Importance of wild crucifers for diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae) and its parasitoids in Kenya.

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Summary

The aim of the present study was to elucidate the role of wild crucifers on diamondback moth (DBM) *Plutella xylostella* (Lepidoptera: Plutellidae) and its associated parasitoids. The study was conducted in four steps. First, surveys were conducted to study diversity and continuity of wild crucifer species in two highland and two mid-altitude semi arid crucifer growing areas of Kenya. Voucher specimens were prepared from the wild crucifer species collected from the field. DBM larvae and pupae were collected from the wild crucifers, taken to the laboratory and observed for DBM adult or parasitoid emergence. Secondly, the suitability of the wild crucifers for egg-laying, development and reproductive potential of DBM was investigated; and thirdly, the effect of DBM reared on wild crucifers on two introduced, exotic parasitoids, *Diadegma semiclausum* (Hymenoptera: Ichneumonidae) and *Cotesia plutellae* (Hymenoptera: Braconidae), were investigated. Screen house trials were used to investigate oviposition preference and parasitism of *D. semiclausum* and *C. plutellae* on Brassica cultivars and wild crucifer species in free choice situation. Finally, immigration of parasitoids from wild crucifers in the field margins into cultivated fields was investigated using artificially DBM-infested potted cabbage plants in a maize field.

Thirteen species of wild crucifers in nine genera were recorded during the two-year study. They were *Raphanus raphanistrum* L., *Erucastrum arabicum* Fisch & Mey., *Sisymbrium officinale* (L.) Scop., *Crambe kilimandscharica* O.E. Schulz, *Capsella bursa-pastoris* (L.) Medic., *Rorippa nudiuscula* (Sond.) Thell., *Ro. micrantha* (Roth) Jonsell, *Ro. microphylla* (Boenn. ex Rchb) Hyl. ex A. & D. Love, *Lepidium bonariense* L., *Coronopus didymus* (L.) Sm., *Brassica rapa* L., *B. juncea* (L). Szern., and *Brassica* species. *Raphanus raphanistrum* was the most dominant species.

Results show that highland areas had significantly higher species diversity and species richness than mid-altitude semi arid areas. Diamondback moth was recovered from ten of the wild crucifer species. Overall, five larval, one larval-pupal and one pupal parasitoid of DBM were recorded: *Diadegma semiclausum*, *Diadegma mollipla*, *Oomyzus sokolowskii*, *Cotesia plutellae, Itoplectis* sp*., Apanteles* sp. and *Brachymeria* species. *Diadegma semiclausum* was the most dominant species. More DBM were recorded on the cultivated than on the wild crucifers in both areas. Higher parasitoid numbers were recovered from the Brassica cultivars than wild crucifers; however, the relative frequency of *D. mollipla*

was higher on wild crucifers than on cabbage and kale. Mid-altitudes areas had higher parasitoid species diversity but generally lower parasitism rates than highland areas. No hyperparasitoids were recovered from both Brassica and wild crucifer species during the two-year study period. Other pests, predators and diseases common to cultivated crucifers were recorded from the wild crucifers, and diseases were more prevalent during the cold dry season.

Laboratory results reveal that DBM preferred wild crucifer species to cabbage and kale for oviposition. Host plant species affected the development and survival of DBM. Larval period was longest on kale and *R. raphanistrum* (10 days) and shortest on *Ro. micrantha* (8.7 days) while pupal weight was significantly higher on DBM reared on kale. Females were significantly heavier than males in all host plant species. Developmental time varied from 14.4 days on *Ro. micrantha* to 18.3 days on *R. raphanistrum*. Adult longevity ranged between 18.2 days on *R. raphanistrum* and 24.7 days on *Ro. nudiuscula*. Moths reared on *Ro. nudiuscula* exhibited the highest fecundity while those reared on cabbage had the lowest and lived longest (24.6 days). DBM on cabbage had the lowest net reproductive rate (95.1) while on kale and *Ro. nudiuscula* the longest generation time of 31.7 days was recorded. The highest intrinsic rate of increase was calculated on *Ro. micrantha* (0.179) and the lowest on kale (0.147). The results indicate that all species studied are suitable hosts for DBM.

DBM reared on cultivated Brassica cultivars and wild crucifer species were used to study the development, survival and reproductive potential of two exotic parasitoids, *Cotesia plutellae* and *Diadegma semiclausum* in the laboratory. Egg-larval period of *C. plutellae* was shortest on DBM reared from *S. officinale* and longest DBM from *R. raphanistrum* while that of *D. semiclausum* was shortest on DBM from *B. juncea* and longer on individuals from cabbage, *E. arabicum*, *Ro. micrantha* and *Ro. nudiuscula*. The pupal weight was higher and the pupal period was longer for *C. plutellae* and *D. semiclausum* that developed on DBM reared on kale and cabbage. Egg-adult development time of *C. plutellae* was significantly longer on DBM from *R. raphanistrum* and shortest on DBM from *S. officinale* while for *D. semiclausum* it was longest on DBM from *Ro. micrantha* and shortest on DBM from *E. arabicum*. Development time of both parasitoids was similar on DBM from cabbage and kale. Mortality was higher on DBM from wild crucifers than on DBM from Brassica cultivars. In spite of these differences, all wild crucifers are suitable for the development of the two parasitoids.

Cotesia plutellae and *D. semiclausum* preferred to oviposit on DBM on the cultivated Brassica cultivars in free choice oviposition preference test. Mortality of parasitised larvae and pupae was higher on the wild species. In general, *D. semiclausum* was more successful in parasitising larvae on any of the hosts than *C. plutellae.* One of the main reasons was the higher loss of larvae exposed to the latter.

Immigration of parasitoids from wild crucifers in the field margins was studied in a maize field where no crucifers were cultivated within 2 km radius. Wild crucifers recorded in the field margins were *E. arabicum, Lepidium bonariense* and *R. raphanistrum*. Parasitoids recovered from exposed, artificially DBM-infested potted cabbage plants were *D. semiclausum, D. mollipla*, *C. plutellae* and *O. sokolowskii*. *Diadegma semiclausum* accounted for 93% of the total parasitism. *Cotesia plutellae* was the only parasitoid recorded already three days after DBM exposure. *Oomyzus sokolowskii* was recovered from day 9 to day 13 with the highest number being recovered 13 days after DBM exposure. Mean number of *D. mollipla* recovered was similar on all days. Significantly higher number of *D. semiclausum* was recovered 13 days after DBM exposure. Highest number of parasitoids was recovered 13 days after DBM exposure and the lowest at 3 days after exposure. Therefore, we can conclude that wild crucifers act as alternative hosts and provide refugia to both DBM and parasitoids. The early recovery of *C. plutellae* shows that parasitoids will be able recolonise the cultivated crops soon after local extinction through pesticide application or harvesting. Higher parasitism rates were recorded from cabbage plants placed next to the field edges. We suggest there is a benefit to leaving weeds as a resource for the natural enemies that inhabit the ecosystems since they act as alternative hosts and provide refugia to the parasitoids that risk extinction from pesticide application.

Keywords: wild crucifers, diversity, refugia, *Plutella xylostella*, *Diadegma semiclausum*, *Cotesia plutellae*, development, reproductive potential, immigration

Zusammenfassung

Ziel der vorliegenden Studie war es, die Bedeutung wilder Cruciferen-Arten für die Entwicklung von *Plutella xylostella* (Lepidoptera: Plutellidae) und assoziierter Parasitoiden-Arten in Gemüseanbaugebieten Ostafrikas zu untersuchen. Die Untersuchungen erfolgten in vier Schritten: Zuerst wurden Aufnahmen im Feld (surveys) durchgeführt, um die Diversität und Beständigkeit im Auftreten wilder Kruziferen-Arten in jeweils zwei Gemüseanbaugebieten im Hochland bzw. auf mittlerem Höhenniveau in Kenia zu erfassen. Belegexemplare der wilden Kruziferen-Arten wurden gesammelt und präpariert. Von den Wildpflanzen wurden Larven und Puppen von *P. xylostella* gesammelt und im Labor bis zum Schlupf adulter *P. xylostella* oder von Parasitoiden gehalten. Zweitens wurde die Eignung der Wildpflanzen für die Eiablage, Entwicklung und das Reproduktionspotential von *P. xylostella* untersucht und drittens wurde der Einfluß von auf den Wildpflanzen angezogenen *P. xylostella* auf zwei in Ostafrika eingeführte Parasitoiden *Diadegma semiclausum* (Hymenoptera: Ichneumonidae) und *Cotesia plutellae* (Hymenoptera: Braconidae) analysiert. In Netzhäusern wurden Präferenzen für die Eiablage und Parasitierungsraten von *D. semiclausum* and *C. plutellae* an verschiedenen Brassica-Sorten und den wilden Kruziferen in Wahlversuchen ermittelt. Letzlich wurde die Einwanderung von Parasitoiden von wilden Kruziferen aus Feldrändern in mit Mais bestellte Kulturflächen mittels in Töpfen ausgebrachter und mit *P. xylostella* besetzter Kohlpflanzen (Fangpflanzen) ermittelt.

13 Arten wilder Kruziferen aus 9 Gattungen wurden während der zweijährigen Aufnahmen erfaßt. Es handelte sich um *Raphanus raphanistrum* L., *Erucastrum arabicum* Fisch & Mey., *Sisymbrium officinale* (L.) Scop., *Crambe kilimandscharica* O.E. Schulz, *Capsella bursa-pastoris* (L.) Medic., *Rorippa nudiuscula* (Sond.) Thell., *Ro. micrantha* (Roth) Jonsell, *Ro. microphylla* (Boenn. ex Rchb) Hyl. ex A. & D. Love, *Lepidium bonariense* L., *Coronopus didymus* (L.) Sm., *Brassica rapa* L., *B. juncea* (L). Szern., und nicht näher determinierte *Brassica*-Species. *Raphanus raphanistrum* war die dominanteste Art.

In den Hochland-Gebieten fand sich eine signifikant höhere Diversität der Arten im Vergleich zu dem auf mittleren Höhenniveau gelegenen semi-ariden Flächen. *P. xylostell*a wurde auf 10 Wildarten gefunden. Insgesamt fanden sich zudem 5 Arten von Larvalparasitoiden, sowie jeweils eine Art von Parasitoiden, die Larven-Puppen und Puppen allein parasitieren: *Diadegma semiclausum*, *Diadegma mollipla*, *Oomyzus sokolowskii*, *Cotesia plutellae, Itoplectis* sp.*, Apanteles* sp. and *Brachymeria* sp.. *Diadegma semiclausum*

war mit Abstand die dominierende Art. In beiden Anbaugebieten wurden höhere Dichten von *P. xylostella* auf den Kulturpflanzen im Vergleich zu den Wildarten gefunden. Ebenfalls wurden mehr Parasitoide an den Brassica-Kulturen als auf den wilden Kruziferen ermittelt. Auffallend war jedoch, dass *D. mollipla* relativ häufiger auf Wildpflanzen auftrat als an Kopf- und Blattkohl. Gebiete auf dem mittleren Höhenniveau wiesen bei den Parasitoiden eine höhere Artendiversität auf, es fanden sich aber duchgehend geringere Parasitierungsraten als im Hochland. Es konnten keine Hyperparasitoide weder auf den untersuchten beiden Brassica-Arten noch auf den wilden Cruciferen während der gesamten Untersuchungsperiode gefunden werden. Zudem wurden auf den wilden Kruziferen auch für die Kulturarten typische Krankheiten und Schädlinge, sowie deren natürliche Gegenspieler, insbsondere Räuber, angetroffen, mit einem deutlichen höheren Besatz während der kühl-trockenen Jahreszeit.

Laboruntersuchungen ergaben, dass *P. xylostella* die wilden Kruziferen-Arten für die Eiablage bevorzugte im Vergleich zu Kopf- und Blattkohl. Die Art der Wirtspflanze beeinflußte zudem die Entwicklung und die Überlebensrate von *P. xylostella*. Die Larvalphase dauerte am längsten auf Blattkohl und *R. raphanistrum* (10 Tage) und war am kürzesten auf *Ro. micrantha* (8.7 Tage), während die Puppengewichte auf Blattkohl signifikant am höchsten waren. Auf allen Wirtspflanzen waren Weibchen signifikant schwerer als Männchen. Die Entwicklungszeit variierte zwischen 14.4 Tagen auf *Ro. micrantha* und 18.3 Tagen auf *R. raphanistrum*. Die Lebensdauer der Adulten schwankte zwischen 18.2 Tagen auf *R. raphanistrum* und 24.7 Tagen auf *Ro. nudiuscula*. *P. xylostella*, die sich auf *Ro. nudiuscula* entwickelten zeigten die höchste Fruchtbarkeit (Fekundität), während diese bei Individuen von Kopfkohl am geringsten war, die aber wiederum die höchste (24.6 Tage) Überlebensrate aufwiesen. Auf Kopfkohl zeigte *P. xylostella* die geringste Nettoreproduktionsrate (95.1) während auf Blattkohl und *Ro. nudiuscula* die längste Generationszeit von 31.7 Tagen gemessen wurde. Die höchste "intrinsic rate of increase" wurde auf *Ro. micrantha* (0.179) und die geringste auf Blattkohl (0.147) bestimmt. Die Ergebnisse ergaben kein einheitliches Bild in den wirtpflanzenspezifischen Entwicklungsparametern, zeigten aber, dass alle geprüften Pflanzenarten geeignete Wirtspflanzen für *P. xylostella* sein können.

Plutella xylostella gezogen auf Kulturarten von Kohl oder auf Wildarten wurden als Wirte genutzt, um die Entwicklung, Überlebensrate und das reproduktive Potential zweier exotischer, in Ostafrika eingeführter Parasitoiden, *Cotesia plutellae* and *Diadegma*

semiclausum unter Laborbedingungen zu bestimmen. Die Ei-Larven Periode von *C. plutellae* war am kürzesten auf *P. xylostella* von *S. officinale* and am längsten auf Wirtsindividuen von *R. raphanistrum,* während die entsprechende Phase bei *D. semiclausum* am kürzesten auf Wirten von *B. juncea* und am längsten auf solchen von Kopfkohl, *E. arabicum*, *Ro. micrantha* and *Ro. nudiuscula* war. Höhere Puppengewichte und längere Puppenperioden wurden für *C. plutellae* and *D. semiclausum* ermittelt, wenn diese sich auf *P. xylostella* von Kopf- und Blattkohl entwickelten. Die Ei-Larven Periode von *C. plutellae* war significant länger auf *P. xylostella von R. raphanistrum* und am kürzesten auf Wirtslarven von *S. officinale* während für *D. semiclausum* diese Phase am längsten auf *Ro. micrantha* und am kürzensten auf *E. arabicum* dauerte. Die Entwicklungszeit beider Parasitoide war auf *P. xylostella* Larven von Kopf- und Blattkohl gleich. Die Mortalität war höher bei Entwicklung an *P. xylostella* von wilden Kruziferen im Vergleich zu solchen von Brassica-Kulturarten. Offensichtlich sind Wirte von allen geprüften Wildarten der Kruziferen für die Entwicklung der beiden Parasitoide geeignet.

Cotesia plutellae and *D. semiclausum* bevorzugten für die Eiablage Wirtslarven auf Kulturbrassicaceen, wenn ihnen die freie Wirtswahl gegeben wurde. Die Mortalität parasitierter Larven und Puppen war auf den Wildarten höher. Insgesamt zeigte sich *D. semiclausum* als erfolgreicher bei der Parasitierung von Larven von *P. xylostella* auf allen Wirtspflanzen im Vergleich zu *C. plutellae.* Ein möglicher Grund ist die weit höhere Abwanderungsrate von Wirtslarven bei Exposition gegenüber *C. plutellae* und damit ein Entkommen der Parasitierung.

Die Einwanderung von Parasitoiden von wilden Kruziferen aus Feldrändern wurde in einem Maisfeld untersucht, in einem Gebiet, in dem in einem Radius von 2 km keine Kulturkruziferen angebaut wurden. Wildarten in den Feldrändern waren *E. arabicum, Lepidium bonariense* and *R. raphanistrum*. Parasitoide, die aus exponierten *P. xylostella* Larven von künstlich befallenen Kohlpflanzen in Töpfen schlüpften, waren *D. semiclausum, D. mollipla*, *C. plutellae* and *O. sokolowskii*. *D. semiclausum* machte dabei 93% aller gefundenen Parasitoide aus. *C. plutellae* war der einzige Parasitoid, der bereits 3 Tage nach der Exposition der Wirtslarven im Feld gefunden wurde. *O. sokolowskii* wurde zwischen dem 9. und 13. Tag, mit der höchsten Anzahl nach 13 Tagen ermittelt. Die mittleren Anzahlen von *D. mollipla* waren an allen Tagen gleich. Von *D. semiclausum* wurden signifikant mehr Parasitoide 13 Tage nach Exposition der Wirtslarven wiedergefunden. Insgesamt wurde die höchste Zahl an Parasitoiden 13 Tage nach Exposition ermittelt, die

geringste nach 3 Tagen. Das läßt den Schluß zu, dass die wilden Kruziferen als alternative Wirte und als Refugien für *P. xylostella* Parasitoide in Phasen dienen können, in denen keine Kulturkruziferen angebaut werden. Das frühe Auftauchen von *C. plutellae* im Feld zeigt prinzipiell, dass die Parasitoids zu einer schnellen Wiederbesiedlung von Kulturflächen aus Quellhabitaten befähigt sind. Höhere Patrasitierungsraten wurden zudem immer auf Kohlpflanzen nahe der Feldränder beobachtet. Es kann angenommen werden, dass es für die Landwirte vorteilhaft ist, Unkräuter (Wildkräuter) als Ressourcen für natürliche Gegenspieler im Agrarökosystem zu belassen, damit sie als alternative Wirtspflanzen und Refugien dienen können und das Risiko einer Auslöschung der emfindlichen Parasitoide bei Pflanzenschutz- und/oder Kulturmassnahmen reduzieren.

Sichworte: Wilde Kruziferen, Diversität, Refugien, *Plutella xylostella*, *Diadegma semiclausum*, *Cotesia plutellae*, Entwicklung, Reproduktion, Einwanderung aus Feldrändern

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Abbreviations

ANOVA:	Analysis of Variance
ASL:	Above sea level
Bt.	*Bacillus thuringiensis*
CAN:	Calcium Ammonium Nitrate
cv.	Cultivar
DBM:	Diamondback moth
DDT:	Dichlorodiphenyltrichloroethane
df	Degrees of freedom
e^{rm}	Finite rate of increase
F:	Statisitcal F-value
FAO:	Food and Agricultural Organization
Fig:	Figure
G	Generation time
GLM:	General Linear Models
GPS:	Global Positioning System
GV:	Granuloviruses
H´	Diversity index
ICIPE:	International Center of Insect Physiology and Ecology
IGR's:	Insect Growth Regulators
IPM	Integrated Pest Management
ln	Natural logarithm
MoARD:	Ministry of Agriculture and Rural Development
ns	Not significant
NPV:	Nucleopolyhedroviruses
Neemroc EC®:	Neem seed oil (NSO)
Neemros®:	Neem kernel cake powder (NKCP)
P:	Probability value for error level
p_i	Proportion of species
PTM	Potato tuber moth
RH	Relative humidity (%)
r_m	Intrinsic rate of increase
Ro	Net reproductive rate

S	Total number of species
SAS:	Statistical Analysis Systems
SE	Standard error of the mean
SNK:	Students Newman Keuls test
sp.	Species
SQRT:	Square Root Transformation
t:	Statistical t-value
Var	Variance
var.	Variety.

CHAPTER ONE

1 General introduction

Crucifers are among the most important vegetables grown in the eight provinces of Kenya. Rift Valley and Central Provinces are the major production areas and contribute over 82 % of the total national production with an average yield of 13.8 tons per hectare (MoARD, 2000). The main crucifer species grown are head cabbage *Brassica oleracea* L. var. *capitata,* kale *B. oleracea* L. var. *acephala*, chinese cabbage *B. rapa* L. (Lour) var, *pekinensis*, cauliflower *B*. *oleracea* L. var. *botrytis*, rape *B. napus* L., radish *Raphanus sativus* L., and broccoli *B*. *oleracea* L. var. *italica*. Kale is mainly produced for home consumption and local marketing while all other species are produced for the market and traded over considerable distances (Macharia et al., 2005). Crucifer production is a major source of income and contributes to poverty alleviation of women and unemployed youth in peri-urban vegetable producing areas. The crucifers also have great nutritional value and their contribution to the vitamins (A, B complex and C) and minerals (potassium, calcium and iron) in the diet is considerable (Tindall, 1983).

Crucifer production is possible throughout the year in areas with favourable weather conditions or where complementary irrigation is possible. In Kenya, crucifers are grown on small-scale farms ranging from 1/8 to 3 acres together with other crops (Macharia et al., 2005). Type of soils, temperatures and precipitation determine the suitability for cultivation of different vegetables over several agro-ecological zones. Most farmers grow vegetables during the rainy season, while those with irrigation facilities undertake cultivation of cruciferous vegetables throughout the year.

However, continuous production is often constrained by insect pests and diseases. Pests associated with crucifers are the diamondback moth (DBM) *Plutella xylostella* L. (Lepidoptera: Plutellidae), cabbage aphid *Brevicoryne brassicae* (L.), green peach aphid *Myzus persicae* Sulzer, false cabbage aphid or turnip aphid *Lipaphis erysimi* (Kaltenbach) (Homoptera: Aphididae), cabbage looper *Trichoplusia ni* Hubner (Lepidoptera: Noctuidae), cutworm *Agrotis* sp., beet armyworm *Spodoptera exigua* Hubner. (Lepidoptera: Noctuidae), cabbage webworm *Hellula undalis* F. (Lepidoptera: Pyralidae), bagrada bug *Bagrada hilaris* Burmeister (Hemiptera: Anthocoridae) and cabbage moth *Crocidolomia binotalis* Zeller (Lepidoptera: Noctuidae) (Adane-Kassa and Abate, 1995; Nyambo and Pekke, 1995; Oduor et al., 1996; Seif and Löhr, 1998). Bacterial, fungal and

viral diseases affect crucifers and are more prevalent during the cold season. The diseases are either seed borne or soil borne and once introduced into the soils, are difficult to control since most farmers rarely practice crop rotation. Most of the common diseases in Kenya include black rot *Xanthomonas campestris* pv. *campestris* Pammel Dowson, powdery mildew *Erysiphe cruciferarum* Opiz ex L. Junell, downy mildew *Peronospora parasitica* (Pers.) Fr., and angular leaf spot *Alternaria brassicae* (Berk) Sacc., (Varela et al., 2003).

Diamondback moth is the most important pest of cultivated crucifers worldwide (Talekar and Shelton, 1993). It is considered a major pest throughout eastern (Ayalew, 2006) and southern Africa (Kfir, 1998). Its exceptional pest status is due to the diversity and abundance of alternative host plants, disruption of its natural enemies, its high reproductive potential and genetic elasticity facilitating rapid development of resistance to insecticides (Mohan and Gujar, 2003; Vickers et al., 2004; Shelton, 2004). The pest has developed resistance to chemical (Kibata, 1996), bio-pesticides like *Bacillus thuringiensis* Berliner (Bt) (Liu et al., 1995; Tabashnik et al., 2003, Sarfraz, 2004) and insect growth regulators (IGR's) (Kobayashi et al., 1992).

Parasitoids play an important role in natural suppression of DBM in cultivated and wild crucifer ecosystems. Parasitic wasps of the genus *Diadegma* (Hymenoptera: Ichneumonidae) and *Cotesia* (Hymenoptera: Braconidae) are major mortality factors of DBM throughout the world (Mustata, 1992; Ooi, 1992). Surveys were conducted to establish the indigenous natural enemies of DBM in East Africa. Average parasitism did not exceed 10 % with low impact on pest population (Oduor et al., 1996). *Diadegma mollipla* one of the parasitoids recovered is considered relative generalist. The species is reported to be indigenous to eastern and southern Africa. Apart from attacking DBM, it was found on potato tuber moth (PTM) *Pytothorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) on potato in Kenya (Lohr and Rossbach, 2004). The original host of *D. mollipla* is unknown (Azidah et al., 2000) since PTM is an introduced species to Africa. The parasitoid was also recovered from DBM on snowpeas (Lohr and Rossbach, 2004). To complement these indigenous species, a classical biological control programme for management of DBM in Kenya was initiated at the International Centre of Insect Physiology and Ecology (ICIPE) in 2000. *Diadegma semiclausum* Hellén) (Hymenoptera: Ichneumonidae), a larval parasitoid of DBM was imported from Taiwan in 2001 and released in two pilot areas located at Taita Taveta and Kiambu Districts from

July 2002. The parasitoid was selected for release in the highlands because it is reported to have the greatest DBM control potential (Lim, 1986, Talekar and Shelton, 1993), it's the principle regulator of DBM worldwide, host specific with high searching efficiency (Wang and keller, 2002). It was found a better candidate for the highlands, which have similar climatic conditions as that of south East Asia where crucifers are grown. The introduction has been a success in New Zealand, Indonesia, Australia, Malaysia, Taiwan and the Philippines and is expected to control DBM effectively. It has since established remarkably well with upto 60 % parasitism (Momanyi et al., 2006; Löhr et al., 2007). The DBM population also declined significantly from 10 to 2 DBM per plant during the hot dry season (Löhr et al., 2007). In the process most farmers have either stopped spraying or reduced their pesticide spray regime (Macharia et al., 2005; Personnal observation).

In March 2003, *C. plutellae* was imported from South Africa and released in the mid-altitude (>1000m) semi arid areas of Yatta and Athi River in June 2004. The parasitoid was selected for release in Kenya because throughout its range, the bio-type from South Africa appears to be the most abundant and effective. Parasitism of *C. plutellae* was found to be low in other countries (Waterhouse and Norris, 1987) while the species from South Africa accounted for over 90 % overall parasitism (Kfir, 2003; Nofemela and Kfir, 2005). It dominates the parasitoid fauna complex despite competition from other primary parasitoids and presence of hyperparsitoids (Mosaine et al., 2003). It was found to be abundant between low (<500m) and mid altitudes (>1000m) (Kfir, 1997; Waladde et al., 2001; Mosaine et al., 2003). However, *C. plutellae* has not established in the release sites, in Kenya possibly due to stiff competition from *D. semiclausum,* which has recorded upto 80 % parasitism (Löhr et al. unpubl. data) or due to lack of host plant species diversity (Kahuthia-Gathu et al., 2006). Good crop management practices with judicious use of insecticides could increase the effectiveness of parasitoids in controlling DBM.

Besides DBM occurrence on cultivated crucifers, it also occurs on cruciferous weeds; *Raphanus raphanistrum* L., *Capsella bursa-pastoris* (L.) Medic., *Rorippa indica* L., *Lepidium virginicum* L. (Harcourt, 1957), *Nasturtium heterophyllum* BL., *Cardamine hirsuta* L. (Kartosuwondo and Sunjaya, 1991) and *Erucastrum arabicum* Fisch and Mey. (FAO, 1987). Other wild crucifers reported to sustain feeding and reproduction of DBM are *Arabis glabra* (L.) Bernh., *Brassica caulorapha* Pasq., *Brassica napobrassica* Mill., *Bunias orientalis* L., *Cardamine amara* L., *Cardamine pratensis* L., *Cheiranthus cheiri* L., *Conringa orientalis* (L.) Dumort, *Erysimum cheiranthoides* L., *Lepidium perfoliatum*

L., *Sinapsis alba* L., and *Thlaspi arvense* L. (Louda 1986; Crafford and Chown, 1987). In Kenya, DBM was recorded on *R. raphanistrum*, *E. arabicum*, *Crambe kilimandscharica* L., *L. bonariense* L., *Sisymbrium officinale* (L.) Scop., *Rorippa nudiuscula* (Sond.) Thell, *Ro. micrantha* (Roth.) Jonsell and *C. bursa-pastoris* (Kahuthia-Gathu et al., 2006).

The abundance of host plants and the action of natural enemies are two key factors that regulate DBM population (Ooi, 1992, Kfir, 2003). Companion plants play several important roles in this regard. They increase the density of parasitoids by habouring and providing refugia when the host plant is absent (Norris and Kogan, 2005), provide nectar and pollen which increase their reproductive potential, increase longevity and provide the much needed energy for longer flights (Idris and Grafius, 1995; Winkler et al., 2006). This may influence the success of biological control agents thus regulating DBM population densities below the economic threshold. Thus habitat management offers an opportunity to increase the impact of parasitoids.

1.1 Justification and rationale

Crucifer production has been seriously affected by DBM, resulting to indiscriminate use of pesticides. The excessive use of pesticides destroys natural bio-control agents existing in the crop ecosystem leading to even more serious outbreaks of DBM and non-target pests. In consequence, the development and implementation of integrated pest management (IPM) programmes are now considered to be the only solution to combat this highly resistant pest (Zhao et al., 1996). The application of IPM gives natural enemies a chance to reduce pest population below the economic threshold. Given the importance of natural enemies in controlling pest populations, attending to their needs should be of primary concern and their conservation is an important consideration in IPM. This is only possible when a more holistic ecological approach is adopted.

Several studies have shown that increased plant diversity can have a substantial effect on on the density, synchronisation and efficiency of natural enemies in the field (Wratten and Thomas, 1990; Thomas et al., 1991). Wild flowers provide the natural enemies with nectar and pollen, which provide energy sources increasing their effectiveness and longevity (Idris and Grafius, 1996; Norris and Kogan, 2000). Moreover many natural enemies need refugia to escape harsh conditions in the field and to maintain source populations. Refugia adjacent to the field can play important role in recolonisation of

fields after pesticide treatments, crop rotations or tillage (Longley et al., 1997; Landis et al*.,* 2000; Idris and Grafius, 2001; Langhof et al. 2003, Norris and Kogan, 2005).

The wild crucifers; *C. bursa-pastoris*, *R. raphanistrum*, *Crambe kilimandscharica* O. E. Schulz, *Lepidium africanum* (Burm. F.) DC., *L. bonariese* L., *Arabidopsis thaliana* (L.) Heynh., and *E. arabicum* were recorded in Kenya (FAO, 1987). However, their importance in the management of DBM associated natural enemies is unknown. No studies dealing with the diversity and the role of cruciferous weeds on DBM and their associated natural enemies in East Africa have been done thus far. Therefore, understanding the role of wild crucifers to both indigenous and exotic parasitoids is of paramount importance.

Hence the described research on diversity of wild crucifer species in Kenya was undertaken, with the aim to investigate the role wild crucifers play in conserving and providing refugia to DBM and its associated natural enemies. Laboratory trials were conducted to evaluate suitability of selected wild crucifer species on oviposition, survival, development and reproductive potential of DBM and its natural enemies. Parasitism rates of *D. semiclausum* and *C. plutellae* were studied on DBM larvae reared on the crucifer species. These studies will help in understanding the role wild crucifers play in conserving and providing natural enemy populations in the absence of brassica crops or after local extinction of natural enemies through inevitable pesticide application. Thus, it will help in redesigning of agro-ecosystems to keep and even to enhance the regulation potential (conservation biocontrol) of natural enemies (Tscharntke and Kruess, 1999; Rauwald and Ives, 2001; Steffan-Dewenter et al., 2001; Bengtsson et al., 2003). This exploration of multifunction agricultural biodiversity is an important future research theme in sustainable agriculture.

