Evaluating the relationship of pollinator attractiveness to floret length in inbred sunflower (Helianthus annuus, Asteraceae) lines

Eric Whitted
Evaluating the Relationship of Pollinator Attractiveness to Floret Length in Inbred Sunflower (*Helianthus annuus*, Asteraceae) Lines

by

Eric Whitted

A creative component submitted to the graduate faculty in partial fulfillment of the requirements for the degree of

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Program of Study Committee:
Dr. Anthony Assibi Mahama, Major Professor
Dr. Thomas Lubberstedt

The student author, whose presentation of the scholarship herein was approved by the program of study committee, is solely responsible for the content of this creative component. The Graduate College will ensure this creative component is globally accessible and will not permit alterations after a degree is conferred.

Iowa State University

Ames, Iowa

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Greatest thanks go to my wife Jennifer and daughters Katelynn and Meredith for putting up with countless late nights, missed events and busy weekends.
ABSTRACT

Sunflowers (*Helianthus annuus* L.) are an important worldwide crop for food, feed and oil. Hybrid sunflower accounts for the majority of crop hectares occupied by sunflower. Its seed production relies solely on the movement of pollen by insects to cross pollinate and fertilize the male-sterile female parent. Managed hives of honey bees (*Apis mellifera*) are placed adjacent to hybrid sunflower seed production fields to carry out the pollination activities. Problems with poor seed set and low yields arise when a parental inbred line is not attractive to bee pollinators. This study characterizes inbred attractiveness to bees, the impact of floret lengths, and examines the relationship between the two. In 2019, 79 male fertile inbreds and 59 male sterile inbreds were planted in a small plot research study at the Corteva™ Agriscience location in Woodland, California, USA. Bee visits to each genotype were recorded during the bloom period. Floret lengths were measured from each genotype using photometry methods. Regression analysis was used to examine the relationship between floret length and bee visitation rates. Bee visitation rates are used to measure the attractiveness of a genotype to bees. The objective of this study was to examine the relationships between sunflower floret length and the visitation rates of pollinators and determine whether floret length could be used to predict pollinator attractiveness.

Bee visitation rates were significantly affected by floret length (p-value = 0.0049), genotype (p-value = 1.092e-13) and observation date (p-value = 1.697e-10). A general linear mixed model was constructed and predicted mean values for bee visits for each genotype were generated. Least squares mean values were generated for each genotype for floret length. Regression of bee visitation rates onto floret lengths reveals little
correlation between the two factors, $R^2 = 0.025$. Correlation slightly improves for male sterile genotypes alone $R^2 = 0.058$ but declines for male fertile genotypes alone $R^2 = 0.002$. These results suggest that for the group of inbreds studied, floret length is not a good predictor of pollinator attractiveness. Future studies will focus on different pollinator survey methods and other floral traits such as visual cues and nectar traits to characterize pollinator attractiveness.
INTRODUCTION

Sunflower as a Crop

Sunflowers and other members of the genus *Helianthus* are native to North America and were domesticated thousands of years ago by Native Americans. Sunflowers have mainly been bred to serve two markets, confection and oil seeds. Oil seed varieties are used to produce sunflower oil that is stable at high cooking temperatures, high in vitamin E, and some varieties have also been bred to have low levels of saturated fat. Confection sunflowers are bred for their edible seeds and are an important part of the snack food market (Long 2019). Sunflowers are also sometimes chopped to produce silage for animal feed.

Modern sunflower (*Helianthus annuus* L.) hybrid seed production systems arose as a result of two significant events. The introduction of open-pollinated, high-oil cultivars from the USSR around 1960 proved useful as a viable source of cooking oil. The 1968 discovery of cytoplasmic male sterility (Leclercq 1969) and subsequent reports of fertility-restoring genes by others enabled relatively easy and inexpensive hybrid seed production utilizing the same biological systems as in corn (*Zea mays* L.) and grain sorghum (*Sorghum bicolor* (L.) Moench). The 1971 release of seven cytoplasmic male-sterile and two fertility-restorer inbred lines by the ARS, USDA and Texas Agricultural Experiment Station provided the source of basic seedstocks which became the foundation for the hybrid sunflower seed industry (Anfinrud 1997).
Hybrid Sunflower Seed Production

Sunflower pollen is relatively large, heavy and sticky, and so wind pollination does not readily occur in sunflower. Hybrid sunflower seed production relies on the movement of pollen by insects to cross pollinate and fertilize the male-sterile female parent. Managed hives of the domestic honey bee (*Apis mellifera*) are relied on for the majority of pollination activity. This cross pollination is, in part, driven by the differential preferences of honey bees for nectar or pollen. Much of pollination is due to incidental contact and transfer as honey bees are seeking and feeding on nectar (Fell 1986).

