Resistance of Some Cultivated Brassicaceae to Infestations by *Plutella xylostella* (Lepidoptera: Plutellidae)

M. SARFRAZ,[1,2], L. M. DOSDALL,[3] AND B. A. KEDDIE[1]

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ABSTRACT Selecting insect-resistant plant varieties is a key component of integrated management programs of oligophagous pests such as diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), but rigorous research on important life history parameters of *P. xylostella* in relation to host plant resistance is rare. We evaluated six conventional brassicaceous species, namely, *Brassica napus* L. 'Q2', *B. rapa* L., *B. juncea* (L.) Czern., *B. carinata* L., *B. oleracea* L., and *Sinapis alba* L., and two herbicide-tolerant cultivars, namely, *B. napus* 'Liberty' and *B. napus* 'Conquest' for their resistance against *P. xylostella.* Brassicaceae species and cultivars varied considerably in their susceptibilities as hosts for *P. xylostella. Sinapis alba* and *B. rapa* plants were highly preferred by ovipositing females and trichome density on adaxial and abaxial leaf surfaces had nonsignificant effects on *P. xylostella* oviposition. Larval survival was similar on the genotypes we tested, but host plants significantly affected larval and pupal developmental time, herbivory, pupal weight, silk weight, adult body weight, forewing area and longevity (without food) of both male and female *P. xylostella.* Larval and pupal development of females was fastest on *B. juncea* and *S. alba*, respectively. Specimens reared on *B. napus* Liberty and *B. oleracea*, respectively, produced the lightest female and male pupae. Defoliation by both female and male larvae was highest on *B. rapa*, whereas least herbivory occurred on *S. alba.* Females reared on *S. alba* were heavier and lived longer in the absence of food than their counterparts raised on other tested host plants. *Brassica oleracea* could not compensate for larval feeding to the level of the other species we evaluated. *B. napus* Conquest, *B. napus* Q2, *B. carinata*, *B. rapa*, and *S. alba* produced, respectively, 1.6-, 1.8-, 1.8-, 3.9-, and 5.5-fold heavier root systems when infested than their uninfested counterparts, suggesting that these species were better able to tolerate *P. xylostella* infestations.

KEY WORDS antixenosis, antibiosis, tolerance, crucifers, diamondback moth

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Host plant resistance has been used effectively in sustainable integrated management programs for several crop pests (Dosdall et al. 1994, 2000; Dent 2000; Raza et al. 2000; Sarfraz et al. 2003, 2006). van Emden (1991) suggested that insecticide concentrations could be reduced three-fold on resistant host plants without appreciable increases in the pest population. Plant resistance can occur through one or a combination of factors involving antibiosis, antixenosis, and tolerance (Painter 1951). Plants responsible for antibiosis may cause reduced insect survival, decreased size or weight, reduced longevity, and reproduction in new generation adults, or they may have an indirect effect by increasing the exposure of the insect to its natural enemies as a result of prolonged developmental time (Dent 2000). Plants that exhibit antixenosis would have reduced initial infestations or a higher emigration rate of the pest than their susceptible counterparts (Teetes 1996, Dent 2000, Sarfraz et al. 2006). Tolerance includes plant responses that minimize the effects of herbivory on the fitness of individual plants (Simms 2000, Tiffin 2000). Herbivores can elicit different physiological responses in infested plants that would not usually occur in noninfested individuals. Such "induced" or "active" tolerance can then lead to compensatory growth of plants as a result of various mechanisms, including enhancement of photosynthetic activity, activation of dormant meristems, and use of stored reserves (Trumble et al. 1993, Tiffin 2000).

Herbicide-tolerant crops have revolutionized agricultural production systems. Several varieties of herbicide-resistant canola, *Brassica napus* L. (Brassicaceae), have been widely planted in the past several years in Canada. It is generally assumed that proteins conferring herbicide tolerance should not affect insects, but to our knowledge no study has compared the life history parameters of any insect pest on conventional and herbicide-tolerant plants, especially Brassicaceae.

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is a destructive insect pest of brassicaceous crops worldwide. It globally requires >US$1.0 billion in estimated annual management costs (Talekar and Shelton 1993). It occurs annually throughout the prairie provinces of Canada wherever

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[1] Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9.

[2] Corresponding author, e-mail: rsarfraz@ualberta.ca.

[3] Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Alberta, Canada T6G 2P5.

brassicaceous crops are grown and can cause substantial crop losses during outbreak years (Dosdall et al. 2004). Under intensive selection pressure, insects often develop high levels of insecticide resistance, and *P. xylostella* is one of the "leaders" among insect pests that are very difficult to control (Mota-Sanchez et al. 2002, Sarfraz and Keddie 2005a). Host plant resistance, therefore, can serve as an important tool for *P. xylostella* management with reduced input of insecticides, but our literature review indicates that extensive studies on plant resistance against *P. xylostella* are rare. The majority of research has focused on comparing selected cultivars within a species (e.g., Hamilton et al. 2005), without providing complete details on life history parameters of *P. xylostella* that are directly related to pest population dynamics. No previous study has compared the compensatory ability of various brassicaceous species and cultivars in the form of root development when infested by *P. xylostella.*

The current study was designed to evaluate eight Brassicaceae commonly available in various crucifer-growing areas worldwide for their resistance against *P. xylostella.* Ovipositional preference (antixenosis) was investigated in a free-choice situation and the potential role of leaf trichome density in antixenosis was determined. For potential antibiotic resistance, several *P. xylostella* life history parameters (i.e., survival, preimaginal developmental time, larval herbivory, pupal weight, silk weight, adult body weight, forewing area, adult longevity, and oviposition of new generation adults) were investigated on all eight Brassicaceae in no-choice tests. Plant compensatory ability (tolerance) in the form of belowground biomass development after *P. xylostella* herbivory also was assessed. A further objective of this study was to provide detailed insights on some key life history traits of both male and female *P. xylostella* when specimens were reared on various host plants.

