

***Plutella xylostella* (diamondback moth) and its parasitoid *Diadegma semiclausum* show different gustatory and longevity responses to a range of nectar and honeydew sugars**

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Abstract

Parasitoids as well as many of their herbivorous hosts, depend on carbohydrate-rich food during the adult stage. Different types of nectar and honeydew vary with regard to their sugar composition. In order to successfully exploit a food source, the insect must show a positive gustatory response to its component sugars and be able to digest and metabolise them. Here we tested the herbivore *Plutella xylostella* L. (Lepidoptera: Plutellidae) and its parasitoid *Diadegma semiclausum* (Hellén) (Ichneumonidae: Campopleginae) with respect to their feeding response and longevity when provided with one of nine sugars (fructose, glucose, lactose, maltose, melibiose, melezitose, raffinose, sucrose, or trehalose). Both species responded to and showed a prolonged life span on a broad range of sugars. The impact of food supply on life span was about sixfold higher for the parasitoid than for the herbivore. In general, there was a good fit between gustatory response and achieved longevity, with some outliers. Both species showed only weak responses to melibiose, which significantly prolonged life span. The parasitoid showed a gustatory response to melezitose, which did not prolong its life span. The parasitoid and its herbivorous host responded differently to trehalose. These differences in gustatory response and longevity show the potential for application of selective sugar sources in conservation biological control. At the same time it also reveals a risk that the indiscriminate application of sugar sources may stimulate herbivory.

Introduction

Many insects depend in their adult stage on carbohydrate-rich food as their main source of energy for longevity, fecundity, and mobility. This is true for many herbivorous species, including Lepidoptera (Romeis et al., 2005), as well as for their parasitoids (Jervis et al., 1996; Wäckers, 2003). An important aspect in nectar exploitation by insects is the morphological fit between their mouth parts and the floral architecture (Jervis, 1998; Winkler et al., 2002, 2003). Floral nectar is generally thought to be the most important food source for Lepidoptera, which often have highly specialised mouth parts (Gilbert & Singer, 1975; Boggs, 1987). Nevertheless, some species also feed on exposed sugar

sources such as extrafloral nectar (Lukefahr, 1960; Beach et al., 1985) and homopteran honeydew. Parasitoids, with their less specialised, short mouth parts (Jervis, 1998) primarily use easily accessible floral nectar (Idris & Grafius, 1995; Wäckers et al., 1996) as well as extrafloral nectar (Bugg et al., 1989), and honeydew (Zoebelein, 1955).

The acceptance of sugar sources such as (extrafloral) nectar and honeydew also depends on their chemical composition. Besides the three dominant sugars (sucrose, glucose, and fructose), nectar and honeydew can contain a number of other saccharides, including maltose, melezitose, melibiose, raffinose, and trehalose. Insects can vary in their gustatory responses to these sugars (Wäckers, 1999) as well as in their capacity to digest and metabolise them.

Most papers have addressed sugar suitability, either from the point of view of the herbivore (Romeis & Wäckers,

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2000; Romeis & Wäckers, 2002), or the parasitoid (Wäckers, 1999, 2001; Beach et al., 2003; Jacob & Evans, 2004). The aspect of gustatory response and the impact of a sugar on longevity are also often investigated separately.

We investigated both the herbivore *Plutella xylostella* L. (Lepidoptera: Plutellidae) and its parasitoid *Diadegma semiclausum* (Hellén) (Ichneumonidae: Campopleginae), with respect to their gustatory response and longevity when provided with one of nine sugars (fructose, glucose, lactose, maltose, melibiose, melezitose, raffinose, sucrose, or trehalose). With the exception of lactose, all these sugars have been reported to occur in nectar or honeydew (Baker & Baker, 1983; Bentley, 1977; Kloft et al., 1985). This comprehensive approach allowed us to investigate whether there are differences in sugar response and physiological use between the herbivore and its natural enemy. Such differences could be exploited in tailoring food sources to selectively support biological control agents, without benefiting herbivores (Wäckers, 1999).

Materials and methods

Plutella xylostella was reared on Brussels sprout plants [*Brassica oleracea* (L.) var. Gemmifera] at 24 ± 2 °C, $30 \pm 10\%$ r.h., and L16:D8. Cages were 38×38 cm in size and 58 cm high, and the ceiling and three side walls were covered with fine metal mesh. The fourth wall was closed by a plexiglas door. For oviposition, adult *P. xylostella* were placed in a cage containing 4–5-week-old plants. After 24 h, the plants were removed and placed into another cage. Plants were watered when necessary. In case the developing larvae depleted the leaf material, fresh plants were added to the cage. After completing the fourth larval stage, larvae pupated on the ceiling of the cage. Pupae were cut off with a razor-blade and either placed individually in glass vials (gustatory response) or in small groups in a separate cage (longevity) under the same climatic conditions.