Production of hybrid seed consists of planting two inbred cultivars in adjacent rows in an alternating pattern of one or multiple male rows in between several female rows (Appendix A.1). One of the lines is a male sterile A line (female) and the other is a male fertile R line (male), providing the pollen needed for fertilization of the sterile female A line. Male rows are destroyed after flowering is complete to prevent harvesting of self-pollinated seed. The hybrid seed produced from the cross pollination is sold to growers and grown in commercial fields for food, feed and oil. Obtaining this cross pollination at a high enough level to generate a profitable amount of hybrid seed is the main challenge in hybrid sunflower seed production.

Individual honey bees tend to prefer foraging on a single flower morphological type during a single trip and subsequent trips. Single bee forage trip switching refers to bees visiting different parental lines on the same foraging trip. Forage trip switching occurs at very low rates and differs between parents with similar morphology and parents with different morphology, 15% - 0%, respectively. Even highly similar parental lines are visited rarely by the same bee on the same foraging trip. It has been proposed that the majority of
pollen transfer occurs within the honey bee hive and at the hive entrance between individual bees that have been foraging on male fertile flowers and bees that have been foraging on male sterile flowers within the same field (Susic 2016). This is important to note because parents that are both equally attractive to pollinators will be visited at about the same frequency, facilitating pollen exchange between bees at the hive to be subsequently carried to the male sterile parent. If one of the parental lines is not attractive to honey bees, then the majority of foraging will occur on only one parent and movement of pollen between parents will be reduced.

Hybrid sunflowers have been bred to be self-fertile. It has been demonstrated that self-fertile hybrid sunflowers also benefit from pollinator activity. These benefits include increased yield, seed mass, increased germination and sometimes increased oil content (Tesfay 2010, Degrandi-Hoffman 2006, DeGrandi-Hoffman 2000, Krause 1981, Chamer 2015, Palmer-Jones 1975). These results have also been confirmed for hybrid confection sunflowers with increased visitation from pollinators resulting in an increase in yield. Benefits were shown to vary across hybrids due to differences in their self-fertility and relative attractiveness to pollinators (Mallinger 2017b, Mallinger 2018). In self-fertile hybrid sunflowers, Hernandez (2008) demonstrated that as much as 30% of the capitulum area must be covered to minimize the development of incompletely developed seeds.
**Flower Structure and Development**

A sunflower capitulum is composed of hundreds or thousands of individual florets. Each floret is a perfect flower possessing male and female organs. Fertilization of a single floret produces a single sunflower seed (Appendix A.4). When florets first open the male anthers emerge. On about the second day, the stigma pushes up from the base of the floret. Any pollen left on the anthers could contact the stigma resulting in self-pollination. In self-fertile cultivars, self-pollination can result in seed set (Degrandi-Hoffman 2006).

Immature sunflower plants exhibit heliotropism. Heliotropism is a dynamic form of phototropism in which aerial portions of the plant follow the movement of the sun throughout the day. During the night sunflowers reorient leaves and apices to face east prior to sunrise. The heliotropism mechanism in sunflowers has been shown to be the result of regulation of differentiated elongation on opposite sides of the stem. This heliotropism ceases as plants mature and stem elongation halts, marking the beginning of flowering. Mature plants remain with the flowering head facing east. Solar tracking behavior in young plants has been shown to increase vegetative biomass. Mature plants that remain in an east facing orientation have been shown to benefit from an increase in pollinator visitation, this is likely due to increased flower temperature in the morning from early sun exposure maximizing the interception of solar radiation (Atamian 2016).

It has been shown that the size of a developing capitulum is significantly influenced by the amount of irradiance intercepted by the plant during vegetative growth. Shading of plants prior to flower initiation reduces the size of the capitulum. A reduction in capitulum size increases competition between individual florets and limits their lateral growth, in turn
reducing seed size. Floret height is largely not affected by floret competition and remains relatively constant (Sinsawat 1993).

**Managed Honey Bee Pollination Services**

Managed honey bee colonies are routinely used in sunflower hybrid seed production. Domestic colonies of honey bees are used to ensure that there is a high enough flower visitation rate to generate the yield needed for profitable commercial production. Honey bees are easily managed, and hives are highly mobile, enabling the rapid deployment of pollination resources. This mobility is desirable as it allows for hives to be moved from field to field and across crops as flowering progresses and pollination services are required.

