta University, Ruiru, Kenya, 160 pp.

Ayalew, G. 2006. Comparison of yield loss on cabbage from diamondback moth, *Plutella xylostella* L. using two insecticides, *Crop Protection* 25(9): 915-919.

Azidah, A. A., Fitton, M. G. and 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.

Badenes-Perez, F. R., Shelton, A. M. and Nault, B. A. 2004. Evaluating trap crops for diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), *Journal of Economic Entomology*, 97: 1365-72.

Barker, A. M. and Maczka, C. J. M. 1996[*]. The relationship between host selection and subsequent larval performance in three free living graminivorous sawflies, *Journal of Ecological Entomology*, 21: 317-327

Barnes, P. W., Ballare, C. L and Caldwell, M. M 1996. Photomorphogenic effects of UV- B radiation on plants: consequences for light competition. *Journal of Plant Physiology*, 148: 15-20.

Bauer, M. E., Kaya, H. K. and Thurston, G. S. 1995[*]. Factors affecting entomopathogenic nematode infection of *Plutella xylostella* on a leaf surface, *Entomologia Experimentalis et Applicata*, 77: 239-250.

Bauer, M. E., Kaya, H. K., Tabashnik, B. E. and Chicutt C. F. 1998. Suppression of diamondback moth (Lepidoptera: Plutellidae) with an entomopathogenic nematode (Rhabditida: Steirnernematidae) and *Bacillus thuringiensis*. Berliner. *Journal of Economic Entomology*, 91: 1089-1095.

Bukovinszky, T., Gols, R., Posthumus, M. A., Vet, L. E. M and van Lenteren, J. C. 2005. Variation in plant volatiles and attraction of the parasitoid *Diadegma semiclausum* (Hellen*), Journal of Chemical Ecology* 31: 461-480.

Buranday, R. P. and Raros, R. S. 1973[*]. Effects of cabbage-tomato intercropping on the incidence and oviposition of the diamondback moth *Plutella xylostella* L. *Philippines Entomologist* 2: 369-374.

Carl, K. 1992[*]**.** Potential for biological control in IPM for vegetable production in africa Pp 203-212 In: Traboulsi, R. (ed.) Proceedings of the regional workshop on the development and application of integrated pest management for vegetable production in Africa, 20-23 November 1992, Dakar, Senegal.

Carter, D. J. 1984. Pest Lepidoptera of Europe with special reference to the British Isles, *Series Entomologia*, 31: 81-83.

Castelo Branco, M and Gatehouse, A. G. 1999. Insecticide resistance in *Plutella xylostella* (Lepidoptera: Yponomeutidae) in the Federal District, Brazil. An. Soc. *Entomol. Brasil*, 26:75-79.

Chapman, J. W., Reynolds, D. R., Smith, A. D., Riley, J. R., Pedgley, D. E. and Woiwod, I. P. 2002. High altitude migration of the diamondback moth *Plutella xylostella* to the U. K.: a study using radar, aerial netting, and ground trapping. *Journal of Ecological Entomology*, 27: 641-650.

Charleston, D. S. and Kfir, R. 2000. The possibility of using indian mustard, *Brassica juncea*, as a trap crop for the diamondback moth, *Plutella xylostella*, in South Africa. *Crop Protection*, 19 (2000) 455-460

Chelliah, S. and Srinivasan, K. 1986[*]**.** Bioecology and management of the diamondback moth in India pp 63-76 61 In: Talekar and Griggs (eds.) Diamondback moth: Proc. 1st Int. Workshop. Shanhua, Taiwan: Asian Vegetable Research and Development Center 471 pp.

Cherry, A. J., Mercadier, G., Meikle, W., Castelo-Blanco, M. and Schroer, S. 2004a[*]**.** The role of entomopathogens in DBM biological control In: Kirk, A. A., Bordat, D. Editors. Improving biocontrol of *Plutella xylostella*. Proceedings of International Symposium, 21-24 October 2002. Montpellier, France. Pp 51-70.

Cherry, A. J., Osae, M. and Djegui, D. 2004b[*]. Relative potency, yield and transmission of a Kenyan isolate of *Plutella xylostella* Granulovirus in a population of diamondback moth from Benin, West Africa. In: Kirk, A. A, Bordat, D. editors. Improving biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. Pp: 158-162.

Cortesero, A. M. and Lewis, W. J. 2000. Understanding and manipulating plant attributes to enhance biological control. *Biological Control*, 17:35-49.

Courtney, S. P, 1982. Co-evolution of pierid butterflies and their cruciferous food plants. V. Habitat selection, community structure and speciation. *Oecologia*, 54: 101-107.

Couty, A., **van Emden, H., Perry, J. N., Hardie, J. I. M., Pickett, J. A. and Lester, J. W. 2006.** The roles of olfaction and vision in host plant finding by the diamondback moth, *Plutella xylostella*. *Physiological Entomology*, 31(2): 134-145.

Deevey, E. S, 1947[*]. Life tables for natural populations of animals, Quarterly Rev. Biology 22: 283-314.

Delvare, G. 2004. The taxonomic status and role of hymenoptera in biological control of DBM, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) In: Kirk, A. A., Bordat, D. editors. Improving biocontrol of *Plutella xylostella*. Proceedings of International Symposium, 21-24 October 2002. Montpellier, France. pp 51-70.

Dennill, G. B. and Pretorius W. L 1995. The status of diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae), and its parasitoids in cabbages in South Africa, *African Entomology*, 3 (1): 65-71.

Dicke, M. 1996. Crop plants affect biological control agents: prospects for breeding for host plant resistance. Bulletin I. O. B. C/ W. P. R. S. 19 (5): 72-80.

Dickson, M. H. and Eckenrode, C. J. 1975. Variation in *Brassica oleracea* resistance to cabbage looper and imported cabbage worm in the green house and field. *Journal of Economic Entomology*, 68: 757-760.