Materials and Methods

Insects and Plants. The laboratory colony of *P. xylostella* was maintained on potted *B. napus* Q2 plants at 22 ± 0.5°C with a photoperiod of 16:8 (L:D) h. Moths collected from different fields in Alberta, Canada, were added to the culture every summer to maintain genetic diversity.

Eight Brassicaceae, namely, *B. napus* 'Q2' (susceptible to both glufosinate ammonium and glyphosate herbicides), *B. napus* 'Liberty' (resistant to glufosinate ammonium), *B. napus* 'Conquest' (resistant to glyphosate), *B. rapa* L. 'Reward', *B. juncea* (L.) Czern. 'Cutlass', *B. carinata* L. (BCA-003), *B. oleracea* L. 'Red Acre', and *Sinapis alba* L. (SAL-004) were grown under greenhouse conditions. Plants were grown individually in 15.2-cm-diameter pots by using Metromix-220 (W. R. Grace & Co., Ajax, Ontario, Canada) as a potting medium and fertilized with 20:20:20 (N–P–K) at 0.5 g per pot when plants were 2 to 3 wk old. Four-week-old plants were used for all experiments.

Oviposition Choice and Trichome Density. Ovipositional preference experiments were conducted with *P. xylostella* in a free-choice situation in five screened cages (120 by 120 by 120 cm) by using a completely randomized design, and each cage was considered a replication. One plant from each species and cultivar was placed randomly in each cage, and 40 plants in total were used in the experiment (i.e., eight plants in each cage). Sixteen 1-d-old adults (two moths per plant) were released in 1:1 (male/female) sex ratio in the middle of each cage and provided a 10% sterile honey solution for adult feeding. Eggs on each plant were counted 2 d after moth release. Leaf discs (area, 1.0 cm^2) were taken from five leaves of each species and cultivar (one leaf from each plant), and trichome densities on adaxial and abaxial leaf surfaces were determined using a dissecting microscope.

Effects of Host Plants on Insect Life History Traits. *Whole Plant Study: Survival of P. xylostella.* More than 100 newly emerged *P. xylostella* were caged and allowed to oviposit on tinfoil sheets treated with an extract of *B. napus* leaves. After 24 h, egg sheets were collected, and incubated in individual plastic cups. Survival from neonate to pupa was assessed in screened cages (40 by 40 by 80 cm), arranged on a greenhouse bench in a completely randomized design with each cage considered one replicate. Each cage contained a single plant; the entire experiment used 80 cages with 10 plants from each species and cultivar. Five plants from each genotype were infested with first instars (at 10 larvae per plant), whereas the remaining plants served as uninfested controls. Plants were observed every 48 h, and the numbers of surviving individuals were recorded. Pupae were harvested, weighed, and kept individually in transparent plastic cups until adult emergence.

Leaf Tissue Study: Preimaginal and Imaginal Parameters. This experiment was conducted in controlled environmental conditions in a growth chamber (22 ± 0.5°C with a photoperiod of 16:8 [L:D] h). Excised leaves were placed on moist filter papers (9 cm in diameter) in plastic containers; four holes were poked in each transparent lid to ensure ventilation and to avoid condensation. For each plant genotype, 100 second instars ($\leq$1 d old) taken from the laboratory colony were introduced into individual plastic containers; in total, 800 larvae were used (one larva per container). Larvae were provided with fresh leaf tissue every 24 h until pupation. Developmental times from second instar to prepupa and from prepupa to pupa were recorded. Pupae were harvested, weighed within 24 h of pupation, returned to their respective containers, and developmental times from pupa to adult emergence were recorded. After adult eclosion, the silk cocoons were also weighed using a Sartorius Supermicro scale (Sartorius Inc., Edgewood, NY). Adults were sexed; 20 pairs were used in the longevity (without food), body weight, and forewing area experiments, whereas 10 pairs were used in the oviposition and longevity (with food) experiments.

To quantify levels of larval feeding, all leaves damaged by *P. xylostella* larvae were scanned daily into a digital format by using a desktop scanner (Umax Powerlook 2100XL Flatbed Scanner, UMAX Technologies Inc., Dallas, TX) and the final version (250 dpi) was

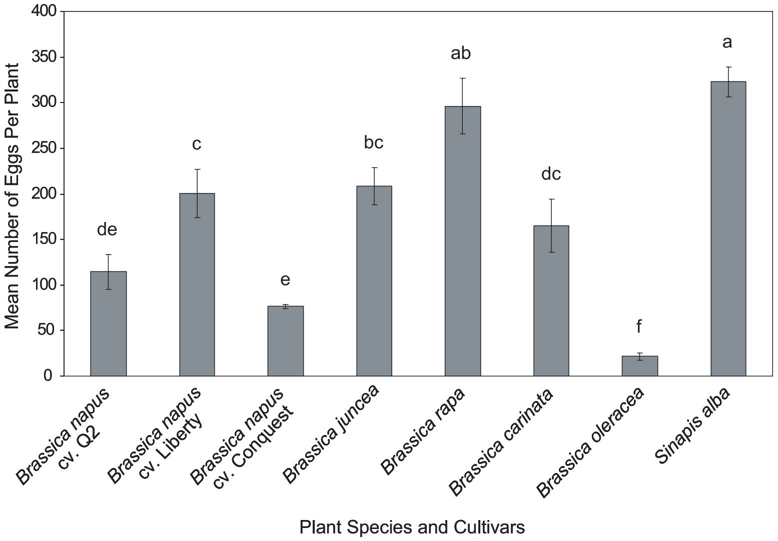

Fig. 1. Ovipositional preference by *Plutella xylostella* in free-choice tests. Means and standard errors are presented; means with different lowercase letters are significantly different from each other (ANOVA and Tukey's mean separation; $P = 0.05$).

saved as a TIFF file without LZW compression. Image J (National Institutes of Health, Bethesda, MD) was used to quantify the amount of leaf area removed due to larval herbivory.