There is much disagreement among studies as to the efficacy of honey bee pollination in sunflower compared to pollination by sunflower specialist and native bees. Much of the discrepancies arise from the context and focus of individual studies. Some studies focus on the benefits of pollinators in self-fertile hybrid fields where managed honey bee colonies are not brought in and native bees (*Melissodes* spp., *Andrena* spp.) dominate the populations (Mallinger 2018). Rader (2009) demonstrated that several wild bee species provide similar visitation and pollen transfer rates as honey bees, but honey bees were more effective pollinators due to high populations from managed hives. Honey bees have also been shown to outperform wild bees in both visitation rates and single-visit contributions to seed set (Pisanty 2014). This is in contrast to Parker (1981), who found honey bees to be the least efficient pollinators of male sterile sunflowers because they rarely visited male fertile flowers and carried less pollen on their body hairs compared to native *Melissodes*. Regardless of which bee species or group is the most efficacious pollinator, most studies agree that both
managed honey bees and native bees do not directly compete for the same resources. Working together, wild and domestic bee groups provide superior pollination services (Sardiñas 2016, DeGrandi-Hoffman 2000). For example, Greenleaf (2006), found that behavioral interactions between wild and honey bees effectively doubled the honey bee pollination services on the average hybrid seed production sunflower field. Pollination services were enhanced by the wild bees essentially disturbing the foraging behaviors of honey bees and causing them to move between male sterile and male fertile blossoms more frequently.

External factors such as pesticide use have also been shown to have a negative impact on pollinator visitation rates to sunflowers. Biweekly applications of carbamate insecticide and fungicide resulted in a 58% decline in honey bee visitation to treated sunflowers when compared to an untreated control (de Oliveira 2019).

Pollinator foraging distances have also been demonstrated to be positively correlated with body size and mass (Cariveau 2016). Foraging distances have an impact on hive placement and maximum field size to ensure pollinators have access to the entire area expected to be pollinated.

**Pollinator Attractiveness**

Many studies have attempted to describe the differential attractiveness of sunflower cultivars (du Toit 1991, Cerrutti 2016, Stejskalova 2018, Rinku 2017) and to classify the diversity and abundance of sunflower pollinators (Westphal 2008, du Toit 1992, Rinku 2017). Shein (1980) demonstrated that there was differential attractiveness between genotypes and that the presence of pollen was not a factor. His results compared the visitation rates to both male sterile and male fertile inbreds. Corolla tube length and stigma
color together were shown to be negatively correlated with honey bee visitation rates. The study could not determine if the reduced visitation rates were due to corolla length independent of stigma color or vice versa. A multi-year study examining nectar quantity and sugar content along with corolla length demonstrated that pollinator visitation rates were significantly impacted by these factors (Mallinger 2017a). The same study also reported that wild bees had a significant preference for male-fertile flowers while honey bees preferred male-sterile flowers. Sunflower pollen seemed not important for the honey bee likely due to the low protein content and insufficient levels of the essential amino acids methionine and tryptophan essential for honey bee development (Nicolson 2013). Other studies also support the findings that increased sunflower corolla lengths decrease pollinator visitation rates (Atlagic 2000). In a two-year study, Portlas (2018) demonstrated that floret lengths differed significantly between inbred lines and explained 52% of the variation in wild bee preference for inbred sunflower lines. Size matching of a pollinator proboscis length and nectar depth is intuitive and has been demonstrated across many pollinator and plant species (Stang 2009). If the nectar reward is inaccessible, then pollinators will not have incentive to visit the flower.

Significant differences in nectar sugar content between genotypes has been reported to have an influence on honey bee attractiveness. Prasifka (2018), highlights several studies that suggest nectar quality in the form of sugar concentrations and ratios of sucrose, fructose and glucose have been implicated in influencing pollinator choice. Zajacz (2008), reported that environmental conditions were also found to influence nectar sugar content and nectar quantity. Abundant precipitation during flowering caused a measurable increase in nectar quantity. It was also shown that excessively cool air temperatures had the effect of increasing nectar sugar content.
**Objective of Study**

Sunflower nectar traits and disc flower corolla length are the two most important parameters of attractiveness to pollinators of sunflower (Joksimović 2003). The objective of this study was to examine the relationships between sunflower floret length and the visitation rates of pollinators, in an attempt to characterize inbred lines of sunflower and use floret length as a predictor of pollinator attractiveness.

