

# Sugar feeding by coccinellids under field conditions: the effects of sugar sprays in soybean

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Received: 26 July 2010 / Accepted: 18 November 2010 / Published online: 5 December 2010  
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**Abstract** Sucrose was applied weekly throughout the growing season at three US locations (South Dakota [SD], Maryland [MD], and Kentucky [KY]), and coccinellids and aphids (*Aphis glycines* Matsumura [Hemiptera: Aphididae]) were sampled 24 h later. Total coccinellid densities were 50–77% greater in sugar-sprayed soybean than in untreated plots. *Coccinella septempunctata* L., *Hippodamia convergens* Guérin-Ménéville, and *Harmonia axyridis* Pallas were more abundant where sugar was applied. *Coleomegilla maculata* (DeGeer) was found in equally low numbers in all treatments. Aphid densities were similar in both treatments, and only reached

economically threatening levels in SD. Coccinellids digested sugar meals within 1 h of consumption (measured using the cold anthrone test). Despite this narrow window of detection, field-collected coccinellids frequently tested positive for fructose. Under natural conditions, sugar is commonly ingested by coccinellids and sugar sprays increase coccinellid densities and their consumption of sugar. Sugar sprays did not enhance biological control of aphids in this experiment.

**Keywords** Anthrone · *Aphis glycines* · Conservation biological control · Food spray · Omnivory · Non-prey foods

Handling Editor: Patrick De Clercq

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## Introduction

Coccinellids feed on a wide range of sugar sources under field conditions (Lundgren 2009a). In particular, they are regular visitors to nectaries, both floral (Bugg 1987; Nalepa et al. 1992; Patt et al. 1997) and extrafloral (Pemberton and Vandenberg 1993), and honeydew coated plant surfaces. Honeydew functions as a contact kairomone for sternorrhynchan-feeding coccinellids, which promotes area-restricted search and oviposition (Carter and Dixon 1984; Evans and Dixon 1986; van den Meiracker et al. 1990), and it also is a food for coccinellid larvae and adults (Putman 1955; Yinon 1969).

Sugar feeding improves the fitness and performance of coccinellids. The flight capacity of *Coccinella*

*septempunctata* L. is increased by sugar feeding (Nedved et al. 2001). In the absence of prey, sugar consumption can increase the survival and longevity of coccinellids (Matsuka et al. 1982; Dreyer et al. 1997; Lundgren 2009a). Feeding on simple carbohydrates alone cannot support coccinellid reproduction, but diets that contain both sugar and prey improve fecundity and other adult performance measurements compared to prey alone (Evans 2000; Lundgren 2009a). Specifically, sugar consumption reduces preoviposition period and increases survival, while decreasing egg resorption during reproductive diapause (Smith and Krischik 1999; Reznik and Vaghina 2006).

Supplementation of available sugar in cropping systems has long shown potential as a means of attracting, conserving and enhancing natural enemies in cropland. Methods of sugar provisioning include planting non-crop plants that produce nectar near crop fields, selection of nectaried crop varieties, and applying food sprays (Lundgren 2009b). Techniques such as habitat manipulations that provide nectar-bearing plants (Agnew et al. 1982; Bugg et al. 1991; Patt et al. 1997), and application of food sprays (Hagen et al. 1970; Wade et al. 2008; Lundgren 2009b; Obrycki et al. 2009) increase coccinellid densities. But no studies have attempted to quantify the degree to which these sugar-augmentation strategies affect the feeding behavior of coccinellids under natural conditions, or indeed whether coccinellids consume sugar in the field at all.

In this study we examined the numerical and feeding response of selected predaceous coccinellid species to weekly applications of sucrose in soybean at three locations across the United States. Soybean was selected as an experimental system because it is a major component of the landscape in the United States, and coccinellids are important predators of the invasive soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae). Specific hypotheses that we tested are that (1) common agricultural coccinellids regularly consume sugar under natural conditions, and (2) early-season sugar sprays aggregate coccinellids to soybean fields, and delay the onset of soybean aphid populations. To test these hypotheses, field sampling was paired with gut content analysis using the cold anthrone test as applied recently for other natural enemy groups (Heimpel et al. 2004; Lee et al. 2006; Taylor and Pfannenstiel 2008). Our intent was to provide information on how an important predator group responds to a common nutrient

in agroecosystems, and to determine if this feeding behavior can be exploited to improve biological control of a serious crop pest.

