

# Oviposition preference and offspring performance of *Crocidolomia pavonana* (Lepidoptera: Pyralidae) on different host plants

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Brassica, insect behaviour, insect biology, pest management, trap cropping

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## Abstract

The cabbage head caterpillar *Crocidolomia pavonana* (Fabricius) (Lepidoptera: Pyralidae) is an increasingly devastating pest on white cabbage (*Brassica oleracea* var. *capitata*) in Uganda. Screen house and field trials were used to assess oviposition preference and offspring performance of *C. pavonana* on six hosts in the genus *Brassica*: kale (*B. oleracea* var. *acephala*), cauliflower (*B. oleracea* var. *botrytis*), broccoli (*B. oleracea* var. *italica*), Chinese cabbage (*B. campestris* spp. *pekinensis*), Indian mustard (*B. juncea* (L.) Czern.) and white cabbage (*B. oleracea* var. *capitata*). To assess oviposition preference, the hosts were offered to *C. pavonana* in multiple-choice (all six); two-choice (cabbage with each of the other hosts) or cabbage-only situations. After specified oviposition periods, egg numbers on individual plants were recorded. To determine *C. pavonana* offspring performance on the six hosts, whole plants were placed in individual cages, where larvae were monitored for development time, pupal weight and foliage consumption. Results of the choice tests indicated that *C. pavonana* preferred Chinese cabbage and broccoli for oviposition. In two-choice arrangements, all the tested host plants were able to greatly reduce oviposition on white cabbage (69–100%) when compared with the monocrop. Chinese cabbage was the most suitable host with regard to *C. pavonana* offspring performance as demonstrated by the shortest development time and highest pupal weight. Chinese cabbage and broccoli can be used as traps for the pest but the resulting larvae should be destroyed regularly to prevent accumulation in the system.

## Introduction

White cabbage (*Brassica oleracea* var. *capitata*) is an important nutritional and economic crop in Uganda; however, its production is greatly constrained by a diverse range of insect herbivores, especially larvae of Lepidoptera, notably the diamondback moth (*Plutella xylostella*: Plutellidae) and the cabbage head caterpillar (*Crocidolomia pavonana*: Pyralidae), two of the most harmful caterpillar pests of cultivated Brassica crops in tropical Africa, South and Southeast Asia, Australia and Pacific islands (Waterhouse and Norris

1987; Sastrosiswojo and Setiawati 1992; Facknath and Kawol 1993; Zhang 1994; Saucke et al. 2000; Morallo-Rejesus and Navasero-Ward 2003; Smyth et al. 2003; BFED 2009). *Crocidolomia pavonana* larvae damage Brassica crops by feeding on leaves, inflorescences and fruits/pods (BFED 2009). Hosts include white cabbage (*B. oleracea* var. *capitata* L.), cauliflower (*B. oleracea* var. *botrytis* L.), Chinese cabbage (*B. campestris* spp. *pekinensis*), turnip (*B. rapa* var. *rapa* L.), broccoli (*B. oleracea* var. *botrytis* L. subvar. *cymosa* Lam.), radish (*Raphanus sativus* var. *hortensis*), kohlrabi (*B. oleracea* var. *gongylodes*) and

mustard (*B. juncea* Coss.) (Gunn 1925; Kalshoven 1981; Sastrosiswojo and Setiawati 1992; BFED 2009). It causes serious damage by preferentially feeding on young leaves and apical meristem, and if plants are attacked during the head formation stage, larvae can tunnel into the head and spoil the harvested crop (Sastrosiswojo and Setiawati 1992; Morallo-Rejesus and Navasero-Ward 2003; Smyth et al. 2003; BFED 2009).

There is an increase in prevalence of *C. pavonana* in Uganda (Karungi et al. 2009), a situation that may perhaps be attributed to climate change as the pest is reported to be favoured by extended dry conditions (Sastrosiswojo and Setiawati 1992; BFED 2009). Another contributing factor may be a reduction in chemical insecticide usage recommended to conserve and promote *Oomyzus sokolowski* (Hymenoptera: Eulophidae) and *Diadegma* spp (Hymenoptera: Ichneumonidae), the parasitoids that have been found to offer effective management of *P. xylostella* in low and highland areas of the country, respectively (Nagawa 2003; ICIPE 2005). Saucke et al. (2000) working in Papua New Guinea also reported that the main conflicting factor in using biological control for *P. xylostella* was the high pest status of the associated *C. pavonana*, which required five to seven insecticide application per cropping period. Strategies to use biological control measures for both pests have been unsuccessful because of the lack of effective natural enemies for *C. pavonana* (Waterhouse and Norris 1989; Saucke et al. 2000). Moreover, *C. pavonana* destructiveness and early attack foiled the development of a composite action threshold concept for *P. xylostella* and its associated pests (Cartwright et al. 1987). There is therefore a need to develop management strategies for *C. pavonana* that are compatible with bio-intensive management of *P. xylostella*.

