

Assessing interspecific variation in nectar and pollen food reward to pollinators under water limitation

Madeline Gregor

University of San Francisco

Wendy Lei

University of San Francisco

Sevan Suni

ssuni@usfca.edu

University of San Francisco

Research Article

Keywords: Nectar, pollen, drought, pollinator, garden, protein

Posted Date: September 30th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-11030702/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Additional Declarations: No competing interests reported.

Abstract

Pollinators obtain food from plants in the form of nectar or pollen. Declines in pollinator populations have led to interest in planting floral enhancements to support pollinator nutrition. However, the way that food rewards vary across plant species, as well as how they might change under expected future climatic scenarios remains poorly understood. We evaluated the quality of nectar and pollen resources produced by four plant species commonly planted to support pollinators in Mediterranean climatic regions, as well as how they varied between high and low water treatments. *Clarkia unguiculata* and *Linaria purpurea* produced higher-quality nectar than *M. elegans* and *Phacelia tanacetifolia*, while the opposite pattern was observed for pollen protein amounts. All species in the low-water treatment had reduced nectar sucrose quantities except *L. purpurea*, which was the only perennial species included. Pollen protein amounts varied substantially among species and remained similar under low water for all species. These results suggest that the carbohydrate resources pollinators obtain from nectar may be compromised, but pollinators foraging primarily for pollen may still be able to obtain pollen with adequate protein content under future climates. *Implications for insect conservation:* Our results highlight the importance of planting diverse plant mixtures to support pollinator acquisition of carbohydrates from nectar and amino acids from pollen.

Introduction

Pollinators enable the reproduction of most wild plant species (Ollerton et al. 2011) and increase seed set in at least 75% of agricultural crops (Kearns et al. 1998). However, declines have been reported in populations of many species (Potts et al. 2010; Zattara and Aizen 2021), which have led to decreased agricultural yields and associated increases in food prices (Murphy et al. 2022). Declines in pollinator populations have also been linked to declines in populations of wild plants (Biesmeijer et al. 2006). The drivers of pollinator decline are wide-ranging and can include pesticide exposure, nutritional deprivation, diseases, land use changes, and climatic changes (Donkersley et al. 2014; Goulson et al. 2015; De Palma et al. 2016; Greenop et al. 2020).

Among the many stressors induced by climate change, drought may have particularly important consequences for plant-pollinator interactions (Brunet et al. 2025). Drought frequency and intensity is projected to increase worldwide in coming decades (Chiang et al. 2021). Effects on pollinators will likely be mediated in part by changes in the food rewards produced by plants (Rering et al. 2020). Pollinators obtain food resources from plants in the form of nectar or pollen, with many pollinator taxa seeking carbohydrate-rich nectar, and others, primarily bees, also gathering pollen that provides a concentrated source of amino acids (Herbert et al. 1977; Thakur and Nanda 2020). Water limitation can reduce the amount or quality of plant reward to pollinators (reviewed in Brunet et al. 2025), which can, in turn, lead to lower pollinator survival and productivity (Wilson Rankin et al. 2020a).

Concern over pollinator decline has led to increasing interest in the establishment of floral enhancements aimed to support pollinators (Requier and Leonhardt 2020). Floral enhancements often include mixtures of plant species that are grown around agricultural fields (Morandin and Kremen 2013) or in urban gardens (Majewska and Altizer 2020). While some floral enhancements have been documented to increase pollinator abundance or richness (Pardee and Philpott 2014; Quistberg et al. 2016; Bennett and Lovell 2019), others seem to have little effect (Glaum et al. 2017). The success of floral enhancements can depend on the spatial scale considered or landscape in which the enhancement is embedded (Janvier et al. 2022; Adedjoja and Mallinger 2025), or on the specific plant species included (Majewska and Altizer 2020). In addition, as climatic changes intensify, it will be important to consider how resilient the chosen plant species are to periods of water limitation, and how the rewards they produce for pollinators may change with water availability.

Past studies on how water limitation affects reward to pollinators tend to reveal decreasing nectar volumes under limited water (Brunet et al. 2025). However, some studies, particularly in field settings, find no decreases in nectar volume under water limitation (Campbell and Wendlandt 2013; Phillips et al. 2018). In addition, effects of water limitation on floral reward may vary across species within the same geographic area (Phillips et al. 2018) or among populations within species (Suni et al. 2020, 2023). These findings suggest that local adaptation to drier conditions may mediate the way that plant reward is

affected by limited water, and they motivate additional research on variation among plant species in food reward under varying water availability.

The current study examined food reward to pollinators under varying moisture conditions produced by four plant species that are commonly planted to support pollinators in Mediterranean climatic regions. Mediterranean regions are characterized by hot, dry summers, and are predicted to experience increasing drought intensity in the future (Essa et al. 2023). The success of pollinator gardens in Mediterranean regions may therefore depend on the inclusion of plant species that maintain the production of nutritional rewards despite the increasingly early onset of dry conditions. We chose to focus on nectar volume and sugar content, because nectar is a key source of carbohydrates for pollinators (Burkle and Irwin 2009; Wilson Rankin et al. 2020b). We also assessed pollen protein content because pollen with higher amino acid content leads to higher pollinator fitness (Génissel et al. 2002; Vanderplanck et al. 2014). Our overall aims were to: (1) assess interspecific variation in nectar and pollen quality among plants commonly planted to support pollinators; (2) assess if traits change under water limitation; and (3) evaluate if trait changes under water limitation vary among species.

Methods

Species selection & greenhouse planting

We worked with local horticulturalists from the plant nursery Home Ground Habitats (Novato, CA) to select outcrossing plant species that have been documented to support pollinators in Mediterranean climatic regions such as in the San Francisco Bay Area of California where the study took place (Ogutcen et al. 2017; Lundin et al. 2019a; Rollings and Goulson 2019). The mission of Home Ground Habitats is to promote the restoration of habitat for pollinator conservation via gardens containing plants derived from wild-sourced seeds or seedlings. We selected four species, including *Clarkia unguiculata* Lindl. ('Elegant clarkia', Onagraceae, annual, endemic in California), *Linaria purpurea* L. ('Purple toadflax', Plantaginaceae, perennial, native to Italy), *Madia elegans* D. Don ('Common madia', Asteraceae, annual, native to the western United States), and *Phacelia tanacetifolia* Benth. ('Lacy phacelia', Boraginaceae, annual, native to the southwestern United States). We chose to include both native and non-native species because non-native plant species have been shown to integrate well into urban plant-pollinator networks (Kovács-Hostyánszki et al. 2022). *Clarkia unguiculata*, *L. purpurea*, and *M. elegans* were obtained from Home Ground Habitats prior to the onset of flowering, with *C. unguiculata* and *M. elegans* in square 10.16 cm pots and *L. purpurea* in round 8.25 cm (radius) x 17 cm (height) pots. *Phacelia tanacetifolia* was grown from seed in the greenhouse at the University of San Francisco, where the experiment took place, in square 10.16 cm pots. We kept plants in the pots they had been grown in prior to purchase so we could begin the water-limitation experiment as soon as possible and to prevent plants requiring an acclimation period after transplanting. There were a total of 154 individual plants included in the experiment (Table 1; Fig. 1).