It has been observed that there is a range of pollinator attractiveness to the inbreds in our breeding program and plantings in hybrid seed production fields. Genotype is the largest contributor to phenotypic variability in corolla length (Joksimović 2003, Atlagic 2003). When an inbred is not well visited by pollinators it results in poor yields and increased costs to produce. It is important to characterize inbred parents for pollinator attractiveness so that they can either be avoided in the breeding pipeline or mitigation efforts be proactively implemented in hybrid seed production fields. Current methods of compensating for an unattractive parental line in a hybrid seed production field are increasing the ratio of male fertile to male sterile rows and increasing the honey bee hive density.
MATERIALS AND METHODS

This study was conducted in a small sunflower field located at the Corteva™ Agriscience research facility in Woodland, CA from June 18th to July 2nd, 2019. Woodland is located within Yolo County in California’s Sacramento Valley. Yolo County is an intensively-farmed agricultural region that contains a mixture of conventionally managed row and orchard crops. Almonds, tomatoes, wine grapes, rice and registered organic production (row crops, produce and rangeland) are the top five commodities according to gross value. Alfalfa hay, walnuts, sunflower seed, nursery products, and cattle are the top ten commodities for 2018. In 2018, 63,012 hectares of sunflower seed crop was harvested (Yolo County Weights and Measures, Crop Statistics). Ninety percent of the hybrid sunflower seed produced in North America originates in the Sacramento valley with Yolo county producing 41% of the certified hybrid sunflower seed (Long 2019).

Honey bee and wild bee visitation rates were observed across a pool of unique sunflower inbred lines within our current breeding and commercial pipeline. Florets from the same lines were also collected, photographed and measured using proprietary photometry methods. Floret length was compared to pollinator visitation rates on an inbred basis. It was hypothesized that the majority of variability in pollinator visitation rates would be explained by floret length, with pollinators preferring a shorter floret length. This study characterizes pollinator attractiveness and floret lengths for the current pool of inbreds in our breeding and commercial pipeline.

Eighty-seven male fertile inbred lines and 71 male sterile inbred lines were planted in single row plots at a population density of 59,305 plants per hectare. Two 5.3m long plots were planted side by side on 152cm raised beds. Spacing between rows was 76cm and a
76cm fallow alley was maintained to separate plots along the rows. Each inbred line represents a unique genotype. Data were not collected on 8 male fertile lines and 12 male sterile lines because seed was not received in time for planting or plot quality was poor. Irrigation was provided via subsurface drip. Male fertile and male sterile entries were blocked separately. A robust male fertile inbred was used as border around the plots and to replace missing entries to draw in pollinators and shield the plots from wind. Two healthy half size bee hives were placed at the northwest and southwest end of the study field. Excess bees were placed at the study field to saturate the area and increase visitation rates to enable a decrease in observation time (Fijen 2017). Normal bee hive density in a hybrid sunflower production field is 3.7 hives per hectare. The study field had the equivalent of 6.4 hives per hectare. The field surroundings consisted of an industrial area of research and seed production facilities to the north and agricultural fields of corn, tomatoes, sunflower, nut trees and fallow areas to the east, south and west (Appendix A.2, A.3).
Figure 1. Field plot layout and orientation. Male fertile lines are in the west (green) block, male sterile lines are in the east (orange) block. Gray represents border rows. Blue boxes represent the approximate locations of bee hives. Each number represents a single row plot, 5.3 meters long, north to south. Each plot is separated by a 76cm fallow alley north to south (range). Each plot is separated east to west by 76 cm row spacing. Each pair of plots (rows), represent a 152cm raised bed.
Honey bee activity data were collected each morning between approximately 8 am and 12 pm depending on temperature. Bee activity has been shown to be greatest in the pre-noon hours and peaks again in the evening (Krause 1981). Honey bee activity commenced each morning earlier than data collection was initiated. Collection of bee visit data was delayed until morning temperatures reached 21 °C to ensure a significant level of activity was reached so as to ensure homogeneity throughout the data gathering time period. This relationship of morning temperatures and commencement of bee activity has been demonstrated in several studies (Krause 1981, Fijen 2017, Puskadija 2007).

Preliminary observations of pollinator activity in the field to be studied were used to determine the number of flowers observed and the length of observation. To obtain accurate visitation rate estimates, a sufficient number of pollinators must be observed. Fijen (2017) reported a strong negative relationship between observation duration and visitation rates, as observation duration decreased with increased visitation rates ($R^2 = 0.85, p < 0.01$). Based on pollinator activity in the field of this study, visitation rate was determined by recording all bees that visited three selected capitula per parental line over a time period of two minutes.

Pollinator visitation observations in each plot began when three representative capitula reached R5.2 flowering stage, where 20% of the florets were at flowering stage (Schneiter 1981). Observations occurred once per day and continued for five consecutive days on representative capitula or until flowering reached R5.9, whichever occurred soonest. For branched male fertile lines, visitation data were collected beginning on the main capitulum and continuing on to an axillary capitulum if the main capitulum exceeded R5.9 during the five-day observation period.
Each significant visit to three representative capitula over two minutes by either a wild bee or a honey bee was recorded. A significant visit consisted of meaningful contact with flowering organs. Bees that contacted flowering organs for less than two seconds were not recorded. Bees that briefly left a flower to hover and reposition were recorded as a single visit, however if the same bee left one observed flower after a significant visit to visit another observed flower within the observation time it was considered two unique visits. Bees that remained on ray florets or other non-flowering areas were not counted.