## Methods

### Field

Coordinated research was replicated at locations in Kentucky (KY), Maryland (MD), and South Dakota (SD). In SD, research was conducted at the Eastern South Dakota Soil and Water Research Farm near Brookings, SD (latitude, longitude: 44.348, -96.811). Soybean (var. Asgrow 1702) was planted on 15-May 2009. In Kentucky at Spindle Top Farm (latitude, longitude: 38.13, -84.52) soybean (Asgrow 4605) was planted on 22-May 2009. In Maryland soybean (var. Doebler's TS219OR) was planted at North Farm, Beltsville Agricultural Research Center (latitude, longitude: 39.034, -76.932), on 2-June 2009. At all locations row spacing was 76 cm and glyphosate was applied for weed control. Plots (5 × 5 m each) were arranged in a randomized complete block design with three replicates in KY and MD and four in SD. These plots were embedded in larger soybean fields with at least 50 m separating plots.

At all locations, weekly applications of 15% sucrose solutions (790 l ha<sup>-1</sup>, total volume of 2 l) were evenly applied to the sugar-sprayed plots beginning on 22-June 2009 (SD and KY) and 6-July 2009 (MD). Sugar was reapplied until soybean aphids exceeded the economic injury level of 690 aphids per plant (Ragsdale et al. 2007) in SD. Plots were sampled on days without rain, after the morning dew had left the plants (i.e., in the afternoon).

### Sampling and lady beetle collection

All plots were sampled for insects 24 h after sugar application using whole plant counts for soybean aphids and sweep samples for coccinellids. To maximize efficiency during aphid sampling, 20 randomly selected plants per plot were examined when 0–80% of plants were infested, ten plants when 81–99% of plants were infested, and five plants were sampled at 100% aphid infestation. Fifty sweep samples (38 cm diameter sweep net) were collected in each plot and coccinellids were counted and identified to species.

Aphids per plant and lady beetles per 50 sweeps were square-root transformed for each location, and treatment means were compared using repeated-measures ANOVA (with treatment as the between-subject variable and sample date as the within-subjects variable). Additionally, seasonal sums of total lady beetles captured per plot at each location, and individual lady beetle species per plot at each location, were compared between treatments and among study locations using two-factor ANOVA (with treatment and location as factors).

All adult lady beetles were placed in individual 1.5 ml centrifuge tubes and stored on dry ice as they were transported to the laboratory. The samples were then stored at  $-20^{\circ}\text{C}$  until their guts were analyzed. In SD, each plot was visually examined for 4 min after sampling, and all lady beetles were hand-collected and the guts of these beetles were also analyzed. Also in SD, coccinellids were collected from other habitats (e.g., wheat, field margins) and tested for sugar feeding.

#### Anthrone test for detection of sugar feeding

Gut content analyses of sugar contents were conducted using methods of van Handel (1985). Thawed coccinellids were rinsed in water to remove any sugar contamination. The entire gut was then dissected in Ringer's solution (0.75 g  $\text{NaCl}_2$ , 0.35 g KCl, 0.28 g  $\text{CaCl}_2$  in 1 l  $\text{H}_2\text{O}$ ) using heat-sterilized tools, and the excised gut was placed directly into 50  $\mu\text{l}$  of 2% sodium sulphate buffer. The guts were ground using a sterile, plastic pestle after the addition of 450  $\mu\text{l}$  of methanol–chloroform (2:1). Samples were centrifuged at 13,200 rpm for 4 min, and the supernatant was split between two glass test tubes (200  $\mu\text{l}$  each). The fluid in each subsample was evaporated to 25  $\mu\text{l}$  at  $90^{\circ}\text{C}$ . Samples were cooled to room temperature, and the subsamples were mixed with either 975  $\mu\text{l}$  of anthrone reagent (318 mg of anthrone [Sigma–Aldrich #319899] dissolved in diluted sulfuric acid [152 ml sulfuric acid and 60 ml water]) or diluted sulfuric acid solution (152 ml sulfuric acid and 60 ml water), and then were incubated at  $34^{\circ}\text{C}$  in a sand bath for 1 h. At this temperature the anthrone reagent changes from yellow to dark green/blue exclusively when in contact with fructose. An aliquot (200  $\mu\text{l}$ ) of each sample was placed on a 96-well plate and optical density was read at 630 nm using a spectrophotometer ( $\mu\text{Quant}$ , BioTek Instruments Inc., Winooski, VT, USA). The

absorbance of the subsample that received sulfuric acid only (i.e., background absorbance) was subtracted from the value of the subsample that received anthrone reagent. Lady beetles of each species (consolidated from at least 25 individuals) were starved for 24 h, and their guts were dissected and centrifuged as described above to be used as negative controls (e.g., unfed controls). At least two wells of each negative control (of each lady beetle species) were included on each plate, and the standard deviation of this control series was calculated for each beetle species on each plate. A sample was considered positive for fructose if the difference in the optical density of the sample exceeded that of its no-anthrone control difference by a threshold value (specifically, three times the standard deviation of the starved beetle control series for each plate, e.g., Lee et al. 2006; Harwood et al. 2007).

