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Development and reproductive potential of diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) on cultivated and wild crucifer species in Kenya

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Abstract. The development, survival and reproductive potential of diamondback moth *Plutella xylostella* (Linnaeus) were studied at 25 ± 1 °C 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 *Rorippa micrantha*. *Rorippa micrantha* was the most preferred species in oviposition choice tests, while cabbage and kale were least preferred. First instar larval mining period differed significantly between plant species with the longest period recorded on cabbage (3.0 days) and the shortest on *R. micrantha* (0.4 days). Pupal weight was significantly lower for larvae reared on *R. nudiuscula*, while those of the others were similar. The developmental period from first instar to adult was the shortest on *R. micrantha* (14.1 days) and the longest on *R. raphanistrum* (15.6 days). Survival to adult was not statistically affected by the host plant species. Adult longevity ranged between 18.2 days on *R. raphanistrum* and 24.7 days on *R. nudiuscula*. The females were significantly heavier than the males on all plant species. However, males lived longer than females. Moths reared on *R. nudiuscula* recorded the highest fecundity (326 eggs), while moths reared on cabbage had the lowest fecundity (262 eggs). Kale and *R. nudiuscula* recorded the longest generation time of 31.7 days, while *E. arabicum* had the highest net reproductive rate (126.4 eggs per day). The highest intrinsic rate of increase was calculated for *R. micrantha* (0.179) and the lowest for kale (0.147). This study shows the suitability of wild crucifers as hosts for *P. xylostella* and indicates that they may play a major role as reservoir for the pest during the absence of cultivated host plants.

Key words: development, diamondback moth, oviposition preference, reproduction, wild crucifers, fitness

Introduction

Diamondback moth (DBM) *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae) is the most important pest of cultivated crucifers worldwide (Talekar and Shelton, 1993). 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). This pest has become the most abundant and damaging pest of cruciferous crops in Kenya and gained economic importance over the years.

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The widespread and intensive use of insecticides and the genetic elasticity of DBM have led to serious problems including insecticide resistance (Kibata, 1997; Mohan and Gujar, 2003; Shelton, 2004; Vickers *et al.*, 2004; Sarfraz *et al.* 2005). Integrated pest management (IPM) systems based on functional biodiversity and ecological engineering have been considered to be the only viable long-term solutions to combat this pest (Verkerk and Wright, 1996; Gurr *et al.* 2003).

In the case of mobile pests and rapidly rotating crops, synchronization of herbivores and natural enemies in time and space is crucial for enhanced conservation biological control, and weeds can play a key role in this process. Weeds growing in the vicinity of field crops of the same plant family often harbour crop pests and provide them with refugia. 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 provide refugia not only for the pests but also for the natural enemies, and can contribute as source habitats of predators and parasitoids for re-colonization of cultivated fields (Longley and Jepson, 1997). Moreover, weeds introduce an element of plant biodiversity that expands the spectrum of natural enemies available to colonize the crop stand (Tscharntke and Kruess, 1999; Rauwald and Ives, 2001). Uncultivated habitats may also offer alternative prey or hosts for predators and parasitoids, and provide food sources such as pollen and nectar 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 were collected in the cabbage and kale growing areas of Kenya; some of them were found to serve as alternative hosts for DBM and harboured a great diversity of natural enemies, with parasitoids being the most important group. The wild crucifers provided refugia to both indigenous and exotic parasitoids that colonized cultivated crops once transplanted (Kahuthia-Gathu, 2007). As the cabbage fields in East Africa are generally small (Macharia *et al.*, 2005), edge effects, with parasitoid reservoirs on 'off-crop' crucifer weeds hosting populations of DBM, can be expected to mitigate pesticide impact on parasitoids. In addition, stable reservoirs outside the crop can enhance the efficient synchronization of parasitoids with a mobile pest, such as DBM, which shows high temporal and spatial variability within fields.

The objective of the present study was to evaluate the performance of DBM on two cultivated *Brassica* cultivars and four commonly found wild crucifer species to assess the role of the latter as alternative hosts for the pest.

