Nectar Production in Oilseeds: Food for Pollinators in an Agricultural Landscape

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ABSTRACT

Pollinating insects are in decline throughout the world, driven by a combination of factors including the loss of forage resources. The maize (*Zea mays* L.)– and soybean [*Glycine max* (L.) Merr.]–dominated agriculture of the Central and Midwestern United States produces a landscape relatively devoid of nectar and pollen resources. Introducing specialty oilseeds into current crop rotations could provide abundant floral resources for pollinating insects as well as a high-value crop for growers. We investigated the nectar sugar resources and insect visitation throughout flower anthesis of nine specialty oilseed crops in west-central Minnesota and eastern South Dakota during the 2013 and 2014 growing seasons. Total sugar produced over anthesis (TS) was highest for echium (*Echium plantagineum* L.) at 472 kg ha $^{-1}$. Canola (*Brassica napus* L.), crambe (*Crambe abyssinica* Hochst.), echium, borage (*Borago officinalis* L.), and cuphea (*Cuphea viscosissima* Jacq. × *Cuphea lanceolata* W. T. Aiton) produced enough sugar in one hectare to supply the annual sugar needs of a least one managed honey bee (*Apis mellifera* L.) colony. Pollinators visited flowers of all crops, with as many as 90 insects min $^{-1}$ observed. Our study is unique as we measured nectar sugar production, flower density, and insect visitation throughout anthesis for multiple specialty oilseed crops, providing a seasonwide perspective of the flux of nectar resources for pollinators. Adding specialty oilseed crops into current crop rotations could aid in reversing pollinator decline by providing forage resources that are lacking in the current agricultural landscape.

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Abbreviations: DS, total daily sugar produced per hectare, s kg ha $^{-1}$ d $^{-1}$; FS, total daily sugar per flower, s µg f $^{-1}$ d $^{-1}$; HPLC, high performance liquid chromatography; NCB, Northern Corn Belt; TS, total sugar produced per hectare over the anthesis period, s kg ha $^{-1}$.

THE PLANTING of specialty oilseed crops represents an important opportunity to improve the health of bees, flies, and other pollinating insects by providing an abundant source of forage resources such as nectar and pollen. Pollinator populations are declining worldwide, from managed colonies of the honey bee to wild populations of bumble bees (*Bombus* spp.) and hover flies (Diptera: Syrphidae) (Ellis et al., 2010; Potts et al., 2010). A number of factors are linked to this decline including habitat loss and fragmentation, disease, parasites, stress, and pesticide exposure (Anderson and East, 2008; Ricketts et al., 2008; Watanabe, 2008; Brown and Paxton, 2009; Szabo et al., 2012). While each factor alone is a problem, the combination of stressors is suggested to be driving the recent pollinator decline (Goulson et al., 2015a).

One-third of the nation's honey-producing colonies reside in the Northern Corn Belt (NCB) during the summer months, which includes Minnesota, North Dakota, and South Dakota, where honey production dropped by one-fourth from 2008 to 2013 (USDA–NASS, 2013a, 2013b). The NCB region is comprised of 26 to 34% arable land; of this area 70 to 86% is field crops of wheat (*Triticum* spp.), soybean [*Glycine max* (L.) Merr.], and maize (*Zea mays* L.; USDA–NASS, 2015). The value of these crops as forage resources for pollinators is limited. Wheat and maize are both

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wind-pollinated and do not produce nectar, though maize pollen is sometimes collected by various insects (Mason and Tracewski, 1982; Flottum et al., 1983; Roulston et al., 2000; Krupke et al., 2012). The anthesis period for maize is approximately 2 wk, which is a brief period of food availability, particularly in a monocropped landscape. In contrast, soybean produces flowers over a longer period, up to nearly 6 wk depending on the cultivar (Metz et al., 1985). In soybean, variable amounts of nectar and pollen are produced on blooms hidden within the plant foliage; being self-fertile, soybean has limited need for pollinating insects (Erickson, 1984) but still attracts some pollinators (Gill and O'Neal, 2015). Conversely, specialty oilseeds, such as canola and oilseed echium (*Echium plantagineum* L.), have bright, visible blooms that are attractive to pollinating insects and that produce copious amounts of nectar and pollen (Maurizio, 1985; Mohr and Jay, 1990; Eberle et al., 2014a). Mass-flowering crops like canola also enhance wild bee abundance and species richness (Holzschuh et al., 2013; Diekotter et al., 2014). While some specialty oilseeds such as camelina [*Camelina sativa* (L.) Crantz] are self-pollinated, insect visitation increases seed production (Groeneveld and Klein, 2014), resulting in a mutualistic interaction, with enhanced forage resources for visiting insects and increased pollination services for the plants.

Numerous specialty oilseeds have the potential to enter or reenter current crop rotations in the NCB. Some have a rich history of cultivation in this region, but are currently planted in a much-reduced acreage compared with the past. For example, flax (*Linum usitatissimum* L.) and sunflower (*Helianthus annuus* L.) reached their peak planting in 1954 and 1979, respectively (USDA–NASS, 2015). Flax, or linseed, is one of the oldest known domesticated crops and is useful both for its fibers, which are processed into linen cloth, and its seed oil, which has fast drying properties appropriate for varnishes, paints, and lacquer (Oplinger et al., 1989b). Sunflower, domesticated from North America, can be used for human food, cooking oil, soaps, animal feed, and biodiesel (Putnam et al., 1990). New crops to this region include calendula (*Calendula officinalis* L.), canola (*Brassica napus* L.), camelina, crambe (*Crambe abyssinica* Hochst.), echium, borage (*Borago officinalis* L.), and cuphea (*Cuphea viscosissima* Jacq. × *Cuphea lanceolata* W. T. Aiton). The oil extracted from the seeds of calendula contain about 60% of the unique lipid calendic acid (C18:3), which has a high rate of oxidation, which is useful for paints, cosmetics, and polymers (Dulf et al., 2013; Eberle et al., 2014b). Canola, with low levels of erucic acid and glucosinolates in seeds, is the edible form of rapeseed. Its oil can be used for human and animal food as well as lubricants and fuel (Oplinger et al., 1989a). Camelina produces an edible seed oil that is high in essential linoleic and α-linolenic fatty acids (Zubr, 1997). Camelina also can be used as feedstock for jet fuel (Gesch and Archer, 2013). Crambe produces a nonedible oil with wide application in the production of lubricants, corrosion inhibitors, and synthetic rubbers (Oplinger et al., 1991). The seeds of echium contain oil high in linoleic, stearidonic, and α- and γ-linolenic acids, which are used in cosmetics and as omega-3 fatty acid alternatives to fish oil (Gray et al., 2010; Eberle et al., 2014b). Borage is also a rich source of γ-linolenic acid as well as linoleic and oleic acids (Gunstone, 1992). Finally, cuphea produces seeds containing medium chain fatty acids like capric acid, and thus is a temperate-climate alternative to tropical-climate-grown palm kernel and coconut oils (Forcella et al., 2005). These nine crops were chosen, in part, because of the range of their flowering dates across species, as well as their adaptability to NCB cropping systems.

We argue that the lack of forage resources is a major culprit underlying many of the problems facing honey bees and wild pollinators and that adoption of alternative oilseeds into current agricultural rotations offers a promising solution. Past work has shown that planting areas adjacent to crops or enhancing roadsides with native wildflowers can provide forage resources and enhance pollinator diversity (Hopwood, 2008; Lentini et al., 2012; Blaauw and Isaacs, 2014). Land taken out of field crop production, such as the USDA–Farm Service Agency's Conservation Reserve Program, also can provide pollinator resources, particularly the critical polyfloral pollen sources found in the Northern Great Plains (Gallant et al., 2014). While each of these efforts has a proven potential to provide good habitat and bolster pollinator populations and pollination services, impact is limited, as efforts are focused on low-quality or marginal land. Here we propose that by integrating specialty oilseeds into NCB cropping systems on highly productive lands we can increase exponentially the availability of rich floral resources on the landscape. Such a change would be a boon for both pollinators and producers. That is, large fields of nectar and pollen producing crops mean abundant resources for pollinators and a high-value harvest of oilseeds that may profit farmers.