Dickson, M. H. and Eckenrode, C. J. 1980. Breeding for resistance in cabbage and cauliflower to cabbage looper, imported cabbage worm and diamondback moth, *Journal of American Society of Horticultural Science*, 105: 782-785.

Dickson, M. H., Eckenrode, C. J. and Lin, J. 1986. Breeding for diamondback moth resistance in *Brassica oleracea* In: Talekar, N. S., Griggs, T. D. (editors). Diamondback Moth Management, Proceedings of the First International Workshop, Asian Vegetable Research and Development Center, Shanhua, Taiwan, Pp 137-143.

Dosdall, L. M., Clayton, G. W., Harker, K. N., O'Donovan, J. T. and Stevenson, F. C, 2004. The effect of soil fertility and other agronomic factors on infestations of root maggots in canola, *Agronomy Journal*, 96: 1306-1313.

Eckenrode C. J., Dickson. M. H. and Lin J. 1986. Resistance in crucifers to diamondback moth and other lepidopterous pests In: Talekar, N. S and Griggs, T. D. (editors). Diamondback moth management Proceedings of the First International Workshop Asian Vegetable Research and Development Center, Shanhua, Taiwan 129-136.

Eigenbrode, S. D. and Espelie, K. E. 1995. Effects of plant epicuticular lipids on insect herbivores, *Annual Review of Entomology*, 40:171-194.

Eigenbrode, S. D. and Jetter, R. 2002. Attachment to plant surface waxes by an Insect predator. *Integrative and Comparative Biology*, 42: 1091-1099.

Eigenbrode, S. D. and Pillai, S. K. 1998. Neonate *Plutella xylostella* responses to surface wax components of a resistant cabbage (*Brassica oleracea*). *Journal Of Chemical Ecology*, 24: 1611-1627.

Eigenbrode, S. D. and Shelton, A. M. 1990. Behaviour of neonate diamondback moth larvae on glossy leaved resistant *Brassica oleracea* L. *Journal of Economic Entomology*, 19: 1566- 1571.

Eigenbrode, S. D., Kabalo, N. N. and Rutledge, C. E. 2000[*]. Potential of Reduced waxbloom oilseed Brassica for insect pest resistance. *Journal of Agricultural and Urban Entomology*, 17: 53-63.

Eigenbrode, S. D., Shelton, A. M. and Dickson, M. H. 1990. Two types of resistance to the diamondback moth (Lepidoptera: Plutellidae) in Cabbage, *Environmental Entomology*, 19(4): 1086-1090.

Eigenbrode, S. D., Stoner, S. D., Shelton, A. M. and Kain, W. C. 1991. Charateristics of leaf waxes of *Brassica oleracea* associated with resistance to diamondback moth. *Journal of Economic Entomology*. 83: 1609- 1618.

Eigenbrode, S. D; Moody, S. and Castagnola, T. 1995[*]. Predators mediate host plant resistance to a phytophagous insect in cabbage with glossy leaf. *Entomologia Experimentalis et Applicata*, 77; 335-342.

Ensign, J. C; Bowen, D. J; Tenor, J. L; Ciche, T. A; Petell, J. K; Strickland, J. A; Orr, G. L; Fatig, R. O; Bintrim, S. B. and French-Constant, R. H 2002[*]. Proteins from the Genus *Xenorhabdus nematophila* are toxic to insects on oral exposure, US patent, No. 0147148 A1

Facknath, S. 1997. Study of botanical pesticides in Mauritius. Proceedings of Expert Group Meeting on Risk Reduction on Agrochemical Development in the Afro-Arab Region Dec. 1996, Mauritius.

Farrar, R. R. Jr. and Ridway, R. L. 1999[*]**.** Relative potency of selected nuclear polyhedrosis viruses against five species of lepidoptera. *Journal of Agricultural and Urban Entomology*, 47: 501-533.

Feeny, P. P. 1976[*]**.** Plant apparency and chemical defense. *Recent Advances in Phytochemistry*, 10: 1-40.

Ferré, J. and van Rie, J. 2002. Biochemistry and genetics of insect resistance to *Bacillus thuringiensis*, *Annual Review of Entomology*, 47: 501-533.

Food and Agriculture Organization of the United Nations, 2003. FAO Production Yearbook.

Fox, L. R and Eisenbach, J. 1992. Contrary choices: possible exploitation of enemy free space by herbivorous insects in cultivated vs. wild crucifers. *Oecologia*, 89: 574-579.

Furlong, M. J. and Wright, D. J. 1994. Examination of stability of resistance and cross-resistance patterns to acylurea insect growth-regulators in-field populations of the

diamondback moth, *Plutella-xylostella*, from Malaysia. *Pesticide Science* 42: 315-326.

Gathu, R. K., Lohr, B. and Poehling, H. M. 2007. Effect of cultivated and wild crucifers on performance of diamondback moth *Plutella xylostella* L. (Lepidoptera: Plutellidae), in Kenya. In press.

Glare, T. R. and OCallaghan, M. 2000. *Bacillus thuringiensis*: Biology, Ecology and Safety. UK: John Wiley and Sons, Ltd. 350 p.

Goolaub, A. 1995[*]. Study of *Bacillus thuringiensis* formulation for the control of some important lepidopteran pests of agriculture. Bsc thesis: Reduit University. In: Facknath, S. 1997. Study of botanical pesticides in Mauritius, Proceedings of Expert Group Meeting on Risk Reduction on Agrochemical Development in the Afro- Arab Region Dec. 1996, Mauritius

Graves, S. D. and Shapiro, A. M, 2003[*]**.** Exotics as host plants of the California butterfly fauna. *Biological Conservation*, 110: 413-433.

Groot, A. T. and Dicke, M. 2002. Insect transgenic plants in a multitrophic context. The Plant Journal, 31: 387-406.

Grzywacz, D., Parnell, M., Kibata, G., Oduor, G., Ogutu, W., Miano, D. and Winstanley, D. 2004[*]**.** The development of endemic Baculoviruses of *Plutella xylostella* (diamondback moth, DBM) for control of DBM in East Africa In: Endersby, N. M., Ridland, P.M, (editors). The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne. Melbourne, Australia: Department of Natural Resources and Environment. Pp 271-280.

