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Plant glucosinolate content increases susceptibility to diamondback moth (Lepidoptera:Plutellidae) regardless of its diet

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Abstract. Glucosinolates are plant defense compounds used in host plant recognition by insects specialized on Brassicaceae, such as the diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae). We tested whether there were differences in oviposition and larval survival among three strains of *P. xylostella* after more than 100 generations continuously reared on cabbage leaves, pea leaves, and wheat germ-casein artificial diet. Pea leaves and wheat germ-casein diet contain no glucosinolates. Tests were conducted with a total of 30 different plant species and their glucosinolate contents were determined. Two-choice oviposition tests (comparing each plant type to *Arabidopsis thaliana* L.) and no-choice oviposition tests showed that, regardless of diet, total glucosinolate content and chemical complexity index for glucosinolates were positively correlated with oviposition preference, total oviposition, and larval survival in *P. xylostella* across the wide range of plants tested. Our research shows that long-term feeding on glucosinolate-free diet hardly affects oviposition preference and larval survival in *P. xylostella.* Our study also suggests that, even when comparing different plant species, glucosinolate content is likely to be associated with host-plant preference and host-plant suitability in *P. xylostella*. This indicates that crop varieties with high glucosinolate content are likely to be more susceptible to damage by *P. xylostella* than crop varieties with lower glucosinolate content. Additional implications of these findings for management of this important pest are discussed. This is the first time that a study includes oviposition preference, total oviposition, larval survival, and glucosinolate content across such a wide range of plant species.

Key words: Brassicaceae, Brassicales, glucosinolates, host-plant preference, oviposition, *Plutella xylostella*

Key message

- We conducted this research to study how plant glucosinolate content and diet affect *Plutella xylostella* oviposition and larval survival.
- Two *P. xylostella* strains reared on glucosinolate-free diet and one strain reared on cabbage were tested on 30 different plant species.
- Regardless of diet, *P. xylostella* oviposition and larval survival were positively correlated with glucosinolate content across the plants tested.
- Crop varieties high in glucosinolates are likely to be more susceptible to *P. xylostella* damage than varieties with lower glucosinolate content.

Introduction

Plant chemistry provides some of the most important cues affecting oviposition behavior in Lepidoptera (Renwick and Chew 1994). Plants in the order Brassicales typically contain glucosinolates, which are used, among other functions, for plant defense (Fahey et al. 2001; Halkier and Gershenzon 2006; Mithen et al. 2010). The main defense mechanism of glucosinolates occurs when they are hydrolyzed by myrosinases upon plant damage, producing compounds that can be toxic to insects, such as isothiocyanates (Bones and Rossiter 1996; Hopkins et al. 2009). However, larvae of the diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), have sulfatases that allow them to desulphate glucosinolates and avoid glucosinolate hydrolysis (Ratzka et al. 2002). For this specialist insect, glucosinolates act as host recognition cues (Badenes-Pérez et al. 2011; Gupta and Thorsteinson 1960a; Møldrup et al. 2012; Sun et al. 2009). Aliphatic, benzenic, and indolic glucosinolates have been shown to be active as oviposition stimulants for *P. xylostella* (Badenes-Pérez et al. 2011; Badenes-Pérez et al. 2010; Møldrup et al. 2012; Sun et al. 2009). Isothiocyanates derived from glucosinolates with sulfur-containing side chains have also been shown to be active as oviposition stimulants for *P. xylostella* (Renwick et al. 2006).

When comparing plants of the same species with different glucosinolate content, experiments conducted with *Arabidopsis thaliana* L., *Barbarea vulgaris* R. Br., and *Brassica napus* L. (Brassicaceae), have shown that *P. xylostella* prefers to oviposit on plants and leaves with high glucosinolate content (Badenes-Pérez et al. 2014; Marazzi and Städler 2004; Sun et al. 2009). Furthermore, in field experiments, larvae of *P. xylostella* were more abundant in lines of *A. thaliana* and *Brassica oleracea* L. with higher glucosinolate content (Bidart-Bouzat and Kliebenstein 2008; Kos et al. 2011). Other studies with *A. thaliana* and *B. oleracea* have found that performance of *P. xylostella* larvae could not be explained by plant glucosinolate content (Mosleh Arany et al. 2008; Müller et al. 2010; Poelman et al. 2008; Sarosh et al. 2010). Another study conducted with *Brassica rapa* L. found that herbivory by *P. xylostella* larvae increased with glucosinolate content until reaching an intermediate maximum, decreasing thereafter (Siemens and Mitchell-Olds 1996).

Plutella xylostella can also oviposit and survive on certain plants outside the order Brassicales that lack glucosinolates and are not its usual host-plants (Gupta and Thorsteinson 1960a; Gupta and Thorsteinson 1960b). For example, in Kenya, *P. xylostella* was found feeding on pea, *Pisum sativum* L. (Fabaceae), next to a cabbage field heavily infested by this insect (Löhr and Gathu 2002). Host-plant preference and host-plant use can also be affected by previous experience (Proffit et al. 2015; Ryan and Bidart-Bouzat 2014). In *P. xylostella*, prior experience contributes to induce oviposition on non-host plants (Wang et al. 2008; Zhang and Liu 2006; Zhang et al. 2007).

To our knowledge, studies addressing the association between host-plant glucosinolate content and preference by *P. xylostella* have been conducted comparing plants of the same or closely-related species. Further research with a wide range of glucosinolate-containing plant species is necessary to study the overall importance of glucosinolates in determining host-plant preference and host-plant suitability in *P. xylostella*. Here, using a wide range of plants, we compare three different *P. xylostella* strains, one reared on cabbage and two reared on glucosinolate-free diets (either artificial wheat-casein diet or pea leaves), to investigate the importance of glucosinolate content in oviposition behavior and larval survival, and to test whether *P. xylostella* loses its ability to use glucosinolates in host-plant preference and host-plant use after many generations of feeding on glucosinolate-free diets.

Materials and methods

Culture of plants and *Plutella xylostella* strains

Plants were selected from all different clades included in the Brassicaceae (Beilstein et al. 2008; Huang et al. 2016). Among the 30 plant species tested, 20 belonged to 11 different subfamilies within the family Brassicaceae (order Brassicales), and 7 belonged to the Brassicales order, but were in the families Caricaceae, Cleomaceae, Gyrostemonaceae, Limnanthaceae, Moringaceae, Resedaceae, and Tropaeolaceae (Bailey et al. 2006) (Table 1). Additionally, 3 plant species belonging to the families Fabaceae (order Fabales) and Phytolaccaceae (order Caryophyllales) were used as control plants without glucosinolates: *Phytolacca americana* L., *Pisum sativum* cultivar Oregon Sugar Pod, and *Vicia faba* L. cultivar Aguadulce. *Pisum sativum* was used because one of the *P. xylostella* strains used was reared on this plant. *Vicia faba* was used as a control without glucosinolates because it is known not to be a host for *P. xylostella* (Badenes-Pérez et al. 2005). Seeds of wild-type *A. thaliana* landrace Columbia-0 were obtained from the European Arabidopsis Stock Center in Nottingham University, Loughborough, UK. Seeds of *Alyssum argenteum* All. were purchased from Jelitto (Schwarmstedt, Germany). *Brassica napus* and *Nasturtium officinale* W. T. Aiton seeds were purchased from Rieger-Hofmann GmbH (Blaufelden-Raboldshausen, Germany). Two different *B. oleracea* varieties were tested, var. *capitata* (i.e., cabbage), cultivar Gloria, and var. *acephala* (i.e., collards), cultivar Green Glaze. Seeds of Green Glaze collards, purchased from Pennington Seed (Madison, GA, US), produce glossy and waxy phenotypes, both of which were tested in our experiments. Seeds of *Cardamine pratensis* L. and *Iberis amara* L. were purchased from Rühlemann´s (Horstedt, Germany). G-type *Barbarea vulgaris* seeds were donated to us by Dr. Niels Agerbirk. All other seeds were purchased from B & T World Seeds (Aigues-Vives, France). Among the plants tested, the *Brassica* spp., *C. papaya*, *M. oleifera*, *P. sativum*, and *V. faba*, were cultivated varieties, while the other plant species were wild. *Arabidopsis thaliana* plants were grown in a climate chamber in short-day conditions to favor plant vegetative growth before bolting (10:14 h light:dark, 21 ± 2º C and 55 ± 5 RH). The rest of the plants used in the experiments were grown in the greenhouse (16:8 h light:dark, 25 ± 3º C). Plants were grown in 7x7x8-cm pots using a peat moss substrate with clay and were fertilized fortnightly with an all-purpose fertilizer (Ferty® 3, Planta Düngemittel GmbH, Regenstauff, Germany). Plants were 5- to 6-wk old at the beginning of the experiments.

Three different strains of *P. xylostella* were used in the experiments. One strain (DBM-C) was collected in a cabbage field in Kenya in 2002 and since then was continually reared on cabbage. Another strain (DBM-G88) was collected in 1988 in Geneva, NY, US, and since then was reared on a wheat germ-casein artificial diet (Shelton et al. 1991). The third strain (DBM-P) was collected in a pea field in Kenya in 2000 and was since then successively reared on pea plants (Löhr and Gathu 2002). Insects of the strains DBM-C and DBM-P were donated to us by Dr. Bernhard Löhr, while insects of the strain DBM-G88 were donated to us by Dr. Anthony Shelton. Insects were reared in environmental growth chambers (16:8 h light:dark, 21 ± 2º C and 55 ± 5 RH). Throughout the experiments, the number of individuals of each strain were always > 250. In the conditions in which they were reared, the three strains of *P. xylostella* completed at least 14 generations per year. Before carrying out the experiments described here, insects reared on glucosinolate-free diet were continuously feeding exclusively on artificial diet for more than 275 generations in the case of DBM-G88, and on *P. sativum* Oregon Sugar Pod plants for more than 100 generations in the case of DBM-P.

