BIOCONTROL SCIENCE AND TECHNOLOGY, 2015
VOL. 26, NO. 1, 104–115
http://dx.doi.org/10.1080/09583157.2015.1078872

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RESEARCH ARTICLE

Plant-mediated vulnerability of an insect herbivore to *Bacillus thuringiensis* in a plant-herbivore-pathogen system

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ABSTRACT

Laboratory studies were performed to explore the effects of host-plant quality on the vulnerability of *Plutella xylostella* to *Bacillus thuringiensis*. *P. xylostella* were kept on different host plants, including *Brassica pekinensis* (Chinese cabbage) cv. Hero, *Brassica oleracea* var. *botrytis* (cauliflower) cv. Royal, and *B. oleracea* var. *capitata* (common cabbage) cv. Globe Master (white cabbage) and cv. Red Dynasty (red cabbage) for at least two generations. These host plants are considered as the high (Chinese cabbage), intermediate (cauliflower and white cabbage) and low-quality (red cabbage) hosts for *P. xylostella*. The vulnerability of the pest larvae was then tested using two formulation of *B. thuringiensis* var. *kurstaki*, including Biolarv® and Biolep®. The results demonstrated that the susceptibility of *P. xylostella* to *B. thuringiensis* was influenced by host-plant quality. Indeed, *B. thuringiensis* acted better on the pest fed on the low-quality host plant compared with that on the high-quality host plant. The interaction between the pathogen and plant quality/resistance resulted in more mortality of the pest larvae, implying a synergistic effect. From a pest management viewpoint, these findings may be promising for the integration of the pathogen and the low-quality/partially resistant host plants against *P. xylostella* in field studies.

ARTICLE HISTORY
Received 2 January 2015
Revised 19 July 2015
Accepted 29 August 2015

KEYWORDS
Plutella; Bacillus; host plant; tritrophic; bottom-up; sustainable strategies

1. Introduction

Host-plant resistance is a paramount component of sustainable pest management (Andrahennadi & Gillott, 1998; Sarfraz, Dosdall, & Keddie, 2006). Plant resistance can happen via one factor or a combination of factors, such as antibiosis, antixenosis and tolerance (Sarfraz, Dosdall, & Keddie, 2007). For example, the mechanism of resistance in glossy *Brassica oleracea* to attack by the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera, Plutellidae) is reduced larval survival (Ulmer, Gillott, Woods, & Erlandson, 2002). Growth and reproduction of insect herbivores are affected by plant quality either via nutritional quality or via the effects of plant defensive compounds (Awmack & Leather, 2002). In

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addition, insect defensive characteristics might be influenced by plant quality variability. Host-plant suitability may indeed alter the fitness costs of pesticide resistance of herbivorous insects (Janmaat & Myers, 2007).

Ecological pest management programmes attempt to combine host-plant resistance with biocontrol, but the compatibility of these two strategies may vary with the specific agro-ecosystem (Karimzadeh, Bonsall, & Wright, 2004; Karimzadeh, Hardie, & Wright, 2013). Host plant may positively or negatively affect the third tritrophic level, including parasitoids, predators and pathogens (Karimzadeh & Wright, 2008; Schuler & van Emden, 2000). The tritrophic interactions between host plants, insect herbivores and their parasitoids (Gols et al., 2007; Karimzadeh et al., 2004, 2013; Sarfraz, Dosdall, & Keddie, 2008; Schuler, Denholm, Clark, Stewart, & Poppy, 2004) or their pathogens (Gassmann, Stock, Tabashnik, & Singer, 2010; Janmaat, Ware, & Myers, 2007; Karimzadeh & Sayyed, 2011; Raymond, Sayyed, & Wright, 2007) are well documented. The plant nutritional, defensive or physical characteristics might mediate such influential multitrophic interactions.