Table 1

For each species grown in the greenhouse common garden (*Clarkia unguiculata*, *Linaria purpurea*, *Madia elegans*, and *Phacelia tanacetifolia*), the family, treatment, number of plants in the greenhouse (Plants), the mean number of flowers per plant for which nectar traits were assessed, along with standard error (Flowers (n)), the mean number of flowers per plant for which percent protein in pollen was assessed, along with standard error (Flowers (p)), and the mean nectar volume, sucrose amount, and protein percent in pollen, along with standard errors. Nectar volume and sucrose amounts were measured for several flowers from each plant, and averages for each species were generated by taking the mean across flowers within individuals and then taking the mean across individuals. Pollen protein was assessed by pooling pollen from multiple flowers from the same individual plant and then assessing percent protein in triplicate. Averages reflect means across replicates for each individual plant followed by taking the mean across individuals within a species. All species are annuals except *Linaria purpurea*, which is a perennial.

Plant species	Family	Treatment	Plants	Flowers (n)	Flowers (p)	Nectar (μL)	Sucrose (mg)	Protein %
<i>C. unguiculata</i>	Onagraceae	High-water	8	3 ± 0.0	3.57 ± 0.3	0.76 ± 0.069	0.84 ± 0.079	9.66 ± 0.37
		Low-water	5	2.6 ± 0.25	2.5 ± 0.39	0.35 ± 0.203	0.40 ± 0.162	11.33 ± 1.03
<i>L. purpurea</i>	Plantaginaceae	High-water	7	3 ± 0.0	7.86 ± 0.55	0.39 ± 0.099	0.41 ± 0.106	10.46 ± 1.20
		Low-water	6	3 ± 0.0	7.5 ± 0.43	0.41 ± 0.081	0.40 ± 0.076	9.21 ± 1.53
<i>M. elegans</i>	Asteraceae	High-water	10	3 ± 0.0	36 ± 2.45	0.002 ± 0.002	0.006 ± 0.002	15.72 ± 1.52
		Low-water	9	3 ± 0.0	37 ± 2.13	0.005 ± 0.003	0.0007 ± 0.0005	16.46 ± 1.62
<i>P. tanacetifolia</i>	Boraginaceae	High-water	3	3 ± 0.0	5.33 ± 0.33	0.042 ± 0.023	0.038 ± 0.024	13.39 ± 1.34
		Low-water	4	3 ± 0.0	5 ± 0.0	0.009 ± 0.005	0.004 ± 0.003	20.74 ± 6.06

Each plant was given a specimen number and then alternating individuals within each species were assigned to either a high or low water treatment. Plants were then randomized with respect to their location in the greenhouse and placed in one of 22 trays. The greenhouse was maintained under a 16-hour light and 8-hour dark cycle, with a temperature target of 10–24°C and a humidity target of 25%.

Water limitation experiment

Floral development (bud and flowering onset) was monitored for each species, and drought treatments were initiated when approximately 50% of individuals of a given species had produced buds. At that time, all plants of that species, including both high and low water treatments, were elevated above their trays to prevent any unintentional water uptake from drainage or runoff. This ensured that excess water from high-water plants could not influence low-water individuals. Following elevation, water was withheld from plants assigned to the low-water treatment until visible signs of wilting appeared, as in (Sun et al. 2023). Control plants received 800 mL of water every three days, an amount previously determined to prevent wilting of these species (Gregor et al., submitted). Once low-water plants began to wilt, they were carefully rewatered from the top with 800 mL and then left un-watered until data was collected. On the day of rewatering, all buds present on each individual plant were marked and only flowers that developed after that point were used for nectar measurements. Only fully open, non-senescent flowers were used for nectar data collection.

We assessed the water status of plants using two different proxies depending on the species. For *L. purpurea*, *M. elegans*, and *P. erecta* we estimated the relative water content of leaves (Raymond Hunt et al. 1987). For *C. unguiculata*, most leaves of the plants in the low-water treatment had senesced, so as a proxy for water status we counted the number of green

leaves present on plants, beginning at the apical meristem and continuing down until 10 leaves per plant were surveyed. The leaves of all *P. tanacetifolia* plants senesced as plants began to flower so we were unable to assess water status for that species. For all other species we ran separate one-tailed t-tests that compared water status between high and low water plants, assuming unequal variance and implemented using the `t.test` function in R (see Table S1 for sample sizes).

Trait measurements

We quantified nectar volume from three flowers per plant using 5 μL microcapillary tubes (Drummond Scientific Company, Broomall, PA) and digital calipers. For each flower, we measured nectar sucrose concentration with a handheld refractometer (Bellingham & Stanley, Weilheim, Germany), recording percent sucrose as % Brix. We then calculated the concentration and total amount of sucrose as in Suni et al. (2020, 2023). For each individual plant, we sampled three flowers, for a total of 154 flowers (Table 1). Flowers were selected according to species-specific floral morphology to facilitate consistency across measurements. For *M. elegans*, one floret was collected from each of three different capitula per individual. For *C. unguiculata*, *L. purpurea*, *P. tanacetifolia*, one flower was sampled from the base, middle, and top of each inflorescence.

We used the percent protein in pollen as a proxy for pollen quality, as in Vaudo et al. (2024) and Ergastolo (2025). We used the Bradford protein assay to measure the concentration of total protein (Bradford 1976), which is robust to different amounts of starting material as long as samples are sufficiently diluted so that absorbance values fall on the linear part of the curve relating absorbance to concentration (Zor and Selinger 1996). To implement the Bradford assay, we used a Pierce Bradford Plus Protein Assay Kit with G-250 dye in a colorimetric reagent (ThermoFisher Scientific, Waltham, MA).

For each plant individual, we removed anthers from several flowers (Table 1) using sterilized tweezers and dried them in a single uncapped 1.5 mL centrifuge tube in an Isotemp oven (Fisher Scientific, Waltham, MA) at 40 °C for 72 h. After drying we vortexed samples to concentrate the pollen, transferred pollen to clean 1.5 mL centrifuge tubes, and weighed the pollen. We added 100 μL of 0.1M NaOH, vortexed for 30 s, centrifuged, pulsed on the vortex, and then left samples at room temperature for 30 min. After 30 min, pollen solutions with greater than 4 mg/mL were further diluted to under that threshold to ensure that absorbance values would fall on the linear part of the absorbance-concentration curve. Diluted pollen solutions were then pipetted up and down and 8 μL of each pollen solution was added to a new tube containing 392 μL Bradford reagent. The mixture was vortexed and centrifuged, and three 100 μL aliquots were pipetted into a 96-well Black Flat Bottom Microplate (Corning, Corning, NY) so that we could run three technical replicates. We popped bubbles if present using a sterilized needle and left the plate at room temperature for 10 min. We determined the absorbance of each well at 595 nm using a Tecan plate reader (Männedorf, Switzerland), the protein concentrations of each sample using a standard curve generated Albumin Standards provided in the Pierce Bradford Plus Protein Assay Kit, and the percent protein of each sample using the original weights of each pollen sample.