The objective of this study was to assess the value of nine specialty oilseed crops for pollinators. We asked two questions: (i) what are the dynamics of nectar production in each crop, and (ii) what are the general patterns of pollinator visitation on these crops? To answer the first question, we sampled nectar production and flower density multiple times throughout anthesis. Nectar production was measured using a novel technique to sample nectar from a variety of flower sizes, and sugar was quantified with high performance liquid chromatography. Concurrent with nectar sampling, we monitored pollinator visitation by measuring the pollinator community during crop anthesis. Using this approach we were able to form a dynamic picture of how pollinators respond to floral resources provided by each crop and how the presence of these crops on the agricultural landscape may benefit pollinator health.

MATERIALS AND METHODS

Study Location

Field measurements of flower density (2013 and 2014) and nectar production (2014) of oilseed crops were conducted at the USDA–ARS Swan Lake Research Farm, Morris, MN (45.68° N, 95.80° W). Soil was a Barnes loam (fine-loamy, mixed, superactive, frigid Calcic Hapludolls). Insect visitation surveys were conducted at the Morris site in 2013 and 2014 and also in 2013 at the USDA–ARS Eastern South Dakota Soil and Water Research Farm, Brookings, SD (44.20° N, 96.47° W). Soil at the Brookings site was a Lamoure silty clay loam (fine-silty, mixed, superactive, calcareous, frigid Cumulic Endoaquolls). Crops in both locations were arranged in a randomized block design with four replications. Plot size was 6.1 by 18.3 m. Seeds of camelina, canola, flax, crambe, calendula, echium, borage, sunflower, and cuphea were sown in no-till wheat stubble in mid-May of 2013 and 2014 (Table 1). Row spacing for sunflower was 76 cm, and 19 cm for all other crops. All crops, except flax, were treated with a preemergent herbicide application of Trifluralin [2,6-dinitro-*N,N*-dipropyl-4-(trifluoromethyl)aniline] at a rate of 0.75 kg ai ha^{-1}. Weeds that escaped herbicide control were manually removed from plots. All crops were fertilized at planting with an application rate of 79–34–34–22 kg ha^{-1} N–P–K–S. In spring of 2014 (May 28 and June 26) canola and crambe were treated with malathoin (O,O-dimethyl dithiophosphate of diethyl mercaptocuccinate) at a rate of 0.84 kg ai ha^{-1} for control of flea beetles. Measurements were collected only during the crop anthesis period, defined as the time from when 30% of the plants in a plot began flowering until fewer than 30% of the plants were still flowering. For all three site years, the season's anthesis period began in late June with camelina and canola and ended in late August to early September with cuphea. Environmental variables of air temperature, solar irradiance, wind speed, and relative humidity were collected on an hourly basis from a fully automated weather station at the Morris location within 400 m of the experimental plots.

Nectar Sugar Production and Flower Density

In 2014, nectar sugar produced over a 2-h period was measured up to three times a day (T1: 0900–1100 h; T2: 1200–1400 h; and T3: 1500–1700 h) for each sampling day during anthesis of each crop (Table 2). Camelina flowers were not open at T1 and therefore were not sampled; flax flowers dropped petals early in the day and were sampled only for T1, except on July 2 and July 7 when they were also sampled at T2.

Flowers were prepared for each standard 2-hr production period by first removing the accumulated nectar. In a randomized complete block design, a set of flowers was marked at the beginning of each sampling period to give five samples per crop per time period. The number of flowers used in a single sample varied by crop and are reported in Table 2. Standing nectar total volume was removed by rinsing or by microcapillary suction according to the corolla structure of the flower. Flowers with an unfused corolla (camelina, flax, crambe, and canola) had their nectaries individually rinsed with two 1-mL streams of deionized water directed through a micropipette. Because the petals were separated, the water was able to drain from the corolla, taking the dissolved standing nectar with it. The standing nectar of flowers with a fused corolla (echium, borage, cuphea, and sunflower [disc flowers]) was removed by inserting a single 5-μL glass microcapillary tube into the base of the corolla near the nectary of the flower to suction the nectar. As this technique is prone to sampling error (Morrant et al., 2009), a baseline measurement using the destructive wash technique below was also taken to adjust for any residual nectar remaining after microcapillary removal. For calendula, the disc flowers were too small for either rinsing or microcapillary suction, thus the standing nectar was not removed, and a baseline measurement was used to calculate total nectar production over the 2-h period. To obtain baseline measurements, two separate sample sets of flowers were removed in each plot and washed as detailed below.

Table 1. Planting rates and depths for oilseeds at the USDA Swan Lake Research Farm, Morris, MN, in May 2013 and 2014 and the USDA–ARS North Central Agricultural Research Laboratory, Brookings, SD, 2013. (Borage and echium seeds from unnamed genetic lines provided by Technology Crops International.)

Crop	Cultivar	Rate	Depth
		kg viable seeds ha^{-1}	cm
Camelina	CO-46	7.8	1.3
Canola	662C-RR	5.6	2.5
Crambe	West Hope	20.2	1.9
Flax	Carter	51.6	2.5
Echium	–	17.4	2.5
Calendula	Carola	10.8	1.3
Borage	–	16.8	3.8
Cuphea	PSR-23	10.8	1.3
Sunflower	Mycogen 1172065	62,535 plants ha^{-1}	2.5

Table 2. Nectar sampling periods, number of samples (sampling days), flowers per sample (for each 2-h sampling period), and standing nectar removal technique at the USDA–ARS Swan Lake Research Farm, Morris, MN, in 2014.

Crop	Sampling period	Sampling days	Flowers per sample	Standing nectar removal technique
Camelina	June 25–July 9	4	4	Rinse
Canola	June 25–July 28	8	2	Rinse
Crambe	July 2–July 22	5	10	Rinse
Flax	July 2–July 24	7	5	Rinse
Echium	July 2–August 19	9	1	Microcapillary
Calendula	July 10–August 19	7	20	None
Borage	July 10–August 19	7	1	Microcapillary
Cuphea	July 17–August 19	6	1	Microcapillary
Sunflower	July 22–August 5	4	3	Microcapillary

Following nectar removal, the individual sample sets of flowers were covered with pollinator exclusion bags for 2 h, allowing nectar to replenish without disturbance from flower visitors. Each sample set of flowers, for baseline or nectar production measurements, were destructively removed from the plant and placed in 1.8-mL microcentrifuge tubes (small flowers: canola, camelina, crambe, calendula, sunflower) or 15-mL Falcon tubes (large flowers: flax, echium, borage, cuphea) containing 500 μL or 1 mL of deionized water, respectively. To wash nectar from the flowers, tubes were agitated manually in the field for 1 min before removing the flowers, reserving the wash solution, and storing it on ice for a maximum of 24 h. The wash solutions from both baseline and nectar production samples were filtered through a 0.2-µm syringe filter (Whatman, GE Healthcare Life Sciences) before sugar concentration analysis.