Plutella xylostella has been reported as the most devastative pest of crucifers worldwide (Furlong, Wright, & Dosdall, 2013; Talekar & Shelton, 1993). In recent decades, resistance in the field to all the classes of synthetic insecticide by *P. xylostella* has occurred (Shelton et al., 1993). This has urgently promoted the assessment of more ecological strategies of pest management, such as biocontrol, host-plant resistance and cultural control. Successful control of *P. xylostella* has been achieved by using different strains of the microbial biopesticide *Bacillus thuringiensis* Berliner (Bacillales, Bacillaceae) or its toxins. Beside its high toxicity to some insect pests, *B. thuringiensis* (*Bt*) has shown little or no toxicity to non-target organisms, including beneficial insects (Tabashnik, Finson, & Johnson, 1991). The *Bt* insecticidal crystal proteins act by binding to and creating pores in insect midgut membranes. In addition, the spores of *Bt* increase the toxicity of its crystals to *P. xylostella* larvae (Liu, Tabashnik, Moar, & Smith, 1998; Schnepf et al., 1998; Syed & Abro, 2003).

The interaction between host-plant suitability and *Bt* may have different effects on the target pest, based on the compatibility of these sustainable strategies. The present study aimed to examine the influence of host-plant suitability on vulnerability of a herbivore (*P. xylostella* larvae) to a pathogen (*Bt*). Here, it was shown that host plant-mediated influences on an insect herbivore can determine host–pathogen interactions. The cascading effect of variation in plant quality on the third trophic level is indicative of a strong bottom-up effect in a plant-herbivore-pathogen system.

2. Materials and methods

2.1. *Plants and insects*

Chinese cabbage (*Brassica pekinensis*) cv. Hero, common cabbage (*Brassica oleracea* var. *capitata*) cv. Globe Master (white cabbage) and cauliflower (*B. oleracea* var. *botrytis*) cv. Royal were grown under greenhouse conditions (25 ± 5°C and L:D 16:8 h) without the application pesticide. In addition, common cabbage cv. Red Dynasty (red cabbage) was grown in the field. The 4–6-week-old Chinese cabbage, and 6–8-week-old common cabbages and cauliflower were used in experiments. *Plutella xylostella* (originally from Isfahan province, central Iran) cultures were maintained on above-mentioned host

plants in ventilated oviposition cages (40 × 40 × 40 cm) under standard constant conditions (25 ± 2°C; 70 ± 5% RH; L:D 16:8 h). Insects were cultured on each host plant for two generations before using them for the experiments (Karimzadeh et al., 2004; Schuler & van Emden, 2000).

2.2. *Herbivore performance*

To obtain synchronized eggs of *P. xylostella*, one plant, 30 pairs (male and female) of newly emerged *P. xylostella* adults (reared from the same host plant), and aqueous honey solution (20%) were placed in each oviposition cage for 24 h. Batches of 10 neonate *P. xylostella* larvae were placed on leaf discs (5.8 cm dia.) within individual Petri dishes (6 cm dia.) containing a moistened filter paper. Leaf discs were cut from randomly selected leaves on different plants for each plant group used in experiments. To prevent starvation of larvae, the leaf discs were replaced every 24 h. Pupae were transferred to separate Petri dishes and kept until eclosion. The experiments were conducted under controlled environment conditions (25 ± 1°C; 65 ± 5% RH; L:D 16:8 h). Life stage and mortality were recorded every 24 h until all insects had either died or emerged as adults. The mean time from oviposition to pupation and eclosion, the survival percentage and pupal weight were calculated (Karimzadeh & Wright, 2008). Each treatment was replicated 17 times, based on the results from a preliminary experiment (Karimzadeh, 2011).