Statistical modeling

We used the `glmmTMB` package (Brooks et al. 2017) to run generalized or general linear mixed models (GLMMs or GLMs) in R (R Core Team 2024), and we examined residuals to determine model fit using the `DHARMA` package (Hartig 2024). To assess drivers of nectar volume and sucrose amount, we ran separate GLMMs with a Tweedie error distribution and log link. Nectar volume or sucrose amount was the dependent variable, plant species, treatment, and their interaction were fixed effects, and plant individual was a random effect. To assess drivers of pollen protein percent, we used a dataset that included the average protein of each of the three technical replicates. We ran a GLM with a Gaussian error distribution and log link. Average protein was the dependent variable, and plant species, treatment, and their interaction were fixed effects.

To evaluate the significance of fixed factors and interactions, we implemented likelihood ratio tests on nested models with and without the factor of interest. To evaluate differences among species and treatment groups given significant model

terms or interactions, we calculated estimated marginal means and pairwise contrasts using the emmeans package (Lenth and Piaskowski 2017) and used the Tukey method for P-value adjustment. We used the package sjPlot to visualize interactions, generate back-transformed model coefficients on the response scale (Est.), calculate R^2 and adjusted R^2 (R^2 adj.) values for GLMs, and calculate marginal (Marg.) and conditional (Cond.) R^2 values for GLMMs.

Results

Across all surveyed species, plants in the low water treatment had lower water status (Table S1). Across species and individuals, plants in the high-water treatment produced average nectar volumes ranging from 0–1.12 μ L, sucrose amounts ranging from 0–1.18 mg, and protein amounts ranging from 4.82–26.47%; while plants in the low-water treatment produced nectar volumes ranging from 0–1.14 μ L, sucrose amounts ranging from 0–1.04 mg, and protein amounts ranging from 4.39–51.16% (see Table 1 for species-level averages).

The way treatment affected nectar volume varied among species ($\chi^2 = 8.50$, $df = 3$, $P = 0.037$, Marg. $R^2 = 0.94$, Cond. $R^2 = 0.96$, Treatment est. = 0.4; Figs. 2 & S1). Similarly, the way treatment affected nectar sucrose varied among species (Interaction est. = 0.46, $\chi^2 = 10.06$, $df = 3$, $P = 0.018$, Marg. $R^2 = 0.96$, Cond. $R^2 = 0.97$; Figs. 2 & S1). *Clarkia unguiculata* had lower nectar volume under low water, while the other three species showed no change (Table 2). The three annual plants (*C. unguiculata*, *M. elegans*, and *P. tanacetifolia*) had lower nectar sucrose under low water, while the perennial (*L. purpurea*) showed no change (Table 2). There was high variation among species in nectar rewards under both high and low water (Fig. 2).

Table 2

For two nectar traits (nectar volume and the amount of sucrose), for four species (*Clarkia unguiculata*, *Linaria purpurea*, *Madia elegans*, and *Phacelia tanacetifolia*), the treatment (High water or Low water), estimated marginal means (EMM) expressed as back-transformed ratios on the response scale, standard error (SE), and 95% confidence interval (CI), and the pairwise contrasts between treatments (LW / HW = the ratio of low water to high water), standard error (SE), Wald test statistic for each contrast (z ratio), and the corresponding P-value. P-values were adjusted using the Tukey method and those that remained significant ($P < 0.05$) are shown in bold.

Trait	Species	Treatment	EMM	SE	CI	Contrast	Ratio	SE	z ratio	P
Nectar (μL)	<i>C. unguiculata</i>	High water	0.75	0.14	0.51–1.09	LW / HW	0.401	0.151	-2.428	0.0152
		Low water	0.30	0.10	0.16–0.57					
	<i>L. purpurea</i>	High water	0.36	0.08	0.23–0.56	LW / HW	1.104	0.371	0.296	0.7673
		Low water	0.39	0.10	0.24–0.64					
	<i>M. elegans</i>	High water	0.0017	0.0011	0.0005–0.006	LW / HW	2.366	1.9	1.072	0.2838
		Low water	0.0041	0.0022	0.0015–0.012					
	<i>P. tanacetifolia</i>	High water	0.039	0.021	0.014–0.11	LW / HW	0.214	0.178	-1.854	0.0637
		Low water	0.008	0.0054	0.0024–0.03					
Sucrose (mg)	<i>C. unguiculata</i>	High water	0.82	0.13	0.6–1.12	LW / HW	0.462	0.136	-2.623	0.0087
		Low water	0.38	0.09	0.23–0.62					
	<i>L. purpurea</i>	High water	0.38	0.07	0.26–0.56	LW / HW	1.012	0.29	0.043	0.9657
		Low water	0.38	0.08	0.25–0.58					
	<i>M. elegans</i>	High water	0.0059	0.0026	0.0025–0.014	LW / HW	0.115	0.113	-2.197	0.028
		Low water	0.0007	0.0006	0.0001–0.004					
	<i>P. tanacetifolia</i>	High water	0.036	0.018	0.013–0.1	LW / HW	0.121	0.11	-2.315	0.0206
		Low water	0.004	0.0033	0.001–0.019					

Madia elegans and *P. tanacetifolia* produced less nectar and nectar with a lower sucrose content than the other two species under both high and low water conditions (Tables 2 & S2). *Madia elegans* produced less nectar and nectar with less sucrose than *P. tanacetifolia* under high water but not under low water (Tables S2 & S3). There was no difference between *C. unguiculata* and *L. purpurea* in nectar volume under high or low water (Tables S2 & S3). *Linaria purpurea* produced less sucrose than *C. unguiculata* under high water but not low water (Tables S2 & S3).

Species varied substantially in the percent protein in their pollen ($\chi^2 = 21.4$, $df = 3$, $P < 0.001$, $R^2 = 0.33$, $R^2 \text{ adj.} = 0.27$; Fig. 3). The way treatment affected pollen protein did not vary among species ($\chi^2 = 3.61$, $df = 3$, $P = 0.31$), and there was no effect of treatment on pollen protein (Est. = 0.16, $\chi^2 = 1.71$, $df = 1$, $P = 0.19$; Fig. 3). *Madia elegans* and *P. tanacetifolia* had higher protein than the other two species, and there was no difference between them (Tables S4 & S5). There was also no difference between *C. unguiculata* and *L. purpurea* in protein amount (Tables S4 & S5).