Gültz, P-G., Muller, E. and Schmitz, K. 1992. Chemical composition and surface structures of epicuticular leaf waxes of *Ginkgo biloba*, *Magnolia grandiflora* and *Liriodendron tulipifera*. *Zeitschrift für Naturforschung*, 47:516–526.

Gupta, P. D. and Thorteinson, A. J. 1960. Food plant relationship of the diamondback moth (*Plutella maculipennis* (Curt.). I. Gustation and olfaction in relation to botanical specification of larva. *Entomoligia Experimentalis et Applicata*. (3): 241-250.

Hamilton, A. J., Endersby, N. M., Ridland, P. M., Zangh, J. and Neal, M. 2005. Effects of cultivar on oviposition preference, larval feeding and development time of diamondback moth *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), of some *Brassica oleracea* vegetables in Victoria. *Australian Journal of Entomology*, 44: 284-287.

Harcourt, D. G 1969. The development of life tables in the study of natural insect populations. Annual Review of Entomology 14: 175-191.

Harcourt, D. G. 1954. The biology and ecology of diamondback moth, *Plutella maculipennis*, Curtis, in Eastern Ontario. PhD. thesis. Cornell Univ., Ithaca N. Y. 107 pp.

Harcourt, D. G. 1957. Biology of the diamondback moth, *Plutella maculipennis* Curtis (Lepidoptera: Plutellidae) in Eastern Ontario Life History, Behaviour and Host Relationship. *Canadian Entomologist*, 89: 554-564.

Harcourt, D. G. 1986. Population dynamics of the diamondback moth in Southern Ontario In: Talekar NS, Editor. Diamondback moth and other Crucifer Pests Proceedings of the First International workshop, 11-15 March 1985 Tainan, Taiwan: AVRDC. Pp 3-16.

Hardy, J. E. 1938. *Plutella maculipennis* Curt. Its natural and biological control in England. Bulletin of Entomological Research, 29: 343-372.

Heckel, D. G., Gahan, L. J., Liu, Y. B. and Tabashnik, B. E. 1999[*]. Genetic mapping of resistance to *Bacillus thuringiensis* toxins in diamondback moth using biphasic linkage analysis**.** Proceedings of the National Academy of Sciences of the United States of America 96**:** 8373-8377.

Herren, H. and Lohr, B. 2001. International Center of Insect Physiology and Ecology (ICIPE). Pesticide Outlook, 12, 192-194

Hillyer, R. J. and Thorsteinson, A. J, 1971. The influence of the host plant or males on programming of oviposition in the diamondback moth, *Plutella maculipennis* (Curt.) lepidoptera, *Canadian Journal of Zoology*, 49: 983-989.

Ho, T.H. 1965. The life history and control of the diamondback moth. Bulletin of Division of Agriculture, Malaysia No. 118, 26 pp.

Hogg, D. B. and Chen, S. Y. 1988. On estimating uncertainty in insect population growth rates obtained from life table experiments. In: Proceedings of the XVIII International Congress of Entomology July 3-9, 1988, Vancouver, BC, Canada. 195 pp.

Hokkanen, H. M. T. 1997*. Role of biological control and transgenic crops in reducing use of chemical pesticides for crop protection. In: Pimentel, D (Ed), Techniques for reducing pesticide use. Economic and environmental benefits, Wiley Chi Chester, pp 103-128.

Holloway, P. J., Hunt, G. M., Baker, E. A. and Macey, M. J. K. 1977. Chemical composition and ultrastructure of the epicuticular wax in four mutants of Pisum sativum. *Chemical Physiology of Lipids*, 20: 141-155.

Honda, K. 1992 Hibernation and migration of the diamondback moth in north Japan 168: 43-50.

ICIPE, 1997. International Center of Insect Physiology and Ecology. Annual Report, 1997.

Inglis, G. D., Goettel, M. S., Butt, T. M. and Strasser, H. 2001*. Use of hyphomycetous fungi for managing insect pests. In: Butt, T. M, Jackson, C. W. and Magan, N, editors. Fungi as biocontrol agents: Progress, Problems and Potential. Wallingford: CABI Publishing. pp 23-69.

Jetter, R. and Riederer, M. 1994. Epicuticular crystals of nonacosan- 10 – ol: *in vitro* reconstitution and factors influencing crystal habits. *Planta*, 195: 257-270.

Jetter, R. and Riederer, M. 1995. *in vitro* reconstitution of epicuticular wax crystals: formation of tubular aggregates by long chain secondary alkendiols. *Botanica acta*, 108: 111-120.

Justus, K., Dosdall, M. L. and Mitchell, B. K. 2000. Oviposition by *Plutella xylostella* (Lepidoptera: Plutellidae) and effects on phylloplane waxiness. *Journal of Economic Entomology*, 92: 1153-1159.

Kadir, H. B. A., Payne, C. C., Crook N. E., Fenlon, J. S. and Winstanley, D. 1999. The comparative susceptibility of the diamondback moth, *Plutella xylostella* and some other Lepidopteran pests of Brassica crops to a range of Baculoviruses. *Biocontrol Science and Technology*, 9: 421-433.

Kakani, V. G., Reddy, K. R., Zhao, D. and Mohammed, A. R. 2003. Effects of ultraviolet-B radiation on cotton (*Gossypium hirsutum* L.) morphology and anatomy. *Annals of Botany*, 91: 817-826.

Kfir, R. 1998. Origin of the diamondback moth (Lepidoptera: Plutellidae). *Annals of the Entomological Society of America*, 91: 164-167.

Kfir, R. and Thomas, J. 2001. Biological control of diamondback moth in the Island of St Hellena. Biocontrol News and Information, 22: 76N.

