NECTAR AVAILABILITY AND PARASITOID SUGAR FEEDING

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INTRODUCTION

Habitat diversification can potentially benefit natural enemies by providing alternative prey, a suitable microclimate, or nectar and pollen (Landis *et al*., 2000). Laboratory and field cage studies demonstrate that parasitoids with access to sugar have greater longevity, fecundity, and more female-biased sex ratios than starved parasitoids (Idris and Grafius, 1995; Dyer and Landis, 1996; Berndt *et al*., 2002). Many parasitoids have been observed to feed on floral nectar in fields (Jervis *et al*., 1993), and crops with nearby flowering vegetation have higher parasitism rates (Landis and Haas, 1992; Zhao *et al.*, 1992; Stephens *et al*., 1998). These studies have led to the hypothesis that diversifying fields with nectar-producing floral vegetation would improve parasitism rates; however, the proportion of parasitoids that utilize floral nectar in these diversified fields is largely unknown. Parasitoids may not feed on nectar in the field as readily as in laboratory and field cage experiments where they are given ample nectar supplies and have no other competitors removing the nectar. Also, the higher parasitism rates in diversified versus simplified habitats may be related to differences in microclimates or in host densities (Baggen and Gurr, 1998) rather than to sugar feeding. In order for floral nectar sources to benefit parasitoids, the nectar supply should be readily available when parasitoids are active and parasitoids must feed from the source. The objectives of this study were (1) to determine the availability of nectar from buckwheat plantings to parasitoids throughout the day and (2) to quantify the proportion of parasitoids feeding from this sugar source.

MATERIALS AND METHODS

Monitoring Nectar Availability

The amount of nectar available to parasitoids was monitored by comparing buckwheat flowers, *Fagopyrum esculentum* Moench, collected in the open field and inside control cages on 1 August 2000. We collected "caged" and "uncaged" buckwheat flowers from two plots: one near cabbage and soybean fields and one near corn and soybean fields. One cage was placed in each site. Cages were 30 x 30 x 61 cm with a mesh size of 2 x 2 mm that served to exclude larger nectar feeders such as bees, syrphid flies, and lepidopterans, but allowed small wasps to enter. We collected 10 uncaged flowers from each site at 7 am. Thereafter, we collected five caged and five uncaged flowers at each site at 10 am, 1 pm, and 4 pm. The amount of nectar was measured immediately by drawing up nectar with a calibrated microcapillary tube while viewing the process under a microscope. The microcapillary tube had been pulled with a PC-10 microelectrode puller (Narishige, East Meadow, New York, U.S.A.) and clipped at the end. Next, flowers were washed to remove remnants of nectar at the base of the corolla and to dissolve any dried nectar residue. We immersed each flower in 200 ¼l of distilled water and washed it using a 100 ¼l pipette tip expelling water back and forth 40 times. Next, the nectar and residual nectar washed from the flower were quantified for fructose and total sugar content using cold and hot anthrone tests (Olson *et al*., 2000). The total sugar content of flowers was determined by combining sugar readings from the nectar extract and residual nectar wash. By comparing flowers from the open field and within field cages, we could assess how nectar removal reduced nectar availability.

Monitoring Sugar Feeding by Parasitic Wasps

Sugar feeding by hymenopteran parasitoids was monitored at a field site with floral nectar and control treatments. The field site consisted of eight 12 x 20 m cabbage plots; four plots were bordered lengthwise by 3 m wide buckwheat strips and four control plots were without buckwheat borders. All cabbage plots were embedded in a soybean field and spaced at least 67 m apart. We captured wasps by sweep netting the buckwheat borders and the soybean borders in control plots. Using small nets (20 cm diameter), we also captured wasps foraging among cabbage plants of the buckwheat and control plots. Live wasps were collected from July through September, when buckwheat flowers were in bloom. Wasps were frozen, sorted and tested for fructose using cold anthrone assays (Olson *et al*., 2000). Fructose does not occur in the hemolymph of insects (Van Handel, 1984) but is a common component of nectar sugars (Van Handel *et al*., 1972) and honeydew (Wäckers, 2001). Therefore, detecting fructose in a wasp indicates that it fed from nectar or honeydew. By monitoring wasps in the borders and among cabbage, we assessed the prevalence of sugar-fed parasitoids and whether buckwheat borders increased the prevalence.