In order to have a selection of options to build upon, cultural practises targeting habitat management to exclude or reduce pest damage on crops of interest should be given due consideration when developing integrated pest management programmes for cabbage pests in general and *C. pavonana* in particular. One such management strategy is trap cropping, which is based on the knowledge that phytophagous insects often demonstrate preferences for particular plants species, cultivars or crop stages in response to different cues (Javaid and Joshi 1995; Shelton and Nault 2004; Shelton and Badenes-Perez 2006). Trap cropping usually involves planting small areas of a preferred crop to particular pests near the crop to be protected to attract, divert, intercept and/

or retain insect pests. The insect pests can therefore be confined to a relatively small area reducing the acreage to be sprayed. Trap cropping has been successfully used in commercial cotton production to manage the lygus bug (*Lygus hesperus*), whereby 5–10 m strips of alfalfa planted in every 100–200 m of cotton have been found to divert the bugs from cotton (Godfrey and Leigh 1994). Another reported success has been in a 'push-pull' approach or stimulo-deterrent diversionary strategy to control the stem borers (*Chilo partellus*) on maize (Khan et al. 2001). In this strategy, which involves combined use of trap and repellent plants, maize is intercropped with a repellent legume such as desmodium, *Desmodium uncinatum* (Fabaceae), or molasses grass, *Melinis minutiflora* (Poaceae) to repel the gravid moths, which are then intercepted by an attractive wild grass such as Napier grass, *Pennisetum purpureum* (Poaceae) planted around the plot perimeter.

If trap cropping systems are to be designed for the cabbage head caterpillar, information about its preference and performance on different host plants is needed. The attractiveness of several host plants at different phenological stages to *C. pavonana* has been studied under laboratory conditions by Smyth et al. (2003). In our study, we investigated oviposition preference (in cages and in field experiments) and performance parameters of *C. pavonana* on six host plants of the same genus.

## Materials and Methods

### Study site

The study was carried out at the Makerere University Agricultural Research Institute, Kabanyolo (MU-ARIK) (0°28'N; 32°27'E; 1200 m a.s.l.) in Uganda in 2007 and 2008. The site's soils are oxisols with a pH 5.6. The area has a bimodal rainfall pattern with April–May and October–November as the wettest months. The mean daily maximum and minimum temperatures of the area were about 28° and 17°C, respectively.

### *Crociodolomia pavonana* culture

A colony of the cabbage head caterpillar was established in a screen house at MUARIK on common cabbage *B. oleracea* var. *capitata* L. (Brassicaceae), cultivar Copenhagen, using late instar larvae collected locally from farmers' cabbage fields. The resulting moths were provided with honey mixed with deionized water at a ratio of 1 : 1 as recommended for

mass rearing (Sastrosiswojo and Setiawati 1992). All the insects used in the trials came from the resulting generation.

### Host plants

The test plants were six cultivated Brassicaceae plants: cabbage (*B. oleracea* var. *capitata* L. cultivar Copenhagen), kale (*B. oleracea* var. *acephala* L. cultivar Thousand headed), cauliflower (*B. oleracea* var. *botrytis* L. cultivar Early snowball), broccoli (*B. oleracea* var. *italica* Plenck cultivar Greens), Chinese cabbage (*B. campestris* L. spp. *pekinensis* cultivar Granat) and Indian mustard (*B. juncea* (L.) Czern). Chinese cabbage and Indian mustard were selected because they have been used successfully as trap crops for *C. pavonana* in Asia and Guam (Srinivasan and Krishna-Moorthy 1991; Sastrosiswojo and Setiawati 1992; Silva-Krott et al. 1995; Muniappan et al. 2001) and have previously been tested in the laboratory (Smyth et al. 2003). Cauliflower, broccoli and kale were included among the test crops because they are commonly grown in Uganda and are known hosts of the pest (Gunn 1925; Kalshoven 1981; Sastrosiswojo and Setiawati 1992). Seeds were obtained from General Allied Uganda Limited, a dealer in agricultural inputs, for all test plants except *B. juncea* that came from Svalöf-Weibull AB.