Kibata, G. N. 1996. Diamondback moth *Plutella xylostella* L. (Lepidoptera: Yponomeutidae), a problem pest of Brassica crops in Kenya In: Farrel, G. and Kibata, G.N. (editors). Proceedings of the First Biennial Crop Protection Conference 27-28 March 1996, Nairobi, Kenya, pp 1-11.

Kimura, K. 1987. What is the rainfall for crops? Noubunkyou, Tokyo, 197 p.

Kirk, A. A., Mercadier, G., Bordat, D., Delvare, G., Pichon, A., Arvanitakis, L., Goudegnon, A. E. and Rincon, C. 2004. Variability in *Plutella* and its natural enemies: implications for biological control. In: Endersby, N. M., Ridland, P.M. editors. The Management of Diamondback moth and other Crucifer Pests, Proceedings of the fourth International Workshop 26-29 November 2001 Melbourne, Melbourne, Australia: Department of Natural Resources and Environment. pp 71-77.

Ko, L.T. and Fang, J. L. 1979. Studies on the biology of the diamondback moth, *Plutella xylostella* L.: life history, annual generations and temperature relations. *Acta Entomologia Sinica*, 22: 310-319.

Kobori, Y. and Amano, H. 2003. Effect of rainfall on a population of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Applied Entomology and Zoology*. 38 (2): 249-253.

Koenig, K., Deogracias, L. and Amend, J. 1993. Mass Rearing and Utilization of *Diadegma semiclausum*, Philippine-German Biological Plant Protection Project, Department of Agriculture, Manila, Philippines

Landolt, P. J. and Phillips, T. W. 1997. Host plant influences on sex pheromone behavior of phytophagous insects. *Annual Review of Entomology*, 42: 371-391.

Larsson, S. and Ekbom, B. 1995[*]. Oviposition mistakes in herbivorous insects: confusion or a step towards a new host plant? *Oikos*, 79:155-160.

Li, Q., Eigenbrode, S., Stringham, G. and Thiagarajah, M. 2000. Feeding and growth of *Plutella xylostella* and *Spodoptera eridania* on *Brassica juncea* with varying glucosinolate concentrations and myrosinase activities. *Journal of Chemical Ecology*, 26:2401-2419.

Lim, G. S. 1992. Integrated pest management of diamondback moth: practical realities. Pp 565-576. In: Talekar, N. S. (editor). Management of diamondback moth and other crucifer pests: Proceedings of the Second International Workshop. Shanhua, Taiwan: AVRDC, pp. 565-576.

Lim, G. S., Sivapragasam, A. and Ruwaida, M. 1986. Impact assessment of *Apenteles plutallae* on diamondback moth using the insecticide check method Pp 195-204 In: Talekar, N. S. and Griggs, T.D. (editor). Diamondback moth Management: Proceedings of the First International Workshop. Shanhua, Taiwan: AVRDC**,** pp. 159-171.

Lin, J., Dickson, M. H. and Eckenrode, C. J. 1984. Resistance of Brassica lines to the diamondback moth (Lepidoptera: Yponomeutidae) in the field, and inheritance of resistance. *Journal of Economic Entomology*, 77: 1293-1296.

Lin, J., Eckenrode, C. J. and Dickson, M. H. 1983. Variation in *Brassica oleracea* resistance to diamondback moth (Lepidoptera: Plutellidae). *Journal of Economic Entomology* 76: 1423-1427.

Liu, S. S., Chen, F. Z. and Zalucki, M. P. 2002. Development and survival of the diamondback moth (Lepidoptera: Plutellidae) at constant and alternating temperatures. *Environmental Entomology*, 31: 221-231.

Liu, S. S., Wang, X. G., Guo, S. J. and He, J. 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.

Löhr, B., and Gathu, R. 2002. Evidence of adaptation of diamondback moth, Plutella xylostella (L.), to pea, Pisum sativum L. *Insect Science and Application*. 22: 161–173.

Löhr, B., and Kfir, R. 2002. Diamondback moth, *Plutella xylostella* L. in Africa. A review with emphasis on biological control. In: Improving Biocontrol of Plutella xylostella, Proceedings of the International Symposium. Montepellier, France.

Lu, L., He, Y., Feng, X. and Chen, H., 2004[*]. Impact of granulosis virus on larval food consumption and development duration of the diamondback moth, *Plutella xylostella* (L) In: Endersby, N. M., Ridland, P. M (editors). The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne. Melbourne, Australia: Department of Natural Resources and Environment. Pp 281-283.

Macharia, I., Löhr, B. and 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.

Madumadu, G. G., Sikinyi, E. O. and Mwamba, D. K. 1991. Vegetables for domestic and export markets. Proceedings of Review Workshop on National Horticultural Research Programme. Thika, Kenya 1991 pp. 41-63.

Magaro, J. J. and Edelson J, V. 1990[*]. Diamondback moth (Lepidoptera: Plutellidae) in south Texas: technique for resistance monitoring in the field. *Journal of Economic Entomology*, 83: 1201-06.

Mahar, A. Munir, .,; Elawad, S., Gowen, S. R. and Hague, N. G. M. 2006. Microbial control of diamondback moth, *Plutella xylostella* L. (Lepidoptera: Yponomeutidae) Using bacteria (*Xenorhabdus nematophila*) and its metabolites from the entomopathogenic nematode *Steinernema carpocapsae*. *Journal of Zhejiang University Science*, 5(10): 1183-1190.

Maia, A. H. N., Luiz, A. J. B. and Campanhola, C. 2002. Statistical inference on associated fertility life table parameters using jackknife technique: Computational aspects. *Journal of Economic Entomology*, 93(2): 511-518.

Marazzi, C. 2003. Plant sulphur nutrition influencing host-plant selection and performance of insect herbivores. PhD thesis. Basel University. Basel, Switzerland. 56 pp.

Markstädler, C., Federle, W., Jetter, R., Riederer, M. and Hölldobler, B. 2000. Chemical composition of the slippery epicuticular wax blooms in Macaranga (Euphorbiaceae) ant-plants. *Chemoecology*, 10: 33-40.