RESULTS

Nectar Availability

The nectar volume, proportion of nectar comprised of fructose, concentration of nectar sugars, and total sugar content of flowers were analyzed separately for flowers collected at the study sites (corn and cabbage fields). Since trends were similar at the two sites, data were pooled. At 7 AM, buckwheat flowers had opened and small quantities of nectar were visible and were extracted from uncaged flowers (Fig. 1). At 10 AM, both uncaged and caged flowers peaked in nectar volume (0.146 ¼l). By the afternoon, nectar was no longer visible nor extractable from uncaged flowers, while caged flowers maintained 60-80% of peak quantities of nectar. This suggests that parasitoids may be limited to finding nectar in the morning hours through competition.

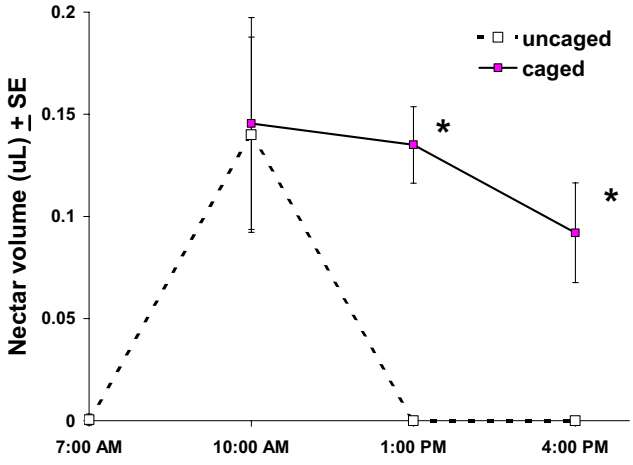

Figure 1. Mean volume of nectar (¼l) ± SE of uncaged and caged flowers from 7 AM to 4 PM. Data from both sites were pooled. Asterisks indicate significant differences between uncaged and caged flowers, $P<0.05$, Wilcoxon test.

Fructose comprised about 50% or more of total sugars within buckwheat nectar (Fig. 2). A few uncaged flowers contained extractable nectar at 7 AM; of these, the sugar concentration of buckwheat nectar was ca. 34% of the total nectar weight (Fig. 3). At 10 AM, sugar concentrations in uncaged flowers and caged flowers were ca. 10%. During the afternoon, the sugar concentration of nectar from caged flowers appeared to increase to ca. 30%.

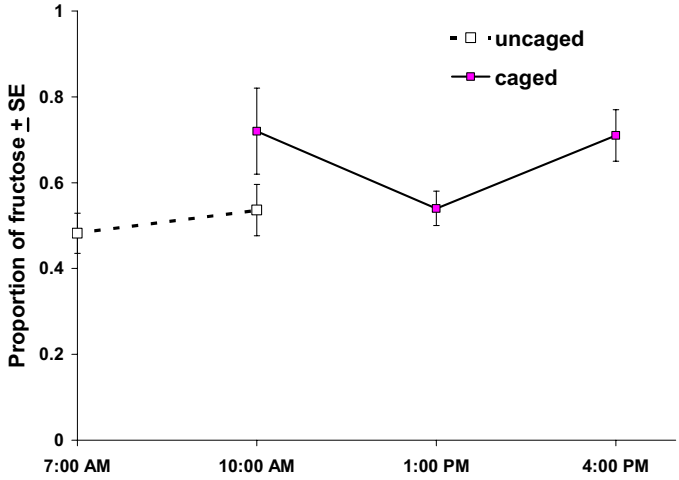

Figure 2. Mean proportion of nectar sugar comprised of fructose ± SE from uncaged and caged flowers at corn and cabbage fields combined, from 7 AM to 4 PM. Uncaged flowers had no visble nectar by 1 PM.

