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

R. Kahuthia-Gathu[1,2], B. Löhr[1], H.M. Poehling[2]* and P.K. Mbugua[3]

[1]International Center of Insect Physiology and Ecology, PO Box 30772, 00100 Nairobi: [2]Universität Hannover, Institute of Plant Protection and Plant Diseases, Herrenhäuser strasse 2, 30419 Hannover, Germany: [3]Kenyatta University, Department of Plant & Microbial Sciences, PO Box 48344, Nairobi

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 an unidentified *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 highlands followed by *E. arabicum*, which was also present and dominant in the semi-arid study sites. Diamondback moth (DBM) was recorded from ten wild crucifer species and *R. raphanistrum* and *E. arabicum* were the preferred host plant species. Overall, four larval, one larval-pupal and one pupal parasitoid of DBM were recorded: *Diadegma semiclausum, D. mollipla, Apanteles sp., Cotesia plutellae, Oomyzus sokolowskii* and *Brachymeria* species, respectively. *Diadegma semiclausum* was the most dominant species on all crucifers. We conclude that wild crucifers act as alternative hosts for DBM and provide refugia for DBM parasitoids, which risk local extinction through pesticide application or competition from introduced exotic parasitoid species. The wild crucifers also act as recolonization sites for DBM parasitoids.

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

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*Author for correspondence
Fax: 0049/511/762301
E-mail: Poehling@ipp.uni-hannover.de

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 & Hector, 2000). Plant diversity affects the population

dynamics of insect herbivores in agricultural (Andow, 1988) and natural communities (Karieva, 1983). Tahvanainen & Root (1972) observed that adult beetles were more abundant on collards *Brassica oleracea* var. *acephala* grown in monocultures than on those grown adjacent to natural vegetation. The 'resource-concentration' hypothesis suggests that the higher herbivore abundance in pure stands is due to the higher probability of host location, long tenure time, higher feeding rates and greater reproductive success of herbivores with narrow host range. Agro-ecosystems that are more diverse in plant species and distribution have been reported to have higher diversity of arthropod communities including herbivore species, predators and parasitoids. In particular, the latter are of special importance in the conservation approach to biological control (Talekar & Shelton, 1993; Kfir & Thomas, 2001; Ohara *et al.*, 2003). Earlier, Altieri (1984) observed that presence of weeds growing outside the crop fields contributed in keeping insect populations below the economic threshold. On the one hand, they provide refuges and, on the other, essential resources such as hosts/prey or alternative food sources (Dennis & Fry, 1992; Landis *et al.*, 2000; Norris & Kogan, 2000). In the case of parasitoids, apart from being a source of hosts, flowering weeds can enhance longevity and effectiveness by providing pollen and nectar (Idris & Grafius, 1995a; Baggen *et al.*, 1999; Landis *et al.*, 2000; Steffan-Dewenter *et al.*, 2001). Wäckers & van Rijn (2005) observed that nectar or pollen feeding is essential for the reproductive success of many insect predators and parasitoids. 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 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 & Shelton, 1993; Reddy *et al.*, 2004). DBM's exceptional pest status is due to the diversity and abundance of host plants, the frequent disruption of its natural enemies communities by broad-spectrum pesticides, its high reproductive potential and genetic elasticity facilitating rapid development of pesticide resistance (Mohan & Gujar, 2003; Shelton, 2004; Vickers *et al.*, 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 & Keddie, 2005).

In a recent classical biological control effort, *Diadegma semiclausum* Hellén (Hymenoptera: Ichneumonidae) was imported from Taiwan and released in the highland areas of Kenya in June 2002. 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 is providing good control of DBM (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; two years after its release very few individuals were recovered (Kahuthia-Gathu *et al.*, unpublished data). However, even in areas with successful establishment, the stability of parasitoid populations is not assured. The presence of other cabbage pests, such as aphids, during the dry season might necessitate pesticide application (Oruku & 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 & Sastrodihardjo, 1986; Verkerk & 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.