Analysis of glucosinolates in the plants tested

Whole plants were harvested (only above-ground plant material was analyzed) and after freeze-drying, glucosinolate content was analyzed as in Badenes-Perez et al. (2010). The procedure included extraction of glucosinolates with room-temperature 80% aqueous methanol containing 4-hydroxybenzylglucosinolate as an internal standard, binding intact glucosinolates to diethylaminoethyl Sephadex columns, treatment with sulfatase, and elution of desulfoglucosinolates. In plant species containing 4-hydroxybenzylglucosinolate, allylglucosinolate was used as an internal standard. Desulfoglucosinolates were separated on reversed-phase chromatography and quantified with a diode array detector at 229 nm (Agilent 1100 HPLC system, Agilent Technologies, Waldbronn, Germany), using a relative response factor of 2.0 and 0.5 for aliphatic and indolic glucosinolates, respectively. We used a relative response factor of 1.0 for the arabinobenzyl, hydroxybenzyl, and methoxybenzyl glucosinolates (the ones most similar to the internal standard), and a relative response factor of 2.0 for the other benzenic glucosinolates. Although there is some error associated with the methodology to determine the relative response factors of glucosinolates, using rounded response factors based on previous studies (Brown et al. 2003; Buchner 1987) is often used as an estimation of the true glucosinolate content in plants (Clarke 2010; Grosser and van Dam 2017). Support in the elucidation of glucosinolate structures was provided by a LC-ESI-IonTrap-MS using a Bruker Esquire 6000 ion trap mass spectrometer (Bruker Daltonics, Bremen, Germany). Further structure confirmation with NMR was necessary in the case of three glucosinolates (3-methoxybenzyl, 3-(hydroxymethyl)pentyl, and 1-methylpropylglucosinolate). NMR spectra were recorded on a Bruker AV500 spectrometer (Bruker Biospin, Rheinstetten, Germany) (Knill et al. 2009). The identities of 3-methylpentylglucosinolate in *C. pratensis,* and of dimeric 4-mercaptobutylglucosinolate and 4-(β-D-glucopyranosyldisulfanyl)butylglucosinolate in *D. muralis* and *E. sativa* were based on previous studies on the glucosinolate content of these plant species (Agerbirk et al. 2010; D'Antuono et al. 2008; Kim et al. 2004). Between 3 and 26 plants of each type were analyzed to determine their glucosinolate content. The highest number of plants analysed (26) was in *A. thaliana* because this was the species most used given that it was the reference species in the two-choice oviposition experiments. This minimum of 3 plants appeared reasonable based on the large amount of plant species included in the study. Glucosinolates were grouped into four chemical classes: aliphatic with sulfur-containing side chains, other aliphatic, benzenic, and indolic. As different glucosinolate types can have either similar or different effects on the oviposition and herbivory of insects specialized on glucosinolate-containing plants (De Vos et al. 2008; Müller 2009; Müller et al. 2010; Sun et al. 2009), we also took into account the effect of the diversity of glucosinolates in each plant species. For this purpose we used the number of different glucosinolates per plant species (glucosinolate richness, *S*) and a chemical chemical complexity index for glucosinolates (CCI) (Becerra et al. 2009; Cacho et al. 2015). The CCI was calculated as the sum of the Shannon´s diversity index from the four chemical classes of glucosinolates (H_A) and the Shannon´s diversity index from the relative concentrations of all individual glucosinolates (H_B) (Becerra et al. 2009). In those cases in which plants contained no glucosinolates and H_A and H_B could not be calculated, their CCI was given a zero value.

Oviposition experiments

Oviposition experiments were conducted in a two-choice fashion in comparison with *A. thaliana* (i.e., one plant of any of the tested types versus one plant of *A. thaliana*) to measure oviposition preference and in a no-choice fashion (i.e., one plant alone) to measure total oviposition (TO). *Arabidopsis thaliana* was chosen as a reference in the two-choice tests because it is the most-widely used model plant, it is easily available, and it contains glucosinolates that have been well-studied. The experimental arenas were 32.5 x 32.5 x 32.5 cm polyester cages with 96 x 26 mesh (MegaView Science Education Services Co., Ltd., Taichung, Taiwan). Multiple cages were used, each of which was considered a replicate. Two pairs of moths (two females and two males, < 3 days old) were released in each cage. To provide a food source for moths, a small plastic cup with a 10 % sugar solution on cotton was placed in the middle of each cage. The experiment was replicated at least three times for each insect strain and plant comparison. Two days after releasing the moths, the number of eggs on each plant was counted in the laboratory. In the two-choice tests, we used an oviposition preference index (OPI), which we calculated as the number of eggs laid on each individual plant divided by the number of eggs laid on the *A. thaliana* plant that it was compared with in the same cage. An OPI = 1 indicated no difference in oviposition preference between *A. thaliana* and the alternative plant species it was compared with; an OPI < 1 indicated that *A. thaliana* would tend to be preferred; and an OPI > 1 indicated that *P. xylostella* would tend to prefer the alternative plant species over *A. thaliana*.

Larval survival experiments

Larval survival experiments with whole plants were conducted with DBM-C and DBM-P larvae. Since the DBM-G88 strain was reared on artificial diet and not on plants, we did not test larval survival in this strain to avoid possible confounding effects between the lack of adaptation to plants and the effect of plant glucosinolate content. Five first-instar *P. xylostella* larvae (<2 d after hatching) were randomly placed on five fully-expanded leaves within each plant. The same procedure was repeated on three plants (n=3) for each plant type. When necessary, in case of extensive defoliation of a plant, larvae were transferred to a new plant of the same age. To prevent larval movement between plants, plants were kept individually in either 32.5 x 32.5 x 32.5 cm cages with 96 x 26 mesh (MegaView Science Education Services Co., Ltd., Taichung, Taiwan) or in larger 61 x 61 x 61 cm cages with 32 x 32 mesh (BioQuip Products, Rancho Dominguez, US). Larval survival was recorded as percentage of individuals that reached pupation per plant.

Statistical analyses

For each plant species, oviposition preference index (OPI) and total oviposition (TO) differences among the three *P. xylostella* strains were analyzed using a Kruskal-Wallis test ($P \leq 0.05$) with SPSS® version 24 (IBM 2017). For each *P. xylostella* strain, data comparing oviposition preference between the different plant types and *A. thaliana* were analyzed using a one-tailed, two-sample test of proportions using STATA® version 14.2 (StataCorp 2015) with significance at $P \leq 0.05$. Differences in larval survival among the three *P. xylostella* strains were also analyzed using a one-tailed, two-sample test of proportions with significance at $P \leq 0.05$. Kruskal-Wallis tests and tests of proportions were performed with untransformed data. Correlations between oviposition, larval survival, and glucosinolate content were performed using one-tailed Spearman´s correlation with SPSS®. Categorical Principal Component Analysis (CATPCA) was done with SPSS® to explore the relationships between glucosinolate content and oviposition and larval survival for each of the *P. xylostella* strains. After the exploratory use of CATPCA, to confirm the effect of glucosinolate content, *P. xylostella* strain, and glucosinolate diversity, on OPI, TO, and larval survival, we used a generalized linear model with a Tweedie probability distribution with log link function by means of the GENLIN procedure SPSS®. This model was chosen after plotting the data and checking that it was the model giving the lowest Akaike information criterion values compared to other models (Poisson and negative binomial). The significance of the variables in the model was assessed using Wald Chi-square tests. Indolic glucosinolates, which were present in the lowest concentrations in the plants tested, were not included in the model because they were negatively correlated to benzenic glucosinolates, which were the glucosinolates present in the highest concentrations in the plants tested (Fig. S1). Prior to performing Spearman´s correlations, CATPCA, and GENLIN analysis, aggregated means were calculated regarding glucosinolate content for each plant type, and regarding OPI, TO, and larval survival for each *P. xylostella* strain. These data were transformed adding 1.0 to all values of each of the variables in order to avoid zero values before GENLIN and CATPCA analysis.

Results

Analysis of glucosinolates in the plants tested

The glucosinolates found in the plants analyzed are shown in Tables 2 and 3. The 38 glucosinolates that we found in these plants included 14 aliphatic glucosinolates with sulfur-containing side chains, 9 other aliphatic glucosinolates, 11 benzenic glucosinolates, and 4 indolic glucosinolates. The indices of glucosinolate diversity in each plant type (S, H_A, H_B, and CCI) are shown in Table 4. Overall, when analyzing the average glucosinolate content of all the plants combined, benzenic glucosinolates were the most abundant glucosinolates in the plants analyzed (12.27 ± 4.82, n=32), followed by other aliphatic glucosinolates (6.88 ± 3.28, n=32), and aliphatic glucosinolates with sulfur-containing side chains (6.55 ± 2.26, n=32) (Table 3, Fig. S2). Benzenic glucosinolates were, thus, the most closely associated with total glucosinolate content (Fig. S2, Tables S1, S2). Content of benzenic glucosinolates was, however, either negatively correlated or not correlated with S, CCI, indolic glucosinolate content, and content of aliphatic glucosinolates with sulfur-containing side chains (Figs. S1, S2, Tables S1, S2). Thus, in the plants analyzed, presence of benzenic glucosinolates was associated with high total glucosinolate content, low content of indolic glucosinolates, low content of aliphatic glucosinolates with sulfur-containing side chains, and low values of S and CCI (low glucosinolate diversity). Aliphatic glucosinolates with sulfur-containing side chains were positively correlated with S and CCI, but their association with indolic and other aliphatic glucosinolates was not significant. Indolic glucosinolates were positively correlated with other aliphatic glucosinolates, and with *S* and CCI. Overall, when analyzing the average glucosinolate content of all the plants combined, indolic glucosinolates were the ones present in the smallest amounts, but the most widespread in the plant species analyzed. The three most widespread glucosinolates in the plant species analyzed were 4-hydroxyindol-3-ylmethylglucosinolate (4-hydroxyglucobrassicin), 4-methoxyindol-3-ylmethyl (4-methoxyglucobrassicin), and indol-3-ylmethylglucosinolate (glucobrassicin).

Oviposition experiments

Two-choice tests

When comparing the three *P. xylostella* strains, there were no significant differences in oviposition preference indices (OPI) ($P = 0.658$) (Tables 5, S4). When analyzing each strain separately in the comparisons with *A. thaliana*, if there were significant differences in oviposition preference, the preferred plant was *A. thaliana*, except in one case, in which *S. officinale* was preferred over *A. thaliana* by DBM-C (Table 5). For the three *P. xylostella* strains, total glucosinolate content, content of benzenic glucosinolates, content of aliphatic glucosinolates without sulfur-containing side chains, and CCI, had a significant positive effect on OPI (Figs. 1, 2A, Tables S3, S4).

No-choice tests

When comparing the three *P. xylostella* strains, there were significant differences in total oviposition (TO) ($P = 0.017$) and across all the plants tested, TO was lowest for DBM-P (Tables 6, S4). When comparing the three *P. xylostella* strains for each plant, there were significant differences in total oviposition (TO) for *C. bursa-pastoris*, *E. cheiri*, and *L. sativum* using Kruskal-Wallis tests (Table 6). There was a significant positive correlation between TO and OPI ($P \leq 0.001$) (Table S3). For the three *P. xylostella* strains tested, there was a significant positive correlation between TO and total glucosinolate content, content of benzenic glucosinolates, content of aliphatic glucosinolates without sulfur-containing side chains, and CCI (Figs. 1, 2B, Tables S3, S4).

