Dynamics of diamondback moth oviposition in the presence of a highly preferred non-suitable host

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Abstract

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), highly prefers to oviposit on yellow rocket, *Barbarea vulgaris* (R. Br.) (Cruciferae) var. *arcuata*, despite larvae not being able to survive on it, suggesting it may have potential as a trap crop. In a no-choice greenhouse experiment, *P. xylostella* laid 28% more eggs on *B. vulgaris* than on cabbage. Within the *B. vulgaris* plant, *P. xylostella* laid 3.7 times more eggs on younger than older leaves. Furthermore, we demonstrated that in the presence of *B. vulgaris* volatiles, *P. xylostella* laid 23% more eggs on cabbage plants than when *B. vulgaris* volatiles were absent. Because increased oogenesis in the presence of *B. vulgaris* could complicate the use of this host as a trap crop for *P. xylostella*, we wanted to examine levels of oogenesis in varying mixtures of cabbage and *B. vulgaris*. In outdoor screenhouse experiments, *P. xylostella* laid a decreasing percentage of eggs on cabbage as the percentage of *B. vulgaris* increased. However, the total number of eggs laid on cabbage did not differ among treatments, suggesting that the presence of *B. vulgaris* may have stimulated *P. xylostella* oviposition. In the field, total oviposition in cabbage plots containing *B. vulgaris* was 6.3 times higher than in cabbage plots without *B. vulgaris*. However, in plots with *B. vulgaris*, *P. xylostella* laid 99% of the eggs on *B. vulgaris* and oviposition on cabbage plants was 6.2 times lower than in the plots without *B. vulgaris*. The results of this study are discussed according to *P. xylostella* egg-laying behavior and life history as it relates to its interaction with *B. vulgaris*.

Introduction

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is considered the most damaging insect pest of cruciferous crops throughout the world (Talekar, 1992). The ability of *P. xylostella* to develop resistance to insecticides (Tabashnik et al., 1990; Shelton et al., 1993; Zhao et al., 2002), combined with general environmental and health concerns, has stimulated interest in developing alternative management techniques such as trap crops (Hooks & Johnson, 2003; Shelton & Badenes-Perez, 2006). *Plutella xylostella* is the insect pest for which most attempts of control through trap cropping have been undertaken and results have been variable (Shelton & Badenes-Perez, 2006). One of the plant species proposed to manage *P. xylostella* is *Barbarea vulgaris* (R. Br.) (Cruciferae) (Idris & Grafius, 1996; Badenes-Perez et al., 2004; Lu et al., 2004; Shelton & Nault, 2004; Badenes-Perez et al., 2005b), a biannual invasive weed

that occurs in temperate regions worldwide (MacDonald & Cavers, 1991; Uva et al., 1997). Given the choice between *B. vulgaris* and various cruciferous crops, *P. xylostella* highly prefers to lay its eggs on *B. vulgaris* despite the fact that its larvae do not survive on it (Idris & Grafius, 1996; Badenes-Perez et al., 2004; Lu et al., 2004; Shelton & Nault, 2004; Badenes-Perez et al., 2005a).

Survival in Lepidoptera is greatly determined by the oviposition behavior of adult females, as immature stages have limited mobility (Renwick, 1989). Among many herbivorous insects, oviposition on newer leaves of a particular host tends to be preferred over oviposition on older leaves (Raupp & Denno, 1983; Steinbauer, 2002; Klemola et al., 2003), which tend to be less suitable for larval development and survival than younger leaves (Larsson & Ohmart, 1988; Raupp et al., 1988; Kause et al., 1999; Rodrigues & Pires-Moreira, 1999). However, it is not known if *P. xylostella* prefers to lay eggs on young leaves within a plant, nor is it known if preference for young leaves is correlated with larval survival on *B. vulgaris*. Ovipositional preference for

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young leaves may increase the chances of larval survival in *B. vulgaris*.