Diadegma semiclausum was reared on *P. xylostella* at 23 ± 2 °C, $60 \pm 10\%$ r.h., and L16:D8. The cages were of the same type as described above for *P. xylostella*. About 30 females and 30 males of *D. semiclausum* were introduced into a cage containing Brussels sprout plants infested with L2 larvae of *P. xylostella*. In case the larvae depleted the leaf material, fresh plants were added to the cage. Parasitoid cocoons were collected and transferred to a climate chamber (21 ± 2 °C, L16:D8, and $60 \pm 10\%$ r.h.). Upon emergence, individuals of both species were only provided with water until used in experiments.

Gustatory response

Two-day-old unfed *P. xylostella* females were used to test the gustatory response. To ensure that the test insects were

water-satiated at the time of the experiment, they were provided with a wet filter paper for a period of 30 min prior to the experiments. In the experiment, one end of a filter paper strip of about 5×70 mm was dipped in a sugar solution and inserted in the vial. Each of the sugars was tested at 1 M, 0.5 M, 0.25 M, and 0.125 M. When the sugar solution was brought into contact with the antennae or tarsi of the moth, the insect either unrolled its proboscis and started feeding (feeding for more than 2 s was recorded as 'acceptance') or failed to do so (recorded as 'non-acceptance'). Each individual was tested only once.

As *D. semiclausum* survives less than 2 days without food, we tested 1-day-old unfed parasitoid females. To ensure that the parasitoid females were water-satiated, they were provided with a wet filter paper for a period of 30 min prior to the experiments. The remaining procedure was similar to the one described by Wäckers (1999) for *Cotesia glomerata*. Parasitoids were transferred to another vial, the bottom of which contained a 3 µl droplet of a sugar solution. The test vial was placed upside down on a wet filter paper in a Petri dish to avoid a concentration increase in the test solution due to evaporation. As soon as the parasitoid made contact with the sugar solution, its feeding response was recorded. The reaction was scored as acceptance (if feeding lasted more than 5 s) or rejection (contact for less than 5 s).

Differences in feeding duration thresholds were chosen intentionally to identify selective sugars which are accepted by *D. semiclausum*, but not by *P. xylostella*. To be conservative, a shorter feeding duration threshold was chosen in the case of *P. xylostella*. For each species, 30 females were tested per sugar concentration.

Longevity response

For the longevity experiment, we used cylindrical cages of 21 cm height and 14.5 cm diameter. The wall was made from a colourless acetate sheet, and plastic Petri dishes formed the base and top. The top had an opening of 10 cm in diameter covered with nylon netting for ventilation.

For both *P. xylostella* and *D. semiclausum*, 4–6 cages with 5–8 females each were prepared to test a minimum number of 30 individuals per sugar (0.5 M in 2.5 ml Eppendorf tubes) and control (water only in 2.5 ml Eppendorf tubes). Females were 0–24 h old and presumably mated. A cotton wick, leading through a hole in the lid of the Eppendorf tube provided access to the sugar solution or water. Sugar solutions were changed every 2–3 days to avoid microbial growth and crystallisation due to evaporation.

Cages were placed in a climate chamber at 22 °C and L16:D8, and checked for surviving individuals once a day. Individual females were considered as replicates in the statistical analysis. The effect of the sugars tested on

Table 1 Response of the herbivore *Plutella xylostella* and its parasitoid *Diadegma semiclausum* to a range of sugars at decreasing concentrations. For each sugar concentration, 30 individuals were tested; numbers indicate percentage positive response

Sugar	<i>Plutella xylostella</i>				<i>Diadegma semiclausum</i>			
	1 M	0.5 M	0.25 M	0.125 M	1 M	0.5 M	0.25 M	0.125 M
Fructose	97	97	96	90	87	83	83	90
Glucose	73	71	40	10	100	90	63	33
Lactose	7	7	3	7	27	23	7	0
Maltose	100	97	97	75	83	73	93	66
Melezitose	100	100	97	95	87	87	90	97
Melibiose	73	7	0	0	33	17	17	10
Raffinose	97	60	17	0	70	23	10	27
Sucrose	97	100	100	90	90	90	70	83
Trehalose	0	17	20	10	80	70	77	50

longevity was analysed using one-way analysis of variance (SPSS 11.0). Any individual that escaped or was killed during the experiment was excluded from the analysis ($n = 4$ for *D. semiclausum*). Multiple comparisons were performed using Tukey's HSD test.

Results

Gustatory response

Plutella xylostella showed a high response to four of the nine sugars (fructose, maltose, melezitose, and sucrose) at all concentrations. In the case of glucose, melibiose, and raffinose, the response to the 1 M solution was high, but the response dropped with decreasing concentration. In the case of lactose and trehalose the response was low, irrespective of the concentration (Table 1).