Nectar solutions were analyzed for sugar content with high performance liquid chromatography (HPLC; Agilent 1260 Infinity Quaternary; BioRad Aminex HPX-87N column at 85°C) at a flow rate of 0.5 µL/min with deionized water as the mobile phase. Sucrose, glucose, and fructose standards were prepared and used for calibration. Outputs generated from the HPLC analysis were in milligrams sugar (sucrose, glucose, or fructose) milliliter^{-1} of solution and were converted to micrograms flower^{-1} (s f^{-1}) for each time period by accounting for the dilution during the flower wash step and the number of flowers per sample. Sugar types were summed to produce the total micrograms nectar sugar flower^{-1} time point^{-1} [$\mathrm{T}_{(1,\,2,\text{ or }3)}$ s f^{-1}].

$$\mathrm{T}_n \text{ s f}^{-1} = \text{s mg mL}^{-1} \times \text{mL wash/flowers sample}^{-1} \times 1000\ \mu\text{g/mg} \qquad [1]$$

The ratios of sucrose, glucose, and fructose sugars as determined from HPLC are included in supplementary material (Sup. 1). Mean sugar production at each time point on each sampling day for echium, borage, cuphea, calendula, and sunflower was corrected by subtracting the mean of the baseline measures on the same sampling day. Total daily sugar per flower (FS; s µg f^{-1} d^{-1}) of each crop was then calculated by summing the mean sugar production per flower for each time period (T_n), a standardized measure of daily sugar content.

$$\text{FS} = \mathrm{T}_1 \text{ s f}^{-1} + \mathrm{T}_2 \text{ s f}^{-1} + \mathrm{T}_3 \text{ s f}^{-1} \qquad [2]$$

Flower density (f ha^{-1}) was measured the same day as nectar sampling in 2014 for each crop using Batcheler-corrected point distance estimation (Rempel et al., 2012; Eberle et al., 2014b) and calculated using Transect Point Density software (Kushneriuk and Rempel, 2009). Calendula capitula and echium, cuphea, and borage flowers were measured in 2013 and 2014; canola, camelina, crambe, and flax flowers were measured in 2014 only. Flower density of calendula was calculated by multiplying the capitula density by the mean number of ray plus disc flowers measured in $n = 20$ flower heads from greenhouse-grown plants. Densities of sunflower capitula were measured after the crop matured using a 16-m transect through the plot and counting capitula in two 1-m^2 quadrats spaced 8 m. Flower density was the product of mean capitula density per ha and the mean number of flowers per capitulum. Flowers per capitulum were estimated from counting the number of disk flower bracts in one-sixth of the flower head for $n = 40$ heads.

Total daily sugar produced per hectare (DS; s kg ha^{-1} d^{-1}) for each crop was calculated by multiplying the FS by the flower density of the crop on the same day, and was plotted for each day sampled.

$$\text{DS} = \text{FS} \times \text{f ha}^{-1} \qquad [3]$$

The total sugar produced per hectare over the anthesis period (TS; s kg ha^{-1}) was calculated by integrating the area under the curve.

$$\text{TS} = \int \text{DS} \qquad [4]$$

This calculation is based on the assumption that each individual flower persists for a single day. For calendula and sunflower, TS was calculated differently, since a capitulum persists longer than a single flower. For calendula, we assumed that a given capitulum matured in 1 wk. Total sugar production over anthesis for calendula was calculated by summing DS instead of integrating under the curve.

$$\text{Calendula TS} = \Sigma\text{DS} \qquad [5]$$

For sunflower, the flower density was a single measure for the entire anthesis period, therefore TS was calculated by multiplying the flower density by the mean FS across all sampling days ($n = 4$), the lowest FS value observed, and the highest FS value observed across all sampling days ($n = 4$).

$$\text{Mean sunflower TS} = \text{FS}_1 + \text{FS}_2 + \text{FS}_3 + \text{FS}_4/4 \times \text{f ha}^{-1} \qquad [6]$$

$$\text{Minimum sunflower TS} = \min \text{FS} \times \text{f ha}^{-1} \qquad [7]$$

$$\text{Maximum sunflower TS} = \max \text{FS} \times \text{f ha}^{-1} \qquad [8]$$

Nectar Sugar Regression Analysis

Linear regressions were performed on the FS as a function of several environmental variables during sampling: day of year, mean temperature, irradiance, mean wind speed, and mean relative humidity. Day of year acts as an indicator of weather, daylength, and also plant maturity (Maurizio, 1985; Mohr and Jay, 1990; Cawoy et al., 2008). Mean temperature, irradiance, mean wind speed, and mean relative humidity affect the actual nectar secretion and concentration via the physiological response of the plant, nectary, and photosynthesis (Corbet and Delfosse, 1984). Before linear regression, highly correlated variables (Pearson correlation coefficient > 0.7) were removed, favoring (in order) day of year, irradiance, temperature, mean wind speed, and mean relative humidity, using the “cor” function in R (R Core Team, 2015). The best-fitting model for each crop was selected in a forward stepwise fashion, with nonsignificant variables (p value > 0.05) sequentially removed, removing the least significant terms first. All regressions were conducted in R.

Pollinator Visitation Sampling

Insect visitation was recorded every 3 to 5 d throughout anthesis on each oilseed crop following methods described by Eberle et al. (2014b). Observers recorded the number of honey bees, bumble bees (*Bombus* spp. and the morphologically similar *Xylocopa* spp.), small bees (all other bees), flies, butterflies, beetles, and other insects visiting flowers over a 2-min period per plot. The “other” insect category was primarily composed of insects that have limited pollination value, mainly small damselflies