Twenty females and 20 males reared from each plant taxon were used to determine their longevity without food. Moths were weighed within 24 h of their death. Their forewings were carefully removed, scanned using a desktop scanner (Umax Powerlook 2100XL Flatbed Scanner, UMAX Technologies Inc.), and their areas were measured using Image J.

Ten pairs of moths of almost the same age (≤1 d old) reared from each plant taxon were released in individual plastic containers (i.e., one pair per cup) containing *B. napus* Q2 leaf discs (area 52.8 cm^2) placed on moist filter papers. In total, 80 cups were used after a completely randomized design, and this experiment was conducted in the growth chamber (22 ± 0.5°C with a photoperiod of 16:8 [L:D] h) where females were allowed to oviposit over an 8-d period. Eggs on both the leaf disc and off the leaf disc (i.e., filter paper, and walls and lids of containers) were recorded daily. Every 24 h, moths were transferred to new containers and provided with fresh leaf discs and food (10% sterile honey solution). After the 8th day, only females were kept in the containers with a continuous supply of 10% honey solution and observed daily until mortality.

Root Mass Development in Response to Insect Herbivory. At the end of the experiment investigating *P. xylostella* survival on whole plants, infested and uninfested (control) plants were uprooted; their roots were carefully washed, air-dried at room temperature, and weighed to determine the effects of aboveground herbivory on root mass (grams, dry weight basis) development.

Statistical Analyses. Transformations [$(x + 0.5)^{0.5}$, $\ln(x + 1)$] were used as necessary to achieve normality and homoscedasticity before analysis (Steel et al. 1997), but untransformed means are presented. Analyses of variance (ANOVA) (PROC GLM) for a completely randomized design were performed to test the differences between treatments, and means were compared at the 5% level of significance using Tukey's studentized range test (Littell et al. 2002, SAS Institute 2004). Correlation (PROC CORR) was used to contrast oviposition preference and trichome density. Correlations also were determined between pupal weight and silk weight, pupal weight and adult weight, pupal weight and longevity without food, pupal weight and forewing area, adult weight and longevity, and pupal weight and oviposition. *t*-tests (PROC TTEST) were performed for pairwise comparison between female and male specimens for their developmental time, larval herbivory, pupal weight, silk weight, adult body weight, forewing area, and longevity (without food) when they were reared on various Brassicaceae. PROC TTEST also was performed for pairwise comparison between root masses of infested and uninfested (control) plants for each plant genotype separately.

Results

Oviposition Choice and Trichome Density. Plant species and cultivars had significant effects on *P. xylostella* oviposition preference ($F = 44.37$, df = 7, $P < 0.0001$). Oviposition on *S. alba* and *B. rapa* were similar, but numbers of eggs deposited on *S. alba* exceeded other plant genotypes (Fig. 1). Females laid 2.8-, 4.2-, and 14.8-fold more eggs on *S. alba* than on *B. napus* Q2, *B. napus* Conquest, and *B. oleracea*, respectively. *B. juncea*, *B. napus* Liberty, and *B. carinata* plants received 1.5-, 1.6-, and 1.9-fold fewer eggs, respectively, than *S. alba.* Mean numbers of eggs deposited on *B. napus* Q2 were statistically similar to those laid on *B. carinata* and *B. napus* Conquest. Among *B.*

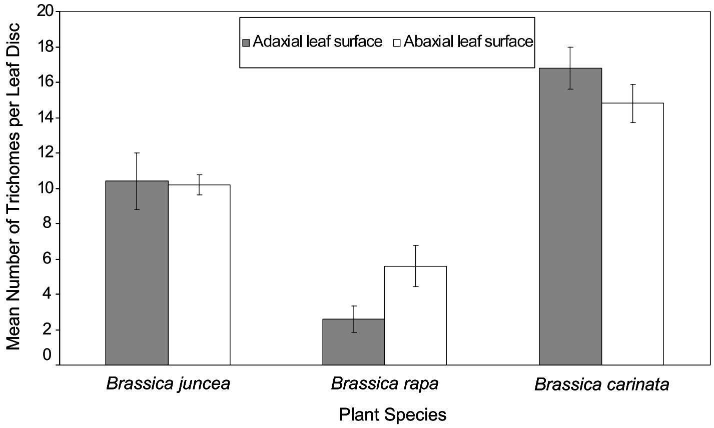

Fig. 2. Trichome density on adaxial and abaxial surface of leaf discs of *Brassica rapa*, *B. juncea*, and *B. carinata*. Means and standard errors are presented. *Brassica napus* Q2, *B. napus* Liberty, *B. napus* Conquest, *B. oleracea*, and *S. alba* are not shown in the figure as they lacked trichomes on the adaxial and abaxial leaf surfaces.

napus cultivars, females deposited 1.7- and 2.6-fold more eggs on Liberty than on Q2 and Conquest, respectively (Fig. 1).

Trichome density varied significantly on adaxial ($F = 95.13$, df = 7, $P < 0.0001$) and abaxial ($F = 126.12$, df = 7, $P < 0.0001$) leaf surfaces among different plant genotypes tested. *B. carinata* had the highest number of trichomes followed by *B. juncea* and *B. rapa* (Fig. 2), whereas *B. napus* Q2, *B. napus* Liberty, *B. napus* Conquest, *B. oleracea,* and *S. alba* lacked trichomes. There was a nonsignificant correlation between oviposition and the overall trichome density ($r = 0.25$, $P = 0.1127$).