The mean proportion of coccinellids testing positive for fructose was tested on arcsine-transformed proportions using a two-factor ANOVA (location and treatment being the factors). This test was not conducted for KY as too few individuals were collected from the untreated plots to serve as a comparison to those collected in the sugar-sprayed soybean.

#### Sugar feeding laboratory assay

Independent laboratory feeding assays were performed to determine the relative rates of fructose digestion by targeted coccinellids (i.e., *C. septempunctata*, *Coleomegilla maculata* [DeGeer], *Harmonia axyridis* Pallas, and *Hippodamia convergens* Guérin-Ménéville). Coccinellids were starved individually in 4-cm diameter plastic Petri dishes for 24 h prior to the assay (they were only provided a water-saturated cotton wick). Each beetle was fed a 15% sucrose solution for ten uninterrupted seconds. Individuals (10–12 per time increment) were then placed in clean 1.5-ml centrifuge tubes and randomly assigned an execution time of 0, 0.5, 1, 2, 4, and 6 h post-ingestion. At the designated times, beetles were frozen at  $-20^{\circ}\text{C}$ , where they remained until they were subjected to the cold anthrone test (as described above). Ten to twelve individuals from each species were starved for 24 h and subjected to the same procedures as those fed sugar solution. The absorbance of these negative controls plus three times their standard deviation was used as a threshold value to

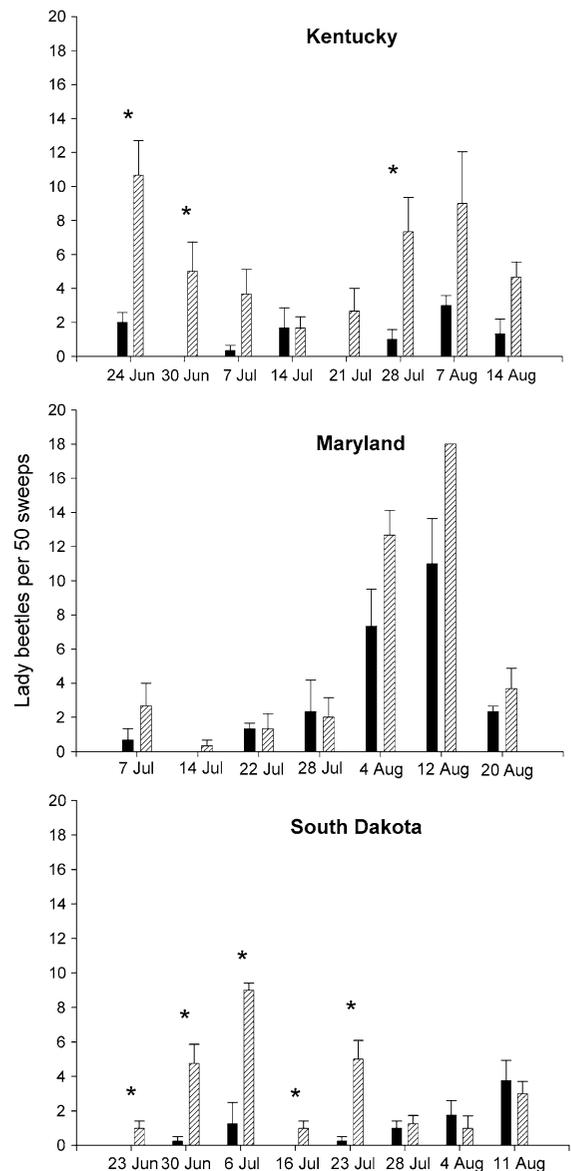
determine how long sugar could be detected in an individual after a small sugar meal.