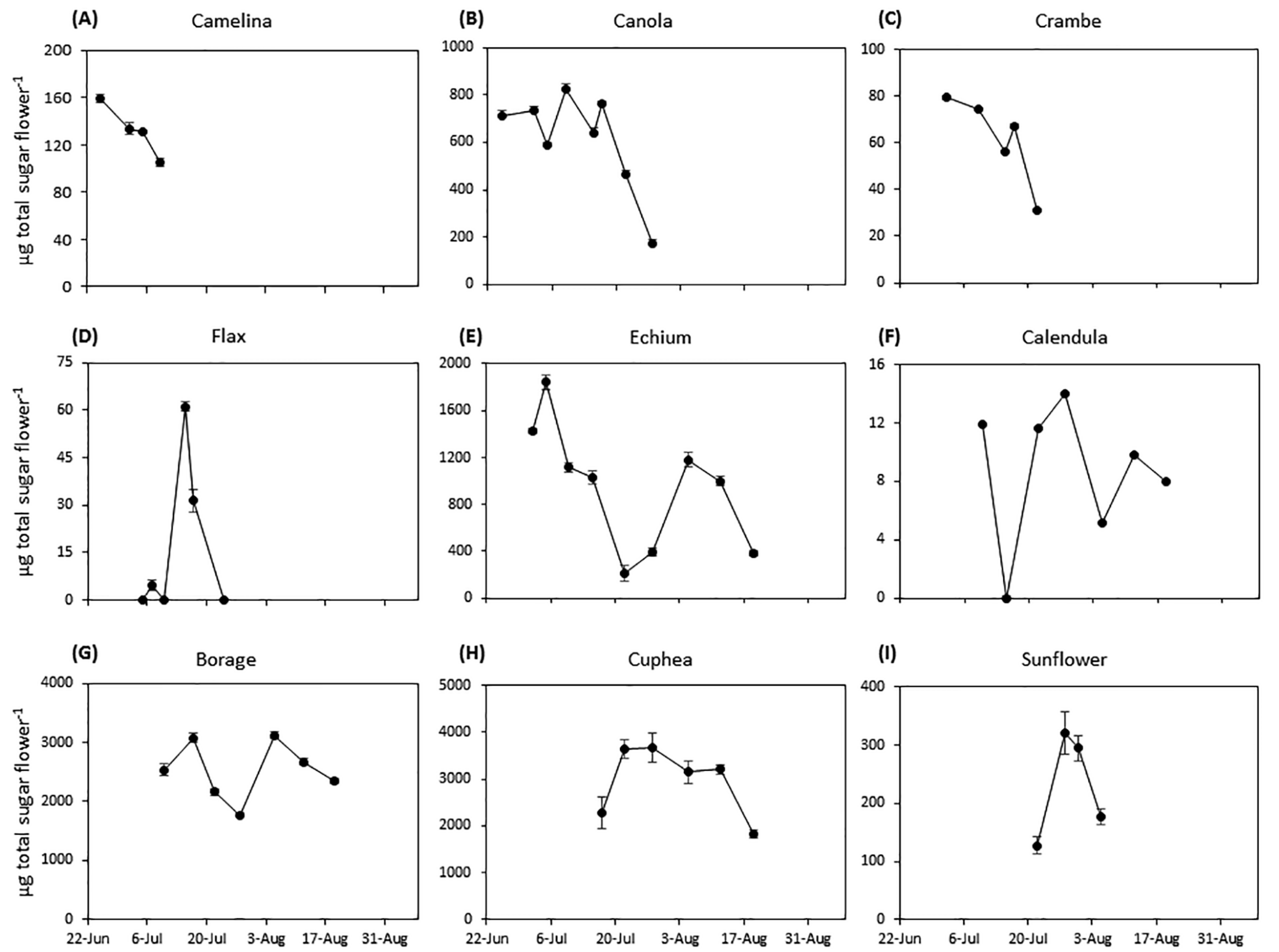

Fig. 1. Total flower sugar production of oilseed crops at the USDA–ARS Swan Lake Research Farm, 2014, summed over three daily sampling periods: 0900–1100, 1200–1400, and 1500–1700 h. Total sugar = sum of sucrose, glucose, and fructose sugars. Values are means, *n* = 5, ±SE.

(Odonata: Zygoptera), lacewing flies (Neuroptera: Chrysididae), and true bugs (Hemiptera) (Proctor et al., 1996). Counts were standardized to insects per observer per min (insects min^{-1}). Total proportions, p_i, of insect groups for each site year were calculated. Total insect visitation for each crop in 2014 was calculated by integrating the area under the curve of the plot of insect visitation. A linear regression was conducted on TS as a function of total insect visitation to relate insect visitation to nectar sugar production.

RESULTS

Nectar Sugar Production and Flower Density

Total flower sugar production for most crops peaked in production at an early or middle date during anthesis, followed by a decline as the crop approached maturity (Fig. 1). For several crops, such as calendula, echium, and borage, FS production was highly variable on one or more days with multiple peaks throughout anthesis. Peak FS was lowest for calendula, flax, crambe, and camelina, ranging from 14 to 160 μg f^{-1}, and highest for borage, echium, and cuphea, ranging from 1900 to 3800 μg f^{-1}. Crambe, calendula, and echium consistently produced more sugar in the 1200 to 1400 h sampling period than in the early or late sampling period (Fig. 2). The other oilseeds showed no clear diurnal trends in peak nectar production.

Flower density displayed a similar pattern to FS, reaching a clear midseason peak before rapidly declining, with peak density ranging from 2 million f ha^{-1} for borage to 300 million f ha^{-1} for crambe (Fig. 3). The sharp peak in density for cuphea in 2013 was not observed in 2014, as the crop was harvested in late August, presumably before the peak was reached. Peak flower density of calendula and borage in 2013 was two and five times higher than the peak measured in 2014, with higher flower density sustained over multiple dates. The error for the 2013 density measurements was also higher, which indicates increased variability among plots. Echium was similar between years, with the exception of the 2013 peak flower density in early August of 85 million f ha^{-1}, compared to a peak of 25 million f ha^{-1} in late July 2014. For sunflower, flower density, which was measured only once at crop maturity, was the lowest of all crops, with only 1.4 million f ha^{-1}.

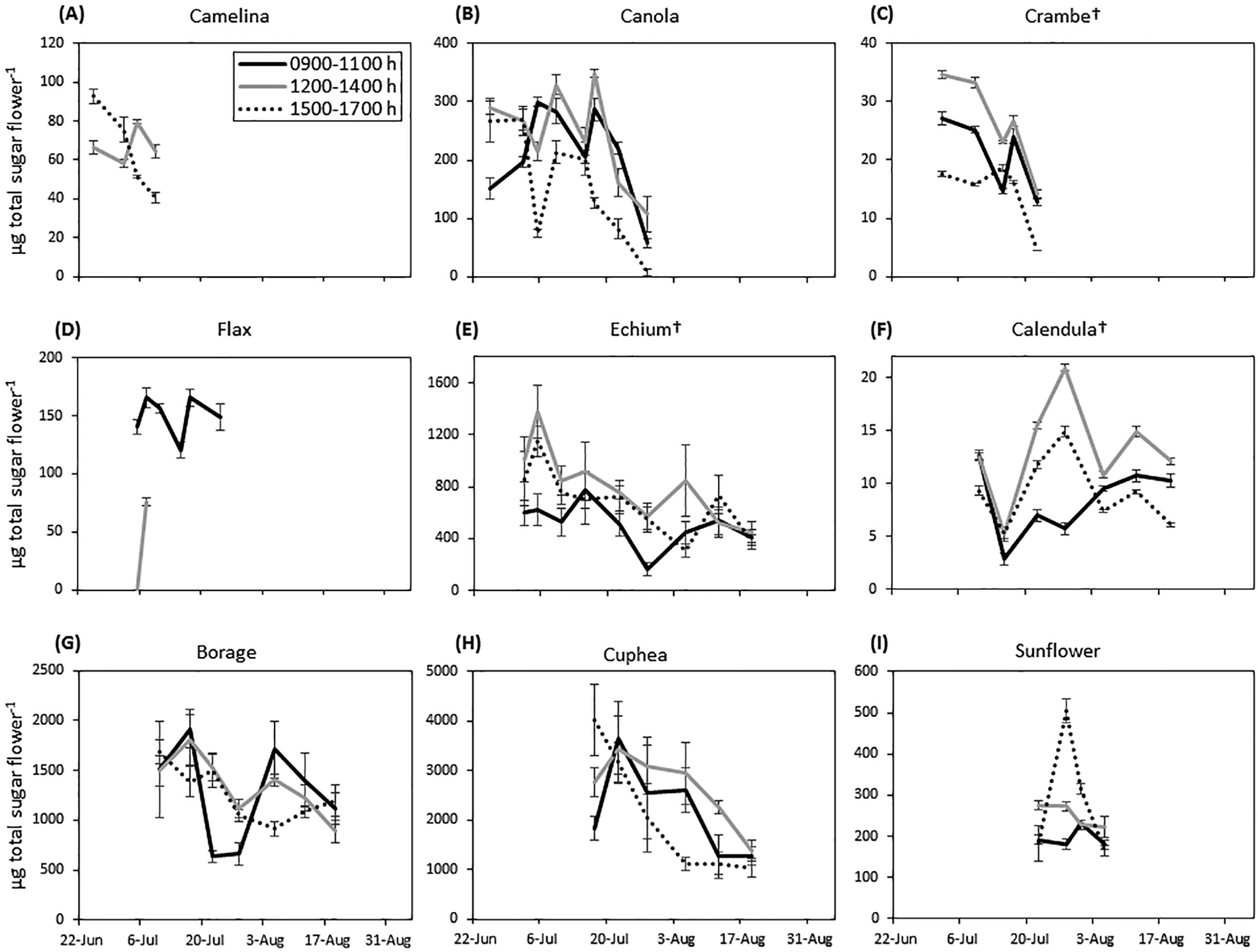

Fig. 2. Diurnal flux of flower sugar (µg sugar flower^{-1} ±SE) of oilseed crops over three daily sampling periods: 0900–1100 (black line), 1200–1400 (gray line), and 1500–1700 (dashed line) h at the USDA–ARS Swan Lake Research Farm, 2014. †Crambe, echium, and calendula exhibited peak sugar production consistently during the 1200–1400 h (gray line) time period.