CHAPTER TWO

2 Literature review

2.1 Diamondback moth *Plutella xylostella*

2.1.1 Origin and distribution of diamondback moth

The diamondback moth, *Plutella xylostella* L., also referred to by the synonym *Plutella maculipennis* (Curt.), belongs to the family Plutellidae, order Lepidoptera. It is an important pest of both cultivated and wild crucifer plants worldwide (Talekar and Shelton, 1993). It is believed to have originated from the Mediterranean region (Harcourt, 1954), which is the origin of some of the most important crucifers (Tsunoda, 1980). However, Kfir (1998) suggested its origin to be South Africa due to the rich fauna of indigenous parasitoids of DBM in the Cape Province indicating a very long association between the pests and the parasitoids. This is also supported by large number of wild crucifers (175 species, of which 32 are exotic) in the region (Jordaan, 1993). Using the same arguments, Liu et al. (2000) are of the view that DBM originated from China. This sporadic pest is now present wherever its host plants exist and is considered to be the most universally distributed of all Lepidoptera. Today, DBM is present in almost all the tropical and subtropical regions of the world including eastern Africa (Ayalew, 2006; Löhr et al., 2007).

2.1.2 Morphology and biology of DBM

Life stages of DBM consist of the egg, four larval instars, pupa and adult. Mating begins on the day of emergence and lasts about one hour. Egg laying begins shortly after dusk and reaches the peak two to four hours later. Females deposit small (0.44 x 0.26mm), oval, yellowish-white eggs singly or in small groups on both sides of the leaves of host plants (Bhalla and Dubey, 1986; Chelliah and Srinivasan, 1986). The eggs are preferentially laid in concavities of the leaves. Just before hatching, the egg darkens and the young larva can be seen coiled beneath the chorion (Harcourt, 1957). The first instar larvae hatch after 3 to 5 days and are barely 0.5 mm long. They mine into the spongy mesophyll leaf tissues where they remain until they moult to the second instar, which exits from the mines and starts feeding on the underside of the leaf. The third and fourth instar larvae are pale green, spindle shaped (about 9 mm long) and feed on the lower leaf

surface. They eat the entire leaf tissue with exception of the upper epidermis, creating a "windowing" effect. The larval period lasts 8-15 days depending on the temperature. When mature, the larva spins a cocoon on the under surface of the leaf and pupates (Harcourt, 1957). The pupa is 7 mm long, brown and encased in a loosely spun, netlike cocoon and the pupal period lasts 3-6 days (Ho, 1965). The emerged adult moth is grayish in color with a maximum wingspan of about 13 mm.

A female can lay on average 188 eggs during its lifetime (Harcourt, 1954). Fecundity is influenced by photoperiod, temperature and condition of larval food. Female adult longevity ranges from 7 to 47 days, with an average of 16.2 days while male longevity ranges from 3 to 58 days with an average of 12.1 days. The development from egg-adult varies from 12 to 20 days depending on environmental conditions (Ooi, 1986; Sarnthoy et al*.,* 1989; Löhr and Gathu, 2002) (Figure 2.1). It is a multivoltine with four to twenty generations in a year in temperate and tropical regions, respectively (Harcourt, 1986; Vickers et al., 2004).

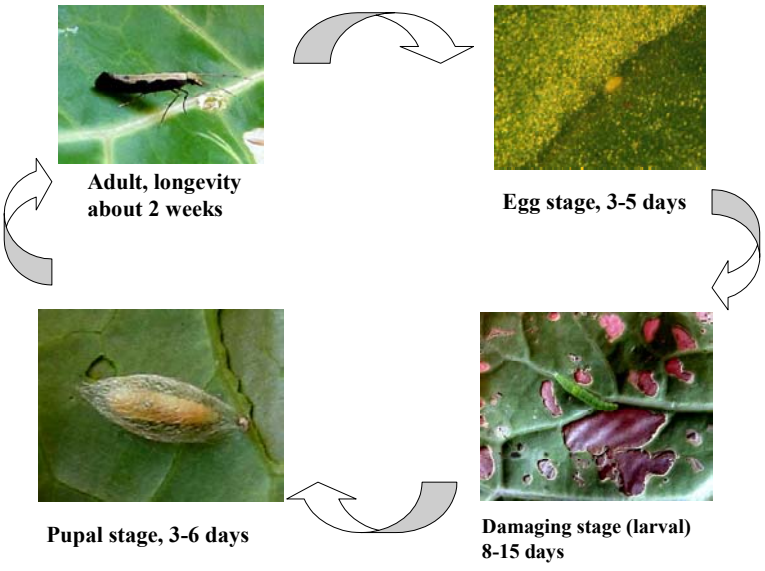


Figure 2.1: Life cycle of the diamondback moth, *Plutella xylostella* L.

Photo source: Dr. B. Lohr:

2.1.3 Host range and host specificity

The host range of DBM was considered to be limited to crucifers that contain mustard oil glucosides (Gupta and Thorsteinson 1960; Hillyer and Thorsteinson, 1971). The mustard oil glucosides act as specific larval feeding stimulants for DBM (Nayar and Thorsteinson, 1963). Sulphur containing glucosinolates or its metabolites like allyl isothiocyanates are present in crucifers and act as oviposition stimulants (Hillyer and Thorsteinson, 1971; Reed et al., 1989). Specialized herbivorous insects often use glucosinolates or isothiocyanates as positive cues for host plant recognition (Schoonhoven, 1972). Isothiocynates may serve to attract such insects to their hosts, whereas glucosinolates often trigger oviposition or feeding after an insect lands on the plant (Chew and Renwick, 1995). About forty plant species containing one or more of these chemicals serve as hosts for the herbivorous insects. Some non-host plants may also contain these stimulants and feeding inhibitors or toxins. Sulphur deficient plants are not attractive to DBM for oviposition (Gupta and Thorsteinson 1960). In 1999, DBM was recorded on snow peas *Pisum sativum* L. (var. Oregon sugar snap) in Naivasha area in the Rift Valley of Kenya, where it had almost completely devastated pea field. Lohr and Gathu (2002) observed that DBM was able to develop and survive on both kale and the pea. However there were variations between the two plants in development time and survival. The pest had a higher percent survival on kale than on peas while development was faster on the former than latter. This is an indication that the pest has broadened its diet by adding snow peas to their normal host range, which is usually known to be restricted to cruciferae (Talekar and Shelton, 1993).

2.1.4 Economic importance of diamondback moth

Diamondback moth is the most destructive insect pest of Brassica crops worldwide (Mustata, 1992; Lim et al., 1996; Verkerk and Wright, 1996). It is the key pest affecting vegetable production in Kenya (Kibata, 1996; Oduor et al., 1996). Control of DBM requires over US$ 1.0 billion in estimated annual management costs (Talekar and Shelton, 1993) in addition to crop loss. In the southeastern USA, it constitutes more than 90% of the guild of defoliating lepidopterans of canola (Ramachandran, 2000). In Texas, it can cause losses of ca. US$ 40-70 million for cabbage and US$ 400,000 for broccoli crops if not treated (Shelton, 2004). In Australia, its control on cabbage and canola

required ca. A$ 12 million and ca. A$ 6 million, respectively (Shelton, 2004). In India, it causes annual losses of ca. US$ 16 million (Mohan and Gujar, 2003a) while a 52 % yield loss has been reported on cabbage (Krishna-Moorthy, 2004). Outbreaks of DBM in Southeast Asia was reported to cause more than 90 % crop loss (Verkerk and Wright, 1996). Sometimes DBM infestations in certain parts of Pakistan and Nicaragua have compelled farmers to plough down their standing crop despite multiple insecticide applications (Perez et al., 2000). Ayalew (2006) reported that in central Rift Valley region of Ethiopia, complete crop failure is common during seasons of heavy DBM infestation. Unfortunaltely, nothing has been published about yield losses in the area of smallholder production in Africa, despite its importance (Kibata, 1996). The pest is difficult to control because of its intrinsic biology and ecology, such as short generation period, high fecundity and sub-optimal biological control (Talekar and Shelton, 1993), and genetic elasticity facilitating rapid development of resistance to insecticides (Vickers et al., 2004).

2.2 Control measures

Various control measures have been used to control DBM populations on crucifers. They include use of insecticides, biopesticides, insect growth regulators IGR's), botanicals, cultural methods, growing of resistant and transgenic crops, and the use of natural enemies. However, DBM has developed resistance to most of the insecticides with time. Resistance is defined as a genetically based decrease in susceptibility of a population over time, in response to long-term exposure to an insecticide. Currently documented cases of resistance to *Bt* in open-field populations of pests are limited to DBM only (Ferre and Van Rie, 2002; Sarfraz, 2004; Sarfraz and Keddie, 2005).

A number of new strategies have been proposed or used to manage the resistance problem. Some are aimed at slowing down the development of resistance such as rotation of pesticides (Liu et al., 1997), provision of refuge to sustain susceptible DBM populations (Shelton et al., 2000) and crop break (Heisswolf et al., 1996). Others are designed to reduce the reliance of insecticides by using alternative management strategies such as mating disruption (Schroeder et al., 2000), use of trap crops (Srinivasan and Krishna-Moorthy, 1991; Ooi, 1992; Charleston and Kfir, 2000) and natural enemies (Talekar and Shelton, 1993; Kfir, 1997).

2.2.1 Chemical control

A wide variety of organophosphates, organochlorides, carbamates and synthetic pyrethroids have been used to control DBM (Morallo-Rejesus, 1986, Sarfraz and Keddie, 2005). In tropical and subtropical areas, crucifer production has been seriously affected in recent years by DBM that has developed resistance to a wide range of insecticides (Wang et al., 1999; Sarfraz and Keddie, 2005; Khaliq et al., 2007), resulting to failure in its control (Sayyed et al., 2002). DBM was the first pest in the world to develop resistance to Dichlorodiphenyltrichloroethane (DDT) (Ankersmit, 1953) and ranks in the top 20 most resistant insect species reported so far (Mota-Sanchez et al., 2002). Resistance of DBM to conventional insecticides has been documented in Malaysia, (Syed, 1992), Taiwan (Sun et al., 1978), Japan (Hama, 1992), Australia (Altmann, 1988) and North America (Tabashnik et al., 1987; Magaro and Edelson, 1990) and on insect growth regulators (IGR's) (Kobayashi et al., 1992).

New insecticides are continuously being developed as existing ones become ineffective as DBM quickly develops resistance to many of these (Ninsin et al., 2000; Shelton, et al., 2000). Examples of these insecticides are avermectins, macrocyclic lactones, oxadiazines, pyrazoles and nereistoxin analogue insecticides (Ninsin, 2004; Sayyed et al., 2004; Sarfraz et al., 2005a). Spinosad, indoxacarb and emamectin benzoate are members of three different classes of insecticides with novel modes of action introduced in recent years (Zhao et al., 2006). Spinosad has a high level of activity against many economically important insect pests and low environmental and human risk (Thompson and Sparks, 2002). However, resistance to these new insecticides has been found in the field and in the laboratory DBM populations. It has been reported on fenvalerate and flufenoxuron (Mohan and Gujar, 2003), abamectin (Feng et al., 2004), permethrin (Endersby et al., 2004), acetamiprid (Ninsin and Miyata, 2003; Ninsin, 2004), indoxacarb and abamectin (Khaliq et al., 2007) and spinosad (Zhao et al., 2002; Sayyed et al., 2004; Khaliq et al., 2007).

Farmers react to the problem of resistance by applying pesticide cocktails, increased dosages and higher frequency of spraying (Kibata, 1996; Samsudin et al., 2004). Apart from increased cost of production, excessive and intensive pesticide use has generated several safety risks to humans, contamination of water, decreased biodiversity, environmental pollution and decimated natural enemy populations (Lim et al., 1986; Idris and Grafius, 1993). There are three main reasons for intensive use of insecticides on

crucifers. Firstly, in many countries synthetic insecticides used to control DBM often eliminates natural enemies, which in turn leads to continued intensive use of insecticides, eventual resistance and control failure (Sayyed et al., 2002). Secondly, DBM is highly migratory (Chapman et al., 2002) and may attain a pest status in areas where its natural enemies are absent and farmers have to rely on insecticides for its control. Thirdly, consumer pressure, i.e. pest damaged/contaminated produce is not acceptable in the market and farmers attempt to grow unblemished vegetables with the use of conventional insecticides.

Parasitoids foraging for host larvae on crops risks coming into contact with insecticides applied for pest control, which might affect them directly by causing mortality or indirectly by impairing their performance. Indoxacarb and spinosad were found to be highly toxic to *C. plutellae* (Haseeb et al*.,* 2004) while indoxacarb, λ-cyhalothrin and spinosad caused 100 % mortality of *D. semiclausum* within 24 hours of ingestion (Xu et al., 2004).

The ability of DBM to resist a wide array of control tactics utilised in its management necessitates the development and implementation of broad based IPM systems including cultural, biological, behavioural and chemical tactics (Liu et al*.*, 1995; Zhao et al*.*, 1996). Sustainable agriculture will rely on alternative interventions to chemical pesticides for pest management that are environmentally friendly. Therefore, conservation and enhancement of natural enemy populations is the cornerstone of successful IPM programmes. Natural enemies reduce pest populations, limit pest damage and keep secondary pests below the economic threshold. A crucifer IPM concept involves minimizing the use of pesticides to ensure no or minimal harm to natural enemies and further augment their efficacy (Hassan, 1989; Gerling and Naranjo, 1998). Such a holistic IPM programme would also safeguard the health of farmers, consumers and the environment.

2.2.2 Cultural control

Cultural control methods involve use of agronomic practices to reduce insect pest abundance and damage below the economic level. Numerous cultural practices such as intercropping, irrigation, residue destruction and trap crops help in regulating DBM population (Srinivasan and Krishna-Moorthy, 1991). Intercropping is a common practice

in the tropics where intensive small-scale farming is practiced. Talekar et al. (1986) reported low incidence of DBM when cabbage was inter-cropped with tomato, dill, garlic, safflower, oat and barley. Intermittent overhead irrigation provides effective economic control of DBM by disrupting adult flight, mating and oviposition, and to some extent washes off the larvae (Talekar et al., 1986). The best time for irrigation is late in the afternoon when moth activities are high. Unfortunately, diseases tend to become a major problem on the crop subjected to overhead irrigation. Crop residue destruction immediately after harvest helps to prevent the pest build-up and subsequent migration to younger plants in adjacent fields (Endersby and Morgan, 1991).

Trap crops are plant stands more attractive to the pest than the target crop and are grown to lure insect pests away from the target crops. For example, Indian mustard, *B. juncea,* when grown adjacent to cabbage crop attracted more DBM for oviposition. Larval survival was lower on mustard, indicating its potential use as a trap crop (Charleston and Kfir, 2000). One of the plant species proposed to manage DBM is yellow rocket *Barbarea vulgaris* (R. Br.) (Shelton and Nault, 2004). Given the choice between *B. vulgaris* and various cruciferous crops, DBM prefers to lay its eggs on *B. vulgaris* despite the fact that its larvae do not survive on it (Shelton and Nault, 2004; Badenes-Perez et al., 2004). Use of trap crops on commercial fields has helped in the reduction of pest populations (Srinivasan and Krishna-Moorthy, 1991). However, it might not be practical and economical in Kenya due to small farm sizes where most of the vegetables are grown.

2.2.3 Botanicals

Various neem formulations have been screened and found to be effective in the control of DBM (Schmutterer, 1992; Javaid et al., 2000). Their complex chemistry makes it hard for DBM to develop resistance. Charleston et al. (2003) observed that neem extracts significantly affected both DBM larvae and adults but had no direct impact on parasitoids *C. plutellae* and *Diadromus collaris* Gravenhorst (Hymenoptera: Ichneumonidae). Akol et al., (2003) found two neem insecticides; Neemroc® and Neemros® safe for *D. mollipla.* The products did not affect the parasitoid's longevity, parasitism rate and foraging behaviour. However, two neem-based commercial products viz., Agroneem® and Neemix® were reported to cause mortality of *D. insulare* and *C. plutellae* and showed adverse effects on parasitism rates (Haseeb et al., 2004; Xu et al., 2004). Saber et al.

(2004) observed that adult emergence of the egg parasitoid, *Trichogramma cacoeciae* Marchal (Hymenoptera: Trichogrammatidae) was significantly reduced (73.3 %) from parasitized eggs of *Sitotroga cerealella* Olivier (Lepidoptera: Gelechiidae) exposed to residues of Neemazal®. These controversial results suggest that efficacy of any azadirachtin-based insecticides on pests and its effects on parasitoids should be thoroughly investigated before widespread use in the field.

2.2.4 Resistant and transgenic varieties

One of the sources of host plant resistance to DBM is the glossy leaf genotype of *B. oleracea* (Lin et al*.,* 1983; Stoner, 1990). Resistant glossy varieties are only effective against the first instar larvae. It was observed that the neonate larvae move faster on glossy resistant than on susceptible leaves with normal wax layers. This suggests that the mechanism of resistance is based on the non-acceptance of first instars, resulting in high net movement and reduced feeding (Eigenbrode and Shelton, 1990; Eigenbrode et al*.,* 1991a). Such varieties with glossy leaves have shown reductions in other lepidopteran pests inhabiting crucifer crops too (Stoner, 1990).

Development of transgenic varieties with built-in resistance to lepidopteran pests is one of the options being considered for DBM control. It involves the insertion of crystal toxin genes (*cry)* from soil bacterium *Bacillus thuringiensis* Berliner (*Bt*) into crop plants. The inserted genes produce toxins in their tissue and thereby protecting the plant from insect feeding damage (Heckel et al., 2001; Zhao et al., 2000). Most Cry proteins have a limited host range, which is believed to be due to the specificity of the binding site (Zhao et al., 2000; Ferré andVan Rie 2002). Transgenic varieties are known to be safe and offer an effective control strategy. Because Cry proteins are non-toxic to natural enemies and to mammals, they have many environmental advantages over chemical insecticides. The single most important threat to their continued efficacy is the evolution of resistance in insect pests and this consideration has dictated deployment strategies for Bt-transgenic plants. Theoretical models show that if two *Bt* genes producing different proteins that target different binding sites in the insect are used simultaneously in the plant, the evolution of resistance can be dramatically delayed relative to single gene plants used sequentially or simultaneously (Zhao et al*.*, 2003). Cry proteins have many environmental advantages over chemical insecticides because they are not toxic to predators and

parasitoids. Chilcutt and Tabashnik, (1999) observed that *Bt* toxins had no detrimental impacts on adult *C. plutellae.* The parasitoid successfully completed its larval development in *Bt*-resistant DBM larvae feeding on *Bt* transgenic crucifers (Schuler et al., 2004). However, the varieties would require less frequent insecticide applications to allow an increased role for the natural enemies (Zhao et al., 2003).

There are attempts of introducing *Bt* cabbages in Asia and East Africa. However, the most challenging aspect, especially in East Africa, is the danger that might be encountered from cross pollination of the *Bt* cabbage from the other Brassica cultivars and the wild crucifers. Most of the farmers do not purchase seeds for planting in every season but rely on those obtained from over grown crops from their farms (personnal observation).

2.2.5 Biological control

Natural enemies play a large role in suppressing DBM population growth (Talekar, 1992). Over 90 parasitoid species have been recorded to attack DBM worldwide, including six species of egg parasitoids, 38 larval and 13 pupal parasitoids (Talekar and Shelton, 1993). In the absence of synthetic insecticides, these parasitoids effectively suppress the pest populations in different parts of the world including Indonesia and Malaysia (Talekar and Shelton, 1993), St Helena (Kfir and Thomas, 2001) and Japan (Noda et al., 2000; Ohara et al., 2003). Mustata (1992) reported 25 parasitoid species from Moldavia (Romania) parasitizing up to 80–90 % of DBM populations. Many countries have developed and implemented a bio-control based IPM approach that has proved successful (Poelking, 1990; Löhr et al., 2007). It involves the importation and release of egg, larval or pupa parasitoids to control the DBM below the economic threshhold. Egg parasitoids belonging to the genera *Trichogramma* and *Trichogrammatoidea* contribute little to biological control of DBM (Talekar and Shelton, 1993). However, larval endoparasitoids belonging to the genera *Diadegma* and *Cotesia* are most predominant and effective in the management of DBM (Fitton and Walker, 1992). *Diadromus collaris*, a pupal parasitoid also exerts significant DBM control (Kfir, 1997, 2004; Kirk et al., 2004).

In Kenya, the parasitoids *D. mollipla, Itoplectis* sp. (Hymenoptera: Ichneumonidae), *Apanteles* sp. (Hymenoptera: Braconidae) and *Oomyzus sokolowskii* (Kurdj.) (Hymenoptera: Eulophidae) were recovered from cabbage growing areas (Kibata, 1996;

Oduor et al., 1996; Löhr et. al., 2007). However, their combined level of parasitism did not exceed 14.5 %, of which *D. mollipla* accounted for 9 % and their impact in the control of DBM was negligible. *Diadegma mollipla* is known to be a generalist parasitoid. It has also been recovered from DBM on pea and potato tuber moth on potato, which could have contributed to the low parasitism. In addition, its original host is not known since potato tuber moth is an introduced species. Lack of intrinsic cues to accept the host plant of DBM may also explain the low parasitation rates by *D. mollipla* as observed by Akol et al. (2003) and Rossbach et al. (2005). Emphasis has been placed on classical biological control when indigenous parasitoid guilds are not able to control the pest. To augment biological control of DBM, *D. semiclausum* was imported from Taiwan and introduced in Kenya in 2002, where it has established in release areas with average parasitism of up to 80 % (Löhr *et. al*., 2007). Success reports have also been recorded in a number of countries through introduction of *C. plutellae* and *D. semiclausum* (Talekar and Shelton, 1993).

2.2.5.1 *Diadegma semiclausum*

Diadegma semiclausum (Hellen) (Hymenoptera: Ichneumonidae) is an effective primary solitary endoparasitoid that attacks all stages of DBM larvae with preference for second and third instars (Talekar and Yang, 1991; Azidah et al*.,* 2000). The species is host specific to DBM (Fitton and Walker, 1992). Because of its great potential to control DBM, it was introduced in New Zealand (Hardy, 1938), Indonesia (Vos, 1953; Sastrosiswojo and Sastrodihardjo, 1986), Malaysia (Ooi, 1992), Taiwan (Talekar andYang, 1991), Philippines (Poelking, 1990) and recently in East Africa (Löhr et al., 2007).

The adult parasitoid emerges from the cocoon, mates immediately, and the female starts ovipositing on DBM larvae (Fitton and Walker 1992). Females lay 300-500 eggs (Abbas, 1988; Winkler et al., 2006). The egg takes about two days to hatch inside the DBM larvae and passes through five larval instars. The larvae feed primarily on the host haemolymph and fat body. Just before pupation, the larva emerges from the prepupal host and spins its own cocoon within the host cocoon, thereby killing the host. The parasitoid pupa is easily recognized by its brownish colour. The life cycle from egg to adult takes 11-29 days. The optimum temperature range for the parasitoid is 15-25°C (Yang et al., 1993). Adults live

from 3-73 days depending on temperature, availability of host and food quality (Talekar and Yang, 1991; Yang et al., 1993).

2.2.5.2 *Cotesia plutellae*

Cotesia plutellae (Kurdjumov) (Hymenoptera: Braconidae) has been recorded in different geographical regions including South Africa, Benin, Martinique, Réunion, Australia, Malysia, Thailand, UK and Taiwan (Rattan et al., 2006). It is a solitary larval endoparasitoid of DBM and prefers ovipositing on the first three larval instars. A female can lay up to 244 eggs depending on the life span. The eggs hatch into larvae just after a day or two within the host's body and only a single wasp develops in each host. The larva feeds on the host haemolymph and fat body, and the mature larva emerge through the side of the host to pupate externally. The larva spins white coloured silken cocoon just outside the host body. Following larval parasitoid egression, the moribund host perishes. The life cycle takes about 15 days at 25°C (Talekar, 1992). The species performs better at higher temperatures and it is considered a good classical biocontrol candidate (Fitton and Walker, 1992). A biotype adapted to semi-arid conditions was studied in South Africa (Nofemela and Kfir, 2005) and released in mid-altitude semi arid areas of Kenya in March 2004.

2.2.5.3 Microbial control agents

Several strains of *Bacillus thuringiensis* Berliner (*Bt*) with different toxins are used to control lepidopteran pests. Unlike most chemical insecticides, which target the nervous system, *Bt* toxins have a unique mode of action. Upon sporulation, certain strains of *Bt* produce crystalline (Cry) protein inclusions. *Bt*-based products are the most promising alternatives to convectional insecticides because of two main reasons. Firstly, they are highly toxic to certain pests and secondly, they are compartible with IPM strategies due to their narrow host specificity, high amenability to genetic engineering and they have little or no harm to non-target organisms (Tabashnik, 1994). When a larva ingests a *Bt* crystal, the crystal dissolves and the Cry protoxins go into solution in the midgut lumen and are converted to activated toxins by the insect's own proteases. These bind to certain sites on the membrane of the midgut, causing formation of pores in the membrane, lysing the epithelial cells and eventually killing the insect (Heckel et al., 2004). The first case of

field resistance to *Bt* was reported from Hawaii in 1990 when DBM populations showed resistance to Dipel® (*Bacillus thuringiensis* subsp. *kurstaki*) (Tabashnik et al., 1990). Resistance of DBM to *B. thuringiensis* has been reported in a number of countries (Tabashnik et al., 2003; Mohan and Gujar, 2003; Sarfraz and Keddie, 2005). It has also been reported in the Philippines (González-Cabrera et al., 2001), Malaysia (Sayyed et al., 2000a), Japan (Maruyama et al., 1999) and the continental USA (Zhao et al., 2000). It is thought to be due to lack of binding of the crystal to the brush-border membrane, either because of strongly reduced binding affinity or complete absence of the receptor molecule (Ferre et al., 1991; Ferre and Van Rie, 2002; Safraz, 2004). Although published reports indicate a lack of cross resistance between some serotypes of *Bt* and thereby offer some hope for managing *Bt* resistance, limiting selection pressure to any of the toxins will be necessary if *Bt* is to remain a durable insecticide complex.

Nucleopolyhedroviruses (NPV) and granuloviruses (GV) have the greatest microbial control potential against insects (Hunter-Fujita et al., 1998). The use of viral pathogens of insects in most agricultural crops takes advantage of their virulence and specificity (Payne, 1982). Their efficacy, specificity and production of secondary inoculum make baculoviruses attractive alternatives to broad-spectrum insecticides. Due to their lack of negative effects on beneficial insects including other biological control organisms, baculoviruses could be ideal components of IPM systems. Unfortunately, the selectivity of many baculoviruses, often targeting only one individual species, coupled with high production cost, has deterred large-scale commercial development. Besides cost and specificity, entomopathogenic viruses present a few drawbacks, which include relatively slow action, sensitivity to ultra-violet light and obligate nature of multiplication. The use of baculoviruses within the IPM context is expected to increase, particularly in developing countries for the control of insects in high value crops grown on small acreages. Fourteen genetic isolates of *P. xylostella* granuloviruses have been reported in Kenya though in small number of infected larvae. The representative samples were from different location and about 96 samples were studied. However, it was stated that the PxGV was the most prevalent disease of DBM in Kenya (Grzywacz et al., 2002). Of the fourteen isolates, none has been commercialized and of the different granuloviruses world over, only *Cydia pomonella* GV and *Adoxophyes orana* GV have been commercialized (Grzywacz et al., 2002). They are potential biopesticides for controlling DBM and have no effects on other Lepidopteran pests and other beneficial natural

enemies such as syrphid and spiders in the field (Grzywacz et al., 2002; Ogutu et al., 2002).

2.3 Wild crucifers

Wild crucifer species occur as weeds within the cultivated crucifer fields or in the neighbouring areas. They can act as alternative hosts and provide refugia to natural enemies during off-season (Landis et al., 2002). Wild crucifers *Nasturtium heterophyllum* and *Cardamine hirsuta* were found to provide refuge to *Diadegma eucerophaga* Horstmann (Kartosuwondo and Sunjaya, 1991) while Kahuthia-Gathu et al. (2006) found *R. raphanistrum*, *E. arabicum*, *C. kilimandscharica* and *S. officinale* provided refuge to *D. semiclausum*, *C. plutellae*, *O. sokolowskii* and *D. mollipla*. They preserve and support natural enemies thereby, contributing to the reduction of pest outbreaks in arable field crops (Landis et al., 2000). Wild and cultivated crucifers have been reported to affect oviposition, survival and development of DBM and its parasitoid, *D. insulare* Cresson (Idris and Grafius, 1996). Idris and Grafius (1997) suggested that presence of wild crucifer *Barbarea vulgaris*, and wild mustard *Brassica kaber* D. C. (Wheeler) in the vicinity of cultivated brassicas could reduce DBM population by increased impact of parasitoids. The efficiency of the parasitoids was enhanced by the supplemental provision of nectar and pollen from the wild crucifers.

Wild flowers are important food sources for parasitoids (Keven, 1975; Fitton and Walker, 1992). In the 1940's, leaving weeds around crop fields was encouraged in South Africa for the purpose of supporting parasitoids and predators that control DBM (Ullyett, 1947). *Diadegma insulare* was found to live longer with higher fecundity when fed on wild flowers of *B. kaber*, *B. vulgaris* or *Daucus carota* L., found around crop fields in North America (Buchholtz et al., 1981). Zhao et al. (1992) observed that parasitism of DBM by *D. insulare* was higher in broccoli fields adjacent to nectar producing plants than in broccoli fields that were not surrounded by nectar producing plants. In Michigan, the presence of wild flowers surrounding the field influenced parasitism rate by *D. insulare* in pesticide treated plots (Idris and Grafius, 1993). Johanowicz and Mitchell (2000) observed alyssum *Lobularia maritime* L. present near the cultivated crucifers prolonged the life span of *C. marginiventris* Cresson and *D. insulare*. The nectar from Pak choi *Brassica campestris* L. was found to prolong the life of *C. rubecula* Marshall (Siekmann,

2002). Thus, presence of wild crucifers around the cultivated fields could increase effectiveness of the recently introduced exotic parasitoids *D. semiclausum* and *C. plutellae*.