Materials and methods

Study site

The experiments were conducted from April to November 2004 at the International Centre 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 °C, 60–80% RH and 12:12 h L:D.

Diamondback moth culture

A colony of DBM was established and maintained in the insectary at ICIPE on common cabbage *Brassica oleracea* var. *capitata* L. (Brassicaceae), cultivar Gloria, from the larvae and pupae originally collected from cabbage grown in Werugha location, Taita-Taveta District, coastal region of Kenya at 03°26′16″S, 38°20′24″E and 1650 m above sea level (masl). The moths were reared as described by Löhr and Gathu (2002) and had no previous encounter with wild crucifers.

Host plants

Two cultivated crucifers, cabbage *B. oleracea* var. *capitata* L. cultivar Gloria, and kale *B. 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. (all Brassicaceae), 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 the highlands and mid-altitude crucifer growing areas of Kenya and the presence of various stages of DBM in the plants during field surveys conducted prior to the experiments. Seeds of the wild crucifers were collected during the surveys, while those of cabbage and kale were purchased from commercial suppliers in Nairobi.

Seedlings were raised in the greenhouse in seedling trays and transplanted 3 weeks after germination into 15-cm diameter plastic pots (2 l). A mixture of garden compost, red soil and sand (2:1:1) was used as the growth medium and no fertilizer was applied. The plants were ready for use in the trials 6 weeks after transplanting. All the plants in these studies were 9 weeks old at the time they were used in the screen houses or laboratory.

Oviposition preference

Choice and no-choice oviposition preference tests were conducted in the screen house using whole plants. The experiments were performed with potted cabbage, kale and *R. raphanistrum* plants grown to the sixth fully extended leaf stage, whereas the wild crucifers *E. arabicum*, *R. micrantha* and *R. nudiuscula* were grown to the 10–15 fully extended leaf stage. In the choice tests, 24 plants, 4 from each host plant species mentioned above, were randomly placed in a cage (1.3 × 2.5 × 1 m) made of muslin cloth with a sleeve on the sides for introducing DBM adults. The plants were placed at a spacing of 30 × 40 cm between plants. Ten pairs of newly emerged and mated DBM were released in the cage and fed on a 10% sugar solution soaked in cotton wool. After 48 h, the plants were removed and the eggs on the upper and lower leaf surfaces counted. The experiment was replicated six times.

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

A second no-choice test was conducted in the laboratory using excised leaves to confirm our earlier results in the screen house. The leaves of the test species were placed individually in a plastic vial (6 cm long × 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 × 20 × 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 a 10% sugar solution soaked in cotton wool. After 48 h, the leaves were removed and the number of eggs on the upper and lower epidermis and on the walls of the plastic vials was counted under the stereomicroscope. The experiment was replicated 15 times for each plant species.

Effect of host plants on egg hatchability

Hatch rate of eggs laid on different crucifer species was determined by excising 15 leaves from each plant species of the oviposition preference experiment. The number of eggs on each leaf was counted. The leaves were placed individually in transparent plastic containers (5 × 6.5 × 7 cm) whose cap had a muslin cloth in the centre for aeration and placed in the incubator at 25 ± 1 °C, 60–80% relative humidity (RH) and 12:12 h (L:D) until the eggs hatched. The number of hatched neonate larvae from each leaf was recorded.

Effect of host plant on larval development and survival

The larvae obtained from the hatch experiment were used in the subsequent experiments on larval development and survival. One hundred and fifty neonate larvae from each plant species were used in the trials. A single larva was picked using a fine camel hairbrush and placed individually in a well-ventilated plastic vial (2.5 × 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 vials were placed in the incubator at 25 ± 1 °C, 60–80% RH and 12:12 h (L:D). The larvae were observed daily until pupation and the leaves changed every 2 days. The duration of larval mining and development period was recorded. The pupa was removed from the vial and weighed within 24 h of pupation using a Mettler electronic scale (Type AM 100; Mettler, Switzerland) and returned to the vial for adult emergence. The newly emerged adults were sexed. The duration of the pupal period and the sex of the adults were recorded.