The weeds introduce an element of biodiversity that expands the spectrum of natural enemies to colonize the crop as the host becomes available. The higher number of natural enemies entering the cabbage fields is related to higher species diversity (Cromartie Jr., 1975; Root & Kareiva, 1984; Lamb, 1989). Pickett & Thompson (1978) suggested that the disappearance of re-colonisation sources leads to extinction of dominant parasitoid populations. Weeds will act as alternative hosts and reservoirs for parasitoid species, which will colonise the cultivated crop, thus, enhancing biological control.

Agnew & 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 rain-fed (mainly producing cabbage) and mid-altitude semi-arid irrigated areas (mainly producing kale) to evaluate the diversity and distribution of wild crucifer species and their role for indigenous and exotic parasitoids. Plant species diversity and parasitoid assemblage from four sites in the two agro-ecological zones were compared to assess the influence of structural characteristics and pest management strategies on these beneficial insects.

Materials and methods

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 to 2293 m and Kinangop from 2343 to 2749 m. Maximum temperatures range between 22°C and 30°C and minimum temperatures between 10°C and 15°C. The rainfall is bimodal and ranges from 1500 to 2000 mm per annum. The long rains occur between March and June and the short rains between October and 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 to 1290 m and Athi River at 1457 to 1527 m. Maximum temperatures range between 25°C and 32°C and minimum temperatures between 5°C and 20°C. The areas receive 500 to 900 mm rainfall per annum and have no distinct seasons. 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.

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 total of 35 and 25 fields were selected in every visit from the highland and mid-altitude semi-arid areas, respectively, and used as the basis for evaluating the diversity of wild crucifers. In the highlands, sampling fields were selected at 2–4 km interval 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 canal (Yatta). A line-transect sampling technique previously 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. The representative wild crucifer species along a 30 m sampling line were sampled by placing a one-metre quadrat frame at the beginning of the transect and recording all wild crucifer species within the frame. The number of plants from each species within the frame was recorded. This procedure was repeated after every 3 m of the line transect to give a total of ten sampling points per transect. We tried to have the line transect perpendicular to the field margins. However, this was not always possible due to the small size of land left fallow and the generally small farm sizes. The number of quadrats varied because some of the selected fields had no wild crucifers recorded.

Samples from each crucifer species were collected and taken to the laboratory for processing and identification. The voucher specimens were identified using various plant identification keys (Ivens, 1967; Agnew & Agnew, 1994). Species were confirmed and deposited at the East Africa Herbarium at National Museums of Kenya.

Sampling of diamondback moth on wild crucifers

To assess DBM incidence on the wild crucifers, a maximum of ten individual plants from each species were selected per quadrat and physically checked for the presence of DBM. The number of DBM larvae and pupae found on each plant were recorded. All 3rd and 4th instar DBM larvae and pupae were collected, kept in labelled (field number, host plant, locality, collection date) plastic containers and taken to the laboratory. The containers were lined with tissue paper at the bottom to absorb excess moisture and closed with a cap containing a fine muslin cloth to enhance ventilation and reduce mould growth. The larvae were kept at room temperature ($23 \pm 2°C$), 50–70% RH and a photo-period of 12:12 h (L:D) and fed on their respective crucifer species when 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 cocoons in gregarious species was recorded.

Data analysis

The diversity and evenness of wild crucifer species was estimated using the Shannon Diversity Index (H′). It is the proportion of species (pi) relative to the 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

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

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

The data of DBM counts on wild crucifers were normalized using a square root transformation (SQRT + 1) before being subjected for analysis using a General Linear Model (GLM) procedure. Means were seperated using the Tukey test (SAS, 2004). 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 parastoids as sum of parasitised cocoons/(DBM + cocoons) × 100. The data for parasitoids recovered from the wild crucifers were arcsine SQRT transformed before anlaysis.