## Results

### Numerical response of aphids and coccinellids to sugar sprays

More adult lady beetles were collected in the sugar-sprayed treatments than in the unsprayed treatments, although there were differences among locations (treatment:  $F_{1,14} = 46.26$ ,  $P < 0.01$ ; location:  $F_{2,14} = 12.44$ ,  $P < 0.01$ ; interaction:  $F_{2,14} = 2.80$ ,  $P = 0.09$ ). Specifically, more coccinellids were collected in the sugar-sprayed treatments in SD ( $F_{1,6} = 50.74$ ,  $P < 0.01$ ) and KY ( $F_{1,4} = 35.64$ ,  $P < 0.01$ ), but numbers were similar in the two treatments in MD ( $F_{1,4} = 3.21$ ,  $P = 0.15$ ; Fig. 1). In both SD and KY there was a significant effect of sample date on coccinellid density (KY:  $F_{7,28} = 4.67$ ,  $P < 0.01$ ; SD:  $F_{7,42} = 9.61$ ,  $P < 0.01$ ), but sample date interacted with the observed treatment effect only in SD (KY:  $F_{7,28} = 2.21$ ,  $P = 0.06$ ; SD:  $F_{7,42} = 9.00$ ,  $P < 0.01$ ; Fig. 1).

Lady beetle species responded differently to the application of sugar. *Coccinella septempunctata* (treatment:  $F_{1,14} = 37.09$ ,  $P < 0.01$ ; location:  $F_{2,14} = 57.21$ ,  $P < 0.01$ ; interaction:  $F_{2,14} = 4.2$ ,  $P = 0.04$ ), *H. convergens* (KY and SD only) (treatment:  $F_{1,13} = 42.46$ ,  $P < 0.01$ ; location:  $F_{1,13} = 49.54$ ,  $P < 0.01$ ; interaction:  $F_{1,13} = 27.23$ ,  $P < 0.01$ ), and *H. axyridis* (treatment:  $F_{1,14} = 26.19$ ,  $P < 0.01$ ; location:  $F_{2,14} = 23.75$ ,  $P < 0.01$ ; interaction:  $F_{2,14} = 9.16$ ,  $P < 0.01$ ) were more abundant in the sugar-sprayed soybeans than in the untreated plots (Table 1). Only in SD, where *H. convergens* was relatively abundant, did we detect increased densities of this species in the sugar-sprayed soybean. *Harmonia axyridis* was more abundant in the sugar-sprayed soybean in both KY and SD, but this difference was not seen in MD. Conversely, numbers of *C. maculata* were unaffected by sugar availability (treatment:  $F_{1,14} = 0.10$ ,  $P = 0.76$ ; location:  $F_{2,14} = 1.22$ ,  $P = 0.32$ ; interaction:  $F_{2,14} = 0.76$ ,  $P = 0.48$ ; Table 1). The densities of other coccinellid species sampled (see Table 1) were similar between sugar-sprayed and untreated soybean in all field locations (treatment:  $F_{1,14} = 2.47$ ,  $P =$



**Fig. 1** Mean (+SE) seasonal abundance of lady beetles in sugar sprayed (hatched bars) and untreated (bold bars) soybean. “\*” represents that treatment means are significantly different on that sampling date ( $\alpha = 0.05$ )

0.14; location:  $F_{2,14} = 1.51$ ,  $P = 0.25$ ; interaction:  $F_{2,14} = 1.60$ ,  $P = 0.24$ ).

Coccinellid larvae were only sampled in MD and SD, and only on the final two sampling dates. There were more larvae collected in SD than MD but no difference was detected between treatments (treatment:  $F_{1,10} = 0.01$ ,  $P = 0.94$ ; location:  $F_{1,10} = 4.89$ ,

**Table 1** Mean ( $\pm$ SE) seasonal abundance of lady beetle species and mean frequency of positive detection of sugar feeding in soybean treated with a sugar spray and untreated soybean in three states