Effects of host plants on adult longevity and reproductive potential

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 h. 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 × 6.5 × 7 cm). This was covered with an inverted transparent plastic container (5 × 6.8 × 12 cm) whose bottom was cut out and replaced with a muslin cloth for ventilation. One pair of adult moths 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 h, the leaf was changed and the number of eggs on the upper and lower leaf surfaces and the walls of the container counted. The procedure was repeated every 48 h until the female died. The longevity of males and females was recorded. The experiment was conducted in an incubator at the conditions stated above. Life table parameters under laboratory conditions were constructed as suggested by Southwood (1978). The observations used for the construction of the life table were developmental

period, survival, fecundity, number of progeny, sex ratio of progeny and adult longevity.

Data analysis

The data of oviposition preference studies in the choice test were analysed using Friedman's non-parametric ANOVA by ranks (Zar, 1996). Egg counts of the no-choice oviposition preference tests were first transformed using SQRT transformation and submitted to one-way ANOVA using the general linear model (GLM) procedure of SAS for PC (SAS Institute, 1999) and the means separated using Tukey's multiple comparison test at $P < 0.05$ (SAS Institute, 1999). 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 ANOVA using the GLM procedure of SAS for PC. Means were separated using Student–Newman–Keuls test (SNK) at $P < 0.05$ (Sokal and Rohlf, 1995). Percentage of 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 percentage of egg hatch was calculated as: (number of eggs hatched/total number of eggs) × 100. The percentage of data was then subjected to one-way ANOVA using the GLM procedure. Life table statistics were calculated using the Jackknife program according to Hulting *et al.* (1990). Differences in intrinsic rate of increase (r_m) were calculated following the protocol of Dixon (1987) and compared with Newman–Keuls tests (Sokal and Rohlf, 1995), based on the Jackknife estimates of variance for r_m values (Meyer *et al.*, 1986). Development time, number of progeny and sex ratio were used to calculate the intrinsic rate of increase in DBM.

Results

Oviposition preference

DBM distinctly preferred some host plants to others in both the choice ($F_{(10,133)} = 7.97$; $P < 0.0001$) and no-choice experiments ($F_{(5,138)} = 10.76$; $P < 0.0001$). In both tests, DBM laid a significantly higher number of eggs on wild crucifers than on cabbage and kale. The highest number of eggs was recorded on *R. micrantha*, while cabbage was the least preferred (Table 1).

In the choice test experiments, the number of eggs oviposited on the wild crucifer plants was significantly higher than that laid on the cabbage and kale. It was also found that DBM laid many eggs on the walls of the pots containing cabbage and kale plants, while this was not found to be the case for the wild crucifers. These results were confirmed with the excised leaves in the laboratory where DBM moths preferred to oviposit on the leaves of wild crucifers, while on cabbage and kale 85% of the eggs were laid on the walls of the plastic container and the plastic vial containing the excised leaf (Fig. 1). The number of eggs laid by DBM on the excised leaves on *R. raphanistrum* and *R. micrantha* was higher on the upper than the lower leaf surface. Significantly higher number of eggs was laid on the lower than the upper leaf surface on all the crucifer species (Fig. 2).

Table 1. Oviposition preference of *Plutella xylostella* on two cultivated *Brassica* cultivars and four wild crucifer species in choice and no-choice tests

Plant species	Number of eggs laid per female in 48 h	
	Choice test	No-choice test
Brassica oleracea var. *acephala*	9.1 ± 2.6c	23.4 ± 2.5b
B. oleracea var. *capitata*	5.6 ± 1.0c	16.9 ± 2.0c
Erucastrum arabicum	29.9 ± 4.7ab	59.4 ± 8.1a
Raphanus raphanistrum	21.7 ± 3.2b	49.8 ± 6.2a
Rorippa nudiuscula	24.6 ± 2.8b	46.6 ± 5.9a
Rorippa micrantha	38.6 ± 6.9a	62.8 ± 7.3a