All crops except for flax showed a distinct peak in DS (kg ha^{-1} d^{-1}), followed by a decline as sugar production and flower density decreased (Fig. 4a–c). Echium and borage both had a decline in DS production on 22 July before rising to a second peak in early August, which corresponded to the decrease in FS at the same time (Fig. 1e, g and Fig. 4b–c). Flax DS, while plotted, was close to zero for all sampling dates, a reflection of limited sugar production and low flower density. Area under the curve calculations revealed a wide range of TS (kg ha^{-1}) production for the oilseed crops, from a low of 3 kg ha^{-1} for flax to a high of 472 kg ha^{-1} for echium (Fig. 4d).

Environmental Correlates to Nectar Sugar Production

Linear regression analysis of FS as a function of environmental conditions resulted in well-fitting models (adjusted $R^2 > 0.9$) for camelina, crambe, and borage (Table 3). Flower sugar production was negatively correlated to day of year in each of these crops, as was wind speed for crambe and borage. In addition, borage FS was positively correlated to irradiance. The best fitting model for echium was less explanatory (adjusted $R^2 = 0.60$), with FS having a positive correlation with temperature and negative correlation with relative humidity. For canola, flax, calendula, cuphea, and sunflower, no significant environmental conditions were found to impact FS production.

Pollinator Visitation

Insect visitation number and duration varied significantly by crop but was relatively consistent across the three site years (Fig. 5). Camelina and flax had the lowest insect activity, with insects visiting for an average of just 7 d, with peak observations of 16 and 15 insects min^{-1}, respectively. On the other end of the spectrum, echium and borage had insect activities for periods longer than 40 d, with peak observations of 56 and 66 insects min^{-1}, respectively. Between these extremes were canola, crambe, and sunflower, with shorter anthesis periods and mid to high insect visitation rates, and calendula and cuphea with long anthesis periods and mid-range insect visitation rates.

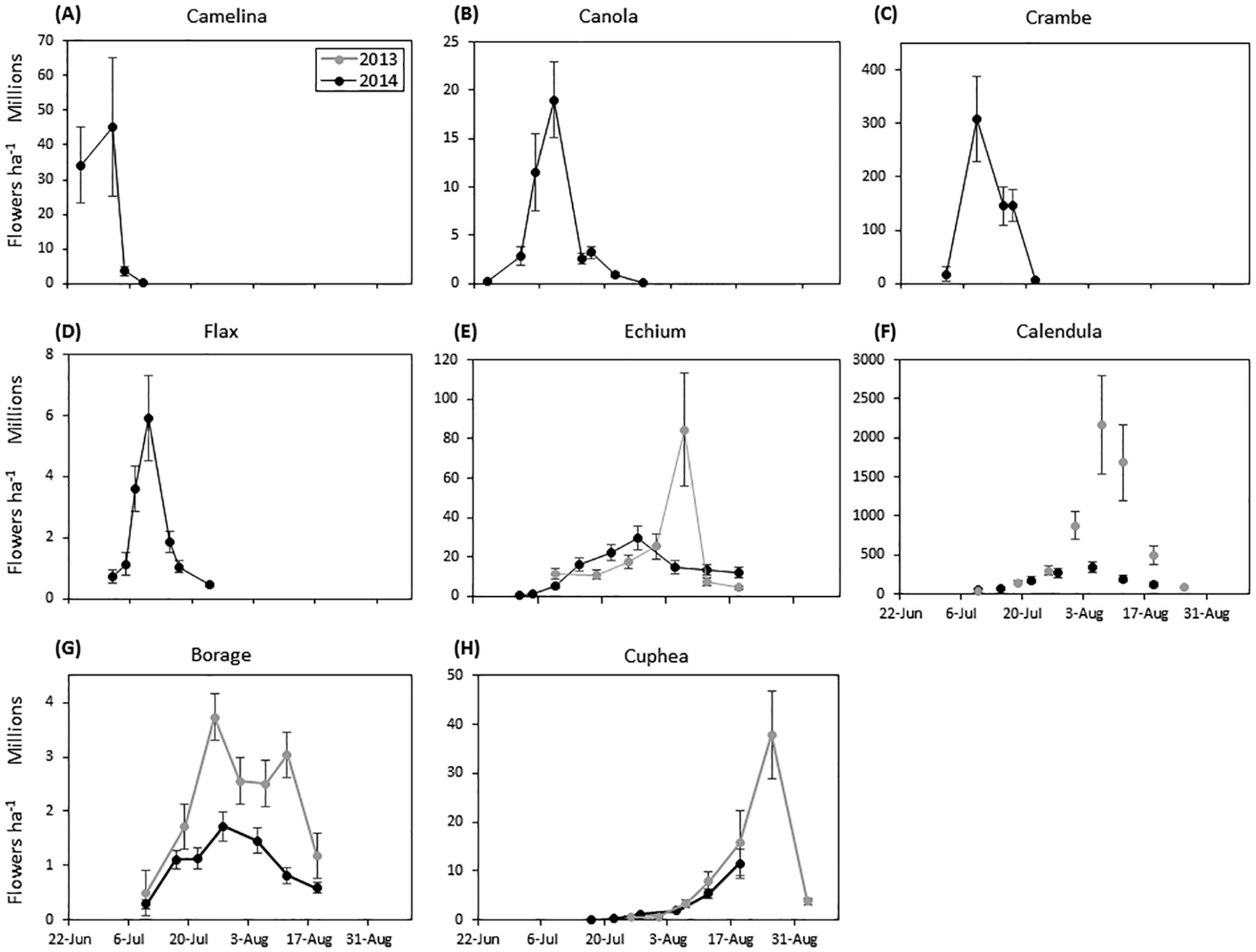

Fig. 3. Flower density of oilseed crops (±SE) at the USDA–ARS Swan Lake Research Farm, 2013 and 2014. No lines were drawn for calendula as flower density estimates were based on capitula density and assumed a 1-wk longevity.

One or more groups of pollinating insects (bees, flies, butterflies, beetles) visited all crops in all years and sites, with differing proportions of each insect group (Table 4). Honey bees comprised the greatest proportion of pollinating insects observed for canola, echium, and borage for all sites and years and for cuphea in Brookings. In Morris, flies were the most commonly observed pollinating insect on camelina, crambe, flax, calendula, and cuphea for both site years. In Brookings, small bees replaced flies as having the highest proportion of visitation for these same crops, with the exception of cuphea. The greatest proportion of visitors to sunflower varied between years and sites, that is, small bees (Morris, 2013), beetles (Brookings, 2013), and flies (Morris, 2014). Small bees and flies were observed on all crops, years, and sites, which is not surprising considering the numbers of species present in these groups. Bumble bees, while representing a small proportion of total counts, were encountered consistently on echium, borage, cuphea, and sunflower. They were seen only on camelina, canola, and flax in Brookings but were never observed to visit crambe or calendula. Butterflies also were low in abundance but were observed on each crop in at least one of the site years. Beetles were often seen on flax, calendula, and sunflower and observed some site years on canola, echium, borage, and cuphea. However, beetles were never observed on camelina or crambe.

Pollinator visitation across oilseed species was found to have a positive but weak linear relationship with TS production (Fig. 6). Flax produced little TS and had correspondingly low insect visitation. Echium produced the most TS in the study and had the highest insect visitation. This trend was not observed for all crops; insect visits to calendula were consistently high for all years and sites though TS production was quite low, suggesting that insects may be collecting a different resource, such as pollen, from this crop. Echium clearly drove the linear relationship between TS and insect visitation, and its removal from the data set results in no observed relationship.