Larval survival experiments

When comparing the two *P. xylostella* strains tested for larval survival on the different plants, there were no significant differences in larval survival between them ($P = 0.971$) (Tables 7, S4). For the two strains of *P. xylostella* in which larval survival was studied (DBM-C and DBM-P), there was a highly significant positive correlation between larval survival on the plants tested and both OPI and TO ($P \leq 0.001$) (Fig. 2, Table S3). In these two strains, there was also a significant positive correlation between larval survival and total glucosinolate content, content of benzenic glucosinolates, content of aliphatic glucosinolates without sulfur-containing side chains, and CCI ($P \leq 0.05$) (Fig. 1, Tables S3, S4).

Discussion

The main purpose of this study was to study how plant glucosinolate content affected susceptibility to *P. xylostella*, measured as oviposition preference and larval survival, under three different diets, two of which lacked glucosinolates. Our research shows that, overall, long-term absence of glucosinolates in the diet of *P. xylostella*, an insect specialized on glucosinolate-containing plants, hardly affects oviposition preference and larval survival. Despite feeding on glucosinolate-free diet for more than 100 generations, DBM-G88 and DBM-P behaved similarly to DBM-C, and their oviposition and larval survival was positively correlated with total glucosinolate content and CCI. This indicates that in *P. xylostella* there is a strong selection for ovipositing on plants with glucosinolates and that glucosinolate sulfatases in *P. xylostella* are not lost after so many generations unused. This also indicates that in *P. xylostella* preimaginal conditioning does not seem to significantly affect adult host-plant choice, as it has also been shown in other insects as opposed to what would be expected from the Hopkins’ host-selection principle (Barron 2001). Studies with the mustard leaf beetle, *Phaedon cochleariae* F. (Coleoptera: Chrysomelidae), an insect specialized in crucifers, also showed no changes in host-plant preference behavior after 10-40 generations being reared on less preferred plants (Kühnle and Müller 2011a; Kühnle and Müller 2011b). The only difference that we could detect among strains is that, overall, total oviposition in DBM-P was lower than in DBM-C and DBM-G88.

The plants involved in this study showed a wide range of glucosinolates that included approximately one fourth of the 142 glucosinolates documented so far (Agerbirk and Olsen 2012; Fahey et al. 2001; Olsen et al. 2016). We did not find any glucosinolates in two of the Brassicaceae species analyzed (*C. bursa-pastoris* and *N. paniculata*), although these species are reported to contain small amounts of glucosinolates (Kjær and Schuster 1972; Okamura et al. 2016). In *L. douglasii*, previous studies reported only the presence of *m*-methoxybenzylglucosinolate (Ettlinger and Lundeen 1956). We confirmed the identity of this glucosinolate based on NMR analysis of the intact glucosinolate, and our data were similar to the NMR data given for 3-methoxybenzylglucosinolate (glucolimnanthin) in a study conducted with *Limnanthes alba* Benth. (Stevens et al. 2009). Besides 3-methoxybenzylglucosinolate as the dominant glucosinolate in *L. douglasii*, we also found 3-hydroxybenzylglucosinolate (glucolepigramin), 4-hydroxyindol-3-ylmethylglucosinolate (4-hydroxyglucobrassicin), and 1-methoxyindol-3-ylmethylglucosinolate (neoglucobrassicin). For *C. cotinifolius*, a previous report indicated only the presence of butylglucosinolate (Bottomley and White 1950). We instead found indol-3-yl-methylglucosinolate as the dominant glucosinolate, followed by 1-methylpropylglucosinolate, 4-hydroxyindol-3-ylmethylglucosinolate, and 1-methoxyindol-3-ylmethylglucosinolate. The benzenic glucosinolates found in some of the plants analyzed, such as 2-phenylethyl- and 2-hydroxy-2-phenylethylglucosinolate, can differ in their production of isothiocyanates and other glucosinolate hydrolysis products (Müller et al. 2018; Pagnotta et al. 2017). However, since feeding by *P. xylostella* circumvents glucosinolate hydrolysis (Ratzka et al. 2002) and we used intact plants in the oviposition bioassays, glucosinolate hydrolysis products should not have played a significant role in the results. Overall, benzenic and aliphatic glucosinolates without sulfur-containing side chains, the most abundant glucosinolates in the plants analyzed, were the most likely to have a significant effect on *P. xylostella* oviposition and larval survival.

Glucosinolates are not the only factors affecting oviposition in *P. xylostella* (Renwick et al. 2006; Sarfraz et al. 2006). Trichome density has also been shown to affect oviposition preference (Handley et al. 2005), while waxes act synergistically with glucosinolates, increasing *P. xylostella* oviposition (Spencer et al. 1999). Glossy cultivars with low amounts of wax on their leaves are preferred by ovipositing *P. xylostella* over waxy cultivars despite lower survival of its larvae (Badenes-Pérez et al. 2004; Eigenbrode and Shelton 1992; Lin et al. 1984; Stoner 1990). However, our study shows that the same type of glossy collards that were preferred by ovipositing *P. xylostella* over waxy plants in Badenes-Pérez et al. 2004 also contain higher glucosinolate content than the waxy collards. Thus, although the oviposition preference of *P. xylostella* for glossy plants has been associated with low amounts of wax (Lin et al. 1984), higher glucosinolate content is also likely to influence this preference. For *P. xylostella* larvae, in addition to glucosinolates, flavonoids from *Brassica oleracea* have also been shown to act as feeding stimulants, while saponins in *B. vulgaris* are associated with feeding deterrence (Agerbirk et al. 2003; Shinoda et al. 2002; van Loon et al. 2002).

Plutella xylostella is a synovigenic species, for which oogenesis can change depending on the host-plant to which females are exposed (Badenes-Pérez et al. 2006). In this study we also show that different host-plants with different glucosinolate content can affect not only oviposition preference, but also total oviposition. In non-preferred plant types without glucosinolates, such as pea, oviposition was very low, even in the DBM-P strain and in a no-choice situation. Even if the insect is able to survive on plants without glucosinolates, the low oviposition on them is likely to result in reduced population growth of the insect.

In our study there was a positive correlation between oviposition preference and larval performance for both DBM-C and DBM-P. This preference-performance correlation has been shown for *P. xylostella* based on studies with 23 different plant types, mainly *Cardamine* and *Brassica* spp. (Zhang et al. 2012). This `mother knows best´ principle is considered to be particularly strong in oligophagous insects (Gripenberg et al. 2010), such as *P. xylostella*. *Limnanthes douglasii* has not been reported as a host-plant for *P. xylostella*, but it appears to be a very attractive and suitable host-plant for this insect. Most of the other plants used in this study have already been reported as host-plants for *P. xylostella* (Newman et al. 2016; Sarfraz et al. 2011; Sarfraz et al. 2010; Talekar and Shelton 1993).

We used a wide range of plant species with different glucosinolate profiles in this study, and so could not compare the effect of individual glucosinolate variation on *P.*

xylostella oviposition and larval survival. However, in studies of different lines of *B. oleracea* with different concentrations of individual glucosinolates, the content of certain individual glucosinolates has been associated with feeding suitability and abundance of *P. xylostella* larvae (Kos et al. 2011; Robin et al. 2017; Santolamazza-Carbone et al. 2014). As glucosinolates can be induced as a result of herbivory, including feeding by *P. xylostella* larvae (Badenes-Pérez et al. 2013; Gols et al. 2008; Textor and Gershenzon 2009), glucosinolate content is likely to have changed during the larval survival experiments compared to the glucosinolate data presented here for intact plants. Our glucosinolate results refer particularly to plants 5-6 weeks old. Ontogenetical changes in glucosinolate content can vary among species, and in the case of annual species, these changes can be very drastic with the onset of reproduction (Boege et al. 2007; Brown et al. 2003).

To our knowledge, this is the first time that a study combines oviposition preference, total oviposition, larval survival, and glucosinolate content across such a large number of plant species. Although in particular comparisons plants with higher glucosinolate content were not necessarily the preferred hosts of *P. xylostella*, in general, glucosinolate content was correlated with oviposition preference, total oviposition, and larval survival. This indicates that, even when comparing different plant species, glucosinolate content is likely to be associated with plant susceptibility to *P. xylostella*, at least with the plants tested here and possibly also with others.

Plutella xylostella is considered one of the most damaging insect pests of cruciferous crops worldwide (Furlong et al. 2013; Zalucki et al. 2012). Even though glucosinolates can provide resistance against generalist herbivores (Jeschke et al. 2017; Rohr et al. 2011; Santolamazza-Carbone et al. 2016), and are considered healthy compounds (Cartea and Velasco 2008; Verkerk et al. 2009), in areas of high incidence of *P. xylostella*, use of crop varieties with low glucosinolate content could reduce *P. xylostella* damage. Even if *P. xylostella* develops on crops with low glucosinolate content, neighboring crops with higher glucosinolate content are likely to be more attractive and susceptible to *P. xylostella* damage. Conversely, when searching for trap crops highly attractive for *P. xylostella*, trap crops with high glucosinolate content are likely to be more effective.

Author contribution statement

FRBP, JG, and DGH conceived and designed the research. FRBP conducted the experiments, analyzed the data, and wrote the paper. JG and DGH provided comments and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical statement This article does not describe any studies that involve human participants. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Table 1. Taxonomy of the plants used in the experiments. Except for *V. faba* and *P. sativum*, which belong to the order Fabales, and *P. americana*, which belongs to the order Caryophyllales, all plants tested belong to the order Brassicales (Bailey et al. 2006).