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

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

Significant differences ($F_{(5,169)} = 10.29$; $P < 0.0001$) were recorded on percentage of egg hatch between different host plants, with eggs laid on *R. micrantha* recording a lower hatch rate (75.1%) than all other test plant species (Table 2). Host plants also significantly affected other biological parameters such as the larval mining period ($F_{(5,750)} = 168.43$; $P < 0.0001$), duration of larval development ($F_{(5,621)} = 15.48$; $P < 0.0001$), pupal weight ($F_{(5,612)} = 4.15$; $P < 0.001$), pupal period ($F_{(5,569)} = 5.9$; $P < 0.0001$) and development time ($F_{(5,568)} = 16.09$; $P < 0.0001$) (Table 3). DBM reared on cabbage had a significantly longer larval mining period than on kale, while those reared on *R. raphanistrum* recorded significantly longer period compared with the other wild crucifer species. The duration of larval mining ranged from 0.4 days on *R. micrantha* to 3.0 days on cabbage. *R. micrantha* recorded a significantly lower larval period (8.7 days) than the other host plant species (Table 3). The larvae reared on cabbage had a significantly shorter larval period than those reared on kale. The pupal weight of DBM reared on kale had the highest mean weight

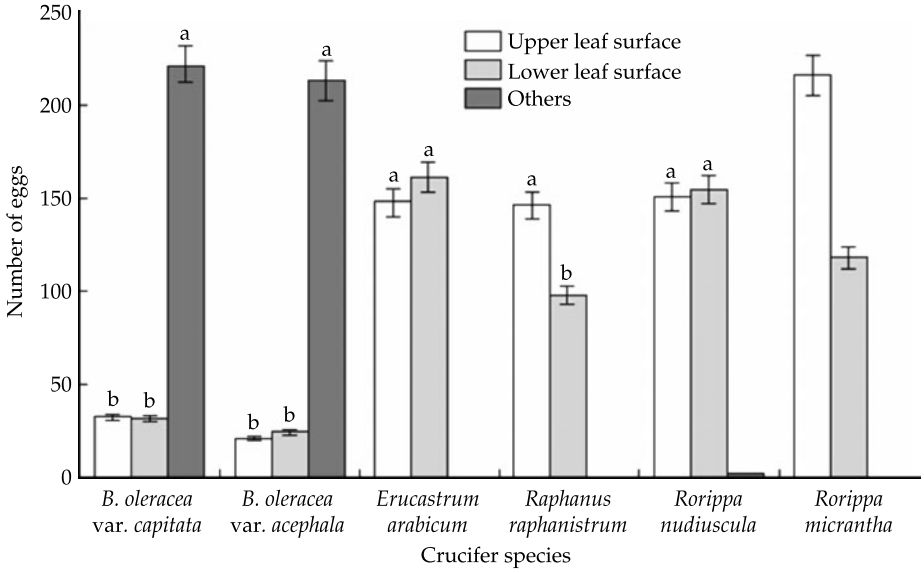

Fig. 1. Effect of two cultivated *Brassica* cultivars and four wild crucifer species on the number and distribution of *Plutella xylostella* eggs on excised leaves

(6.1 mg), while those on *R. raphanistrum* the lowest (5.6 mg).

DBM reared on *R. nudiuscula* recorded the shortest pupal period of 5.1 days, while those reared on kale and *R. raphanistrum* recorded significantly longer development period than the other crucifer species. Kale recorded significantly longer development time than cabbage, while that of *R. raphanistrum* and *E. arabicum* was longer than *R. micrantha* and *R. nudiuscula*.

Overall, the development time of DBM ranged between 14.1 days in *R. micrantha* and 15.6 days in *R. raphanistrum*. Larval mortality was higher than pupal mortality on all the test plants. The highest larval mortality was recorded on *E. arabicum*, while cabbage and kale had the lowest (Fig. 3).