DISCUSSION

Our findings demonstrate that specialty oilseed crops have plentiful nectar sugar resources available for pollinating insects. The availability of this resource is tied to the flux in diurnal and season-long nectar production as well as the

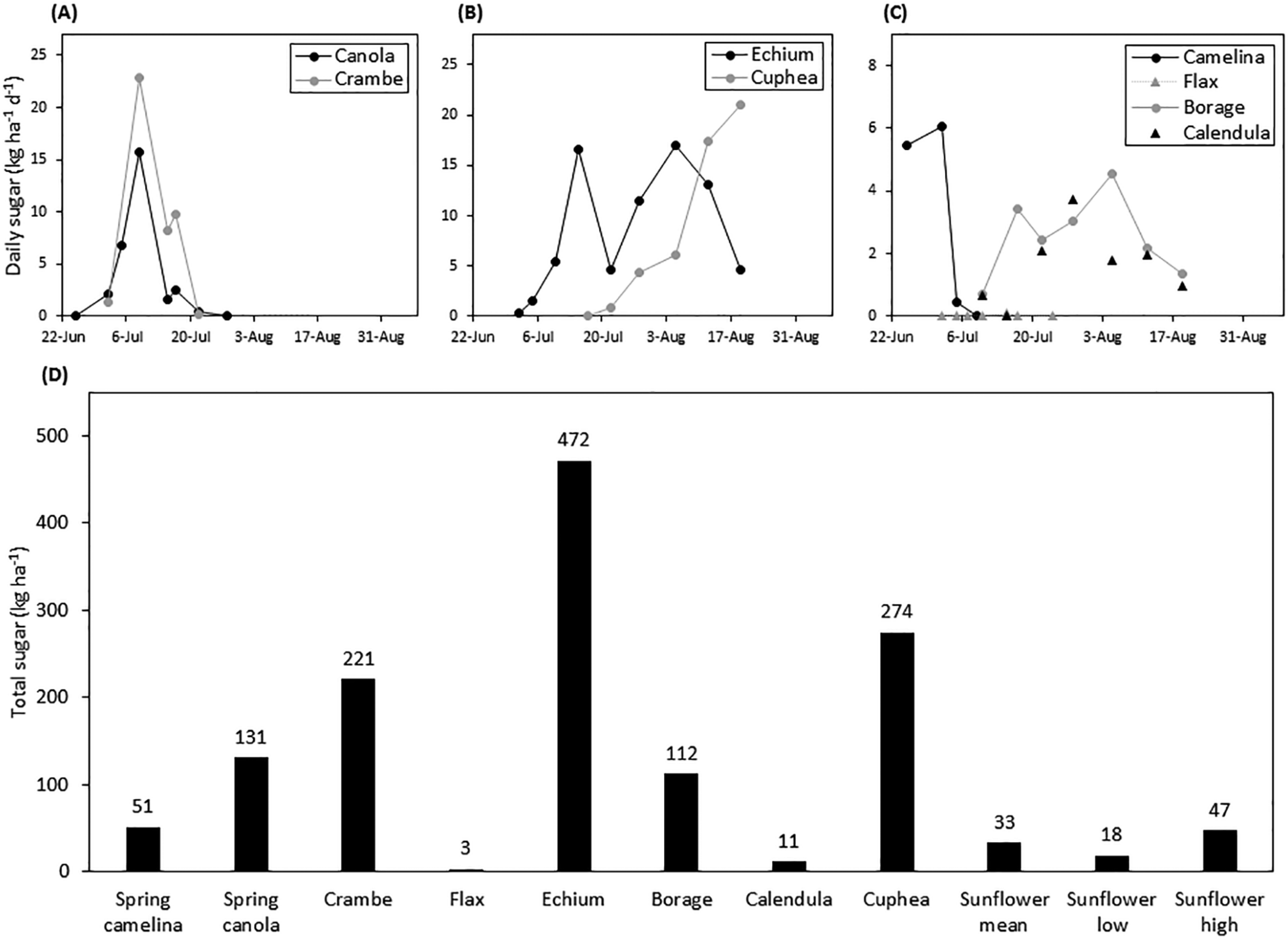

Fig. 4. A–C. Daily sugar (kg ha^{-1} d^{-1}) produced by oilseed crops at the USDA–ARS Swan Lake Research Farm, Morris, MN, in 2014. D. Total sugar (kg ha^{-1}) values calculated from the area under curve of daily sugar production. Refer to flower sugar production (Fig. 1) and flower density (Fig. 3) for error estimates of daily sugar and flower density.

dynamics of flower density as the crops mature. Our data also show that a diverse array of pollinating insects readily visit specialty oilseed crops, with certain groups more commonly encountered on some crops than others. This work confirms that mass-flowering oilseed crops are attractive to pollinating insects and are a valuable source of nectar forage.

Specialty Oilseed Crops Produce Abundant Nectar

Total sugar production was measured successfully for the nine oilseed crops in this study, seven of which produced TS of at least 30 kg ha^{-1}. Our study is unique because we sampled nectar production and flower density multiple times during anthesis (Table 2), while other studies of nectar secretion dynamics for these same crops included only one or very few days of sampling during anthesis (Corbet and Delfosse, 1984; Hadisoesilo and Furgala, 1986; Mohr and Jay, 1990; Patten et al., 1993). Previous studies found sugar production in canola, borage, echium, and sunflower to be 980 to 1700, 200 to 4900, 635, and 120 to 490 μg sugar flower^{-1}, respectively (Hadisoesilo and Furgala, 1986; Mohr and Jay, 1990; Patten et al., 1993; Eberle et al., 2014b). Our measured production of 170 to 830, 1770 to 3120, 210 to 1840, and 130 to 320 μg sugar flower^{-1} for canola, borage, echium, and sunflower, respectively, are within the previously measured ranges for these crops (Fig. 1). The wide range of sugar production within each crop suggests that plant-breeding programs could select for nectar production through larger nectary size, nectar concentration, secretion rate, or other related attributes. Conversely, selection for agronomic traits such as early maturation or determinate growth habit might decrease total nectar production over anthesis by shifting plant resources from flower and nectar synthesis to seed production.

Sugar production measured in our study likely underestimates the DS, as it excludes any secretion in the 1-h gap separating each sampling period. Nectar is also readily absorbed by flowers, an issue that influences any estimation of maximum nectar secretion, particularly if the interval between secretion and sampling is high (Burquez

Table 3. Linear regression of environmental parameters correlated to oilseed flower sugar production during field study at the Swan Lake Research Farm, Morris, MN, May–August 2014.