CHAPTER THREE

3 Diversity, distribution and role of wild crucifers in major cabbage and kale growing areas of Kenya

Abstract

An investigation of the diversity and distribution of wild crucifer species and their importance for cultivated crucifers was conducted during 2005 and 2006 in the highland and mid-altitude semi-arid areas of Kenya. Thirteen species of wild crucifers in nine genera were recorded: *Raphanus raphanistrum, Erucastrum arabicum, Sisymbrium officinale, Crambe kilimandscharica, Capsella bursa-pastoris, Rorippa nudiuscula, Ro. micrantha, Ro. microphylla, Lepidium bonariense, Coronopus didymus, Brassica rapa, B. juncea and Brassica* species. Highland areas had significantly higher species diversity and species richness than mid-altitude semi-arid areas. Species richness, diversity and evenness varied with season and location. *Raphanus raphanistrum* was the dominant non-cultivated species in the highland, followed by *E. arabicum*, which was also present and dominant in the semi-arid study sites. Diamondback moth (DBM), *Plutella xylostella* L., was recorded from ten wild crucifer species and *R. raphanistrum* and *E. arabicum* were the preferred host plant species. DBM numbers on wild crucifers were lower than on cabbage and kale in adjacent fields. Overall, five larval, one larval-pupal and one pupal parasitoid of DBM were recorded: *Diadegma semiclausum, D. mollipla, Itoplectis* sp. (highland only), *Cotesia plutellae* and *Apanteles* sp. (both semi-arid areas only), *Oomyzus sokolowskii* and *Brachymeria* species. *Diadegma semiclausum* was the most dominant species on all crucifers. Spatial niche separation was observed in Athi River where *Apanteles* and *Brachymeria* were collected on *E. arabicum* only. Higher numbers of *D. mollipla* were recovered from wild crucifers than cabbage and kale. We conclude that wild crucifers act as alternative hosts for DBM and provide refugia for parasitoids when the crop is absent and may help in recolonisation of cultivated crops after local extinction of parasitoids through pesticide application.

Keywords: species diversity, parasitoids, diamondback moth, conservation biological control, cruciferous weeds, recolonisation, agro-ecological systems

3.1 Introduction

In natural and agricultural systems, species counts are used as a measure of diversity. Species diversity however, is both a function of the number of species, and the evenness in distribution of abundances of species (Magurran, 1988; Purvis and Hector, 2000). Plant diversity affects the population dynamics of insect herbivores in agricultural (Andow, 1988) and natural communities (Karieva, 1983). Agroecosystems that are more diverse in plant species and distribution have been reported to have higher diversity of arthropod communities including herbivore species as well as predators and parasitoids. In particular the latter are of special importance regarding conservation biocontrol (Talekar and Shelton, 1993; Kfir and Thomas, 2001; Ohara et al., 2003). Earler, Altieri (1984) observed that presence of weeds growing outside the crop fields can contribute in keeping insect populations below economic threshold. On the one hand they provide refuges, and on the other essential resources such as hosts/prey or alternative food sources (Dennis and Fry, 1992; Norris and Kogan, 2000; Landis et al., 2000). In case of parasitoids apart from being convenient hosts, flowering weeds can enhance longevity and effectiveness by providing pollen and nectar (Idris and Grafius, 1995; Baggen et al., 1999; Landis et al., 2000; Steffan-Dewenter et al., 2001). It's been established that nectar- or pollen-feeding is essential for the reproductive success of many insect predators and parasitoids (Wäckers andvan Rijn, 2005). Varying rainfall amount and temperatures also increase or restrict the abundance of parasitoid species by determining the presence or absence of essential resources (Quayle et al., 2003). Thus, the assemblage of parasitoids in a particular habitat will depend on host-related and environment-related biotic and abiotic factors and might result in different degrees of biological control of pests.

The diamondback moth (DBM) *Plutella xylostella* Linnaeus (Lepidoptera: Plutellidae) is the most important pest of cultivated crucifers worldwide (Talekar and Shelton, 1993; Reddy et al., 2004). Its exceptional pest status is due to the diversity and abundance of the host plants, most common disruption of its natural enemies communities by broad-spectrum pesticides, its high reproductive potential and genetic elasticity facilitating rapid development of pesticide resistance (Mohan and Gujar, 2003; Vickers et al., 2004; Shelton, 2004). The pest has developed resistance to most chemical (Kibata, 1996) and bacterial insecticides (Liu et al., 1995; Tabashnik et al., 2003; Heckel et al., 2004; Sarfraz, 2004; Sarfraz and Keddie, 2005).

In one of the recent classical biological control efforts, *Diadegma semiclausum* Hellén (Hymenoptera: Ichneumonidae) was imported from Taiwan and released in the highland areas of Kenya. In addition, a *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae) biotype from South Africa was released in 2004 in mid-altitude semi arid areas. *Diadegma semiclausum* has successfully established and it is providing excellent control of DBM (Momanyi et al. 2006; Löhr et al., 2007). This has resulted in farmers reducing pesticide application while others have stopped spraying against DBM altogether in the highland areas where *D. semiclausum* was released (Löhr et al., 2007). However, *C. plutellae* has not established in the mid-altitude semi arid areas, 2 years after the release since very few individuals were recovered (Kahuthia-Gathu et al., unpubl. Data). However, presence of other cabbage pests such as aphids during the dry season might necessitate pesticide application (Oruku and Ndung'u, 2001). The use of broad-spectrum insecticides may be detrimental to the introduced parasitoids and result in pest resurgences as observed in Asia (Sastrosiswojo and Sastrodihartjo, 1986; Verkerk and Wright, 1997). We believe that the presence of wild crucifers in field margins can prevent large-scale elimination of parasitoids and thus stabilize the crucifer growing system.

Agnew and Agnew (1994) recorded 42 wild crucifers species in 19 genera in Kenya. However, their occurrence and distribution in major cabbage and kale growing areas is unknown. Even less known is the role they play in providing refugia for DBM and its parasitoids. Therefore, detailed surveys were conducted in two agro-ecological zones, highland rainfed (mainly cabbage-producing) and mid-altitude semi-arid, irrigated areas (mainly producing kales) to evaluate the diversity and distribution of wild crucifer species, and their role for indigenous and exotic parasitoids. Our working hypothesis was that wild crucifers act as alternative host plants and provide refugia to parasitoids when the crop is absent or in case of local parasitoid extinction in crucifer fields through application of broad-spectrum pesticides. Plant species diversity and parasitoid assemblage of four sites in two agroecological zones were compared to assess the influence of structural charteristics and pest management strategies on these beneficial insects.

3.2 Materials and methods

3.2.1 Study sites

Two sites each from major highland and mid-altitude semi-arid crucifer growing areas were selected for the studies. The highland sites were located in Central Province of Kenya and comprised of Naro Moru with an altitude ranging from 1893 m to 2293 m and Kinangop from 2343 m to 2749 m. Maximum temperatures range between 22ºC to 30ºC and minimum temperatures between 10 ºC to 15 ºC. The rainfall is bimodal and ranges from 1500 mm to 2000 mm per annum. The long rains occur between March-June and short rains October-December. Soils are mostly of volcanic origin and relatively fertile. Both cabbage and kale are grown in the region with the former being the dominant crop.

The mid-altitude semi arid study areas were located in Eastern Province of Kenya and comprised of Yatta at 1220 m to 1290 m and Athi River at 1457 m to 1527m. Maximum temperatures range between 25 ºC to 32 ºC and minimum temperatures between 5 ºC to 20 ºC. The areas receive 500 mm to 900 mm rainfall per annum. Rainfall is unreliable and farmers supplement by irrigation. Black cotton soils are predominant in both areas. As temperatures are usually too high for head cabbage, kale is the crop grown in both areas.

3.2.2 Data collection

Surveys were conducted quarterly during the hot dry (January-March), long rainy (April-June), cold dry (July-September) and short rainy seasons (October-December) of 2005 and 2006. A line-transect sampling technique as described by Grieg-Smith (1983) was used to evaluate the diversity and distribution of wild crucifer species in the uncultivated land neighbouring the cabbage or kale fields. We tried to have the line transect perpendicular to the field margin. However, this was not always possible due to small size of land left fallow and the generally small farm sizes. The representative wild crucifer species along a 30m sampling line were sampled by placing a one-meter square frame at the beginning of the transect and recording all wild crucifer species within the frame. The number of plants of each species within the frame was recorded. This procedure was repeated after every 3m of the line transect for ten sampling points per transect.

A total of 35 and 25 fields were sampled every visit from the highland and mid-altitude semi arid areas, respectively. The difference in number of fields was due to the low number of cultivated kale fields in the latter during the dry periods of the year. In the highlands, sampling fields were selected at 2-4 km intervals because of the large area under cabbage unlike in the mid-altitude areas where most of the kale fields were located close to each other along the river valley (Athi River) or irrigation channel (Yatta).

Mature seeds were harvested from wild crucifers, put in poly bags and labeled (date, species, location) for use in laboratory and screen house trials. Voucher specimen of each crucifer species were collected and taken to the laboratory for processing and identification. They were identified using various plant identification keys (Ivens, 1967; Agnew and Agnew, 1994). Species were confirmed and deposited at the East Africa Herbarium at National Museums of Kenya.

Global Positioning System (GPS) (Garmin Geko 101) readings of longitudes, latitudes and altitude from each field sampled were recorded for mapping (Figure 3.1).

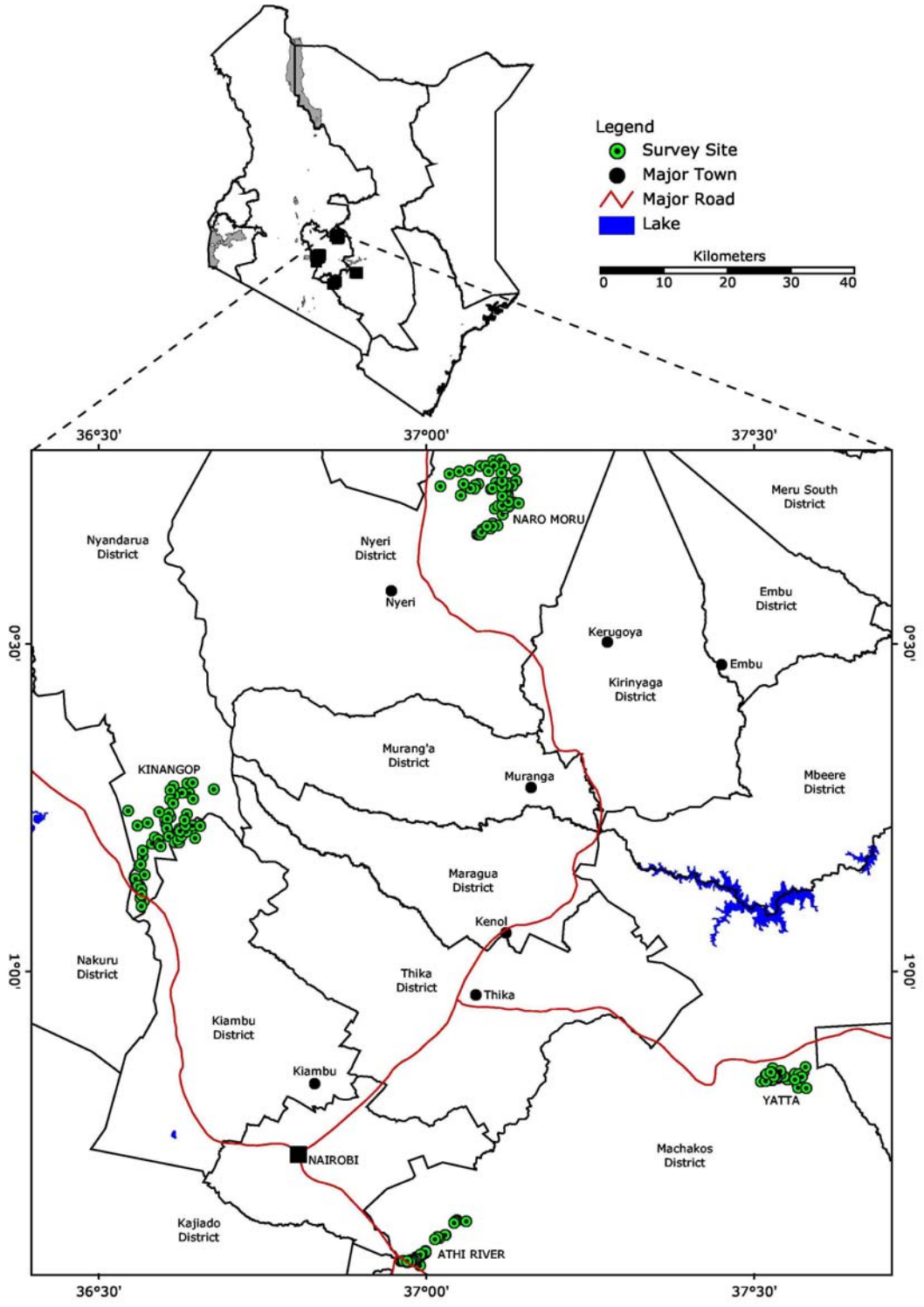


Figure 3.1: Map of Kenya showing the survey sites in highland and mid-altitude semi arid areas where cabbage and kale are grown, respectively

3.2.3 Sampling of diamondback moth on cultivated and wild crucifers

Diamondback moth was sampled on cabbage *Brassica oleracea* var *capitata* L. in the highlands and on kale, *B. oleracea* var. *acephala* L. in the mid-altitude semi arid areas. From each field, ten plants of cabbage or kale, and a maximum of ten wild crucifer plants (per quadrat) of each species were selected at random from the field and physically checked for presence of DBM. To assess DBM incidence on the wild crucifers, an individual plant from each species was selected from each quadrat. The number of DBM larvae and pupae found on each plant were recorded. All third and fourth instar larvae and pupae were collected and kept in labeled (field number, host plant, locality, collection date) plastic containers then taken to the laboratory. The containers were lined with tissue paper at the bottom to absorb excess moisture and closed with cap containing a fine muslin cloth to enhance ventilation and reduce mould growth. The larvae were kept at room temperature (23±2ºC), 50-70 % RH and a photoperiod of 12:12 (L:D) hour and fed on their respective crucifer species where necessary until pupation. The pupae were then placed individually in clean plastic vials, plugged with cotton wool and observed daily for DBM or parasitoid emergence. The parasitoids species were identified, adults sexed and recorded. The number of parasitoids emerging from single cocoon in gregarious species was recorded.

Presence of other pests, diseases and natural enemies found on the wild crucifers was also recorded. Samples were collected and taken to the lab for identification while some were preserved in 70% alcohol for confirmation.

3.3 Data analysis

The diversity and evenness of wild crucifer species was estimared using the Shannon Diversity Index (H′). It is the proportion of species (pi) relative to total number of species (S) summed up and multiplied by natural logarithm of this proportion (ln pi) (Magurran, 1988). The product is summed across species and multiplied by (-1) Rosenzweig, 1995). $H' = -p_i \ln p_i$, where $p_{i,} = n_i/N$. Evenness was calculated by dividing H' by ln S.

Variance in diversity was estimated using the formula

Var $H' = (p_{i-} (\ln p_{i)^2} - (p_i \ln p_{i)^2})/_{N-}(_{S-1/2N^2})$.

A t-test was performed to test for differences in diversity indices between seasons using the formula t= *H*'1- *H*'2/(Var *H*'1+ Var *H*'2)^½ (Batten, 1976; Magurran, 1988).

One Way Analysis of Variance (ANOVA) was used to analyse data on DBM counts on cabbage and kale. The means were separated using the Student Newman Keuls test (SNK) (SAS, 2004 SAS Institute Inc.). The data of DBM counts on wild crucifers were normalized using square root transformation (SQRT+1) before being subjected for analysis using General Linear Model (GLM). Means were seperated using Tukey test (SAS, 2004, SAS Institute Inc.,). Parasitism rates for solitary parasitoids were calculated as the sum of parasitoids divided by total number of adults (DBM + parasitoids)*100 while that of gregarious parasitoids as sum of parasitised cocoons/(DBM + cocoons)*100. The data for parasitoids recovered from the wild crucifers were arsine SQRT transformed before anlaysis.

3.4 Results

3.4.1 Diversity and distribution of wild crucifers

Thirteen wild crucifer species from nine genera were recorded from over 480 fields sampled. A total of twelve species were recorded in the highlands and two species in the mid–altitude semi arid areas (Plates 3.1-3.14). *Erucastrum arabicum* Fisch & Mey., *Raphanus raphanistrum* L.*, Capsella bursa-pastoris* (L.) Medic.*, Lepidium bonariense* L.*, Crambe kilimandscharica* O.E. Schulz., *Coronopus didymus* (L.) Sm.*, Brassica* sp., *Brassica juncea* (L.) Czern., *Rorippa microphylla* (Boenn. ex Rchb.) Hyl. ex A. Löve & D. Löve, *Brassica rapa* L.*, Rorippa nudiuscula* (Sond.) Thell., and *Sisymbrium officinale* (L.) Scop.*,* were found in Kinangop and Naro Moru (Table 3.1 and3.2). *Rorippa micrantha* (Roth.) Jonsell., and *E. arabicum* were the only species recorded in Yatta and Athi River. Due to the low numbers obtained, analysis on diversity was not calculated in Yatta and Athi River. *Erucastrum arabicum* was the only species recorded in both highlands and mid-altitude areas. *Raphanus raphanistrum* and *E. arabicum* were recorded throughout the sampling period of 2005 and 2006 in the highland areas of Naro Moru and Kinangop. *Raphanus raphanistrum* was the most dominant and abundant species in both areas. *Rorippa nudiuscula* and *B. rapa* were recorded from Kinangop only but with very low frequencies (Table 3.2).

Plate 3.1: *Raphanus raphanistrum* L.

Plate 3.2: *R. raphanistrum* at the background of cabbage

Plate 3.3: *Rorippa nudiuscula* (Sond.) Thell.

Photos taken by Kahuthia-Gathu

Plate 3.4: *Erucastrum arabicum* Fisch & Mey.

Plate 3.5: *Capsella bursa pastoris* (L.) Medic.

Plate 3.6: *Crambe kilimandscharica* O.E. Schulz

Plate 3.7: *Rorippa microphylla* (Boenn. ex Rchb.) Hyl. ex A. & D. Löve

Plate 3.8: *Rorippa micrantha* (Roth.) Jonsell

Plate 3.9: *Coronopus didymus* (L.) Sm

Plate 3.10: *Brassica* sp.

Plate 3.11: *Brassica* sp. fruiting bodies

Plate 3.12: *Brassica juncea* (L.) Szern

Plate 3.13: *Sisymbrium officinale* (L.) Scop

Plate 3.14: *S. officinale* fruiting bodies

Photos by Kahuthia-Gathu

A significant difference in species richness was observed between the highlands and mid-altitude semi-arid areas. The highlands recorded an average of six species while the average in mid-altitude areas was one species only. The average number of crucifer species was similar between the highland areas of Kinangop and Naro Moru, and also between mid-altitude semi-arid areas of Athi River and Yatta (see also table 3.4).

Diversity indices and evenness differed significantly between seasons and regions. In Naro Moru, the diversity index ranged between 0.82 and 1.35. The highest diversity index of 1.663 and 1.05 was recorded during the short rains while the lowest index of 0.924 and 0.820 during the cold dry season in 2005 and 2006, respectively (Table 3.1). In Kinangop, the highest index of 1.203 and 1.021 was recorded during the hot dry and cold dry reasons, while the lowest index of 0.839 and 0.434 during the hot dry and cold dry seasons in 2005 and 2006, respectively (Table 3.2). Highest species evenness of 0.841 and 0.639 was recorded during the hot dry season, while lowest evenness of 0.526 and 0.494 during cold dry and short rain seasons in 2005 and 2006, respectively in Naro Moru. However, the highest species evenness of 0.578 and 0.552 was recorded during the hot dry and short rainy season, while the lowest species evenness of 0.468 and 0.395 during cold dry and hot dry season in 2005 and 2006, respectively in Kinangop. Diversity index was higher in 2005 than in 2006 in Naro Moru.

Species diversity indices and species richness for Yatta and Athi River were not calculated since only two crucifer species were recorded and the number of quadrats containing a particular species was too low. At certain periods no wild crucifer species was recorded from the quadrats. Species diversity differed significantly between hot dry and long rainy season of 2005 ($t=6.01$, $df=448$, $P<0.001$), between short rainy and dry season of 2005-2006 ($t=8.9$, $df= 363$, $P<0.001$) and between cold dry and short rainy season of 2006 ($t=3.18$, $df= 511$, $P<0.001$) in Naro Moru (Table 3.1). In Kinangop area, significant differences were observed between hot dry and long rainy season of 2005 ($t=3.09$, $df=439$, $P<0.001$) and 2006 ($t=4.88$, $df=245$, $P<0.001$), respectively, and between short rainy and hot dry season of 2005-2006 ($t=4.10$, $df= 114$, $P<0.001$) (Table 3.2). Athi River recorded higher number of quadrats with *E. arabicum* while Yatta had more quadrats with *Ro. micrantha*.

Table 3.1: Diversity index and seasonal occurrence of wild crucifer species in the highlands, cabbage growing area of Naro Moru, Central Province of Kenya

Crucifer species	Number of quadrats with crucifers(2005)				Number of quadrats with crucifers (2006)			
	Hot dry	Long rains	Cold dry	Short rains	Hot dry	Long rains	Cold dry	Short rains
Raphanus raphanistrum	52	158	102	112	90	155	134	233
Erucastrum arabicum	66	112	26	111	49	21	55	77
Rorippa nudiuscula	-	-	-	-	-	-	-	-
Brassica juncea	4	-	-	-	-	-	-	10
Capsella bursa-pastoris	31	5	2	14	-	-	2	7
Lepidium bonariense	16	4	5	9	10	30	-	28
Rorippa microphylla	-	-	6	-	1	-	-	6
Coronapus didymus	-	5	-	4	-	-	-	-
Sisymbrium officinale	-	-	3	-	-	4	10	-
Crambe kilimandscharica	-	4	-	-	-	-	-	-
Brassica sp.	-	4	-	-	-	-	-	-
Number of species	5	6	6	5	4	4	4	6
Total number of quadrats	169	292	144	250	150	214	201	361
Diversity Index	1.353	0.956	0.924	1.663	0.886	0.886	0.820	1.05
Evenness	0.841	0.534	0.526	0.663	0.639	0.494	0.592	0.588
Variance	0.0019	0.0024	0.0077	0.0023	0.0029	0.0045	0.0028	0.0027

Table 3.2: Diversity index and seasonal occurrence of wild crucifer species in the highlands, cabbage-growing area of Kinangop in Central Province of Kenya

Crucifer species	Number of quadrats with crucifers(2005)				Number of quadrats with crucifers(2006)			
	Hot dry	Long rains	Cold dry	Short rains	Hot dry	Long rains	Cold dry	Short rains
Raphanus raphanistrum	136	262	265	180	101	244	186	284
Erucastrum arabicum	4	29	31	12	7	33	4	18
Rorippa nudiuscula	7	-	-	-	-	-	-	-
Brassica juncea	3	-	-	-	-	-	4	31
Capsella bursa- pastoris	32	30	32	25	-	40	23	-
Lepidium bonariense	2	5	1	2		4	4	19
Rorippa microphylla	16	10	-	-	-	-	-	23
Coronapus didymus	10	-	7	22	6	7	14	11
Sisymbrium officinale	-	-	--	-	-	1	15	-
Crambe kilimandscharica	-	10	10	-	-		3	-
Brassica rapa	-	-	-	-	-	5	-	-
Species no.	8	6	6	5	3	7	8	6
Total number of quadrats	210	346	346	241	114	334	253	386
Diversity Index	1.203	0.896	0.839	0.861	0.434	0.927	1.021	0.989
Evenness	0.578	0.500	0.468	0.535	0.395	0.476	0.491	0.552
Variance	0.0062	0.0037	0.0034	0.0042	0.0067	0.0036	0.0061	0.0034

3.4.2 Incidence of DBM on wild crucifers

Diamondback moth was collected from ten of the wild crucifer species found in the field during the survey (Tables 3.3 and 3.4). DBM was present in 10 out of the 12 wild crucifers recorded in the highlands, while no DBM was found on *C. didymus* and *B. rapa*. The pest was present on *R. raphanistrum* throughout the sampling period. The highest population of 2.24 DBM/plant was recorded during the hot dry season of 2006 from *R. raphanistrum* in Kinangop and during the cold dry season of 2005 in Naro Moru 1.57 DBM/plant. The highest population of 1.4 DBM/plant was recorded during the long rainy season of 2005 in Athi River from *E. arabicum*. No DBM was collected from *E. arabicum* and *Ro. micrantha* in Yatta during 2005 (Table 3.4).

3.4.3 Incidence of DBM on cabbage and kale

Diamondback moth populations varied significantly between seasons in the highlands and mid-altitude semi arid areas in 2005 and 2006 (Table 3.5). The population of DBM was generally higher on kale than on cabbage. The highest mean of 3.6 and 2.0 DBM/plant was recorded during the hot dry season in 2005 in Kinangop and Naro Moru, respectively while the lowest (0.2 DBM/plant) during the short rains and cold dry season in Naro Moru and Kinangop, respectively (Table 3.5). However, in 2006, a higher mean of 1.5 and 1.0 DBM/plant was recorded from Kinangop and Naro Moru during the hot dry and long rain seasons, respectively, while the lower mean was 0.4 and 0.3 DBM/plant during the short rain season in Kinangop and Naro Moru, respectively. When the data was pooled together, Kinangop had higher DBM population than Naro Moru in 2005 and 2006.

In the semi-arid areas, Athi River recorded significantly higher DBM populations than Yatta in both years. The highest population of 5.2 DBM/plant was recorded in Athi River during the long rainy season of 2005, while the lowest was 0.6 DBM/plant during the hot dry season of 2006. In Yatta, the highest mean of 2.9 DBM/plant was recorded during the long rainy season of 2006, while the lowest was 0.6 DBM/plant during the short rain season of 2005 (Table 3.5). When the data on DBM population was pooled together, higher DBM per plant were recorded on cabbage in Kinangop than Naro Moru in both years. Higher DBM per plant on kale was also recorded in Athi River than Yatta in both years

Table 3.3: Seasonal variation of diamondback moth (*Plutella xylostella*) numbers per plant on wild crucifer species in two highland crucifer growing areas namely Naro Moru and Kinangop in Central Province of Kenya.

Wild crucifer species	2005				2006			
	Hot dry	Long rains	Cold dry	Short rains	Hot dry	Long rains	Cold dry	Short rains
Naro Moru								
Raphanus raphanistrum	0.31±0.10	0.16±0.04	1.57±0.23	0.19±0.07	0.16±0.05	1.38±0.24	0.55±0.09	0.6±0.09
Eucastrum arabicum	0.18±0.09	0.14±0.05	0.19±0.10	0	0	0.38±0.29	0.05±0.03	0.12±0.08
Brassica juncea	0	-	-	-	-	-	-	1.2±0.68
Capsella bursa-pastoris	0.35±0.25	0	0	0	-	-	0	0
Lepidium bonariense	0.19±0.10	0	0	0	0	0.25±0.25	-	0
Rorippa microphylla	-	-	0	-	0	-	-	1.5±0.96
Coronopus didymus	-	-	-	0	0	-	-	-
Sisymbrium officinale	-	0.20±0.20	0	-	-	0	0	-
Crambe kilimandscharica	-	1.0±0.41	-	-	-		-	-
Brassica sp.	-	0	-	-	-	-	-	-
Kinangop								
Raphanus raphanistrum	2.08±0.23	0.76±0.09	0.30±0.05	1.39±0.23	2.24±0.49	0.43±0.06	1.25±0.17	1.01±0.12
Eucastrum arabicum	0.25±0.25	0.79±0.26	0.61±0.27	0	0	0.15±0.08	0	0.56±0.28
Rorippa nudiuscula	0.74±0.42	-	-	-	-	-	-	-
Brassica juncea	0	-	-	-	-	-	0	-
Capsella bursa-pastoris	0.84±0.33	0	0	0	-	0	0	0
Lepidium bonariense	0	0	0	0	-	0	0	0
Rorippa microphylla	1.70±0.67	0.70±0.42	-	-	-	-	-	0.74±0.27
Coronopus didymus	0	-	0	0	0	0	0	0
Sisymbrium officinale	-	-	-	-	-	0	0	0.74±0.27
Crambe kilimandscharica	-	1.2±0.55	0	-	-	-	2.2±0.79	-
Brassica rapa	-	-	-	-	-	0	-	-

NB: - refers to absence of wild crucifer during a certain season

Table 3.4: Seasonal variation of diamondback moth (*Plutella xylostella*) numbers per plant on wild crucifer species in two mid-altitude semi arid crucifer growing areas of Eastern Province of Kenya.

Crucifer species	2005				2006			
	Hot dry	Long rains	Cold dry	Short rains	Hot dry	Long rains	Cold dry	Short rains
Athi River								
E. arabicum	-	1.4 ± 0.19	-	0.08 ± 0.06	0.06 ±0.06	0.13 ± 0.05	0	0.21 ± 0.08
Ro. micrantha	-	-	-	0	-	0	0	0.1 ± 0.06
Yatta								
E. arabicum	-	0	0	-	-	0	-	-
Ro. micrantha	-	0	0	-	0.2 ± 0.2	0.17 ± 0.05	0	0.07 ± 0.05

NB: - refers to absence of wild crucifer during a certain season

Table 3.5: Seasonal variation of diamondback moth (*Plutella xylostella*) numbers per plant on cultivated crucifers in highland (Kinangop and Naro Moru) and mid-altitude, semi-arid (Athi River and Yatta) crucifer growing areas of Kenya.

Site	Seasons	2005	2006	Site	2005	2006
Highlands		Mean ± SE	Mean ± SE	Mid-altitude	Mean ± SE	Mean ± SE
Naro Moru	Hot dry	1.99 ± 0.13a	0.66 ± 0.06b	Athi River	1.39 ± 0.12c	2.50 ± 0.18a
	Long rains*	0.76 ±0.07b	1.01 ± 0.07a		5.20 ± 0.33a	2.25 ± 0.13a
	Cold dry	0.96 ± 0.09b	0.93 ± 0.07a		2.77 ± 0.18b	0.58 ± 0.10c
	Short rains	0.24 ± 0.04c	0.33 ± 0.03c		1.49 ± 0.11c	1.49 ± 0.13b
	Yearly average	0.98 ± 0.05	0.72 ± 0.03		2.75 ±0.12	1.72 ± 0.07
Kinangop	Hot dry	3.62 ± 0.20a	1.52 ± 0.13a	Yatta	0.36 ± 0.02d	1.25 ± 0.12b
	Long rains*	0.55 ± 0.05c	0.27 ± 0.04c		1.06 ± 0.12b	2.85 ± 0.19a
	Cold dry	0.27 ± 0.03d	1.07 ± 0.08b		2.05 ± 0.16a	0.73 ± 0.10c
	Short rains	2.20 ± 0.04b	0.41 ± 0.04c		0.60 ± 0.08c	0.72 ± 0.10c
	Yearly average	1.66 ± 0.08	0.82 ± 0.04		1.01 ± 0.06	1.38 ± 0.07

For each site and year, means within a column followed by the same letter do not differ significantly at $P<0.05$ (SNK)
* On long rains, for Athi River and Yatta it is characterized by temperatures above 35°C
Sampling was done on cabbage in the highlands and on kale in mid-altitude areas

3.4.4 Parasitoid fauna on wild crucifers

Six primary parasitoid species were recovered from DBM collected from 7 wild crucifers species (Table 3.6). The parasitoids were recorded from one and seven wild crucifer species in mid-altitude semi arid areas and highlands, respectively. Four species were larval parasitoids (*D. semiclausum* and *Diadegma mollipla* (Holmgren) (both Hymenoptera: Ichneumonidae), *Cotesia plutellae* (Kurdjumov) and *Apanteles* sp. (both Hymenoptera: Braconidae), one a larval-pupal (*Oomyzus sokolowskii* (Kurdjumov) (Hymenoptera: Eulophidae), and one a pupal parasitoid (*Brachymeria* sp., Hymenoptera: Chalcidae). Higher parasitoid species (6 species) were recovered from wild crucifer in mid-altitude areas than in the highlands (3 species). Highest parasitism rates in the highland were observed on *Ro. microphylla*, followed by *R. raphanistrum, C. bursa-pastoris* and *E. arabicum*. In mid-altitude semi arid areas, parasitoids were recovered in Athi River only, from DBM collected from *E. arabicum*. *Diadegma semiclausum* was the dominant and abundant species in the highlands representing over 80 % of the total number recorded. Six parasitoid species were recovered from Athi River and *D. mollipla* was the dominant species. However, parasitism was lower than in the highlands. No parasitoids were recovered from *Ro. micrantha* and *E. arabicum* in Yatta.