Effects of Host Plant Genotypes on Insect Life History Parameters. Survival from neonate to pupa and from pupa to adult was statistically similar on whole plants of all eight Brassicaceae we tested (Table 1). Host plant genotypes significantly affected larval and pupal developmental time of females ($F = 20.67$, df = 7, $P < 0.0001$ and $F = 4.50$, df = 7, $P = 0.0002$, respectively) and males ($F = 29.16$, df = 7, $P < 0.0001$ and $F = 9.92$, df = 7, $P < 0.0001$, respectively). Prepupal developmental time was significantly affected for males ($F = 2.14$, df = 7, $P = 0.0432$), but not for females ($F = 1.97$, df = 7, $P = 0.0633$). Host plants had significant effects on foliage consumption by individual female and male larvae ($F = 7.72$, df = 7, $P < 0.0001$ and $F = 3.12$, df = 7, $P = 0.0045$, respectively). Pupal weight and silk weight differed significantly for females ($F = 28.27$, df = 7, $P < 0.0001$ and $F = 10.88$, df = 7, $P < 0.0001$, respectively) and males ($F = 14.08$, df = 7, $P < 0.0001$ and $F = 8.37$, df = 7, $P < 0.0001$, respectively) when reared on various host plant genotypes. Host plants significantly affected adult body weight, forewing area, and longevity (without food) of females ($F = 21.17$, df = 7, $P < 0.0001$; $F = 10.05$, df = 7, $P < 0.0001$; and $F = 31.24$, df = 7, $P < 0.0001$, respectively) and males ($F = 9.20$, df = 7, $P < 0.0001$; $F = 7.00$, df = 7, $P < 0.0001$; and $F = 7.03$, df = 7, $P < 0.0001$, respectively).

Table 1. Mean percentage of survival (± SE) of *P. xylostella* from neonate to pupa and pupa to adult on whole plants of different Brassicaceae

Host plant genotype	% survival	
	Neonate to pupa	Pupa to adult
B. napus Q2	72.00 ± 3.74a	97.5 ± 2.5a
B. napus Liberty	80.00 ± 8.37a	96.00 ± 2.45a
B. napus Conquest	80.00 ± 4.47a	94.28 ± 3.50a
B. juncea	86.00 ± 4.00a	92.70 ± 4.64a
B. rapa	86.00 ± 6.78a	95.78 ± 2.59a
B. carinata	78.00 ± 7.35a	90.92 ± 3.97a
B. oleracea	69.00 ± 6.78a	91.58 ± 3.55a
S. alba	82.00 ± 4.90a	100.00 ± 0.00a

Means in a column followed by the same letter do not differ significantly ($P = 0.05$) using analysis of variance and Tukey's studentized range test.

Female larval development was fastest on *B. juncea,* whereas male larvae developed faster on *B. napus* Liberty than on other plants we tested. Female and male pupae developed fastest on *S. alba* and *B. napus* Conquest, respectively (Table 2). Both female and male larvae consumed largest leaf area of *B. rapa,* whereas male larvae had least foliage consumption on *B. napus* Liberty. Female and male pupae were lighter in weight on *B. napus* Liberty and *B. oleracea*, respectively, than on other tested plant species and cultivars (Table 2). Female specimens reared on *S. alba* produced more silk than those on other host plants tested. Male specimens reared on *B. napus* Conquest produced significantly more silk than those on *B. juncea* and *B. carinata* (Table 2). Heaviest females were produced on *S. alba*, whereas males were heaviest on *B. napus* Liberty (Table 3). Female moths reared on *B. napus* Conquest had the largest forewings, whereas male moths reared on *B. napus* Liberty had the smallest forewings. Female and male specimens reared on *B. napus* Liberty and *B. oleracea* lived for the shortest time in the absence of food; longevity of females reared on the tested Brassicaceae, however, did not differ significantly when food was provided (Table 3). For female specimens reared on various host plant genotypes, a significant correlation was found be-

Table 2. Mean ± SE developmental time, foliage consumption, pupal weight, and silk weight of *P. xylostella* female and male specimens when reared on leaf tissue of various Brassicaceae

Host plant genotype	Developmental time (d)						Foliage consumed (cm²)		Pupal wt (mg)		Silk wt (mg)	
	Larva to prepupa		Prepupa to pupa		Pupa to adult							
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
B. napus Q2	6.40 ± 0.15a	5.60 ± 0.18dc	1.00 ± 0.00a	0.90 ± 0.05ab	4.30 ± 0.11b	5.30 ± 0.15cd	3.02 ± 0.13b	2.13 ± 0.16ab	7.28 ± 0.06dc	5.52 ± 0.06a	0.26 ± 0.01b	0.21 ± 0.00ab
B. napus Liberty	5.60 ± 0.11bc	4.10 ± 0.12e	0.85 ± 0.05a	1.00 ± 0.00a	4.70 ± 0.11ab	5.70 ± 0.18abc	2.96 ± 0.16b	1.95 ± 0.01b	6.29 ± 0.18e	5.83 ± 0.08a	0.22 ± 0.01b	0.21 ± 0.01ab
B. napus Conquest	5.40 ± 0.18bc	5.80 ± 0.14c	0.95 ± 0.03a	0.80 ± 0.06ab	4.30 ± 0.11b	5.10 ± 0.07d	2.65 ± 0.19b	2.45 ± 0.10ab	7.64 ± 0.14bc	5.84 ± 0.09a	0.26 ± 0.01b	0.24 ± 0.01a
B. juncea	5.00 ± 0.18c	6.10 ± 0.12bc	0.80 ± 0.06a	0.75 ± 0.06b	4.90 ± 0.19a	5.60 ± 0.11bcd	2.54 ± 0.16b	2.24 ± 0.18ab	7.71 ± 0.07bc	5.72 ± 0.03a	0.24 ± 0.01b	0.20 ± 0.00bc
B. rapa	6.50 ± 0.15a	6.50 ± 0.15ab	0.85 ± 0.10a	0.85 ± 0.10ab	4.70 ± 0.15ab	6.20 ± 0.17a	3.75 ± 0.24a	2.56 ± 0.14a	8.04 ± 0.15ab	5.89 ± 0.17a	0.25 ± 0.01b	0.21 ± 0.01ab
B. carinata	6.90 ± 0.19a	6.80 ± 0.22a	0.95 ± 0.03a	0.90 ± 0.05ab	4.40 ± 0.15ab	6.10 ± 0.12ab	2.62 ± 0.03b	2.08 ± 0.09ab	7.60 ± 0.16bc	5.63 ± 0.16a	0.22 ± 0.01b	0.17 ± 0.01c
B. oleracea	6.80 ± 0.14a	6.10 ± 0.16bc	1.05 ± 0.36a	0.95 ± 0.03ab	4.90 ± 0.12a	6.00 ± 0.10ab	3.03 ± 0.09b	2.20 ± 0.07ab	6.93 ± 0.09d	4.62 ± 0.12b	0.24 ± 0.01b	0.22 ± 0.00ab
S. alba	5.70 ± 0.11b	5.10 ± 0.16d	0.90 ± 0.05a	0.90 ± 0.05ab	4.20 ± 0.09b	5.30 ± 0.15cd	2.37 ± 0.11b	1.97 ± 0.16b	8.57 ± 0.14a	5.79 ± 0.11a	0.38 ± 0.04a	0.23 ± 0.01ab