Mayhew, P. J. 1997[*]. Adaptive patterns of host plant selection by phytophagous insects. Oikos, 79: 417-428.

McDonald, G. and Cole, P.G. 1991[*]. Factors influencing oocyte development in *Mythimna convecta* (Lepidoptera:Noctuidae) and their possible impact on migration in eastern Australia. Bulletin Entomological Research, 81:175-184.

Megallona, E. D. 1986. Developments in diamondback moth management in the Philippines In: Talekar, N. S. and Griggs, T. D. (editors). Diamondback moth management. Proceedings of the 1st International Workshop. Shanhua, Taiwan: AVRDC. pp 423-436.

Messenger, P. S. 1964. Use of life tables in a bioclimatic study of an experimental aphid-braconid wasp host parasite system. *Ecology*, 45: 119-131.

Meusel, I., Neinhuis, C;., Markstädter, C. and Barthlott, W. 1999. Ultrastructure, chemical composition, and re-crystallization of epicuticular waxes: transversely ridged rodlets. *Canadian Journal of Botany*, 77: 706-720.

Meyer, J. S., Igersoll, C. G., MacDonald, L. L. and Boyce, M. S. 1986. Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. *Ecology*, 67:1156-1166.

Mitchell, E. R., Hu G. Y. and Okine, J. S. 1997. Diamondback moth (Lepidoptera: Plutellidae) infestation and parasitism by *Diadegma insulare* (Hymenoptera: Ichneumonidae) in Collard Georgias and adjacent cabbage fields. *Florida Entomologist*, 80(1): 54-62.

Mohan, M. and Gujar, G. T. 2003. Larval variation in susceptibility of the diamondback moth, *Plutella xylostella* (Linneaus) to insecticides and detoxification enzymes. *Crop Protection*, 22: 495-504.

Momanyi, C., Löhr, B. and Gitonga, L. 2006. Biological impact of the exotic parasitoid *Diadegma semiclausum* (Hellen), of diamondback moth, *Plutella xylostella* (L.), in Kenya. *Biological Control*, 38 (2): 254-263.

Mota-Sanchez, D., Bills, P. S. and Whalon, M. E. 200.2 Arthropod resistance to pesticides: status and overview. In: Pesticides in agriculture and the environment. Wheeler, W. B. (Editor). New York: Marcel Dekker, 241-272.

Mustafa, G. 1992. Role of parasitoid complex in limiting the population of diamondback moth in Moldavia, Romania. In: Talekar, N.S. (editor). Management of diamondback moth and other crucifer pests. Proceeding of the Second International Workshop. Shanhua, Taiwan: AVRDC. Pp 203-221

Myers, J. H., Boettner, G. and Elkinston, J. 1997. Maternal effects on Gypsy moth: only sex ratios vary with population density. *Ecology*: 79(1): 305-314.

Nakahara, L. M., McHugh, J., Otsuka, C. K., Funusaki, G. Y. and Lai, P. Y 1986[*]. Integrated control of diamondback moth and other insect pests using an overhead sprinkler system, an insecticide and biological control agents in watercress farm in Hawaii. In: Talekar, N. S and Griggs, T. D. (editor). Proceedings of the First International Workshop on Diamondback moth Management, Shanhua, Taiwan: AVRDC. 1985. Pp. 403-413.

Nayar, J. K. and Thorsteinson, A. J. 1963. Further investigations into the chemical basis of the insect-host plant relationship in an oligophagous insect *Plutella maculipennis* Curtis (Lepidoptera: Plutellidae). *Canadian Journal of Zoology*, 41: 923-29.

Nel, A., Krause, M., Ramautar, N. and van Zyl, K. 1999. A guide for the control of plant pests. National Department of Agriculture, Republic of South Africa, 38th Edition, 220 pp.

Nemoto, H., Sekijima, Y. and Shibukawa, S. 1985[*]. Application of an immunological method for the identification of predators of diamondback moth *Plutella xylostella* (Lepidoptera: Yponomeutidae) in cabbage fields: evaluation of the precipitation reaction especially the micro-ouchterlony method. *Japan Journal of Applied Entomology and Zoology*, 29: 61-66.

Ninsin, K. D. 2004. Acetamiprid resistance and cross-resistance in the diamondback moth *Plutella xylostella*. *Pest Management Science*, 60: 839-841.

Noda, T; Miyai, S; Takashino, K. and Nakamura, A. 2000. Density suppression of *Plutella xylostella* (Lepidoptera: Plutellidae) by multiple releases of *Diadegma*

semiclausum (Hymenoptera: Ichneumonidae) in cabbage fields in Iwate, Northern *Japan. Applied Entomology and Zoology*, 35: 557-563.

Nyambo, B. and Pekke, A. 1995. Brassica Planning workshop for Eastern and southern Region, Lilongwe-Malawi, 15-18 May 1995. GTZ IPM Horticulture, Nairobi.

Nylin, S. and Janz, N. 2000. Butterfly host plant choice in the face of possible confusion, *Journal of Insect Behaviour*, 13: 469-482.

Oduor, G. I., Löhr, B. and Seif, A. A. 1996. Seasonality of major cabbage pests and incidence of their natural enemies in central Kenya In: Sivapragasam, A., Loke, W. H., Hussan, A. K. & Lim, G. S (Editors). The management of diamondback moth and other crucifer pests. Proceedings of the Third International Workshop, 29 October - 1 November 1996, Kuala Lumpur, Malaysia, Malaysian Agricultural Research and Development Institute (MARDI), pp. 37–43.

Ohara, Y; Takafuji, A and Takabayshi, J. 2003. Response of host infested plants in females of *Diadegma semiclausum* Hellen (Hymenoptera: Ichneumonidae). *Applied Entomology and Zoology*, 38: 157-162.