Females of synovigenic insect species mature eggs throughout their adult life, whereas pro-ovigenic species emerge with a fixed number of eggs ready to lay (Papaj, 2000). In *P. xylostella*, oogenesis has been shown to increase in the presence of a host plant (cabbage) as compared to a non-host plant (beans) (Hillyer & Thorsteinson, 1969). It is not known, however, how exposure to different cruciferous plants, even if they are non-suitable hosts for larval development, can affect oogenesis and total oviposition in *P. xylostella*. Oogenesis in *P. xylostella* also may increase in the presence of *B. vulgaris*. Shelton & Nault (2004) reported that when *P. xylostella* was offered cabbage or broccoli plants alone vs. a 70 : 30 mixture of cabbage/broccoli and *B. vulgaris* plants, the total number of eggs laid on all plants in the treatment with *B. vulgaris* was 1.6–3 times greater than in the broccoli treatment alone. However, in one experiment 1.2 times more eggs were laid in the treatment with cabbage alone than in the treatment with *B. vulgaris*. Additional studies are needed to confirm that *B. vulgaris* is responsible for increased oogenesis in *P. xylostella* as well as identifying the mechanism involved.

The objectives of this research were to compare *P. xylostella* oogenesis and oviposition dynamics in cabbage alone or in mixtures with *B. vulgaris* under laboratory, screenhouse, and field conditions. Additionally, *P. xylostella* ovipositional preference and larval survival within *B. vulgaris* plants were studied.

Materials and methods

Experiments were conducted at the New York State Agricultural Experiment Station in Geneva, NY, USA, in 2003. *Plutella xylostella* used in all experiments originated from a population collected in cabbage fields in Camilla, GA, USA, in 2003. After collection from the field, *P. xylostella* colonies were maintained in the laboratory on a wheat germ-casein artificial diet (Shelton et al., 1991). 'Bobcat' cabbage (Reed's Seeds, Cortland, NY, USA) and G-type (glabrous) *B. vulgaris* plants were used in our experiments. *Barbarea vulgaris* seeds were obtained from wild plants growing near Ithaca, NY, USA. All plants used in the experiments were initially grown using Cornell mix soil substrate (one peat moss : two vermiculite) in 15-cm pots. Plants were grown first in the greenhouse and then moved outdoors at least 2 weeks before experiments began. All plants used in this study were 12 weeks old at the time they were used either in laboratory and screenhouse experiments or transplanted into the field. Plants did not flower during the time they were used in the experiments (both cabbage and *B. vulgaris* are biennial). Prior to experimentation, plants were fertilized weekly with an all-purpose 15-30-15 fertilizer (Wilson Laboratories Inc., Springdale, CT, USA). *Plutella xylostella* adults released at the beginning of each experiment were always <2 days old.

Host-dependent oogenesis

Experiments were conducted in screened cages $60 \times 60 \times 45$ cm. Total oviposition was recorded when moths were provided either cabbage or *B. vulgaris*. Two mated females were placed in each cage. A 25-ml Erlenmeyer flask with a 10% sugar solution and dental wick (Absorbal, Wheat Ridge, CO, USA) was placed in each cage to provide a food source for moths. The number of eggs laid was recorded 3 days after the moths were released. Total oviposition was compared between moths provided with either cabbage or *B. vulgaris* plants. Treatments were located in separated greenhouses with the same environmental conditions (23 ± 3 °C). Each treatment was replicated 15 times.

Ovipositional preference and larval survival on *Barbarea vulgaris* leaves of different age within a plant

Experiments were conducted in growth chambers (22 ± 1 °C and 60 ± 5% r.h.). Ovipositional preference was assessed in plexiglass tubes 3.75 cm (interior diameter) by 12 cm (length). One single female moth was placed in each tube, where it was only offered two 6.4 cm^2 circular disks of the abaxial side of *B. vulgaris* leaves. For each tube, the ends of a single tube were attached to two leaves, a younger/smaller leaf (<3.0 cm maximum leaf diameter) and an older/larger leaf (>6.0 cm maximum leaf diameter), of the same *B. vulgaris* plant with the help of rubber bands and parafilm. Each two-choice comparison was replicated 10 times. The number of eggs laid for each leaf age was recorded 2 days after the moth was released. Larval survival was assessed by using a pin to randomly attach groups of 10 *P. xylostella* eggs (<2 days old and laid on small pieces of aluminum foil) to six leaves within a *B. vulgaris* plant: three younger/smaller leaves (<3.0 cm maximum leaf diameter) and three older/larger leaves (>6.0 cm maximum leaf diameter). The same procedure was repeated on three plants, so nine leaves were used in total per treatment. Plants were inspected every 2 days to record survival of larvae.

