

Water availability affects nectar sugar production and insect visitation of the cup plant *Silphium perfoliatum* L. (Asteraceae)

Anna Lena Mueller¹  | Christian A. Berger² | Siegfried Schittenhelm³  |
Burkhard Stever-Schoo³ | Jens Dauber^{1,4}

¹Thünen Institute of Biodiversity,
Braunschweig, Germany

²Department of Life Sciences and
Engineering, TH Bingen University of
Applied Science, Bingen am Rhein, Germany

³Institute for Crop and Soil Science,
Julius Kühn-Institute (JKI), Braunschweig,
Germany

⁴Institute of Geoecology, Technische
Universität Braunschweig, Braunschweig,
Germany

Correspondence

Anna Lena Mueller, Thünen Institute of
Biodiversity, Bundesallee 65, Braunschweig
38116, Germany.
Email: mueller_annalena@posteo.de

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Abstract

The perennial cup plant (*Silphium perfoliatum* L.) is considered as an alternative feedstock to maize for biogas plants. Due to its ecological advantages of an extensive management and function as food resource for pollinators, it can be grown in Ecological Focus Areas (EFAs) since 2018. However, studies at the Julius Kühn-Institute in Braunschweig (Germany) showed that the assumed advantage of the cup plant of a high drought tolerance could not be confirmed regarding aspects of crop production and yield. We complemented this experiment by assessing how different soil moisture conditions affect the production of floral resources and insect visitation. In 2014, we sampled three irrigated and three rainfed plots of the cup plant. We quantified the nectar volume and sugar mass per inflorescence, the number of inflorescences per plant and calculated the total nectar sugar production. We further counted insect visitation on the inflorescences. Due to reduced numbers of inflorescences per plant and an earlier harvest, the estimated nectar sugar production was 58 kg/ha regarding irrigated and 20 kg/ha regarding rainfed plots. Honeybee visitation per inflorescence was about twice as high in the irrigated plots. Furthermore, the early harvest is a disadvantage for wild pollinators with a late activity period.

KEYWORDS

bioenergy, drought stress, floral resources, irrigation, pollinators

1 | INTRODUCTION

Maize (*Zea mays* L.) is the dominant energy crop in Germany, cultivated on about one million hectares for the production of biogas (about one third of the total maize acreage) (FNR, 2019). This dominance of maize as energy crop raised concern about environmental sustainability and preservation of biodiversity (Gevers, Høye, Topping, Glemnitz, & Schröder, 2011; Wiehe, von Ruschkowski, Rode, Kanning, & Haaren, 2009). An alternative feedstock for biogas production is the cup plant *Silphium perfoliatum* L. (Asteraceae). Although the cup

plant is semi-domesticated, its methane yield per hectare is promising, even if it usually does not reach that of maize yet (Gansberger, Montgomery, & Liebhard, 2015; Haag, Nägele, Reiss, Biertümpfel, & Oechsner, 2015). Potential economic disadvantages may be compensated by environmental benefits, because the cup plant as a perennial crop is grown without tillage and low herbicide input, preventing soil erosion, improving the soil humus content and promoting soil biodiversity (Gansberger et al., 2015; Schorpp & Schrader, 2016).

Furthermore, the cup plant is recommended as food resource for honeybees in agricultural landscapes (Decourtye, Mader, & Desneux,

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2010). Due to its late flowering period from July to September and its comparably high pollen production, it may be of particular importance for winter bee rearing as well as feeding (Mueller et al., 2020). In contrast to maize, a pollen-only resource, its disc florets produce both, pollen and nectar. However, nectar sugar might be the limiting resource for winter bee feeding especially with decreasing numbers of open inflorescences at the end of the flowering period (Mueller et al., 2020). With respect to wild pollinators, the cup plant flowers to a time when bumblebees rear the new hibernating queens (Amiet & Krebs, 2012). It was further shown that the cup plant can be of special importance for some hoverfly species with a late activity period at the end of the flowering period (Mueller & Dauber, 2016). However, the benefit as late food resource for pollinators can be reduced by an early cup plant harvest before the end of the flowering period (Mueller & Dauber, 2016).

Due to its ecological advantages, this alternative energy crop can be grown in Ecological Focus Areas (EFAs) since 2018, which are part of the direct payments regulation of the EU's common agricultural policy (European Parliament, 2017). Therefore, it is predicted that the area in Germany that is currently cultivated with the cup plant of about 2,000 ha (Schittenhelm & Grunwald, 2018) will further increase in the short term by about 1,100 ha (Fachverband Biogas e.V., 2018).