Family	Subfamily	Species	Common name
Brassicaceae	Aethionemeae	*Aethionema cordifolium* DC.	Lebanon stone cress
Brassicaceae	Alysseae	*Alyssum argenteum* All.	Yellow tuft
Brassicaceae	Camelineae	*Arabidopsis thaliana* (L.) Heynh.	Thale cress
Brassicaceae	Arabideae	*Arabis caucasica* Willd.	Mountain rock cress
Brassicaceae	Cardamineae	*Barbarea vulgaris* R.Br.	Wintercress
Brassicaceae	Biscutelleae	*Biscutella laevigata* L.	Buckler mustard
Brassicaceae	Brassiceae	*Brassica juncea* (L.) Czern.	Indian mustard
Brassicaceae	Brassiceae	*Brassica napus* L.	Canola
Brassicaceae	Brassiceae	*Brassica oleracea* var. *capitata* L.	Cabbage
Brassicaceae	Brassiceae	*Brassica oleracea* var. *acephala* L.	Glossy collard greens
Brassicaceae	Brassiceae	*Brassica oleracea* var. *acephala* L.	Waxy collard greens
Brassicaceae	Euclidieae	*Bunias orientalis* L.	Turkish rocket
Brassicaceae	Camelineae	*Capsella bursa-pastoris* (L.) Medik.	Shepherd´s purse
Brassicaceae	Cardamineae	*Cardamine pratensis* L.	Cuckoo flower
Brassicaceae	Brassiceae	*Diplotaxis muralis* (L.) DC.	Annual wall rocket
Brassicaceae	Brassiceae	*Eruca sativa* Mill.	Arugula, rucola
Brassicaceae	Camelineae	*Erysimum cheiri* (L.) Crantz	Wallflower
Brassicaceae	Iberideae	*Iberis amara* L.	Bitter candytuft
Brassicaceae	Lepidieae	*Lepidium sativum* L.	Garden cress
Brassicaceae	Camelineae	*Neslia paniculata* (L.) Desv.	Ball mustard
Brassicaceae	Cardamineae	*Nasturtium officinale* W. T. Aiton	Watercress
Brassicaceae	Sisymbrieae	*Sisymbrium officinale* (L.) Scop.	Hedge mustard
Caricaceae	-	*Carica papaya* L.	Papaya
Cleomaceae	-	*Cleome spinosa* L.	Spider flower
Fabaceae	-	*Pisum sativum* L.	Pea
Fabaceae	-	*Vicia faba* L.	Faba bean
Gyrostemonaceae	-	*Codonocarpus cotinifolius* (Desf.) F.Muell.	Bell-fruit tree
Limnanthaceae	-	*Limnanthes douglasii* R. Br.	Douglas' meadowfoam
Moringaceae	-	*Moringa oleifera* Lam.	Drumstick tree
Phytolaccaceae	-	*Phytolacca americana* L.	Pokeweed
Resedaceae	-	*Reseda odorata* L.	Common mignonette
Tropaeolaceae	-	*Tropaeolum majus* L.	Garden nasturtium

Table 2. Glucosinolate side chains found in the plants analyzed, grouped into four chemical classes: aliphatic with sulfur-containing side chains (AS), other aliphatic (AO), benzenic (BEN), and indolic (IN).

Abbreviation	Glucosinolate	Common Name	Chemical Class
A	Allyl, 2-Propenyl	Sinigrin	AO
2AB	2-Arabinobenzyl	-	BEN
B	Benzyl	Glucotropaeolin	BEN
D4MB	Dimeric 4-mercaptobutyl	-	AS
4GDB	4-(β-D-Glucopyranosyldisulfanyl)butyl	Diglucothiobeinin	AS
3OHB	3-Hydroxybenzyl	Glucolepigramin	BEN
4OHB	4-Hydroxybenzyl	Sinalbin	BEN
R2OH3B	2(*R*)-Hydroxy-3-butenyl	Progoitrin	AO
3OHMP	3-(Hydroxymethyl)pentyl	-	AO
4OHI3M	4-Hydroxyindol-3-ylmethyl	4-hydroxyglucobrassicin	IN
R2OH2PE	2(*R*)-Hydroxy-2-phenylethyl	Glucosibarin	BEN
S2OH2PE	2(*S*)-Hydroxy-2-phenylethyl	Glucobarbarin	BEN
I3M	Indol-3-ylmethyl	Glucobrassicin	IN
4MB	4-Mercaptobutyl	Glucosativin	AS
3MOHB	3-Methoxybenzyl	Glucolimnanthin	BEN
4MOHB	4-Methoxybenzyl	Glucoaubrietin	BEN
1MOI3M	1-Methoxyindol-3-ylmethyl	Neoglucobrassicin	IN
4MOI3M	4-Methoxyindol-3-ylmethyl	4-methoxyglucobrassicin	IN
M	Methyl	Glucocapparin	AO
1ME	1-Methylethyl	Glucoputranjivin	AO
1MP	1-Methylpropyl	Glucocochlearin	AO
2MP	2-Methylpropyl	-	AO
3MP	3-Methylpentyl	-	AO
4MSOB	4-(Methylsulfinyl)butyl	Glucoraphanin	AS
10MSOD	10-(Methylsulfinyl)decyl	Glucocamelinin	AS
7MSOH	7-(Methylsulfinyl)heptyl	Glucoibarin	AS
9MSON	9-(Methylsulfinyl)nonyl	Glucoarabin	AS
8MSOO	8-(Methylsulfinyl)octyl	Glucohirsutin	AS
5MSOP	5-(Methylsulfinyl)pentyl	Glucoalyssin	AS
3MSOP	3-(Methylsulfinyl)propyl	Glucoiberin	AS
3MSOOP	3-(Methylsulfonyl)propyl	Glucocheirolin	AS
4MTB	4-(Methylthio)butyl	Glucoerucin	AS
8MTO	8-(Methylthio)octyl	-	AS
3MTP	3-(Methylthio)propyl	Glucoiberverin	AS
4P	4-Pentenyl	Glucobrassicanapin	AO
2PE	2-Phenylethyl	Gluconasturtiin	BEN
2RB	2-(α-L-Rhamnopyranosyloxy)benzyl	-	BEN
4RB	4-(α-L-Rhamnopyranosyloxy)benzyl	-	BEN

Table 3. Mean ± SE glucosinolate content (μmol g^{-1} plant dry weight) in the plants used in the experiments. From the total glucosinolate content the percentage of individual glucosinolates and the percentage of glucosinolates according to chemical class is also shown. Four glucosinolate classes were considered: aliphatic with sulfur-containing side chains (AS), other aliphatic (AO), benzenic (BEN), and indolic (IN).

Plant species	Replicates	Total glucosinolates (% AO, BEN, IN, and AS)	Identity of glucosinolates identified (% of total glucosinolates)
A. cordifolium	5	24.9 ± 5.2 (0%, 0%, 1.15%, 98.85%)	3MSOOP (63.85%), 3MSOP (26.72%), 8MSOO (6.70%), 3MTP (1.06%), 4MOI3M (0.58%), 4OHI3M (0.57%), 7MSOH (0.29%), 4MSOB (0.22%)
A. argenteum	5	1.4 ± 0.3 (0%, 0%, 75.32%, 24.68%)	5MSOP (75.32%), I3M (18.94%), 4OHI3M (4.33%), 4MOI3M (1.41%)
A. thaliana	26	17.6 ± 0.4 (0%, 0%, 14.81%, 85.19%)	4MSOB (65.00%), I3M (11.10%), 3MSOP (9.56%), 8MSOO (5.15%), 4MTB (4.50%), 4MOI3M (2.22%), 1MOI3M (1.23%), 7MSOH (0.97%), 4OHI3M (0.26%)
A. caucasica	3	20.8 ± 18.2 (60.03%, 0%, 0.78%, 39.19%)	1ME (53.43%), 9MSON (32.70%), 1MP (4.48%), 10MSOD (3.19%), 2MP (2.12%), 8MSOO (1.77%), 4MTB (1.53%), 4MOI3M (0.52%), 4OHI3M (0.26%)
B. vulgaris	3	35.6 ± 4.2 (0%, 81.60%, 18.40%, 0%)	S2OH2PE (80.88%), I3M (17.26%), 4MOI3M (0.80%), R2OH2PE (0.72%), 4OHI3M (0.34%)
B. laevigata	5	30.8 ± 3.4 (0%, 0%, 42.23%, 57.77%)	8MSOO (57.77%), I3M (42.23%)
B. juncea	3	97.9 ± 1.9 (95.70%, 0%, 4.17%, 0.13%)	A (95.70%), 1MOI3M (1.52%), 4MOI3M (1.16%), I3M (1.03%), 4OHI3M (0.46%), 3MSOP (0.13%)
B. napus	5	6.1 ± 1.7 (28.38%, 0%, 71.62%, 0%)	I3M (58.96%), 2OH3B (19.09%), 4P (9.28%), 1MOI3M (5.50%), 4MOI3M (4.71%), 4OHI3M (2.45%)
B oleracea capitata	7	8.0 ± 1.5 (25.13%, 0%, 59.04%, 15.83%)	I3M (52.66%), A (24.13%), 3MSOP (15.06%), 4MOI3M (3.88%), 1MOI3M (1.72%), 2OH3B (1.00%), 4OHI3M (0.78%), 4MSOB (0.77%)
B. oleracea acephala (glossy)	4	28.4 ± 4.1 (11.30%, 0%, 75.93%, 12.77%)	I3M (65.61%), 3MSOP (10.02%), A (9.19%), 1MOI3M (7.27%), 4MSOB (2.43%), 4MOI3M (2.23%), 2OH3B (2.11%), 4OHI3M (0.82%), 5MSOP (0.31%), 3MSOOP (0.01%)
B. oleracea acephala (waxy)	7	14.6 ± 2.7 (47.60%, 0%, 32.97%, 19.43%)	A (46.98%), I3M (24.39%), 3MSOP (18.88%), 4MOI3M (4.34%), 4OHI3M (2.69%), 1MOI3M (1.56%), 2OH3B (0.61%), 4MSOB (0.48%), 5MSOP (0.06%), 3MSOOP (0.01%)
B. orientalis	3	33.3 ± 2.9 (0%, 99.66%, 0.34%, 0%)	4OHB (96.47%), 4MOHB (3.19%), 4MOI3M (0.23%), 4OHI3M (0.06%), I3M (0.05%)
C. bursa-pastoris	3	0 ± 0 (0%, 0%, 0%, 0%)	-
C. pratensis	5	27.1 ± 7.6 (95.10%, 0%, 4.90%, 0%)	3OHMP (93.92%), I3M (4.51%), 3MP (1.18%), 4OHI3M (0.39%)