Effect of plant volatiles in host-dependent oogenesis

Experiments were conducted in screened cages $60 \times 60 \times 45$ cm. Total oviposition in *P. xylostella* was compared between moths exposed to plant volatiles from only cabbage and moths exposed to volatiles from cabbage and *B. vulgaris*. Three mated *P. xylostella* females were placed in each cage containing a cabbage plant, on which they were able to lay eggs, and either a cabbage or a *B. vulgaris* plant physically concealed by being covered with cheese cloth. The mesh of the cloth was small enough to prevent oviposition on the

covered plant, but allow the release of plant volatiles. A 25-ml Erlenmeyer flask with a 10% sugar solution and dental wick was placed in each cage to provide a food source for moths. Oviposition was measured daily over a 7-day period by replacing the cabbage plant exposed to *P. xylostella* every 24 h. Treatments were located in separate growth chambers with the same environmental conditions (22 ± 1 °C and 60 ± 5% r.h.). Each treatment was replicated 10 times.

Oviposition in cabbage and *Barbarea vulgaris* mixtures

Experiments were conducted in $4.7 \times 3.2 \times 2.5$ m outdoor screenhouses that were covered with a transparent fiberglass roof. Plants were moved to the screenhouses 24 h before experimentation. There were six treatments containing a systematic mixture of cabbage and *B. vulgaris* plants (0, 4, 8, 16, 24, and 32% of plants were *B. vulgaris*) and all treatments included a total of 25 plants (Badenes-Perez et al., 2005b). Adults of *P. xylostella* were released at a rate of 1.5 per plant (38 total) from a plastic container placed on top of a wooden platform (80 cm above ground) in the middle of the screenhouse. Adults were released in a 1 : 1 sex ratio. A 50-ml Erlenmeyer flask with a 10% sugar solution and dental wick was placed at the release point to provide a food source for moths. Two days after releasing the moths, the number of eggs on each plant was counted in the laboratory using a dissecting microscope. Treatments were randomly assigned to screenhouses and treatments were replicated three times. Multiple screenhouses were used, each of which was considered a replicate or block.

Oviposition in a cabbage field with a *Barbarea vulgaris* trap crop

Cabbage and *B. vulgaris* plants were planted in rows separated by 0.9 m with 0.45 m spacing between adjacent plants within rows (Badenes-Perez et al., 2005b). Plots had 14 rows with 18 plants each. A treatment with a solid planting of cabbage was compared to a treatment with 28% *B. vulgaris* in which rows 1, 2, 13, and 14 were planted with *B. vulgaris*, while the remainder was cabbage. Each plot was surrounded by 3.5 m of bare soil plus two rows of 'Seneca Indian' corn (Johnny's Seeds, Albion, ME, USA) to provide a physical barrier for minimizing insect movement between plots. A randomized complete block design was used with six plots for each treatment. Field plots were conventionally tilled and fertilizer and herbicide were applied according to current recommendations (Reiners et al., 2003). Prior to the beginning of the experiment, natural infestations of *P. xylostella* in the field were very low (<0.1 larvae per plant) and, to reduce them further, approximately 1 week before *P. xylostella* release plots were sprayed with *Bacillus thuringiensis* var. *kurstaki* [DiPel® Pro DF, 1.0 kg a.i. ha^{-1} (Valent BioSciences Corporation, Libertyville, IL, USA)]. To ensure a high and temporarily predictable *P. xylostella* infestation, 126 moths

were released on the west side of each plot, 0.5 m outside the middle of the first row, simulating the arrival of moths to the field from one side of the field. Approximately 3 days after moths were released in the field, 30 plants (12% of the plot total) were randomly collected from each plot (eight plants from rows 1, 2, 13, and 14 and 22 plants from rows 4–13). The numbers of *P. xylostella* eggs per plant were counted in the laboratory using a dissecting microscope.