### Oviposition preference

Oviposition preference was studied in the screen house as well as in the field. The screen house was a building with walls made of metal screen mesh and a roof made of transparent slates; there was no climate control and the light conditions approximated L12 : D12. The screen house trial began in November 2007. Seedlings were raised in a screen house in seedling trays filled with sterilized soil for 4 weeks. Individual seedlings were then transplanted into 15-cm diameter plastic pots, where they were maintained for 4 weeks. The plants were therefore 8 weeks old when first exposed to *C. pavonana* in the screen house. At this time, the plants were at the pre-flowering stage with 7 to 11 leaves with the bases of the stems and leaves still visible from above. This stage was chosen because we wanted to evaluate preference around the time of highest oviposition of *C. pavonana* on cabbage; Smyth et al. (2003) reported that 7- to 8-week-old seedlings (stage 4 in Smyth et al. 2003) were preferred when compared with older plants (stage 5). Two-choice and multi-

ple-choice tests were carried out to compare oviposition preference of *C. pavonana* using whole plants. In the two-choice (paired) tests, 8 eight-week-old plants (all pre-flowering), 4 of cabbage and 4 of another host (cauliflower, broccoli, Chinese cabbage, kale or mustard) were randomly put in a cage (1 m × 1 m × 1 m) made of muslin cloth and glass in a wooden framework. A control of eight cabbage plants (cabbage-only) was also included. Three pairs of newly emerged moths were introduced into the cages. In the multiple-choice (mixture) tests, two plants of each of the six hosts (=12 plants) were randomly put in a cage (1 m × 1.5 m × 1 m), four pairs of newly emerged moths were then introduced into the cages. In all the cages, moths were provided with diluted honey. After 7 days, the plants were removed from the cages and thoroughly examined for eggs. All the tests were replicated eight times.

In the field trial, season one began in March 2008 and the trial was repeated in October 2008; plots had either a two-choice treatment, a mixture of all plants or a cabbage monoculture control. Seedlings were sown in trays filled with sterilized soil for germination and kept in the trays for 4 weeks. Seedlings were transplanted into individual plots of 3 m × 2 m at a plant-spacing of 60 cm × 30 cm. Each two-choice (paired) and cabbage monocrop plot contained 40 plants evenly distributed into four rows; five cabbage plants and five plants of another host were randomly assigned into each row (=20 cabbage plants : 20 other host plants per plot; fig. 1). There were five combinations: (i) cabbage : cauliflower, (ii) cabbage : broccoli, (iii) cabbage : Chinese cabbage, (iv) cabbage : kale, (v) cabbage : Indian mustard and a control plot (vi) of a cabbage monocrop. In addition, plots containing a mixture of the plants were planted in individual plots of 3.3 m × 2 m four-row plots, 12 plants, two of each of the six

|         | 1      | 2      | 3      | 4       | 5      | 6       | 7       |
|---------|--------|--------|--------|---------|--------|---------|---------|
| Block 1 | CB: CF | CB: BC | CB: CC | CB: IM  | CB: CB | CB: KL  | MIXTURE |
| Block 2 | CB: CC | CB: CF | CB: IM | MIXTURE | CB: BC | CB: CB  | CB: KL  |
| Block 3 | CB: KL | CB: CB | CB: CF | MIXTURE | CB: BC | CB: IM  | CB: CC  |
| Block 4 | CB: CB | CB: CC | CB: BC | CB: CF  | CB: KL | MIXTURE | CB: IM  |

**Fig. 1** Field layout and a schematic representation of the paired and mixture arrangements for *C. pavonana* oviposition preference (where, CB : CF = cabbage : cauliflower; CB : BC = cabbage : broccoli; CB : CC = cabbage : Chinese cabbage; CB : KL = cabbage : kale; CB : IM = cabbage : Indian mustard and CB : CB = cabbage monocrop).

hosts were randomly assigned to a row (=48 plants/plot). There were four replications for each plot, arranged in blocks (fig. 1). Individual plots were separated by 1-m alleys, whereas blocks were separated by 2-m alleys. Hand weeding was performed two times in each season; manual watering was only carried out when the conditions necessitated. The trials were planted in an area where cabbage, which had recently been harvested, had been infested with the cabbage head caterpillar; thus, we assumed that the population of *C. pavonana* would be high enough to cause a natural infestation.