3.4.5 Parasitoid fauna on cabbage and kale

In addition to the species mentioned on wild crucifers, *Itoplectis* sp. (Hymenoptera: Ichneumonidae) was found in low numbers in the highlands on cabbage. *Diadegma semiclausum*, was the dominant species in the highland throughout the sampling period of 2005 and 2006. Parasitism rates ranged between 45 % to 79 % in Kinangop and between 60 % to 84 % in Naro Moru (Table 3.7). *Diadegma mollipla* was collected during the hot dry season of 2005 in Kinangop only. However, in 2006 this species was present in low numbers during the cold dry and short rainy seasons in Naro Moru and Kinangop. Parasitism by *O. sokolowskii*, a larval-pupal parasitoid was low and ranged between 0 % and 1.2 %.

Six primary parasitoid species were collected from kale in Yatta and Athi River (Table 3.8). They included *D. semiclasusm, D. mollipla, O. sokolowskii, Apanteles* sp*., Cotesia plutellae, Brachymeria* species. *Diadegma mollipla* and *O. sokolowskii* were the dominant species in 2005. However, in 2006 *D. semiclasusm* became the most dominant

species. Recovery of *D. semiclausum* started in Yatta during the long rainy season of 2005 followed by Athi River during the cold dry season. *Cotesia plutellae* was not recovered in 2005 from Athi River and Yatta despite its initial release in March 2005. However, during the long rains of 2006 *C. plutellae* was recorded from Yatta with parasitism rates of 0.5 % while in Athi river the parasitoid was recovered throughout except during the cold dry season; parasitism rates ranged between 0 and 26.9 %. Despite *O. sokolowskii* being recovered throughout, parasitism rates were low and ranged between 0 and 16 % in Athi River and Yatta.

Total parasitism for the two years combined was higher in the highland areas than in the mid-altitude semi areas. Kinangop recorded the highest parsitism rates of 71 % compared to 63 % in Naro Moru on cabbage while in the semiarid areas on kale Yatta recorded 43 % and Athi river 41 %. Overall, *D. semiclausum* accounted for highest parasitism rates in the four areas. The sex ratio of *O. sokolowskii* wasps that emerged from the parasitised pupae of DBM were female biased. Females constituted 70 % of the total number of adults and very few pupae produced females only. The number of parasitoids per pupa ranged between 3 and 17 and a pupa had a mean of 9.2 adult wasps.

Table 3.6: Parasitism rates and parasitoid species recovered from diamondback moth collected from various wild crucifers in mid-altitude semi arid of Athi River and Yatta crucifer growing areas of Kenya.

Parasitoid species	Wild crucifer species						
	Raphanus raphanistrum	*Erucastrum arabicum*	*Brassica juncea*	*Capsella bursa-pastoris*	*Rorippa microphylla*	*Sisymbrium officinale*	*Crambe kilimandscharica*
Naro Moru							
Diadegma semiclausum	36.1 ± 3.1	16.5 ± 6.1	0	0	41.1 ± 4.9		25
Diadegma mollipla	3.6 ± 1.2	7.0 ± 3.9	0	25	5.7 ± 5.7		
Oomyzus sokolowskii	0.5 ± 0.58	0	0	0	0		
Kinangop							
Diadegma semiclausum	33.6 ± 2.6	11.0 ± 6.8	0	19.1 ± 2.4	39.7 ± 8.4	0	
Diadegma mollipla	6.3 ± 1.3	3.4 ± 3.4	7.1 ± 3.6	19.1 ± 2.4	0	4.2 ± 4.2	
Oomyzus sokolowskii	0	0	3.6 ± 3.6	0	0	0	
Athi River							
Diadegma semiclausum		7.4 ± 2.9					
Diadegma mollipla		10.4 ± 3.5					
Apanteles sp.		9.24 ± 3.5					
Brachymeria sp.		0.2 ± 0.2					
Oomyzus sokolowskii		1.0 ± 0.7					
Cotesia plutellae		1.3 ± 0.9					
Yatta							
Diadegma semiclausum		0					
Diadegma mollipla		0					
Apanteles sp.		0					
Brachymeria sp.		0					
Oomyzus sokolowskii		0					
Cotesia plutellae		0					

Table 3.7: Seasonal variation (Mean ± SE) of diamondback moth (*Plutella xylostella*) parasitism on cabbage in two highland crucifer growing areas of Naro Moru and Kinangop in Central Province of Kenya

Year	Parasitoid species	Naro Moru				Kinangop			
		Hot dry	Long rains	Cold dry	Short rains	Hot dry	Long rains	Cold dry	Short rains
2005	*D. semiclausum*	70.1±4.88a	70.4±3.42a	71.7±3.6a	84.5±4.6	45.2±4.15a	76.0±4.0	63.3±5.76	62.5±4.01
	D. mollipla	0	0	0	0	3.1±3.12b	0	0	0
	Itoplectis sp.	3.2±3.12b	0	0	0	0	0	0	0
	O. sokolowskii	1.2±1.12b	0.4±0.4b	0.4±04b	0	0.2±0.20b	0	0	0
	n	498	242	308	68	641	162	72	475
	df	3,128	3,116	3,128	3,68	3,124	3,80	3,64	3,124
	F	415.4	382.6	333.5	72.2	232.6	120	234.2	267
	p	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001
2006	*D. semiclausum*	68.9±4.22	60.3±4.05a	63.8±3.96a	77.8±4.15a	56.5±4.26	78.3±5.79	51.1±3.85a	74.5±4.68a
	D. mollipla	0	0	0.57±0.43b	0.6±0.59b	0	0	3.6±1.75b	2.24±1.57b
	Itoplectis sp.	0	0.61±0.61b	0	0	0	0	0	0
	O. sokolowskii	0	0	0.91±0.64b	0	0	0	0.3±0.26c	0.5±0.58c
	n	175	283	271	107	462	99	383	120
	df	3,88	3,128	3,132	3,105	3,116	3,80	3,116	3,100
	F	267	215	255.6	345	175	182	138	220
	p	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001

*Means within a column followed by the same letter do not differ significantly at P<0.05, PROC GLM (SNK test)

Table 3.8: Seasonal variation (Mean ± SE) of diamondback moth (*Plutella xylostella*) parasitism on kale in two mid-altitude semi-arid crucifer growing areas of Athi River and Yatta in Eastern Province of Kenya

Year	Parasitoid	Athi River				Yatta			
2005	species	Hot dry	Long rains	Cold dry	Short rains	Hot dry	Long rains	Cold dry	Short rains
	D. semiclausum	0	0	25.5±4.6a	32.1±5.8a	0	0.4±0.4b	29.6±6.2a	40.3±9.2a
	D. mollipla	3.1±2.9a	7.2±3.6a	9.0±2.3c	0.8±0.6b	1.4±1.4b	10.4±6.3ab	9.1±4.2b	5.1±4.4b
	O. sokolowskii	7.2±3.0a	2.3±1.2ab	16.3±2.9b	10.2±2.4b	15.8±6.3a	21.2±7.5a	7.4±2.2b	2.6±1.6b
	Apanteles sp.	0	3.6±1.6ab	4.5±1.6c	4.2±1.6b	0	1.6±0.9b	0	0.4±0.4b
	C. plutellae	0		0	0	0	0	0	0
	Brachymeria sp	0	1.4±1.0ab	0	0	0	0.4±0.4b	0	0
	n	183	645	303	209	63	181	296	106
	Df		5,162	5,156	5,132	5,66	5,126	5,138	5,132
	F		2.46	16.27	20.0	5.76	4.56	12.96	14.4
	p	ns	<0.05	<0.0001	<0.0001	<0.001	<0.001	<0.0001	<0.0001
2006	*D. semiclausum*	9.6±3.4a	30.4±5.7a	52.3±8.2a	63.8±5.5a	16.1±5.3a	33.0±5.2a	47.2±8.0a	42.7±7.0a
	D. mollipla	0.5±0.5b	5.1±2.2b	0	0	0	11.9±2.8b	3.1±2.5b	3.7±1.6b
	O. sokolowskii	1.8±1.2b	4.9±2.1b	7.7±3.4b	1.9±1.1b	1.8±1.5b	1.9±0.7c	3.3±2.0b	0
	Apanteles sp.	4.9±2.3ab	5.1±1.5b	0	0.2±0.1b	6.8±4.7b	4.0±2.1c	1.3±0.9b	0
	C. plutellae	1.1±0.5b	26.9±7.1a	0	1.3±0.8b	0	0.5±0.3c	0	0
	Brachymeria sp	0.1±0.1b	0.7±0.5b	0	1.1±0.5b	1.3±0.8b	2.0±0.7c	0	0.9±0.6b
	n	499	303	98	250	240	551	91	114
	Df	5,138	5,126	5,102	1,144	5,126	5,144	5,114	5,102
	F	4.07	10.52	33.76	123.29	4.44	23.24	28.18	33.43
	p	0.001	<0.0001	<0.0001	<0.0001	<0.001	<0.0001	<0.0001	<0.0001

*Means within a column followed by the same letter do not differ significantly at P<0.05, PROC GLM, (SNK test)

3.4.6 Other pests, predators and parasitoids

Apart from DBM, a wide range of other pests and diseases were associated with the wild crucifers *R. raphanistrum, E. arabicum*, *Ro. microphylla* and *Ro. micrantha* (Plate 3.15-3.18). They included the cabbage aphid *Brevicoryne brassicae* L., the false cabbage aphid *Lipaphis erysimi* Kaltenbach (both Homoptera: Aphididae), cabbage looper *Trichoplusia ni* Hubner. (Lepidoptera: Noctuidae), African bollworm *Helicoverpa armigera* Hubner (Lepidoptera: Noctuidae), cabbage sawfly *Athalia* sp. (Hymenoptera: Tenthredinidae), cabbage webworm *Hellula undalis* Fabricius (Lepidoptera: Pyralidae), whiteflies *Aleyrodes proletella* L. (Homoptera: Aleyrodidae), thrips *Frankliniella* sp. (Thysanoptera: Thripidae), leaf miner *Liriomyza brassicae* (Riley) (Diptera: Agromyzidae), flea beetles *Phyllotreta cruciferae* Goeze (Coleoptera: Chrysomelidae), red spider mite *Tetranychus urticae* Koch., bagrada bug *Bagrada cruciferarum* Kirkaldy (Hemiptera: Pentatomidae) and *Spodoptera exigua* Hubner (Lepidoptera: Noctuidae) (Table 3.9). The diseases *Erysiphe cruciferam* Opiz ex L. Junell and downy mildew, *Peronospora parasitica* (Pers.) Fr., were observed mainly on *R. raphanistrum, E. arabicum, Ro. micrantha, B. juncea* and *S. officinale* while alternaria leaf spot, *Alternaria brassicae* (Berk.) Sacc., on *R. raphanistrum* only. The diseases were more prevalent during the cold season.

A number of beneficial insects were noted on the wild crucifers. The predators included coccinellids, hoverfly larvae as well as spiders. Spiders were abundant in Athi River and Yatta. Coccinelid larvae and ladybird beetles were mainly found on aphid infested crucifer species. The aphid parasitoid *Diaeretiella rapae* M'Intosh (Hymenoptera: Braconidae) was recovered from mummies of *B. brassicae* collected from *R. raphanistrum* and *E. arabicum* (Table 3.9).

Plate 3.15: *Helicoverpa armigera* and mildew on *Rorippa micrantha*

Plate 3.16: Bagrada bug *Bagrada hilaris* on *Rorippa micrantha*

Plate 3.17: Saw fly larvae *Athalia* sp. on *Ro. micrantha*

Plate 3.18: Powdery mildew on *Sisymbrium officinale*

Photos taken by Kahuthia-Gathu

Table 3.9: Occurrence of other pests, parasitoids and predators associated with wild crucifer species found in highland (Kinangop and Naro Moru) and mid-altitude semi arid (Athi River and Yatta) crucifer growing areas of Kenya in 2005 and 2006.

	Wild crucifer species in 4 crucifer growing areas								
	Athi River		Yatta		Kinangop		Naro Moru		
Pest species	*Rorippa micrantha*	*Erucastrum arabicum*	*Rorippa micrantha*	*Erucastrum arabicum*	*Raphanus raphanistrum*	*Erucastrum arabicum*	*Raphanus raphanistrum*	*Erucastrum arabicum*	*Brassica juncea*
Helicoverpa armigera	x	xx	xx		x	x	xx	x	
Spodoptera sp.		x							
Athalia sp.		xx	x			x	xxx	x	
Hellula undalis	x	xx	x			xx	xx	x	
Trichoplusia ni	x	x	x			x	xx	x	
Bagrada cruciferarum	x	x	xx	x					
Lipaphis erysimi		xx				xx	xx	xx	
Brevicoryne Brassicae		xxx	xx		xxx	xx	xxx	xx	
Tetranychus urticae		x	x				x		
Phyllotreta cruciferae	x	xx	x	xx	xx	xx	xx	xx	
Frankliniella sp.		x							
Aleyrodes proletella		x	x						
Liriomyza sp.		x		x		x	x	x	
Parasitoids									
Diaeretiella rapae		xx	xx		xx	xx		xx	
Predators									
Spiders	xx	xx	xx	xx					
Coccinelids		x			x	xx	xx	x	x

NB: x = scarce, xx= common and xxx= frequent presence of the pests, predators and parasitoids on the wild crucifer species

3.5 Discussion

The importance of landscape aspects and particularly diversity of plant species in areas surrounding crop fields, for the management of crop pests has received considerable attention over the last years. Higher plant diversification is assumed to enhance the population of natural enemies, which migrate to crop fields, attack the pests and thereby contribute to a better pest control (Boller et al., 2004; Yann et al., 2007; Olson andWackers, 2007; Bullock et al., 2007). Comparing the literature (from other agroecosystems) and our data the most consequent or logic deduction from our finding, from the practical point of view, is that the existence of wild crucifers in the vicinity of cabbage and kale fields can be expected to provide the capacity for reorganization after disturbance, or resilience as suggested by Bengtsson et al. (2003) and Tscharntke et al. (2005). Hickman and Wratten (1996) and Dyer and Landis (1997) related the number of natural enemies entering the crop field to higher diversity of surrounding vegetation of wheat and maize field, respectively. Pickett and Thompson (1978) suggested that, the disappearance of re-colonisation sources leads to extinction of dominant populations. Hence, agricultural landscape must have both early and late succession plants to support a high biodiversity, and thereby provide the capacity to recover from agricultural disturbance (Bengtsson et al., 2003).

Higher species richness of wild crucifers and higher species dominance by particular species was observed in the highland than mid altitude, semi-arid growing areas. Variation in species diversity and richness has been attributed to differences in amount of rainfall, soil type and over altitude gradient (Cowling, 1990; Montana and Valiente-Banuet, 1998; Suddarapandian and Swamp, 2000). Simmons and Cowling (1996) observed that species diversity changed along soil fertility and geographical gradients in South Africa's Cape Peninsula. Thompson et al., (2005) suggests that the species richness of a community is determined by the soil fertility. Soil fertility limits the number of plant species that can establish in a restored site (Pywell et al., 2003). The higher species diversity in Kinangop than in Naro Moru can be attributed to higher altitude and more rainfall in the former. Higher species diversity recorded mainly during the hot dry season was attributed to most of the farmers leaving the land fallow especially where there was no water to supplement irrigation. The strong influence of seasons on the abundance and diversity of wild crucifers in the highland is a good indication of the relevance of rainfall. In contrast, only two species were found in the semi-arid areas. Their abundance

fluctuated less between the seasons and thus they seem to be much better adapted to water stress than most highland species. *Erucastrum arabicum* was the only species found growing in both highland and semi-arid areas, and was co-dominant in the former and dominant in the latter. We assume that adaptation to growing in dry conditions is a rare trait in crucifers and this is most likely factor responsible for low species diversity in the semi-arid areas. This might also explain why *Ro. micrantha* was only found growing in areas of continuous water flow. Species richness in mid- altitude semi arid areas was limited by water scarcity as observed by Montana and Valiente-Banuet (1998).

Under the "enemies hypothesis" (Root, 1975; Russell, 1989; Wolfe, 2002), weeds introduce an element of biodiversity that expands the spectrum of natural enemies to colonize the crop as the host becomes available (Longley et al., 1997). Weeds are an important part of the vegetative diversity and help in maintaining and augmenting natural enemies' populations (Hooks and Johnson, 2003). This in turn leads to an increase in the number and abundance of species of beneficial insects (Landis et al., 2000; Norris and Kogan, 2005). Weeds can be even more important when they are sharing pests and natural enemies with the cultivated crop (Tscharntke and Kruess, 1999; Kremen, et al., 2002). In such cases, the crops will act as a source of species invading the weeds (Tscharntke et al., 2005) thus, enhancing biological control. Of all wild crucifers collected, *R. raphanistrum* was the most dominant and abundant species in the highlands and it was also observed to flower for extended periods. Importance of flowering plants to parasitoids in providing nectar and pollen in crucifer growing systems has documented by Idris and Grafius (1995) and Winkler et al. (2006). They observed that wildflowers increased the longevity and fecundity of *D. insulare* while Lee et al. (2006) observed that presence of flowering crucifers inside cabbage fields increased parasitism rates. In other studies, *Diadegma semiclausum* showed significant differences in longevity when provided with different sugar solutions (Winkler et al., 2005). This is in accordance with many reports stressing the importance of carbohydrate-rich foods for adult insects.

Russell (1989) postulated that the closer the companion plants are to the cash crop the more effective they are in regulating pest populations. Therefore, the small farm sizes and closeness of wild crucifer species to cultivated crucifer crops in Kenya might have an impact on the management of DBM. It is our opinion that the cruciferous weeds should be left growing along field edges and the surrounding uncultivated areas to provide nectar and refugia to parasitoids.

Diamondback moth numbers were generally low during the surveys, and much lower than those reported by Löhr et al. (2007) on cabbage in highland growing areas with similar growing conditions. The introduction of an exotic larval parasitoid, *D. semiclausum* into the system about two years before this work was started must have contributed to the low DBM numbers. The parasitoid has also lead to a significant DBM population reduction in the pilot release areas (Löhr et al., 2007). DBM populations were higher on kale than on cabbage, and higher on the cultivated crop than on the wild crucifers. Karieva (1983) and Andow (1988) observed that specialist herbivores exhibit lower population densities in diverse habitats containing host plants and nonhost plants compared with simple habitats containing host plants only. Lack of diversity and frequent disturbances through pesticide application on the cultivated crop could have resulted in higher DBM population. The low DBM numbers on wild crucifers could be associated with higher species diversity and high predation in the uncultivated fields. A variety of predators including spiders, were found feeding on the DBM. The results are supported by the findings of Liljesthrom et al. (2002), who found that spiders more abundant in uncultivated insecticide free areas. There was also a general decline in DBM numbers from 2005 to 2006 in the highland areas most probably it is still attributed to the release and establishment of the exotic parasitoids.

Other than DBM, a number of pests, predators and diseases were recorded from the wild crucifers. The numbers were relatively low though not quantified, compared to those on the cultivated crop. *Brevicoryne brassicae* was one of the major pests found on the wild crucifers and seem to be controlled easily by the coccinelids that were found on the weeds. Although powdery mildew was found on the wild crucifers, it was more pronounced on the cultivated crop an indication that its presence on the weeds might not be of great economic importance. However, the weeds could be the source of crop infestation necessitating further investigation. Most of the diseases are easily controlled if detected early. In mid-altitude semi arid areas spiders were found on the plants. However, we cannot deduce their importance in the control of DBM since no further observations were made.

Diseases such as powdery mildew *Erysiphe cruciferarum* Opiz ex L. Junell, downy mildew *Peronospora parasitica* (Pers.) Fr., and angular leaf spot *Alternaria brassicae* (Berk) Sacc., as reported byVarela et al. (2003) were more prevalent during the cold season. Most farmers tend to spray the crop intensively with cocktails more so if attacked

during head formation. However, many are not able to detect the symptoms early enough and this affects the yield. The extensive use of chemicals could lead to elimination of the parasitoids, but with the wild crucifers growing around, they will provide the refugia. Presence of predators on wild crucifers was an indication that they acted as a reservoir or provided refugia. This is of great ecomonic importance because they will act as recolonisation site especially when the farmers spray the crop or harvest leading to their elimination. Presence of other pests on the wild crucifers such as leaf miners and red spider mites when pea and tomato crop was absent, respectively might pose a risk once the crop is planted. However, we hypothesize that the off crop areas function to stabilize the parasitoid populations, which over-weigh the risk of being an important source for the pests.

The number of parasitoids in the cabbage growing areas was significantly higher than in kale growing areas. These could be due to continuous cabbage growing all the year round and abundance of wild crucifer species. Parasitoids strongly respond to vegetation complexity (Marino andLandis, 1996). However, the difference in parasitoid numbers and assemblage may be related to climatic variations. The continuous cropping in the highlands may be partly offering a more stable environment where both DBM and its parasitoids co-exist for a long time. Large patches observed in the cabbage growing areas with wild crucifers may have contributed to high parasitoid numbers. Kruess and Tscharntke (2000) observed that percent parasitism of the weevil *Oxystoma ochropus* was an increasing function of area, doubling from 35 % on the smallest to 70 % on the largest meadows. Other important effects of flowering weeds (food sources) include increased attraction, retention, parasitism and efficiency of natural enemies in the fields. Thies and Tscharntke (1999) observed that parasitism of rape pollen beetle increased with increasing non-crop habitat. Stapel et al. (1997) observed that female *Microplitis croceipes* Cresson (Hymenoptera: Braconidae), a larval parasitoid of *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) stayed longer and parasitised more host larvae found on patches of nectaried cotton plants than on nectariless cotton plants. Zhao et al. (1992) observed that parasitism of DBM by *D. insulare* (Cresson) (Hymenoptera: Ichneumonidae) was higher in broccoli fields adjacent to nectar producing plants than in broccoli fields that were not surrounded by nectar producing plants. In Michigan, presence of wild flowers surrounding the field influenced parasitism rates by *D. insulare* (Idris and Grafius 1993).

Very low numbers of *D. mollipla* were recovered from the wild crucifers and kale, none from Naro Moru and only 1 parasitoid wasp from Kinangop on cabbage. Some of the main reasons that could have led to these include the following: *D. mollipla* is considered relative generalist, The species is reported to be indigenous to eastern and southern Africa, and apart from attacking DBM, it is also known as a parasitoid of potato tuber moth (PTM) *Pytothorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) on potato and tobacco in southern Africa and on potato in Yemen (Kroshel, 1993). The original host of *D. mollipla* is unknown (Gupta, 1974; Azidah et al., 2000) since PTM is an introduced species to Africa. Oduor et al. (1996) observed that *D. mollipla* was the most abundant species of DBM in eastern African highlands. However, overall field parasitism was less than 20 %, with *D. mollipla* accounting for 9%. The parasitoid has also been recovered from DBM on snowpeas, where it recorded significantly higher parasitism rates compared to that of DBM on cabbage (Lohr and Rossbach, 2004). Lack of intrinsic cues to accept the host plant of DBM may also explain the generally low parasitation rates observed in the laboratory (Akol, 2003). Rossbach et al., (2005) observed that *D. mollipla* was not attracted by the chemical odors produced by kale and this could have also contributed to the low parasitism. Absence of *D. mollipla* on cabbage in the highlands two years after the introduction of *D. semiclausum* could be due to stiff competition the parasitoid is facing from *D. semiclausum*, which is known as a DBM specialist with a high searching efficiency (Wang and keller, 2002). This could have forced *D. mollipla* to search for DBM from the wild crucifers, which are the alternative hosts.

Oomyzus sokolowskii is a gregarious larval-pupal parasitoid that attacks DBM (Fitton and Walker, 1992) and has been introduced in tropical and subtropical regions to control DBM (Talekar and Hu, 1966) and is adapted to high temperature conditions. They were abundant in the mi-altitude semi arid areas throughout the sampling period while in the highlands their occurrence was mainly during the hot seasons. Parasitism rates ranged between 0 % and 21.2 % in the mid-altitude semi arid areas and, 0 % and 1.2 % in the highlands. Parasitism by *O. sokolowskii* decreased with the increase in parasitism rates by *D. semiclausum*. This could be due to the low numbers of fourth instar DBM larvae and pupae available for *O. sokolowskii* to parasitise.

The wild crucifers seemed to play a role in the conservation of parasitoids *D. semiclausum, D. mollipla, O. sokolowskii, Apanteles* and *Itoplectis* species. The

apparent levels of parasitism differed between plants and parasitoid species. Although parasitism rates by each parasitoid species were low, when summed up, the total contribution was quantitatively high. It is our opinion that average parasitism rates of about 60 % must be reached in order to have significant influence on the pest population dynamics. Of particular importance was *R. raphanistrum*, which had the highest number of parasitoids species recorded. Momanyi et al. (2006) and Löhr et al. (2007) showed that *D. semiclausum* is very competitive and displaced indigenous parasitoids from cabbage fields even before it had become firmly established in the highlands of Kenya. The data shows that this not the case on wild crucifers, where significant numbers of *D. mollipla* were collected in the highlands and semi-arid areas. *Diadegma semiclausum* could have forced *D. mollipla* to search for prey from the wild crucifers available. Therefore, we can conclude that wild crucifers provided refugia and conserved the indigenous parasitoid species displaced in the cultivated environment.

Much to our surprise *D. semiclausum*, considered a parasitoid for cool highland areas (Talekar and Shelton, 1993), was recovered from the mid-altitude semi arid areas that are hot and dry. The large numbers recovered show that the parasitoid can thrive under these conditions, even though their seasonality indicates their susceptibility to high temperature conditions. *Cotesia plutellae* was released in March 2005 in Yatta and Athi River. However, only very low numbers have been recovered since then. On the contrary, the parasitoid has become established within Lake Victoria region and spread over 200 km from the release sites in Uganda into western Kenya (ICIPE, unpublished data). Remarkably also, is the complete absence of hyper-parasitoids in both highland and mid-altitude semi arid areas, which could have contributed to the successful establishment and spread of *D. semiclausum*.

In conclusion, wild crucifer species should play an important role in Kenya in the conservation and enhancement of parasitoid populations by providing refugia in times of absence of the crop, a reservoir for recolonisation of fields after local elimination of parasitoid through broad-spectrum pesticides and a source of nectar. The more diverse ecosystem helps to stabilize the pest population by favouring density–dependent responses of the pest's natural enemies. Furthermore, they seem to conserve indigenous parasitoid species that were displaced from cultivated areas after the introduction of a superior competitor. Therefore, there should be no total field free of weeds if parasitoids have to function effectively and less pesticides used in the control of DBM. Research on

weed-insect interactions, especially that dealing with the role of diversity in relation to beneficial arthropods, frequently suggests that there is a benefit to leaving weeds as a resource for beneficials (Norris and Kogan, 2005).

CHAPTER FOUR

4 Development and reproduction of diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae) on cultivated Brassica cultivars and wild crucifer species in Kenya

Abstract:
The development, survival and reproductive potential of diamondback moth, *Plutella xylostella* L., were studied at 25 ± 1 ºC in the laboratory in response to two cultivated *Brassica oleracea* cultivars (cabbage *B. oleracea* var. *capitata* and kale *B. oleracea* var. *acephala*) and four wild crucifer species (*Erucastrum arabicum*, *Raphanus raphanistrum, Rorippa nudiuscula* and *Ro. micrantha*). *Rorippa micrantha* was the most preferred species in oviposition choice tests, while cabbage and kale were least preferred. First instar larval mining was longest on cabbage (3.0 days) and shortest on *Ro. micrantha* (0.4 days). Pupal weight was significantly higher for larvae reared on kale while the others were comparable. Survival to adult was comparable in all the species studied. The developmental period from first instar to adult varied from 14.4 days on *Ro. micrantha* and 18.3 days on *R. raphanistrum*. Adult longevity ranged between 18.2 days on *R. raphanistrum* and 24.7 days on *Ro. nudiuscula*. The females were significantly heavier than males on all plant species. However, males lived longer than females. Moths reared on *Ro. nudiuscula* lived longest (24.6 days) and recorded the highest fecundity (326 eggs) while moths reared on cabbage had the lowest fecundity (261 eggs). Moth on cabbage had lowest net reproductive rate (Ro) (95.1 expected females per female) while on kale and *Ro. nudiuscula* the longest generation time of 31.7 days was recorded. The highest intrinsic rate of increase was calculated on *Ro. micrantha* (0.179) and the lowest on kale (0.147). The results indicate that all the species studied are suitable hosts for DBM.

Key words; Diamondback moth, development, survival, fecundity, life table, longevity

4.1 Introduction

The diamondback moth *Plutella xylostella* L. (Lepidoptera: Plutellidae) is the most important pest of cultivated crucifers worldwide (Talekar and Shelton, 1993). It is believed to have originated from the Mediterranean region (Harcourt, 1962). However, Kfir (1998) suggested its origin to be South Africa due to the rich fauna of indigenous parasitoids of DBM and the diversity of wild crucifers in the Cape Province indicating a very long association between the pests and the parasitoids. Using the same arguments, Liu et al (2000) are of the view that DBM originated from China. Virtually, DBM occurs wherever crucifer crops are grown and it is believed to be the most universally distributed of all Lepidoptera (Talekar and Shelton, 1993). Today, DBM is present in almost all the tropical and subtropical regions of the world including eastern Africa (Ayalew, 2006; Löhr et al., 2007). The pest has become the most abundant and damaging pest of cruciferous crops in Kenya and has gained economic importance over the years (Kibata, 1996). The annual cost of controlling DBM worldwide is estimated to be over US$ 1.0 billion (Talekar and Shelton, 1993) in addition to crop loss. The larvae feed on many plants in the crucifer family such as cole crops and on several greenhouse and ornamental plants (Talekar and Shelton, 1993; Reddy et al., 2004). There are numerous crucifer plants which are not consumed by man, are considered as weeds and consumed by the DBM when its favoured hosts are absent and provide a crucial link in maintaining DBM populations (Talekar and Shelton, 1993). The main crucifer species grown are cabbage, kale, Chinese cabbage, cauliflower, radish and broccoli. Crucifer production is a major source of income and contributes to poverty alleviation of unemployed in vegetable production areas. They are produced throughout the year in areas with favourable weather conditions or where supplimentary irrigation is possible. The widespread and intensive use of insecticides has led to serious problems of insecticide resistance (Kibata, 1996; Mohan and Gujar, 2003; Vickers et al., 2004; Shelton, 2004; Sarfraz et al., 2005). Integrated pest management systems based on functional biodiversity and ecological engineering have been considered to be the only viable long-term solutions to combat the pest (Verkerk and Wright, 1996; Gurr et al. 2004).