Besides the ecological advantages, the cup plant was initially characterized as drought tolerant due to its large root system and cup-shaped water collecting leaf axils (Gansberger et al., 2015). Drought resistance of crops is becoming of major importance, not only to face impacts of climate change (IPCC, 2014), but in particular in the context of energy crop production. In regions where energy crops are largely promoted, targeting the reduction of fossil energy use, the demand for arable land has increased and the use of marginal soils became regionally profitable even when prone to risk of drought (Wright & Wimberly, 2013). Furthermore, the "food versus fuel" debate led to the discussion if and under what conditions energy crop production could be limited to marginal land to secure fertile arable land for food production (Dauber et al., 2012).

In this context, the impact of different water regimes—irrigated versus rainfed—on various aspects of plant production was assessed at the Julius Kühn-Institute for Crop and Soil Science in Braunschweig, Germany, by comparing the biogas crops cup plant, maize and lucerne-grass. The study year 2014 was characterized by an optimal precipitation for plant growth. In that year, water consumption of the cup plant was significantly higher than that of maize and lucerne-grass, while water use efficiency, that is the amount of dry matter produced per amount of water needed, was highest for maize. As a consequence, dry matter yield and methane yield per hectare of irrigated cup plants were 30% and 34%, respectively, higher than those of the rainfed cup plants. In contrast, maize yields were not significantly affected by additional irrigation and were significantly higher compared to both, irrigated and rainfed cup plants (Schoo, Kage, & Schittenhelm, 2017; Schoo, Wittich, Böttcher, Kage, & Schittenhelm, 2017). Hence, the expected drought tolerance of the cup plant could not be confirmed regarding aspects of crop production and yield.

Floral resources needed by pollinators are also affected by drought stress: studies comparing irrigated with less or non-irrigated non-crop plants showed that limited water supply can reduce the nectar volume per flower (Carroll, Pallardy, & Galen, 2001; Petanidou, Goethals, & Smets, 1999; Waser & Price, 2016; Zimmerman, 1983), sugar mass per flower (Petanidou et al., 1999; Waser & Price, 2016), pollen grains per flower (Waser & Price, 2016), number of flowers (Su et al., 2013) or flower size (Carroll et al., 2001; Su et al., 2013) and can shorten flowering periods (Halpern, Adler, & Wink, 2010; Petanidou et al., 1999). Reduced nectar volume per flower can in turn reduce the number of flowers visited per plant (Zimmerman, 1983). Hence, an open question is whether and to what extent the environmental advantage of the cup plant as food resource for pollinators can be sustained under drought conditions.

Therefore, we complemented the experiment of Schoo, Kage, et al. (2017), Schoo, Wittich, et al. (2017) by comparing the irrigated and rainfed plots of the cup plant regarding (a) the current and total nectar and nectar sugar production and (b) the insect visitation on the inflorescences.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental set-up

The experiment was conducted in 2014 on an experimental field (52.296 °N, 10.438 °E, altitude 76 m) at Braunschweig, located in northern central Germany (Schoo, Wittich, et al., 2017). The experiment was laid out according to a two-factorial split-plot design with four replications of the respective water regime, that is with and without additional irrigation. The plot size amounted to 240 m² (40 × 6 m). The field plots of the cup plant had already been established in 2012. The cup plant was planted at a density of 4 plants/m².

The irrigated plots' target soil moisture of 50% to 80% available water capacity (AWC) was attained by overhead irrigation with a travelling sprinkler. Because of their high water consumption, the cup plant plots for technical reasons were additionally watered by means of drip tubes. Rainfall in 2014 was 360 mm on the field site, and the irrigated cup plant plots received an additional irrigation of 230 mm (from May to July). In 2014, mean soil moisture of irrigated and rainfed plots of the cup plant was 53% AWC and 50% AWC, respectively, during the growing season and 52% AWC and 43% AWC, respectively, during the flowering period (for further details see Table 1). Fertilizers were applied crop specific taking account of the residual nutrient contents and the expected nutrient removal and were 170 kg N/ha for both irrigated and rainfed cup plants. In May 2014, the cup plant was treated with boscalid and pyraclostrobin against grey mould (*Botrytis cinerea*). Harvesting took place when the dry matter content reached between 25% and 30%. Hence, rainfed cup plant plots were harvested at August 6, irrigated cup plant plots at August 14. Details of the cultural practices are presented in Schoo, Wittich, et al. (2017).