Ooi, P. A. C. 1981*. Microbial Control of the Diamondback moth in the Cameron Highlands in Malaysia. *Malays. Appl. Biol*. 10: 49-56

Ooi, P. A. C. 1992. Role of parasitoids in managing diamondback moth in the Cameron highlands, Malaysia. In: Talekar, N. S. (editor). Diamondback moth and other crucifer pests: Proceedings of the Second International Workshop. Tainan, Taiwan. 10-14 Dec. 1990, pp 255-262.

Poelking, A. 1992. Diamondback moth in the Philippines and its control with Diadegma semiclausum. In N. S. Talekar (ed.). Diamondback moth and other crucifer pests. Proceedings of the second International workshop. Tainan, Taiwan, 10-14 December.

Ramachandran, S., Buntin, G. D. and All, J. N. 2000. Response of canola to simulated diamondback moth (Lepidoptera: Plutellidae) defoliation at different growth stages. *Canadian Journal of Plant Science*, 80:639-646.

Ratzka, A., Vogel, H. and Kliebenstein, D. L. 2002. Disarming the mustard oil bomb. Proceedings of the National Academy of Sciences USA, 99:11223-11228.

Reed, D. W., Pivnick, K. and Underhill, E. W. 1989. Identification of chemical oviposition stimulants for the diamondback moth, *Plutella xylostella* present in three species of Brassicaceae. *Entomological Experimentalis et Applicata*, 53: 227-286.

Renwick, J. A. A. and Chew, F. S. 1994. Oviposition in Lepidoptera. *Annual Review of Entomology* 39: 377-400.

Renwick, J. A. and Huang, X. 1994*. Interacting chemical stimuli mediating oviposition by Lepidoptera. In: N Ananthakrishan, (editor). Functional dynamics of phytophagous insects. Oxford and IBH publishing Co., New Delhi, pp. 79-94.

Renwick, J. A. A., Radke, C. D. and Sachdev-Gupta, K. S., 1992. Leaf surface chemicals stimulating oviposition by Pieris rapae (Lepidoptera: Pieridae) on cabbage. *Chemoecology* (Historical Archives) 3: 33-38.

Robert, H., Verkerk, J. and Wright, D. J. 1996. Multitrophic interactions and management of the diamondback moth: a review. Bulletin of Entomological Research, 86: 205-216.

Rossbach, A., Lohr, B. and Vidal, S. 2006. Does a specialist parasitoid adapt to its host on a new host plant? *Journal of Insect Behaviour*, 18(4), 491-493.

Said, M. and Itulya, F. M. 2003. Intercropping and nitrogen management effects on diamondback moth damage and yield of Collard Georgias in the highlands of Kenya. *African Crop Science Journal*, 11 (1): 35-42.

Salas, M. D., Mendoza, B., Salazar, E. and Rivera, B. M. 1993[*]. Supervivencia y reproduction de la Palomilla Dorso de Diamante en Cruciferas. *Turrialba*, 43: 242-246.

Salinas, P. J. 1986. Studies of diamondback moth in Venezuela with reference to other Latin-American countries In: Talekar, N. S, and Griggs, T. D (editors). Diamondback moth Management: Proceedings of First International Workshop. Shanhua, Taiwan. AVRDC, pp 17-24.

Sarfraz, M. 2004. Interaction between diamondback moth and *Bacillus thuringiensis*. Outlooks on Pest Management, 15: 167-171.

Sarfraz, M., Dosdall, L. M. and Keddie, B. A. 2005. Spinosad: a promising tool for integrated pest management. Outlooks on Pest Management, 16: 78-84.

SAS Institute. 1999. SAS/STAT. The SAS system for Windows, Version 8.0 SAS Institute, Cary, NC.

Sastrosiswojo, S. and Sastrodihardjo, S. 1986. Status of biological control of diamondback moth by introduction of parasitoid *Diadegma eucerophaga* in Indonesia. In: N. S. Talekar and T. D. Griggs (Editor). Diamondback moth management. Proceedings of the First International Workshop. Shanhua, Taiwan. AVRDC, pp185-194.

Saucke, H., Doyi, F. and Schmutterer, H. 2000*. Biological and integrated control of *Plutella xylostella* (Lepidoptera: Yponomeutidae) and *Crocidolomia pavonana* (Lepidoptera: Pyralidae) in Brassica crops in Papua New Guinea. *Biocontrol Science and Technology*, 5: 595-600.

Sayyed, A. H., Omar, D. and Wright, D. J. 2004*. Genetics of spinosad resistance in a multi-resistant field selected population of *Plutella xylostella*. *Pesticide Management Science,* 60: 827-832.

Schmutterer, H. 1995. The Neem tree: source of unique natural products for integrated pest management, medicine, industry and other purposes. New York: VCR publishers Inc., 695 pp.

Schmutterer, H. 1997. Side effects of neem (*Azadirachta indica*) products on insect pathogens and natural enemies of spider mites and insects. *Journal Applied Entomology*, 121: 121-128.

Schroer, S., Sulistyanto, D. and Ehlers, R. U. 2005. Control of *Plutella xylostella* using polymer-formulated *Steinernema carpocapsae* and *Bacillus thuringiensis* in cabbage fields. *Journal Applied Entomology*, 129 (4): 198-204.

Schuler, T. H. and van Emden, H. F. 2000. Resistant cabbage cultivars change the susceptibility of *Plutella xylostella* to *Bacillus thuringiensis*. *Agricultural and Forest Entomology*, 2: 33-38.

Seif, A. A and Lohr, B. 1998. Brassica Planning Meeting for Eastern and Southern Africa Region, Icipe, Duduville, Nairobi, Kenya. 12- 22 May. GTZ- IPM Horticulture, Nairobi

Shelton, A. M. 2004*. Management of the diamondback moth: déjà vu all over again? In: Endersby NM, Ridland PM, (editors). Management of the diamondback moth and

other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne. Melbourne, Australia, pp 3-8.

Shelton, A. M. and Badenes-Perez, F. R. 2006. Concepts and application of trap cropping in pest management. *Annual Review of Entomology*, 51: 285-308.

Shelton, A. M. and Nault, B. A. 2004. Dead-end trap cropping: a technique to improve management of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Crop Protection*. 23: 497- 503.