Plants were inspected from transplanting, but data collection commenced 4 weeks after transplanting (plants were 8 weeks old), at which time *C. pavonana* egg batches were first observed in the field. Data collection was carried out once a week thereafter for 1 month. In each plot, 10 plants of cabbage and 10 plants of the other host crop in the two-choice trial and 5 of each host type in the mixture, were randomly sampled and examined for eggs. The number of *C. pavonana* eggs per sampled plant was then recorded and removed. Cabbage aphids (*Brevicoryne brassicae* (L.)) were present in the field and generally in higher numbers on cabbage than on the other plant species (U. Lubanga, personal observation).

### Offspring performance

This trial was carried out in the screen house in September 2008 and was repeated in second round in November 2008. Seedlings were raised similarly to those in the oviposition preference screen house trial. A potted plant (8 weeks old) of each of the six host crops was put in individual 1 m<sup>3</sup> cages. On each plant, four first instar *C. pavonana* larvae randomly taken from a culture maintained on common cabbage at MUARIK were introduced to the whorl region of each of the plants using fine brushes. Each host crop was assigned to three cages (replications) and the experiment was carried out twice (total = 24 larvae/host plant). The larvae assigned to the different host plants did not vary in length ( $F = 0.60$ ; d.f. = 5, 138;  $P = 0.70$ ). The larvae were observed every other day with data being collected on growth as well as damage being inflicted on plants. Pupae from each cage were removed and weighed using an electronic scale (Casio and Satwick from Devyani Investments Ltd in Uganda) and then returned for adult emergence. Pupal weight was included as a parameter to indicate fitness. Pupal weight has been used as a performance parameter for other Lepidoptera: for example Tammaru et al. (2002) showed

that pupal weight can be a reliable index of adult fitness for a Lymantrid moth. Accumulation of reserves for moths feeding on cabbage can be greatly influenced by differences in the suitability of the host plant species (Idris and Grafius 1996; Van Dam et al. 2000; Kahuthia-Gathu et al. 2008). Plant damage (consumption of foliage) was included as an indication of feeding preference and suitability and was assessed for each individual plant in each cage using a visual rating scale of between 1 and 6, where: 1 = 1–5% of foliage eaten; 2 = 6–15%; 3 = 16–30%; 4 = 31–45%; 5 = 46–75% and 6 = 76–100% eaten).

### Data analysis

Statistics were calculated using SAS for Windows version 9.1 (SAS Institute, Cary, NC, USA). All data were analyzed using ANOVA (proc GLM). During preliminary analyses, there were no significant interactions with the season or round in which the trial was conducted as a factor; as such subsequent analyses were performed with data pooled over seasons or rounds.

For oviposition preference in cages in the screen house where all plant species were mixed, a completely randomized experimental design was used and analysis was performed using a one-way ANOVA with the factor plant species and each cage was a replicate. For the two-choice (paired) situation in cages in the screen house a completely randomized experimental design was also used and analyzed using a one-way ANOVA to test the difference between number of eggs laid on cabbage and the total number of eggs laid in the different combinations. All multiple comparison tests for means for different plants were performed using Bonferroni *t*-tests.

For the field trials, a randomized complete block experimental design was used with the following seven treatments: (i) cabbage : cauliflower, (ii) cabbage : broccoli, (iii) cabbage : Chinese cabbage, (iv) cabbage : kale, (v) cabbage : Indian mustard, (vi) monoculture cabbage and (vii) a mixture of all six plant species. Initially, an ANOVA with the factors block, plant species, treatment and date of egg counts was performed. The interactions between date and the other factors were calculated, but none were statistically significant. In a second step, an ANOVA with block, plant species, treatment and the interaction between plant species and treatment was performed. The following pre-determined contrasts were tested using a least squared means *t*-test with Bonferroni adjustment: (i) Number of eggs laid on cabbage in monocrop compared with number of eggs

on cabbage in all other treatments, (ii) number of eggs laid on cabbage compared with number of eggs laid on trap crop in two-choice plots, (iii) number of eggs laid on different plants in the mixed plots.

To determine the influence of host plant on damage by larvae, a repeated measures analysis of variance was used to analyze the data for foliage damage over time. For larval development time and final pupal weights, a completely randomized experimental design was used and analyzed using an ANOVA with host plant as factor. All comparison tests for means for different plants were performed using Bonferroni *t*-test.

## Results

### Oviposition preference of *Crociodolomia pavonana*

Results from both the screen house and field trials indicated that all five potential trap crops under trial reduced the number of eggs laid on cabbage by 69–100% (tables 1 and 2).