Crop	Coefficients	Estimate	Std. error	*t* value	*P* value	Model fit (adjusted R^2)
Camelina	Day of year	−3.7	0.59	−6.3	0.025	0.93
Crambe	Day of year	−2.4	0.14	−16.9	0.004	0.99
	Wind speed	−2.9	0.32	−8.9	0.013	
Echium	Temperature	150.0	52.15	2.9	0.028	0.60
	% Relative humidity	−72.4	20.04	−3.6	0.011	
Borage	Day of year	−23.1	3.98	−5.8	0.010	0.95
	Irradiance	0.3	0.04	8.5	0.003	
	Wind speed	−147.6	17.90	−8.2	0.004	

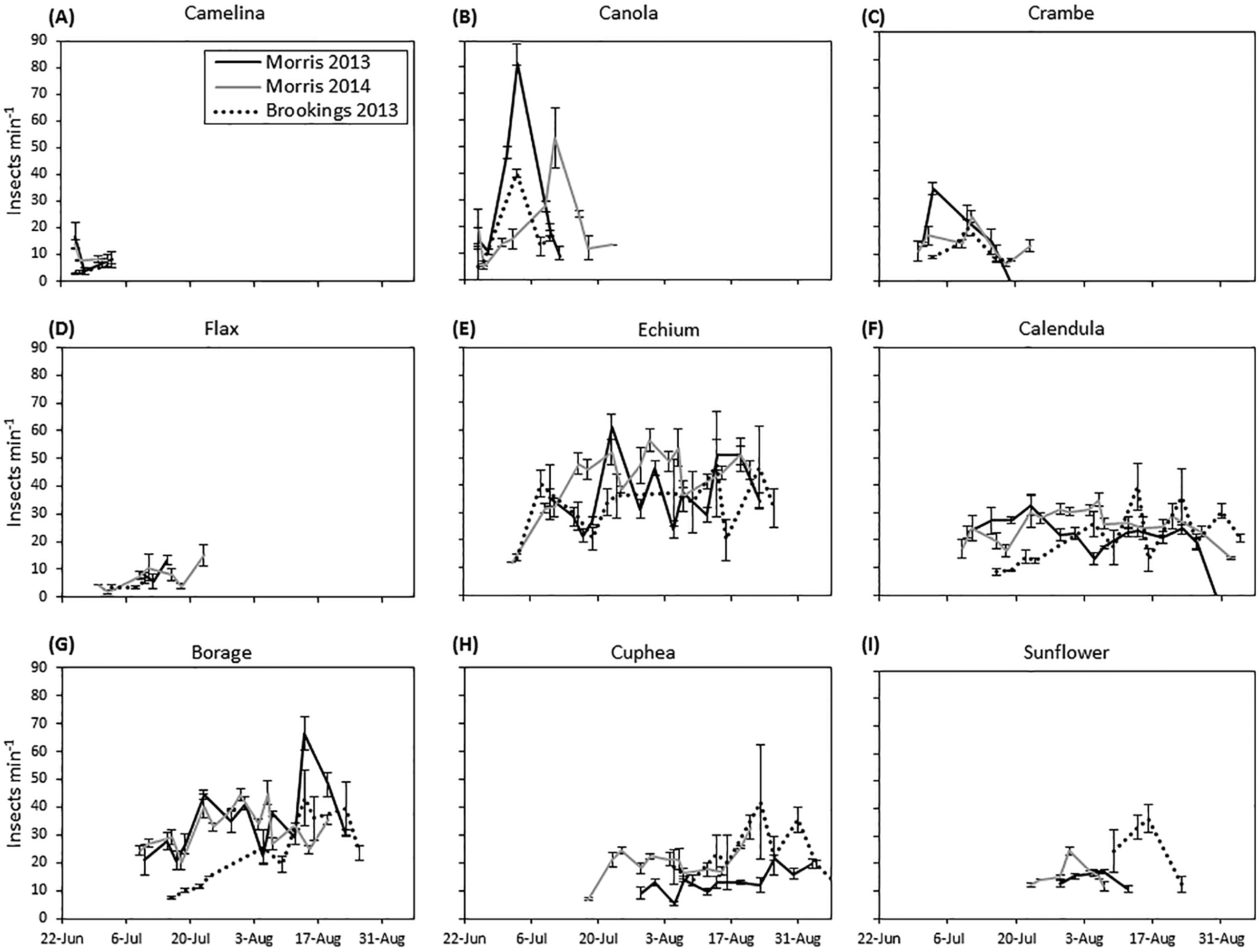

Fig. 5. Insect visitation (insects min^{-1} ±SE) on oilseed crops from 2013 to 2014 at the USDA–ARS Swan Lake Research Farm, Morris, MN, and the USDA–ARS North Central Agricultural Research Laboratory, Brookings, SD. Black line = Morris 2013; gray line = Morris 2014; dotted line = Brookings 2013. Insect visitation is standardized to counts per one observer in 1 min.

and Corbet, 1991). Furthermore, our DS did not account for sugar production after 1700 h and before 0900 h. Flower sugar produced at this time may be significant, assuming that flower-visiting insects actively foraged and that flowers were receptive at those times. While flowers of camelina, crambe, flax, calendula, and sunflower were open only during daylight hours, canola, echium, borage, and cuphea flowers persisted longer, with the possibility of having sugar production at night. We were able to minimize some of these issues, with 2-h sampling intervals conducted at three times spread out during the day and sampling multiple times throughout anthesis, providing a very detailed picture of sugar produced by each crop.

Table 4. Average insects per minute for the entire anthesis period. Insect group proportions (honey bees, bumble bees, small bees, flies, butterflies, beetles, and other) are based on total counts throughout anthesis at the USDA–ARS Swan Lake Research Farm, Morris, MN, and the USDA–ARS North Central Agricultural Research Laboratory, Brookings, SD. Bumble bees includes the genera *Bombus* and *Xylocopa.* Small bees include all bees except for the genera *Apis*, *Bombus*, and *Xylocopa*.

	Average insects min^{-1}	Honey bees	Bumble bees	Small Bees	Flies	Butterflies	Beetles	Other
Camelina								
Morris 2013	8.8	0	0	0.20	0.58	0.02	0	0.21
Morris 2014	9.4	0.01	0	0.15	0.39	0	0	0.43
Brookings 2013	4.1	0.18	0.01	0.39	0.19	0.11	0	0.11
Canola								
Morris 2013	29.9	0.63	0	0.05	0.14	0	0.01	0.16
Morris 2014	21.6	0.47	0	0.08	0.31	0.02	0	0.12
Brookings 2013	16.0	0.65	0.01	0.24	0.05	0.03	0	0.02
Crambe								
Morris 2013	18.6	0	0	0.04	0.65	0	0	0.30
Morris 2014	13.5	0.01	0	0.04	0.71	0.02	0	0.22
Brookings 2013	11.4	0.11	0	0.63	0.08	0.02	0	0.16
Flax								
Morris 2013	8.9	0	0	0.03	0.38	0.06	0.01	0.53
Morris 2014	7.2	0	0	0.03	0.67	0.02	0	0.27
Brookings 2013	4.2	0.12	0.01	0.34	0.18	0.06	0.01	0.30
Echium								
Morris 2013	36.7	0.56	0.06	0.08	0.23	0	0	0.07
Morris 2014	43.7	0.55	0.07	0.04	0.27	0.01	0	0.06
Brookings 2013	32.9	0.28	0.03	0.24	0.02	0.01	0.03	0.41
Calendula								
Morris 2013	22.3	0	0	0.21	0.56	0.01	0.03	0.19
Morris 2014	25.3	0	0	0.12	0.62	0.01	0.06	0.20
Brookings 2013	20.5	0.04	0	0.16	0.09	0.01	0.28	0.42
Borage								
Morris 2013	34.7	0.61	0.02	0.06	0.22	0	0	0.08
Morris 2014	32.6	0.48	0.04	0.03	0.36	0.01	0	0.09
Brookings 2013	23.1	0.25	0.05	0.09	0.01	0	0.30	0.29
Cuphea								
Morris 2013	13.3	0.28	0.03	0.13	0.41	0.01	0	0.15
Morris 2014	21.0	0.29	0.03	0.04	0.45	0.01	0	0.18
Brookings 2013	22.3	0.10	0.05	0.05	0.02	0.01	0.05	0.72
Sunflower								
Morris 2013	14.5	0.19	0	0.58	0.19	0	0.01	0.03
Morris 2014	15.9	0.23	0.01	0.23	0.47	0.01	0.01	0.04
Brookings 2013	26.7	0.28	0.02	0.02	0.03	0	0.51	0.13

Flower Sugar Production Is Influenced by Complex Factors

Sugar production varied diurnally and seasonally in our study. Our methods captured the relatively wide range in FS throughout anthesis, which is likely due to differences in temperature and relative humidity throughout the sampling period as well as other factors unexplained by the regression model (Table 3). Mohr and Jay (1990) showed that nectar secretion and sugar concentration are affected by temperature and relative humidity in canola. Other studies have shown that management inputs such as fertilizers (Hoover et al., 2012) and pesticides (Stoner and Eitzer, 2012) can alter nectar sugar composition, extending to negative effects on pollinator survival and colony fitness (Whitehorn et al., 2012, Goulson, 2015b). We evaluated the nectar production of crops grown under the recommended grower guidelines for each crop, but a follow-up study looking at the impact of alternative agronomic practices on nectar production could be done to determine how to maximize nectar production from the crops.