Shelton, A. M. and Wyman, J. A. 1992. Insecticide resistance of diamondback moth in North America In: Talekar, N. S. (editor) 1992. Management of Diamondback moth and other crucifer pests. Proceeding of the Second International Workshop, Shanhua, Taiwan: AVRDC pp 447-54.

Shelton, A. M; Cooley, R. J; Croening, M. K; Wilsey, W. T. and Eigenbrode, S. D. 1991. Comparative analysis of two rearing procedures for diamondback moth (Lepidoptera: Plutellidae). *Journal of Entomological Science*, 26: 17-26.

Sivapragasam, A., Ito, Y. and Saito, T. 1988. Population fluctuation of the diamondback moth, *Plutella xylostella* (L) on cabbage in *Bacillus thuringiensis* sprayed and non sprayed plots and factors affecting within- generation survival of immatures. *Research in Population Ecology*, 30: 329-342.

Southwood, T. R. E. 1978. The construction, description and analysis of age specific life tables, ecological methods with particular reference to the study of insect population. 2nd Edition, Chapman and Hall, London, UK. Pp 356-385.

Spencer, J. L., Pillai, S. and Bernays, E. A. 1999. Synergism in the Oviposition Behaviour of *Plutella xylostella*: Sinigrin and Wax Compounds. *Journal of Insect Behaviour*, 12: 483-499.

Stefanescu, C., Jubany, J. and Dantart, J, 2006. Egg laying by the butterfly *Iphiclides podalirius* (Lepidoptera: Papilionidae) on alien plants: a broadening of host range or oviposition mistake.*Animal Biodiversity and Conservation*, 29(1): 83-90.

Stoner, K. A. 1990. Glossy leaf wax and plant resistance to insects in *Brassica oleracea* under natural infestation. *Environmental Entomology*, 19: 730-739.

Stork, N. E. 1980a[*].. Environmental analysis of adhesion of chrysopolina polita (Chrysomelidae: Coleoptera) on a variety of surfaces. *Journal of Experimental Biology*. 88: 91-107.

Sun, C. N. 1992. Insecticide resistance in diamondback moth. In: Talekar, N. S (Editor). Diamondback moth and other crucifer pests. Proceedings of the second International Workshop, Tainan, Taiwan. 10-14 Dec. 1990: Asian Vegetable Research and Development Center. Pp 419-426.

Syed, T. S. and Abro, G. H. 2003. Effect of Brassica vegetable hosts on biology and life table parameters of *Plutella xylostella* under laboratory conditions. Pakistani *Journal of Biological Sciences*, 6 (22): 1891-1896.

Tabashnik, B. E; Finson, N; Johnson, M. W. and Moar, W. J. 1993[*]. Resistance to toxins from *Bacillus thuringiensis* subsp. *Kurstaki* causes minimal cross-resistance to *B. thuringiensis* subsp. *Aizawai* in diamondback moth (Lepidoptera: Plutellidae). *Applied and Environmental Microbiology*, 59:1332-1335.

Talekar, N. S. 1992. Introduction of *Diadegma semiclausum* for the control of diamondback moth in Taiwan. In Talekar, N. S. (editor). Diamondback moth and other crucifer pests: Proceedings of the second International Workshop, Tainan, Taiwan. 10-14 Dec. 1990, pp 263-270.

Talekar, N. S. and Shelton, A. M. 1993. Biology, ecology and management of the diamondback moth**.** *Annual Review of Entomology*, 38: 275-301.

Talekar, N. S. and Yang, J. C. 1991. Characteristic of parasitism of Diamondback moth by two larval parasites. *Entomophaga*, 36: 95-104.

Talekar, N. S., Liu, S., Chen, C. and Yiin, Y. 1994. Characteristics of oviposition of diamondback moth (Lepidoptera: Yponomeutidae) on cabbage. *Zoological Studies*, 33:72-77.

Talekar, N. S., Su, F. C. and Lin, M. Y. 2003. How to produce safer, leafy vegetables in net houses and net tunnels, Asian Vegetable Research Development Center, Shanhua, Tainan, Taiwan. 18 pp.

Tarumoto, I. 2005. Glossiness of leaf blades of sorghum (Sorghum bicolor L. Moench): its visual and ultrastructural studies. JARQ, 39 (3): 153-160.

Terry, I; Bradley, J. P. R. and van Duyn, J. W 1989. Establishment of early instar *Heliothis zea* on soybeans. *Entomologia Experimentalis et Applicata,* 51: 233-240.

Tevini, M and Steinmuller, D. 1987. Influence of light, UV-B radiation and herbicides on wax biosynthesis of cucumber seedlings. *Journal of Plant Physiology*, 131: 111-121.

Theunissen, J. and Ouden, H. D. 1987*. Tolerance levels and sequential sampling tables for supervised control in cabbage crops. Mitteilungen der Schweizer *Entomologischen Gesellschaft*, 60: 243-248.

Thomas, W. P. and Ferguson, A. M. 1989*. *Plutella xylostella* (L.), Diamondback moth (Lepidoptera: Ypnomeutidae). In: Technical communication institute of biological control, Wallingford, Oxon, UK, 10: 135-142.

Thompson, J. N. and Pellmyr, O. 1991. Evolution of oviposition behavior and host preference in Lepidoptera. *Annual Review of Entomology*, 36: 65-89.

Toepfer, S. and Kuhlmann, U. 2006. Constructing lifetables for the invasive maize pest *Diabrotica vigifera vigifera* (Col.; Chrysomelidae) in Europe. *Journal of Applied Entomology*, 130(4), 193-205.

Uematsu, H. and Sakanoshita, A, 1989. Possible role of cabbage leaf waxbloom in suppressing diamondback moth *Plutella xylostella* (Lepidoptera: Yponomeutidae) oviposition. *Applied Entomology and Zoology*, 24: 253-257.