2.3. *Dose-response bioassays*

Plutella xylostella larvae were treated with two commercial formulations of *B. thuringiensis* var. kurstaki, including Biolarv® (3A3B 5%; Agrimix, Roma, Italy) and Biolep® (10^8 cell/ml; Tabiatgera, Karaj, Iran), both containing δ–endotoxin crystals and viable spores. The test products were freshly prepared in distilled water with Tween20® (0.02%) as a surfactant. To determine CFU three concentrations of Biolarv® (10^{-3}, 10^{-6} and 10^{-9}) and Biolep® (10^{-6}, 10^{-9} and 10^{-12}) suspensions were prepared. The suspensions (100 µl) were then spread on the surface of nutrient agar (Merk®, Germany) plates, which were incubated for 24 h at 27°C. Each concentration was replicated four times. The visible colonies were counted and used as an index for calculating CFU (Izadyar, Talebi-Jahromi, Askary, & Rezapanah, 2003). To perform the bioassay, the leaf discs (5.8 cm dia.) of the host plants were immersed in the test solution for 10 s, and then kept on a corrugated sheet of aluminium foil with the adaxial leaf surface uppermost for 2 h at room temperature to dry up. Control leaf discs were immersed in distilled water containing Tween20® (0.02%). The leaf discs were then transferred to individual plastic Petri dishes (6 cm dia.) containing a moistened filter paper. Five third-instar larvae of *P. xylostella* were then placed on each leaf disc. The leaf discs were then replaced every 24 h with fresh, untreated ones. Mortality was recorded after five days. Six concentrations were used for Biolarv (3.75×10^{-1}, 3.75×10^{1}, 3.75×10^{3}, 3.75×10^{5}, 3.75×10^{7}, 3.75×10^{9} CFU/ml) and Biolep (2.95×10^{2}, 2.95×10^{4}, 2.95×10^{6}, 2.95×10^{8}, 2.95×10^{10}, 2.95×10^{12} CFU/ml). All the concentrations as well as the control treatment were replicated eight times. All the bioassays were performed under the standard environment conditions (25 ± 2°C; 70 ± 5% RH; L:D 16:8 h; Karimzadeh & Sayyed, 2011; Sayyed, Raymond, Ibiza-Palacios, Escriche, & Wright, 2004). In all the experiments, the institutional and national guidelines

for the care and use of laboratory animals (Institutional Animal Care and Use Committee Guidebook) were followed.

2.4. *Statistical analysis*

Differences in the survival rates among host-plant types were analyzed using logistic analysis of deviance (binomial error). The developmental periods and pupal weight were analyzed using nested ANOVA, where the individual larvae were nested within Petri dishes, and Petri dishes were nested within plants. For these data, a Petri dish (containing 10 individual larvae) was considered as a replication, and the treatments (four host plants) were replicated 17 times. The dose-response data were corrected using Abbott's formula and analyzed using probit analysis, where regression lines were fitted to dose-mortality data on a log-probit scale, and the estimated LC50s and associated confidence intervals (CI) were then calculated from the estimated linear regression parameters. In addition, to compare the independent and combined effects of host plants and *Bt* formulations, differences in percentage mortalities between host-plant types, *Bt* formulations and concentrations were analyzed using Analysis of Covariance after correction, and arcsine transformation. For these data, a Petri dish (containing five individual larvae) was considered as a replication, and the treatments (six different concentrations of each *Bt* formulation, as well as the control) were replicated eight times. Pairwise comparisons were performed using Least Significant Difference (LSD) or Tukey's Honestly Significant Difference (HSD; Crawley, 2013; Day & Quinn, 1989). All statistical analyses were completed in *R* 2.10.0 (R Development Core Team).

3. Results

3.1. *Host-plant effects on* P. xylostella *performance*

There was a significant effect of host plant on *P. xylostella* larval periods ($F_{3,76} = 101.19$, $P < 0.001$). The mean larval period of *P. xylostella* on the red cabbage (16.89 ± 0.53 days) was significantly greater than that on white cabbage (11.32 ± 0.28 days), cauliflower (10.29 ± 0.27 days) or Chinese cabbage (8.10 ± 0.07 days; Table 1). However, no significant influence of host plants on the pupal period of *P. xylostella* was observed ($F_{3,76} = 1.54$, $P = 0.19$; Table 1). In addition, when sum of larval and pupal period was analyzed, there was a significant effect of host plant ($F_{3,76} = 9.73$, $P < 0.001$); such that the shortest and longest developmental period of *P. xylostella* was obtained when the insect fed on Chinese cabbage (11.71 ± 0.46 days) and red cabbage (20.98 ± 2.00 days), respectively (Table 1). The effect of host plant on the pupal weight of *P. xylostella* was also significant

Table 1. Host-plant effects on developmental periods and pupal weight of *P. xylostella*.