Results

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. *Erucastrum arabicum* Fisch & Mey., *Raphanus raphanistrum* L., *Capsella bursa-pastoris* (L.) Medic., *Lepidium bonariense* L., *Crambe kilimandscharica* O.E. Schulz., *Coronopus didymus* (L.) Sm., an unidentified *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 (tables 1 and 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 done for the mid-altitude areas. *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 highland areas. *Rorippa nudiuscula* and *B. rapa* were recorded from Kinangop only, but with very low frequencies.

A notable 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 Kinangop and Naro Moru and also between mid-altitude semi-arid areas Athi River and Yatta (see also table 4).

Diversity indices and evenness differed significantly between seasons and regions. In Naro Moru, the diversity index ranged between 0.820 and 1.663. The highest diversity indices of 1.663 and 1.050 were recorded during the short rains, while the lowest indices of 0.924 and 0.820 were recorded during the cold dry season in 2005 and 2006, respectively (table 1). In Kinangop, the highest indices of

Table 1. Diversity index and seasonal occurrence of wild crucifer species in the highlands cabbage growing area of Naro Moru 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	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	1.050
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 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

1.203 and 1.021 were recorded during the hot dry and cold dry seasons, and the lowest indices of 0.839 and 0.434 were recorded during the hot dry and cold dry seasons in 2005 and 2006, respectively (table 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 was recorded during cold dry and long 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 was recorded during cold dry and hot dry season in 2005 and 2006, respectively, in Kinangop.

Species diversity differed significantly between hot dry and long rainy season of 2005 ($t = 6.01$, $n = 448$, $P < 0.001$), between short rainy and dry season of 2005–2006 ($t = 8.9$, $n = 363$, $P < 0.001$) and between cold dry and short rainy season of 2006 ($t = 3.18$, $n = 511$, $P < 0.001$) in Naro Moru (table 1). In the Kinangop area, significant differences were

observed between hot dry and long rainy season of 2005 ($t = 3.09$, $n = 439$, $P < 0.001$) and 2006 ($t = 4.88$, $n = 245$, $P < 0.001$), respectively, and between short rainy and hot dry season of 2005–2006 ($t = 4.10$, $n = 114$, $P < 0.001$) (table 2).

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.

Incidence of DBM on wild crucifers

Diamondback moth was collected from ten out of the 12 wild crucifers recorded in the highlands, while no DBM was found on *C. didymus* and *B. rapa* (tables 3 and 4). The pest was present on *R. raphanistrum* throughout the sampling period. In 2006, the highest population of 1.03 DBM per plant

Table 3. Seasonal variation on mean number of diamondback moth per plant±SE on wild crucifer species in the highland crucifer growing areas of Naro Moru from Central Province of Kenya.

Wild crucifer species	Number of DBM per plant in 2005				Number of DBM per plant in 2006			
	Hot dry	Long rains	Cold dry	Short rains	Hot dry	Long rains	Cold dry	Short rains
Raphanus raphanistrum	0.03 ± 0.03 $n=423$	0.06 ± 0.02 $n=715$	1.08 ± 0.27 $n=200$	0.07 ± 0.04 $n=419$	0.09 ± 0.05 $n=341$	0.45 ± 0.14 $n=491$	0.21 ± 0.06 $n=354$	0.12 ± 0.02 $n=1193$
Eucastrum arabicum	0.15 ± 0.11 $n=162$	0.06 ± 0.03 $n=362$	0.16 ± 0.08 $n=26$	0 $n=26$	0 $n=259$	0.11 ± 0.11 $n=25$	0.009 ± 0.01 $n=151$	0.02 ± 0.01 $n=156$
Brassica juncea	0 $n=5$	–	–	–	–	–	–	0.22 ± 0.20 $n=10$
Capsella bursa-pastoris	0.14 ± 0.14 $n=157$	0 $n=13$	0 $n=3$	0 $n=15$	–	–	0 $n=2$	0 $n=7$
Lepidium bonariense	0.07 ± 0.06 $n=56$	0 $n=4$	0 $n=5$	0 $n=9$	0 $n=15$	0.25 ± 0.25 $n=30$	–	0 $n=37$
Rorippa microphylla	–	–	0 $n=7$	–	0	–	–	1.25 ± 0.63 $n=8$
Coronopus didymus	–	–	–	0 $n=6$	0 $n=2$	–	–	–
Sisymbrium officinale	–	0.20 ± 0.20 $n=11$	0 $n=4$	–	–	0 $n=4$	0 $n=10$	–
Crambe kilimandscharica	–	1.0 ± 0.41 $n=4$	–	–	–	–	–	–
Brassica sp.	–	0 $n=4$	–	–	–	–	–	–
Number of DBM sampled	60	47	155	21	16	223	81	172