TABLE 1 Weekly mean air temperature, rainfall, irrigation and available water capacity (AWC) of soils in cup plant plots during the sampling period in 2014

| Calendar week | 27 June 30–July 6 | 28 July 7–July 13 | 29 July 14–July 20 | 30 July 21–July 27 | 31 July 28–Aug. 3 | 32 Aug. 4–Aug. 10 | Flowering period |
|--------------------------------|----------------------|----------------------|-----------------------|-----------------------|----------------------|----------------------|---------------------|
| Air temp. [°C] | 18.2 | 18.4 | 22.2 | 21.0 | 20.9 | 19.1 | 20.0 |
| Rainfall [mm] | 5 | 21 | 0 | 26 | 50 | 18 | 120 |
| Irrigation [mm] | 20 | 20 | 0 | 60 | 0 | 0 | 100 |
| AWC [%] of the cup plant plots | | | | | | | |
| Irrigated | 52 | 55 | 51 | 46 | 53 | 56 | 52 |
| Rainfed | 41 | 42 | 39 | 37 | 45 | 51 | 43 |

Samplings and observations for the present study were conducted along the 40 m length sides of the plots, because due to the high density of the cup plant, entering the plots without damaging the plants would not have been possible. The supply of nutrients and water may be higher and the shadowing lower at plot edges. To reduce these possible effects, we selected the plot edges that were facing maize plots which were similar in crop height with the cup plant of about 3 m, avoiding effects of different shading (Pacini & Nepi, 2007). Hence, three irrigated and three rainfed cup plant plots met this condition and were sampled. Absolute amounts of floral resources might still be slightly overestimated, but as we aimed for comparing the cup plant growing under equal conditions except the water regimes, the study design is appropriate to detect possible relative differences.

2.2 | Nectar volume and sugar mass per disc floret

The sampling of nectar started in the 29th calendar week (July 14 to 20) with the inflorescences concluding the growth of the main stems (primary inflorescences). In the 30th calendar week (July 21 to 27), inflorescences of the first side branches (secondary inflorescences) and, in the 31st calendar week (July 28 of August 3), inflorescences of the second branching degree (tertiary inflorescences) were sampled. The sampling ended after harvesting of the rainfed plots.

To quantify nectar volume and sugar mass per disc floret, inflorescences were isolated with bags of non-woven fabric prior to the opening of the disc florets to avoid nectar removal by insects. As nectar sugar accumulates in the disc florets until midday (Mueller et al., 2020), nectar was collected between 12 and 2 p.m. using microcapillary tubes (Drummond Microcaps[®], 0.25 and 0.50 μ l) inserted to the disc florets. The sugar concentration was measured using two hand-held refractometers for low volume (Eclipse Refractometer by Bellingham and Stanley 45–81 (0–50°Bx) and 45–82 (45–80°Bx)). The Brix reading was corrected for air temperature data provided by the German Weather Service (DWD) situated nearby the experimental field. Sugar mass per disc floret was calculated as described by Galetto and Bernardello (2005).

One irrigated and one rainfed plot could be sampled per day, alternately beginning with an irrigated or rainfed plot. Four to eight inflorescences were selected per plot, and one disc floret of each

inflorescence was sampled. Over the flowering period, six sampling days could be realized (two per week or branching degree, respectively) resulting in 75 samples in total.

2.3 | Number of disc florets and inflorescences

We collected four inflorescences per plot and branching degree (sum of 72 primary to tertiary inflorescences from the 29th to the 31st calendar week, see above) to count the number of disc florets per inflorescence.

From the 29th calendar week on, for seven plants per plot, the flowering and withered inflorescences of each stem were counted every week on the same plants until harvest, rainfed plots until the 31st calendar week and irrigated plots until the 32nd calendar week (August 4 to 10), respectively. Floral buds that had dried out before they started to present the disc florets were not counted.

2.4 | Insect visitation

Insect visitation on flowers can be studied on a per-area level (e.g. Power & Stout, 2011) or on a per-flower level (e.g. Rader et al., 2009). In our study, all plots were within easy reach by all insects (range of nearest neighbour distances between plots: 5 to 14 m). Comparing the water regimes, an equal insect visitation on a per-flower level (here: inflorescence) but a different insect visitation on a per-area level (here: equal to a per-plot level) would therefore reflect a different number of flowering inflorescences in irrigated and rainfed plots, with an equal distribution of insect visitors over all available resources within the experimental field. In contrast, a different insect visitation on a per-inflorescence level would show a preference for one water regime although the given resources in the other water regime could also be reached easily, reflecting a true preference for one water regime.

Therefore, we measured insect visitation by counting the number of insect visits on ten inflorescences per five minutes (including multiple counting of one insect in case of multiple landings within the ten inflorescences) at three selected sampling points on one irrigated and one rainfed plot, respectively, per sampling day. The respective three counts per plot were summed up to 15 min. We differentiated between

honeybees (*Apis mellifera* L.), bumblebees (*Bombus* spec.), hoverflies (Syrphidae) and other insects. With respect to honeybees, eight bee hives of a local beekeeper were situated nearby the plots. Observations were made, once in the morning (between 9 a.m. and 12 p.m.), and once in the afternoon (between 2 and 5 p.m.), when weather allowed a day-long sampling (no rain, temperature > 18°C, wind speed < 3 Bft). The sampling ended after the harvest of the rainfed plots. Eight sampling days were realized, whereof two counts in the morning had to be skipped due to weather conditions (28 observations in total).