C. papaya	4	4.1 ± 1.3 (0%, 99.72%, 0.28%, 0%)	B (99.72%), I3M (0.28%)
C. spinosa	4	39.9 ± 6.1 (97.44%, 0%, 2.56%, 0%)	M (97.44%), I3M (1.64%), 4OHI3M (0.84%), 4MOI3M (0.08%)
C. cotinifolius	3	10.4 ± 1.6 (≥9.57%, ≥0%, ≥85.81%, ≥0%)	I3M (72.15%), 4OHI3M (10.83%), 2MP (9.57%), 1MOI3M (2.83%), other (4.62%)*
D. muralis	7	30.7 ± 4.9 (≥4.25%, ≥0%, ≥0.58%, ≥89.65%)	D4MB (33.12%), 4GDB (28.13%), 4MTB (11.69%), 4MB (8.54%), 4MSOB (7.87%), R2OH3B (4.25%), 4OHI3M (0.46%), 5MSOP (0.30%), 4MOI3M (0.12%), other (5.52%)*
E. sativa	7	37.4 ± 2.6 (≥4.18%, ≥0%, ≥0.46%, ≥90.29%)	D4MB (32.39%), 4GDB (24.63%), 4MB (14.31%), 4MTB (11.25%), 4MSOB (7.32%), R2OH3B (4.18%), 5MSOP (0.35%), 4MOI3M (0.27%), 4OHI3M (0.19%), 3MTP (0.05%), other (5.06%)*
E. cheiri	4	16.3 ± 6.5 (0%, 0%, 0%, 100.00%)	3MSOOP (59.35%), 3MTP (25.10%), 3MSOP (14.98%), 4MSOB (0.57%)
I. amara	4	53.8 ± 9.8 (0%, 0%, 0.06%, 99.94%)	3MSOP (85.71%), 3MTP (13.85%), 4MSOB (0.37%), 4MOI3M (0.06%)
L. sativum	3	120.5 ± 7.0 (0%, 99.95%, 0%, 0.05%)	B (99.95%), 3MSOP (0.05%)
L. douglasii	4	49.4 ± 10.2 (0%, 99.97%, 0.03%, 0%)	3MOHB (93.61%), 3OHB (6.36%), 4OHI3M (0.02%), 1MOI3M (0.01%)
M. oleifera	5	28.0 ± 2.5 (0%, 100.00%, 0%, 0%)	4RB (87.94%), 4OHB (10.52%), B (1.54%)
N. officinale	14	17.5 ± 1.5 (0%, 92.93%, 0%, 7.07%)	2PE (92.93%), 8MSOO (3.31%), 7MSOH (2.39%), 8MTO (1.37%)
N. paniculata	3	0 ± 0 (0%, 0%, 0%, 0%)	-
P. americana	3	0 ± 0 (0%, 0%, 0%, 0%)	-
P. sativum	3	0 ± 0 (0%, 0%, 0%, 0%)	-
R. odorata	4	89.8 ± 18.0 (0%, 93.88%, 6.12%, 0%)	2RB (92.96%), I3M (6.12%), 2AB (0.91%)
S. officinale	3	33.8 ± 2.8 (93.84%, 0%, 6.16%, 0%)	1ME (84.90%), 2MP (8.94%), I3M (5.19%), 4OHI3M (0.97%)
T. majus	3	28.0 ± 12.4 (0%, 100.00%, 0%, 0%)	B (99.66%), 4MOHB (0.34%)
V. faba	3	0 ± 0 (0%, 0%, 0%, 0%)	-

Glucosinolate abbreviations were: Allyl (A), 2-Arabinobenzyl, (2AB), Benzyl (B), Dimeric 4-mercaptobutyl (D4MB), 4-(*β*-D-Glucopyranosyldisulfanyl)butyl (4GDB), 3-Hydroxybenzyl (3OHB), 4-Hydroxybenzyl (4OHB), 2(*R*)-Hydroxy-3-butenyl (R2OH3B), 3-(Hydroxymethyl)pentyl (3OHMP), 4-Hydroxyindol-3-ylmethyl (4OHI3M), 2(*R*)-Hydroxy-2-phenylethyl (R2OH2PE), 2(*S*)-Hydroxy-2-phenylethyl (S2OH2PE), Indol-3-ylmethyl (I3M), 4-Mercaptobutyl (4MB), 3-Methoxybenzyl (3MOHB), 4-Methoxybenzyl (4MOHB), 1-Methoxyindol-3-ylmethyl (1MOI3M), 4-Methoxyindol-3-ylmethyl (4MOI3M), Methyl (M), 1-Methylethyl (1ME), 3Methylpentyl (3MP), 1-Methylpropyl (1MP), 2-Methylpropyl (2MP), 4-(Methylsulfinyl)butyl (4MSOB), 10-(Methylsulfinyl)decyl (10MSOD), 7-(Methylsulfinyl)heptyl (7MSOH), 9-(Methylsulfinyl)nonyl (9MSON), 8-(Methylsulfinyl)octyl (8MSOO), 5-(Methylsulfinyl)pentyl (5MSOP), 3-(Methylsulfinyl)propyl (3MSOP), 3-(Methylsulfonyl)propyl (3MSOOP), 4-(Methylthio)butyl (4MTB), 8-(Methylthio)octyl (8MTO), 3-(Methylthio)propyl (3MTP), 4-Pentenyl (4P), 2-Phenylethyl (2PE), 2-(α-L-Rhamnopyranosyloxy)benzyl (2RB), 4-(α-L-Rhamnopyranosyloxy)benzyl (4RB).

Table 4. Glucosinolate richness (*S*), Shannon´s diversity index for the four glucosinolate classes (H_A), Shannon´s diversity index for the relative concentrations of all individual glucosinolates (H_B), and chemical complexity index for glucosinolates (CCI) for each of the plant types tested. Values based on means across replicates.

	S	H_A	H_B	CCI*=H_A+H_B
A. cordifolium	8	0.693	0.958	1.651
A. argenteum	4	0.693	0.724	1.417
A. thaliana	9	0.693	1.240	1.933
A. caucasica	9	1.099	1.209	2.308
B. vulgaris	5	0.693	0.568	1.261
B. laevigata	2	0.693	0.681	1.374
B. juncea	6	1.099	0.238	1.337
B. napus	6	0.693	1.243	1.936
B. oleracea (cabba.)	8	1.099	1.283	2.382
B. oleracea (g. co.)	10	1.099	1.232	2.331
B. oleracea (w. co.)	10	1.099	1.370	2.469
B. orientalis	5	0.693	0.167	0.860
C. bursa-pastoris	0	n/a	n/a	0
C. pratensis	4	0.693	0.273	0.966
C. papaya	2	0.693	0.019	0.712
C. spinosa	4	0.693	0.139	0.832
C. cotinifolius	14	0.693	0.802	1.495
D. muralis	12	1.099	1.568	2.667
E. sativa	12	1.099	1.610	2.709
E. cheiri	4	0.000	0.970	0.970
I. amara	4	0.693	0.431	1.124
L. sativum	2	0.693	0.004	0.697
L. douglasii	5	0.693	0.240	0.933
M. oleifera	3	0.000	0.414	0.414
N. officinale	4	0.693	0.329	1.022
N. paniculata	0	n/a	n/a	0
P. americana	0	n/a	n/a	0
P. sativum	0	n/a	n/a	0
R. odorata	3	0.693	0.282	0.975
S. officinale	4	0.693	0.553	1.246
T. majus	2	0.000	0.023	0.023
V. faba	0	n/a	n/a	0

*In plants without glucosinolates, in which the H_A and H_B indices could not be calculated, their CCI was given a zero value.

Table 5. Two-choice oviposition preference index (OPI) in three *P. xylostella* strains reared on cabbage (DBM-C), artificial diet (DBM-G88), and pea (DBM-P). Data were analyzed using a one-tailed, two-sample test of proportions comparing the relative percentages of all eggs laid on the plant being tested and on *A. thaliana* ($P \leq 0.05$) (n = 3). OPI given as means found across replicates (mean ± SE). Significant differences are shown in bold type.

	OPI, test statistic, and *P*-value		
	DBM-C	DBM-G88	DBM-P
A. cordifolium	0.69 ± 0.26, *z*=0.59, *P*=0.278	0.33 ± 0.18, *z*=1.37, *P*=0.085	**0.20 ± 0.10, _z_=1.67, _P_=0.048***
A. argenteum	**0.08 ± 0.02, _z_=2.11, _P_=0.018***	0.59 ± 0.05, *z*=0.64, *P*=0.262	0.38 ± 0.15, *z*=1.18, *P*=0.120
A. caucasica	0.43 ± 0.05, *z*=0.98, *P*=0.164	3.42 ± 0.85, *z*=1.27, *P*=0.101	1.55 ± 0.64, *z*=0.20, *P*=0.422
B. vulgaris	2.70 ± 0.99, *z*=0.98, *P*=0.164	2.31 ± 0.39, *z*=0.93, *P*=0.176	1.60 ± 0.29, *z*=0.54, *P*=0.295
B. laevigata	0.87 ± 0.06, *z*=0.20, *P*=0.422	1.27 ± 0.16, *z*=0.24, *P*=0.403	0.97 ± 0.36, *z*=0.20, *P*=0.422
B. juncea	1.71 ± 0.25, *z*=0.59, *P*=0.278	2.17 ± 0.25, *z*=0.88, *P*=0.189	1.39 ± 0.21, *z*=0.34, *P*=0.366
B. napus	1.46 ± 0.04, *z*=0.44, *P*=0.330	2.33 ± 0.59, *z*=0.83, *P*=0.202	2.48 ± 0.83, *z*=0.88, *P*=0.188
B. oleracea (cabba.)	0.24 ± 0.06, *z*=1.52, *P*=0.064	**0.16 ± 0.10, _z_=1.81, _P_=0.035***	**0 ± 0, _z_=2.45, _P_=0.007***
B. oleracea (g. co.)	0.51 ± 0.04, *z*=0.78, *P*=0.217	0.35 ± 0.09, *z*=1.22, *P*=0.110	0.54 ± 0.09, *z*=0.73, *P*=0.231
B. oleracea (w. co.)	**0.04 ± 0.01, _z_=2.25, _P_=0.012***	**0.03 ± 0.01, _z_=2.30, _P_=0.011***	**0.02 ± 0.02, _z_=2.35, _P_=0.009***
B. orientalis	**0.18 ± 0.10, _z_=1.76, _P_=0.039***	**0.07 ± 0.04, _z_=2.11, _P_=0.018***	0.24 ± 0.02, *z*=1.52, *P*=0.064
C. bursa-pastoris	**0.03 ± 0.03, _z_=2.30, _P_=0.011***	**0 ± 0, _z_=2.45, _P_=0.007***	0.51 ± 0.40, *z*=1.22, *P*=0.110
C. pratensis	0.71 ± 0.16, *z*=0.49, *P*=0.312	0.29 ± 0.01, *z*=1.32, *P*=0.093	0.30 ± 0.08, *z*=1.32, *P*=0.093
C. papaya	**0.05 ± 0.05, _z_=2.25, _P_=0.012***	**0.03 ± 0.03, _z_=2.35, _P_=0.009***	**0 ± 0, _z_=2.45, _P_=0.007***
C. spinosa	**0.09 ± 0.05, _z_=2.06, _P_=0.020***	**0.06 ± 0.03, _z_=2.16, _P_=0.016***	**0.06 ± 0.03, _z_=2.20, _P_=0.014***
C. cotinifolius	**0.01 ± 0.01, _z_=2.40, _P_=0.008***	**0.03 ± 0.03, _z_=2.30, _P_=0.011***	**0.06 ± 0.03, _z_=2.16, _P_=0.016***
D. muralis	1.51 ± 0.17, *z*=0.49, *P*=0.312	1.99 ± 0.65, *z*=0.64, *P*=0.262	8.20 ± 6.41, *z*=1.18, *P*=0.120
E. sativa	1.35 ± 0.25, *z*=0.29, *P*=0.384	1.96 ± 0.39, *z*=0.73, *P*=0.231	1.55 ± 0.28, *z*=0.49, *P*=0.312
E. cheiri	**0.22 ± 0.18, _z_=1.71, _P_=0.043***	0.84 ± 0.25, *z*=0.34, *P*=0.366	0.79 ± 0.13, *z*=0.34, *P*=0.366
I. amara	0.72 ± 0.46, *z*=0.78, *P*=0.217	1.82 ± 0.94, *z*=0.34, *P*=0.366	0.61 ± 0.13, *z*=0.64, *P*=0.262
L. sativum	4.28 ± 1.74, *z*=1.18, *P*=0.120	2.45 ± 0.16, *z*=1.03, *P*=0.152	4.87 ± 2.38, *z*=1.32, *P*=0.093
L. douglasii	3.84 ± 0.86, *z*=1.37, *P*=0.085	4.39 ± 1.16, *z*=1.42, *P*=0.078	3.58 ± 1.08, *z*=1.22, *P*=0.110
M. oleifera	**0 ± 0, _z_=2.45, _P_=0.007***	**0 ± 0, _z_=2.45, _P_=0.007***	**0 ± 0, _z_=2.45, _P_=0.007***
N. officinale	0.72 ± 0.10, *z*=0.39, *P*=0.348	1.23 ± 0.39, *z*=0.15, *P*=0.442	2.48 ± 1.76, *z*=0.34, *P*=0.366
N. paniculata	**0 ± 0, _z_=2.45, _P_=0.007***	**0 ± 0, _z_=2.45, _P_=0.007***	**0 ± 0, _z_=2.45, _P_=0.007***
P. americana	**0 ± 0, _z_=2.45, _P_=0.007***	**0 ± 0, _z_=2.45, _P_=0.007***	**0 ± 0, _z_=2.45, _P_=0.007***
P. sativum	**0 ± 0, _z_=2.45, _P_=0.007***	**0 ± 0, _z_=2.45, _P_=0.007***	**0.01 ± 0.01, _z_=2.40, _P_=0.008***
R. odorata	0.36 ± 0.30, *z*=1.47, *P*=0.071	**0.04 ± 0.04, _z_=2.30, _P_=0.011***	0.23 ± 0.08, *z*=1.57, *P*=0.058
S. officinale	**6.67 ± 2.04, _z_=1.67, _P_=0.048****	4.04 ± 0.76, *z*=1.42, *P*=0.078	4.47 ± 1.43, *z*=1.42, *P*=0.078
T. majus	0.04 ± 0.04, **_z_=2.16, _P_=0.016***	**0 ± 0, _z_=2.45, _P_=0.007***	0.35 ± 0.19, *z*=1.37, *P*=0.085
V. faba	**0 ± 0, _z_=2.45, _P_=0.007***	**0 ± 0, _z_=2.45, _P_=0.007***	**0 ± 0, _z_=2.45, _P_=0.007***