In the cage trials, performed in the screen house, egg distribution by *C. pavonana* varied significantly when all the six hosts (cabbage, cauliflower, broccoli, Chinese cabbage, kale and Indian mustard) were offered together (ANOVA:  $F = 27.9$ ;  $d.f. = 5, 30$ ;  $P < 0.001$ ). More eggs were oviposited on Chinese cabbage and broccoli compared with the other crops with Indian mustard receiving the least number of eggs (fig. 2a). When each of the five potential trap crops were paired with cabbage (two-choice test), all the companion crops used received more eggs than the cabbage with the exception of Indian mustard (table 1). The number of eggs laid on the potential trap crops in the two-choice tests also varied significantly (ANOVA:  $F = 10.2$ ,  $d.f. = 4, 25$ ,  $P < 0.001$ ) with Chinese cabbage, broccoli and cauliflower receiving more eggs compared with kale and Indian mustard (table 1). There were significantly fewer eggs oviposited on cabbage plants grown in combination with another host crop compared with cabbage plants grown alone (table 1;  $F = 15.3$ ,  $d.f. = 5, 30$ ,  $P < 0.0001$ ).

| Treatments                | No. eggs laid on cabbage | No. eggs laid on trap crop(s) | % Reduction in No. eggs on cabbage because of trap crop* |
|---------------------------|--------------------------|-------------------------------|--|
| Cabbage-only (control)    | 77.00 ± 9.42a            |                               |  |
| Cabbage : Broccoli        | 13.33 ± 6.25b            | 89.00 ± 13.46a                | 82.7   |
| Cabbage : Cauliflower     | 6.17 ± 3.92b             | 73.33 ± 10.33ab               | 92.0   |
| Cabbage : Chinese cabbage | 17.00 ± 6.20b            | 103.7 ± 08.42a                | 78.0   |
| Cabbage : Kale            | 11.67 ± 5.35b            | 31.33 ± 14.35bc               | 84.8   |
| Cabbage : Indian mustard  | 23.67 ± 7.74 b           | 21.16 ± 08.48c                | 69.3   |

Values in the same column followed by different letters are significantly different ( $P < 0.05$ ); Bonferroni *t*-test was used for comparison in screen house trials and least squared means *t*-test with a Bonferroni adjustment for field trials.

\*% Reduction in No. eggs on cabbage = [(No. eggs on cabbage in monoculture – No. eggs on cabbage in combination)/No. eggs on cabbage as a monoculture] × 100.

**Table 1** Oviposition preference (mean ± SE, no. eggs laid/plant) of *C. pavonana* on different hosts in the screen house

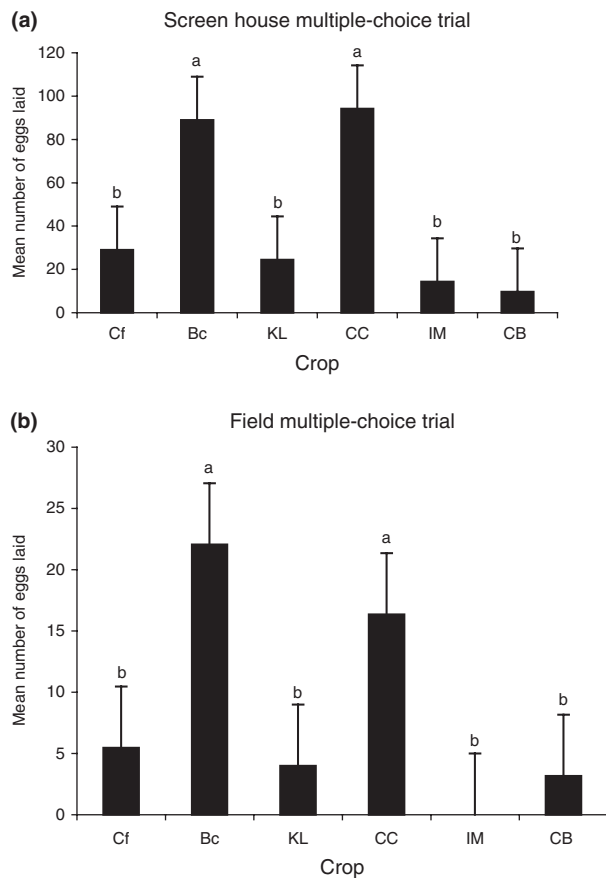
| Treatments                | No. eggs laid on cabbage | No. eggs laid on trap crop(s) | % Reduction in No. eggs on cabbage because of trap crop* |
|---------------------------|--------------------------|-------------------------------|--|
| Cabbage-only (control)    | 22.16 ± 4.78a            |                               |  |
| Cabbage : Broccoli        | 3.66 ± 1.61b             | 17.88 ± 4.50a                 | 83.5   |
| Cabbage : Cauliflower     | 2.22 ± 1.61b             | 3.34 ± 1.49bc                 | 90.0   |
| Cabbage : Chinese cabbage | 0.00 ± 0.00b             | 9.31 ± 2.31abc                | 100.0  |
| Cabbage : Kale            | 2.59 ± 1.26b             | 6.84 ± 2.07abc                | 88.3   |
| Cabbage : Indian mustard  | 1.66 ± 1.16b             | 0.00 ± 0.00c                  | 92.5   |