After each count of insect visitation for 15 min per plot and daytime, we observed single individuals of the respective taxa (honeybees, bumblebees and hoverflies) and counted the time spent on one inflorescence. Therewith, we aimed to differentiate whether a higher number of insect visits reflect a preference for a given water regime or are simply the result of a faster switch between inflorescences (e.g. as a result of resource depletion). Depending on insect density, the visit duration of 15 individuals per taxa was measured per observation (28 in total) if possible, resulting in 328 samples of honeybees, 249 samples of bumblebees and 168 samples of hoverflies.

2.5 | Statistical analyses

We conducted data analyses with R, version 3.3.2 (<http://www.R-project.org/>) and applied (generalized) linear mixed effects models ((G)LMM) using the packages “lme4” (Bates, Mächler, Bolker, & Walker, 2015). The variable “water regime” (two levels: irrigated and rainfed) was considered in all models as fixed factor.

The response variables “nectar volume per disc floret” and “sugar mass per disc floret” were square root-transformed to meet normality assumption of residuals in LMMs. The variables “sampling day” nested in “branching degree” (three levels: primary, secondary and tertiary inflorescences, corresponding to 29th, 30th and 31st calendar week) and “plot” were considered as random effects.

To model the response variable “disc florets per inflorescence,” LMM was applied considering the variables “branching degree” and “plot” as random effects.

To account for temporal pseudoreplication regarding the response variables “flowering inflorescences per plant” and “total number of inflorescences per plant,” one model per calendar week was performed considering the variable “plot” as random effect. GLMMs were applied using negative binomial distribution due to overdispersion in Poisson models.

To model the response variables “honeybee, bumblebee and hoverfly visits per 10 inflorescences in 15 min,” GLMMs were applied using negative binomial distribution as well. “Calendar week” and its interaction with “water regime” were additionally included into the fixed structure. The variables “plot” and “daytime” nested in “sampling day” formed the random structure.

The response variables “duration of honeybee, bumblebee and hoverfly visits per inflorescence” were log-transformed to meet normality assumption of residuals in LMMs. The fixed and random structure was according to the models on insect visitation.

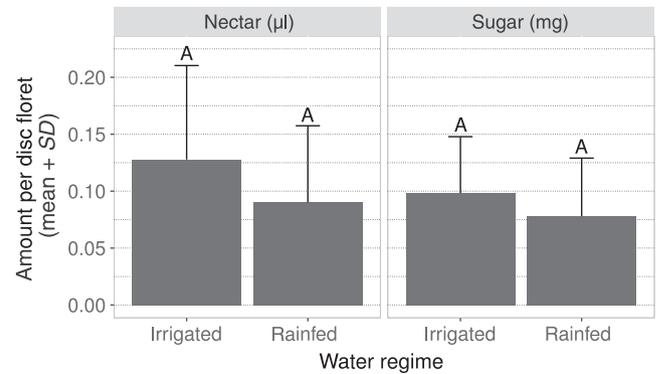


FIGURE 1 Nectar volume and sugar mass per disc floret of the cup plant grown in irrigated and rainfed plots. The same letters indicate that neither the nectar volume nor the sugar mass differs significantly between irrigated and rainfed plots ($p(\text{LRT}) > .05$)

Likelihood ratio test (LRT) was used for model selection (see Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

3 | RESULTS

3.1 | Nectar volume and sugar mass per disc floret

Although mean nectar volume per disc floret was higher in irrigated compared to rainfed plots (Figure 1), the difference was not significant ($p(\text{LRT}) = .194$). Mean sugar concentration of nectar was slightly lower in irrigated plots (mean = 64°Bx, $SD = 9$) in comparison with rainfed plots (mean = 68°Bx, $SD = 8$). Hence, sugar mass per disc floret did not differ significantly ($p(\text{LRT}) = .238$) between irrigated plots (mean = 0.10 mg, $SD = 0.05$, range: 0.03–0.23, $n = 38$) and rainfed plots (mean = 0.08 mg, $SD = 0.05$, range: 0–0.26, $n = 37$) (Figure 1).

3.2 | Number of disc florets and inflorescences

The number of disc florets per inflorescence did not significantly differ ($p(\text{LRT}) = .407$) between irrigated plots (mean = 161.2, $SD = 37.2$) and rainfed plots (mean = 152.0, $SD = 40.9$).