Species	Location	Seasonal mean		Percentage of positive for fructose	
		Sugar spray	Untreated	Sugar spray	Untreated
<i>Coccinella septempunctata</i>	Kentucky	0.50 $\pm$ 0.07a	0.04 $\pm$ 0.04b	66.67 $\pm$ 17.64	–
	Maryland	2.28 $\pm$ 0.22a	1.09 $\pm$ 0.25b	78.48 $\pm$ 6.09a	14.85 $\pm$ 5.70b
	South Dakota	0.66 $\pm$ 0.11a	0.19 $\pm$ 0.08b	94.74 $\pm$ 3.24a	25.00 $\pm$ 25.00b
	All	1.10 $\pm$ 0.27a	0.42 $\pm$ 0.17b	87.78 $\pm$ 4.37a	20.65 $\pm$ 13.69b
<i>Coleomegilla maculata</i>	Kentucky	0.17 $\pm$ 0.11	0.04 $\pm$ 0.04	25.00 $\pm$ 25.00	–
	Maryland	0.14 $\pm$ 0.08	0.24 $\pm$ 0.05	55.00 $\pm$ 5.00a	25.00 $\pm$ 25.00b
	South Dakota	0.25 $\pm$ 0.09	0.22 $\pm$ 0.09	90.00 $\pm$ 10.00a	19.44 $\pm$ 10.01b
	All	0.19 $\pm$ 0.05	0.17 $\pm$ 0.05	78.33 $\pm$ 9.81a	21.67 $\pm$ 9.72b
<i>Harmonia axyridis</i>	Kentucky	4.67 $\pm$ 0.85a	1.04 $\pm$ 0.15b	54.66 $\pm$ 9.57	50.00 $\pm$ 50.00
	Maryland	3.24 $\pm$ 0.38	2.00 $\pm$ 0.46	57.91 $\pm$ 5.95a	15.61 $\pm$ 6.90b
	South Dakota	0.72 $\pm$ 0.09a	0.31 $\pm$ 0.15b	90.06 $\pm$ 6.48a	60.11 $\pm$ 4.05b
	All	2.66 $\pm$ 0.61a	1.04 $\pm$ 0.27b	76.28 $\pm$ 7.70a	41.04 $\pm$ 9.61b
<i>Hippodamia convergens</i>	South Dakota	1.09 $\pm$ 0.14a	0.16 $\pm$ 0.03b	83.56 $\pm$ 8.11a	22.22 $\pm$ 10.39b
Other	Kentucky <sup>a</sup>	0.21 $\pm$ 0.04a	0.04 $\pm$ 0.04b	16.67 $\pm$ 16.67	–
	Maryland <sup>b</sup>	0.14 $\pm$ 0.08	0.24 $\pm$ 0.24	33.33 $\pm$ 33.33	0.00 $\pm$ 0.00
	South Dakota <sup>c</sup>	0.53 $\pm$ 0.19	0.16 $\pm$ 0.03	38.61 $\pm$ 10.69	16.67 $\pm$ 16.67
	All	0.32 $\pm$ 0.09	0.15 $\pm$ 0.07	36.35 $\pm$ 13.87	10.00 $\pm$ 10.00

<sup>a</sup> *Cycloneda munda*

<sup>b</sup> *Brachiacantha* sp., *Cycloneda munda*, *Hippodamia convergens*, *Propylea quatuordecimpunctata*

<sup>c</sup> *Brachiacantha* sp., *Cycloneda munda*, *Hippodamia parenthesis*, *Scymnus* sp

Treatment means within a row followed by different letters are significantly different from one another ( $\alpha = 0.05$ )

$P = 0.05$ ; interaction:  $F_{1,10} = 0.00$ ,  $P = 0.95$ ). Abundances of larvae in MD were  $1.33 \pm 0.88$  and  $0.33 \pm 0.33$  larvae in sugar-sprayed plots and  $0.33 \pm 0.33$  and  $1.33 \pm 1.33$  (mean  $\pm$  SE) larvae in unsprayed plots on 12-Aug and 20-Aug, respectively. Abundances of larvae in SD were  $0.25 \pm 0.25$  and  $5.50 \pm 0.87$  larvae in sugar-sprayed plots and  $0.25 \pm 0.25$  and  $5.75 \pm 2.50$  larvae in unsprayed plots on 4-Aug and 11-Aug, respectively.