Values in the same column followed by different letters are significantly different ( $P < 0.05$ ); Bonferroni *t*-test was used for comparison in screen house trials and least squared means *t*-test with a Bonferroni adjustment for field trials.

\*% Reduction in No. eggs on cabbage = [(No. eggs on cabbage in monoculture - No. eggs on cabbage in combination)/No. eggs on cabbage as a monoculture] × 100.

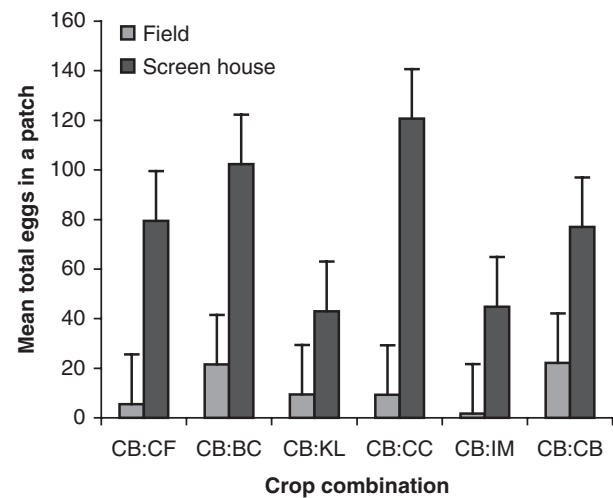
**Table 2** Oviposition preference (mean ± SE, No. eggs laid/plant) of *C. pavonana* on different hosts in the field





**Fig. 2** Egg distribution (number of eggs/plant) by *C. pavonana* when offered multiple hosts (where Cf = cauliflower, Bc = broccoli, KL = Kale, CC = Chinese cabbage, IM = Indian mustard, CB = cabbage). Bars marked with different letters are significantly different ( $P < 0.05$ ); Tukey's test was used for comparison in screen house trials and least squared means *t*-test for field trials.

In the field trials, there was also significant variation in egg distribution between host crops ( $F = 20.2$ , d.f. = 5, 520,  $P < 0.0001$ ) and treatments ( $F = 13.2$ , d.f. = 6, 520,  $P < 0.0001$ ). The interaction between crop and treatment was not significant ( $F = 0.65$ , d.f. = 5, 520,  $P = 0.67$ ). Cabbage as a monocrop received significantly more eggs than cabbage in any other combination (dual choice and mixed plots; table 2). The number of eggs laid on broccoli ( $P < 0.0014$ ) was significantly higher than the number of eggs laid on cabbage in two-choice plots. There was no statistical difference in the two-choice plots between the number of eggs laid on cabbage and the number of eggs laid on Chinese cabbage, cauliflower, kale or Indian mustard. There were no *C. pavonana* eggs found on cabbage plants that were paired with Chinese cabbage in the field trial (table 2). Consider-



**Fig. 3** Total eggs oviposited by *C. pavonana* in the paired host crops' patches for cages in the screen house (exposed to three pairs of moths/cage) or plots in the field under natural infestation (where CB : CF = cabbage : cauliflower, CB : BC = cabbage : broccoli, CB : CC = cabbage : Chinese cabbage, CB : KL = cabbage : kale, CB : IM = cabbage : Indian mustard and CB : CB = cabbage monocrop).

ing plots where all host crops were present, broccoli and Chinese cabbage received significantly more eggs than the other plant species (fig. 2b).