At the beginning of the flowering period, cup plants in irrigated and rainfed plots produced an equal number of (flowering) inflorescences (Figure 2). However, with ongoing flowering, cup plants produced significantly more (flowering) inflorescences in the irrigated plots. The irrigated cup plants produced a mean number of 34 inflorescences between the 31st and 32nd calendar week, while rainfed plots were already harvested (Figure 2).

3.3 | Total sugar supply

By multiplying the mean sugar mass per disc floret (0.09 mg) and the mean number of disc florets per inflorescence (156.6) with the

mean number of inflorescences per plant counted during the last sampling before harvest (105.3 in the 32nd calendar week in irrigated plots and 36.3 in the 31st calendar week in rainfed plots) and by considering a stand density of 4 plants/m², we estimated total nectar sugar production of the cup plant over the flowering period, namely 58 kg/ha for the irrigated plots, and 20 kg/ha for the rainfed plots.

3.4 | Insect visitation

During seven hours of observation ($n = 28$ observations of 15 min on 10 inflorescences of the cup plant), we counted 607 visits of honeybees, 446 visits of bumblebees, 248 visits of hoverflies and 110 visits of other insects, mainly butterflies (Lepidoptera) and other Diptera. Honeybee, bumblebee and hoverfly visitation was influenced by the variable calendar week (Table 2). Honeybee visitation was decreasing over the flowering period, bumblebee visitation fluctuated over the three weeks, and hoverfly visitation raised in the 31st calendar week (Figure 3). Only honeybee visitation could also be explained by the variable water regime reflecting a higher honeybee visitation in irrigated plots in comparison with rainfed plots in all calendar weeks.

One honeybee visit per inflorescence lasted on average 18.8 s ($SD = 15.6$, $n = 196$) in irrigated plots and 22.8 s ($SD = 20.3$, $n = 132$) in rainfed plots that of one bumblebee on average 12.0 s ($SD = 9.2$, $n = 156$) in irrigated plots and 11.9 s ($SD = 9.3$, $n = 93$) in rainfed plots and that of one hoverfly on average 22.8 s ($SD = 22.4$, $n = 92$) in irrigated plots and 23.4 s ($SD = 25.4$, $n = 76$) in rainfed plots. Neither the variables water regime and calendar week nor their interaction were significant due to the LRT ($p(\text{LRT}) > .05$ in all model comparisons).

4 | DISCUSSION

4.1 | Production of floral resources

The water regime had no significant effect on the supply of floral resources per inflorescence of the cup plant, neither regarding the nectar volume and sugar mass per disc floret nor the number of disc florets per inflorescence. However, with a difference of 0.04 μl , the mean nectar volume per disc floret showed at least a tendency to be higher in irrigated plots, but due to a higher mean sugar concentration of nectar in rainfed plots, this difference was less pronounced regarding the sugar mass per disc floret. The decisive factor for the production of floral resources over the flowering period had been the number of inflorescences per cup plant. In the rainfed plots, the cup plant produced only 60% of the number of inflorescences compared to the irrigated plots up to the 30th calendar week and 50% up to the 31st calendar week. This increasing difference between irrigated and rainfed plots over the flowering period also affected the current availability of floral resources. While the number of flowering inflorescences in the rainfed plots was reduced by a factor of 1.7 in the 30th calendar week, it was

reduced by a factor of 2.9 in the 31st calendar week. In summary, these results show that the drought stressed cup plants had less power to develop inflorescences in higher branching degrees, but those inflorescences that could have been developed produced a comparable amount of nectar sugar. In addition, the rainfed plots were harvested about one week before the irrigated plots as a result of earlier maturation. Hence, irrigated plots could develop even more inflorescences during the additional week and the total nectar sugar production was about three times higher in the irrigated compared to the rainfed cup plant plots. As the study year was characterized by an optimal precipitation for plant growth (see above), resource reduction might be even more pronounced in drier years. Although the focus of the present study was on the nectar sugar production, it should be mentioned that pollen production was also affected by water availability. We did not proof whether the pollen quantity per disc floret differed between irrigated and rainfed plots, but a mean difference of 69 inflorescences per cup plant comparing irrigated and rainfed plots until harvest most likely affected pollen quantity as well.

It should further be pointed out that the irrigated plots were also harvested before the end of the flowering period to the time of highest methane yield. A late harvest together with maize in one operation at the end of the flowering period is only realized in small commercial cup plant fields when the higher yields would not cover the costs of a separate, early harvest (see Mueller et al., 2020).