Observations began each day at an entry chosen by a random number generator and continued sequentially. Starting observations alternated each day between male sterile and male fertile blocks. A general linear mixed model was constructed and predicted mean values for bee visits for each genotype were generated (Table A.1, Table A.2). The model used is:

\[ Y_{ijk} = \mu + F_i + G_j + D_k + \varepsilon_{ijk} \]

- \( Y_{ijk} \) = bee visitation rate of the ith floret length on the jth genotype on the kth collection date
- \( \mu \) = overall mean
- \( F_i \) = the effect of the ith floret length, a random effect
- \( G_j \) = the effect of the jth genotype, a fixed effect
- \( D_k \) = the effect of the kth collection date, a random effect
- \( \varepsilon_{ijk} \) = residual variation, a random effect

In addition to bee visitation and floret measurement data discussed below, data were collected on the following traits for each line: flowering start date, 50% flowering date, last flowering date, and plant height.

Three representative capitula at stage R5.9-R6 were removed from each plot, tagged with identification and transported into the lab in mesh harvest bags. Florets were removed from an approximately 3 cm diameter area located equidistant from the center and edge of
each sunflower capitulum (Appendix A.5). Under normal growing conditions at anthesis there is not a significant difference in floret height between the outer and inner positions (Sinsawat 1993). Florets were removed from the capitulum and imaged within 48 hours of harvesting the capitulum from the plant. Florets removed from the capitulum quickly desiccated and deteriorated within hours but remained fresh and viable if left attached to the capitulum for up to 48 hours at room temperature.

Floret samples were imaged immediately after removal from the capitulum to avoid desiccation and the resulting size shrinkage. The number of florets sampled varied for each genotype (Table A.1, Table A.2). For each plot, floret samples were removed from each of three capitula (Appendix A.5), combined, sifted to remove debris (Appendix A.6), and placed within the outlined focal area on a blue foam board in preparation for imaging (Appendix A.7). Florets were arranged to minimize touching and overlap in order to facilitate image processing following image capture. Imaging took place within a proprietary fixed camera photometry box using a Canon EOS Rebel T2i camera and proprietary image capture software. The fixed camera setup allows for the use of a single calibration factor to convert pixels to length measurements in millimeters.

Floret images were processed using proprietary software. Each floret in an image was identified and annotated with a unique number. Output files consisted of the length measurement, in number of pixels, of each individual floret. Floret measurement data were analyzed to remove incorrectly measured florets. Incorrect measurements occur occasionally when florets are grouped together or unnecessarily split by the image processing software (Appendix A.8). Floret length measurements were converted from number of pixels to
millimeters. R package lsmeans (Lenth 2016) was used to generate least squares mean values for floret lengths by genotype (Table A.1, Table A.2).

Bee visitation data and floret measurements were analyzed using JMP v14.2.0 (JMP), R v3.5.1 (R Core Team 2018), R package lme4 (Bates 2015), R package lsmeans (Lenth 2016) and R package predictmeans (Luo 2018). To protect Corteva™ Agriscience intellectual property, inbred lines were identified by random alphanumeric characters in place of actual inbred codes.
RESULTS

Bee Visitation Rates

Bee visitation rate observations (n = 689) were converted to visits per minute and exhibit a significant skewness to the right (Appendix A.9). The visitation data were analyzed using ANOVA to identify factors that significantly contributed to the variability in bee visitation rates. Floret length (p-value = 0.0049), genotype (p-value = 1.092e-13) and observation date (p-value = 1.697e-10) were significant factors accounting for the variability in bee visits (Table 1). Given these results, the null hypothesis that no difference in floret length and pollinator attractiveness among inbreds is rejected. This is consistent with previous studies that have confirmed cultivar flowering date does not have a significant influence on the level of attractiveness for honey bees and that cultivar genotype is a significant factor in the level of attractiveness for honey bees (Cerrutti 2016, Sapir 2009). A Tukey-Kramer comparison of mean bee visitation rates revealed significant differences in bee visitation rates across collection dates (Table 2) and genotypes (Table A.1, Table A.2).
Table 1. ANOVA of effect of floret length (p-value = 0.0049), genotype (p-value = 1.092e-13) and observation date (p-value = 1.697e-10) on bee visitation rate (Num visits/min).

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<th>Df</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
<th>F value</th>
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<td>Observation Date</td>
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<td>71.43</td>
<td>5.1022</td>
<td>5.7493</td>
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<td>Residuals</td>
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<td>472.12</td>
<td>0.8874</td>
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Table 2. Collection dates, times, weather conditions and mean bee visitation rates. Means not connected by the same letter are significantly different (α = 0.05).