Statistical analyses

Treatments in all experiments were analyzed using analysis of variance (ANOVA) with the PROC GLM procedure of SAS® (SAS Institute Inc., 2004). When significant treatment differences were indicated by a significant F-test at P≤0.05, means were separated by Fisher's protected least significant difference (SAS Institute Inc., 2004). For the experiment testing the effect of plant volatiles on *P. xylostella* oogenesis, a random coefficient model in which replicate was nested within treatment and day, fitted as a random effect, was used with the PROC MIXED procedure of SAS® (SAS Institute Inc., 2004) to compare day-by-day oviposition on cabbage in the presence or absence of *B. vulgaris*. In order to normalize the residuals, a natural $\log(x + 1)$ function was used to transform data. Although all tests of significance were based on the transformed data, only untransformed data are presented.

Results

Host-dependent oogenesis

Plutella xylostella females provided with *B. vulgaris* laid 27.8% more eggs than those provided with cabbage ($F_{1,28} = 4.58$, P<0.05).

### Ovipositional preference and larval survival on *Barbarea vulgaris* leaves of different age within a plant

Plutella xylostella laid 3.7 times more eggs on younger than on older *B. vulgaris* leaves ($F_{1,18} = 9.71$, P<0.01). No larvae survived on any of the tested *B. vulgaris* leaves.

Effect of plant volatiles in host-dependent oogenesis

Plutella xylostella cumulative oviposition on cabbage increased following a logarithmic growth curve and was higher in the presence of *B. vulgaris* volatiles as compared with oviposition in the presence of cabbage volatiles ($F_{1,18} = 4.20$, P<0.05; Figure 1). After 7 days, total oviposition in the treatment with *B. vulgaris* was 23.4% higher than in the treatment with cabbage only.

Oviposition in cabbage and *Barbarea vulgaris* mixtures

In cabbage–*B. vulgaris* mixtures in screenhouses, the percentage of eggs laid on cabbage decreased following a
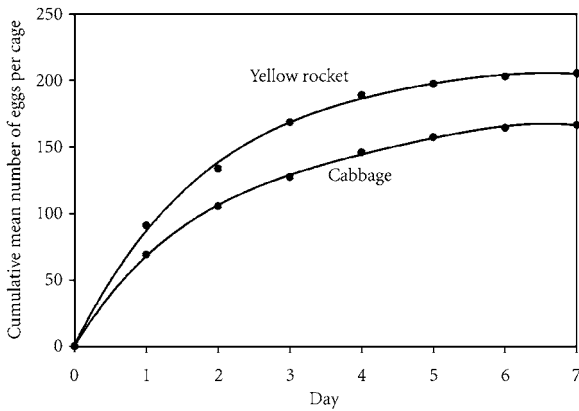
Figure 1 Daily cumulative oviposition by *Plutella xylostella* females on cabbage plants contained in cages with or without simultaneous exposure to volatiles from *Barbarea vulgaris*. Cages with and without *B. vulgaris* were located in separate environmental chambers.

quadratic relationship (r = 0.95, y = −0.01x^2 + 0.68x + 0.80, n = 18, P<0.001; Figure 2A) as the percentage of *B. vulgaris* increased. Compared with the linear decrease that would be expected from equal ovipositional preference for cabbage and *B. vulgaris* and the percentage of cabbage and *B. vulgaris* plants present in the experimental arena, the observed oviposition decrease confirms previous studies of *P. xylostella* ovipositional preference for *B. vulgaris* (Badenes-Perez et al., 2004). However, the number of eggs laid on cabbage did not differ among treatments with an increasing percentage of *B. vulgaris* plants ($F_{5,12}$ = 0.44, P>0.05; Figure 2B). This suggests that the presence of *B. vulgaris* may have stimulated total oviposition, which was confirmed by plotting total oviposition with increasing percentage of trap crops (r = 0.52, y = 0.03x + 2.04, n = 18, P<0.05; Figure 2C).

Oviposition in a cabbage field with a *Barbarea vulgaris* trap crop

Total oviposition in plots with *B. vulgaris* was 6.3 times higher than oviposition in plots with only cabbage ($F_{1,10}$ = 34.20, P<0.001; Figure 3A). However, 99.1% of all eggs laid in plots with the cabbage–*B. vulgaris* mixture were laid on *B. vulgaris* ($F_{1,28}$ = 141.74, P<0.001; Figure 3B). Consequently, oviposition on cabbage was 6.2 times lower in the mixture treatment than in cabbage alone ($F_{1,10}$ = 433.88, P<0.001; Figure 3C).