Diadegma semiclausum showed a high response to five of the nine sugars (fructose, maltose, melezitose, sucrose, and trehalose) irrespective of the concentration. In the case of glucose and raffinose the response was high to the 1 M solution, but dropped with decreasing concentration.

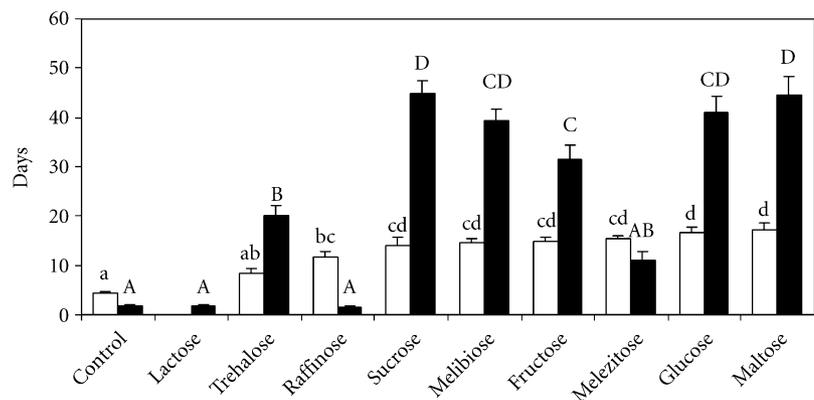
Lactose and melibiose elicited low responses, even at high concentrations (Table 1).

Longevity

Plutella xylostella longevity differed distinctly between individuals provided with different sugar solutions ($F = 16.5$, d.f. = 8, $P = 0.000$). Individuals fed a trehalose diet did not show an increase in longevity relative to control individuals kept with only water. All other sugars significantly increased longevity compared to the control. Glucose and maltose yielded the highest average longevity, but differed significantly only from the control, lactose, trehalose, and raffinose (Figure 1).

Diadegma semiclausum also showed significant differences in average longevity when provided with different sugar solutions ($F = 65$, d.f. = 9, $P = 0.000$). Three sugars (lactose, raffinose, and melezitose) failed to increase longevity over the water control. The other six sugars significantly increased longevity. Sucrose and maltose yielded the highest average longevity, but did not differ significantly from melibiose and glucose (Figure 1).

Figure 1 Longevity (mean + SE) of *Plutella xylostella* (white bars) and *Diadegma semiclausum* (black bars) when provided with water only (control) or one of nine different sugars (0.5 M). Treatments within insect species labelled with the same letter are not significantly different (ANOVA, Tukey's test; $\alpha = 0.05$).



Discussion

Gustatory response

The herbivore *P. xylostella* accepts a wide range of sugars, in contrast to other lepidopteran herbivores feeding on cabbage. In *Pieris brassicae* (Romeis & Wäckers, 2000) and *Pieris rapae crucivora* (Kusano & Sato, 1980) feeding is mainly, if not exclusively, elicited by sucrose and to a lesser extent by fructose. Percival (1961) found that plant families with deep-tubed flowers tend to produce sucrose-rich nectar, whereas those with open or shallow-tubed flowers tend to be hexose-rich. The sugar acceptance of *P. xylostella* and *Pieris* spp. on a gustatory level correlates with the flower visited by these herbivores in the field. Observations on standardised flower plots indicated that *P. xylostella* visits a broad range of flower species having exposed as well as hidden nectar, whereas *P. rapae* and *P. brassicae* visit a restricted number of flower species with hidden nectar (K. Winkler, 2005). Choosing selective food plants which benefit the natural enemy but not the herbivore, is therefore more difficult for *P. xylostella* than for *P. rapae* and *P. brassicae*.

The parasitoid *D. semiclausum* also responds to a wide range of sugars. In contrast to *P. xylostella*, the parasitoid showed a positive response to the honeydew sugar trehalose. This gustatory response might facilitate the exploitation of honeydew as a ubiquitous food source.

Compared with data from the parasitoid *C. glomerata* (Wäckers, 1999), *D. semiclausum* responds to a broader range of sugars. Sucrose, fructose, and glucose elicited high responses in both species. The response to maltose, melezitose, and trehalose was high in *D. semiclausum* but moderate in *C. glomerata*. *Diadegma semiclausum* showed a moderate response to lactose, raffinose, and melibiose, sugars to which *C. glomerata* did not respond at all. The egg parasitoid *Anaphes iole* showed strong responses to sucrose, maltose, glucose, and melezitose. This species is less sensitive to fructose and responded poorly to trehalose (Beach et al., 2003).