4.2 | Insect visitation

In the irrigated plots, honeybee visitation per inflorescence was on average about twice as high as in the rainfed plots. Considering an equal amount of resources of single inflorescences and an equal time spent on one inflorescence comparing irrigated with rainfed plots, this may not reflect a higher number of visited inflorescences per honeybee during one collecting flight in irrigated plots, but a higher ratio of honeybees to inflorescences in irrigated plots. In contrast, bumblebee and hoverfly visitation was not affected by the water regime. These patterns may reflect combined effects of general high honeybee abundance and competition effects, as well as foraging behaviour and seasonal activity periods as follows:

Eight honeybee hives were placed right by the experimental field. Multi-annual honeybee colonies have a maximum size of about 30,000 adults (VDRB, 2011) compared to bumblebee colonies with a maximum of 50 to 600 adults depending on the species (Hagen & Aichhorn, 2014). Furthermore, general abundance of wild living bumblebees and hoverflies depends on the requirements of nesting or larval sites, respectively, and, thus, on landscape composition (e.g. Kennedy et al., 2013; Sjödin, Bengtsson, & Ekblom, 2008). Worker honeybees returning from a collecting flight brief other worker bees the direction where to find attractive floral resources by their waggle dance or indicate nearby resources by a circular dance, and honeybees show pronounced flower constancy (VDRB, 2011). Hence, a comparatively high honeybee activity within the experimental field

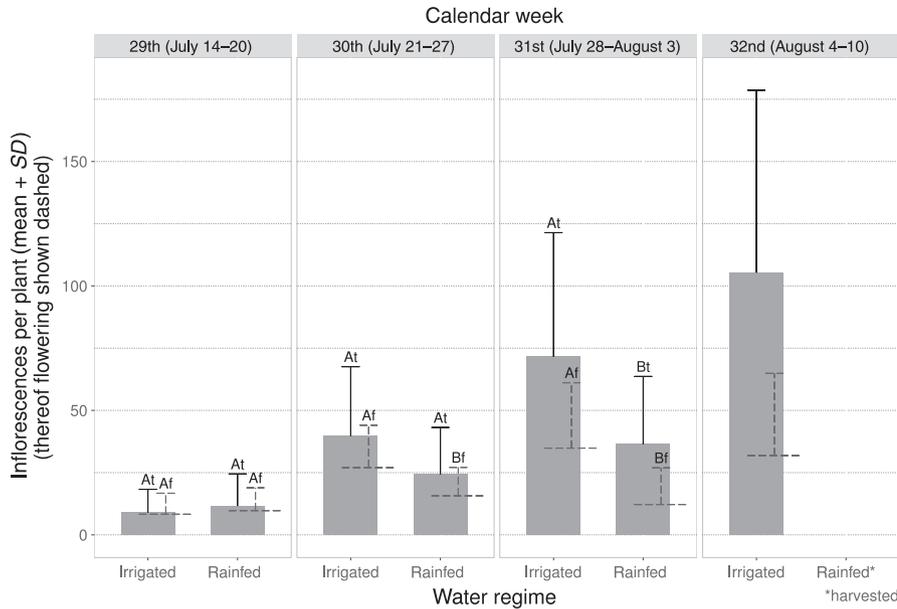


FIGURE 2 Inflorescences per cup plant grown under different water regimes. Different letters indicate a significant difference ($p(\text{LRT}) < .05$) between irrigated and rainfed plots regarding the total number of inflorescences per plant (sum of withered and flowering inflorescences, marked with “t”) as well as the number of flowering inflorescences per plant (marked with “f”) for each calendar week, respectively

| Model no. | Explanatory variables | df | AIC | Test | Chisq | $pr(>\text{Chisq})$ |
|--------------------------------------------------------------------|-----------------------|----|--------------|----------|--------|---------------------|
| Response variable: Honeybee visits on 10 inflorescences in 15 min | | | | | | |
| 1 | WR + CW +WR: CW | 10 | 215.2 | | | |
| 2 | WR + CW | 8 | 215.4 | 1 vs. 2 | 4.221 | .121 |
| 3a | WR | 6 | 227.4 | 2 vs. 3a | 16.027 | <.001 |
| 3b | CW | 7 | 221.2 | 2 vs. 3b | 7.836 | .005 |
| Response variable: Bumblebee visits on 10 inflorescences in 15 min | | | | | | |
| 1 | WR + CW +WR: CW | 10 | 208.8 | | | |
| 2 | WR + CW | 8 | 209.0 | 1 vs. 2 | 4.237 | .120 |
| 3a | WR | 6 | 216.4 | 2 vs. 3a | 11.422 | .003 |
| 3b | CW | 7 | 207.0 | 2 vs. 3b | 2e-04 | .988 |
| Response variable: Hoverfly visits on 10 inflorescences in 15 min | | | | | | |
| 1 | WR + CW +WR: CW | 10 | 168.7 | | | |
| 2 | WR + CW | 8 | 170.2 | 1 vs. 2 | 5.447 | .066 |
| 3a | WR | 6 | 183.1 | 2 vs. 3a | 16.990 | <.001 |
| 3b | CW | 7 | 168.2 | 2 vs. 3b | 0.043 | .836 |

Note: Generalized linear mixed effects models (GLMMs) were applied with the variables water regime (WR, two levels: irrigated and rainfed plots) and calendar week (CW, 3 levels: 29th to 31st) as well as their interaction as fixed structure. The variables “plot” and “daytime” nested in “sampling day” formed the random structure.