Discussion

These studies provide insight into *P. xylostella* oogenesis and oviposition dynamics, the potential use of *B. vulgaris* as a trap crop, and the potential of *P. xylostella* to increase

its host range to include *B. vulgaris*. Isothiocyanates (volatile compounds) have been shown to stimulate oogenesis in *P. xylostella* (Hillyer & Thorsteinson, 1969). In *B. vulgaris*, sulphur-containing isothiocyanates have been identified as active oviposition stimulants for *P. xylostella* (A Renwick, pers. comm.). Given that, as a general rule, oviposition begets oogenesis (Papaj, 2000), the same volatile compounds acting as oviposition stimulants also may be responsible for the increased oogenesis observed in this study, but this hypothesis remains to be tested. It is noteworthy that while in general insect oogenesis has been shown to increase with
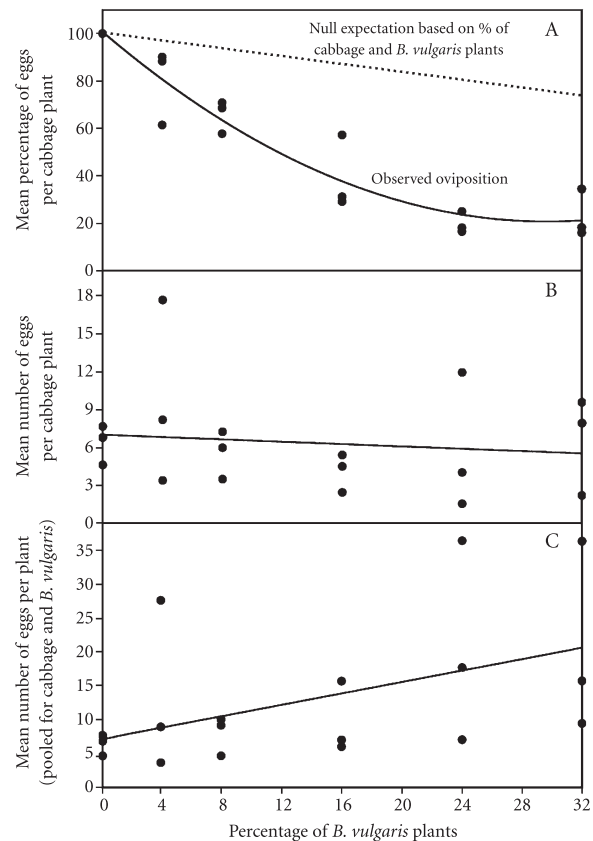
Figure 2 Data from screenhouse experiment showing *Plutella xylostella* oviposition (A) as percentage of eggs laid on cabbage (following quadratic regression equation y = −0.01x^2 + 0.68x + 0.80, n = 18, r = 0.95, P<0.001) compared to null expectation based on equal ovipositional preference for cabbage and *Barbarea vulgaris* plants; (B) as mean number of eggs laid on cabbage (y = 2.05 − 0.05x, n = 18, r = 0.21, P>0.05); and (C) as total oviposition, pooled from eggs laid on cabbage and *B. vulgaris* plants, with an increasing percentage of *B. vulgaris* plants (following linear regression equation y = 0.03x + 2.04, n = 18, r = 0.52, P<0.05). Data in Figure 2A were presented as a non-linear segmented regression model in Badenes-Perez et al. (2005b).
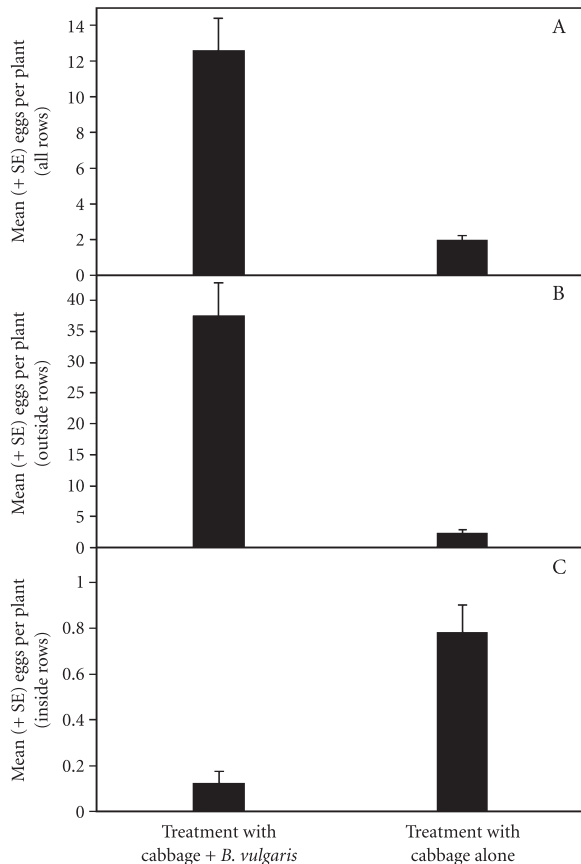
Figure 3 Mean (+ SE) number of *Plutella xylostella* eggs in a treatment with cabbage and *Barbarea vulgaris* compared and a treatment with cabbage alone. Data shown (A) as eggs laid for each treatment (pooled for all rows); (B) as eggs laid on outside rows (rows 1, 2, 13, and 14), where *B. vulgaris* was located in the treatment containing it; and (C) as eggs laid on the inside rows (rows 3–12).