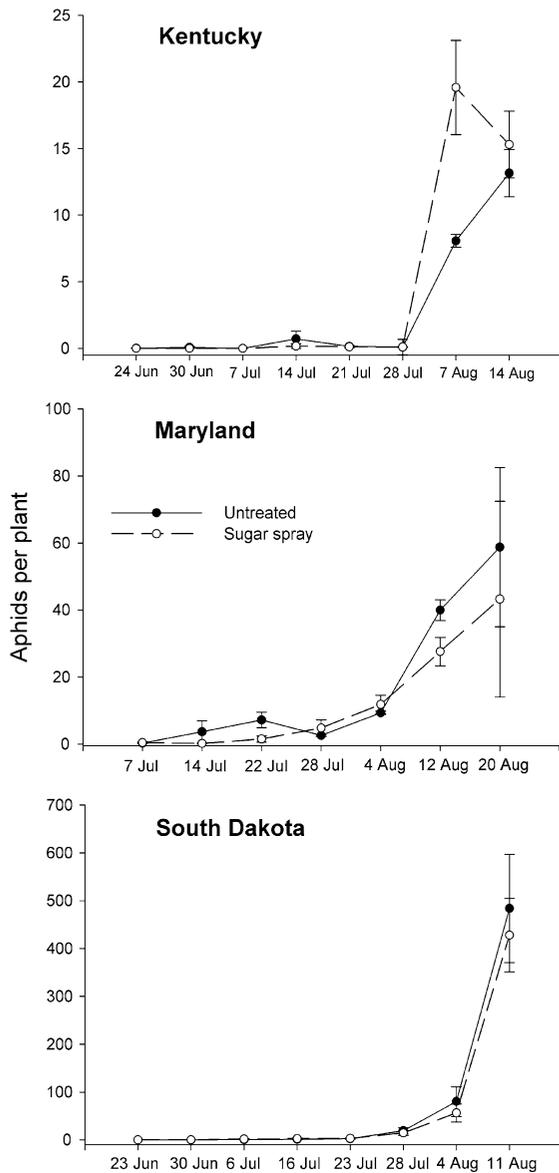
Aphid populations increased over the season (KY:  $F_{7,28} = 224.6$ ,  $P < 0.01$ ; MD:  $F_{6,24} = 14.16$ ,  $P < 0.01$ ; SD:  $F_{7,42} = 89.11$ ,  $P < 0.01$ ) and peaked in August at all locations, although densities were at least tenfold higher in SD than at the other two locations. Sugar-sprayed and unsprayed treatments had similar aphid densities at all locations (KY:  $F_{1,4} = 3.16$ ,  $P = 0.15$ ; MD:  $F_{1,4} = 1.15$ ,  $P = 0.34$ ; SD:  $F_{1,4} = 0.08$ ,  $P = 0.78$ ; Fig. 2). This lack of treatment effect was consistent over the season (KY:  $F_{7,28} = 8.42$ ,  $P < 0.01$ ; MD:  $F_{6,24} = 0.62$ ,  $P = 0.58$ ; SD:  $F_{7,42} = 0.20$ ,  $P = 0.88$ ), with the

exception of 7-Aug in KY where aphids per plant were significantly higher in the sugar-sprayed soybean ( $F_{1,4} = 14.89$ ,  $P = 0.02$ ).

Sugar feeding by lady beetles in the field and in the laboratory

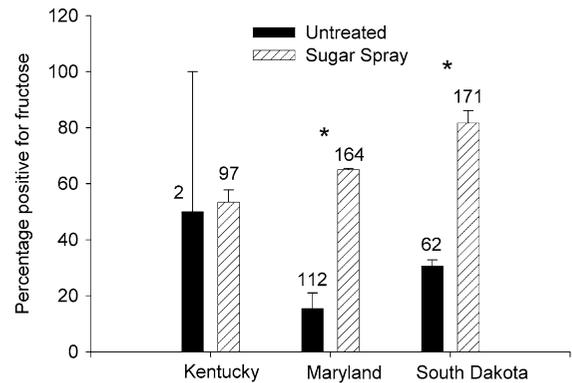
Coccinellids from sugar-sprayed plots consumed fructose more frequently than those from unsprayed plots (treatment:  $F_{1,10} = 123.37$ ,  $P < 0.01$ ; location:  $F_{1,10} = 14.09$ ,  $P < 0.01$ ; interaction:  $F_{1,10} = 0.88$ ,  $P = 0.37$ ; Fig. 3). A higher percentage of coccinellids tested positive for the presence of fructose in SD than in the other two locations. In SD, 20.6% of 165 coccinellids collected in other habitats tested positive for fructose.

Species tested positive for fructose at different frequencies (Table 1). *Coccinella septempunctata* (treatment:  $F_{1,10} = 12.35$ ,  $P < 0.01$ ; location:  $F_{1,10} = 1.80$ ,  $P = 0.21$ ; interaction:  $F_{1,10} = 0.14$ ,  $P = 0.72$ ), *C. maculata* (treatment:  $F_{1,10} = 15.72$ ,



**Fig. 2** Mean ( $\pm$ SE) seasonal abundance of *Aphis glycines* in untreated soybean and soybean treated weekly with sugar spray. Note the differences in the y-axis scales

$P < 0.01$ ; location:  $F_{1,10} = 3.82$ ,  $P = 0.09$ ; interaction:  $F_{1,10} = 3.49$ ,  $P = 0.10$ ) and *H. axyridis* (treatment:  $F_{1,10} = 18.80$ ,  $P < 0.01$ ; location:  $F_{1,10} = 20.67$ ,  $P < 0.01$ ; interaction:  $F_{1,10} = 0.34$ ,  $P = 0.57$ ) from sugar-sprayed soybean tested positive for fructose more frequently than those collected in untreated soybean (Table 1). This treatment effect was also seen in *H. convergens* in SD ( $F_{1,7} = 14.73$ ,  $P < 0.01$ ; Table 1). There was no difference in the