Longevity response

Both the herbivore and the parasitoid showed a prolonged longevity on a wide range of sugars. This is in accordance with many reports stressing the importance of carbohydrate-rich foods for adult insects. However, in the current study, the food supply had a far more pronounced effect on the life span of the parasitoid (up to a 24-fold increase) as compared to the herbivore (up to a fourfold increase). A similar difference in effect was found for the herbivore *P. brassicae* (threefold) and its parasitoid *C. glomerata* (15-fold) (Wäckers, 2001).

There is limited information available on the longevity of lepidopteran species exposed to sugars other than sucrose. Like *P. xylostella*, *P. brassicae* lived significantly longer on

sucrose, fructose, glucose, and raffinose (Romeis & Wäckers, 2000). Whereas melibiose decreased the life span of *P. brassicae* compared to the control, *P. xylostella* survived well on this sugar.

Diadegma semiclausum did not survive long on raffinose and lactose. Inability to use these two sugars was also found for the parasitoid *C. glomerata* and honeybees (Wäckers, 2001, and references therein). The longevity of *D. semiclausum* on melibiose was as good as on glucose and fructose. Although this sugar has been qualified as unsuitable for bees, it seems to be suitable for parasitoids like *C. glomerata*, as well as some Diptera (Wäckers, 2001, and references therein).

Similar to the differences in the gustatory response, the honeydew sugar trehalose has a disparate effect on the longevity of the two species tested here. While *P. xylostella* did not obtain a measurable longevity bonus from trehalose as compared to water, *D. semiclausum* showed a significantly longer life span on this sugar (20 days) than on water (1.8 days). Nevertheless, the increase in life span on trehalose was not as substantial as on fructose, glucose, sucrose, maltose, or melibiose. The impact of melezitose also differed between the two species. While *P. xylostella* survived on melezitose as long as on sucrose, this sugar did not extend *D. semiclausum* survival beyond control levels. The effect of trehalose and melezitose on longevity has been tested in two other parasitoids. *Bathyplectus curculionis* survival on trehalose and melezitose was as great as on sucrose and honey, but shorter than on glucose or fructose (Jacob & Evans, 2004). In *C. glomerata* the increase in life span was highest on sucrose, fructose, and glucose, moderate on melezitose and lowest on trehalose, but still significantly higher than in the control (Wäckers, 2001). Our data confirm the overall pattern that honeydew-specific sugars appear to be less suitable as food sources, compared to the nectar sugars sucrose, fructose, and glucose (Wäckers, 2000). However, the differences in sugar utilisation between species demonstrates that we can not implicitly generalise, even within an order or family.

Relationship between gustatory response and longevity

Plutella xylostella showed a good fit between gustatory response and longevity, as it showed the highest responses to fructose, maltose, melezitose, and sucrose, which are also suitable in increasing longevity. The unsuitable sugar trehalose, on the other hand, did not elicit a feeding response. In this case we do not know whether the short longevity is due to the lack of sugar uptake or due to the poor nutritional suitability of this sugar. Melibiose is somewhat exceptional, as it evoked only a weak response (at lower concentrations), but appeared to be suitable for increasing longevity.

In addition, *D. semiclausum* showed a general fit between gustatory response and longevity. In this species there are two clear outliers. As in *P. xylostella*, melibiose elicited only a weak response, but appeared to be suitable for increasing longevity. In contrast, the gustatory response to melezitose was as high as to sucrose, but survival was significantly poorer. The phenomenon that sugars elicit a feeding response without being nutritionally suitable has been reported for a number of other insects (Dethier et al., 1956; Dethier, 1968; Nettles & Burks, 1971; Romeis & Wäckers, 2002).

Providing food sources in the field to boost biocontrol

The limited ability of parasitoids to exploit flowers can restrict their longevity in nature as well as in agroecosystems. As *D. semiclausum* survives less than 2 days without food, it is fully dependent on carbohydrate feeding to achieve at least some of its reproductive potential. It is quite probable that these parasitoids feed on honeydew in the field (Wäckers & Steppuhn, 2003), even though this might be a suboptimal food (Leius, 1961; Elliot et al., 1987; Wäckers, 2001).

Providing natural sugar sources or applying sugar sprays to crops is one possible approach within conservation biological control to attract and/or retain beneficial insects (McEwen & Liber, 1995; Cañas & O'Neil, 1998). The differences in gustatory response between the herbivore and its parasitoid as reported in this study, show the potential for the application of selective sugar sources. At the same time it also reveals the risk that indiscriminate use of sugar sources may result in a reverse selectivity: supporting herbivores without benefiting their antagonists. Raffinose, which evoked a gustatory response in both species but only prolonged life span in the herbivore, might be an example that may result in such a negative scenario. In contrast, trehalose, which evoked a gustatory response and prolonged life span in the parasitoid but not in the pest, would selectively promote the parasitoid. As parasitoid longevity on this sugar was considerably longer than on water, provision of this sugar in the field might result in strongly increased lifetime fecundity, and thus, in better pest reduction.

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