A number of authors have investigated various aspects of host plant relationship of DBM. Large differences were found between different crucifer species/ varieties in the number of eggs laid and survival (Lin et al., 1983). Gupta and Thornsteinson (1960) observed that DBM could be reared on a variety of leguminous plants but their survival varied with

species. Yamada (1983) reported that DBM reared on three wild crucifers *Capsella bursa-pastoris*, *Rorippa palustris* and *Ro. indica*) had similar performance to those reared on cultivated crop. However, Wakisaka et al (1991) observed that *Capsella bursa-pastoris* was a less suitable host for DBM than cultivated crop but DBM depends on the weeds in absence of the crop. Mohamad et al. (1994) studied the influence of wild crucifers on biological traits of DBM and observed that female adults reared from cabbage and wild crucifers, with lower weight had lower fecundity. These findings suggest that cruciferous weeds are able to sustain feding and reproduction of the DBM.

In case of mobile pests and fast rotating crops, synchronisation of herbivores and natural enemies in time and space is crucial for enhanced conservation biocontrol. Weeds can play a key role in that case. Weeds growing in the vicinity of field crops of the same plant family often harbour crop pests and provide them with refugia. Therefore, presence of wild crucifer stands adjacent to cultivated crop might also act as trap crop, which lure insect pests away from the target crops thus helping in the reduction of DBM populations below the economic threshold. In the case of DBM, they can provide a crucial link for maintaining populations when the crop is not in cultivation (Talekar and Shelton, 1993; Begum et al., 1996). However, uncultivated weedy habitats do not only provide refugia for the pests but also for natural enemies. As such, they can contribute as source habitats for recolonization of cultivated fields by predators and parasitoids (Longley et al., 1997). Moreover weeds introduce an element of plant biodiversity that expands the spectrum of natural enemies available to colonise the crop stand (Tscharntke and Kruess, 1999; Rauwald and Ives, 2001). Uncultivated habitats also offer alternative hosts for predators and parasitoids, and provide food sources like pollen and nectar necessary for natural enemies (de Snoo, 1999; Landis et al., 2000). This may enhance the number and diversity of biological control agents entering a field (Zhao et al., 1991; Hickman and Wratten, 1996; Dyer and Landis, 1997).

Numerous wild crucifer species in the cabbage and kale growing areas of Kenya were found to serve as alternate hosts for DBM (Gathu et al., unpubl. data). As cabbage fields in East Africa are generally small (Macharia et al., 2005), edge effects can be expected to lead to fast and massive immigration of DBM into newly planted fields, in case the wild crucifers are able to sustain a significant pest population. Therefore, the objective was first to evaluate the performance of the diamondback moth on two cultivated *Brassica* cultivars and four wild crucifer species in terms of oviposition preference, larval

development and reproductive potential. The trials were conducted in the laboratory under standard conditions.

4.2 Materials and Methods

4.2.1 Study site

The experiments were conducted at the International Center of Insect Physiology and Ecology (ICIPE) headquarters in Nairobi, Kenya. The studies were conducted in an incubator (Rumed®, Rubarth Apparate GmbH, Laatzen, Germany) at 25 ± 1 ºC, 60-80 % RH and 12:12 L/D.

4.2.2 Diamondback moth culture

A colony of DBM was established and maintained in the insectary at ICIPE on common head cabbage *Brassica oleracea* var. *capitata* L. cultivar Gloria from larvae and pupae originally collected from cabbage grown in Werugha Location, Taita Taveta District, Coastal region of Kenya at 03°26'16''S, 38º20'24''E and altitude 1650 m. The moths were reared as described by Löhr and Gathu (2002) and had no previous encounter with wild crucifers.

4.2.3 Host plants

Two cultivated crucifers, head cabbage *B. oleracea* var. *capitata* L. cultivar Gloria, and kale, *Brassica oleracea* var. *acephala* L. cultivar Thousand headed, and four wild crucifers, *Erucastrum arabicum* Fisch. & Mey., *Raphanus raphanistrum* L., *Rorippa micrantha* (Roth.) Jonsell, and *Rorippa nudiuscula* (Sond.) Thell., were selected for use in experiments on development and reproductive potential of DBM. The rationale for the selection of the wild crucifer species was their common occurrence in or on the highlands and mid-altitude crucifer growing areas, and presence of various stages of diamondback moth on the plants during field surveys conducted prior to the experiments. Seeds of the wild crucifers were collected during the survey while those of cabbage and kale were purchased from the agrochemical shops. Seedlings were raised in the greenhouse in seedling trays and transplanted three weeks after germination into 15 cm diameter plastic

pots (2 litres). A mixture of red soil, garden compost and sand (mixing ratio 2:1:1) was used as the growth medium and no fertilizer was applied. The plants were ready for use in the trials six weeks after transplanting. All the plants in these studies were nine weeks old at the time they were used in the screen houses or laboratory.

4.2.3.1 Oviposition preference

Choice and no choice oviposition preference tests were conducted in the screen house using whole plants from both cultivated Brassica cultivars and wild crucifer species. The experiments were performed with potted cabbage, kale and *R. raphanistrum* plants grown to the sixth fully extended leaf stage, whereas *E. arabicum, Ro. micrantha* and *Ro. nudiuscula* were grown to the 10-15 fully extended leaf stage. In the choice tests, four plants from each host plant species mentioned above were randomly placed in a cage (1 m × 1.3 m × 2.5 m) made of muslin cloth with a sleeve on the sides for introducing DBM adults (Plate 4.1). Ten pairs of newly emerged and mated DBM adults from cabbage culture were released in the cage and fed on 10% sugar solution soaked in cotton wool. After 48 hours, the leaves were removed and the number of eggs on the upper and lower leaf surface recorded. The experiment was replicated six times.

Plate 4.1: Experimental setup for choice oviposition preference tests

In the no choice tests, four plants of the same cultivar or species were placed in a cage (1 m × 1 m × 1 m) made from muslin cloth with a sleeve on the sides for introducing DBM adults. Four pairs of newly emerged and mated DBM adults from cabbage culture were released into each cage and fed on 10 % sugar solution soaked in cotton wool. After 48 hours, the plants were removed and the number of eggs on upper and lower leaf surface recorded. The experiment was replicated six times for each *Brassica* cultivar and the wild crucifer species.

A second no choice test was conducted in the lab using excised leaves to confirm our earlier results in the screen-house where DBM had also laid eggs at the stem-soil interface and on the plastic pots, with cabbage and kale as host plants. Leaves of the test species were placed individually in a plastic vial (6 cm long by 2.5 cm diameter) containing tap water to prevent the leaf from drying. The mouth of the vial was covered with cotton wool to prevent DBM from drowning. Two leaves of the same species were exposed in a perspex cage (20 cm × 20 cm × 30 cm) simultaneously to gravid females. Five pairs of newly emerged and mated adult moths from the cabbage culture were released into each cage with the host plant leaves and fed on 10 % sugar solution soaked in cotton wool. After 48 hours, the leaves were removed and the number of eggs on upper leaf surface, lower leaf surface and on the walls of the plastic vials recorded. The experiment was replicated fifteen times for each plant species.

4.2.3.2 Effect of host plants on egg hatchability

Hatchability of eggs laid on different crucifer species was determined by taking fifteen leaves from each plant species from the oviposition preference test. The number of eggs on each leaf was recorded. The leaves were then placed individually in transparent plastic containers (5 cm × 6.5 cm × 7 cm) whose cap had a muslin cloth in the center for aeration and placed in the incubator at 25 ± 1 ºC, 60-80 % RH, 12:12 h (L: D) until the eggs hatched. The number of hatched neonate larvae from each leaf was recorded.

4.2.3.3 Effect of host plant species on development, survival and reproductive potential of DBM

One hundred and fifty neonate DBM larvae from each plant species were used in the trials. A single larva was picked using a fine camel hair brush and placed individually in

a well ventilated plastic vial (2.5 cm × 6 cm) with a piece of fresh leaf from the test plants. A piece of tissue paper was placed in the vial to absorb excess moisture and keep the leaf fresh. The mouth of the vial was covered with cotton to allow ventilation and placed in the incubator at 25 ± 1 ºC, 60-80 % RH, 12:12 h (L: D). The larvae were observed daily for any mortality until pupation while the leaves were changed every two days. The duration of larval mining and larval development period was recorded. The pupa was removed from the vial and weighed within 24 hours of pupation using a Mettler electronic scale (Type AM 100, Mettler, Switzerland) and returned to the vial for adult emergence. The duration of the pupal period and sex of newly emerged adult moths were recorded.

The adults from the previous experiment were used for longevity and reproductive potential studies. Newly emerged females were paired with males reared from the same plant species and allowed to mate for 24 hours. A single detached leaf from the respective host plant species in a plastic vial as described before was placed in a clear conical plastic container (5 cm × 6.5 cm × 7 cm). This was covered with an inverted transparent plastic container (5 cm × 6.8 cm × 12 cm) whose bottom was cut out and replaced with a muslin cloth for ventilation. One pair of adult moth was released in the plastic container for egg laying on the same plant species it had been reared on. The moths were fed a 10 % sugar solution soaked in cotton wool. After 48 hours the leaf was changed and the number of eggs on both leaf surfaces (upper and lower) as well as on the walls of the container recorded. The procedure was repeated every 48 hours until the female died. The longevity of males and females was recorded. The experiment was conducted in an incubator at the conditions stated above.

4.2.3.4 Life table parameters

Life table parameters were constructed as suggested by Southwood (1978) and calculated using the jackknife method. DBM eggs were collected from the culture and kept in the incubator for hatching. Upon hatching, the larvae were transferred individually to leaves from different host plants placed in well-ventilated vials using a fine camel hairbrush. The experiment was conducted in the incubator at 25±2 ºC, 60-80 % RH, 12:12 h (L: D) and the developmental period, fecundity, progeny, sex ratio and adult longevity of each individual recorded. The age of each individual (pivotal age, x) was measured since the

egg was laid; the first age class for the adults was 1. egg census was made at two days interval. For adults the probability of surviving upto age class x (l_x) and the expected number of offspring (m_x) for a female in age class x.

4.3 Data analysis

The data on oviposition preference studies in choice test was analyzed using Friedman's Non-parametric Analysis of Variance by Ranks (Zar, 1996). No choice oviposition preference tests was first transformed using SQRT transformation and submitted to one-way Analysis of Variance (ANOVA) using the general linear model procedure of SAS for PC (SAS Institute, 2004) and the means separated using Tukey's Multiple Comparison test at P<0.05 (SAS Institute, 2004). The data on DBM development, duration of larval mining and total larval period, pupal weight, pupal period, fecundity and adult longevity were subjected to one-way analysis of variance (ANOVA) using the general linear model procedure of SAS for PC. Means were separated using Student Newman Keuls test (SNK) at P<0.05 (Sokal and Rohlf, 1995). Percent survival until adult and egg hatch from different host plants were calculated as (number of emerged adults/total number of neonate larvae exposed)*100 while percent egg hatch was calculated as (number of eggs hatched/total number of eggs)*100. The percentage data was then subjected to one-way ANOVA using GLM procedure. Life table statistics were calculated using Jackknife program according to Hulting et al., (1990). Differences in r_m value were calculated following the protocol of Dixon (1987).

4.4 Results

4.4.1 Oviposition preference

Diamondback moth distinctly preferred some host plants to others in both choice (F= 7.97; df = 10, 133; P<0.0001) and no choice experiments (F=10.76; df=5, 138; P<0.0001). In both tests, the DBM laid significantly higher number of eggs on wild crucifers than on cabbage and kale. The eggs were deposited in batches of 7 to 13 eggs. The highest number of eggs was recorded on *Ro. micrantha* while cabbage was the least preferred (Table 4.1). The number of eggs on cabbage and kale was similar in choice test experiment. In the no choice test, DBM laid eggs on the walls of the plastic pot with cabbage and kale. Significantly higher number of eggs was laid on the upper leaf surface

than on the lower surface on all the crucifer species. These results were confirmed with excised leaves in the laboratory where preferential oviposition on leaves was observed on *R. raphanistrum*, *E. arabicum, Ro. micrantha* and *Ro. nudiuscula* while on head cabbage and kale, 85% of the eggs were laid on the walls of the plastic container and the vial containing the excised leaf (Fig. 4.1). Females deposited significantly more eggs on the stem near the soil surface than on the leaves on cabbage and kale. However, all eggs on the wild crucifers were deposited on leaves and none on the stem.

Table 4.1: Number of eggs laid (Mean ± SE) per female DBM in 48 hours in choice and no-choice oviposition preference tests, and their distribution on the leaf surface on two cultivated Brassica cultivars and four wild crucifer species

Plant species	Number of eggs laid in 48 hours per female		Egg distribution on leaf surface	
	Choice test	No choice test	Upper surface	Lower surface
B. oleracea var. *acephala*	9.1 ± 2.6c	23.4 ± 2.5b	6.4 ± 1.1a	2.8 ± 1.9b
B. oleracea var. *capitata*	5.6 ± 1.0c	16.9 ± 2.0c	4.7 ± 0.9a	0.9 ± 0.3b
Erucastrum arabicum	29.9 ± 4.7ab	59.4 ± 8.1a	21.2 ± 3.1a	8.7 ± 1.9b
Raphanus raphanistrum	21.7 ± 3.2b	49.8 ± 6.2a	13.4 ± 2.2a	8.3 ± 1.9b
Rorippa nudiuscula	24.6 ± 2.8b	46.6 ± 5.9a	18.8 ± 1.9a	5.8 ± 1.1b
Rorippa micrantha	38.6 ± 6.9a	62.8 ± 7.3a	29.0 ± 5.4a	9.6 ± 1.9b

*Means in the same column (number of eggs) and same row on egg distribution followed by the same letter do not differ significantly at $P<0.05$ (SNK test).

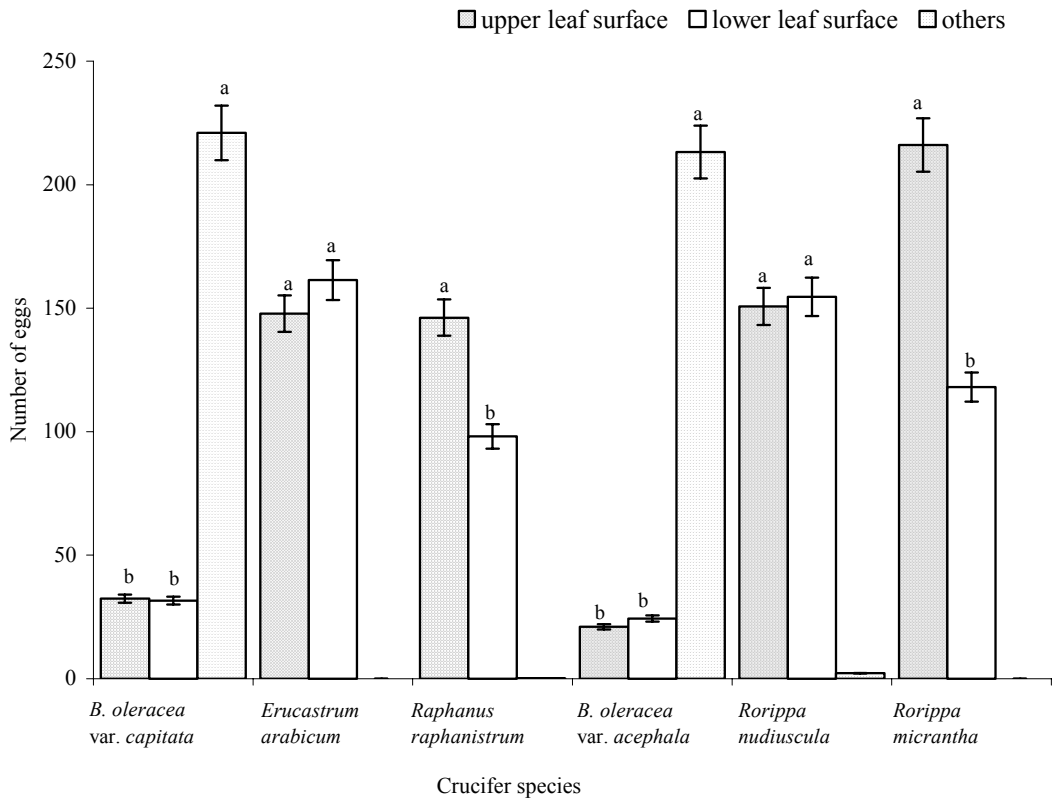


Figure 4.1: Number and distribution of DBM eggs on excised leaves in no choice test on two cultivated Brassica cultivars and four wild crucifer species

4.4.2 Effect of host plant on egg hatchability

Significant differences (F=10.29; df=5,169; P<0.0001) were recorded on percent egg hatch between different host plants. Percent egg hatch was similar on all test plants except *Ro. micrantha* which recorded the lowest percent egg hatch of 75.1 % while the others had over 90 % of the eggs hatching (Table 4.2).

Table 4.2: Mean (± SE) of percent egg hatch of eggs oviposited by DBM on two cultivated Brassica cultivars and four wild crucifer species

Plant species	% Egg hatch
B. oleracea var. *acephala*	92.2 ± 1.2a
B. oleracea var. *capitata*	93.6 ± 1.5a
Erucastrum arabicum	90.8 ± 2.1a
Raphanus raphanistrum	93.4 ± 2.2a
Rorippa nudiuscula	89.8 ± 1.8a
Rorippa micrantha	75.1 ± 3.8b

Means ± SE in the same column followed by the same letter do not differ significantly at P=0.05 (Tukey test

4.4.3 Development and survival of DBM on Brassica cultivars and wild crucifers

Host plants significantly affected the larval mining period (F=168.43; df=5, 750; P<0.0001), duration of larval development (F=15.48; df=5, 621; P<0.0001), pupal weight (F=4.15; df=5, 612; P<0.001), pupal period (F=5.9; df=5, 569; P<0.0001) and development time (F=16.09; df=5, 568; P<0.0001) (Table 4.3). The duration of larval mining ranged from 0.4 on *Ro. micrantha* to 3.0 days on cabbage. The longest larval period of 10.0 days was recorded from DBM reared on kale and *R. raphanistrum* while the shortest period of 8.7 days from DBM reared on *Ro. micrantha.* Pupae reared on kale had the highest mean weight of 6.1 mg while those reared on *R. raphanistrum* the lowest weight of 5.5 mg. *Raphanus raphanistrum* induced the longest pupal period of 5.6 days while pupae from *Ro. nudiuscula* developed fastest with a mean of 5.1 days. Development time ranged between 14.1 days from DBM reared on *Ro. micrantha* and 15.6 days from DBM reared on *R. raphanistrum*. Larval mortality of DBM was significantly higher than pupal mortality on all test plants (Figure 4.2). The highest larval mortality was recorded on *E. arabicum* followed by *R. raphanistum*, and *Ro. nudiuscula,* while *Ro. micrantha* had the highest pupla mortality and *R. raphanistrum* the lowest. There was no significant difference in percent survival of DBM from larval to adult stage

(*F*=1.53; df=5, 19; P=0.23). Percentage survival to adult ranged between 69 % in *Ro. micrantha* and 81 % in *R. raphanistrum* (Table 4.2). Females had significantly (*F*= 50.0; df= 1, 5; P <0.0001) heavier pupal weight than males in all host plants while males lived longer (*F*= 34.28; df =1, 5; P <0.0001) than females.

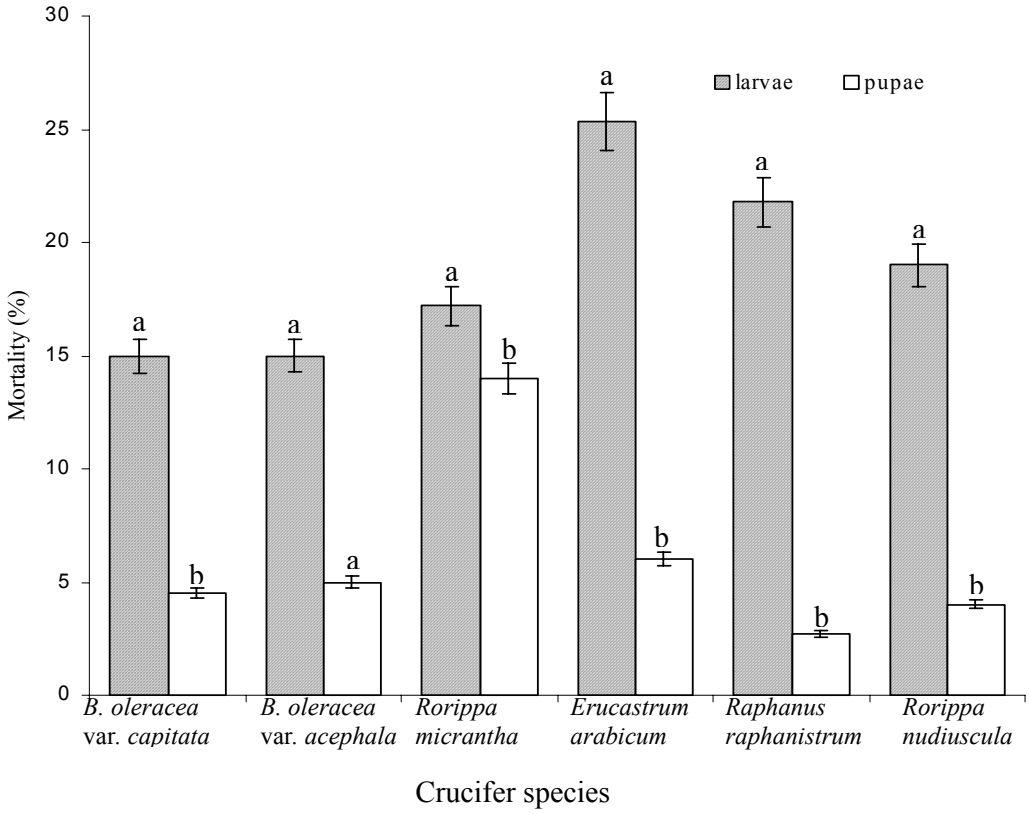


Figure 4.2: Mean percent larval and pupal mortality (± SE) of DBM reared on two cultivated Brassica cultivars and four wild crucifer species

Table 4.3: Mean (value ± SE) of mining, larval and pupal period, development time and survival to adult of the diamondback moth on two cultivated brassica cultivars and four wild crucifer species

Plant species	Mining period (days)	Larval period (days)	Pupal period (days)	Pupal weight (mg)	Development period (days)	% survival to adult
B. oleracea var. *acephala*	2.0 ± 0.08c	10.0 ± 0.11a	5.4 ± 0.06a	6.05 ± 0.09a	15.4 ± 0.14a	80 ± 4.1a
B. oleracea var. *capitata*	3.0 ± 0.07a	9.5 ± 0.95b	5.4 ± 0.06a	5.68 ± 0.07b	14.9 ± 0.11bc	80 ± 4.7a
Erucastrum arabicum	1.4 ± 0.09d	9.7 ± 0.12ab	5.5 ± 0.07a	5.68± 0.09b	15.1 ± 0.13ab	69 ± 6.6a
Raphanus raphanistrum	2.7 ± 0.08b	10.0 ± 0.13a	5.6 ± 0.07a	5.59 ± 0.09b	15.6 ± 0.14a	81 ± 2.9a
Rorippa nudiuscula	0.8 ± 0.08e	9.5 ± 0.11b	5.1 ± 0.09b	5.69 ± 0.11ab	14.5 ± 0.15cd	78 ± 4.7a
Rorippa micrantha	0.4 ± 0.06f	8.7 ± 0.09c	5.4 ± 0.07a	5.69 ± 0.12ab	14.1 ± 0.14d	69 ± 2.0a

*Means ± SE in the same column followed by the same letter do not differ significantly at P=0.05 (Tukey test).

4.4.4 Adult longevity and fecundity

Longest adult longevity was recorded on DBM reared on *Ro. nudiuscula* 24.7 days, which was significantly (F= 8.53; df = 5, 401; P <0.0001) longer than DBM reared on the other host plant species (Table 4.4). Shortest adult longevity of 18.2 days was recorded on DBM reared on *R. raphanistrum* Host plant species had significant influence on fecundity (F=4.74; df=5,212; P<0.005). Females reared on *Ro. nudiuscula* had the highest mean fecundity of 326.7 eggs while those reared on cabbage had the lowest fecundity of 261.6 eggs.

Table 4.4: Adult longevity and fecundity of diamondback moth (mean ± SE) reared on two cultivated Brassica cultivars and four wild crucifer species

Plant species	Adult longevity (days)	Fecundity
B. oleracea var. *acephala*	20.7 ± 0.86b	285.3 ± 10.4ab
B. oleracea var. *capitata*	19.0 ± 0.93b	261.6 ± 7.1b
Erucastrum arabicum	18.5 ± 0.73b	309.4 ± 10.3a
Raphanus raphanistrum	18.2 ± 0.62b	264.7 ± 12.7b
Rorippa nudiuscula	24.7 ± 0.87a	326.7 ± 18.9a
Rorippa micrantha	20.4 ± 0.64b	312.1 ± 17.1a

*Means ± SE in the same column followed by the same letter do not differ significantly P=0.05(SNK test).

4.4.5 Life table parameters

The intrinsic rate of increase (r*m*) was highest on *Ro. micrantha* (0.179) and lowest on kale (0.147) (Table 4.5). The net reproductive rate (Ro), which is a product of mean total fecundity, survival and sex ratio differed significantly between host plant species. The highest Ro value of 126.4 expected females per female was recorded from DBM reared on *E. arabicum,* while the lowest Ro value of 95.1 expected females per female from DBM reared on cabbage. The shortest generation time (G) of 26.9 days was recorded on *Ro. micrantha* while the highest 31.7 days was recorded on *Ro. nudiuscula* and kale. Highest finite rate of increase (e^{rm}) of 1.20 was recorded on DBM reared on *Ro. micrantha* while the lowest 1.15 on DBM reared on cabbage. Over 80 % of the total

fecundity was laid within 7 days of adult emergence despite most of the female adults living upto 23 days after emergence (Figure 4.3).

Table 4.5: Effect of two cultivated Brassica cultivars and four wild crucifer species on life table parameters of the diamondback moth under laboratory conditions

Plant species	Intrinsic rate of increase (r_m)	Net reproductive rate (Ro)	Generation time (days)	Finite rate of increase e^{rm}
B. oleracea var. *acephala*	0.147 ± 0.002e	106.0 ± 3.9c	31.7	1.16
B. oleracea var. *capitata*	0.159 ± 0.002cd	95.1 ± 2.6d	28.6	1.17
Erucastrum arabicum	0.177 ± 0.002ab	126.4 ± 4.2a	27.4	1.19
Raphanus raphanistrum	0.161 ± 0.002c	104.0 ± 5.0cd	28.9	1.18
Rorippa nudiuscula	0.150 ± 0.002e	116.4 ± 6.3b	31.7	1.16
Rorippa micrantha	0.179 ± 0.001a	124.9 ± 5.9a	26.9	1.20

*Means ± SE in the same column followed by the same letter do not differ significantly at P=0.05 (SNK test).

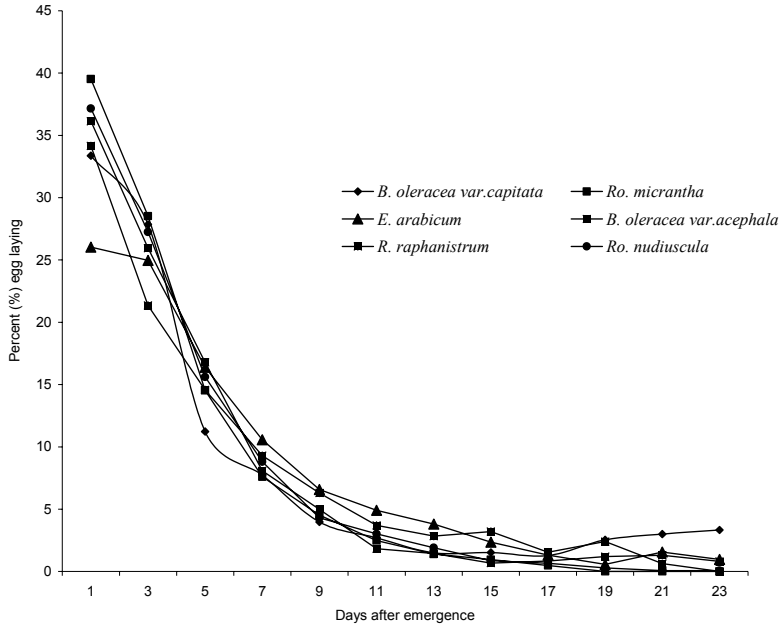


Figure 4.3: Mean oviposition dynamics per female DBM on two cultivated Brassica cultivars and four wild crucifer species in different days after adult emergence.

4.5 Discussion

In our studies, wild crucifers were more attractive to ovipositing females than the cultivated *Brassica* (cabbage and kale) cultivars: in choice tests, females laid more eggs on all wild crucifers and four and nine times more on *Ro. micrantha* than on cabbage and kale. Higher numbers of eggs were recorded on the upper leaf surface in both choice and no-choice tests on potted plants as well as on detached leaves. Normally DBM is known to oviposit mainly on the upper surface (Justus et al., 2000). On cultivated Brassica cultivars (cabbage and kale), a number of eggs were laid near the soil-stem interface and on the walls of the plastic pots in both choice and no choice oviposition preference tests. Depositing of the eggs on the stem near the soil surface could be as a result of DBM developing behavioural resistance through selection of oviposition site as observed by (Safraz et al., 2005). Host finding and host acceptance are two distinct processes and often different cues are involved. Semiochemicals are important for long-range orientation (Bernays and Chapman, 1994, Hardie et al. 2001) and green leaf volatiles (Reddy and Guerrero, 2000) have been identified to play a major role in host-finding behaviour of diamondback moth; some of the chemicals involved have also been determined (Reed et al., 1989). Vision was shown to be of minor importance in the case of DBM in relation to olfaction (Couty et al., 2006).