host quality (Hopkins & Ekbom, 1999; Papaj, 2000), in this study *P. xylostella* oogenesis was higher with a non-suitable host (*B. vulgaris*) than with a suitable host (cabbage). The combination of increased oogenesis and preferential oviposition on *B. vulgaris* increases the chances of *P. xylostella* adaptation to *B. vulgaris* because the probability of a larva surviving on *B. vulgaris* increases with the number of eggs laid on it due to genetic variation in the insects.

In this study, screenhouse and field experiments differed in that, in the screenhouse, the presence of *B. vulgaris* as a trap crop did not significantly reduce oviposition on cabbage, while in the field it did. Although this difference could be attributed to the different experimental design in the screenhouse, in the field (spatial arrangements of *B. vulgaris* and cabbage and/or location where moths were released), this is not likely the case. Shelton & Nault (2004) conducted an experiment with a similar experimental

design in an outdoor screenhouse that resulted in a reduction in oviposition in cabbage similar to that observed in the field in this experiment. Alternatively, the difference in oviposition may have been due to a limited number of plants and a relatively confined area in the screenhouse compared with the field. To a certain extent, oviposition in most insects is distributed among host patches, not only as a diversifying risk-spreading (bet-hedging) strategy, but also to avoid density-dependent effects from competitors, predators, or other factors (Hopper, 1999). Even if there is a strong preference for a certain plant type, oviposition will also occur on other host plants, especially if there is a limited number of preferred plants available, such as in the case of the 25-plant host patch in the experimental arena of the screenhouse experiment described here. Conditions of limited space, such as those in a screenhouse or a cage, have also been reported to result in aberrant oviposition in other Lepidoptera in host-plant mixtures, supposedly because of insect excitation after contact with a highly preferred host (Withers & Barton Browne, 1998; Steinbauer, 2002). High density of moths has further been shown to result in unexpected oviposition behavior in experiments with other Lepidoptera (Steinbauer, 2002), and this could also be the case here, where 1.5 moths per plant (higher than typical naturally occurring infestations) were released in the screenhouse experiment as compared to 0.5 moths per plant released in the field experiment.

In cabbage and collard plants, *P. xylostella* larval survival has been shown to be higher on younger than on older leaves (Badenes-Perez et al., 2005a). Although no *P. xylostella* larvae survived on *B. vulgaris* regardless of leaf age, *P. xylostella* preferred to oviposit on young *B. vulgaris* leaves. Saponins acting as feeding deterrents have been identified as responsible for the lack of survival of *P. xylostella* larvae on *B. vulgaris* (Shinoda et al., 2002; Agerbirk et al., 2003). Contents of saponins in leaves have been shown to increase with leaf age in several plants (Carlsson, 1980; Potter & Kimmerer, 1986), perhaps making survival of *P. xylostella* more likely if eggs are laid on younger rather than older leaves. However, preferential oviposition on young leaves could also be the result of other factors, such as increased shelter from biotic and abiotic mortality factors for eggs and larvae as a consequence of young leaves being located in the interior of the plant, or a response to higher concentration of oviposition stimulants in young leaves. Measurements of the content of triterpenoid saponins and oviposition stimulants in *B. vulgaris* leaves of different age are necessary to test these hypotheses.