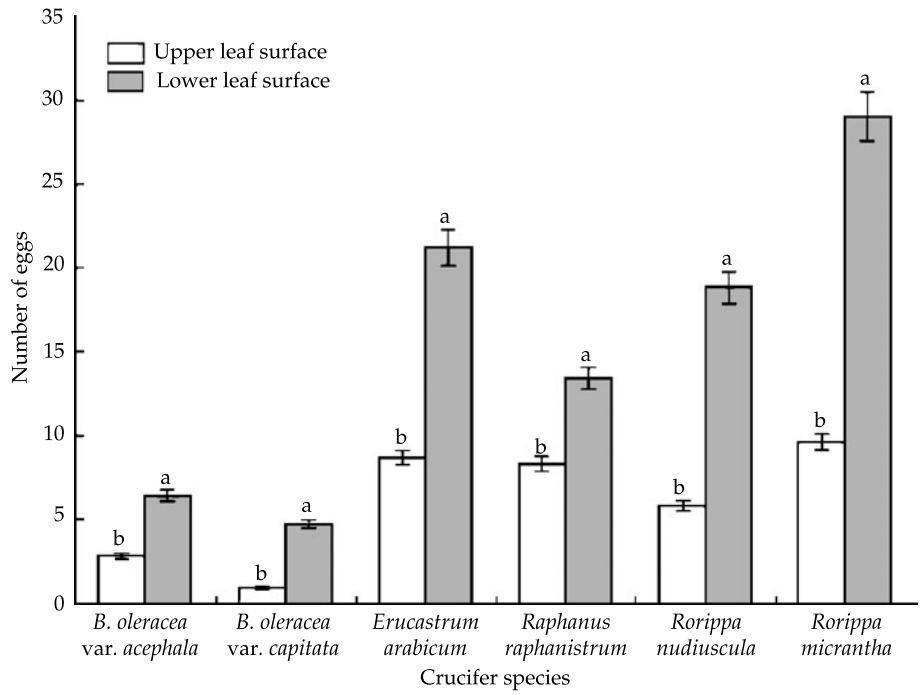

Fig. 2. Distribution of *Plutella xylostella* eggs on the leaf surface on two cultivated *Brassica* cultivars and four wild crucifer species

Table 2. Mean percentage of egg hatch of eggs oviposited by *Plutella xylostella* on two cultivated *Brassica* cultivars and four wild crucifer species

Plant species	Percentage of egg hatch
Brassica 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 in the same column followed by the same letter do not differ significantly at $P < 0.05$ (SNK test).

However, pupal mortality was significantly higher on *R. micrantha* and the lowest on *R. raphanistrum*. Larval and pupal mortality on both cabbage and kale were similar. There was no significant difference between host plant species in percentage of survival of DBM to adult stage ($F_{(5,19)} = 1.53$; $P = 0.23$). Percentage of survival to adult ranged between 69% in *R. micrantha* and 81% in *R. raphanistrum* (Table 3). Females had significantly ($F_{(1,5)} = 350.0$; $P < 0.0001$) heavier pupal weight than males in all host plants, while males lived longer ($F_{(1,5)} = 34.28$; $P < 0.0001$) than females.

Adult longevity and reproductive potential

Adult longevity differed significantly between host plants ($F_{(5,401)} = 8.53$; $P < 0.0001$). Adults lived for a significantly longer period if they had been feeding on *R. raphanistrum* than on any of the other plants. Host plant species had significant influence on fecundity ($F_{(5,212)} = 4.74$; $P < 0.005$). Females reared on *R. nudiuscula*, *R. micrantha* and *E. arabicum* recorded significantly higher mean fecundity than cabbage. Females reared on *R. nudiuscula* had the highest mean fecundity (326.7 eggs), while those reared on cabbage had the lowest (261.6 eggs) (Table 4).