Physical and gustatory stimuli guide host acceptance (Justus and Mitchell, 1996; Badenes-Perez et al., 2004) and for DBM, non-volatiles such as glucosinolates are important for oviposition (Renwick and Radke, 1990). Leaf surface wax also plays a role in DBM host acceptance as glossy phenotypes are associated with increased oviposition but reduced larval survival (Eigenbrode et al., 1991b). Total leaf area and leaf shape do not seem to be major factors: Badenes-Perez et al. (2004) observed that in choice tests, the number of eggs laid on glossy collards, yellow rocket and Indian mustard were higher than on waxy collards and cabbage. Glossy and waxy collards and cabbage had similar and significantly larger leaf areas than Indian mustard and yellow rocket. This coincides with our results where *E. arabicum*, *Ro. micrantha, R. raphanistrum* and *Ro. nudiuscula* had significantly higher number of eggs although the leaf area was smaller than those of the cultivated species. *Raphanus raphanistrum* and *E. arabicum* had the surfaces covered with hairs while kale, cabbage, *Ro. nudiuscula* and *Ro. micrantha* had no hairs and their surfaces were very smooth and shiny. Current knowledge does not allow us to clearly determine what makes the wild crucifers more attractive for ovipositing females

nevertheless; our findings allow us to draw some conclusions. We hypothesize the existence of volatiles responsible for distance attraction as oviposition in all choice and no-choice tests was on or in close vicinity to the host plants. We can further conclude that wild crucifers were favoured in the host acceptance process because of the higher number of eggs laid on the leaf itself instead of the pot or vial holding the plant/leaf in the case of the cultivated crucifers. The reasons, however, are not evident. We assume that leaf surface wax and tactile stimuli (trichomes and hairs, prominent leaf veins) must have played a role in our studies, as there is no distinct leaf surface wax in any of the wild crucifers studied and also leaf structure and texture is very different from the cultivated species.

Substantial larval mortality is commonly observed and affects particularly early stages of DBM (Zalucki et al., 2002). Variation in host-plant quality can be expected to affect larval development, survival and pupal weight, which in turn can determine fecundity (Idris and Grafius, 1996). The crucifers are a large and diverse family with a long list of secondary metabolites, some of them highly toxic (Agrawal and Kurashige, 2003; Wittstock et al., 2003). It is therefore not surprising, that different crucifer species vary considerably in their suitability for DBM. Mortality can also be due to environmental conditions, host plant species, their nutritional quality and secondary metabolites (Biever and Boldt, 1971; Begum et al., 1996; Syed and Abro, 2003). We can exclude environmental conditions as all our plants were raised in the greenhouse. We found higher larval mortality on wild crucifers tested compared to cultivated Brassica cultivars but the opposite in oviposition preference. Badenes-Perez et al. (2004) recorded 18 times more eggs on *B. juncea,* 12 times more on yellow rocket (*Barbarea vulgaris* (L.) R. Br.) and three times more on glossy collard than on cabbage. Yet yellow rocket does not support larval development in spite of its attractiveness for oviposition and has even been termed a “dead end trap crop” (Lu et al., 2004; Shelton andNault, 2004). A clear indication that the choice a female makes for egg laying may not always be the best for survival of the progeny. In evolutionary terms, this seems counter-intuitive. It appears that females make a host selection with insufficient information: they cannot always identify the absence of vital nutritional substances or the presence of metabolites that may not be conducive for the development of immature stages (Biever and Boldt, 1971; Begum et al., 1996; Syed and Abro, 2003).

Larval mining is a normal feeding habit for the DBM. Upon hatching, the first instar neonate larvae mines into the spongy mesophyll leaf tissues where they remain until they moult to the second instar, which exits from the mines and starts feeding on the underside of the leaf. Longer larval mining period observed on cabbage kale and *R. raphanistrum* could have been due to difference in leaf thickness other than suitability of the host. However, no measurements were taken on leaf thickness.

Larval duration can be greatly influenced by differences in the suitability of plant species (Idris andGrafius, 1996). This did not seem to be the case with the wild crucifers we tested: even though DBM on *Ro. micrantha* had the shortest larval period, pupal weight was similar to the best-performing host plants while larvae reared on *R. raphanistrum* had the longest larval period combined with lowest weight. Sant et al. (1982) and Reddy et al. (2004) reported the shortest larval development on cauliflower, cabbage and radish compared to turnip and mustard contrary to our findings where *Ro. micrantha* recorded the shortest larval period compared to kale, cabbage, *E. arabicum*, *R. raphanistrum* and *Ro. nudiuscula*. The pupal weight of diamondback moth reared on *B. oleracea* var. *acephala* were significantly higher than those reared from *B. oleracea* var. *capitata* and the wild crucifers. Similarly, Muhamad et al. (1994) and Begum et al. (1996) showed that diamondback moth reared from cabbage was larger than those reared from wild crucifers.

As far as performance of adults reared from wild crucifers is concerned, all wild species produced females that laid more eggs and only for *Ro. micrantha* than for all others. Our observations of similar or even higher intrinsic rates of increase of DBM raised on wild than on cultivated crucifers is contrary to much of the conventional wisdom: Bigger and Fox (1997) who observed that DBM reared on cabbage and kale had higher survival than on *C. bursa-pastoris*. Sant et al. (1982) and Reddy et al. (2004) observed higher larval survival on head cabbage compared to turnip (*Brassica rapa* L.) and mustard (*Brassica napus* L.). Idris and Grafius (1996) observed higher survival on kale than on cabbage and wild radish *R. raphanistrum*. Wakisaka et al. (1992) recorded significantly reduced fecundity of larvae reared on *C. bursa-pastoris* compared to broccoli and head cabbage. Begum et al. (1996) showed that female *P. xylostella* reared on *Ro. indica* and *Lepidium virginicum* (L.) Hiern. were less fecund than those reared on head cabbage. However, Muhamad et al. (1994) and Begum et al. (1996, 1997) obtained larger and more fecund females from cabbage than from wild crucifers. Similar observations were made for

another crucifer specialist: Benrey et al. (1997) observed that *P. rapae* performed better on cultivated cabbage than on a wild crucifer *Lunaria annua* L.

The use of intrinsic rate of increase integrates the effects of mortality and fertility factors into single value. The results of life table corroborated with our hypothesis that there are siginificant differences between cultivated Brassica cultivars and the wild crucifer species. Similarly, the results were comparable with that of Syed and Abro (2003). They obtained intrinsic rate of increase between 0.24 on *B. oleracea botrytis* and 0.181 on *Raphanus sativa*. However they obtained a higher intrinsic rate of increase from DBM reared on *B. oleracea* var. *capitata* of 0.228 and a lower generation time of 18.8 days while in our studies, DBM reared on the same species had an intrinsic rate of 0.159 and generation time of 28.6 days. Unfortunately, they have not stated at what temperatures they conducted the experiments in the laboratory, as this could have been the reason for the differences since the tread seems to be the same. The study is of economic importance as a parameter for checking population icrease in the field.

If we follow Kfir's suggestion (Kfir, 1998) that the diamondback moth is an African species, our findings appear less surprising. The species might have been associated with wild African crucifers for a long enough time to allow for co-evolution to take its course and bring about high survival on plant species highly attractive for oviposition.

In conclusion, oviposition preference and life table studies revealed that some common wild crucifers of Kenya were highly attractive to ovipositing females, allowed for larval and pupal development which resulted for some species in higher intrinsic rates of increase of the pest than the cultivated species. Since DBM was able to develop on the wild crucifers in the laboratory, we assume that those will act as its alternative hosts in the field as well. If these plants are also attractive to parasitoids, they should provide refugia to parasitoids in the fields when the crucifer crop is absent. This is particularly important for the recently introduced parasitoid, *D. semiclausum*, which has provided good control of the pest in Kenya but is susceptible to local extinction through application of broad-spectrum pesticides.

CHAPTER FIVE

5 Effect of cultivated and wild crucifer species on development, reproductive potential and parasitism of *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae) and *Diadegma semiclausum* (Hellen) (Hymenoptera: Ichneumonidae)

Abstract

The parasitoids *Cotesia plutellae* and *Diadegma semiclausum* found on cultivated and wild crucifers in Kenya are important larval parasitoids of diamondback moth *Plutella xylostella*. Parasitoid fitness, fecundity and sex ratio can, directly or indirectly, be affected by the plant the herbivorous host feeds on. We studied the development, survival, fecundity and parasitism of both parasitoids on DBM raised on two cultivated Brassica cultivars (cabbage and kale) and six wild crucifers (*Erucastrum arabicum*, *Raphanus raphanistrum*, *Rorippa micrantha*, *Ro. nudiuscula, B. juncea* and *Sisymbrium officinale*). Egg-larval period of *C. plutellae* was shortest on *S. officinale* (7.0 days) and longest on *R. raphanistrum* (9.3 days) while that of *D. semiclausum* was shortest on *B. juncea* (6.7 days) and longer on cabbage, *E. arabicum*, *Ro. micrantha* and *Ro. nudiuscula*. Longer pupal period and heavier pupae of *C. plutellae* and *D. semiclausum* were recorded on kale (2.11 mg) and cabbage (5.06 mg), respectively. Egg-adult development time of *C. plutellae* was significantly longer on *R. raphanistrum* (15.2 days) and shortest on *S. officinale* (11.9 days) while that of *D semiclausum* was longest on *Ro. micrantha* (16.1 days) and shortest on *E. arabicum* (12.4 days). Development time of both parasitoids was similar on cabbage and kale. On all crucifer species females were heavier and took longer to develop than males. Reproductive potential of *C. plutellae* and *D. semiclausum* was lower on *B. juncea* (108 eggs) and *Ro. nudiuscula* (167), respectively. More females emerged from cabbage than from other plant species. Larval and pupal mortality of parasitoids was higher on wild crucifers than on cultivated crucifers. Significantly more adults emerged from cultivated than from wild crucifers. Parasitism was higher on cabbage and kale than on wild crucifers. Higher number of DBM larvae not re-collected from the plant (dropped to the ground), was recorded in the trials where DBM was exposed to *C. plutellae* than to *D. semiclausum*. The results suggest that wild crucifers growing around the cultivated fields can support

the parasitoids. They can conserve and provide refugia to parasitoids, which lowers risk of local extinction from pesticide application.

Key words: *Diadegma semiclausum*, *Cotesia plutellae*, diamondback moth, development, mortality, fecundity, parasitism

5.1 Introduction

Parasitoids are very important natural enemies of Brassica pests (Billqvist and Ekbom, 2001). They complete their larval development on a single host. Their survival and fitness are intrinsically linked to the quality and fate of their host (Godfray, 1994; Quicke, 1997). Variation in host-plant quality is known to affect the body size of herbivorous insects (Bjorkman, 2000; de Bruyn et al., 2002). Many studies have demonstrated that plant quality can influence parasitoid performance directly or indirectly through development of the phytophagous host (Fox et al., 1996; Turlings and Benrey, 1996; Benrey et al., 1997). Nutrition of the host is considered by many authors to be important for the development of parasitoids (Salt, 1938). The suitability for parasitoids depends largely on quality of the host plant the insect feeds on (Benrey et. al., 1997). The effects of resource variation on insects also influence development, survival, fecundity and size of natural enemies (Sumerford et al., 2000; Teder and Tammaru, 2002) and their sex ratio (Kester and Barbosa, 1991). Some host plants lack nutritional compounds required for successful insect development (Clancy and Prince, 1987). Longer development time due to poor host plant quality may increase the chances of exposure to natural enemies (Awmack and Leather, 2002). The effects of food plant on host quality, and subsequently on development of parasitoids, may be directly due to the presence of allelochemicals in host tissues (via sequestration), or allelochemicals in the diet of the herbivore may reduce its consumption efficiency leading to indirect reduction of developmental conditions for the parasitoid on smaller hosts. On the other hand compensation of the host may occur in spending more time feeding, thereby extending the temporal exposure to their natural enemies (‘slow-growth-high-mortality hypothesis’, *sensu* Clancy and Price; 1987; Damman, 1987), a secondary function of reduced herbivore performance on more toxic host species. This could provide a longer time period for parasitation and increase in parasitation rates.

Apparent levels of parasitism by the same parasitoids have frequently been observed to differ between plants species or cultivars (Price et al., 1980; Verkerk and Wright, 1996; Billqvist and Ekbom, 2001) and plant morphology (e.g. presence of hairs, spines, tough foliage, trichomes and density of grandular trichomes) (Fujiwara et al., 2000). In addition to host species, size and age of the host are also known to affect the size and performance of natural enemies (Neveu et al., 2000). Plant attributes like the provision of host finding cues or shelter mediate the efficiency of natural enemies (Cortesero et al., 2000). For example, *Diadegma semiclausum* (Hellen) (Hymenoptera: Ichneumonidae), a specialist parasitoid of DBM relies on plant related cues to locate its host (Ohara et al., 2003, Rossbach et al., 2005).

Crucifers are very diverse and contain a long list of secondary metabolites some of which are highly toxic (Fox et al., 1996; Agrawal and Kurashige, 2003; Wittstock et al., 2003). They are known to affect interactions between plants, herbivores and natural enemies up to the fourth trophic level (Harvey et al., 2003; Soler et al., 2005). Some species contain toxic allelochemicals (glucosinolates, isothiocyanates) that kill insects (Fox et al., 1996). Herbivores that specialize on glucosinolate-containing plants have some mechanisms of overcoming toxicity of their host. Diamondback moth (DBM) *Plutella xylostella* L. (Lepidoptera: Plutellidae), and *Pieris rapae* L. (Lepidoptera: Pieridae) avoid the formation of isothiocyanate hydrolysis products in their digestive tract, which are deleterious to larval growth and survival (Agrawal and Kurashige, 2003).

Several studies have reported that the performance of koinobiont and idiobiont parasitoids can be detrimentally affected by the presence of allelochemicals in the host's diet (Barbosa et al., 1986; Gunasena et al., 1990). These effects are more apparent in koinobiont endoparasitoids. Koinobionts are parasitoids that initially allow the host to continue developing after oviposition. Hosts continue to feed and grow during much of the course of parasitism (Harvey et al., 1994). The parasitoid larvae cannot excrete toxins contained in their diet until after voiding of the meconium, which occurs after egression and before pupation (Quicke, 1997). Consequently, the allelochemicals consumed by the host are stored by the parasitoid larva until much later in development (Barbosa et al., 1986). Idiobionts on the other hand kill or paralyse their hosts at the time of oviposition. The latter have an advantage of having a wider host range and are typically ectoparasitoids that feed from the surface of their hosts, while koinobionts have a narrow host range and are endoparasitoids. Therefore, there is no accumulation of any toxic

substances in idiobionts. Sheehan and Hawkins (1991) and Althoff (2003) supported the hypothesis that koinobionts are more host-specific than idiobionts.

Understanding the relative importance of wild crucifers to parasitoids is of economic importance in enhancing the management of DBM. The objective of our study was to examine the effect of two Brassica cultivars and six wild crucifer species on development, survival and reproductive potential of exotic larval parasitoids *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae) and *D. semiclausum.* Both were introduced to Kenya for a biological control project of DBM, the former in the highlands and latter in mid-altitude semi arid areas from South Africa and Taiwan, respectively. These are predominant parasitoids of DBM as observed by Ooi (1992) and Talekar and Shelton (1993). The studies were conducted to evaluate whether the parasitoids would develop on DBM found on the wild crucifer species, the wild crucifers act as refugia for parasitoids, which could later recolonise the new crop once it is cultivated and whether the wild crucifers will support parasitoids, which can reduce the risk of local extinction due to heavy pesticide application.

5.2 Materials and methods

5.2.1 Host plants

Two cultivated Brassica cultivars (head cabbage *B. oleracea* var. *capitata* and kale *B. oleracea* var. *acephala*) and six wild crucifers (*Erucastrum arabicum* Fisch. & Mey., *Raphanus raphanistrum* L., *Rorippa micrantha* (Roth.) Jonsell, *Ro. nudiuscula* (Sond.) Thell., *Brassica juncea* Czern., and *Sisymbrium officinale* (L.) Scop., were used in laboratory trials at the International Center of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya. The selection of wild crucifer species was based on their common occurrence in highland and mid-altitude semi arid areas and presence of DBM on the host plant during the surveys conducted earlier (see chapter 1). The seedlings were raised in the greenhouse from seeds collected from the fields. They were transplanted into 15 cm diameter plastic pots three weeks after germination. A mixture of red soil, garden compost and sand (2:1:1) was used as the growth medium. Calcium Ammonium Nitrate (CAN) fertilizer was used as top dressing two weeks after transplanting. The plants were used in the trials six weeks after transplanting.

5.2.2 Diamondback moth culture

A colony of DBM was established and maintained in the insectary on cabbage *Brassica oleracea* var. *capitata* L., cultivar Gloria. The DBM larvae and pupae were originally collected from cabbage grown in Werugha Location, Taveta District, Coastal Region of Kenya at 03°26'16'' S, 38º20'24'' E and 1650 m above sea level. The moths were reared as described by Löhr and Gathu (2002). Sub colonies of DBM were also established on the Brassica cultivars and the wild crucifer species and maintained in the insectary at 23 ± 2 ºC and used in development and reproductive potential studies of *C. plutellae* and *D. semiclausum* in the laboratory and screen house. The DBM were reared on the respective host plants for at least one generation before the trials.

5.2.3 *Cotesia plutellae* culture

Ten potted cabbage plants with 100 second instar DBM larvae each were placed in a screen house measuring 4 by 3 by 2 meters. Twenty pairs of a day old mated naïve *C. plutellae* adults were released and allowed to parasitise freely. The wasps were fed on 10 % honey solution soaked in cotton wool. The larvae were allowed to complete their development on the cabbage until pupation. The parasitised pupae were harvested using a pair of soft forceps and put in a clean ventilated plastic container and kept in the laboratory at temperature 23 ± 2 ºC for adult emergence. The *C. plutellae* culture was maintained in the screen house.

5.2.4 *Diadegma semiclausum* culture

A potted cabbage plant with 200 early third instar DBM larvae was placed in a perspex cage (20 cm × 20 cm × 40 cm) with muslin sleeve on one side of the cage. Ten pairs of a day old mated *D. semiclausum* were introduced into the cage through the sleeve to oviposit. The wasps were provided with a diet of 10 % honey solution soaked in cotton wool. After 24 hours the exposed larvae were removed and placed in ventilated plastic containers (20 cm × 10 cm × 5 cm) lined with tissue at the bottom to absorb excess moisture. Fresh cabbage leaves were added as required until the larvae pupated. The parasitised pupae were harvested and put in clean plastic containers for adult emergence. The *D. semiclausum* culture was established and maintained in the laboratory at temperature 23 ± 2 ºC.

5.3 Effect of crucifer species on development of *C. plutellae* and *D. semiclausum*

Studies on development of *C. plutellae* on the Brassica cultivars and wild crucifers were conducted in the laboratory at controlled temperature (25 ± 1 ºC). Each test plant was infested with 200 second instar DBM larvae obtained from the respective host plant species. The plants were placed individually in perspex cage (30 cm × 30 cm × 25 cm) with a muslin sleeve on one side of the cage. Six pairs of newly mated naive *C. plutellae* were introduced into the cage through the sleeve and allowed to parasitise. A streak of 10 % honey on saturated cotton wool was placed inside the container to provide nutrition for the parasitoids. Twenty four hours later, the plants were removed from the cages. One hundred 100 of the exposed DBM larvae from each host plant were picked using a soft camel brush and placed individually in plastic containers containing a leaf from the respective host plant. The containers were lined with tissue paper at the bottom to absorb excess moisture and covered with a cap line with muslin cloth for ventilation. They were placed in an incubator (Rumed ® Rubarth Apparate GmbH, Germany) at 25 ± 1 ºC, 60-80 % relative humidity (RH) and 12:12 L/D. The leaves from respective test plants were changed every two days until the larvae pupated. Spinning of the cocoon was considered as an indicator of distinguishing between larval and pupal period. The parasitised pupae were weighed within 24 hours of pupation to the nearest 0.01 milligram using a Mettler electronic scale (Type AM 100, Mettler, Switzerland). The weighed pupae were placed individually in plastic vials for adult emergence. Egg-larval and pupal period of parasitoid was recorded. Developmental time was recorded as the number of days between parasitism and adult emergence.

The procedure mentioned above was repeated using the parasitoid *D. semiclausum*.

5.3.1 Effect of crucifer species on reproductive potential of *C. plutellae*

The reproductive potential of *C. plutellae*, a preovigeneous species was determined by counting the number of eggs in the ovaries. In *C. plutellae,* the egg load is complete immediately after adult emergence while ovaries of *D. semiclausum* matures continuously over longer time. Twenty five, one day old female *C. plutellae* from each test plants from the above experiment were picked at random and killed by keeping them in the freezer for half an hour. Each female was then placed in a petri dish with 10 % saline solution and the abdomen split open using a pair of dissecting pins to expose the

ovaries. The ovaries were removed from the abdomen by pulling out the ovipositor with a pair of forceps and isolated using a pin. They were placed on a microscope slide with a drop of 10 % saline solution and split open under the dissecting microscope (Olympus, Tokyo Japan). The number of eggs were counted with a tally counter and recorded.

5.3.2 Effect of crucifer species on reproductive potential and parasitism of *D. semiclausum*

Twenty newly emerged *D. semiclausum* females from each test plant from the above development experiment were placed individually in clean plastic vials (1.5 cm × 7.5 cm) and paired with males from respective test plants and left to mate for 24 hours. A leaf from the respective test plant was placed in a ventilated plastic container (10 cm diameter and 25cm height) and infested with 35 early third instar DBM larvae. To prevent the leaf from wilting, the petiole was wrapped with cotton wool soaked in water. A pair of three-day-old mated naive *D. semiclausum* was introduced in the container and allowed to oviposit. After every 24 hours, each pair was transferred to another plastic container with a leaf infested with 35 DBM larvae and the process was repeated for seven days. The adult wasps were fed on 10 % honey solution soaked in cotton wool. The exposed larvae were transferred into ventilated plastic containers (10 cm diameter and 6.5 cm height) lined with tissue paper to absorb excess moisture. Leaves from respective test plants were added as required until the larvae pupated. The containers were checked daily for any dead larvae, which was recorded and dissected under the dissecting microscope to check if they were parasitised. On pupation, the parasitised pupae from individual females were placed in clean ventilated plastic containers (5 cm diameter and 4 cm height) and observed daily for adult emergence. The number of emerged DBM and parasitoids were recorded and sex of the latter noted. After all the wasps had emerged, the cocoons were checked and the number that failed to emerge as adult recorded. All cocoons that failed to emerge were recorded as dead pupae

5.3.3 Effect of crucifer species on body size

Twenty-five newly emerged male and female parasitoids from each test plant were killed by placing them in the freezer for half an hour. Each wasp was placed in a petri dish with 70 % alcohol and the left forewing and left hind tibia removed using a pair of forceps

under the dissecting microscope. The forewing and hind tibia were placed on a microscope slide using a soft camel hairbrush and a drop of water added to spread the wing. The lengths were measured to the nearest 0.01 mm using an ocular micrometer fitted on the dissecting microscope. The measurements were taken under magnification of ×6.4 and ×16 for forewing and hind tibia, respectively. The calibration was done for each magnification as shown; for magnification of ×16, length of each graduation mark was 0.03034 mm while that of ×6.4 was 0.077 mm.

The actual length was calculated by multiplying the size on the ocular micrometer with that of the magnification used. The wing load was expressed as the ratio of the pupal weight to forewing length. The length of forewing and tibia are correlated with size or pupal weight (Muhamad et al., 1994).

5.3.4 Effect of crucifer species on rate of DBM parasitism by *D. semiclausum* and *C. plutellae* (choice test)

Choice test parasitism studies by *C. plutellae* and *D. semiclausum* were conducted using two cultivated cultivars (*Brassica oleracea* var. *capitata* and *Brassica oleracea* var. *acephala*) and four wild crucifers (*R. raphanistrum, E. arabicum, Ro. nudiuscula* and *Ro. micrantha*). A day before parasitism was measured five potted plants from each host plant species were infested with 25 second instar DBM larvae each to inflict damage and release of semio-chemicals necessary for parasitoid attraction. The plants were randomly placed in the screen house (4 m × 3 × m 2 m) at 0.5 meters apart (Plate 5.1). Ten pairs of a day old naive *C. plutellae* were introduced in the screen house for oviposition and fed on 10 % honey solution soaked in cotton wool. After 24 hours, the plants with exposed DBM were cut, placed in clean plastic containers (20 cm × 15 cm × 8 cm) lined with tissue paper and taken to the laboratory. The containers were kept at 25 ºC, 60-80 % RH and LD 12:12 h photoperiod for larval development. Leaves from respective test plants were added until the larvae pupated. On pupation, the number of DBM were recorded, the parasitised pupae harvested and kept individually in clean plastic vials (1.5 cm × 7 cm) for adult emergence. The emerged adult parasitoids were sexed and recorded. The experiment was replicated four times.

The procedure stated above was repeated using ten pairs of three-day-old naive *D. semiclausum* and the plants were infested with 25 third instar DBM larvae. The experiment was replicated four times.

Plate 5.1: Experimental setup for free choice parasitism tests

Photo by Kahuthia-Gathu

5.4 Data analysis

The data on development (egg-larval period, pupal period and pupal weight), number of DBM parasitised, dead parasitised larvae, unemerged pupae, emerged adult wasps and unaccounted larvae of *C. plutellae* and *D. semiclausum* from the crucifer species were subjected to one-way Analysis of Variance (ANOVA) using general linear model (SAS Institute, 2004). The data on fecundity was subjected to square root transformation before analysis. The means were separated using Student Newman Keuls (SNK) test at $P<0.05$ where significant difference were recorded (Sokal and Rohlf, 1995). Percent parasitism was calculated as (total number parasitised/total number exposed)*100 while percent pupal mortality was calculated as (difference between the total number pupated and total number emerged) divided by the total pupated*100. The data on pupal weight, fecundity, forewing length and hind tibia was subjected to Pearson's Correlation Coefficients using SAS program to find if there any relationship between morphological structures and

weight of *C. plutellae* and *D. semiclausum* obtained from DBM reared on cultivated Brassica cultivars and the wild crucifer species.

5.5 Results

5.5.1 Effect of crucifer species on development and reproductive potential of *Cotesia plutellae*

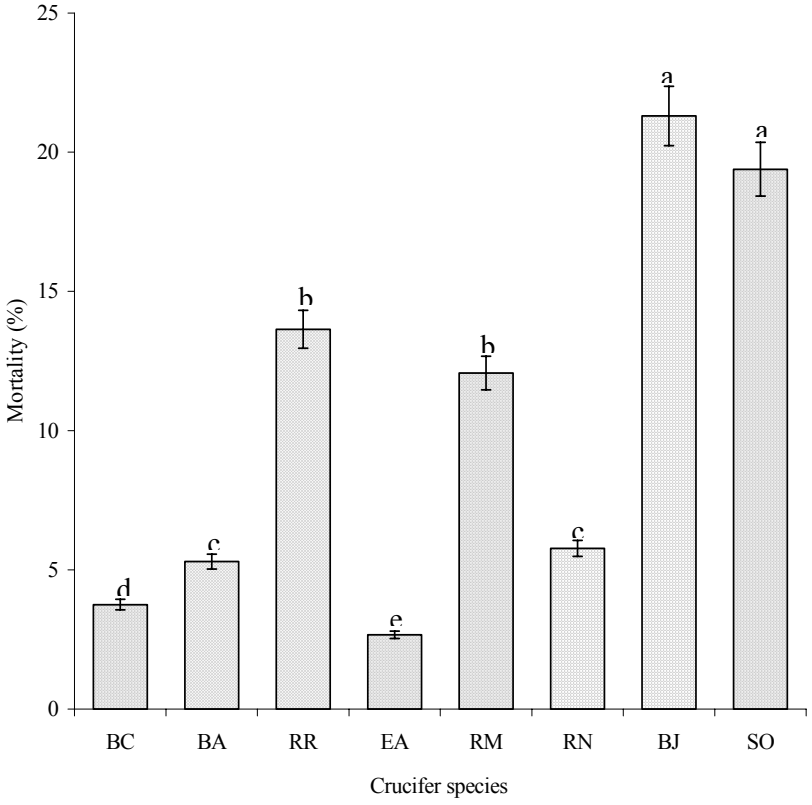
Host plant species affected the egg-larval period (F=166.59; df=7, 1077; P<0.0001), pupal weight (F=30.67; df=7, 1067; P<0.0001), pupal period (F=133.57; df=7, 962; P<0.0001) and development time (F=300.97; df=7, 962; P<0.0001) of *C. plutellae* (Table 5.1). Parasitoids from DBM reared on *S. officinale* had shortest egg-larval period of 7.4 days while those on *R. raphanistrum* recorded the longest period of 9.3 days. Pupae were significantly heavier on kale and cabbage than on wild crucifers. The cocoon weight ranged between 1.67mg on *Ro. micrantha* and 2.11mg on kale. *Cotesia plutellae* reared from DBM on kale recorded the longest pupal period while those on *E. arabicum*, *B. juncea* and *S. officinale* had the shortest. Total development time also differed between crucifer species and ranged between 11.9 days on *S. officinale* and 15.2 days on *R. raphanistrum*. Egg-larval period, pupal weight and development time of *C. plutellae* were similar on cabbage and kale. Females were significantly heavier (F=31.08; df=1, 960; P<0.0001) and had longer development time (F=67.29; df=1, 966; P<0.0001) than males. Generally, pupal mortality of *C. plutellae* was higher on wild crucifers than on cabbage and kale with *B. juncea* recorded the highest percent pupal mortality (22 %) (Figure 5.1).

Host plant species also affected the reproductive potential of *C. plutellae* (F=2.35; df=7, 212; P<0.02). The number of eggs ranged between 108 from *C. plutellae* reared on *B. juncea* and 126 on cabbage (Table 5.1).