Most ovipositing Lepidoptera prefer to oviposit on hosts where their larvae are able to survive, but there are cases in which the correlation between oviposition preference and larval performance is poor and several hypotheses, acting

independently or in concert, have been put forward to interpret this apparently non-adaptive behavior (Courtney, 1982; Thompson, 1988; Courtney & Kibota, 1989; Thompson & Pellmyr, 1991; Larsson & Ekbom, 1995; Nylin & Janz, 1999; Thompson, 1999; Janz, 2002). It is not clear whether *P. xylostella* oviposition behavior on *B. vulgaris* should be interpreted as a non-adaptive mechanical response to cues specific from cruciferous hosts, or a teleological behavior geared to improve fitness through a potential host expansion. Given that no *P. xylostella* larvae survive on *B. vulgaris*, there cannot be selective advantage in *P. xylostella* oviposition on *B. vulgaris* and it is likely that the behavior is non-adaptive.

Both *P. xylostella* and *B. vulgaris* arrived first to New York and other northeastern states of the USA in the 1800s (Nuttall, 1818; Fitch, 1856). *Plutella xylostella* was reported for the first time in the USA in 1855 (Fitch, 1856), spreading throughout all the USA by 1883 (Riley, 1883), while *B. vulgaris* is thought to have been introduced to the USA around 1800 (Nuttall, 1818). In western New York, *B. vulgaris* is a common weed in fields of cruciferous crops (Root & Tahvanainen, 1969, FR Badenes-Perez, unpubl.) and thus, sympatry between *B. vulgaris* and *P. xylostella* has occurred for about 150 years (about 750 generations of the insect), which could be sufficient for adaptation to or avoidance of *B. vulgaris* to occur in *P. xylostella*. However, our observations in western New York (Ithaca and Geneva) as well as a 3-year study recording insect fauna associated with *B. vulgaris* in a wide variety of habitats in Ithaca, NY, USA (Root & Tahvanainen, 1969), have never indicated survival of *P. xylostella* on *B. vulgaris*. Lack of *P. xylostella* larval survival associated with high ovipositional preference on *B. vulgaris* has been recorded over several years in different populations of *P. xylostella* in various parts of the USA (Idris & Grafius, 1996; Badenes-Perez et al., 2004; Shelton & Nault, 2004; Badenes-Perez et al., 2005a; Badenes-Perez et al., 2005b) and also in China (Lu et al., 2004). Both *P. xylostella* and *B. vulgaris* are thought to be native to the Mediterranean region of Europe (Hardy, 1938; MacDonald & Cavers, 1991). Adaptation to *B. vulgaris* (or avoidance of it) may have evolved in *P. xylostella* in these and other areas where *B. vulgaris* and *P. xylostella* have coexisted for thousands of years, but there are no references to confirm this hypothesis. A geographic mosaic with adaptation to *B. vulgaris* by certain populations of the flea beetle, *Phyllotreta nemorum* L., has been shown as a result of different levels of interaction between *P. nemorum* and *B. vulgaris* in different parts of Denmark (de Jong et al., 2001) and this could also be the case of *P. xylostella*.