	Developmental periods (mean ± SE; days)			Pupal weight
Host plant	L_1-Adult	Pupal	L_1-pupa	(mean ± SE; mg)
Chinese cabbage	11.71 ± 0.46 a	3.61 ± 0.20 a	8.10 ± 0.07 a[a]	4.32 ± 0.06 a
White cabbage	15.05 ± 0.71 ab	3.73 ± 0.32 a	11.32 ± 0.28 b	3.81 ± 0.11 ab
Cauliflower	14.44 ± 0.54 ab	4.15 ± 0.24 a	10.29 ± 0.27 b	3.80 ± 0.06 b
Red cabbage	20.98 ± 2.00 b	4.09 ± 0.44 a	16.89 ± 0.53 c	3.66 ± 0.19 b

[a]The different letters within columns show a significant ($P < 0.05$) difference (Tukey's HSD).

Table 2. Host-plant effects on survival rate of *P. xylostella*.

Host plant	Survival rate (mean ± SE; %)		
	L_1-pupa	Pupal	L_1-adult
Chinese cabbage	83.53 ± 5.42 a[a]	85.92 ± 3.55 a	71.76 ± 6.08 a
Cauliflower	68.24 ± 5.09 ab	90.52 ± 3.02 a	61.75 ± 4.94 ab
White cabbage	47.65 ± 5.97 b	90.12 ± 3.91 a	42.94 ± 5.74 b
Red cabbage	20.00 ± 4.62 c	82.35 ± 5.26 a	16.47 ± 3.83 c

[a]The different letters within columns show a significant ($P < 0.05$) difference (Tukey's HSD).

($F_{3,76} = 26.97$, $P < 0.001$; Table 2). The mean pupal weight of *P. xylostella* on Chinese cabbage (4.32 ± 0.06 mg) was significantly greater than cauliflower (3.80 ± 0.06 mg) and red cabbage (3.66 ± 0.19 mg; Table 1). Host plant had significant influences on the larval ($F_{3,80} = 52.83$, $P < 0.001$) and on L_1-adult ($F_{3,80} = 44.14$, $P < 0.001$) survival rate of *P. xylostella*. Mean survival rate of both the larvae and the sum of larvae and pupae of *P. xylostella* was significantly greater on Chinese cabbage compared with common cabbages (Table 2). But no significant difference for pupal survival rate ($F_{3,75} = 1.78$, P = 0.13) between the host plants was found.

3.2. *Host-plant effects on the* Bt *dose-mortality response*

The results of CFU test showed that the number of viable spores of Biolarv® and Biolep® were 3.75×10^{11} and 2.95×10^{14} CFU/ml, respectively (Table 3). The probit analysis showed that LC_{50} of Biolarv® significantly varied among host plants; such that LC_{50} of Biolarv® was significantly greater on Chinese cabbage compared with red cabbage. However, there was no significant difference between LC_{50} of Biolep® on different host plants (Table 3). The analysis of covariance (Table 4) showed that both the host plant ($F_{3,368} = 15.43$, $P < 0.001$) and *Bt* formulation ($F_{1,368} = 7.63$, $P < 0.01$) had significant effects on the mortality of *P. xylostella* larvae; the proportion mortality of *P. xylostella* larvae was highest and lowest on red cabbage (0.68) and Chinese cabbage (0.38), respectively (Table 5; Figure 1). Furthermore, the proportion *P. xylostella* larvae killed by Biolarv® (0.57) was significantly greater than that for Biolep® (0.49). There was, however, no significant interaction ($F_{3,368} = 0.54$, P = 0.65) between host plant and formulation for their effects on *P. xylostella* larval mortality (Table 4). In addition, there was a significant

Table 3. The effects of host-plant species on the susceptibility of *P. xylostella* larvae to *B. thuringiensis*.

Bt Formulation	Number of viable spores (CFU/ml)	Host plant	Lethal dose (gr/ml or ml/ml)[a]		Slope± SE	*P*
			LC_{50}	95% CI ($n = 8$)		
Biolarv®(WP)	3.75×10^{11}	Chinese cabbage	2.3×10^{-4}	7.99×10^{-6}–1.94×10^{-1}	0.45 ± 0.08	<0.001
		White cabbage	1.24×10^{-5}	1.53×10^{-6}–3.4×10^{-3}	0.51 ± 0.08	<0.001
		Cauliflower	9.45×10^{-6}	9.83×10^{-7}–2.40×10^{-2}	0.43 ± 0.08	<0.001
		Red cabbage	1.97×10^{-7}	8.33×10^{-8}–3.19×10^{-6}	0.40 ± 0.07	<0.001
Biolep®(SC)	2.95×10^{14}	Chinese cabbage	4.20×10^{-4}	2.23×10^{-5}–4.8×10^{-1}	0.57 ± 0.07	<0.001
		White cabbage	8.99×10^{-5}	4.49×10^{-6}–0.17×10^{-1}	0.42 ± 0.08	<0.001
		Cauliflower	1.35×10^{-5}	2.29×10^{-6}–5.90×10^{-4}	0.57 ± 0.07	<0.001
		Red cabbage	4.35×10^{-6}	6.91×10^{-7}–9.40×10^{-4}	0.45 ± 0.08	<0.001