The effects of host plant on life table parameters were calculated on the basis of the development time, fecundity, survival and sex ratio. The net reproductive rate (R_0), which is a product of mean total fecundity, survival rate and sex ratio, was significantly higher for DBM reared on *E. arabicum* (126.4) and the lowest on cabbage (95.1). There was some variation in the mean generation time (G) of DBM fed on different host plants. The shortest generation time was recorded on *R. micrantha* (26.9 days), while the highest on *R. nudiuscula* and kale (31.7 days). The intrinsic rate of increase (r_m) differed significantly between the host plant species and was the highest (0.179) on *R. micrantha* and the lowest (0.147) on kale (Table 5).

Discussion

In our studies, the wild crucifers were more attractive to ovipositing DBM females than the cultivated *Brassica* (cabbage and kale) cultivars. In the choice tests, females laid more eggs on all wild crucifers and four and nine times more on *R. micrantha* than on cabbage and kale, respectively. This high rate of oviposition on *R. micrantha* was recorded in both the choice and no-choice tests and on potted entire plants as well as detached leaves. Badenes-Perez *et al.* (2004) reported similar observations. The workers recorded 18 and 12 times more eggs, respectively, on the cruciferous weeds *Brassica juncea* (L.) Czern. and yellow rocket *Barbarea vulgaris* R.Br. than on cabbage. Furthermore, large differences were observed in our trials in the placement of the eggs. While virtually all eggs were deposited on the plant or on the detached leaves of the wild crucifers, most eggs were laid off target in the case of the cultivated crucifers. The numbers and placement of the eggs is the result of a whole sequence of behavioural steps that start with long-range attraction mediated by semiochemicals (Bernays and Chapman, 1994; Hardie *et al.* 2001) and green leaf volatiles (Reddy and Guerrero, 2000). Both have been identified to play a major role in host plant-finding behaviour of DBM. These seem to have been present in all the test plants, resulting in oviposition in all tests. The on-target placement

Table 3. Development and percentage of survival of adult *Plutella xylostella* on two cultivated and four wild crucifer species

Plant species	Mining period (days)	Larval period (days)	Pupal period (days)	Pupal weight (mg)	Development period	Percentage of survival to adult
Brassica 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 ± 0.09b	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's test).

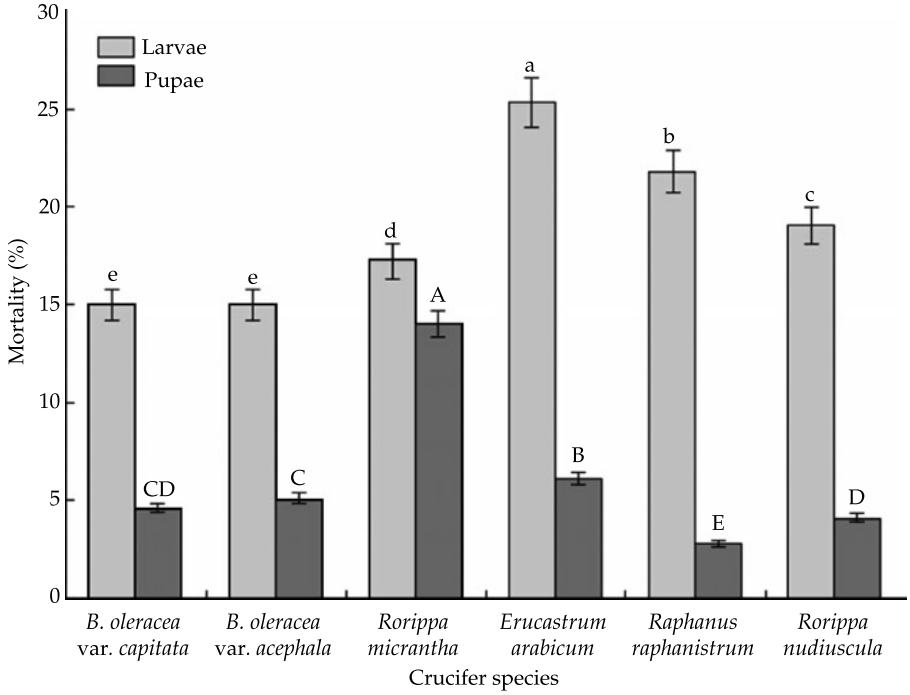

Fig. 3. Mean larval and pupal mortality of *Plutella xylostella* reared on two cultivated *Brassica* cultivars and four wild crucifer species

of eggs on the wild crucifers indicates that these provide additional stimuli to probing females after first contact with the plant surface and indeed non-volatiles such as glucosinolates are known to play a role in DBM oviposition (Renwick and Radke, 1990).