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<tr>
<th>Date</th>
<th>Time Start</th>
<th>Temp °C Start</th>
<th>Time End</th>
<th>Temp °C End</th>
<th>Observations</th>
<th>Mean Bee Visits/Min</th>
</tr>
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<td>6/18/2019</td>
<td>8:50</td>
<td>27</td>
<td>10:40</td>
<td>30</td>
<td>Moderate light breeze, sunny</td>
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<td>10:50</td>
<td>28</td>
<td>Very light breeze, sunny</td>
<td>1.08bcd</td>
</tr>
<tr>
<td>6/20/2019</td>
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<td>2:15</td>
<td>29</td>
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<tr>
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<tr>
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<td>10:20</td>
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<td>1.27abcd</td>
</tr>
<tr>
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<td>9:30</td>
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</table>
Floret Lengths

Floret length is much easier to measure than functional corolla depth and has been shown to be highly correlated ($R^2 = 0.78$) to corolla depth (Portlas 2018). For this study, floret length will be used as a proxy for corolla length. Floret length observations ($n = 19994$) (Table A.1, Table A.2) show a nearly normal distribution with very slight skewness to the right (Appendix A.10). Floret length observations were analyzed using ANOVA to test the null hypothesis that there is no difference in floret length across genotypes. It was found that genotype contributes significantly (p-value = 2.2e-16) to the variability in floret length (Table 3). Given this, the null hypothesis that there is no difference in floret length across genotypes is rejected. A Tukey-Kramer comparison of mean floret lengths revealed significant differences in floret lengths across genotypes (Table A.1, Table A.2).

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<th>F value</th>
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</table>

Floret Lengths and Bee Visitation Rates

A regression of bee visitation rates onto floret lengths (Table A.1, Table A.2) reveals little correlation between the two factors, $R^2 = 0.025$ (Figure 2). Correlation slightly improves for male sterile genotypes alone $R^2 = 0.058$ (Figure 3) but declines for male fertile genotypes alone $R^2 = 0.002$ (Figure 4). For both male fertile and male sterile genotypes, floret length would not be a good predictor of bee visitation rates, accounting for zero (Figure 4) and 6% (Figure 3) of the variability, respectively. Although the correlations are weak, the negative trend in bee visitation rates is expected as floret length increases. The slightly
positive trend seen in the male fertile genotypes is likely due to the extremely poor correlation and floret length having little influence on bee visitation rates.

Figure 2. Regression of bee visitation rates onto floret length for $n = 138$ male fertile and male sterile inbred lines.
Figure 3. Regression of bee visitation rates onto floret length for $n = 59$ male sterile inbred lines.

Figure 4. Regression of bee visitation rates onto floret length for $n = 79$ male fertile inbred lines.
DISCUSSION

Most previous studies focused on self-fertile hybrid fields where the majority of the populations were wild bees. In contrast to other studies (Parker 1981, Mallinger 2017a, Mallinger 2018) honey bees accounted for the majority of pollinators present in this study. This was a result of the saturation of the study with honey bee hives. There was still a surprising abundance of wild bees (Melissodes spp.) present within this field of study. Their abundance was likely due to the large amount of sunflower and other flowering crop cultivation coupled with many field edges and natural habitats suitable for ground nesting native bees (Saez 2012). Studies performed within the same general area as the current study (Yolo county, CA) observed native ground nesting bees in a variety of habitats including within the sunflower crop fields and at field edges with populations and nesting sites being most abundant at field edges (Sardiñas 2016, Sardiñas 2015).

Bee visitation data exhibited significant variability due to both genotype (Table A.1, Table A.2), floret length and observation date (Table 2). Similar findings have been reported in other studies. Genotype has been reported to be a significant source of variability in bee visitation rates in both hybrid (Portlas 2018, Rinku 2017, du Toit 1988, Krause 1981) and inbred sunflowers (Shein 1980, Mallinger 2017a). Environmental conditions that would vary by observation dates such as temperature (Telfay 2010) and wind speed (Fijen 2017) have been identified as factors that significantly influence bee foraging activity.

During this study, three dates, June 18, 21 and 22, had mean visitation rates that varied significantly from all other observation dates (Table 2). The observation date of June 18th, the first date of bee observation, had the highest mean observation rate of 2.17 bees/min. This high observation rate was likely due to the recent movement of the bee hives to the
study field. One of the hives was moved to the study field more than 24 hours before the first observation date, the other hive was moved to the study field in the evening before the first date of observation. The recent movement of the hives likely had the bees unsettled and forced them to increase scouting and foraging activities in an effort to establish the most efficient and productive foraging routes and targets (Delaplane 2013). The other two dates, June 21st and 22nd, had mean bee visitation rates (0.88 and 0.66, respectively) that were significantly lower than the remaining observation dates. The low visitation rates on these dates were likely due to windy conditions (Table 2). Winds were mostly blocked by the large building structures directly adjacent to the field but still had a significant impact on honey bee foraging activities.