Table 5.1: Effect of two cultivated Brassica cultivars and six wild crucifer species on development, fecundity and sex ratio of *Cotesia plutellae*

Plant species	Egg-larval period (days)	Pupal weight (mg)	Pupal period (days)	Development time (days)	Fecundity	Sex ratio
B. oleracea var. *acephala*	7.9 ± 0.06c	2.11 ± 0.02a	6.3 ± 0.06a	14.2 ± 0.07c	112 ± 4.4ab	1:0.57
B. oleracea var. *capitata*	8.1 ± 0.04c	2.04 ± 0.02a	6.0 ± 0.05b	14.1 ± 0.05c	126 ± 2.7a	1:0.90
Raphanus raphanistrum	9.3 ± 0.08a	1.78 ± 0.03cd	6.0 ± 0.09b	15.2 ± 0.10a	119 ± 5.9ab	1:0.48
Erucastrum arabicum	7.4 ± 0.04e	1.85 ± 0.03bc	4.9 ± 0.04d	12.2 ± 0.05e	107 ± 3.8ab	1:0.59
Rorippa micrantha	8.7 ± 0.08b	1.67 ± 0.04e	6.1 ± 0.07b	14.7 ± 0.09b	116 ± 6.8ab	1:0.46
Rorippa nudiuscula	8.1 ± 0.02c	1.94 ± 0.03b	5.4 ± 0.05c	13.5 ± 0.06d	120 ± 3.6ab	1:0.70
Brassica juncea	7.6 ± 0.06d	1.74 ± 0.03d	4.7 ± 0.06d	12.2 ± 0.09e	108 ± 3.9b	1:0.32
Sisymbrium officinale	7.0 ± 0.04f	1.91 ± 0.03b	4.9 ± 0.04d	11.9 ± 0.06f	113 ± 3.7ab	1:0.42

*Means ± SE within column followed by the same superscript letter are not significantly different at P=0.05 (SNK test)



BC- *B. oleracea* var. *capitata*, BA- *B. oleracea* var. *acephala*, RR- *R. raphanistrum* EA- *E. arabicum,* RM – *Ro. micrantha,* RN- *Ro. nudiuscula,* BJ- *B. juncea* and *S. officinale*

Figure 5.1: Percent pupal mortality of *C. plutellae* from DBM reared on two cultivated Brassica cultivars and six wild crucifer species

5.5.2 Development of *Diadegma semiclausum*

Significant differences were recorded on egg-larval period (F=38.79; df=6, 957; p<0.0001), pupal weight (F=17.32; df=6, 956; P<0.0001) and development time (F=50.48; df=6, 851; P<0.0001) of *D. semiclausum* between different crucifer species (Table 5.2). The egg-larval period of larvae reared from DBM on *B. juncea* was significantly shorter (6.7 days) than on cabbage, *E. arabicum*, *Ro. micrantha* and *Ro. nudiuscula*. Pupae from DBM reared on cabbage recorded higher weight than on kale

and the wild crucifer species. Pupae from DBM reared on *R. raphanistrum* recorded the lowest weight (4.14 mg) while those reared on cabbage had the highest (5.06 mg). Pupal period and development time was significantly shorter on *E. arabicum* (4.37 days) than on other species. Development time was similar on cabbage and kale and significantly shorter on *E. arabicum* (12.4 days). Female wasps were significantly heavier (F=27.34; df=1, 788; P<0.0001) and took longer to develop (F=26.44; df=1, 788; P<0.0001) than males.

Table 5.2: Effect of two cultivated Brassica cultivars and five wild crucifer species on development and fecundity of *Diadegma semiclausum*

Crucifer species	Egg-larval period (days)	Pupal weight (mg)	Pupal period (days)	Development time (days)	Fecundity
B. oleracea var. *acephala*	7.3 ± 0.08b	4.72 ± 0.07b	7.8 ± 0.06c	15.9 ± 0.11b	217 ± 4.0a
B. oleracea var. *capitata*	7.7 ± 0.06a	5.06 ± 0.07a	7.9 ± 0.05c	15.5 ± 0.08ab	223 ± 3.9a
Raphanus raphanistrum	7.1 ± 0.11c	4.14 ± 0.07d	8.2 ± 0.08b	15.2 ± 0.12b	200 ± 6.1a
Erucastrum arabicum	7.6 ± 0.04a	4.37 ± 0.07c	7.2 ± 0.08e	12.4 ± 0.27d	226 ± 3.8a
Rorippa micrantha	7.6 ± 0.06a	4.79 ± 0.07b	8.5 ± 0.08a	16.1 ± 0.08a	216 ± 7.4a
Rorippa nudiuscula	7.6 ± 0.10a	4.64 ± 0.06b	8.1 ± 0.09b	14.3 ± 0.29c	167 ± 17.7b
Brassica juncea	6.7 ± 0.03d	4.78 ± 0.06b	7.5 ± 0.07d	14.0 ± 0.10c	196 ± 6.0a

*Means ± SE within column followed by the same superscript letter are not significantly different at P=0.05 (SNK test)

5.5.3 Effect of crucifer species on parasitism and reproductive potential of *D. semiclausum*

Host plant species had a strong influence on parasitism of DBM by *D. semiclausum* (F=6.16; df=6,134; P=0.001) (Table 5.3). The number of parasitised DBM larvae was similar in all host plant species except *Ro. nudiuscula*. Larval mortality of *D. semiclausum* was also affected by the plant species (F=20.12; df=6,134; P<0.0001). *Brassica juncea* recorded the highest number (94.8) of dead larvae while kale, cabbage and *Ro. nudiuscula* had the lowest. Host plants had significant effect on the number of pupae that failed to emerge as adult wasps (F=18.49; df=6,134; P<0.0001). Although on *Ro. nudiuscula* lower number of dead larvae was observed, which was similar to cabbage and kale, it carried the highest number of unemerged pupae while cabbage and kale carried the lowest number of unemerged pupae. A significant difference was found in the proportion of *D. semiclausum* surviving to adult stage (F=29.9; df=6,134; P<0.0001) between the host plant species. DBM from cabbage and kale give significantly higher adult wasps emergence that the wild crucifers. *Rorippa nudiuscula* and *B. juncea* had the lowest number of emerged adult wasps. Despite similar number of parasitised DBM larvae between the cultivated (cabbage and kale) and the wild crucifers, the number of emerged adult wasps was higher on the former than latter. Host plant species also affected the sex ratio, which ranged between 1:0.2 on *B. juncea* and 1:0.44 on kale.

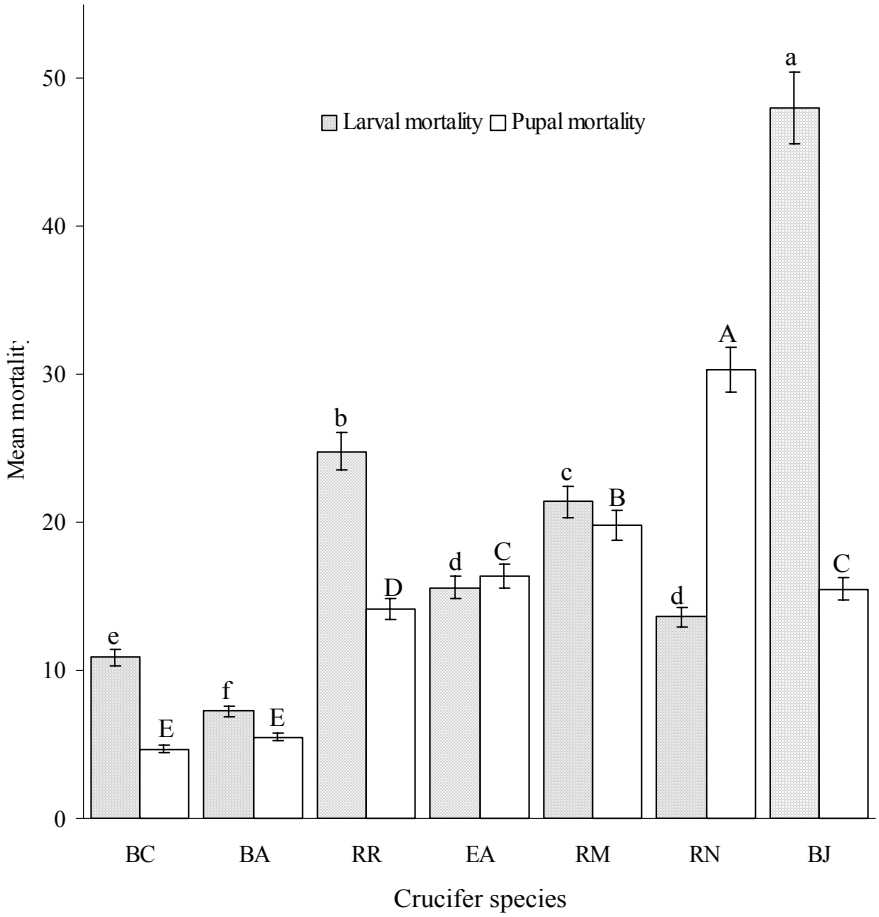
Parasitism rates differed significantly (F=3.95; df=6,130; P=0.001) and ranged between 75 % on *Ro. nudiuscula* and 92 % on *E. arabicum*. Host plant species had a significant effect on percent larval (F=20.54; df=6,134; P<0.0001) and pupal mortality (F=32.4; df=6,134; P<0.0001) of *D. semiclausum*. Percentage of dead parasitised larvae was highest on *B. juncea* (48 %) and lowest on cabbage (7.2 %). The proportion of parasitised pupae that failed to emerge as adults was significantly higher on wild crucifer species than on cabbage and kale. Larval and pupal mortality of *D. semiclausum* from DBM reared on different host plant species differed significantly. *Diadegma semiclausum* from DBM reared on *B. juncea* had the higherst larval mortality, while that from cabbage had the lowest. However, pupal mortality was highest on *D. semiclasusm* from DBM reared on *Ro. nudiuscula* (30.2 %) and lowest on cabbage (4.7 %) on (Fig. 5.2). The reproductive potential of *D. semiclausum* differed between host plant species. It was

similar in both cultivated and wild crucifer except on *Ro. nudiuscula*, which recorded the lowest (167) (Table 5.2).

Table 5.3: Mean (± SE) of parasitised DBM larvae, dead parasitised larvae, pupae that failed to emerge as adults and emerged adult wasps and their sex ratio from 245 third instar DBM exposed to *D. semiclausum* on two cultivated Brassica cultivars and five wild crucifer species

Crucifer species	Total parasitised DBM larvae	Dead parasitised larvae	Un-emerged pupae	Emerged adult wasps	Sex ratio
B. oleracea var. *acephala*	217.3 ± 4.0a	22.8 ± 3.8c	10.2 ± 1.3d	185.9 ± 6.7a	1:0.44
B. oleracea var. *capitata*	223.1 ± 3.9a	15.5 ± 3.5c	12.0 ± 2.0d	195.6 ± 7.7a	1:0.37
Raphanus raphanistrum	200.3 ± 6.1a	47.9 ± 5.5b	27.6 ± 2.5c	124.7 ± 9.7c	1:0.43
Erucastrum arabicum	226.5 ± 3.8a	35.0 ± 4.9b	37.2 ± 2.3bc	154.0 ± 7.2b	1:0.39
Rorippa micrantha	216.3 ± 7.4a	47.0 ± 7.7b	43.3 ± 4.0ab	125.9 ± 8.0c	1:0.38
Rorippa nudiuscula	167.1 ± 17.7b	23.4 ± 4.6c	49.7 ± 6.3a	94.0 ± 11.0d	1:0.30
Brassica juncea	196.4 ± 6.0a	94.8 ± 10.0a	31.0 ± 4.1c	70.6 ± 8.3d	1:0.20

*Means under the same column followed by the same letter are not significantl different at P < 0.05, SNK test



BC- *B. oleracea* var. *capitata*, BA- *B. oleracea* var. *acephala*, RR- *R. raphanistrum* EA- *E. arabicum*, RM - *Ro. micrantha*, RN- *Ro. nudiuscula* and BJ- *B. juncea*.

Figure 5.2: Mean percent larval and pupal mortality of *D. semiclausum* from DBM reared on two cultivated Brassica cultivars and five wild crucifer species. Bars with the same letter do not differ significantly to SNK test at P=5 %

5.5.4 Effect of host plants on body size of *Cotesia plutellae* and *D. semiclausum*

Host plant species affected the body size of *C. plutellae*. Significant differences were recorded on hind tibia (F=15.05; df=7,591; P<0.0001) and forewing (F= 19.32; df=7,591; P<0.0001) length of *C. plutellae* (Table 5.4). The length of hind tibia ranged between 0.77 mm and 0.83 mm while forewing length ranged between 2.42 mm and 2.60 mm on *B. juncea* and kale, respectively.

Hind tibia (F= 17.45; df=6, 571; P<0.0001) and forewing (F=17.29; df=6, 570; P<0.0001) length of *D. semiclausum* differed significantly between host plant species (Table 5.4).

Diadegma semiclausum from DBM reared on *Ro. micrantha* had longest hind tibia length. Hind tibia and forewing lengths of *D. semiclausum* from cabbage, kale, *R. raphanistrum*, *Ro. nudiuscula* and *B. juncea* were similar and differed from those on *Ro. micrantha* and *Ro. nudiuscula*. A highly significant positive correlation was observed between pupal weight and hind tibia of *C. plutellae* from DBM reared on all crucifer species, with cabbage and kale recording the lowest (r=0.48) (Table 5.5). All species recorded significant positive correlation between pupal weight and forewing length at P=0.05. However, no correlation was found between hind tibia length and fecundity of *C. plutellae* from DBM reared on cabbage (r=0.43, P=0.43) and kale (r=0.27, P=0.27). Significant positive association between forewing and fecundity at was observed on *C. plutellae* from DBM reared on *R. raphanistrum* (r=0.76, P<0.0001), *E. arabicum* (r=0.59, P=0.0008), *Ro. micrantha* (r=0.6, P=0.0009), *Ro. nudiuscula* (r=0.43, P=0.03) and kale (r=0.43, P=0.02) at P=0.05.

Table 5.4: Mean ± SE of forewing and hind tibia lengths of *C. plutellae* and *D. semiclausum* from DBM reared on two cultivated Brassica cultivars and six wild crucifer species

Crucifer species	*Cotesia plutellae*		*Diadegma semiclausum*	
	Hind tibia length (mm)	Forewing length (mm)	Hind tibia length (mm)	Forewing length (mm)
B. oleracea var. *acephala*	0.83 ± 0.005a	2.60 ± 0.01a	1.21 ± 0.08b	3.49 ± 0.02a
B. oleracea var. *capitata*	0.81 ± 0.004b	2.55 ± 0.01b	1.21 ± 0.01b	3.54 ± 0.02a
Raphanus raphanistrum	0.80 ± 0.006bc	2.52 ± 0.02bc	1.16 ± 0.01b	3.40 ± 0.03a
Erucastrum arabicum	0.78 ± 0.005cd	2.44 ± 0.01de	1.03 ± 0.05c	3.04 ± 0.14b
Rorippa micrantha	0.79 ± 0.006cd	2.45 ± 0.02de	1.28 ± 0.02a	3.12 ± 0.03b
Rorippa nudiuscula	0.78 ± 0.004d	2.48 ± 0.01cd	1.17 ± 0.01b	3.45 ± 0.03a
Brassica Juncea.	0.77 ± 0.006d	2.42 ± 0.01e	1.15 ± 0.01b	3.42 ± 0.02a
Sisymbrium officinale	0.81 ± 0.005bc	2.50 ± 0.01cd	-	-

*Means within column followed by the same superscript letter are not significantly different at P=0.05 (SNK test)

*No experiments were conducted on *D. semiclasusm* from DBM reared on *S. officinale* because the seeds did not germinate

Table 5.5: Pearson correlation coefficients between pupal weight, fecundity and morphological structure of *Cotesia plutellae* obtained from DBM reared on two cultivated Brassica cultivar and four wild crucifer species

Crucifer species		Pupal weight	Hind tibia	Forewings	Fecundity
B. oleracea var. *capitata* (n=38)	Pupal weight	1.00			
	Hind tibia	0.48 (P=0.002)	1.00		
	Forewing	0.50 (P=0.002	0.78 (P<0.0001)	1.00	
	Fecundity	0.33 (P=0.04)	0.13 (P=0.27)	0.31(P=0.05)	1.00
B. oleracea var. *acephala* (n=28)	Pupal weight	1.00			
	Hind tibia	0.48 (P=0.02)	1.00		
	Forewing	0.58 (P=0.001)	0.58 (P=0.001	1.00	
	Fecundity	0.52 (P=0.005)	0.22 (P=0.27)	0.43 (P=0.02)	1.00
Rorippa micrantha (n=27)	Pupal weight	1.00			
	Hind tibia	0.66 (P=0.0002)	1.00		
	Forewing	0.76 (P<0.0001)	0.85 (P<0.0001)	1.00	
	Fecundity	0.45 (P<=0.02)	0.56 (P<0.0001)	0.6 (P=0.0009)	1.00
Erucastrum arabicum (n=29)	Pupal weight	1.00			
	Hind tibia	0.78 (P<0.0001)	1.00		
	Forewing	0.70 (P<0.0001)	0.80 (P<0.0001)	1.00	
	Fecundity	0.58 (P=0.001)	0.60 (P=0.0005)	0.59 (P=0.0008)	1.00
Raphanus raphanus (25)	Pupal weight	1.00			
	Hind tibia	0.89 (P<0.0001)	1.00		
	Forewing	0.90 (p<0.0001)	0.95 (P<0.0001)	1.00	
	Fecundity	0.73 (P<0.0001)	0.76 (P<0.0001)	0.76 (P<0.0001)	1.00
Rorippa nudiuscula (n=26)	Pupal weight	1.00			
	Hind tibia	0.53 (P=0.005)	1.00		
	Forewing	0.57 (P=0.002)	0.56 (P=0.003)	1.00	
	Fecundity	0.41 (P=0.04)	0.47 (P=0.002)	0.43 (P=0.03)	1.00

5.5.5 Effect of host plants species on parasitism of DBM by *D. semiclausum* and *C. plutellae*

Host plant species had a significant effect (F=6.13; df=5,114; P<0.001) on the number of larvae parasitised by *D. semiclausum*, with kale recording the highest mean (11.8) and *E. arabicum* the lowest (6.2) (Table 5.6). Cabbage and kale recorded significantly (F=11.8; df=5,114; P<0.0001) higher number of emerged adult wasps than wild crucifer species. Mean number of dead parasitised larvae and pupae that failed to emerge as adults were similar in all species. However the number of DBM larvae that could not be accounted for was significantly higher (F=6.09; df=5,114; P<0.0001) on the wild crucifers, and ranged from 4.7 in kale to 12.3 on *R. raphanistrum*.

Table 5.6: Parasitism of DBM by *Diadegma semiclausum* on two cultivated Brassica cultivars and four wild crucifer species in a free choice situation

Species	Parasitised larvae	Emerged adults	Dead parasitised larvae	Unemerged parasitised pupae	Larvae not re-collected
B. oleracea var. *capitata*	11.8±0.8a	10.5±0.7a	0.1±0.05a	1.3±0.2a	4.7±0.9c
B. oleracea var. *acephala*	11.2±1.0ab	10.0±1.0a	0.2±0.16a	1.0±0.2a	7.7±1.3bc
Raphanus raphanistrum	7.5±0.8c	4.8±0.6b	0.3±0.09a	2.4±0.5a	12.3±1.1a
Erucastrum arabicum	6.2±0.7c	4.2±0.6b	0.4±0.13a	1.7±0.4a	11.8±1.0ab
Rorippa micrantha	8.8±1.1bc	5.8±0.9b	0.4±0.18a	2.7±0.7a	8.3±1.5abc
Rorippa nudiuscula	8.5±0.8bc	5.9±0.7b	0.5±0.25a	2.1±0.4a	10.2±1.1ab

*Means in the same column followed by the same letter do not differ significantly at P=0.05 (SNK test)

Each plant was initially infested with 25 third instar DBM larvae

The number of parasitised larvae, emerged adult wasps, dead parasitised larvae and unemerged pupae of *C. plutellae* was similar in all host plant species (Table 5.7). Cabbage, kale and *E. arabicum* did not record any dead parasitised larvae and all parasitised pupae emerged into adults in all test plants. Cabbage and kale had significantly lower (F= 21.2;

df=5,114; P<0.0001) number of DBM larvae not accounted for than wild crucifers. Over 50 % of the 25 infested larvae on the wild crucifers could not be accounted.

Diadegma semiclausum recorded higher parasitism than *C. plutellae* while number of DBM larvae not accounted for was higher in the latter than former (Table 5.6 and5.7). The number of emerged adults of both parasitoid species was similar with cabbage and kale recording a higher mean than wild crucifers.

Table 5.7: Parasitism of DBM by *Cotesia plutellae* on cultivated and wild crucifer species in a free choice situation

Species	Total larvae parasitised	Emerged adult wasps	Dead parasitised larvae	Unemerged parasitised pupae	Larvae not accounted
B. oleracea var. *capitata*	1.2 ± 0.3a	1.2 ± 0.3a	0a	0	5.9 ± 1.3c
B. oleracea var. *acephala*	1.3 ± 0.5a	1.3 ± 0.5a	0a	0	3.8 ± 0.9c
Raphanus raphanistrum	1.8 ± 0.5a	1.2 ± 0.3a	0.6 ± 0.4a	0	19.2 ± 1.2a
Erucastrum arabicum	0.8 ± 0.2a	0.8 ± 0.2a	0a	0	19.1 ± 1.3a
Rorippa micrantha	2.5 ± 0.6a	2.3 ± 0.6a	0.2 ± 0.2a	0	13.8 ± 1.8b
Rorippa nudiuscula	1.8 ± 0.5a	1.1 ± 0.3a	0.7 ± 0.4a	0	16.1 ± 1.9ab

*Means in the same column followed by the same letter do not differ significantly at P=0.05 (SNK test)

* Each plant was initially infested with 25 late second instar DBM larvae

5.6 Discussion

The results reveal that different host plant species affected growth, development, survival and reproductive potential of both *C. plutellae* and *D. semiclausum* at the third trophic level differently. The parasitoids reacted differently to various host plant species in terms of larval period, pupal weight, pupal period and development time. This could be due to the differences in nutritional quality of the host plants. Obviously, these effects are not restricted to herbivores, but may trickle up to the third and fourth trophic levels (Sznajder and Harvey, 2003; Ode et al., 2004) and influence the allocation of resources for parasitoids or predators (Shi et al., 2002). It was observed that egg-larval period of *C. plutellae* was shortest on larvae reared on *S. officinale* and longest on *R. raphanistrum* while that of *D. semiclausum* was shortest on *B. juncea* and

longest on *E. arabicum*, *Ro. micrantha* and *Ro. nudiuscula.* The cocoon of *C. plutellae* from larvae reared on cabbage and kale had the heaviest weight while those on *Ro. micrantha* the lowest contrary to that of *D. semiclausum* where cocoons from kale recorded the heaviest weight and those from *R. raphanistrum* the lowest. This was reflected in growth and development of DBM where the larvae reared on kale recorded the heaviest pupal weight (Gathu et al., unpubl.data). Pupal duration of *C. plutellae* was shortest on *E. arabicum*, *B. juncea* and *S. officinale* and longest on kale. However, pupal duration of *D. semiclausum* was shortest on larvae reared *E. arabicum* and longest on *Ro. micrantha*.

Development time of *C. plutellae* was shortest on both *E. arabicum* and *Ro. micrantha* and longest on *R. raphanistrum* while that of *D. semiclausum* was shortest on *E. arabicum* and longest on *Ro. micrantha*. This diverse picture of reactions triggered by the different crucifer species makes it difficult to give convincing explanations. Moreover we can only mention a very few papers dealing directly with a comparable topic. Harvey and Wagenaar, (2006) observed that *Cotesia rubecula* Marshall (Hymenoptera: Braconidae) developed faster on *Pieris rapae* L., (Lepidoptera: Pieridae) reared on *B. oleracea* than on *S. officinale* while their pupal weight was similar. Slow growth of *C. plutellae* and *D. semiclausum* on *R. raphanistrum* and *Ro. micrantha,* respectively may be due to the direct encounter with host plant allelochemicals in the herbivore haemolymph as suggested by Bowers (2003). The effects are especially apparent in koinobiont endoparasitoids (Askew and Shaw 1986) since the larvae do not excrete toxins contained in the diet until after voiding of the meconium, which occurs after egression and before pupation (Quicke, 1997).

Partial explanation why the crucifer species affected the parasitoids differently despite both being koinobionts could be that *C. plutellae* being a haemolymph feeder does not consume all the host tissues prior to egression compared as to *D. semiclausum*. As a result it has been suggested that host quality can vary independently of host size (Harvey et al., 1999). The difference in the host plant species may have directly or indirectly affected the allocation of the nutritional resources within the parasitoids. It has been shown that allocation of resources to body size and fecundity can vary in *C. plutellae*. Shi et al. (2002) observed that fecundity of *C. plutellae* was highest when the host was in third instar at the time of parasitism.

The difference in pupal weight, forewing and hind tibia lengths showed that host plant species had a significant effect on the parasitoids but does not give indication on suitability of the host plants. There was positive correlation between pupal weight and fecundity, and pupal weight and forewing length of *C. plutellae* on all the crucifer species. However, no correlation was found between fecundity and hind tibia length on on *C. plutellae* from DBM reared on both cabbage and kale. Therefore, wing length can be used as a measure of reproductive potential for parasitoids as observed by Mohamad et al. (1994). However, the size of *C. plutellae* has been shown not to be a reliable indicator of fitness as some experiments found that the largest females are not those with the highest fecundity (Shi et al., 2002).

Intra and inter-specific difference in plant quality can profoundly influence the behaviour of herbivorous insect (Harvey and Wagennar, 2006). For example, morphological traits such as hairs, trichomes, or adhesive glands on the leaf surface may inhibit herbivore colonization or movement on the plants and the effects may trickle to the third and fourth trophic levels impeding the searching efficiency of parasitoids (Sznajder and Harvey, 2003; Harvey et al., 2005). They are manifested through reduced growth rate, small adult size or increased mortality. Negative impact on parasitoids fitness may occur either directly (when the developing parasitoids encounter either plant toxins or metabolites in the haemolymph or tissue of its herbivore host) or indirectly (when the parasitoid fitness suffers owing to compromised host size or quality) (Barbosa et al., 1986; Sznajder and Harvey, 2003). Several studies have reported that allelochemicals in the host diet affects growth, development and survival of less adapted parasitoids (Havill and Raffa, 2000). Although similar number of parasitised DBM larvae by *D. semiclausum* was recorded on cultivated cultivars (cabbage and kale) and wild crucifers *R. raphanistrum*, *Ro. micrantha, B. juncea* and *S. officinale,* significant differences were recorded on number of emerged adult wasps. Cabbage and kale recorded a higher number of emerged adults than the wild crucifers. This was due to the larger number of *D. semiclausum* dying during the larval and pupal stages on wild crucifers than on cultivated cultivars. Gathu et al. (2007) observed that DBM reared on wild crucifers had a higher mortality than cabbage and kale. The difference in mortality and adult emergence suggests that the wild crucifers are less suitable for development of *D. semiclausum* than cabbage and kale although they can act as alternative hosts. It could also be attributed to varying quantities

of toxic chemicals in wild crucifers, which seems to have affected both DBM and parasitoids.

The nutritional characteristics of the host's food plant can affect the sex ratio of parasitoids by influencing sex allocation or by differentially affecting survival of sexes. Higher number of females recorded on *D. semiclausum* from DBM reared on cabbage than on wild crucifers might be attributed to plant quality and allocation of resources. Kester and Barbosa (1991) observed that host plant quality positively correlated with sex ratio of parasitoids.

The results also reveal that the wild crucifers *R. raphanistrum*, *Ro. micrantha, B. juncea*, *S. officinale* and *Ro. nudiuscula* supported parasitoid development. This evidence confirms a certain degree of suitability of the wild crucifer species as alternative host plants or refugia sites. Kartosuwondo and Sunjaya (1990) observed that DBM reared on *Nasturtium heterophyllum* BL., and *Cardamine hirsuta* L., in the laboratory were able to support *D. semiclausum*. The performance of both *C. plutellae* and *D. semiclausum* was better on cabbage and kale than on wild crucifers. Harvey and Wagenaar (2006) observed that *Pieris rapae* L., (Lepidoptera: Pieridae) and *Cotesia rubecula* Marshall (Hymenoptera: Braconidae) developed most successfully on *B. oleracea* and *Raphanus sativus* L., than on wild species *S. officinale*. Benrey et al., (1997) found that *P. rapae* and its parasitoid *C. glomerata* performed better on cultivated cabbage than on a wild crucifer *Lunaria annua*. The difference in performance could have been a result of presence of glucosinolates. Several species of cultivated and wild crucifers produce different concentrations of glucosinolates (Nayar and Thornsteinson, 1963; Simmonds, 1979). Harvey and Wagenaar (2006) reported that work in progress by Gols et al. (unpubl. data) have shown that glucosinolate profiles in the feral populations of *Brassica oleracea* are qualitatively and quantitatively similar to those in cultivars but much lower than in wild species. This might partially explain the differences in suitability of the wild crucifer species used during the study.

Different parasitism levels were recorded between cultivated and the wild crucifer species with *D. semiclausum* recording higher parasitism rates on the former than latter. Talekar and Yang (1991) demonstrated in a laboratory choice test that levels of parasitism by *D. semiclausum* and *C. plutellae* differed significantly among four Brassica species tested. Verkerk and Wright (1997) observed in the field that *D. semiclausum* seemed to exert more control of DBM population on cabbage than on Chinese cabbage.

Other than DBM being lost to predators in the field, Momanyi et al. (2005) observed that 70 % of the DBM found on the floor of the cage were parasitised. Our results on parasitism by *C. plutellae* and *D. semiclausum* in the screenhouse where predators were excluded show similar observations. Over 70 % of total DBM exposed to *C. plutellae* were not recovered from the plants. This is an indication that most of the DBM dropped to the ground due to parasitoid disturbance do not find their way back onto the plant. Wang and Keller (2002) observed that upon disturbance, the DBM drops by the web and *C. plutellae* exhibits a fixed host searching behaviour, by persuing the DBM down the silken thread and spending a significantly greater proportion of time on the ground. It is also possible that most of the larvae do not find their way back to the plant. Upon dropping to the ground, they could be eaten by the ants on the ground and thus, the parasitoids have no chance of multiplying and establishing.

This might explain to some extent why *C. plutellae* has not spread and established in the mid-altitude semi arid areas where it was released in March 2004. Lack of wild crucifers species diversity and species richness in the mid-altitude semi arid areas could have also affected their spreading (Kahuthia-Gathu et al., 2006).

In conclusion, the wild crucifer species in the fields will be able to support and conserve the introduced exotic parasitoids *C. plutellae* and *D. semiclausum* especially in areas where farmers continue spraying their crops against DBM and aphids. This might cause damage to target and no-target organisms within the treated areas (Holland et al., 2000). Owing to temporal dynamics, wild crucifers in the uncultivated fields will provide refugia and act as reservoir for parasitoids when the crop is absent. Other than providing refugia, the wild crucifers might serve as food and energy source for parasitoids, which increases their efficiency and longevity. Wildflowers have been reported as important food sources for adult parasitoids (Kevin, 1973; Idris and Grafius, 1995). This interaction between wild crucifers and parasitoids can form a basis for increasing biodiversity and enhance DBM management. The information obtained from the studies will help in the management of parasitoid species, which are at risk of local extinction from pesticide application.

CHAPTER SIX

6 The role of field margin habitats on recolonisation of Brassica crops by parasitoids of *Plutella xylostella* L. (Lepidoptera: Plutellidae)

Abstract

The immigration of diamondback moth parasitoids from field margins was studied in a maize field where no crucifers were cultivated within a radius of 2 kilometers. DBM infested potted cabbage plants were placed at different distances from the field edges and sampled from 3 to 13 days after exposure. Three larval and one larval-pupal parasitoid were recovered. *Diadegma semiclausum* (Hellen) was the dominant species accounting for 93 % parasitism. *Diadegma mollipla* (Holmgren), *Cotesia plutellae* Kurdjumov and *Oomyzus sokolowskii* Kurdjumov were also recovered but in low numbers. *Cotesia plutellae* was recovered from infested plants within 3 days of exposure. Significantly higher number of parasitoids was recovered 13 days after exposure. Cabbage plants placed at 6 meters from the field edges had higher parasitism than at 16 meters. Over 70 % of the infested DBM larvae could not be accounted. The wild crucifers found in the field margins were *Erucastrum arabicum* Fisch & Mey*, Lepidium bonariense* L., and *Raphanus raphanistrum* L. We conclude that wild crucifers provide refuge to DBM parasitoids, from where they can colonise the crop once cultivated or immigrate after local extinction through pesticide application. The retention and rational management of cruciferous weeds within field margins can be crucial tool to enhance the populations of biological control agents and conserve the DBM parasitoid species, thus improving biological control against DBM.