Significant p -values of the LRT ($p(\text{LRT}) < .05$) and final models in bold.

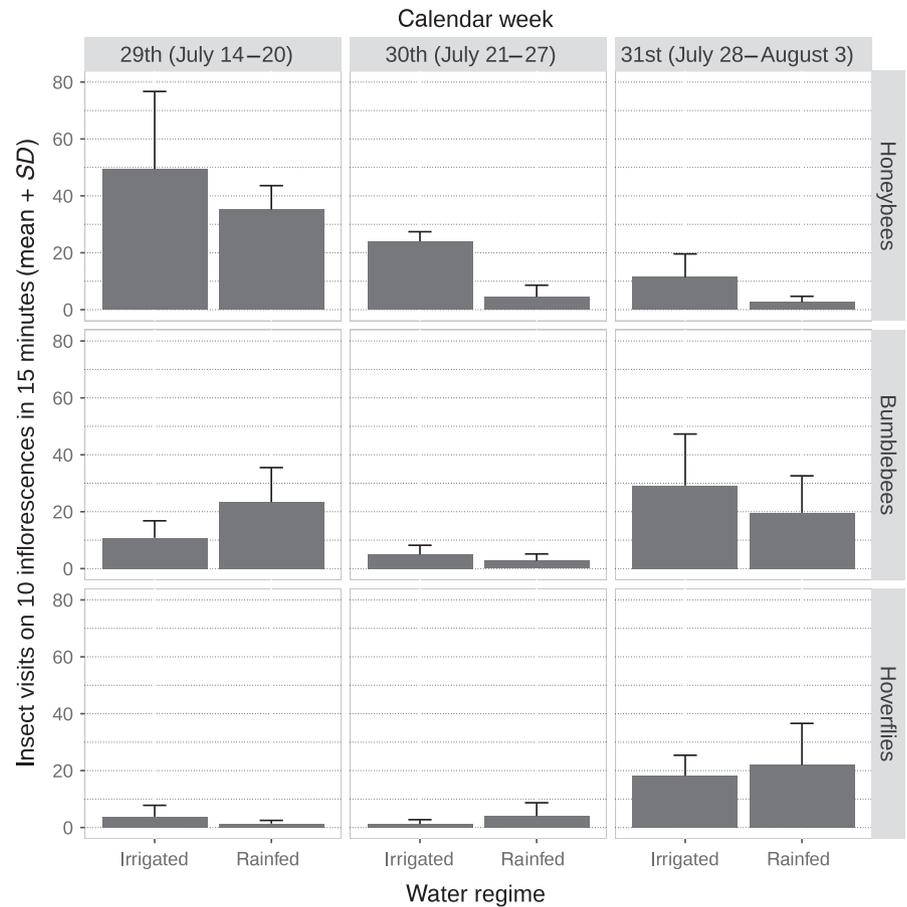
could be expected. However, as both irrigated and rainfed plots were located in close proximity, higher honeybee visitation in irrigated plots is a result of local orientation to higher flower densities instead of an indication by other worker bees.

Flower constancy in bumblebees is less pronounced, and resource selection orientates more on qualitative characteristics (Leonhardt & Blüthgen, 2012). Furthermore, bumblebees extend their forage breadth with increasing pollinator abundance (Fontaine, Collin, & Dajoz, 2008). Decreased bumblebee visitation in the 30th calendar week may therefore reflect both a preference

for and a displacement to other surrounding resources. We observed *Phacelia* and mustard fields in the vicinity whose blossom was decreasing in the 31st calendar week. The missing impact of the water regime on bumblebee visitation may further reflect a shift to the rainfed plots of lower densities of inflorescences, less visited by honeybees (Walther-Hellwig et al., 2006). As a consequence, possible positive reactions to high densities of inflorescence that could be expected for bumblebees as well (Hegland & Boeke, 2006) have not been observed due to superimposing effects.