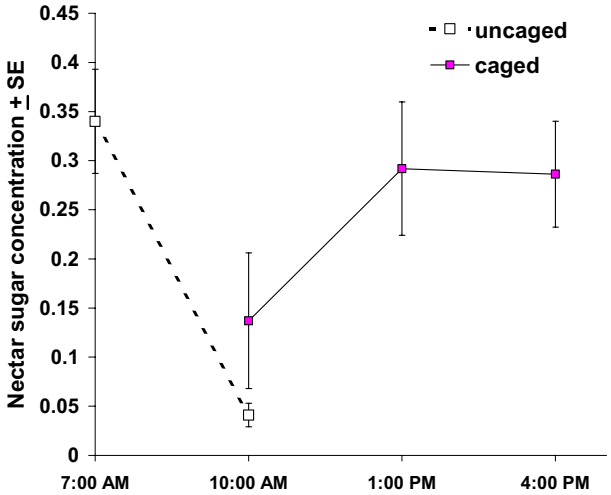

Figure 3. Mean concentration of nectar sugars ± SE of uncaged and caged flowers at both sites from 7 AM to 4 PM (weight of sugar / weight of nectar). Uncaged flowers had no visible nectar by 1 PM.

Total sugar content of uncaged flowers was about 14 µg at 7 AM (Fig. 4). Although both uncaged and caged flowers had similar quantities of nectar at 10 AM (Fig.1), uncaged flowers had significantly lower sugar content than caged flowers (Fig. 4). By 1 PM, uncaged flowers no longer contained visible nectar (Fig. 1), but some residual sugar was detected from the floral wash (Fig. 4). The ability of parasitoids to utilize the dried nectar residues is unknown. Even if parasitoids are capable of eating solidified sugar sources, the overall available sugar decreases by afternoon. On the other hand, caged flowers continued to maintain high levels of total sugar throughout the afternoon (Fig. 4), suggesting that large-sized nectar feeders remove significant amounts of nectar from floral plantings, reducing benefits to parasitoids.

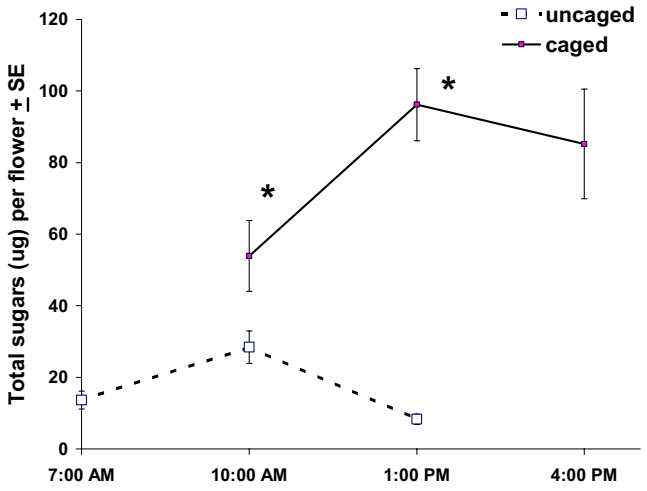

Figure 4. Mean total sugar content (µg) ± SE per flower of uncaged and caged buckwheat flowers from 7 AM to 4 PM. Total sugar content includes extracted nectar and dried residues collected from the floral wash. Asterisks indicate significant differences between caged and uncaged flowers, $P<0.05$, Wilcoxon test.

Sugar Feeding by Parasitic Wasps

Since buckwheat nectar consists of more than 50% fructose, wasps that fed on buckwheat nectar should have fructose in their guts. Of all collected ichneumonoid and chalcidoid wasps, 72% collected from buckwheat borders fed on sugars, whereas 60% collected from soybean borders (control plots) fed on sugars (Fig. 5). As expected, significantly more wasps in buckwheat borders were sugar-fed than in soybean borders. For wasps foraging within plots, the proportion of sugar-fed wasps did not differ between buckwheat and control treatments (Fig. 5). Overall the majority of wasps in the field had fed on sugar. Floral nectar sources increased the incidence of sugar feeding for wasps found within the floral border but had no effect on the proportion of fed wasps foraging among the cabbage.