Discussion

Our investigation of nectar and pollen reward produced by plants commonly planted to support pollinators in Mediterranean climate zones revealed substantial interspecific differences in nectar quality and pollen protein percentages as well as differences in the way water limitation affected nectar quality. Among the plant species assessed, *M. elegans* and *P. tanacetifolia* produced low-quality nectar even under well-watered conditions, while *C. unguiculata* and *L. purpurea* produced higher-quality nectar. *Clarkia unguiculata* and *L. purpurea* may therefore better provision pollinators that visit plants for nectar rewards and be useful choices to include in floral enhancements. Furthermore, *C. unguiculata* has been shown to establish readily in experimental gardens, exhibit high abundance, be phenologically persistent, and support specialist pollinators such as bees in *Anthophora*, *Bombus*, *Halictus*, *Lasioglossum*, *Megachile*, and *Melissodes* (Müller et al. 2025). Similarly, *L. purpurea* planted in community gardens has been shown to be visited by bees in more than 10 genera (Pawelek et al. 2016; Frankie et al. 2019).

While our results suggest that *M. elegans* and *P. tanacetifolia* may not provision pollinators with high quality nectar rewards on a per visit basis, these species can exhibit large floral displays, such that *P. tanacetifolia* can have hundreds of flowers (Petanidou 2003; Leach et al. 2021; Giovanetti et al. 2022), and *M. elegans* can have multiple inflorescences per plant (calflora.org). It is therefore possible that pollinators would be able to obtain meaningful energetic rewards from nectar after visiting multiple flowers or inflorescences. Indeed, past work that examined visitation to *P. tanacetifolia* in experimental plots within agricultural fields found that honey bees readily visit *P. tanacetifolia* for both nectar and pollen (Giovanetti et al. 2022). That study also recorded visits to *P. tanacetifolia* by wild bees in several genera (*Bombus*, *Halictus*, and *Hyleus*), as well as visits from Lepidopterans (Giovanetti et al. 2022). Other work found moderate visitation to *P. tanacetifolia* relative to other plant species in experimental plots and no visitation by honey bees despite their presence (Leach et al. 2021). On the other hand, *P. tanacetifolia* has been highlighted as a useful species for honey production via visitation by honey bees (Żarczyński et al. 2025). *Phacelia tanacetifolia* is grown worldwide to support pollinators, and it is possible that regional variation in reward production explains some of the discrepancies among these studies. Regarding *M. elegans*, past work evaluating pollinator visitation in outdoor plots found high visitation by honey bees, but no visitation by wild bees (Lundin et al. 2019b). In contrast, another study that observed visitation in gardens started from seed mixes found that *M. elegans* did support specialist pollinators, despite receiving visits during a relatively narrow phenological (Müller et al. 2025). However, neither of those studies specified whether the bee pollinators observed were visiting plants to obtain nectar or pollen, so it is possible that they were in fact collecting pollen given the relatively high pollen protein amounts produced by *M. elegans*. Given that most non-bee pollinators visit flowers primarily for nectar (Rader et al. 2020; Raguso 2020), it would be useful for future studies to evaluate the extent to which they visit *M. elegans* versus other species that grow nearby in diverse plant communities.

While we are unaware of previous work on nectar quality for most species evaluated here, we can draw comparisons to past work on *P. tanacetifolia*. The nectar volumes and sucrose amounts we found under well-watered conditions are within the ranges reported by a past study that sowed seeds at field sites in Greece that varied in aridity (Petanidou 2003). That study found nectar volumes were higher at xeric sites earlier in the season while they were higher at mesic sites later in the season, suggesting plasticity in response to climate. The current study also found evidence for plasticity in nectar volume and sucrose amount; although the quantities we found under the low-water treatment were lower than those reported by Petanidou (2003). It is possible that the lower amounts we found are due to our lower-water treatment imposing conditions that were more xeric than those at the xeric sites in Petanidou (2003). Another study evaluated nectar quality at sites in

Turkey that experienced a mixture of rainy and sunny weather and reported higher nectar volumes and sucrose amounts than those in our study and that of Petanidou (2003). This further reinforces the role that plasticity plays in mediating nectar quality in different environments (Dorey and Schiestl 2022) and suggests that as drought frequency intensifies in the future, the nectar resources provided to pollinators from *P. tanacetifolia* may be reduced. It is worth noting that despite the overall low amounts of nectar produced and decreases under low water conditions, there is evidence that *P. tanacetifolia* replenishes its nectar (Petanidou 2003; Owayss et al. 2020), so pollinators may be able to obtain energetic rewards somewhat consistently throughout the day in irrigated urban gardens.

The way the low water treatment affected nectar volume varied among species, with reductions occurring only for *C. unguiculata* and no changes observed for the other three species. However, despite the decreases observed for *C. unguiculata*, nectar volumes under the low-water treatment were still much higher than those of the two other annual species assessed (*M. elegans* and *P. tanacetifolia*). Nectar volume is a highly liable trait that often responds negatively to water limitation (Brunet et al. 2025), so it is interesting that no significant decreases were observed for the majority of species surveyed here. It is possible that since the plants used in this study are native to Mediterranean climatic regions, they may be somewhat well-adapted to low-water conditions (Ramírez-Valiente et al. 2022) and be able to maintain nectar production under drought.

Despite the similarity across treatments in nectar volume for most species, sucrose amounts were reduced for all three annual species examined, while perennial *L. purpurea* showed no reduction under low water. Effects of water limitation on sucrose content vary across plant taxa (reviewed in Kuppler and Kotowska 2021), and decreases are sometimes mediated by a decrease in sucrose relative to total sugars (Rering et al. 2020), which was not assessed in this study. We speculate that the perennial life history of *L. purpurea* may have played a role in its drought response. Perennial plants are often thought to be more drought resistant due to greater investment in belowground structures than annual plants, which this can facilitate water uptake and mitigate negative consequences of low soil moisture (Zwicke et al. 2015). However, perennials can use other strategies to respond to drought (Blumenthal et al. 2020), and other traits such as taller plant height with higher leaf N has been shown to be associated with drought resistance regardless of life history (Worthy et al. 2026). In addition, local adaptation within species can lead to variation across populations in drought response (Sun et al. 2020), so future work that includes larger sample sizes of annual and perennial plants, and incorporates seed provenance and measurements of growth-related traits would be useful to clarify drivers of sucrose content under drought.

Plant species varied substantially in the percent protein in their pollen. Interestingly, the species that produced the lowest nectar quality in this study (*M. elegans* and *P. tanacetifolia*) produced higher pollen protein amounts than the higher-quality nectar producers (*C. unguiculata* and *L. purpurea*). These results are consistent with past work evaluating pollen protein percentages for *C. unguiculata* and *P. tanacetifolia* growing in field plots around agricultural fields in the Central Valley of California, which found higher protein in the pollen of *P. tanacetifolia* than *C. unguiculata* (Page et al. 2024). While the protein percentages reported by Page et al. (2024) for *C. unguiculata* are similar to what we observed under the high-water treatment ($8.0 \pm 0.01\%$ versus $9.66 \pm 0.37\%$), the pollen protein percentages we found for *P. tanacetifolia* are approximately half of those reported in Page et al. (2024), as well as those reported in another study (Vergun et al. 2023). We speculate the higher pollen protein amounts observed in Page et al. (2024) and Vergun et al. (2023) may be due to higher climatic water deficits in their field plots relative to our greenhouse, since climatic water deficit has been shown to drive higher pollen protein amounts within species in the field (Vaudo et al. 2024b).