Table 4. Seasonal variation on mean number of diamondback moth per plant±SE on wild crucifer species in the highland crucifer growing areas of Kinangop from Central Province of Kenya.

Wild crucifer species	Number of DBM per plant in 2005				Number of DBM per plant in 2006			
	Hot dry	Long rains	Cold dry	Short rains	Hot dry	Long rains	Cold dry	Short rains
Raphanus raphanistrum	0.84 ± 0.29 $n=390$	0.29 ± 0.07 $n=262$	0.19 ± 0.04 $n=549$	0.91 ± 0.25 $n=314$	1.03 ± 0.59 $n=168$	0.09 ± 0.02 $n=1522$	0.37 ± 0.09 $n=590$	0.29 ± 0.06 $n=1077$
Eucastrum arabicum	0.13 ± 0.13 $n=14$	0.17 ± 0.17 $n=45$	0.53 ± 0.49 $n=49$	0 $n=17$	0 $n=7$	0.05 ± 0.03 $n=94$	0 $n=4$	0.15 ± 0.15 $n=25$
Rorippa nudiuscula	0.74 ± 0.42 $n=95$	–	–	–	–	–	–	–
Brassica juncea	0	–	0.67 ± 0.27	–	–	–	0 $n=4$	–
Capsella bursa-pastoris	0.12 ± 0.09 $n=95$	0 $n=43$	0 $n=32$	0 $n=26$	–	0 $n=99$	0 $n=25$	0 $n=55$
Lepidium bonariense	0 $n=4$	0 $n=6$	0 $n=1$	0 $n=2$	–	0 $n=4$	0 $n=4$	0 $n=25$
Rorippa microphylla	1.70 ± 0.67 $n=21$	0.70 ± 0.42 $n=16$	–	–	–	–	–	0.49 ± 0.37 $n=35$
Coronopus didymus	0 $n=20$	–	0 $n=7$	0 $n=22$	0 $n=6$	0 $n=7$	0 $n=14$	0 $n=12$
Sisymbrium officinale	–	–	1.50 ± 0.96	–	–	0 $n=3$	0 $n=10$	0.49 ± 0.77 $n=35$
Crambe kilimandscharica	–	1.20 ± 0.55 $n=10$	0 $n=10$	–	–	–	1.68 ± 1.43 $n=18$	–
Brassica rapa	–	–	–	–	–	0 $n=15$	–	–
Number of DBM sampled	330	240	99	251	226	110	265	313

was recorded during the hot dry season in Kinangop and, in 2005 during the cold dry season in Naro Moru, 1.08 DBM per plant, both from *R. raphanistrum*. The highest population of 0.66 DBM per 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 5).

Parasitoid fauna on wild crucifers

Six primary parasitoid species were recovered from DBM larvae or pupae collected from seven wild crucifers species (table 6). Four larval parasitoid species, *D. semiclausum* and *Diadegma mollipla* (Holmgren) (both Hymenoptera: Ichneumonidae), *Cotesia plutellae* (Kurdjumov) and *Apanteles*

Table 5. Seasonal variation on mean number of diamondback moth per plant $\pm$ SE on wild crucifer species in two mid-altitude semi-arid crucifer growing areas of Athi River and Yatta from Eastern Province of Kenya.