The total number of eggs oviposited in a given patch (cage or plot) varied significantly depending on the host crops combinations in screen house and field trial (ANOVA:  $F = 5.18$ , d.f. = 5, 30,  $P = 0.0015$  and  $F = 7.23$ , d.f. = 5, 168,  $P = 0.001$ , respectively). In the screen house, highest number of eggs was laid in the cabbage + Chinese cabbage patch and this was followed closely by the number of eggs in the cabbage + broccoli patch. In the field, it was the cabbage + broccoli patch that had the highest total eggs and this was comparable to monocrop cabbage (fig. 3).

#### Offspring performance of *Crociodolomia pavonana*

In our study, depending on host type, *C. pavonana* took 26–31 days to complete its life cycle. This is in line with results from Indonesia (Sastrosiswojo and Setiawati 1992) for temperatures between 26° and 33°C. In our study, larval survival was very high (95.8% survived and reached adulthood). The high survival could be explained by the procedure we used, i.e. using whole plants of known host crops under semi-natural conditions.

Host crop type significantly affected *C. pavonana* development time ( $F = 55.1$ ; d.f. = 5, 137;  $P <$

**Table 3** Offspring performance (mean  $\pm$  SE) of *C. pavonana* on different hosts

| Host crop       | Weight of pupae (gm) | Days to adult emergence |
|-----------------|----------------------|-------------------------|
| Cabbage         | 0.180 $\pm$ 0.021ab  | 20.5 $\pm$ 0.21c        |
| Broccoli        | 0.189 $\pm$ 0.011ab  | 23.8 $\pm$ 0.24ab       |
| Cauliflower     | 0.154 $\pm$ 0.020b   | 24.0 $\pm$ 0.25a        |
| Chinese cabbage | 0.244 $\pm$ 0.015a   | 20.6 $\pm$ 0.28c        |
| Kale            | 0.146 $\pm$ 0.015b   | 23.7 $\pm$ 0.20b        |
| Indian mustard  | 0.169 $\pm$ 0.022ab  | 23.9 $\pm$ 0.20ab       |

Values in the same column followed by different letters are significantly different ( $P < 0.05$ ). Bonferroni *t*-tests were used for comparison. Performance was assessed following the fate of 24 two-day-old larvae per host crop to adult emergence.

0.0001). Development was significantly fastest on cabbage and Chinese cabbage and longest on cauliflower (table 3). Weight of pupae also varied significantly with host crop type ( $F = 3.9$ ; d.f. = 5, 30;  $P = 0.008$ ). The heaviest pupae were recorded on Chinese cabbage (table 3).

The extent of foliage damage (consumption) by *C. pavonana* did not vary significantly among host plants (repeated measures ANOVA:  $F = 2.3$ ; d.f. = 5, 30;  $P = 0.07$ ). There was an effect over time (Wilks' test:  $F = 126.1$ ; d.f. = 8, 23;  $P = 0.001$ ) because damage increased as the larvae grew. There was, however, no interaction between host plant and time (Wilks' test:  $F = 1.4$ ; d.f. = 40, 103;  $P = 0.0.11$ ) for foliage damage.

## Discussion

Results on oviposition preference in choice tests showed that gravid *C. pavonana* females were able to evaluate and discriminate among same-genus host crops. Broccoli and Chinese cabbage were the most preferred hosts for oviposition in choice arrangements in both field and screen house experiments. The high attraction of *C. pavonana* to Chinese cabbage is in agreement with findings from Guam (Muniappan and Marutani 1992; Silva-Krott et al. 1995) and laboratory studies at Cornell University with an insect culture from Indonesia (Smyth et al. 2003). Smyth et al. (2003) found that pre-flowering Chinese cabbage was consistently chosen over head cabbage regardless of the phenological stage of the head cabbage. The result that *C. pavonana* is highly attracted to broccoli is reported for the first time.

In two-choice (host plants paired with cabbage) arrangements, both in the screen house and in the field, all the host plants that were used as

companions to cabbage were able to greatly reduce oviposition on white cabbage (69–100%) when compared with the monocrop. This may happen in two ways: by attracting *C. pavonana* away from white cabbage or by rendering the patch less favourable and thereby reducing the numbers of eggs laid. The first scenario is in agreement with results obtained for *P. xylostella* where inclusion of more preferred Brassica host plants with white cabbage were shown to reduce numbers of eggs on the white cabbage (Luther et al. 1996; Mitchell et al. 2000; Asman 2002; George et al. 2009). On the contrary, some studies have shown that main crops in mixed-Brassica-cropping systems sustain lower pest damage compared with simple plantings because of reduced tenure time by the ovipositing female (Tukahirwa and Coaker 1982; Elmstrom et al. 1988; Garcia and Altieri 1992; Hooks and Johnson 2003), which could explain the second scenario. For *C. pavonana*, it appears that Chinese cabbage and broccoli pull the moth away from the cabbage because total number of eggs in the two-choice tests was comparable to that laid in cabbage monoculture. The second scenario may explain reductions in the numbers of eggs on cabbage paired with Indian mustard as the total number of eggs laid in a patch was lower than that laid in a monocrop.