Our finding no effect of watering treatment on pollen protein amounts highlights the importance of pollen to plant reproduction and is consistent with plants having evolved a range of mechanisms to prevent the loss of male reproductive potential via compromised pollen (Borghi et al. 2019). While work on how water stress affects total pollen protein amounts is scant, two experimental studies on bee-pollinated plants also found a similar lack of effect of watering treatment on protein amounts (Descamps et al. 2021a, b). Most other studies that have examined effects of water stress on pollen in the context of pollinator nutrition have focused on pollen *production* (Borghi et al. 2019), with some finding no change under reduced water (Rering et al. 2020; Descamps et al. 2021b) and others finding a decrease in pollen amounts under water

stress (Waser et al. 1996; Wilson Rankin et al. 2020a). Therefore, even if the amount of protein available for pollinator consumption is not reduced on a per-flower basis, it is possible that a reduction in total pollen production may still compromise pollinator acquisition of adequate food resources. In addition, the amount of protein in pollen can be reduced by heat stress (Descamps et al. 2021a, b), but not in all cases (Russo et al. 2019), so future work that examines differences among plant species in the response of pollen protein to the multiple stressors expected under future climate change will be useful.

Conclusions

Overall, we found high variation among plants species commonly planted to support pollinators in nectar quality and pollen protein amount, with two species producing higher-quality nectar but lower-quality pollen (*C. unguiculata* and *L. purpurea*) and the other two producing higher-quality pollen and lower-quality nectar (*M. elegans* and *P. tanacetifolia*). The variation across species and fact that all plants surveyed produced either high-quality nectar or pollen highlights the importance of including a diverse mixture of plant species in floral enhancements. Our finding that the one perennial species included maintained sucrose levels under low water, while the three annual species did not, suggests that including perennial plants may facilitate the success of pollinator gardens under future climate change, and motivates additional research on potential differences with life history. Our results regarding pollen quality suggest that plant species identity is more important than the amount of water plants receive in explaining variation in pollen protein amounts. Additionally, they suggest that for insects that consume pollen, future drought may not compromise their ability to obtain nutritional resources from the plants evaluated here. That said, other work has shown a decrease in overall pollen production under drought, raising the possibility that despite no change in protein amounts, nutritional resources for pollinators may still be reduced under future climates.

Statements and Declarations

The authors declare no conflict of interest

Acknowledgements

We thank the support staff of the Biology Department, including J. Oda and M. Helm, and A. Chen Hsin Yang for help with data collection. This work was funded by a grant to S. Suni from the Faculty Development Fund at the University of San Francisco and a scholarship to M. Gregor from the Santa Clara Chapter of the California Native Plant Society.

Author Contributions

All authors contributed to the study conception and design. Data collection was performed by Madeline Gregor and Wendy Lei with help from Sevan Suni, analyses were performed by Sevan Suni, and the manuscript was written by Sevan Suni with input from Madeline Gregor and Wendy Lei.

Data Availability

The data and code used in analyses are available online: [dataset] Data and code for "Assessing interspecific variation in nectar and pollen food reward to pollinators under water limitation", Dryad online data repository, DOI: <https://doi.org/10.5061/dryad.70rxwdcfn>

AI Statement

Claude (free version, Anthropic, 2026) was used for digitizing lab notebooks and creating .csv files containing raw data that were checked by the authors for accuracy (used on July 1, 2026).

References

1. Adedija OA, Mallinger RE (2025) Landscape context mediates the effect of pollinator garden enhancements on pollinator visitation and plant-pollinator interactions. *Landsc Ecol* 40:116. <https://doi.org/10.1007/s10980-025-02135-8>
2. Bennett AB, Lovell S (2019) Landscape and local site variables differentially influence pollinators and pollination services in urban agricultural sites. *PLoS ONE* 14:e0212034. <https://doi.org/10.1371/journal.pone.0212034>
3. Biesmeijer JC, Roberts SPM, Reemer M et al (2006) Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* 313:351–354. <https://doi.org/10.1126/science.1127863>
4. Blumenthal DM, Mueller KE, Kray JA et al (2020) Traits link drought resistance with herbivore defence and plant economics in semi-arid grasslands: The central roles of phenology and leaf dry matter content. *J Ecol* 108:2336–2351. <https://doi.org/10.1111/1365-2745.13454>
5. Borghi M, De Perez L, Yoshida T, Fernie AR (2019) Flowers and climate change: a metabolic perspective. *New Phytol* 224:1425–1441. <https://doi.org/10.1111/nph.16031>
6. Bradford MM (1976) A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Anal Biochem* 72:248–254. [https://doi.org/10.1016/0003-2697\(76\)90527-3](https://doi.org/10.1016/0003-2697(76)90527-3)
7. Brooks M, Kristensen K, van Benthem KJ et al (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J* 9
8. Brunet J, Inouye DW, Wilson Rankin EE, Giannini TC (2025) Global change aggravates drought, with consequences for plant reproduction. *Ann Botany* 135:89–104. <https://doi.org/10.1093/aob/mcae186>
9. Burkle L, Irwin R (2009) Nectar Sugar Limits Larval Growth of Solitary Bees (Hymenoptera: Megachilidae). *Environ Entomol* 38:1293–1300. <https://doi.org/10.1603/022.038.0441>
10. Campbell DR, Wendlandt C (2013) Altered precipitation affects plant hybrids differently than their parental species. *Am J Bot* 100:1322–1331. <https://doi.org/10.3732/ajb.1200473>
11. Chiang F, Mazdiyasni O, AghaKouchak A (2021) Evidence of anthropogenic impacts on global drought frequency, duration, and intensity. *Nat Commun* 12:2754. <https://doi.org/10.1038/s41467-021-22314-w>
12. De Palma A, Abrahamczyk S, Aizen MA et al (2016) Predicting bee community responses to land-use changes: Effects of geographic and taxonomic biases. *Sci Rep* 6. <https://doi.org/10.1038/srep31153>
13. Descamps C, Boubnan N, Jacquemart A-L, Quinet M (2021a) Growing and Flowering in a Changing Climate: Effects of Higher Temperatures and Drought Stress on the Bee-Pollinated Species *Impatiens glandulifera* Royle. *Plants* 10:988. <https://doi.org/10.3390/plants10050988>
14. Descamps C, Quinet M, Jacquemart A-L (2021b) Climate Change–Induced Stress Reduce Quantity and Alter Composition of Nectar and Pollen From a Bee-Pollinated Species (*Borago officinalis*, Boraginaceae). *Front Plant Sci* 12:755843. <https://doi.org/10.3389/fpls.2021.755843>
15. Donkersley P, Rhodes G, Pickup RW et al (2014) Honeybee nutrition is linked to landscape composition. *Ecol Evol* 4:4195–4206. <https://doi.org/10.1002/ece3.1293>
16. Dorey T, Schiestl FP (2022) Plant phenotypic plasticity changes pollinator-mediated selection. <https://doi.org/10.1111/evo.14634>. *Evolution* evo.14634
17. Ergastolo A (2025) Ecological and nutritional drivers of floral fidelity in wild pollinators. Master's Thesis in Biology, University of San Francisco
18. Essa YH, Hirschi M, Thiery W et al (2023) Drought characteristics in Mediterranean under future climate change. *npj Clim Atmos Sci* 6:133. <https://doi.org/10.1038/s41612-023-00458-4>
19. Frankie G, Feng I, Thorp R et al (2019) Native and non-native plants attract diverse bees to urban gardens in California. *J Poll Ecol* 25. [https://doi.org/10.26786/1920-7603\(2019\)505](https://doi.org/10.26786/1920-7603(2019)505)
20. Génissel A, Aupinel P, Bressac C et al (2002) Influence of pollen origin on performance of *Bombus terrestris* micro-colonies. *Entomol Exp Appl* 104:329–336. <https://doi.org/10.1046/j.1570-7458.2002.01019.x>