The differences in off-target egg laying may also be due to differences in leaf morphology between the tested plant species, including leaf vein characteristics, pubescence and the presence of depressions in the leaf surface, all of which can have an effect on oviposition. In addition, Eigenbrode *et al.* (1990, 1991) showed that leaf surface wax also plays a role in DBM host acceptance. Glossy (non-waxy) phenotypes were associated with increased oviposition but reduced larval survival. In this study, the leaf surfaces differed greatly between the host plant species, with *R. raphanistrum* and *E. arabicum* having pubescent surfaces compared with the glabrous kale and cabbage. Leaf surface wax can also be implicated, as *R. raphanistrum* and *E. arabicum* do not show any conspicuous wax deposits and *R. nudiuscula* and *R. micrantha* have smooth shiny leaf surfaces while both cultivated crucifers are waxy. All these reasons may also have contributed to the higher egg numbers on wild crucifers.

Total leaf area and leaf shape do not seem to be the major factors in determining the number of eggs oviposited on the different host plant species. In our study, *E. arabicum*, *R. micrantha*, *R. nudiuscula* and *R. raphanistrum* recorded significantly higher number of eggs despite the leaf area being significantly smaller than those of the cultivated species. This concurs with the observations made by Badenes-Perez *et al.* (2004), where more eggs were oviposited on Indian mustard and yellow rocket than cabbage despite their smaller leaf area.

Table 4. Adult longevity and fecundity of *Plutella xylostella* reared on two cultivated and four wild crucifer species

Plant species	Adult longevity (days)	Fecundity (number of eggs)
Brassica 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).

Table 5. Effect of two cultivated and four wild crucifer species on life table parameters of *Plutella xylostella*

Plant species	Intrinsic rate of increase (r_m)	Net reproductive rate (R_0)	Generation time (days)
Brassica oleracea var. *acephala*	0.147 ± 0.002e	106.0 ± 3.9cd	31.7
B. oleracea var. *capitata*	0.159 ± 0.002c	95.1 ± 2.6e	28.6
Erucastrum arabicum	0.177 ± 0.002a	126.4 ± 4.3a	27.4
Raphanus raphanistrum	0.161 ± 0.002b	104.0 ± 5.0de	28.9
Rorippa nudiuscula	0.152 ± 0.002d	116.4 ± 6.5abc	31.7
Rorippa micrantha	0.179 ± 0.001a	124.9 ± 5.9ab	26.9

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

DBM development and larval survival varied considerably in our study within the wild crucifers and between the wild and cultivated species. Variable results with DBM reared on different cultivated and wild cruciferous host plants have also been reported by other authors. Idris and Grafius (1996) showed that DBM reared on cultivated *Brassica* cultivars had a shorter larval duration and development time than the wild crucifers due to the suitability of the crops. Sant *et al.* (1982) and Reddy *et al.* (2004) reported the shortest larval development time on cauliflower, cabbage and radish compared with turnip and mustard.