Key words: Field margins, immigration, parasitism, parasitoids, wild crucifers

6.1 Introduction

Diamondback moth (DBM) *Plutella xylostella* L., (Lepidoptera: Plutellidae) is the most important pest of cultivated crucifers worldwide (Talekar and Shelton, 1993). It is considered a major pest throughout eastern (Ayalew, 2006) and southern Africa (Kfir, 1998). Its exceptional pest status is due to the diversity and abundance of alternative host plants, disruption of its natural enemies, its high reproductive potential and genetic elasticity facilitating rapid development of resistance to insecticides (Mohan and Gujar, 2003; Shelton, 2004). Most insecticides are not effective against DBM, which has developed resistance to chemical (Kibata, 1996) and bacterial insecticides (Tabashnik et al., 2003, Sarfraz and Keddie, 2005). Parasitoids play an important role in natural suppression of DBM in cultivated and wild ecosystems. *Diadegma* (Hymenoptera: Ichneumonidae), *Cotesia* (Hymenoptera: Braconidae) and *Diadromus* species (Hymenoptera: Ichneumonidae), which attack larval and pupal stages of DBM dominate the parasitoid communities (Talekar and Shelton, 1993).

Cultural practices can affect natural enemy population density and species diversity, and manipulation of these practices can provide the foundation for conservation biological control. Parasitoids strongly respond to vegetation complexity (Marino andLandis, 1996); in particular, plants within field boundaries may enhance parasitoid activity within the crop by providing essential ressources. Wild flowers support parasitoids with pollen and nectar for nutrition of adults (Fitton and Walker, 1992; Steppuhn and Wackers, 2004; Tenhumberg et al., 2006). Kahuthia-Gathu et al. (2006) already showed that wild crucifers can provide a refuge for DBM parasitoids. Other authors corroborate this finding; Kartosuwondo and Sunjaya (1991) observed that the wild crucifers *Nasturtium heterophyllum* BL., and *Cardamine hirsuta* L., provided refuge to *Diadegma eucerophaga* Horstmann, on insecticide-treated cabbage plots. Moreover there are strong indications that such refuge habitats can influence the pest dynamics in the crop. Zhao et al., (1992) observed that parasitism of DBM by *D. insulare* (Cresson) (Hymenoptera: Ichneumonidae) was higher in broccoli fields adjacent to nectar producing plants than in broccoli fields that were not surrounded by nectar producing plants. In Michigan, presence of wild flowers surrounding the field influenced parasitism rates by *D. insulare* in pesticide treated plots (Idris and Grafius 1993). Johanowicz and Mitchell (2000) suggested that planting of selected wild flowers into Brassica crops could enhance the control of DBM by parasitic wasps.

Recolonisation may take place after harvesting or local extinction from two different sources of parasitoids. Firstly, the source of recovery might be located within the treated fields, i.e. parasitoids that emerge from the cocoons that offer protection against e.g. pesticides. Secondly, parasitoids originate from populations in adjacent untreated wild crucifers found in the field margins. Its not clear whether parasitoids within off-crop habitats actually contribute to recolonisation of field crops after depletion of the population. The studies were conducted to clarify the question of a possible recolonisation process, which is associated with migration.

In order to further support this beneficial role of crop adjacent vegetation such as field boundaries with wild crucifers it is necessary to analyse more in detail the movement (or dislocation, distribution) from such boundary refuges into the fields. Our objective was to evaluate the effect of field margins on recolonisation potential of host crops by parasitoids. Studies were conducted using artificially DBM infested cabbage plants placed at different distances from the field boundaries and evaluating immigrating parasitoid species and parasitism rates.

6.2 Material and methods

6.2.1 Host plants

The seedlings of cabbage *Brassica oleracea* var. *capitata* L. cv. Gloria were raised in the greenhouse at the International Center of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya. The seeds were planted on seedling trays and transplanted into 15 cm diameter plastic pots three weeks after germination. A mixture of red soil, garden compost and sand (mixing ratio 2:1:1) was used as the growth medium. Fertilizer (CAN) was added as top dressing three weeks after transplanting. The cabbage plants were ready for use six weeks after transplanting. They were used in maintenance of the DBM culture and for the field trials.

6.2.2 Diamondback moth culture

A colony of DBM was established and maintained in the insectary on cabbage at 23 ± 2 ºC, 50-70 % RH and LD 12:12 h photoperiod. The DBM larvae and pupae were originally collected from cabbage grown in Werugha Location, Taveta District, Coastal

Region of Kenya (geographical co-ordinates: 03°26'16'' S, 38º20'24'' E and 1650 m altitude). The moths were reared as described by Löhr and Gathu (2002).

6.2.2.1 Effect of field margins on recolonisation of crops by DBM parasitoids

The trials were conducted at the Kenya Agricultural Research Institute (KARI), Muguga from January to March 2007 in maize fields. The site was selected because there was no cultivated Brassica crop within a radius of 2 kilometers. The field size measured 45 m by 36 m, a representative of many farm sizes under crucifers in Kenya. Thirty potted cabbage plants with six fully formed leaves were selected and the leaves marked 1 to 6 starting from the lower leaves. Random numbers were generated from 1 to 6 for use in data collection. Each plant was infested with 60 newly emerged first instar DBM larvae, 10 on each leaf and left in the greenhouse for five hours for the larvae to mine before transferring the potted cabbage plants to the field. The plants were placed within a growing maize field (crop at 1.5 m height during the first exposure) at a distance of 6 meters within and 6 meters between rows (Fig. 6.1).

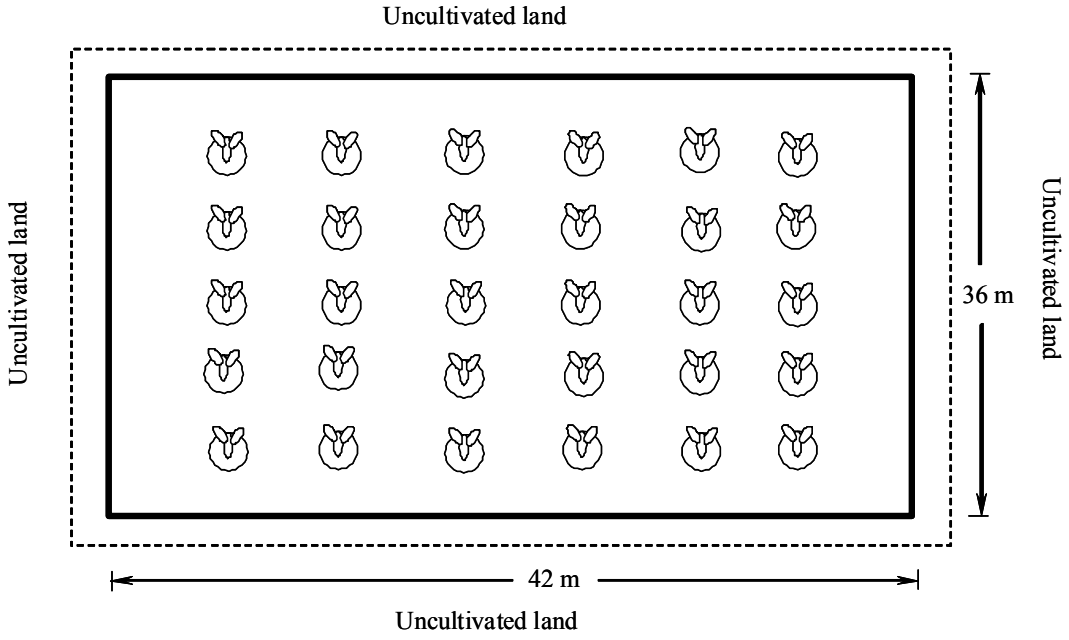


Figure 6.1: Schematic layout of potted cabbage (*Brassica oleracea* var. *capitata*) plants in a maize filed at Kenya Agricultural Research Institute (KARI), Muguga, Kenya. Pots were placed at a spacing of 6 m by 6 m. Beyond the dotted line was uncultivated field full of various weeds.

The first and the last rows were placed 6 meters away from the field margins. Sampling started 3 days after exposure in the maize field and was repeated after every alternate day for two weeks. Each day, a leaf was excised from each cabbage plant and placed individually in a clean ventilated plastic container (20 cm × 15 cm × 8 cm) lined with tissue paper at the bottom to absorb excess moisture. The container was covered with a lid containing a muslin cloth for ventilation. On the last day of data collection, the remaining younger leaves were excised, placed in plastic containers. The containers were taken to the laboratory and kept at 23 ± 2 °C, 50-70 % RH and photoperiod of 12:12 h (L:D) for larval development. Cabbage leaves were added if necessary until the larvae pupated. On pupation, the unparasitized pupae of DBM and parasitised pupae were placed individually in clean plastic vials (1.5 cm × 7 cm) and plugged with cotton wool for ventilation and observed daily for adult emergence. The number of adult DBM and parasitoids recovered on each leaf were recorded. The experiment was replicated four times with five days interval between each setup. Wild crucifer species found growing in the field margins were surveyed during the trials and recorded. However, no quantitative data was collected from them.

6.3 Data analysis

The number of DBM recovered, DBM not re-collected and those parasitised were subjected for analysis using General Linear Model (GLM) and the means seperated at P=0.05 using Students Newman Keuls (SNK) test (SAS Institute, 2004). Parasitism rates for parasitoids were calculated as the sum of total parasitoids divided by total number of adults (DBM + parasitoids) multiplied by 100.

6.4 Results

6.4.1 Parasitoid species

Three larval parasitoids *Diadegma semiclausum* and *Diadegma mollipla* (Ichneumonidae), *Cotesia plutellae* (Braconidae) and one larva-pupal parasitoid *Oomyzus sokolowskii* (Eulophidae) were recorded from DBM on the artificially infested potted cabbage plants (Table 6.1). *Diadegma semiclausum* was the dominant species in the area and accounted for 93 % parasitism. The number of parasitised larvae collected tended to increase with time of exposure. The mean number of *D. semiclausum* per plant ranged

between 0 at 3 days of exposure and 2.7 per plant after 13 days of exposure. *Cotesia plutellae* was the only parasitoid recorded even 3 days after exposure and attacked the DBM larvae during the early larval instar stages. *Oomyzus sokolowskii* were recorded between 9 and 13 days after exposure, with the latter recording the highest number. Both *D. semiclausum* and *D. mollipla* were recovered on all days except at 3 days after exposure. A highest mean of 2.8 parasitoids per plant was recovered 13 days after exposure.

Table 6.1: Parasitoid species collected and their mean number (± SE) recovered from artificially infested potted cabbage plants placed in a maize field at different days of exposure

	Mean ± SE of parasitoid numbers per plant				
Days after exposure	*Diadegma semiclausum*	*Diadegma mollipla*	*Oomyzus sokolowskii*	*Cotesia plutellae*	Total number of parasitoids
3	0d	0a	0b	0.04 ± 0.02a	0.04 ±0.02c
5	0.16 ± 0.05cd	0.01 ± 0.01a	0b	0.04 ± 0.03a	0.21 ± 0.06bc
7	0.37 ± 0.07bc	0.02 ± 0.01a	0b	0a	0.39 ± 0.08bc
9	0.59 ± 0.01b	0.01 ± 0.01a	0.01 ± 0.01b	0a	0.60 ± 0.11b
11	0.50 ± 0.1bc	0.01 ± 0.01a	0.01 ± 0.01b	0a	0.52 ± 0.1b
13	2.65 ± 0.2a	0.03 ± 0.03a	1.15 ± 0.34a	0a	2.80 ± 0.2a

*Means ± SE in the same column followed by the same letter do not differ significantly at P<0.05 (SNK test). * Six plants were used in each row. On each plant, six fully-grown leaves were infested with ten first instar DBM larvae each

6.4.2 Parasitism and number of DBM recovered

Parasitism rates on the potted cabbage plants differed significantly (F=3.70; df=4, 115; P=0.007) with distance from the field margins. Highest parasitism of 25 % was recorded at 6 m on the eastern (E) edge row while that on the western (W) edge rows at the same placement distance had 22 % and the one placed at 12 m on the same side had 20 % (Fig 6.1). The center row and the one at 12m from the eastern edge had lower parasitism of 11 %. Over 70 % of the DBM larvae infested on the cabbage could not be re-collected (Table 6.2). The mean number of DBM not recollected (lost) and those recovered did not differ significantly between rows.

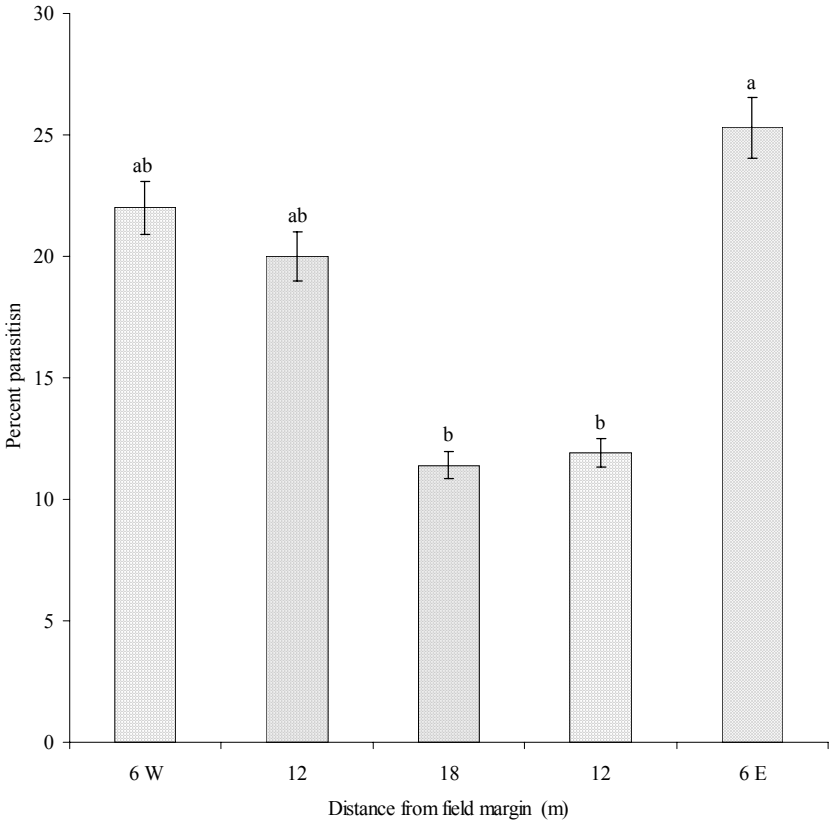


Figure 6.2: Mean percent parasitism of DBM from infested potted cabbage plants placed at various distances from the field margin

Table 6.2: Number of DBM (Mean ± SE) recovered, parasitised and DBM not recollected (DBM lost) per plant from the artificially infested cabbage plants with 60 first instar neonate DBM larvae

Rows	DBM recovered	Parasitised DBM	DBM not recollected
6m-W	17.9 ± 1.2a	5.4 ± 0.7a	42.2 ± 1.1a
12m	16.1 ± 1.1a	5.1 ± 0.7a	43.9 ± 1.1a
18m	15.2 ± 1.0a	3.3 ± 0.5b	44.8 ± 1.0a
12m	16.8 ± 0.9a	3.3 ± 0.5b	43.1 ± 0.9a
6m-E	19.3 ± 2.1a	5.4 ± 0.8a	40.8 ± 2.1a

*Means in the same column followed by the same letter do not differ significantly at $P<0.05$ (SNK test).

6.4.3 Wild crucifer species

During the four months trial, the wild crucifer species *E. arabicum*, *L. bonariense* and *R. raphanistrum* were recorded in the uncultivated field margins surrounding the maize crop. *E. arabicum* and *R. raphanistrum* were the dominant species in the area. *Raphanus raphanistrum* was observed to flower for long and it could have provided the parasitoids with nectar for diet.

6.5 Discussion

Recovery of parasitoids from infested potted cabbage plants in the maize fields was a clear indication that parasitoids migrated from the cruciferous weeds found in the field margins. This is because there was no crucifer crop within 2 km radius from the trial site. The parasitoids used the semio-chemicals produced to search for infested cabbage plants which had been placed in the maize field. They could have been attracted by plant volatiles emitted by the cabbage plants following DBM infestation as observed by De Moraes et al. (1998) and Turlings et al. (2002). Refuges in different parts of the agro-ecosystem ("on farm area") can act as a reservoir and provide refugia to parasitoid population during off-season, which colonized the crop. These findings suggest the wild crucifers will help in conserving and enhancing local populations of natural enemies.

Recovery of parasitoids as early as the third day after infestation shows that the parasitoids will be able to colonise the cultivated crop immediately after transplanting from uncultivated margins with wild crucifers thereby attacking DBM on the cultivated crop. This might help in checking pest population growth and reducing crop damage. Pickett and Thompson (1978) suggested that the disappearance of re-colonisation sources leads to extinction of parasitoid populations. Therefore, presence of cruciferous weeds might act as alternative hosts for parasitoid species invading the crop as the host becomes available thus, enhancing biological control. Thus, maintaining them in the field margins may increase the recolonisation process. Non-crop plants, however growing in uncultivated field could become invasive, reducing crop yield, or provide a reservoir for the pests. Despite these potential negative effects, in many circumstances habitat diversity within fields may benefit the crops (Gliessman 1998). Kahuthia-Gathu et al. (2006), observed that the assemblage of wild crucifers had negligible DBM population compared to the cultivated Brassica cultivars. Therefore, it is unlikely that these weeds

could become a major source of DBM infestation. Many studies demonstrate that pest outbeaks are more likely to occur in weed-free fields than in diversified crop systems (Root, 1973).

Out of the total DBM larvae and pupae collected from the infested cabbage plants, 36.4 % were parasitised (See Chapter 6) unlike in the surveys where 60.7 % were parasitised (See Chapter 3). The difference in parasitism might be as a result of the short period of cabbage exposure contrary to the latter where there was continous crop production. *Diadegma semiclausum* dominated the parasitoid fauna and accounted for 93 % parasitism in both cases. These could be due to its high searching efficiency (Wang and Keller, 2002) or their dominance on the cruciferous weeds. The relative fast recovery of parasitoids on all rows placed at different distances from the field margin is an indication that recolonisation of parasitoids will be possible even over distances of 150 meters after local depletion or elimination. The small farm size in Kenya (Macharia et al., 2005) will be an advantage because of the close proximity of even field centers to field margins and the high border to area ratio. Schellhorn and Silberbauer (2004) observed that *D. semiclausum* had dispersed 108 m away from the broccoli field five days after spraying. Several authors have observed long-distance dispersal of other parasitoids after field release. Langhof et al. (2005) observed that *Aphis colemani* Viereck (Hymenoptera: Braconidae), a parasitoid of *Myzus persicae* (Sulzer) (Hemiptera Aphididae) dispersed up to 16 m from the release points after 5 days. Sallam et al. (2001) observed that *Cotesia flavipes* (Hymenoptera; Braconidae) a parasitoid of *Sesamia calamistis* dispersed over 64 m in its life-time (2-6 days). However, Antolin and Strong (1994) observed that *Anagrus delicalus* (Mymaridae: Hymenoptera), an egg parasitoid of planthopper *Prokelesia marginata* (Delphacidae: Homoptera), a common insect pest of cordgrass *Spartina alterniflora* dispersed for about 1 km in Florida salt marsh.

The recovery of *D. mollipla* from the infested cabbage plants is an indication that the wild crucifers function in particular as alternative host and refugia for that parasitoid species, which seems to be diminishing from the cultivated crop by the strong competition with *D. semiclausum*. This is evidenced from the observations made by Kahuthia-Gathu et al. (2006) where *D. mollipla* was only recovered from the wild crucifers and none from the cabbage crop.

Over 70 % of total DBM infested could not be re-collected. They might have been lost to predators such as spiders and birds found in the maize fields or washed of by irrigation.

Others could have been lost due to disturbance by the parasitoids during oviposition. Wang and Keller (2002) observed that upon disturbance, DBM drops by the web and *D. semiclausum* sits motionless near the silken thread waiting for the suspended larvae to climb up and then attack it again but sometimes they follow the silken thread and sting the suspended larvae, which could drop to the ground. They observed that, unlike other host specific parasitoids, *C. plutellae* exhibits a fixed host searching behaviour, by pursuing the DBM down the silken thread and spending a significantly greater proportion of time on the ground. Momanyi (2005) observed that 70 % of the larvae recovered from the ground in the field simulated screen house studies were parasitised. Therefore, the data on parasitism rates might be higher than recorded.

In conclusion, there should be no field free from cruciferous weeds in order to provide a reservoir and refugia to parasitoids from where they can colonise the crop once cultivated or immigrate after local extinction through pesticide application. Wild crucifers might be crucial in providing refuge to parasitoids after disturbance through cultivation or harvesting. Therefore conservation and rational management of weeds is recommended to improve biological control against DBM.

CHAPTER SEVEN

7 General conclusions

Habitat type, quality, spatial arrangement and connectivity of habitats within an area are known to influence biological diversity and ecosystem structure. Thirteen species of wild crucifers in nine genera were recorded: *Raphanus raphanistrum, Erucastrum arabicum, Sisymbrium officinale, Crambe kilimandscharica, Capsella bursa-pastoris, Rorippa nudiuscula, Ro. micrantha, Ro. microphylla, Lepidium bonariense, Coronopus didymus, Brassica rapa, B. juncea and Brassica* species. *Raphanus raphanistrum* was the dominant species in the highland, followed by *E. arabicum*. The latter was the only species found in the two agro-ecological regions, and dominant in the mid-altitude semi-arid study sites. Highland areas had significantly higher species diversity and species richness than mid-altitude semi-arid areas. Species diversity, richness and evenness varied with season and location. They have been attributed by many authors to differences in amount of rainfall, soil type and over altitude gradient (Cowling, 1990; Montana and Valiente-Banuet, 1998; Suddarapandian and Swamp, 2000). Simmons and Cowling (1996) observed that species diversity changed along soil fertility and geographical gradients in South Africa's Cape Peninsula. Thompson et al. (2005) suggests that the species richness of a community is determined by the soil fertility. Soil fertility limits the number of plant species that can establish in a restored site (Pywell et al., 2003).

The strong influence of seasons on the abundance and diversity of wild crucifers in the highland is a good indication of the relevance of rainfall. We assume that adaptation to growing in dry conditions is a rare trait in crucifers and this is most likely also the factor responsible for low species diversity in the mid-altitude semi-arid areas. This might also explain why *Ro. micrantha* was only found growing in areas of continuous water flow. Species richness in mid-altitude semi-arid areas was limited by water scarcity. Similar observations were made by Montana and Valiente-Banuet (1998). Varying rain intensity and temperatures might increase or restrict the abundance of parasitoid species by determining the presence or absence of essential resources (Quayle et al., 2003).

Presence of wild crucifers might play an important role in providing the parasitoids with essential food as they were found to flower for long. The flowers provide parasitoids with pollen and nectar, which is necessary for provision of protein and carbohydrates for flight

(Idris and Grafius, 1995; Baggen et al., 1999; Landis et al., 2000; Winkler et al., 2006). They enhance foraging, which increases parasitism, longevity, and parameters determining effectiveness as natural enemies (Landis et al., 2000; Steffan-Dewenter et al., 2001). Wäckers and van Rijn (2005) observed that nectar or pollen feeding is essential for the reproductive success of many parasitoids. Most parasitoids visit flowers upon emergence before searching for prey. Considering the small farm sizes and closeness of wild crucifer species to Brassica crops in Kenya this patchy environment may favour dislocation of parasitoids between boundary and crop habitats and can play an important role in the control of DBM.

Another observation from this study is that the higher diversity of host plant species supported the higher parasitoid density. Continuous cabbage cropping in the highlands might have offered a more stable environment for parasitoids. The results support the hypothesis that undisturbed habitats are necessary to preserve natural enemies. Therefore, higher plant diversification is assumed will enhance the population of natural enemies, which migrate to crop fields, attack the pests and thereby contribute to a better control of pests as reported by Norris and Kogan (2005). Higher parasitoid diversity in the mid-altitude semi-arid areas could have been due lack of competition from the exotic introduced parasitoid *D. semiclausum*. The parasitoids differed in their potential contribution to DBM control by having different parasitism rates. Although parasitism rates by each parasitoid species were low, when summed up, the total contribution was quantitatively high. This might have contributed to increase the parasitism leading to low DBM population on the plant. Thus, the assemblage of parasitoids in a particular habitat will depend on host-related and environment-related factors and might result in different degrees of biological control of pests.

Higher species diversity observed in the highlands might allow faster reorganization after local parasitoid extinction due to pesticide application, which is a common process and immigration is of major importance. During heavy DBM infestation, many farmers tend use pesticide cocktails, increased dosages and increase the frequency of pesticide application to control the pest, thus eliminating the natural enemies from the cultivated crop. The process of recolonisation might be faster and more intensive in the highlands than in mid-altitude semi-arid areas due to diversity and large number of parasitoids recorded, in accordance with the insurance hypothesis of biodiversity (Loreau, et al., 2003). However, if not checked the disappearance of recolonisation sources might lead to

extinction of the dominant parasitoid population resulting in pest outbreaks. Hence there must be a mosaic of well connected early and late succession plants to support species diversity and thereby a capacity to recover from disturbances such as pesticide application. During the hot dry seasons, the crops are mainly attacked by *Brevicoryne brassicae* (Ndung'u and Oruku, 2001), forcing the farmers to spray the crop intensively to avoid losing the crop. The problem is usually severe when the crop is attacked during head formation stage. Farmers tend to use pesticide cocktails against the diseases (powdery mildew and angular leaf spot), which are prevalent during the cold season.

The introduced exotic parasitoid *D. semiclausum* seems to have displaced the indigenous parasitoids from the cultivated crop to wild hosts. This was evidenced by absence or relatively low number of indigenous parasitoids on cultivated crop than on wild crucifers. Absence of *D. mollipla* on cultivated crucifers could be due to the stiff competition the parasitoid is facing from *D. semiclausum,* which is known as a specialised DBM parasitoid. Compared to other parasitoids, *D. semiclausum* has high searching efficiency (Wang and Keller, 2002), and has the ability to discriminate previously parasitised DBM larvae to avoid multiparasitism and superparasitism (Bolter and Laing, 1983). On the contrary, *D. mollipla* is considered a relative generalist parasitoid and has been known to attack DBM on crucifers and snowpeas as well as potato tuber moth on potato and tobacco.

All crucifer species included in the studies were suitable for DBM and parasitoid development. Higher survival and performance on cultivated cultivars than on wild crucifers might be a result of high nutritional quality on the former. Higher number of DBM eggs on the wild crucifers than on Brassica cultivars in choice tests however is an indication of long term adaptation of the DBM to the endogenous wild crucifers. They can act as a kind of "dead end" trap plant if found growing within crucifer fields, thus reducing DBM population on the cultivated crop.

Performance and reproductive potential of DBM was lower on wild crucifers compared to development on crop cultivars. Heavier cocoon weight and similar development time on Brassica cultivars could be due to comparable host plant quality after all they are the same species but different varieties. Presence of toxic allelochemicals in the host's diet might have been responsible for higher larval and pupal mortality and low adult emergence on wild crucifers than on Brassica cultivars. Mortality induced by the wild crucifers was more apparent regarding parasitoids than on DBM. This could be due to the

parasitoids being koinobionts, which do not excrete the toxic allelochemicals until pupation. However wild crucifers fulfill the basic requirements for parasitoid development and therefore wild crucifers in the fields will be able to support parasitoid development by acting as alternative hosts if more convenient crop/host combinations are scarce.

Higher parasitism rates recorded in the screenhouse on cabbage and kale than on wild crucifers confirm the efficient adaptation of the natural enemies to the cultivated crucifers and the potential of adapted parasitoids to control DBM population, and to reduce crop damage and the indiscriminate use of pesticides. These in turn will result in faster establishment and spread of parasitoids. Why *C. plutellae* has so far not established in the mid-altitude semi-arid areas remains speculative. However, we can hypothesize from our observations that one reason could be the escape behaviour of DBM larvae to the ground, when disturbed by the parasitoid, not finding their way back onto the plants. Upon dropping to the ground, they could be eaten by the ants on the ground and thus, the parasitoids have no chance of multiplying and establishing.

Presence of *D. semiclausum, O. sokolowskii, C. plutellae* and *D. mollipla* on artificially infested potted cabbage plants within the maize field showed that migration had taken place from the wild crucifers found in the field margins. Wild crucifers in the surrounding maize fields could have been the only source of the parasitoids since there was no other Brassica crop cultivated nearby. First parasitoids were recovered within two days of placing DBM-infested cabbage in the field and parasitism was higher next to field edges. Such fast immigration of parasitoids into areas with newly established hosts and successful location of even isolated patches fields shows the potential of parasitoids to recolonize field plots after disturbance, e.g. through pesticide application or harvesting. Local parasitoid extinction is a common process that can be compensated by immigration in such a patchy environment. The results corroborate the hypothesis that wild crucifers from field margins are important sources for recolonisation of parasitoids (Landis et al., 2000; Idris and Grafius, 2001; Langhof et al. 2003). In addition, presence of weeds maintains and augments natural enemies populations (Hooks and Johnson, 2003). On the other hand such wild crucifer populations adjacent to field plots are potential refuges for the pest too. From our data we cannot exclude a potential role of such sites for DBM population recovery, too. However we hypothesize that the off crop areas function to

stabilize the more sensitive parasitoid populations overweight the risk of being an important source for the high mobile pest.

In conclusion the wild crucifers might have played a role in the rapid establishment and spread of the introduced exotic parasitoid *D. semiclausum* in the highland crucifer growing areas and will help to sustain the parasitoid population furtheron in case of disturbances.

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Special dedication

My adorable children

Joan Gathu & *Edgar Kahuthia*

(My source of inspiration)

My loving husband

D Gathu Kariuki.

My caring parents

Lillian Muthoni & *Bedan Kahuthia*.

Who inspired me through the Hyena's motto of ''Ngone kana Ngone'.

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Kahuthia-gathu R., Löhr, B., Poehling H-M. & Mbugua P.K. (2007). Diversity, distribution and role of wild crucifers in major cabbage and kale growing areas of Kenya. (Submitted to Bulletin of Entomological Research)

Tagungsbeiträge

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Declaration by candidate

I, Ruth Kahuthia-Gathu, declare that this thesis, entitled **" The importance of wild crucifers for diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) and its parasitoids in Kenya"** is an original piece of work conducted by myself and has not been submitted for a degree in any other University.

Hannover, 1st June 2007

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