21. Giovanetti M, Malabusini S, Zugno M, Lupi D (2022) Influence of Flowering Characteristics, Local Environment, and Daily Temperature on the Visits Paid by *Apis mellifera* to the Exotic Crop *Phacelia tanacetifolia*. *Sustainability* 14:10186. <https://doi.org/10.3390/su141610186>
22. Glaum P, Simao M-C, Vaidya C et al (2017) Big city *Bombus*: using natural history and land-use history to find significant environmental drivers in bumble-bee declines in urban development. *R Soc open sci* 4:170156. <https://doi.org/10.1098/rsos.170156>
23. Goulson D, Nicholls E, Botías C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347. <https://doi.org/10.1126/science.1255957>
24. Greenop A, Mica-Hawkyard N, Walkington S et al (2020) Equivocal Evidence for Colony Level Stress Effects on Bumble Bee Pollination Services. *Insects* 11:191. <https://doi.org/10.3390/insects11030191>
25. Hartig F (2024) Residual Diagnostics for Hierarchical ## (Multi-Level / Mixed) Regression Models_. R package version 0.4.7, ## <http://florianhartig.github.io/DHARMA/>
26. Herbert EW, Shimanuki H, Caron D (1977) Optimum protein levels required by honey bees (Hymenoptera, Apidae) to initiate and maintain brood rearing. *Apidologie* 8:141–146. <https://doi.org/10.1051/apido:19770204>
27. Janvier AJ, Ulyshen MD, Braman CA et al (2022) Scale-dependent effects of landscape context on urban bee diversity. *J Insect Conserv* 26:697–709. <https://doi.org/10.1007/s10841-022-00402-6>
28. Kearns CA, Inouye DW, Waser NM (1998) Endangered Mutualisms: The Conservation of Plant-Pollinator Interactions. *Annu Rev Ecol Syst* 29:83–112. <https://doi.org/10.1146/annurev.ecolsys.29.1.83>
29. Kovács-Hostyánszki A, Piross IS, Shebl MA (2022) Non-native plant species integrate well into plant-pollinator networks in a diverse man-made flowering plant community. *Urban Ecosyst* 25:1491–1502. <https://doi.org/10.1007/s11252-022-01242-7>
30. Kuppler J, Kotowska MM (2021) A meta-analysis of responses in floral traits and flower–visitor interactions to water deficit. *Glob Change Biol* 27:3095–3108. <https://doi.org/10.1111/gcb.15621>
31. Leach M, Dibble AC, Stack LB et al (2021) The Effect of Plant Nutrition on Bee Flower Visitation. *J Kansas Entomol Soc* 94:277–300
32. Lenth RV, Piaskowski J (2017) emmeans: Estimated Marginal Means, aka Least-Squares Means. 2.0.3
33. Lundin O, Ward KL, Williams NM (2019a) Identifying native plants for coordinated habitat management of arthropod pollinators, herbivores and natural enemies. *J Appl Ecol* 56:665–676. <https://doi.org/10.1111/1365-2664.13304>
34. Lundin O, Ward KL, Williams NM (2019b) Identifying native plants for coordinated habitat management of arthropod pollinators, herbivores and natural enemies. *J Appl Ecol* 56:665–676. <https://doi.org/10.1111/1365-2664.13304>
35. Majewska AA, Altizer S (2020) Planting gardens to support insect pollinators. *Conserv Biol* 34:15–25. <https://doi.org/10.1111/cobi.13271>
36. Morandin LA, Kremen C (2013) Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol Appl* 23:829–839. <https://doi.org/10.1890/12-1051.1>
37. Müller U, Borchardt K, Britzman A, Williams NM (2025) Seed mix performance and species network roles as a framework to select candidate key resources for pollinator habitat. *Ecosphere* 16:e70492. <https://doi.org/10.1002/ecs2.70492>
38. Murphy JT, Breeze TD, Willcox B et al (2022) Globalisation and pollinators: Pollinator declines are an economic threat to global food systems. *People Nat* 4:773–785. <https://doi.org/10.1002/pan3.10314>
39. Ogutcen E, Theriault J, King DB, Vamosi JC (2017) Diversification rates in Antirrhineae (Plantaginaceae): The contribution of range shifts and pollination modes. *Perspectives in Plant Ecology. Evol Syst* 26:39–52. <https://doi.org/10.1016/j.ppees.2017.04.001>
40. Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120:321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>