Means in a column followed by the same letter do not differ significantly ($P = 0.05$) using analysis of variance and Tukey's studentized range test.

tween pupal weight and silk weight ($r = 0.43$, $P < 0.0001$), pupal weight and adult weight ($r = 0.50$, $P < 0.0001$), pupal weight and longevity (without food) ($r = 0.60$, $P < 0.0001$), pupal weight and forewing area ($r = 0.50$, $P < 0.0001$), and adult weight and longevity (without food) ($r = 0.45$, $P < 0.0001$). For male specimens, a significant correlation was found between pupal weight and silk weight ($r = 0.21$, $P = 0.0078$), pupal weight and adult weight ($r = 0.27$, $P = 0.0007$), pupal weight and longevity (without food) ($r = 0.40$, $P < 0.0001$), and adult weight and longevity (without food) ($r = 0.19$, $P = 0.0168$), but a nonsignificant correlation existed between pupal weight and forewing area ($r = 0.01$, $P = 0.8542$).

Female and male specimens exhibited significant differences in various life history traits when reared on the same host plant genotype (Table 4). Female pupal development was significantly faster than their male counterparts on all the crucifers tested in this study. In addition, females were heavier and lived longer than males in the absence of food (Table 4).

Over the 8-d oviposition period, females deposited significantly different numbers of total eggs on the leaf discs ($F = 110.96$, df = 7, $P < 0.0001$), total eggs off the leaf discs ($F = 34.74$, df = 7, $P < 0.0001$), and overall eggs (on the discs and off the discs) ($F = 137.37$, df = 7, $P < 0.0001$) when they were raised on the Brassicaceae tested in this study. Females raised on *B. napus* Conquest and *B. juncea* deposited the most total eggs (436.80 ± 6.69 and 401.60 ± 7.51, respectively), whereas females from *B. oleracea* laid the fewest eggs (180.40 ± 6.86). Overall oviposition of females reared on *B. napus* Q2, *B. rapa*, and *B. carinata* did not differ significantly (Table 5). Females reared on *B. napus* Conquest exhibited less discrimination between substrates and deposited the most eggs off the leaf disc followed by females raised on *B. juncea* and *S. alba* (Table 5). A nonsignificant correlation was found between oviposition and pupal weight ($r = 0.11$, $P = 0.3130$).

Root Mass Development in Response to Insect Herbivory. Insect herbivory had a highly significant effect on root mass development in a multiple comparison ($F = 9.42$, df = 15, $P < 0.0001$). Pairwise comparisons for each genotype indicated that infested *B. napus* Q2 ($t = 7.37$, df = 8, $P < 0.0001$), *B. napus* Conquest ($t = 2.97$, df = 8, $P = 0.0179$), *B. rapa* ($t = 12.30$, df = 8, $P < 0.0001$), *B. carinata* ($t = 2.99$, df = 8, $P = 0.0174$), and *S. alba* ($t = 15.90$, df = 8, $P < 0.0001$) had significantly more robust root systems than their uninfested counterparts. However, the root masses of *B. napus* Liberty ($t = 0.84$, df = 8, $P = 0.4245$), *B. juncea* ($t = 0.44$, df = 8, $P = 0.6703$) and *B. oleracea* ($t = -2.20$, df = 8, $P = 0.0587$) did not differ significantly between infested and uninfested plants (Fig. 3).

Discussion

Oviposition Choice and Trichome Density. *S. alba* was the host plant most preferred by *P. xylostella* among the Brassicaceae evaluated and this may be attributed to morphological and chemical properties of the species. For example, *S. alba* has a glossy phylloplane (Justus et

Table 3. Mean (± SE) adult body weight, forewing area, and longevity of female and male *P. xylostella* when reared as larvae on different Brassicaceae

Host plant genotype	Adult body weight (mg)		Forewing area (cm^2)		Longevity without food (d)		Longevity with food (d)
	Female	Male	Female	Male	Female	Male	Female
B. napus Q2	2.58 ± 0.06b	1.54 ± 0.05ab	0.15 ± 0.00bc	0.13 ± 0.00bc	8.20 ± 0.14b	5.40 ± 0.11ab	23.20 ± 0.86a
B. napus Liberty	2.09 ± 0.05c	1.65 ± 0.04a	0.14 ± 0.04c	0.12 ± 0.00c	6.50 ± 0.11d	5.00 ± 0.10bc	24.80 ± 1.62a
B. napus Conquest	2.50 ± 0.07bc	1.24 ± 0.01c	0.17 ± 0.00a	0.15 ± 0.00a	7.30 ± 0.18c	5.80 ± 0.14a	25.20 ± 1.11a
B. juncea	2.35 ± 0.07bc	1.11 ± 0.02c	0.15 ± 0.00bc	0.13 ± 0.00bc	8.10 ± 0.19b	5.50 ± 0.11ab	24.40 ± 1.33a
B. rapa	2.43 ± 0.11bc	1.28 ± 0.07bc	0.16 ± 0.00ab	0.14 ± 0.00ab	8.20 ± 0.14b	5.10 ± 0.24bc	24.60 ± 2.38a
B. carinata	2.41 ± 0.16bc	1.13 ± 0.09c	0.16 ± 0.00ab	0.14 ± 0.00ab	6.90 ± 0.12dc	5.40 ± 0.15ab	25.00 ± 1.18a
B. oleracea	2.35 ± 0.10bc	1.15 ± 0.10c	0.14 ± 0.00c	0.15 ± 0.00a	6.70 ± 0.29dc	4.50 ± 0.11c	22.60 ± 1.21a
S. alba	3.55 ± 0.04a	1.15 ± 0.04c	0.16 ± 0.00ab	0.13 ± 0.00bc	9.50 ± a0.15	5.30 ± ab0.15	24.00 ± 0.084a