Host expansion involves, first, female attraction and stimulation to oviposit on a new host (or accidental placement of eggs/larvae on the host), and second, survival and adequate development of immature stages of the insect on the new host. Unlike other cases where the primary barrier for host expansion has been shown to be behavioral (i.e., no oviposition on the plant) rather than physiological (i.e., no survival of larvae) (Karowe, 1990), the inability of *P. xylostella* larvae to survive on *B. vulgaris* is the only obstacle to host expansion. The known ability of *P. xylostella* to develop resistance to all major groups of insecticides (Talekar & Shelton, 1993) indicates high genetic plasticity in this insect. Host expansion is more likely to occur in plants that are closely related to the plant species already present in the host range of the insect (Fraser & Lawton, 1994). In *P. xylostella*, some populations have adapted to peas, a non-cruciferous host (Löhr & Gathu, 2002), and thus, adaptation to *B. vulgaris*, a cruciferous plant, is feasible. Furthermore, *P. xylostella* can use other plant species in the genus *Barbarea* as a host, such as *Barbarea verna* (Miller) (A Renwick, pers. comm.). Additionally, in western New York, other insect pests of cruciferous crops, such as *Pieris rapae* (L.) and *Agrotis ipsilon* Hufnagel, use *B. vulgaris* as a host, especially at the beginning and end of the growing season when no other host plants are available (Root & Tahvanainen, 1969; Busching & Turpin, 1977; Huang et al., 1994). These factors, combined with the high ovipositional preference and increased oviposition on *B. vulgaris*, suggests that *P. xylostella* could potentially adapt to *B. vulgaris*.

Fitness costs aside, three factors may decrease the possibility of *P. xylostella* adaptation to *B. vulgaris* in western New York. First, within a geographical area, the natural habitat of *B. vulgaris* only seems to overlap with that of *P. xylostella* in limited cases, decreasing the selection pressure on *P. xylostella* to adapt to *B. vulgaris*. *Plutella xylostella* is mainly associated with agricultural production of cruciferous crops (Talekar & Shelton, 1993), whereas *B. vulgaris* tends to occupy grassland, roadsides, and ruderal and waterside habitats, being particularly abundant on early successional stages in open habitats following soil disturbance (Root & Tahvanainen, 1969; Roberts, 1986; Rich, 1987; MacDonald & Cavers, 1991; Castroviejo et al., 1993). As a result of the soil disturbance associated with common practices for growing cruciferous crops, *B. vulgaris* can be common in fields with cruciferous crops (Root & Tahvanainen, 1969; FR Badenes-Perez, unpubl.). Yet, current weed management practices may eliminate most *B. vulgaris* from these fields (Reiners et al., 2005). Second, obligate requirements for vernalization in *B. vulgaris* (MacDonald & Cavers, 1991) limit its interaction with overwintering *P. xylostella*, which cannot survive in cold winters (Talekar & Shelton, 1993). The cold winters in western New York allow *P. xylostella* to complete a maximum of six generations per year, further decreasing its exposure to *B. vulgaris* (Talekar & Shelton, 1993). Furthermore, *P. xylostella* populations arriving to

New York State seem to come from the southern USA (Smith & Sears, 1982; Shelton et al., 1996), where *B. vulgaris* is less common (MacDonald & Cavers, 1991). Third, in fields containing a cabbage crop with a high percentage of *B. vulgaris*, *P. xylostella* also oviposits on cabbage plants, even if in reduced numbers (Badenes-Perez et al., 2005b). *Plutella xylostella* oviposition and survival also occur on *Capsella bursa-pastoris* (L.) Medicus, *Sinapis arvensis* L., and other cruciferous weeds in western New York (Talekar & Shelton, 1993; FR Badenes-Perez, unpubl.). Because of higher *P. xylostella* larval survival on cabbage and various cruciferous weeds, panmixia between a larger *P. xylostella* population not adapted to *B. vulgaris* and a hypothetical, much less common, *B. vulgaris*-adapted *P. xylostella* population is likely to dissolve any emerging *B. vulgaris*-adapted genes in *P. xylostella*.

In summary, *P. xylostella* shows high ovipositional preference for *B. vulgaris*, but larvae do not survive on it, suggesting that it may be useful as a trap crop. However, *P. xylostella* shows increased oogenesis in the presence of *B. vulgaris*, which could favor adaptation to *B. vulgaris*, reducing its long-term potential as a trap crop. However, without explicit estimates of behavioral and genetic variation in *P. xylostella* populations in habitats with different exposure to *B. vulgaris*, it is difficult to predict the role of the various aspects of *P. xylostella* oviposition behavior in adapting to *B. vulgaris*. Limited selection pressure on *P. xylostella* to adapt to *B. vulgaris* as well as gene flow conferred by insect movement and panmixia are likely to prevent adaptation.

Acknowledgements

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