41. Owayss AA, Shebl MA, Iqbal J et al (2020) *Phacelia tanacetifolia* can enhance conservation of honey bees and wild bees in the drastic hot-arid subtropical Central Arabia. J Apic Res 59:569–582. <https://doi.org/10.1080/00218839.2020.1735731>
42. Page ML, Francis JS, Müller U, Williams NM (2024) Wildflower plantings and honeybee competition impact nutritional quality of wild bee diets. J Appl Ecol 61:3104–3113. <https://doi.org/10.1111/1365-2664.14813>
43. Pardee GL, Philpott SM (2014) Native plants are the bee's knees: local and landscape predictors of bee richness and abundance in backyard gardens. Urban Ecosyst 17:641–659. <https://doi.org/10.1007/s11252-014-0349-0>
44. Pawelek JC, Frankie GW, Thorp RW, Przybylski M (2016) Modification of a community garden to attract native bee pollinators in Urban San Luis Obispo, California. Urban Horticulture: Ecology, Landscape, and Agriculture. Apple Academic Press, Inc.. 3333 Mistwell Crescent, Oakville, ON L6L 0A2 Canada
45. Petanidou T (2003) Introducing plants for bee-keeping at any cost? – Assessment of *Phacelia tanacetifolia* as nectar source plant under xeric Mediterranean conditions. Plant Syst Evol 238:155–168. <https://doi.org/10.1007/s00606-002-0278-x>
46. Phillips BB, Shaw RF, Holland MJ et al (2018) Drought reduces floral resources for pollinators. Glob Change Biol 24:3226–3235. <https://doi.org/10.1111/gcb.14130>
47. Potts SG, Biesmeijer JC, Kremen C et al (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
48. Quistberg RD, Bichier P, Philpott SM (2016) Landscape and Local Correlates of Bee Abundance and Species Richness in Urban Gardens. Environ Entomol 45:592–601. <https://doi.org/10.1093/ee/nvw025>
49. R Core Team (2024) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <<https://www.R-project.org/>
50. Rader R, Cunningham SA, Howlett BG, Inouye DW (2020) Non-Bee Insects as Visitors and Pollinators of Crops: Biology, Ecology, and Management. Annu Rev Entomol 65:391–407. <https://doi.org/10.1146/annurev-ento-011019-025055>
51. Raguso RA (2020) Don't forget the flies: dipteran diversity and its consequences for floral ecology and evolution. Appl Entomol Zool 55:1–7. <https://doi.org/10.1007/s13355-020-00668-9>
52. Ramírez-Valiente JA, Santos Del Blanco L, Alía R et al (2022) Adaptation of Mediterranean forest species to climate: Lessons from common garden experiments. J Ecol 110:1022–1042. <https://doi.org/10.1111/1365-2745.13730>
53. Raymond Hunt E, Rock BN, Nobel PS (1987) Measurement of leaf relative water content by infrared reflectance. Remote Sens Environ 22:429–435. [https://doi.org/10.1016/0034-4257\(87\)90094-0](https://doi.org/10.1016/0034-4257(87)90094-0)
54. Requier F, Leonhardt SD (2020) Beyond flowers: including non-floral resources in bee conservation schemes. J Insect Conserv 24:5–16. <https://doi.org/10.1007/s10841-019-00206-1>
55. Rering CC, Franco JG, Yeater KM, Mallinger RE (2020) Drought stress alters floral volatiles and reduces floral rewards, pollinator activity, and seed set in a global plant. Ecosphere 11:e03254. <https://doi.org/10.1002/ecs2.3254>
56. Rollings R, Goulson D (2019) Quantifying the attractiveness of garden flowers for pollinators. J Insect Conserv 23:803–817. <https://doi.org/10.1007/s10841-019-00177-3>
57. Russo L, Vaudo AD, Fisher CJ et al (2019) Bee community preference for an invasive thistle associated with higher pollen protein content. Oecologia 190:901–912. <https://doi.org/10.1007/s00442-019-04462-5>
58. Suni S, Kuwana A, Ibañez N (2023) Responses of floral traits to water limitation across soil types and along climatic gradients. Flora 304:152295. <https://doi.org/10.1016/j.flora.2023.152295>
59. Suni SS, Ainsworth B, Hopkins R (2020) Local adaptation mediates floral responses to water limitation in an annual wildflower. Am J Bot 107:209–218. <https://doi.org/10.1002/ajb2.1434>
60. Thakur M, Nanda V (2020) Composition and functionality of bee pollen: A review. Trends Food Sci Technol 98:82–106. <https://doi.org/10.1016/j.tifs.2020.02.001>

61. Vanderplanck M, Moerman R, Rasmont P et al (2014) How Does Pollen Chemistry Impact Development and Feeding Behaviour of Polylectic Bees? PLoS ONE 9:e86209. <https://doi.org/10.1371/journal.pone.0086209>
62. Vaudo AD, Dyer LA, Leonard AS (2024a) Pollen nutrition structures bee and plant community interactions. Proc Natl Acad Sci USA 121. <https://doi.org/10.1073/pnas.2317228120>
63. Vaudo AD, Lin E, Luthy JA et al (2024b) Do past and present abiotic conditions explain variation in the nutritional quality of wildflower pollens for bees? Evol Ecol 38:941–955. <https://doi.org/10.1007/s10682-024-10313-4>
64. Vergun O, Grygorieva O, Lidiková J et al (2023) Nutritional composition of *Phaeclia tanacetifolia* Benth. Bee pollen and inflorescences. Agrobiodiversity for improving nutrition, health, and life quality 7:. <https://doi.org/https://doi.org/10.15414/ainhlq.2023.0011>
65. Waser NM, Chittka L, Price MV et al (1996) Generalization in Pollination Systems, and Why it Matters. Ecology 77:1043–1060. <https://doi.org/10.2307/2265575>
66. Wilson Rankin EE, Barney SK, Lozano GE (2020a) Reduced Water Negatively Impacts Social Bee Survival and Productivity Via Shifts in Floral Nutrition. J Insect Sci 20:15. <https://doi.org/10.1093/jisesa/ieaa114>
67. Wilson Rankin EE, Barney SK, Lozano GE (2020b) Reduced Water Negatively Impacts Social Bee Survival and Productivity Via Shifts in Floral Nutrition. J Insect Sci 20:15. <https://doi.org/10.1093/jisesa/ieaa114>
68. Worthy SJ, Luong JC, Wainwright BE et al (2026) Growth form and lifespan of herbaceous species mediate the role of traits in short-term drought response. Nat Ecol Evol 10:512–522. <https://doi.org/10.1038/s41559-026-02989-4>
69. Żarczyński PJ, Mackiewicz-Walec E, Krzebietke SJ et al (2025) *Phacelia tanacetifolia* Benth. as a Multifunctional Plant: Support for Pollinators and Sustainable Agricultural Practices. Agronomy 15:1843. <https://doi.org/10.3390/agronomy15081843>
70. Zattara EE, Aizen MA (2021) Worldwide occurrence records suggest a global decline in bee species richness. One Earth 4:114–123. <https://doi.org/10.1016/j.oneear.2020.12.005>
71. Zor T, Selinger Z (1996) Linearization of the Bradford Protein Assay Increases Its Sensitivity: Theoretical and Experimental Studies. Anal Biochem 236:302–308. <https://doi.org/10.1006/abio.1996.0171>
72. Zwicke M, Picon-Cochard C, Morvan-Bertrand A et al (2015) What functional strategies drive drought survival and recovery of perennial species from upland grassland? Ann Botany 116:1001–1015. <https://doi.org/10.1093/aob/mcv037>