Means in a column followed by the same letter do not differ significantly ($P = 0.05$) using analysis of variance and Tukey's studentized range test.

al. 2000), and *P. xylostella* prefers to oviposit on glossy substrates rather than on their nonglossy counterparts (Eigenbrode et al. 1991a,b; Justus et al. 2000; Shelton and Nault 2004). Furthermore, *S. alba* plants contain higher concentrations of aromatic glucosinolates (mainly hydroxybenzyl and benzyl), whereas alkenyl/aliphatic and indolyl glucosinolates predominate in *Brassica* species (Mewis et al. 2002, Sarfraz et al. 2006). *P. xylostella* survival was similar on the Brassicaceae we tested (see Effects of Host Plant Genotypes on Insect Life History Parameters), suggesting that plants such as *S. alba* that received more eggs would have higher larval infestations, and this is in accordance with previous reports. For example, significantly more *P. xylostella* larvae were reported on *S. alba* than on *B. juncea* and *B. napus* under field conditions (Brown et al. 1999). By contrast, *S. alba* plants were less susceptible than other Brassicaceae to infestations by crucifer specialists such as the cabbage maggot, *Delia radicum* (L.) (Diptera: Anthomyiidae) (Dosdall et al. 2000); the flea beetles *Phyllotreta cruciferae* (Goeze) and *Phyllotreta striolata* (F.) (Coleoptera: Chrysomelidae) (Lamb 1984, Bodnaryk and Lamb 1991, Palaniswamy and Lamb 1992); and the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae) (Brown et al. 1999, Kalischuk and Dosdall 2004). These differences in susceptibility are perhaps not surprising because different crucifer specialists are known to vary in their responses to different glucosinolates. For example, indolyl glucosinolates had greater stimulatory effects than aromatic and alkenyl glucosinolates in *Pieris rapae* (L.) (Lepidoptera: Pieridae), *D. radicum,* and *Delia floralis* (Fallén) (Diptera: Anthomyiidae) (Renwick et al. 1992, Simmonds et al. 1994, Roessingh et al. 1997). Some evidence exists that extracts from *S. alba* contained an unknown deterrent for *P. xylostella* oviposition (Reed et al. 1989), but diverse morphologies and chemistries probably override such compounds when whole plants (instead of extracts) of *S. alba* are presented to females along with other Brassicaceae.

Brassica napus Conquest showed higher levels of antixenotic resistance for ovipositing females than *B. napus* Liberty, but *B. napus* Q2 and Conquest were preferred equally for oviposition by *P. xylostella.* There is considerable evidence that differences in resistance can vary significantly among cultivars within the same species (Dosdall et al. 2000, Hamilton et al. 2005). Trichome density on adaxial and abaxial leaf surfaces did not contribute to this difference in resistance, because the *B. napus* cultivars we tested lack trichomes (see Oviposition Choice and Trichome Density). Further research is required to investigate the mechanisms involved in this antixenosis.

We found a nonsignificant correlation between oviposition and overall trichome density, but these results do not support previous reports. For example, a negative relationship was observed between trichome density and *P. xylostella* oviposition on *Arabidopsis thaliana* L. (Handley et al. 2005). By contrast, *P. xylostella* oviposition on Chinese cabbage, *Brassica rapa* L. ssp. *pekinensis* (Lour.) 'New King', was significantly correlated with trichome density (Talekar et al. 1994). We hypothesize that when a range of plant genotypes with diverse morphologies were provided in a choice situation, trichome density as a factor regulating *P. xylostella* oviposition was not of sole importance.

Effects of Host Plants on Insect Life History Traits. Charleston and Kfir (2000) reported that *P. xylostella* larval survival was significantly lower on *B. juncea* than on cabbage, *B. oleracea* variety *capitata;* broccoli, *B. oleracea* variety *italica;* cauliflower, *B. oleracea* variety *Botrytis;* and Chinese cabbage, *B. rapa* ssp. *pekinensis* and suggested that *B. juncea* could be used as trap crop in cabbage-growing regions. Badenes-Perez et al. (2004) concluded that percentage survival from egg to pupation was higher on *B. juncea* than on *B. oleracea,* but our findings indicated that insect survival did not differ among Brassicaceae plants tested. Larval development was faster and females were more fecund on *B. juncea* than on *B. oleracea,* suggesting that *B. juncea* planted along with *B. oleracea* as trap crop could instead serve as a nursery crop for *P. xylostella* in situations where growers are unable to manage pest insects on *B. juncea* in time. Measuring defoliation is a useful tool for evaluating host plant resistance (Jansky et al. 1999), but to our knowledge, no previous study has compared *P. xylostella* herbivory on various Brassicaceae. Our digital analyses demonstrated that *B. rapa* was highly susceptible to larval herbivory, whereas all the other genotypes we tested were equivalent in their resistance in terms of foliage consumption.