*_A. thaliana_ preferred

**_S. officinale_ preferred

Table 6. Total oviposition (TO) in non-choice tests (mean ± SE) for each of the tested plants and for the three *P. xylostella* strains reared on cabbage (DBM-C), artificial diet (DBM-G88), and pea (DBM-P). Differences in TO among *P. xylostella* strains were analyzed using a Kruskal-Wallis test ($P \leq 0.05$) (n = 3). Significant differences are shown in bold type.

	Number of eggs mean ± SE		
	DBM-C	DBM-G88	DBM-P
A. cordifolium	22.33 ± 2.40	31.00 ± 6.43	13.67 ± 1.76
A. argenteum	91.00 ± 23.69	70.67 ± 17.28	52.00 ± 24.70
A. thaliana	52.67 ± 5.24	85.33 ± 11.46	54.67 ± 10.10
A. caucasica	63.00 ± 11.27	74.33 ± 12.68	44.33 ± 15.01
B. vulgaris	44.67 ± 10.68	67.00 ± 18.77	19.67 ± 6.67
B. laevigata	50.00 ± 13.65	65.00 ± 19.35	45.00 ± 4.51
B. juncea	37.33 ± 5.70	81.33 ± 14.84	63.00 ± 18.68
B. napus	75.00 ± 3.05	62.33 ± 13.20	10.33 ± 3.28
B. oleracea (cabbage)	34.33 ± 6.39	54.67 ± 5.24	21.33 ± 7.31
B. oleracea (glossy collards)	55.00 ± 4.16	59.67 ± 12.35	14.33 ± 2.33
B. oleracea (waxy collards)	27.33 ± 4.91	42.00 ± 12.00	26.33 ± 5.78
B. orientalis	22.67 ± 7.17	22.00 ± 2.52	15.67 ± 8.25
C. bursa-pastoris	**15.33 ± 2.91**	**0.00 ± 0.00**	**1.33 ± 1.33**
C. pratensis	45.67 ± 3.53	28.67 ± 5.24	19.33 ± 2.33
C. papaya	5.67 ± 5.67	74.00 ± 24.01	22.33 ± 16.37
C. spinosa	55.33 ± 8.41	35.33 ± 0.88	20.00 ± 1.53
C. cotinifolius	40.33 ± 12.20	39.67 ± 12.17	45.00 ± 14.11
D. muralis	51.00 ± 5.51	65.33 ± 10.71	49.33 ± 24.39
E. sativa	90.00 ± 16.56	95.33 ± 7.36	63.33 ± 17.49
E. cheiri	**58.67 ± 2.33**	**43.00 ± 3.79**	**21.00 ± 3.61**
I. amara	37.33 ± 8.21	53.00 ± 10.97	16.00 ± 9.64
L. sativum	**82.67 ± 8.41**	**122.67 ± 8.17**	**60.67 ± 9.53**
L. douglasii	60.33 ± 6.77	74.67 ± 10.68	71.00 ± 6.56
M. oleifera	4.33 ± 2.19	2.67 ± 2.67	0.00 ± 0.00
N. officinale	63.33 ± 5.90	61.33 ± 17.53	62.33 ± 7.36
N. paniculata	3.00 ± 1.15	3.67 ± 2.03	0.33 ± 0.33
P. americana	1.33 ± 0.67	0.00 ± 0.00	0.00 ± 0.00
P. sativum	1.00 ± 1.00	0.00 ± 0.00	0.67 ± 0.67
R. odorata	3.00 ± 3.00	2.67 ± 1.45	0.00 ± 0.00
S. officinale	43.67 ± 1.45	77.33 ± 8.95	70.67 ± 3.84
T. majus	16.33 ± 14.38	4.67 ± 4.67	10.67 ± 3.71
V. faba	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Table 7. Survival of *P. xylostella* from first-instar larvae to pupae (mean ± SE) for insect strains reared on cabbage (DBM-C) and pea (DBM-P). Data comparing survival of DBM-C and DBM-P larvae were analyzed using a one-tailed, two-sample test of proportions ($P \leq 0.05$) (unless otherwise indicated n = 3-7).

	Survival of larvae (%) per plant		
	DBM-C	DBM-P	Test statistic and *P*-value
A. cordifolium	13.3 ± 6.7	32.0 ± 4.9	z=0.59, P=0.277
A. argenteum	20.0 ± 8.2	13.3 ± 6.7	z=0.24, P=0.404
A. thaliana	46.7 ± 17.6	40.0 ± 11.5	z=0.17, P=0.431
A. caucasica	25.0 ± 18.9	6.7 ± 6.7	z=0.62, P=0.267
B. vulgaris	0.0 ± 0.0	0.0 ± 0.0	n/a
B. laevigata	46.7 ± 6.7	33.3 ± 6.7	z=0.35, P=0.367
B. juncea	66.7 ± 6.7	66.7 ± 6.7	z=0.00, P=0.500
B. napus	73.3 ± 6.7	66.7 ± 6.7	z=0.16, P=0.436
B. oleracea (cabba.)	33.3 ± 6.7	26.7 ± 6.7	z=0.16, P=0.436
B. oleracea (g. co.)	6.7 ± 6.7	13.3 ± 6.7	z=0.24, P=0.403
B. oleracea (w. co.)	46.7 ± 6.7	33.3 ± 6.7	z=0.35, P=0.363
B. orientalis	13.3 ± 6.7	20.0 ± 11.5	z=0.23, P=0.409
C. bursa-pastoris	20.0 ± 11.5	13.3 ± 6.7	z=0.23, P=0.409
C. pratensis	66.7 ± 6.7	46.7 ± 6.7	z=0.49, P=0.310
C. papaya	0.0 ± 0.0	0.0 ± 0.0	n/a
C. spinosa	6.7 ± 6.7	13.3 ± 6.7	z=0.24, P=0.403
C. cotinifolius	6.7 ± 6.7	6.7 ± 6.7	z=0.00, P=0.500
D. muralis	53.3 ± 17.6	46.7 ± 17.6	z=0.15, P=0.442
E. sativa	13.3 ± 6.7	26.7 ± 6.7	z=0.43, P=0.334
E. cheiri	50.0 ± 12.9	20.0 ± 20.0	z=0.89, P=0.187
I. amara	40.0 ± 14.1	13.3 ± 6.7	z=0.78, P=0.217
L. sativum	60.0 ± 11.5	66.7 ± 6.7	z=0.18, P=0.429
L. douglasii	66.7 ± 6.7	53.3 ± 17.6	z=0.35, P=0.363
M. oleifera	10.0 ± 10.0	10.0 ± 5.8	z=0.00, P=0.500
N. officinale	40.0 ± 11.5	46.7 ± 6.7	z=0.17, P=0.431
N. paniculata	0.0 ± 0.0	0.0 ± 0.0	n/a
P. americana	0.0 ± 0.0	0.0 ± 0.0	n/a
P. sativum	0.0 ± 0.0	20.0 ± 11.5	z=0.82, P=0.207
R. odorata	20.0 ± 20.0	17.1 ± 6.8	z=0.12, P=0.451
S. officinale	66.7 ± 6.7	50.0 ± 17.3	z=0.45, P=0.326
T. majus	24.0 ± 14.7	20.0 ± 8.7	z=0.17, P=0.434
V. faba	0.0 ± 0.0	0.0 ± 0.0	n/a

Figure Legends:

Figure 1. CATPCA plots showing the relationships between oviposition preference index (OPI), total oviposition (TO), and larval survival, for three *P. xylostella* strains and total glucosinolate content (TOTAL GLUC), aliphatic glucosinolates with sulfur-containing side chains (AS), other aliphatic glucosinolates (AO), benzenic glucosinolates (BEN), indolic glucosinolates (IN), glucosinolate richness (*S*), and chemical complexity index for glucosinolates (CCI). Component loadings of CATPCA plots were rotated using Varimax with Kaiser normalization. The three *P. xylostella* strains were DBM-C (A1, B1, and D1), DBM-G88 (B1 and B2), and DBM-P (C1, C2, and D2). Component loadings of CATPCA plots were rotated using Varimax with Kaiser normalization.