Ulmer, B., Gillot, C., Woods, D, and Erlandson, M. 2002. Diamondback moth, *Plutella xylostella* (L) Feeding and Oviposition Preferences on glossy and waxy *Brassica rapa* (L) Lines. *Crop Protection*, 21: 327-331.

Vandenberg, J. D., Shelton, A. M., Wise, W. T. and Ramos, M. 1998*. Assessment of *Beauveria bassiana* sprays for control of diamondback moth (Lepidoptera: Plutellidae) on crucifers. *Journal of Economic Entomology*, 91. 3: 624-630.

Varela, A. M., Seif, A. A. and Löhr, B. 2003. A guide to IPM in brassica production in Eastern and Southern Africa, ICIPE Science Press Publication.

Vattanatangum, A. 1988*. Country review paper: Thailand. Informal Expert Consultation on IPM on Major Vegetable crops in Asia, 14-16 Nov 1988, RPA (FAO), Bangkok, 5p.

Verkerk, R. H. J. and Wright, D. J, 1994a. Interactions between the diamondback moth *Plutella xylostella* L. and glasshouse and outdoor-grown cabbages. *Annals of Applied Biology*, 125: 477-488.

Verkerk, R. H. J. and Wright, D. J. 1994b. The potential for induced extrinsic host plant resistance in IRM strategies targeting the diamondback moth. In: Proceedings of the Brighton Crop Protection Conference. Pests and Diseases - 1994. Farnham, British Crop Protection Council, pp 457-462.

Verkerk, R. H. J. and Wright, D. J. 1996. Common cabbage resistance mechanisms against the diamondback moth: still an open book? *Annals of Applied Biology*, 128:571-577.

Verkerk, R. H. J., Leather, S. R. and Wright, D. J. 1998. The potential for manipulating crop pest natural enemy interactions for improved insect pest management. Bulletin of Entomological Research, 88: 493-501.

Vickers, R. A., Furlong, M. J., White, A. and Pell, J. K. 2004*. Initiation of fungal epizootics in diamondback moth populations within a large field cage: proof of concept of auto-dissemination. *Entomologia Experimentalis et Applicata* 111: 7-17.

Vogel, H., Kroymann, J., Ratzka, A. and Mitchell-Olds, T. 2004*. Coping with glucosinolates: disarming the mustard oil bomb. In: Endersby, N. M., Ridland P. M. (Editors). Proceedings of the Fourth International Workshop on the Management of Diamondback moth and other Crucifer Pests, 15-26 November 2001, Melbourne. Melbourne, Australia: Department of Natural Resources and Environment, pp 159.

Vu, V. M. 1988*. Country Review Paper, Vietnam Informal Expert Consultation on IPM in Major Vegetable Crops in Asia, 14- 16 November, 1988 RAPA (FAO), Bangkok, 11 pp.

Wakisaka, S., Tsukuda, R. and Nakasuji, F, 1992. Effects of natural enemies, rainfall, and temperature and host plants on survival and reproduction of the diamondback moth. In: Talekar, N. S (editor). Diamondback moth and other crucifer pests. Proceedings of the second International Workshop, Tainan, Taiwan. 10-14 Dec. 1990: Asian Vegetable Research and Development Center, 15-26.

Wang, X. 2002. Patch Exploitation by the parasitoid of *Plutella xylostella*: from individual behavior to population dynamics. *Australian Journal of Entomology*, 41(3): 282-284.

Wang, X. G. and Keller, M. A. 2002. A comparison of host-searching efficiency of two larval parasitoids of *Plutella xylostella*. *Ecological Entomology*, 27: 104-115.

Wang, X. P., Fang, Y. L. and Zhang, Z. N. 2005. Effect of male and female multiple mating on the fecundity, fertility and longevity of diamondback moth, *Plutella xylostella* (L.). *Journal of Economic Entomology*, 129(1): 39-42.

Wang, X; Duff, J., Keller, M. A., Zalucki, M. P. Liu, S. and Bailey, P. 2004. Role of *Diadegma semiclausum* (Hymenoptera: Ichneumoidae) in controlling *Plutella, xylostella* (Lepidoptera, Plutellidae): cage exclusion experiments and direct observation. *Biocontrol*, 14 (6): 571-586.

Waterhouse, D. F. and Norris, K. R. 1987*. Biological control - Pacific prospects. Melbourne, Australia: Inkata Press.

Wemin, J. and Wesis, P. 2004. Evaluation of four insecticides as part of an integrated pest management strategy for diamondback moth *Plutella xylostella* L. in the highlands of Papua New Guinea. In: Price (Editor). Pest and disease incursions: risks, threats and management in Papua New Guinea. Pp 49-56.

Wermelinger, B; Oertli, J. J. and Baumgartner, J. 1991*. Environmental factors affecting the life tables of *Tetranichus urticae* (Acari: Tetranychidae) III host plant nutrition. *Experimental and Applied Acarology*, 12: 259-274.

Whitecross, M. I. and Armstrong, D. J. 1995. Environmental effects on epicuticular waxes of *Brassica napus* (L.). *Australian Journal of Botany*, 20(1): 87-95.

Wilding, N. 1986. The pathogens of diamondback moth and their potential for its control: a review. In: N. S. Talekar and T. D. Griggs (Editors). Diamondback moth management. Proceedings of the First International Workshop. Shanhua, Taiwan. AVRDC. Pp 219-232.

Yang, G., Wiseman, B. R., Espelie, B. R. and Isenhour, D. J. 1993. Effects of corn foliar cuticular lipids on the movement of fall armyworm (Lepidoptera: Noctuidae) neonate larvae. *Florida Entomologist*, 76: 302-316.

Yaseen, M. 1975[*]**.** Biology, seasonal incidence and parasitoids of *Plutella xylostella* (L.) in Trinidad and the introduction of exotic parasitoids into the Lesser Antilles. In: C. W. D. Brathwaite, R. H. Phelpa, F. Bennette (editors). *Crop Protection in the Caribbean*. Trinidad: Univ. West Indies, pp 237-44.

[*] Seen only as abstract