[a]LC_{50} units for Biolarv® and Biolep®, respectively.

Table 4. Analysis of covariance of the effects of host plant, *Bt* formulation and concentration on *P. xylostella* mortality.

Source	Df	Sum Sq	Mean Sq	*F* value	*P* value
Plant	3	4.38	1.46	15.43	<0.001
Formulation	1	0.72	0.72	7.63	<0.01
Concentration	1	72.36	72.36	765.16	<0.001
Plant: Formulation	3	0.15	0.05	0.54	0.65
Plant: Concentration	3	1.10	0.37	3.88	<0.01
Formulation: Concentration	1	0.06	0.06	0.63	0.43
Plant: Formulation: Concentration	3	0.29	0.10	1.02	0.39
Residuals	368	34.80	0.10		

Table 5. The effects of host-plant species on the mortality of *P. xylostella* larvae by *B. thuringiensis*.

	Proportion mortality of *P. xylostella* larvae (mean ± SE)[a]		
	Bt formulation		
Host plant	Biolarv®	Biolep®	Overall
Chinese cabbage	0.42 ± 0.08	0.33 ± 0.08	0.38 ± 0.06 a[b]
White cabbage	0.53 ± 0.08	0.50 ± 0.07	0.52 ± 0.05 b
Cauliflower	0.58 ± 0.08	0.51 ± 0.08	0.54 ± 0.06 b
Red cabbage	0.75 ± 0.07	0.61 ± 0.08	0.68 ± 0.05 c
Overall	0.57 ± 0.04 A[c]	0.49 ± 0.04 B	

[a]The mean proportional mortality of the total bioassay doses.
[b]The different letters within the column show a significant ($P < 0.05$) difference (Tukey's HSD).
[c]The different capital letters within the row show a significant ($P < 0.05$) difference (Tukey's HSD).

interaction ($F_{3,368} = 3.88$, $P < 0.01$) between plant type and *Bt* concentration (Table 4); as it can be seen more clearly in Figure 1, for the Biolep formulation there is a significant difference in mortality among the plant species at the lower concentrations but not at the higher concentrations.

4. Discussion

Using the laboratory experiments we demonstrate that host plant quality-mediated effects on an insect herbivore might be determinative in host–pathogen interactions. In particular, it was indicated that the species of the host plant may influence the susceptibility of the diamondback moth to *Bt*. Host-plant quality clearly had a direct effect on the herbivore performance; the different stages of *P. xylostella* developed faster and performed better on the high-quality host plant (Chinese cabbage) compared with intermediate (white cabbage and cauliflower) or low-quality (red cabbage) host plants. In addition, the lowest LC_{50} value of *Bt* against *P. xylostella* larvae fed on red cabbage compared with other host plants demonstrated that the entomopathogen acts better on the herbivore larvae that suffered from low plant quality. Such an indirect effect of plant quality on the third trophic level is indicative of a strong bottom-up cascading effect in a tritrophic system.

The plant characteristics, such as trichomes, domatia or semiochemicals, may have direct or indirect (through alteration of herbivore physiology or behaviour) effects on natural enemies. For example, diverse life history traits of viral pathogens and parasitoids can be affected by variation in host-plant chemistry (Karimzadeh et al., 2004; Raymond et al., 2002). The plant nutritional, defensive or physical characteristics can