TABLE 2 Likelihood ratio test (LRT) for model selection regarding insect visitation

FIGURE 3 Number of honeybee, bumblebee and hoverfly visits on 10 inflorescences in 15 min comparing irrigated and rainfed plots of the cup plant



Hoverfly visitation increased at the end of the flowering period in comparison with the previous two weeks, but in contrast to bumblebees, this may not be associated with competition effects at times of high honeybee visitation, but confirms the above mentioned general late activity peaks of the most abundant species like *Eristalis tenax* L., as it was observed in cup plant fields and surrounding habitats by Mueller and Dauber (2016). Hoverfly density may increase with flower density when comparing similar habitats on separated study areas (Power & Stout, 2011), but Hegland and Boeke (2006) found that hoverfly activity is not influenced by flower density comparing patches within a distinct area. They explained this lack of relationship with lower requirements of hoverflies in comparison with bumblebees and hence a less targeted and less optimized foraging behaviour. However, although the lower flower densities of rainfed plots did not affect hoverfly visitation in comparison with irrigated plots, the early harvest of the cup plant, especially of the rainfed plots, is a disadvantage for those hoverfly species with a late activity period.

4.3 | Cultivation of the cup plant

Facing an increasing demand for agricultural land and the possible impacts on biodiversity mentioned above, cropping systems have to be optimized to enable an efficient but ecologically sustainable production of food and energy. Schoo, Kage, et al. (2017)

showed that a high water availability is needed to achieve high dry matter yields of the cup plant, but they pointed out that a less efficient use of agricultural land must be set against possible ecological benefits. In case of pollinators, the provision of sufficient and diverse floral resources throughout the season is of vital importance. Although the present study confirms that nectar sugar production of the cup plant is strongly affected by drought stress, the rainfed cup plants still produced a nectar sugar amount of about 20 kg/ha over a flowering period of about three weeks. Considering that the sugar requirements of a medium sized beehive are about 60 to 80 kg/year (VDRB, 2011), this is still a considerable amount, even if it might be slightly overestimated due to possible edge effects mentioned above. Therefore, a replacement of maize as a pollen-only resource by the cup plant is still beneficial for pollinators even on sites with an insufficient water supply. However, the cultivation of the cup plant on drier sites traditionally used as grassland, that can provide high amounts of floral resources (Baude et al., 2016), is not recommended for both economic and ecological reasons. From a pollinator's perspective, a replacement of maize by the cup plant on a small-scale, for example along field margins or ditches, might be more advantageous than a large-scale production of the cup plant, because yield losses caused by an insufficient water supply and a late joint harvest would be acceptable, especially if greening requirements can thereby be fulfilled. But also, pure cup plant crops instead of maize can be ecologically reasonable, for example at sites with

high erosion risk on slopes of low mountain ranges. It should be mentioned that there is ongoing research for the material usage of the cup plant, for example for particleboards, insulating material or paper production (BioSC, 2019; Klímek, Meinlschmidt, Wimmer, Plinke, & Schirp, 2016). A material usage might lead to later harvests after the flowering period and in this context, the maximum potential production of floral resources could be achieved on a large-scale production under optimal growing conditions.

However, in contrast to wild flower mixes, the cup plant is still a monofloral bee pasture. Therefore, it is further important to consider which alternative crops could have been chosen instead. As our study was conducted on one experimental site and in one year only, further research is needed to relate locations with different water availability as well as years of different precipitation to the number of inflorescences per cup plant, as this is the decisive parameter for the quantity of floral resources, and to compare the results with other alternative nectar-producing energy crops or EFA measures like land lying fallow for melliferous plants.

5 | CONCLUSIONS

We compared cup plants of three irrigated and rainfed plots, respectively, regarding nectar sugar production and insect visitation. Neither the nectar volume nor the sugar mass per disc floret and the number of disc florets per inflorescence were affected by the water regime. However, the number of (flowering) inflorescences per plant was higher in irrigated plots. In addition, rainfed plots were harvested about one week before irrigated plots as a result of earlier maturation. Hence, mean nectar sugar production was about three times higher in irrigated plots. It can be assumed that pollen supply differed by the same amount. The different flower densities influenced honeybee visitation per inflorescence, which was about twice as high in irrigated plots. Furthermore, the earlier harvest is a disadvantage for wild pollinators with a late activity period. However, a replacement of maize as a pollen-only resource by the cup plant is still considered to be beneficial for pollinators even on sites with an insufficient water availability, especially when a late joint harvest together with maize can be obtained. Further research is needed to compare locations of different water availability regarding the number of inflorescences per cup plant and compare it with other alternative nectar-producing energy crops or EFA measures to develop efficient but ecologically sustainable cropping systems.

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ORCID

Anna Lena Mueller  <https://orcid.org/0000-0002-5573-5034>

Siegfried Schittenhelm  <https://orcid.org/0000-0002-2743-0989>

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