Several Brassica plant-specific factors affect oviposition choice: thickness of wax layer, morphology and biochemical composition of the plant leaf, as well as physiological age being among the most significant factors when choosing the suitable oviposition sites (Bernays and Chapman 1994; Broad et al. 2008). In Brassica specialists, glucosinolates and their volatile hydrolysis products seem to be the main attractants and oviposition stimulants (Reed et al. 1989; Pivnick et al. 1994; Renwick 2002; Badenes-Perez et al. 2004). Besides plant volatiles, Lepidoptera also seems to rely on vision and mechanoreception for host recognition and oviposition (Tabashnik 1985; Spencer et al. 1999; Kahuthia-Gathu et al. 2008). Therefore, differences in host volatiles and/or leaf morphology between the tested plant species, including leaf vein characteristics, pubescence and presence of depressions in the leaf surface could have had an effect on oviposition decisions by the moths.

Significant effects of Brassica host plant type on offspring performance of *C. pavonana* were demonstrated in our study. Host plant type differentially affected *C. pavonana* development time and pupal mass. The shortest development time for *C. pavonana* and heaviest pupae were produced on Chinese

cabbage. Thus, Chinese cabbage was both a very attractive host plant for oviposition and a very good substrate for offspring performance for *C. pavonana*, a result that supports the preference–performance linkage hypothesis (Singh and Singh 1982; Leyva et al. 2000) and the optimality theory (Thompson and Pellmyr 1991; Barker and Maczka 1996), which suggest that ovipositing females should choose plant species that maximise progeny fitness. In contrast, broccoli although as highly preferred for oviposition as Chinese cabbage, showed lower offspring performance when compared with Chinese cabbage. Eigenbrode and Shelton (1990, 1992) as well as Charleston and Kfir (2000) found a negative relationship between preference and performance of *P. xylostella* on Brassica host plants as a consequence of leaf wax characteristics; they demonstrated that a reduced wax load (glossiness) favoured oviposition by *P. xylostella* but reduced larval survival. They estimated that the hue associated with normal leaf wax was highest on cabbage, followed by cauliflower, broccoli, Indian mustard and finally Chinese cabbage. Our results on oviposition preference and offspring performance did not have a specific trend that can be attributed to glossiness and this could mean that *C. pavonana* may be different from *P. xylostella* in responding to leaf glossiness. Charleston and Kfir (2000) working with *P. xylostella* found that broccoli although not very preferred for oviposition, had high larval fitness rates, which is opposite to the results for *C. pavonana*. These contrasts suggest that the two Brassica specialist moths are probably different with regard to host plant preference and suitability.

Great attraction powers for oviposition are very important in selecting a trap crop; indicating the potential of both Chinese cabbage and broccoli as trap crops for *C. pavonana*. However, the high offspring performance and hence high turnover on Chinese cabbage may serve as a source for subsequent infestations in cabbage, unless proper management procedures for the ensuing larvae are applied. Highly attractive crops that are naturally suitable hosts for target pest development can be rendered dead-end trap crops by treating them with conventional or biological insecticides (Shelton and Nault 2004; Shelton and Badenes-Perez 2006). In this case, only the trap crop would be sprayed if insecticides are to be used; greatly minimizing usage and negative impacts. Despite this drawback, Chinese cabbage may have a higher chance of being acceptable to growers over broccoli because of its relatively lower logistic and agronomic requirements.

All of the trap crop plants used in this study, except Indian mustard, have an economic value of their own. Broccoli, and to a lesser extent Chinese cabbage, are among the low volume-high margin fresh vegetables in Uganda (Bear and Goldman 2005). Growing of properly managed strips of these crops among white cabbage could be advantageous to the peri-urban growers as they would probably be able to sell the products at a good price in the city. However, rural growers might prefer trap crops that require low inputs even if they have little or no commercial value. As such, future studies should focus on assessing the efficacy of less intensive crops and wild crucifer species as trap crops for *C. pavonana* for the rural peasant growers.

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