**Fig. 3** Mean ( $\pm$ SE) percentage of individual lady beetles collected in sugar-sprayed and untreated soybean that tested positive for the presence of fructose. “\*” indicates significantly different treatment means ( $\alpha = 0.05$ ), and the number of lady beetles assayed are indicated above each bar

proportion testing positive for sugar feeding in other lady beetle species collected in MD and SD (treatment:  $F_{1,10} = 1.44$ ,  $P = 0.26$ ; location:  $F_{1,10} = 0.00$ ,  $P = 0.98$ ; interaction:  $F_{1,10} = 0.24$ ,  $P = 0.63$ ; Table 1).

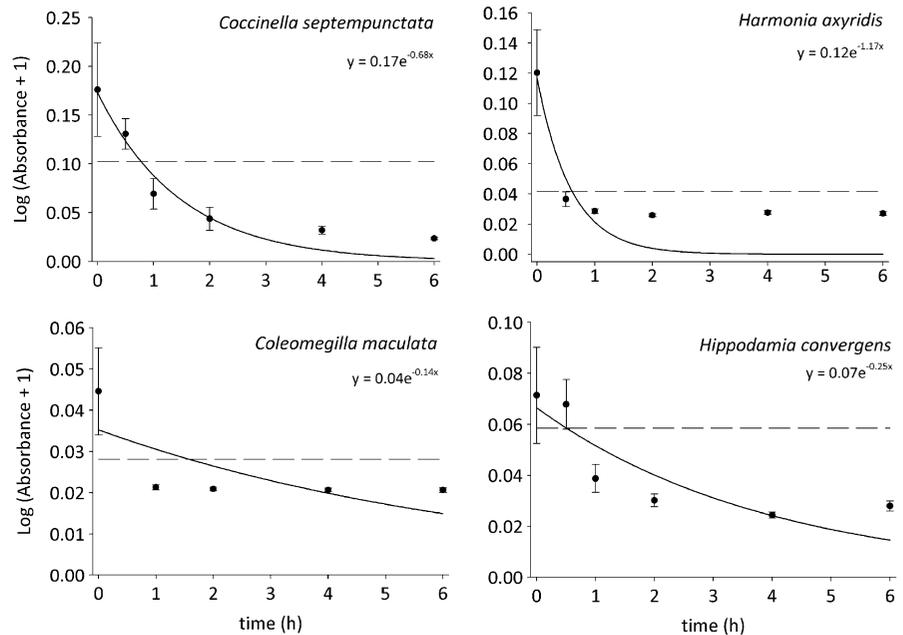
#### Sugar feeding laboratory assay

Sucrose was completely digested within 1–2 h of ingestion (Fig. 4). With the criteria for a positive being the average of 24 h starved individuals plus three standard deviations, the window for detection of sugar ingested in a 10 s feeding event in a starved beetle is less than 1 h (Fig. 4).

#### Discussion

This study demonstrates that adult coccinellids commonly feed on sugar in the field. The addition of a sucrose spray in soybean elevated the abundances of coccinellids, and the availability of sugar often affected the feeding behavior of this group. Thus, the availability of sugar within a habitat functions by both altering the foraging behavior of lady beetles (Carter and Dixon 1984; Van Der Werf et al. 2000; Křivan 2008), and serve as an important component of their diets under natural conditions, but both of these patterns depend on the coccinellid species in question.

**Fig. 4** Detection of fructose (using the cold anthrone test) in four species of lady beetles fed sucrose in the laboratory. Optical densities were recorded at 630 nm. Error bars represent SE. Dashed lines represent detection thresholds determined as sum of average of 12 starved individuals of the same species and three times the standard deviation. Regression lines represent exponential decay rates



Several species of aphidophagous coccinellids were more abundant in soybean that had weekly applications of sucrose sprays than in untreated soybean, a trend commonly observed in other cropping systems (Ewert and Chiang 1966; Schiefelbein and Chiang 1966; Evans and Swallow 1993; Evans and Richards 1997; Wade et al. 2008; Lundgren 2009b). When all locations were examined together, coccinellids were much more abundant in sugar-sprayed soybean than in untreated soybeans. This treatment effect was seen in KY and SD but not in MD. Even though coccinellid densities were not significantly different between treatments in MD, it is notable that coccinellids were more abundant on sugar-sprayed soybean on all but one sampling date. The lack of treatment effect in MD was largely driven by *H. axyridis*, which had equivalent densities in the two treatments. In KY and SD, this species was more abundant in sugar-sprayed soybean. The effect of increased numbers of coccinellids in the sugar-sprayed soybean in SD waned late in the season. This corresponds to an increase in the aphid populations in both treatments, as well as in the surrounding soybean. We found that the effects of sugar applications diminished as aphid populations increased; this trend is in accord with observations of Schiefelbein and Chiang (1966) and Carlson and Chiang (1973), who reported that sugar sprays do not concentrate coccinellids in corn when aphids were at

high densities. It is also noteworthy that coccinellids were fairly rare in soybeans during the first part of the growing season of our study, and the trends we observed may be stronger in more coccinellid-rich habitats.