Crucifer species	Number of DBM per plant in 2005				Number of DBM per plant in 2006			
	Hot dry	Long rains	Cold dry	Short rains	Hot dry	Long rains	Cold dry	Short rains
Athi River								
E. arabicum	–	0.66 + 0.14 n = 547	–	0.26 + 0.04 n = 57	0.08 + 0.08 n = 105	0.02 + 0.009 n = 524	0 n = 11	0.04 + 0.02 n = 1049
Ro. micrantha	–	–	–	0 n = 6	–	0 n = 25	0 n = 105	0.002 + 0.002 n = 435
DBM sampled		361		15	9	14	0	28
Yatta								
E. arabicum	–	0 n = 3	0 n = 1	–	–	0 n = 12	–	–
Ro. micrantha	–	0 n = 15	0 n = 65	–	0.25 + 0.25 n = 10	0.17 + 0.05 n = 164	0 n = 63	0.02 + 0.02 n = 227
DBM sampled		0	0		4	10	0	7

Table 6. Parasitism rates $\pm$ SE and parasitoid species recovered from diamondback moth collected from wild crucifers in highland crucifer growing areas of Central Province and mid-altitude semi-arid areas of Eastern Province of Kenya. Means $\pm$ SE followed by same letters within a column are not significantly different at $P < 0.05$ (SNK).

Site	Parasitoid species	Percent parasitism $\pm$ SE on wild crucifer species						
		Raphanus raphanistrum	*Erucastrum arabicum*	*Brassica juncea*	*C. bursa-pastoris*	*Rorippa microphylla*	*Sisymbrium officinale*	*Crambe kilimandscharica*
Naro Moru	*D. semiclausum*	36.1 + 3.1a	16.5 + 6.1a	0	0	41.1 + 4.9a		38.9 + 15.6a
	D. mollipla	3.6 + 1.2b	7.0 + 3.9b	0	29.2 + 4.2a	5.7 + 5.7b		
	O. sokolowskii	0.5 + 0.58c	0	0	0	0		
	DBM collected (*n*)	405	49	6	15	10	0	16
Kinangop	*D. semiclausum*	33.6 + 2.6a	11.0 + 6.8a	0	19.1 + 2.4a	39.7 + 8.4a	0	
	D. mollipla	6.3 + 1.3b	3.4 + 3.4a	7.1 + 2.2a	19.1 + 2.4a	0	4.2 + 4.2a	
	O. sokolowskii	0	0	3.6 + 3.6a	0	0	0	
	DBM collected (*n*)	989	49	17	20	36	14	0
Athi River	D. semiclausum		7.4 + 2.9a					
	D. mollipla		10.4 + 3.5a					
	Apanteles sp.		9.24 + 3.5a					
	Brachymeria sp.		0.2 + 0.2c					
	O. sokolowskii		1.0 + 0.7bc					
	C. plutellae		1.3 + 0.9b					
	DBM collected (*n*)		265					

sp. (both Hymenoptera: Braconidae), one larval-pupal parasitoid *Oomyzus sokolowskii* (Kurdjumov) (Hymenoptera: Eulophidae) and one pupal parasitoid (*Brachymeria* sp., Hymenoptera: Chalcidae) were collected. Whereas in the highland areas only *D. semiclausum*, *D. mollipla* and *O. soko-lowskii* could be found, all six species mentioned above were recovered from *E. arabicum* in the mid-altitude semi-arid area of Athi River. The highest parasitism rates in the highlands 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, whereas at Athi River *D. mollipla* was the dominant species. However, parasitism was lower than in the highlands.