Figure 2. Correlation between plant glucosinolate content and oviposition preference index (OPI) (A) and total oviposition (TO) (B) for three *P. xylostella* strains. The OPI for each plant type was calculated as the number of eggs laid on each individual plant divided by the number of eggs laid on the *A. thaliana* plant that it was compared with in the same cage, while TO indicates the total number of eggs laid per plant. The lineal trend lines are solid for the DBM-C strain, long-dashed for the DBM-G88 strain, and with short dashes for the DBM-P strain.

Fig. 1

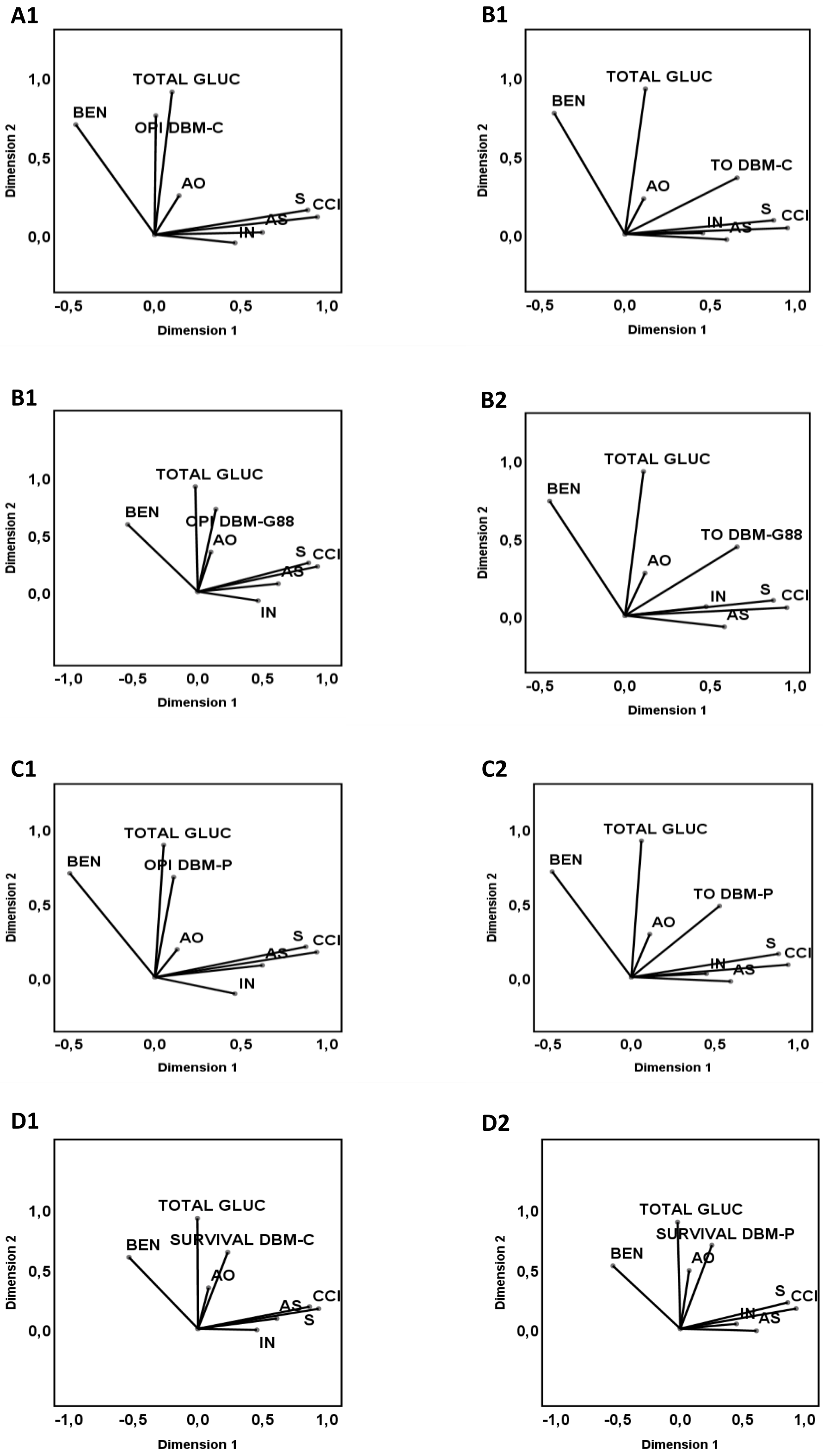
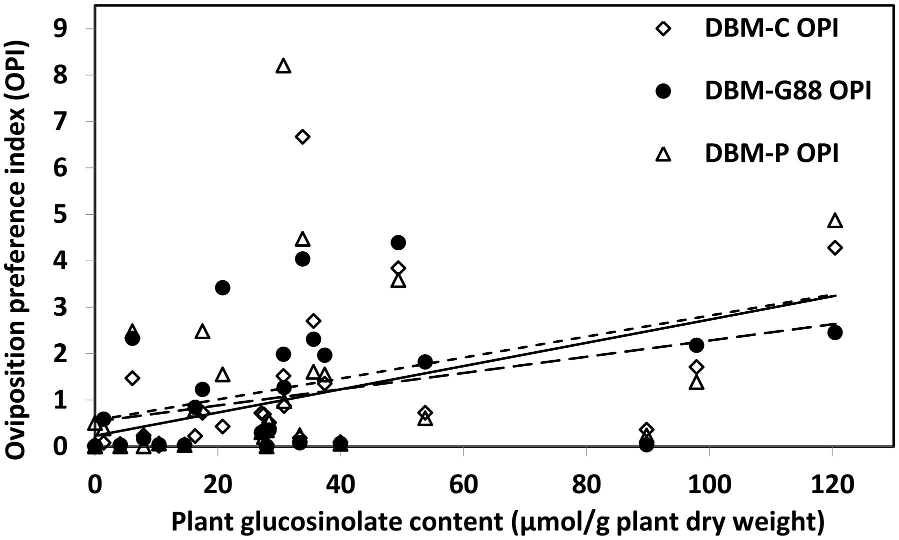

A1
TOTAL GLUC
BEN
OPI DBM-C
AO
S
CCI
AS
IN
Dimension 2
Dimension 1
-0,5
0,0
0,5
1,0
B1
TOTAL GLUC
BEN
TO DBM-C
AO
IN
S
CCI
AS
B1
TOTAL GLUC
BEN
OPI DBM-G88
AO
S
CCI
AS
IN
-1,0
B2
TOTAL GLUC
BEN
TO DBM-G88
AO
IN
S
CCI
AS
C1
TOTAL GLUC
BEN
OPI DBM-P
AO
S
CCI
AS
IN
C2
TOTAL GLUC
BEN
TO DBM-P
AO
S
CCI
IN
AS
D1
TOTAL GLUC
BEN
SURVIVAL DBM-C
AO
AS
CCI
S
IN
D2
TOTAL GLUC
SURVIVAL DBM-P
BEN
AO
S
CCI
IN
AS

Fig. 2

A


DBM-C OPI
DBM-G88 OPI
DBM-P OPI
Oviposition preference index (OPI)
0
1
2
3
4
5
6
7
8
9
0
20
40
60
80
100
120
Plant glucosinolate content (µmol/g plant dry weight)

B

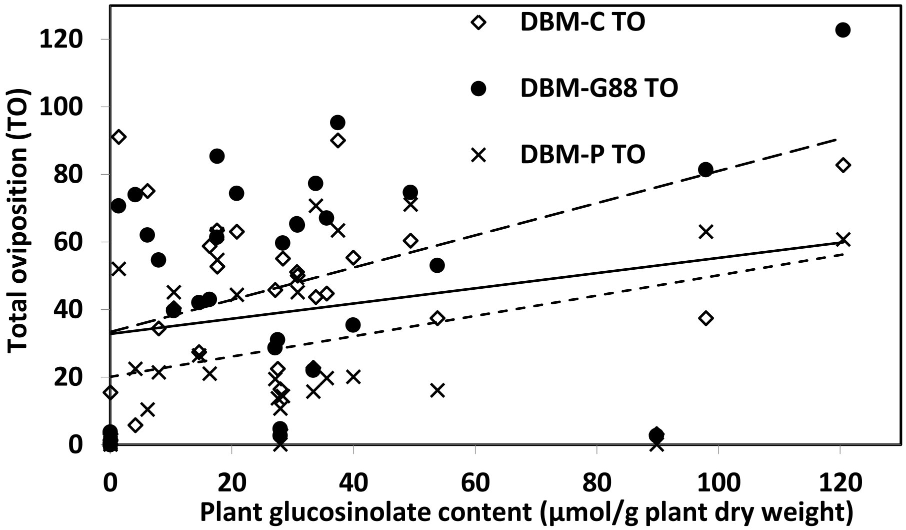

DBM-C TO
DBM-G88 TO
DBM-P TO
Total oviposition (TO)
0
20
40
60
80
100
120
0
20
40
60
80
100
120
Plant glucosinolate content (µmol/g plant dry weight)

Table S1. Significance of correlations between plant glucosinolate content and glucosinolate diversity in the plants tested. Correlations were analyzed statistically using one-tailed Spearman´s rho correlations (n = 32). Four different classes of glucosinolates were distinguished, aliphatic with sulfur-containing side chains (AS), other aliphatic (AO), benzenic (BEN), and indolic (IN). The effect of the diversity of glucosinolates was analyzed with the glucosinolate richness (*S*) and the chemical complexity index for glucosinolates (CCI) of each plant. Significant *P*-values (*P* ≤ 0.05) are shown in bold type.

	P-value of Spearman´s rho correlation					
	Total glucosinolates	AO	BEN	IN	AS	*S*
CCI	*P*=0.105	***P*≤0.001**	***P*=0.031**	***P*≤0.001**	***P*≤0.001**	***P*≤0.001**
S	*P*=0.054	***P*≤0.001**	*P*=0.118	***P*≤0.001**	***P*=0.002**	
AS	*P*=0.109	*P*=0.289	***P*=0.018**	*P*=0.114		
IN	*P*=0.084	***P*≤0.001**	*P*=0.104			
BEN	***P*=0.008**	***P*=0.004**				
AO	*P*=0.133					

Table S2. Model summary and component loadings of the different CATPCA for glucosinolate content of the plants tested, oviposition preference index (OPI) and total oviposition (TO) in the three strains of *P. xylostella* (DBM-C, DBM-G88, and DBM-P), and larval survival (LS) in DBM-C and DBM-P. Variables related to glucosinolate content included total glucosinolate content (TOTAL GLUC), aliphatic glucosinolates with sulfur-containing side chains (AS), other aliphatic glucosinolates (AO), benzenic glucosinolates (BEN), indolic glucosinolates (IN), glucosinolate richness (*S*), and chemical complexity index for glucosinolates (CCI). Component loadings were rotated with Varimax with Kaiser normalization. Model summary include Cronbach´s Alpha (CA), Eigenvalue, and percentage of variance accounted for (% VAF).