Curiously, line type (male fertile or male sterile) did not contribute significantly to the variability in bee visitation rates. This is likely due to the method used to collect the bee visitation data. A single male fertile plant consists of many branches with functional capitula that contribute to the reproductive surface area presented in addition to the primary capitulum. In contrast, a male sterile plant does not have branches and presents a single primary capitulum. With its many branches, a male fertile plant will also flower over a duration two to three times longer than a male sterile plant. Given the branched structure of male fertile plants, it was not feasible to count all bee visitors to flowering capitula on branches, hence only visitors to the main capitulum were counted. Bee visits to a branch were only counted if the primary capitulum completed flowering during the observation time. Essentially, only a small portion of the reproductive surface and flowering duration for a male fertile plant was assessed compared to the entire reproductive area and majority of flowering duration for a male sterile plant. This morphological difference coupled with the
data collection method is likely a significant source of error and does not allow for a direct comparison of bee visitation rates between male fertile and male sterile genotypes. Therefore, male sterile and male fertile genotypes were separated and evaluated independently (Table A.1, Table A.2).

Bee visitation rates for male fertile genotypes (n = 79, mean = 1.12, sd = 0.47) were less variable than male sterile genotypes (n = 59, mean = 1.62, sd = 0.74). It is likely that true visitation rates to male fertile genotypes was not meaningfully assessed by this study. Due to the branched, multi-capitula nature of male fertile plants, actual visitation rates are likely much higher than observed. This fits well with observations in hybrid seed production fields where male fertile lines have not experienced issues with poor pollinator visitation rates.

Male sterile lines have been observed to have a much wider range of desirability for pollinators. Through hybrid seed production experiences two male sterile lines, FFY31A and BYW67A, have demonstrated poor pollinator attractivity. The pollinator visitation data collected in this study supports those observations. FFY31A had the lowest predicted mean visitation rate (0.33 bees/min) among all male sterile lines. BYW67A at a predicted mean visitation rate of 1.09 bees/min, ranked in the bottom 20% of male sterile lines (Table A.1).

Floret measurement via photometry methods proved to be a viable and robust measurement method. The sheer number of florets that were measured (19,994) far outnumbers any known study to date. The number of florets measured for each genotype ranged from 63 to 237. The large volume of florets measured provides the ability to generate a very precise and accurate estimate of floret length for each genotype.

The poor correlation of floret length and bee visitation rates indicate that for the group of inbreds studied, floret length is not a useful factor for predicting pollinator
visitation. Studies that show a significantly greater relationship between floret length and pollinator visitation indicate that longer florets present a physical barrier to a pollinator reaching the nectar reward (Portlas 2018, Mallinger 2017a). The pollinator proboscis is not long enough to extend to the nectar at the bottom of the corolla tube. In this study mean floret length ranges from 5.6mm to 8.4mm. The corolla tube that must be spanned by a pollinator proboscis represents approximately 70% of the entire floret length. Given that the mean functional length of the honey bee proboscis is approximately 7.0mm (Waddington 1987), the floret lengths observed in this study would not pose a physical barrier to pollinator foraging activities.

Studies that have found a significant negative correlation between floret length and pollinator visitation rates used genotypes that have longer floret lengths that would pose a physical barrier to honey bee foraging activities. In addition, several studies focus mainly on wild bee visitation rates (Portlas 2018). Wild bee pollinators of sunflower, with the exception of the rare bumble bee, are smaller in body size than the honey bee. Bee body size is a reliable indicator of functional proboscis length (Cariveau 2016). Wild bees, with shorter proboscis, would be more sensitive to floret lengths as a barrier to foraging activities.
CONCLUSION

This study successfully measured floret lengths for all genotypes sampled. In characterizing bee visitation rates, this study was successful for male sterile genotypes. Male fertile genotypes presented a unique challenge for properly measuring bee visitation rates and will require a change in protocol for future assessments. It is likely that future studies will focus on male sterile genotypes because that is where issues with poor pollinator visitation have been observed both in this study and in hybrid seed production fields. Bee visitation data for male sterile genotypes from this study will be used to rank the inbreds studied in order of relative pollinator attractiveness. Inbreds with demonstrated poor pollinator attractiveness in hybrid seed production fields, such as FFY31A and BYW67A mentioned above, can be used as benchmarks for pollinator visitation rates of an inbred. Inbreds that rank near or below benchmarks will likely have low rates of pollinator visitation. Efforts to mitigate the effects of poor pollinator visitation rates can then be implemented proactively to help ensure profitable hybrid seed production yields. This dataset also provides a good foundation for male sterile genotypes to build on with multiyear observations.