Table 4. Pairwise comparison between female and male *P. xylostella* for some key life history parameters when reared on the same host plant genotype

Parameter	*B. napus* Q2		*B. napus* Liberty		*B. napus* Conquest		*B. juncea*		*B. rapa*		*B. carinata*		*B. oleracea*		*S. alba*	
	t	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*T*	*P*	*t*	*P*	*t*	*P*	*t*	*P*
Larval developmental time	3.36	0.0018	8.89	<0.0001	−1.74	0.0893	−5.08	<0.0001	0.00	1.0000	0.34	0.7362	3.31	0.0021	3.13	0.0034
Prepupal developmental time	2.18	0.0356	−2.85	0.0070	2.28	0.0285	0.62	0.5372	0.00	1.0000	0.87	0.3888	1.14	0.2595	0.00	1.0000
Pupal developmental time	−5.54	<0.0001	−4.81	<0.0001	−6.37	<0.0001	−3.16	0.0031	−6.64	<0.0001	−8.67	<0.0001	−6.85	<0.0001	−6.35	<0.0001
Herbivory (per larva)	4.35	<0.0001	6.17	<0.0001	0.98	0.3353	1.27	0.2115	4.30	0.0001	5.69	<0.0001	7.07	<0.0001	2.05	0.0478
Pupal wt	20.13	<0.0001	2.37	0.0231	10.91	<0.0001	26.09	<0.0001	9.23	<0.0001	8.88	<0.0001	15.89	<0.0001	15.23	<0.0001
Silk wt	5.01	<0.0001	1.19	0.2419	1.70	0.0971	5.60	<0.0001	4.24	0.0001	3.69	0.0007	3.52	0.0012	4.05	0.0002
Adult body weight	14.06	<0.0001	6.56	<0.0001	12.86	<0.0001	16.19	<0.0001	8.92	<0.0001	7.01	<0.0001	8.37	<0.0001	41.68	<0.0001
Forewing area	3.28	0.0022	2.29	0.0278	5.03	<0.0001	4.30	0.0001	6.07	<0.0001	3.23	0.0026	−0.58	0.5668	4.47	<0.0001
Adult longevity without food	15.76	<0.0001	9.75	<0.0001	6.64	<0.0001	11.69	<0.0001	11.22	<0.0001	7.65	<0.0001	7.03	<0.0001	19.74	<0.0001

Table 5. Mean ± SE eggs deposited per female of new generation adults reared as larvae on various brassicaceous species and cultivars

Host plant genotype	Oviposition over an 8-d period		
	Eggs on leaf disc	Eggs off leaf disc	Total no. of eggs
B. napus Q2	161.30 ± 8.26c	68.20 ± 9.30dc	229.50 ± 7.40c
B. napus Liberty	201.50 ± 6.73b	74.20 ± 3.52c	275.70 ± 8.45b
B. napus Conquest	310.20 ± 3.80a	126.60 ± 4.29a	436.80 ± 6.69a
B. juncea	302.20 ± 8.47a	99.40 ± 3.36b	401.60 ± 7.51a
B. rapa	151.50 ± 5.97c	60.00 ± 4.45dc	211.50 ± 8.30c
B. carinata	159.70 ± 6.50c	54.40 ± 3.58d	214.10 ± 7.56c
B. oleracea	112.20 ± 5.33d	68.20 ± 3.51dc	180.40 ± 6.86d
S. alba	195.90 ± 5.49b	94.00 ± 6.40b	289.90 ± 2.29b

Means in a column followed by the same letter do not differ significantly ($P = 0.05$) using analysis of variance and Tukey's studentized range test.

Our study indicated that females reared on *S. alba* developed into heavier pupae and produced more silk than on all other host plant genotypes we tested; evidently, heavier pupae will require more silk for better attachment to the substrate. Pupal weight is often considered a good indicator of offspring fitness, because heavier pupae are known to produce larger and more fecund adults than their smaller counterparts (Barah and Sengupta 1991, Armbruster and Hutchinson 2002), but to our knowledge, this has never been reported previously for *P. xylostella.* Our study is the first evidence to suggest that different plant genotypes affect female pupal weights differently, and, in turn, can influence adult body weight, longevity (without food), and forewing area. However, a nonsignificant correlation between pupal weight and forewing area of males suggested that it was the food plant that affected wing size and not the pupal weight. Although oviposition differed significantly among females raised on various host plants, a nonsignificant correlation between pupal weight and oviposition indicated that parameters such as oviposition depend, at least in part, on other environmental factors in addition to host plants. However, food plants affected the oviposition site selection by new generation adults. For example, females reared on *B. napus* Conquest exhibited less discrimination between substrates and deposited the most eggs off the leaf disc compared with females raised on other tested host plants.

Among genotypes we evaluated, greatest levels of overall antibiotic resistance were observed in *B. napus* Liberty and *B. oleracea.* For example, females reared on *B. napus* Liberty had lighter pupal weights, less silk, lighter adult body weights and reduced longevity (without food) compared with other plant genotypes tested. Similarly, *B. oleracea* had higher antibiotic resistance against *P. xylostella* females than *S. alba* as indicated by slower larval and pupal development, lighter pupal weight, less silk, lower body weight, shorter forewings, reduced longevity without food, and reduced reproduction of new generation adults. Such antibiotic effects could cause reductions in fitness of *P. xylostella;* for example, prolonged developmental time could increase the exposure of the insect