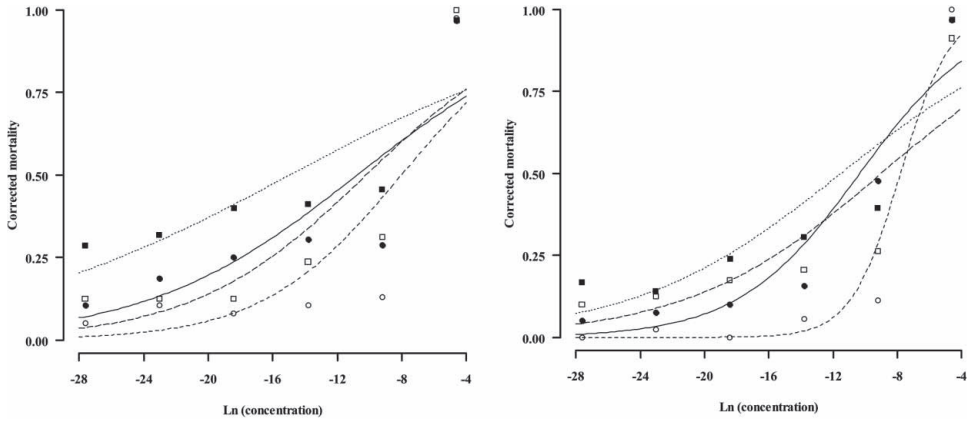

Figure 1. Dose-responsive curves for Biolarv (left) and Biolep (right) on different host plants. Solid (filled circle), dashed (empty circle), dotted (filled square) and long-dashed (empty square) lines (points) represent cauliflower, Chinese cabbage, red cabbage and white cabbage, respectively.

mediate such determinative interactions between plants, herbivores and natural enemies (Awmack & Leather, 2002). The different plant suitability to *P. xylostella* observed in the present study may be due to the presence and extent of nutritional factors and feeding stimulants (Syed & Abro, 2003); Chinese cabbage showed to be the most qualified host for *P. xylostella*, which completed its larval development fastest on this plant compared with other host plants. The longer developmental times of insect herbivores on low-quality plants may increase the exposure time to natural enemies (Awmack & Leather, 2002). In addition, the greatest pupal weight of *P. xylostella* fed on Chinese cabbage might have increased the fitness and performance of *P. xylostella* on such a plant. The insect life-history parameters such as fecundity, longevity and survival rate may vary with body size, as indicative of fitness (Karimzadeh et al., 2004). Apart from other factors, fecundity of an insect greatly depends on body weight or size (Begum, Ritusko, & Fujisaki, 1996; Miller, 1957; Syed & Abro, 2003). The plant-mediated variation in insect fecundity has paramount implications for population ecology and pest management through the manifestations of the intrinsic rate of increase and economic injury threshold, respectively (Awmack & Leather, 2002; Carey, 2001; Karimzadeh et al., 2004).

Host plants can mediate the interactions among insect herbivores and their pathogens; such that the vulnerability of insects to infection and the production and persistence of entomopathogens may be greatly affected by the variations in plant chemistry and structure (Cory & Hoover, 2006). Plants influences on the insect–entomopathogen interactions can occur via leaf surface (for example, leaf alkaline exudates containing basic ions that can inactivate baculoviruses, or leaves with reduced wax bloom increase adhesion and germination of the fungal conidia on the insect cuticle), plant architecture (for example, the degree of shading can influence the time entomopathogens persist before degradation by UV irradiation), or phytochemicals (for example, biologically activated phytochemicals can bind to occlusion bodies in the larval midgut and reduce the subsequent infectivity of the virus to host insects) (Duffey, Hoover, Bonning, & Hammock, 1995; Kouassi, Lorenzetti, Guertin, Cabana, & Mauffette, 2001). In addition, plant allelochemicals and nutrients