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. Higher plant diversity is assumed to enhance the population of natural enemies, which migrate to crop fields, attack the pests and, thereby, contribute to better pest control (Root, 1973; Boller *et al.*, 2004; Bullock *et al.*, 2007; Olson & Wackers, 2007; Yann *et al.*, 2007). Comparing the literature (from other agroecosystems) and our data, the most logical deduction, 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 recoloniza-tion after disturbance, or resilience (Bengtsson *et al.*, 2003; Tscharntke *et al.*, 2005). Hickman & Wratten (1996) and Dyer & Landis (1997) related the number of natural enemies entering the crop field to higher diversity of vegetation surrounding wheat and maize fields, respectively.

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 altitude gradient (Cowling, 1996; Montana & Valiente-Banuet, 1998; Suddarapandian & Swamp, 2000). Simmons & 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. This could have applied in our research because the highlands had rich volcanic soils and this is where higher species diversity was recorded. 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 their land fallow, especially where there was no water to supplement rainfall. 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 a key 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 & Valiente-Banuet (1998).

Under the 'enemies hypothesis' (Root, 1973; Russell, 1989; Wolfe, 2002), weeds introduce an element of biodiversity that expands the spectrum of natural enemies to colonize the crop (Longley *et al.*, 1997). The hypothesis predicts a positive correlation between plant species richness and natural enemy abundance, which results in the regulation of herbivores at lower levels in diverse vegetation than in pure stands. Weeds are an important part of the vegetative diversity and help in maintaining and augmenting natural enemy populations (Landis *et al.*, 2000; Hooks & Johnson, 2003, Norris & Kogan, 2005). Weeds can be even more important when they share pests and natural enemies with the cultivated crop (Tscharntke & Kruess, 1999; Kremen *et al.*, 2002). This is of special importance in a 'crucifer system' because of the relative strong association of herbivores and their most efficient specialized natural enemies, such as the parasitoids, to a narrow host plant range. 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 been documented (Idris & Grafius, 1995b; Winkler *et al.*, 2005). 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 crop the more effective they are in regulating pest populations because some natural enemies have only a limited spatial dispersal potential. Therefore, the

small farm sizes and proximity of wild crucifer species to cultivated crucifer crops in Kenya might favour the natural management of DBM since wild crucifers in boundary vegetation could provide a complete set of important resources for parasitoids such as hosts and nutrition (e.g. nectar). Possibly, wild crucifers in uncultivated areas will also provide reservoirs of the pest levelling off the positive effect for the parasitoid population. However, DBM populations on the wild crucifers were always much lower (1:5) compared to that reported on cultivated crucifer crop (Löhr *et al.*, 2007; Kahuthia-Gathu *et al.*, in press). Karieva (1983) and Andow (1988) observed that specialist herbivores exhibit lower population densities in diverse habitats containing host plants and non-host plants compared with simple monoculture areas covered by host plants only. This might be due to higher probability of host location, host finding, higher feeding rates and greater reproductive success of the herbivores. The low DBM numbers on wild crucifers could also be associated with higher species diversity and high predation in the uncultivated areas. Some of the wild crucifers being relatively smaller than the cultivated cultivars could have affected the DBM numbers. A variety of predators, including spiders, were found feeding on the DBM. The results are supported by the findings of Liljesthrom *et al.* (2003), who found that spiders were more abundant in uncultivated insecticide-free areas. Also, in our study we found many natural enemies, especially predators on the wild crucifers, but their abundance was not quantified. We hypothesize that the off crop areas provide only a minor risk of being a substantive source for the pests and that their function to stabilize the parasitoid populations is overweighing. However, this must remain speculative until a broad comparison between field plots, with and without neighbouring off crop areas, is performed.