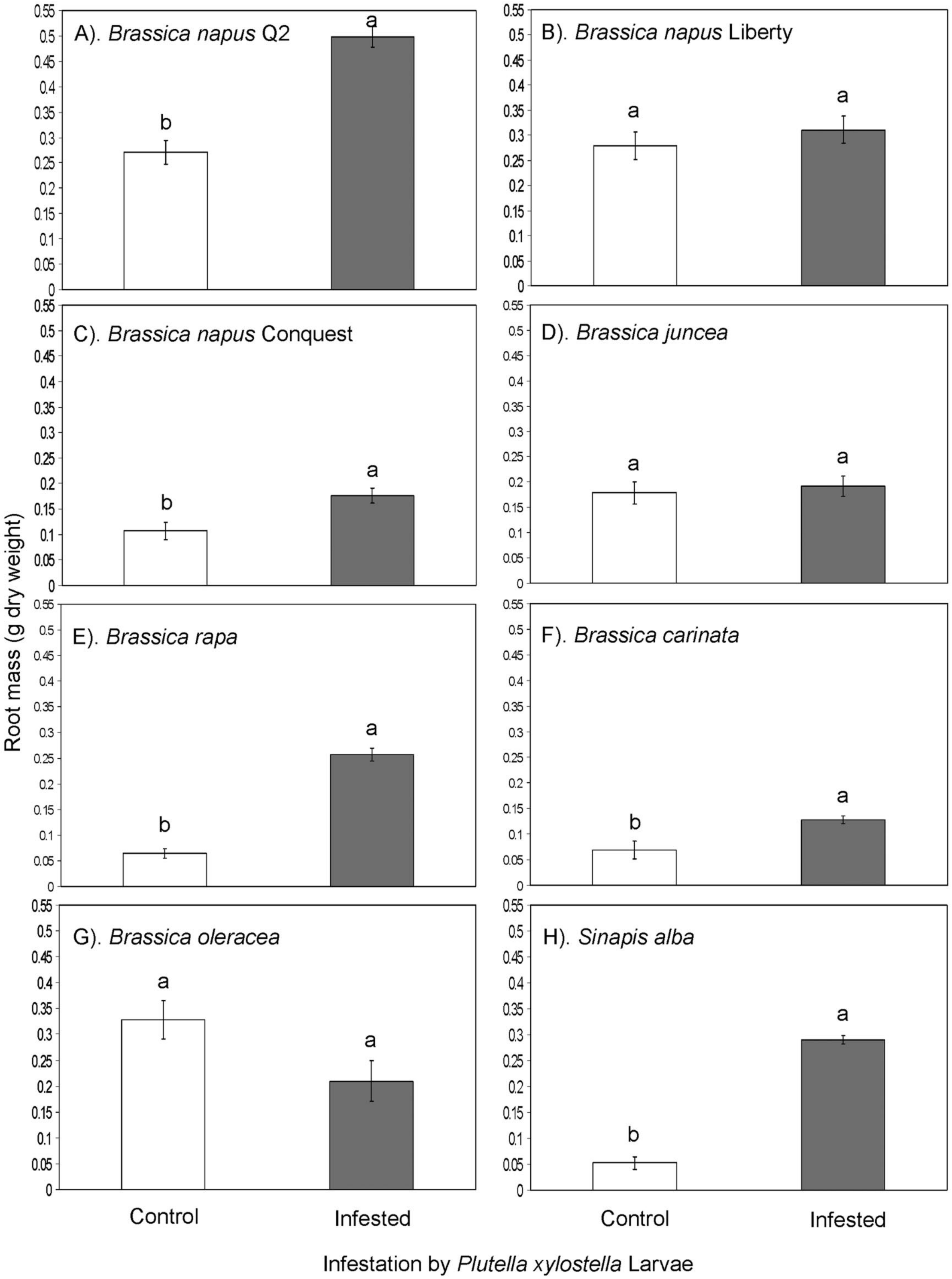

Fig. 3. Root mass development of various Brassicaceae species and cultivars when infested and noninfested by *P. xylostella* larvae. Means and standard errors are presented; in each graph, means with different lowercase letters are significantly different from each other at $P = 0.05$.

to its natural enemies. Reduced longevity when food is limiting could impair reproductive success if females are not in the habitats of favorable host plants. Reduced wing area could also affect fitness. *P. xylostella* adults are highly migratory (Talekar and Shelton 1993, Chapman et al. 2002, Sarfraz et al. 2005b), and moths with larger wings fly more actively than those with smaller wings (Muhamad et al. 1994, Begum et al. 1996). Female moths reared on *B. napus* Liberty and *B. oleracea* had the smallest forewings, suggesting that they would have reduced dispersal capability than those fed on plants such as *B. napus* Conquest, *B. rapa*, *B. carinata,* and *S. alba.*

Root Mass Development in Response to Insect Herbivory. This is the first study to suggest that when under stress from *P. xylostella* herbivory, host plants compensate by increasing their root masses. For example, *B. napus* Q2, *B. napus* Conquest, *B. rapa*, *B. carinate,* and *S. alba* plants infested with *P. xylostella* had significantly more robust root systems that their uninfested counterparts. Greater root mass development in infested plants could enable more efficient extraction from the soil of elements such as nitrogen and sulfur that are required in the defense responses by plants. Plants also can increase their net aboveground productivity when infested (Belsky 1986 and references therein). However, not all Brassicaceae we tested had similar compensatory capabilities: the root masses of *B. napus* Liberty, *B. juncea,* and *B. oleracea* did not differ significantly between infested and uninfested plants (Fig. 3).

In conclusion, comparisons of conventional (*B. napus* Q2) and herbicide-tolerant (*B. napus* Liberty and Conquest) canola cultivars determined that females of *P. xylostella* deposited significantly more eggs on Liberty than on Conquest or Q2. Although our results seem to indicate that *B. napus* Liberty modified to express the *bar* gene also conferred greater susceptibility to ovipositing females, this cannot be concluded from our study. To answer this question would require comparisons of the same *B. napus* germplasm with and without the *bar* gene. However, our results indicate that species and cultivars of Brassicaceae vary considerably in their suitabilities as hosts for *P. xylostella,* and these differences could perhaps be exploited by producers. For example, *B. oleracea* cannot compensate for larval feeding to the level of the other species we evaluated, so it may be appropriate to plant an alternative crop in areas where *P. xylostella* populations annually reach high densities. None of the Brassicaceae we evaluated is a suitable candidate for *P. xylostella* trap cropping. However, *S. alba* plants were highly preferred by ovipositing females, consequently producers of this crop must be especially vigilant in monitoring *P. xylostella* infestations and applying chemical control measures when populations reach economic threshold densities. Finally, the greater propensity for *P. xylostella* females to oviposit on *S. alba* points to an opportunity to genetically modify this crop by introducing genes that express an antibiotic effect. The susceptible host could then become a dead-end trap for *P. xylostella,* and so enhance sustainable management of this pest.

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