In addition to variability of FS production throughout anthesis, flower density of each oilseed during the same period is a major factor driving DS and TS production. We observed large variability in flower density between 2013 and 2014 (Fig. 3). For example, borage flower density in 2013 was nearly two times higher than in 2014. Differences in weather between 2013 and 2014 may explain some of the observed differences in flower density. May of 2014 had a

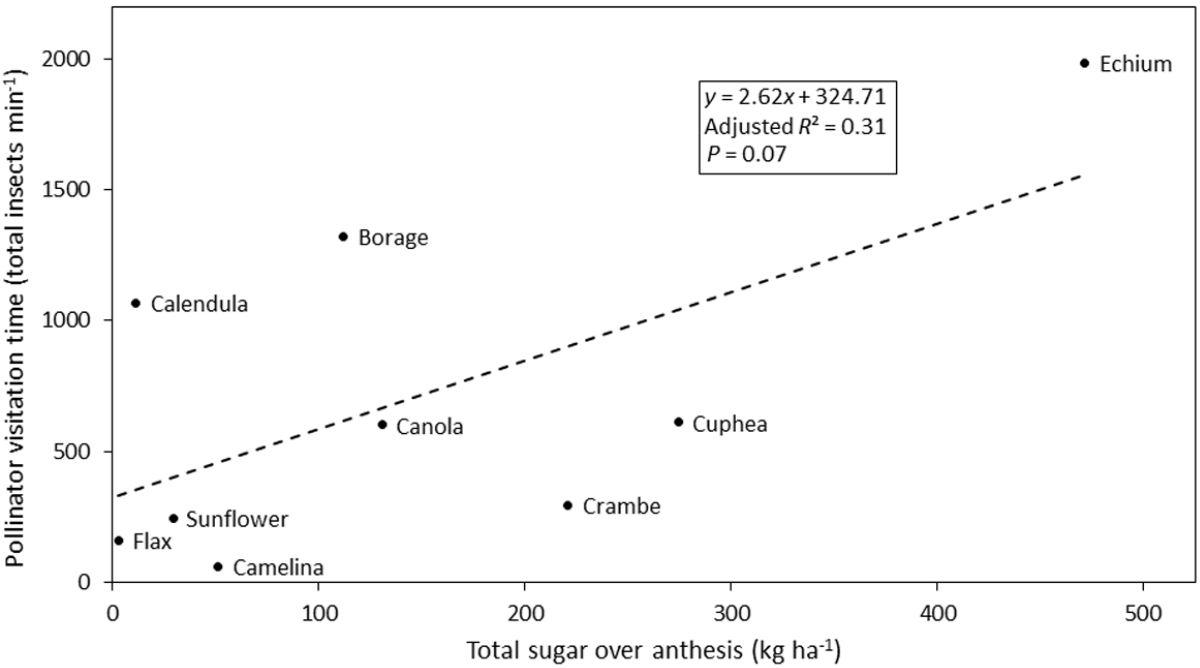

Figure 6. Linear regression of total insect visitation time, generated from area-under-the-curve calculations of 2014 total insect visitation (Fig. 5), as a function of total sugar production over anthesis (kg ha^{-1}).

warmer, sunnier, and wetter early growing period (Supplementary Table 2), and July 2014 was cooler with about half the rainfall of 2013. For cuphea, we know that timing of harvest caused the major difference in peak flower production between the 2 yr. In 2014 the lower pods of the cuphea were shattering and the crop was harvested to avoid additional seed loss. Understanding the forces driving flower density will require more investigation but may lead to improved management for promotion of flowering.

Diverse Pollinators Visited Oilseed Flowers

Our study suggests that planting multiple oilseed crops in both number and in temporal extent (i.e., across the growing season) would attract the largest diversity of insect visitors. Honey bees were the predominant insect visitor on most crops, most particularly on canola, echium, and borage; echium is a well-known melliferous plant with high honey bee activity documented in southeastern Australia (Corbet and Delfosse, 1984). Bumble bees were a more discerning group, only found visiting echium, borage, cuphea, and sunflower; borage has been previously shown to be highly attractive to both honey bees and bumble bees (Patten et al., 1993). Patterns of visitation are less clear with the highly speciose small bee and fly groups. These pollinators visited all the crops, suggesting that to support their diversity a similar diversity of specialty oilseed crops should be planted.

The sugar needs of a normal-sized honey bee colony range from 120 to 225 kg yr^{-1} (Standifer et al., 1977; Standifer, 1980; Seeley, 1985; Axel et al., 2011). On the basis of our results, approximately one hectare of canola, crambe, echium, borage, or cuphea would supply this annual need; the highly productive echium could support two to three colonies. Although honey bee colonies can gain weight foraging for nectar and pollen over a 14-wk period (Seeley and Visscher, 1985), a single crop such as echium, which flowers profusely for 7 wk, would not be an adequate supply. Honey bee colonies would need additional resources earlier or later in the season. The forage needs of native pollinator communities are much less understood. Scheper et al. (2014) suggested the number of food sources is important for supporting different specializations and dietary needs of native insects. Additionally, a diverse cropping arrangement would ensure multiple or overlapping periods of floral resources, important to the different emergence, life cycle, and activity periods for certain native species (Riedinger et al., 2014). Recent studies have investigated oilseed rape as a resource for wild pollinators and have concluded that mass-flowering crops such as this benefit species richness and abundance. Specifically, adequate and nearby nesting sites are necessary for wild pollinators. Evidence suggests that decreased proximity and increased size of seminatural areas relative to mass-flowering crops is important for groups such as the cavity-nesting bee families Megachilidae and Colletidae (Holzschuh et al., 2013; Diekotter et al., 2014;) and ground-nesting species including bumble bees, and hover flies (Riedinger et al., 2014). A specifically designed study looking at the long-term health of honey bee colonies or native pollinator populations when diverse oilseeds are introduced into the landscape would further test the value of these crops as forage resources for pollinators.

CONCLUSIONS

Our study is unique in that we estimated production of flowers and nectar sugar throughout the entire anthesis period for a number of different oilseed crops, providing a seasonwide perspective of the flux of nectar resources for pollinators. We carefully considered the nectar volumes in the flowers of our study, used a modified rinse-wash method for flowers with nectar volumes ≤1 µL, and followed with HPLC analysis of our nectar wash for all samples. Furthermore, we took into account the dynamic nature of nectar secretion and concentration by removing standing nectar, excluding insects, and sampling several times a day across anthesis. Many of these oilseeds produce abundant amounts of sugar in their nectar and would provide a great nectar resource for pollinators of all taxonomic groups that were recorded visiting the flowers, including European honey bees, native bees, hover flies, beetles, and butterflies. By introducing these oilseeds into the typical maize-soybean rotation in the NCB, much needed nectar resources could be provided to pollinators. As a lack of forage resources is linked to declines in pollinating insect biodiversity and honey production from managed honey bees, oilseeds such as these represent an important opportunity to improve pollinator health within agricultural landscapes.

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