The objective of this study was to identify a simple and reliable method for determining pollinator attractiveness in sunflower inbreds by measuring floret length. In an effort to narrow the scope of this study the important nectar traits were ignored. Given the weak association found between pollinator visitation rates and floret length, other characteristics including visual cues, nectar quality and nectar quantity should be examined in future studies.

Many studies have also focused on pollinator attractiveness and the association with nectar quantity and quality. Future efforts to characterize inbreds for pollinator attractiveness
should include examining nectar quality using NIR analysis or microcapillary tubes and a refractometer to assess sugar concentration (Human 2013, Zajacz 2011). Multiyear data will be needed as nectar characteristics are greatly affected by environmental conditions. The high environmental variability and the labor-intensive nature of nectar collection and assessment raise concerns as to whether it is a practical option for large scale use.

Another promising avenue to pursue would be phenotyping sunflower lines for their ultraviolet (UV) floral patterning in conjunction with pollinator visitation rates to see if the UV floral pattern plays a significant role in pollinator attractiveness (Moyers 2017). Floral displays often include UV absorbing pigmentation patterns as nectar guides for pollinators, commonly referred to as the UV bullseye. Phenotyping for the relative size of the UV bullseye would be relatively inexpensive, easy to measure and adaptable for large scale use.
REFERENCES


Cerrutti N, Pontet C. (2016). Differential attractiveness of sunflower cultivars to the honeybee Apis mellifera L. OCL, 23, D204.


Vear, F. M Pham-Delegue, Denis Tourville de Labrouhe, R Marilleau, Y Loublier, et al. (1990). Genetical studies of nectar and pollen production in sunflower. Agronomie, EDP Sciences, 10 (3), pp.219-231. <hal-00885284>


APPENDIX A.

Figure A.1  This figure illustrates the alternating row pattern of a sunflower hybrid seed production field. Male fertile rows have begun to flower while male sterile rows are a couple days behind, this is done on purpose to help ensure purity.
Figure A.2 Field of study looking towards the southwest. Hive placement and subsurface drip irrigation is shown as well as the robust male fertile border planted as a windbreak.
Figure A.3  Field of study looking towards the north with production plant in background. Hive placement is shown as well as the robust male fertile border planted as a windbreak. The immediate foreground and field to the right is fallow, the field to the left is immature sunflower.
Figure A.4 This figure illustrates the basic sunflower reproductive organs. Florets were removed from the sepals and immature seeds for imaging.
Figure A.5  Sunflower capitulum that has had a floret sample removed. The center and edges of the capitulum are avoided to ensure a uniform floret sample. Note the white sepals that must be removed from the sample prior to imaging. Ray petals are removed for picture clarity.
Figure A.6 Method of sifting florets to remove debris and sepals. This process is necessary to provide the best possible image for processing. Foreign debris in the image can cause excessive errors and complicate floret measurements.
Figure A.7 Arrangement of florets in preparation for imaging. Florets are arranged within the focal area to minimize overlap and touching. The blue background provides contrast for better discrimination of the florets.
Figure A.8  Portion of a processed image with florets annotated with measurement boxes in red. Floret numbers #141, 162, 173 and 176 are correctly identified and measured. The floret represented by #142 and 134 has been unnecessarily split by the software. Florets represented by #131 could not be distinguished as separate by the software due to excessive overlap. Erroneous measurements were removed from the dataset.
Figure A.9  Distribution and summary statistics for bee visitation data.

Figure A.10  Distribution and summary statistics for floret length data.
Table A.1  Mean bee visitation rates and floret lengths for male sterile (A line) genotypes. Mean bee visitation rates not connected by the same letter are significantly different ($\alpha = 0.05$). Mean floret lengths not connected by the same letter are significantly different ($\alpha = 0.05$).

<table>
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<th>Coded Inbred Name</th>
<th>Material Type</th>
<th>Mean Bee Visits/Min</th>
<th>Bee Visits/Min SE</th>
<th>Floret Length Least Squares Mean</th>
<th>Number of Florets Measured</th>
<th>Floret Length SE</th>
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<td>8.039a</td>
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Table A.2  *Mean bee visitation and floret lengths for male fertile (R line) genotypes. Mean bee visitation rates not connected by the same letter are significantly different (α = 0.05). Mean floret lengths not connected by the same letter are significantly different (α = 0.05)*.

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<th>Floret Length Least Squares Mean</th>
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