The number of parasitoids recorded in the cabbage growing areas was significantly higher than in kale growing areas. Out of the total 2441 and 3545 DBM collected from Naro Moru and Kinangop, 1520 and 1704 parasitoids emerged, respectively; while in Athi River and Yatta, 962 and 649 parasitoids emerged from 2756 and 1649 DBM collected, respectively. These differences could be due to continuous cabbage growing all the year round and an abundance of wild crucifer species. Parasitoids strongly respond to vegetation complexity (Marino & Landis, 1996). The difference in parasitoid numbers and assemblage may be related to climatic variations between the two agro-ecological zones. The continuous cropping in the highlands may offer a more stable environment where both DBM and its parasitoids can co-exist for a long time. The large patches with wild crucifers observed in the cabbage growing areas may have contributed to high parasitoid abundance. Thies & Tscharntke (1999) described increasing parasitism of rape pollen beetle in non-crop habitat area. Kruess & Tscharntke (2000) observed that percent parasitism of the weevil *Oxystoma ochropus* increased with area, doubling from 35% on the smallest to 70% on the largest meadows. As mentioned above, one key factor supporting parasitoid abundance and efficacy is the supply of convenient food for the adults. Stapel *et al.* (1997) ascertained that female *Microplitis croceipes* Cresson (Hymenoptera: Braconidae), a larval parasitoid of *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae), stayed longer and parasitised more host larvae 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.

A surprising result in our study was the very low occurrence of the endemic parasitoid species *D. mollipla*. This species was recovered almost entirely from the wild crucifers and kale, none from Naro Moru and only one parasitoid wasp from Kinangop on cabbage. *Diadegma mollipla* is considered to be a 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) *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) on potato and tobacco in southern Africa and on potato in Yemen (Kroschel, 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 an abundant and widely distributed parasitoid of DBM in eastern African highlands. Overall, field parasitism was less than 20%, with *D. mollipla* accounting for 9%. One reason could be a lack of strong intrinsic cues from the typical crucifer host plants of DBM. This may also explain the generally low parasitism rates observed in the laboratory on crucifers (Akol et al., 2003). Moreover, Rossbach et al. (2005) observed that *D. mollipla* was not attracted by the chemical odours produced by kale, and this could have also contributed to the low parasitism. The parasitoid also has been recovered from DBM on snowpeas, where significantly higher parasitism rates were recorded compared to that of DBM on cabbage (Löhr & Rossbach, 2004). This might be due to the host plant not being attractive to the other DBM parasitoids. Momanyi et al. (2006) and Löhr et al. (2007) observed 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. Absence of *D. mollipla* on cabbage in the highlands two years after the introduction of *D. semiclausum* may indicate the stiff competition this species is facing from *D. semiclausum*, a DBM specialist with a high searching efficiency (Wang & Keller, 2002). This could have forced *D. mollipla* to search for DBM from the wild crucifers, which are the alternative hosts; consequently, significant numbers of *D. mollipla* were collected in the highlands and semi-arid areas on the wild crucifers only. *Oomyzus sokolowskii* is a gregarious larval-pupal parasitoid that attacks DBM (Fitton & Walker, 1992) and has been introduced in tropical and subtropical regions to control DBM (Talekar & Hu, 1966) and is adapted to high temperature conditions. They were abundant in the mid-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 4th instar DBM larvae and pupae available for *O. sokolowskii* to parasitize.

Much to our surprise, *D. semiclausum*, considered a parasitoid for cool highland areas (Talekar & 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, relative humidity and vapour pressure deficit

(VPD). Since March 2005 when *Cotesia plutellae* was released in Yatta and Athi River, very low numbers have been recovered from the kale fields. On the contrary, the parasitoid has become established within the Lake Victoria region and spread over 200 km from the release sites in Uganda into western Kenya (ICIPE, unpublished data). Remarkable, also, is the complete absence of hyper-parasitoids in both highland and mid-altitude semi-arid areas, which may have contributed to the successful establishment and spread of *D. semiclausum*.

In conclusion, wild crucifer species will 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 recolonization of fields after local elimination of parasitoids. 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.

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