Model summary for glucosinolate content

	TOTAL GLUC	AO	BEN	IN	AS	*S*	CCI	CA	Eigenvalue	% VAF
Dimension 1	0.124	0.113	-0.437	0.470	0.614	0.894	0.946	0.702	2.512	35.887
Dimension 2	0.950	0.237	0.751	0.025	0.000	0.128	0.051	0.411	1.543	22.043
Total	-	-	-	-	-	-	-	0.879	4.055	57.929

Model summary for OPI DBM-C

	OPI DBM-C	TOTAL GLUC	AO	BEN	IN	AS	*S*	CCI	CA	Eigenvalue	% VAF
Dimension 1	0.008	0.102	0.142	-0.457	0.466	0.625	0.888	0.944	0.691	2.527	31.584
Dimension 2	0.754	0.904	0.243	0.699	-0.053	0.015	0.155	0.111	0.564	1.973	24.659
Total	-	-	-	-	-	-	-	-	0.889	4.499	56.244

Model summary for OPI DBM-G88

	OPI DBM-G88	TOTAL GLUC	AO	BEN	IN	AS	*S*	CCI	CA	Eigenvalue	% VAF
Dimension 1	0.141	-0.019	0.104	-0.543	0.466	0.622	0.857	0.926	0.693	2.522	32.528
Dimension 2	0.719	0.917	0.340	0.589	-0.078	0.072	0.252	0.220	0.562	1.943	23.282
Total	-	-	-	-	-	-	-	-	0.887	4.465	55.809

Model summary for OPI DBM-P

	OPI DBM-P	TOTAL GLUC	AO	BEN	IN	AS	*S*	CCI	CA	Eigenvalue	% VAF
Dimension 1	0.112	0.056	0.131	-0.491	0.464	0.624	0.877	0.940	0.693	2.533	31.657
Dimension 2	0.673	0.888	0.180	0.703	-0.114	0.079	0.200	0.164	0.530	1.855	23.191
Total	-	-	-	-	-	-	-	-	0.882	4.388	54.848

Model summary for TO DBM-C

	TO DBM-C	TOTAL GLUC	AO	BEN	IN	AS	*S*	CCI	CA	Eigenvalue	% VAF
Dimension 1	0.622	0.100	0.134	-0.439	0.458	0.605	0.865	0.952	0.742	2.837	35.466
Dimension 2	0.371	0.933	0.248	0.756	-0.024	-0.059	0.140	0.091	0.468	1.672	20.900
Total	-	-	-	-	-	-	-	-	0.889	4.509	56.366

Model summary for TO DBM-G88

	TO DBM-G88	TOTAL GLUC	AO	BEN	IN	AS	*S*	CCI	CA	Eigenvalue	% VAF
Dimension 1	0.527	0.028	0.125	-0.513	0.463	0.603	0.858	0.937	0.733	2.750	34.372
Dimension 2	0.550	0.934	0.296	0.686	0.025	-0.044	0.207	0.164	0.529	1.805	22.564
Total	-	-	-	-	-	-	-	-	0.892	4.555	56.936

Model summary for TO DBM-P

	TO DBM-P	TOTAL GLUC	AO	BEN	IN	AS	*S*	CCI	CA	Eigenvalue	% VAF
Dimension 1	0.455	-0.008	0.120	-0.534	0.454	0.608	0.860	0.927	0.722	2.680	33.499
Dimension 2	0.560	0.924	0.326	0.659	0.006	-0.020	0.255	0.185	0.529	1.808	22.600
Total	-	-	-	-	-	-	-	-	0.888	4.488	56.099

Model summary for LS in DBM-C

	LS DBM-C	TOTAL GLUC	AO	BEN	IN	AS	*S*	CCI	CA	Eigenvalue	% VAF
Dimension 1	0.186	-0.036	0.097	-0.554	0.463	0.623	0.849	0.924	0.695	2.529	31.616
Dimension 2	0.656	0.922	0.372	0.571	-0.061	0.087	0.236	0.234	0.541	1.866	23.326
Total		-	-	-	-	-	-	-	0.883	4.395	54.942

Model summary for LS in DBM-P

	LS DBM-P	TOTAL GLUC	AO	BEN	IN	AS	*S*	CCI	CA	Eigenvalue	% VAF
Dimension 1	0.192	-0.058	0.076	-0.562	0.462	0.627	0.845	0.918	0.696	2.525	31.557
Dimension 2	0.738	0.896	0.501	0.492	-0.026	-0.003	0.272	0.251	0.578	1.978	24.723
Total		-	-	-	-	-	-	-	0.889	4.502	56.281

Table S3. Significance of correlations between plant glucosinolate content, two-choice oviposition preference index (OPI), no-choice total oviposition (TO) and larval survival (LS) in three *P. xylostella* strains reared on cabbage (DBM-C), artificial diet (DBM-G88), and pea (DBM-P). Correlations were analyzed statistically using one-tailed Spearman´s rho correlations ($P \leq 0.05$) (n = 31). Significant correlations are shown in bold type.

	P-value of Spearman´s rho correlation								
	DBM-C OPI	DBM-G88 OPI	DBM-P OPI	DBM-C TO	DBM-G88 TO	DBM-P TO	DBM-C LS	DBM-P LS	Total glucosinolates
DBM-C OPI	-	***P*≤0.001**	***P*≤0.001**	***P*≤0.001**	-	-	***P*≤0.001**	-	***P*≤0.001**
DBM-C TO	***P*≤0.001**	-	-	-	***P*≤0.001**	***P*≤0.001**	***P*≤0.001**	-	***P*=0.025**
DBM-C LS	***P*≤0.001**	-	-		***P*≤0.001**	-	-	***P*≤0.001**	***P*=0.017**
DBM-G88 OPI	***P*≤0.001**	-	***P*≤0.001**	-	***P*≤0.001**	-	-	-	***P*≤0.001**
DBM-G88 TO	-	***P*≤0.001**	-	***P*≤0.001**	-	***P*≤0.001**	-	-	***P*=0.004**
DBM-P OPI	***P*≤0.001**	***P*≤0.001**	-	-	-	***P*≤0.001**	-	***P*≤0.001**	***P*≤0.001**
DBM-P TO	-	-	***P*≤0.001**	***P*≤0.001**	***P*≤0.001**	-	-	***P*≤0.001**	***P*=0.011**
DBM-P LS	***P*≤0.001**	-	-	-	-	***P*≤0.001**	***P*≤0.001**	-	***P*=0.012**

Table S4. Effect of plant glucosinolate content, glucosinolate diversity, and DBM strain on two-choice oviposition preference index (OPI), no-choice total oviposition (TO), and larval survival (LS) in three *P. xylostella* strains reared on cabbage (DBM-C), artificial diet (DBM-G88), and pea (DBM-P). Four different classes of glucosinolates were distinguished, aliphatic with sulfur-containing side chains (AS), other aliphatic (AO), benzenic (BEN), and indolic (IN). The effect of the diversity of glucosinolates was analyzed with the glucosinolate richness (*S*) and the chemical complexity index for glucosinolates (CCI) of each plant. The generalized linear model used was based on a Tweedie probability distribution with log link function ($P \leq 0.05$) (n = 31). The slope estimate was set to zero for the strain DBM-P. Significant *P*-values are shown in bold type.

	Wald-chi square	*P*	Slope Estimate	SE
OPI				
Strain DBM-C	0.82	0.364	-0.116	0.128
Strain DBM-G88	0.30	0.583	-0.070	0.127
S	2.19	0.139	-0.045	0.030
CCI	11.59	**≤0.001**	0.475	0.139
AO	11.32	**≤0.001**	0.009	0.003
BEN	29.47	**≤0.001**	0.010	0.002
AS	2.75	0.097	0.008	0.005
TO				
Strain DBM-C	3.96	**0.047**	0.337	0.170
Strain DBM-G88	7.93	**0.005**	0.470	0.167
S	1.14	0.285	-0.035	0.033
CCI	24.66	**≤0.001**	0.847	0.164
AO	10.10	**≤0.001**	0.011	0.003
BEN	18.79	**≤0.001**	0.011	0.002
AS	0.59	0.443	0.004	0.006
LS				
Strain DBM-C	0.01	0.971	0.002	0.043
S	2.56	0.109	-0.019	0.012
CCI	6.69	**0.010**	0.138	0.053
AO	14.26	**≤0.001**	0.004	0.011
BEN	6.39	**0.011**	0.002	0.001
AS	0.26	0.611	0.001	0.002

The *P*-values of the generalized linear model used for OPI, TO, and LS were highly significant ($P \leq 0.001$) based on Omnibus tests

Figure S1. Correlation between indolic and benzenic glucosinolate content (μmol/g plant dry weight) in the plants tested.

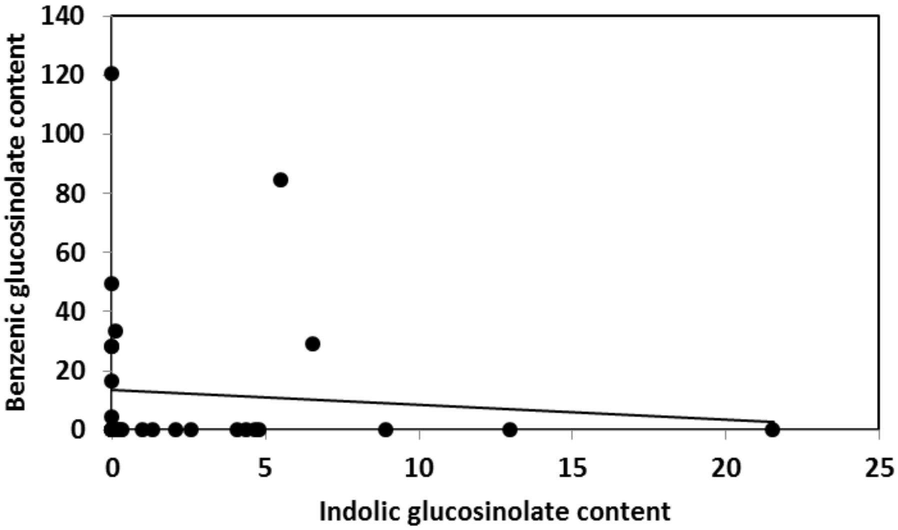


Figure S2. CATPCA plot showing the relationships between total glucosinolate content (TOTAL GLUC), aliphatic glucosinolates with sulfur-containing side chains (AS), other aliphatic glucosinolates (AO), benzenic glucosinolates (BEN), indolic glucosinolates (IN), glucosinolate richness (*S*), and chemical complexity index for glucosinolates (CCI) in the plants analyzed. The component loadings of the CATPCA plot were rotated using Varimax with Kaiser normalization.