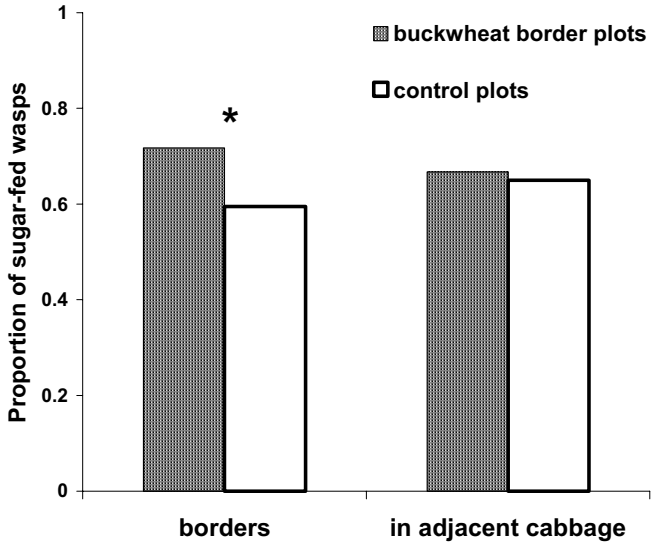

Figure 5. Proportion of sugar-fed wasps found in the borders (n=400, 121 respectively) and in adjacent cabbage of buckwheat or control plots (n=27, 20). Asterisk indicates a significant difference $P<0.05$, Pearson Chi-square.

DISCUSSION

Diversifying agroecosystems with floral vegetation may increase nectar sources available to parasitoids for maintenance and reproduction. However, floral vegetation may not benefit parasitoids under certain conditions. First, nectar available to parasitoids may be diminished in the field by other nectar feeders that consume comparatively larger quantities of nectar. This field study demonstrated that nectar was mainly available to parasitoids during the morning hours, and competing nectar feeders were likely responsible for removing most of the nectar in the afternoon. Therefore, parasitoids were limited to a few hours to utilize floral sources. This limitation stresses the importance of parasitoid activity coinciding with nectar availability.

Second, an abundance of floral nectar may not be beneficial if parasitoids do not readily respond to and feed on it. Generally, parasitoids are expected to find floral nectar sources since they are innately attracted to floral colors and odors and can learn to orient to cues associated with previous feeding experiences (Lewis and Takasu, 1990; Wäckers, 1994; Patt *et al*., 1999). Nevertheless, while parasitoids readily find nectar in laboratory or small field arenas, the degree to which unconfined parasitoids utilize nectar sources has not been determined. By assaying field-collected wasps for fructose, we found that a majority of wasps in the field were sugar-fed. Wasps within the buckwheat borders fed on sugar proportionately more than wasps in soybean borders, suggesting that the presence of buckwheat nectar increased sugar intake. Though wasps were likely using buckwheat nectar, the nectar source did not appear to retain the wasps in the vicinity, contrary to what has been observed in past studies (Takasu and Lewis, 1995; Stapel *et al*., 1997). The similar proportions of sugar-fed wasps in cabbage plots near or far from buckwheat borders may suggest that the wasps fed on alternative sugar sources or wasps dispersed at least 67 m between treatments. We consider between-treatment movement to be a likely possibility since the field was kept free of flowering weeds, aphids were in very low abundance, and parasitoids were unable to feed from the narrow soybean flowers in the laboratory (Lee and Heimpel, unpub. data). Provided that parasitoids are capable of dispersing long distances, the benefits derived from floral habitats might extend relatively far into the field.

ACKNOWLEDGMENTS

We thank Tim Winkler and Kara Ferguson for field assistance. We also thank the organizers of the conference for the opportunity to present our research.

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