can affect pathogen fitness through the alteration of the physiology, growth and behaviour of the insect host. Entomopathogens could benefit from plants through the additional persistence on plant surface, encountering higher host populations, and increased host vulnerability to pathogens (Elliot et al., 2000). From the evolutionary point of view, this is a paramount role that plants play in the evolution of insect–pathogen interactions. From a pest management viewpoint, however, the increased fitness costs of an insect herbivore on poor quality plants would intensify the susceptibility of the insect to pathogens, mainly viruses and bacteria. Here, it was also demonstrated that food plants of *P. xylostella* play an important role in the pathogenicity of *Bt*, as the higher concentrations of *Bt* were needed to control *P. xylostella* larvae on a high-quality host plant (Chinese cabbage) compared with intermediate (white cabbage and cauliflower) or low-quality (red cabbage) host plants. Although the effects of plant resistance/quality/genotype on the interactions between *P. xylostella* and its parasitoids or predators are well documented (Eigenbrode, Moodie, & Castagnola, 1995; Gols et al., 2007; Karimzadeh et al., 2004, 2013; Karimzadeh & Wright, 2008; Liu & Jiang, 2003; Reddy, Tabone, & Smith, 2004; Sarfraz et al., 2008; Schuler et al., 2003, 2004; Verkerk & Wright, 1997), tritrophic studies focusing on the effects of plant characteristics on the interactions between *P. xylostella* and its pathogen or even on more complex interactions are rare (Karimzadeh & Sayyed, 2011; Raymond et al., 2007). The present study, in this regard, revealed a strong effect of plant quality/suitability for *P. xylostella* on the host–pathogen interaction, which is important from pest management point of view. Previous studies have also shown differential food plant-mediated effects of *Bt* on other insects, such as *Lymantria dispar* (L.) (Lepidoptera, Erebidae), *Trichoplusia ni* (Hübner) (Lepidoptera, Noctuidae), *Spodoptera littoralis* (Boisduval) (Lepidoptera, Noctuidae) and *Helicoverpa zea* (Boddie) (Lepidoptera, Noctuidae) (Bell, 1978; Farrar, Martin, & Ridgway, 1996; Janmaat et al., 2007). Some secondary plant compounds have been reported to affect *Bt* efficiency on control of herbivorous insects. For example, tannins and phenolic glycosides present in the foliage of aspen have changed the impact of *Bt* or its delta endotoxins on *L. dispar* larvae (Awmack & Leather, 2002).

The observed antagonistic/synergistic interactions between host plants of *P. xylostella* and *Bt* provide an additional advantage for the use of low-quality/partially resistant plants in *Bt*-based pest management programmes against *P. xylostella*. The growth and adaption of *P. xylostella* populations on such host plants would be slower. Moreover, such a synergism might result in a better control of *P. xylostella* by *Bt* or other pathogens, predators and parasitoids (Awmack & Leather, 2002; Verkerk, Leather, & Wright, 1998). In addition, low plant quality or plant defensive chemicals may favour *Bt* resistance management. For example, fitness costs of *Bt* resistance in *P. xylostella* have been higher on the low-quality plants (Raymond, Wright, & Bonsall, 2011). Increased accumulation of gossypol (a cotton defensive chemical) in pink bollworm (*Pectinophora gossypiella*) may also contribute to fitness costs associated with resistance to *Bt* toxins (Williams et al., 2011).

The host plant influences on the efficiency of other entomopathogens have been also reported. For instance, feeding on different food plants caused significant variation of *Leptinotarsa decemlineata* (Say) (Coleoptera, Chrysomelidae) to attack by the fungus *Beauveria bassiana* (Hare & Andreadis, 1983). In another study, Poprawski and Jones (2001) have shown that mycosis from two different fungi, *B. bassiana* and

Paecilomyces fumosoroseus, in nymphs of *Bemisia argentifolii* Bellows and Perring (Hemiptera, Aleyrodidae) varied between the different host plants. The influence of food plants on the vulnerability of *Spodoptera frugiperda* (J. E. Smith) and *L. dispar* to a nuclear polyhedrosis viruses have also been documented (Keating, Yendol, & Schultz, 1988). In addition, Gassmann et al. (2010) have shown plant-mediated resistance to entomopathogenic nematodes in *Grammia incorrupta* (Hy. Edwards) (Lepidoptera, Erebidae).

The present study indicated that host-plant resistance can be successfully combined with the entomopathogenic bacterium *B. thuringiensis* in sustainable pest management of *P. xylostella*. Further studies are, however, needed to explore the mechanisms by which resistant crucifers increase the vulnerability of *P. xylostella* larvae to *Bt*, and to test the consequence of such a combination in field.

Acknowledgements

We thank the late Dr Ali H. Sayyed (Department of Biochemistry, School of Life Sciences, University of Sussex, Brighton, UK) for advising on bioassays.

Disclosure statement

No potential conflict of interest was reported by the authors.

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