Although coccinellids frequently consumed fructose under untreated conditions, they ate it more frequently when soybeans were treated with sucrose than when soybeans were untreated (Fig. 3). Depending on location, species sampled, and time of year, 10–60% of the coccinellids collected from untreated soybean consumed sugar. These results are particularly significant considering that all of the coccinellid species assayed in the laboratory digested sugar meals within 1 h of ingestion (Fig. 4). Gut analyses of this nature need to be interpreted with care, since the digestion, and thus detection, of food in coccinellids is influenced by numerous factors (Sunderland 1996; Weber and Lundgren 2009b; Lundgren and Weber 2010). Nevertheless, our data strongly suggests that these insects must consume sugar very frequently for us to register such a large proportion of positive samples, even within soybeans that did not receive sugar supplements. This suggests that sugar is likely an important dietary component for coccinellids in agroecosystems.

Within the greater coccinellid community, individual species responded differently to the application of sugar in both their numbers and in their

feeding behavior. As mentioned earlier, *H. axyridis* was equally abundant between the treatments in MD, but was more abundant in sugar-sprayed soybean in both SD and KY. *Coccinella septempunctata* was more abundant in the sugar-sprayed plots at all locations, as was *H. convergens* in SD (the only location where this species was abundant). In contrast, similar densities of *C. maculata* were observed in the two treatments at all locations, but this species was infrequently collected. As for their feeding behavior, *H. axyridis* collected from untreated soybean were more frequently positive for sugar feeding than other coccinellids (Table 1). This is especially stark in comparison to *C. septempunctata*. It may be that *H. axyridis* is more vagile than the other species, and the individuals we collected may have recently been in a different habitat than the untreated soybean. Coccinellids are known to have very different diets under field conditions, depending on relative food availability, species-specific characteristics, and landscape structure (Triltsch 1999; Harmon et al. 2000; Lundgren et al. 2004; Weber and Lundgren 2009a; Davidson and Evans 2010). We believe that all of these intrinsic and extrinsic characteristics could explain the species-specific responses observed in numerical and feeding responses in this study.

Despite elevated coccinellid densities in the sugar-spray plots, aphid densities were similar to the untreated soybean at all points in the season. Therefore, early-season application of sugar sprays is likely not a viable option for increasing early season soybean aphid control. Soybean aphids may not be a good prey item for coccinellids due to their defenses or their potentially low nutritional quality (Toft 2005; Butler and O'Neil 2006). For example, a recent study showed that *C. maculata* did not digest soybean aphids consistently over their larval life like they did other foods (Lundgren and Weber 2010). It is also worth noting that provision of sugar does not necessarily enhance biological control since parasitism rates are sometimes unaffected when a habitat is sprayed with sugar sprays (Lundgren et al. 2002; Rogers and Potter 2004), and the sudden abundance of other non-prey foods can detract from predation in other systems (Dennis and Sotherton 1994; Cottrell and Yeargan 1998; Lundgren et al. 2004; Spellman et al. 2006). Clearly, more research on how the availability of non-prey foods (including sugar) affects

predation and foraging behavior is required in order to optimally conserve natural enemies within cropland.

**Acknowledgments** The authors are grateful for the technical help of Janet Fergen, Mallory Johnson, and Chloe Kruse at the South Dakota location. In Maryland, Keri Athanas, Holly Badin, Meiling Webb, and Michael Athanas performed field sprays, samplings and collections. Thanks also to BARC Farm Crew for planting the crop in spite of unfavorable weather. In Kentucky, we thank Sarah Thompson and Karindah Sudarmadji for assisting in the field and laboratory. We also thank Dr. Ricardo Bessin for accommodating our use of soybean fields. J. P. Michaud (Kansas State University) and Jana Lee (USDA-ARS, Corvallis, OR) provided helpful comments on an earlier draft of this manuscript. Mention of any proprietary products does not constitute endorsement by the USDA.

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