Pupation at the end of the larval period is generally determined by the nutritional stage attained by the larva. Once sufficient reserves are accumulated for successful pupation and adult emergence, larvae pupate. The accumulation of reserves can be greatly influenced by the differences in the suitability of the host plant species (Idris and Grafius, 1996; van Dam *et al.*, 2000). The pupal weights of DBM reared on *B. oleracea* var. *acephala* were significantly higher than those reared on *B. oleracea* var. *capitata* and the wild crucifers. Similarly, Muhamad *et al.* (1994) and Begum *et al.* (1996) showed that DBM adults reared on the cabbage were larger than those reared on the wild crucifers. In all cited cases, no reasons were given for these differences. In our case, we tried to shed some light on the factors behind the differences using correlation analysis between larval duration and pupal weight. However, the correlations were generally weak and even in the case of *R. nudiuscula* and *R. raphanistrum*, the negative relationship was not strong enough to warrant further investigation.

We observed significantly higher larval mortality on three out of the four tested wild crucifers than on the cultivated species. However, these differences were levelled out during the pupal stage. This, like most of our results on larval development and survival, is in contrast to the studies of a number of authors and might be attributable to the specific aim of our study and the resulting selection of plant species for our experiments. We wanted to demonstrate the importance of the wild crucifers as hosts for DBM, and thus the selection criterion of potential host plants was the presence of larvae and pupae during surveys in the field. The case of *Capsella bursa-pastoris* (L.) Medic. might serve as a sample to illustrate this. It is a common species in the Kenyan highlands and the previous studies of Bigger and Fox (1997) observed reduced survival of DBM reared on this species compared with cabbage and kale. However, as we did not find DBM on this species in the field, it was not included in our work because it did not fit our criteria.

The crucifers are a large and diverse family with a long list of secondary metabolites, some of them being highly toxic (Agrawal and Kurashige, 2003; Wittstock *et al.*, 2003). Badenes-Perez *et al.* (2004) recorded 12 times higher oviposition on yellow rocket than on cabbage. Yet, yellow rocket does not support larval development and has even been termed a 'dead-end trap crop' (Lu *et al.*, 2000; Shelton and Nault, 2004), a clear indication that the choice a female makes for egg laying may not always be the best for the survival of the progeny. In evolutionary terms, this seems counter-intuitive. However, if one considers that DBM may be a South African species (Kfir, 1998), the choice of *B. vulgaris*, a species endemic to North America, as preferred host for egg laying could be excused. It appears that in the absence of a co-evolutionary history, females may select a host plant based on the insufficient information as on semiochemicals only and not always identify the absence of vital nutritional substances or the presence of harmful metabolites that may be disadvantageous for the development of immature stages (Biever and Boldt, 1971; Begum *et al.*, 1996; Syed and Abro, 2003).

The results from the study showed that adults reared on the wild crucifers produced females that were more fecund than those reared on the cultivated *Brassica* crucifers. Wakisaka *et al.* (1992) recorded significantly reduced fecundity of larvae reared on *C. bursa-pastoris* compared with broccoli and cabbage. Begum *et al.* (1996) showed that female *P. xylostella* reared on *R. indica* and *Lepidium*

virginicum (L.) Hiern. were less fecund than those reared on cabbage. Muhamad *et al.* (1994) and Begum *et al.* (1996) 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 *Pieris rapae* (Linnaeus) (Lepidoptera: Pieridae) performed better on cultivated cabbage than on a wild crucifer *Lunaria annua* L.

In our case, the wild crucifers were all suitable for DBM development and this is best documented from the life table statistics, in particular the intrinsic rate of increase, where all biological parameters are combined. All the wild crucifers were either similar to or even significantly better hosts than the cultivated species. If we follow Kfir's suggestion that DBM is an African species (Kfir, 1998), our findings appear unsurprising. DBM may have been associated with wild African crucifers for long enough to allow for co-evolution to take its course and bring about high survival on plant species highly attractive for oviposition.

Since DBM was able to develop on the wild crucifers in the laboratory, it is probable that these species act as alternative hosts for DBM in the field as well. If these plants are also attractive to parasitoids, they should provide refugia to them in the fields when the crucifer crop is absent. This is particularly important for the recently introduced parasitoid *Diadegma semiclausum* (Hellen) (Hymenoptera: Ichneumonidae), which has provided good control of the pest in Kenya, but is susceptible to local extinction through application of broad-spectrum pesticides.

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