Figures

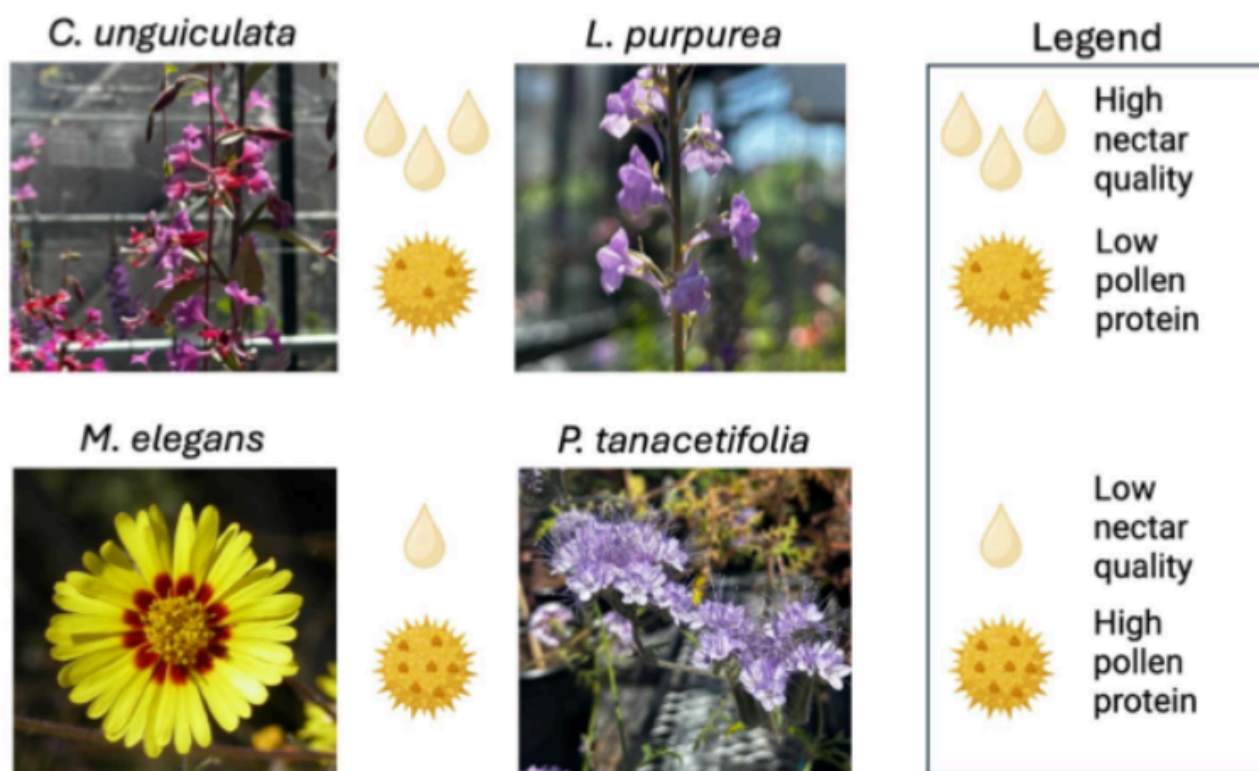


Figure 1

The species grown in the greenhouse common garden and for which nectar quality and pollen protein percent were assessed, including *Clarkia unguiculata*, *Linaria purpurea*, *Madia elegans*, and *Phacelia tanacetifolia*. High nectar quality reflects high volumes and sucrose content, while low nectar quality reflects low volumes and sucrose content.

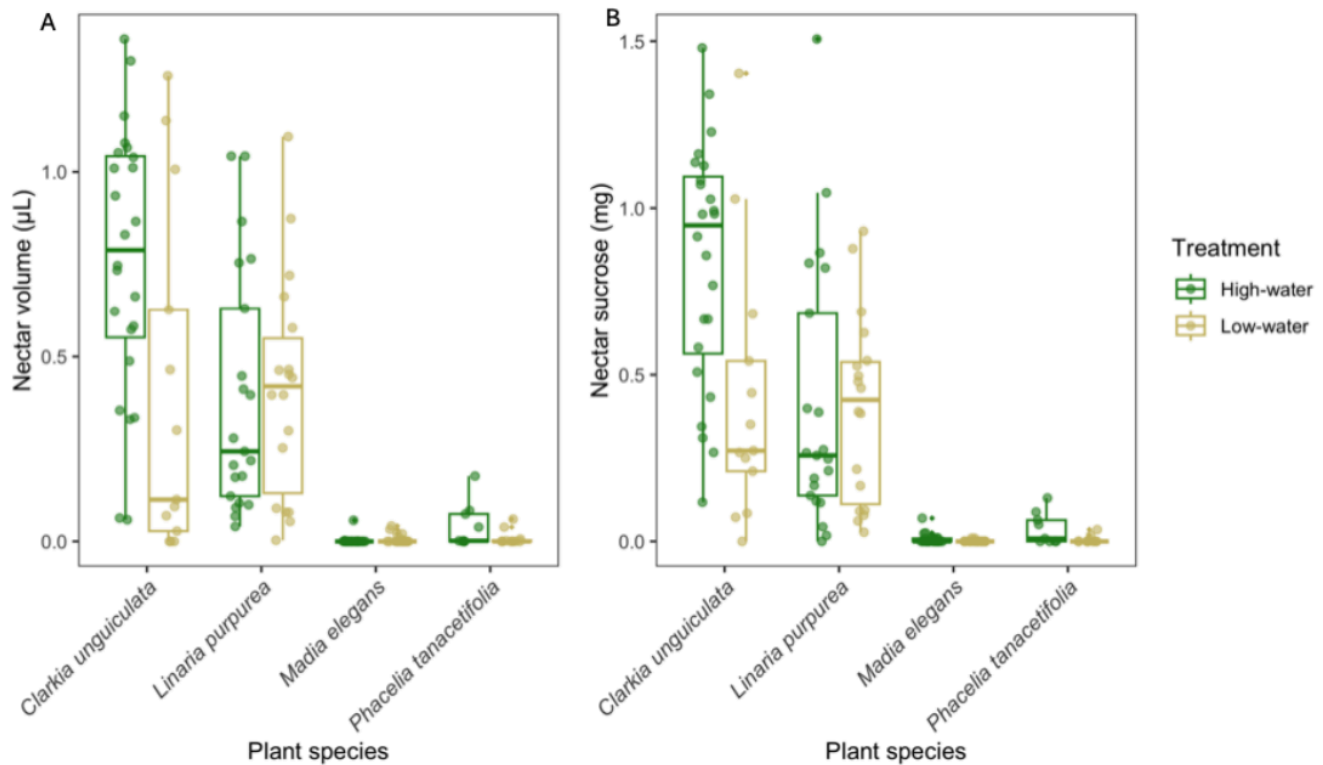


Figure 2

The volume of nectar (panel A) and amount of sucrose (panel B) found in flowers of plant species commonly planted to support pollinators and grown in a greenhouse common garden under high and low-water conditions. Plots are boxplots and points represent nectar volumes of individual flowers. Colors reflect treatment, with green representing high-water and tan representing low water. Plots represent boxplots with outliers designated by diamonds, and points are actual data points that have been jittered for clarity.

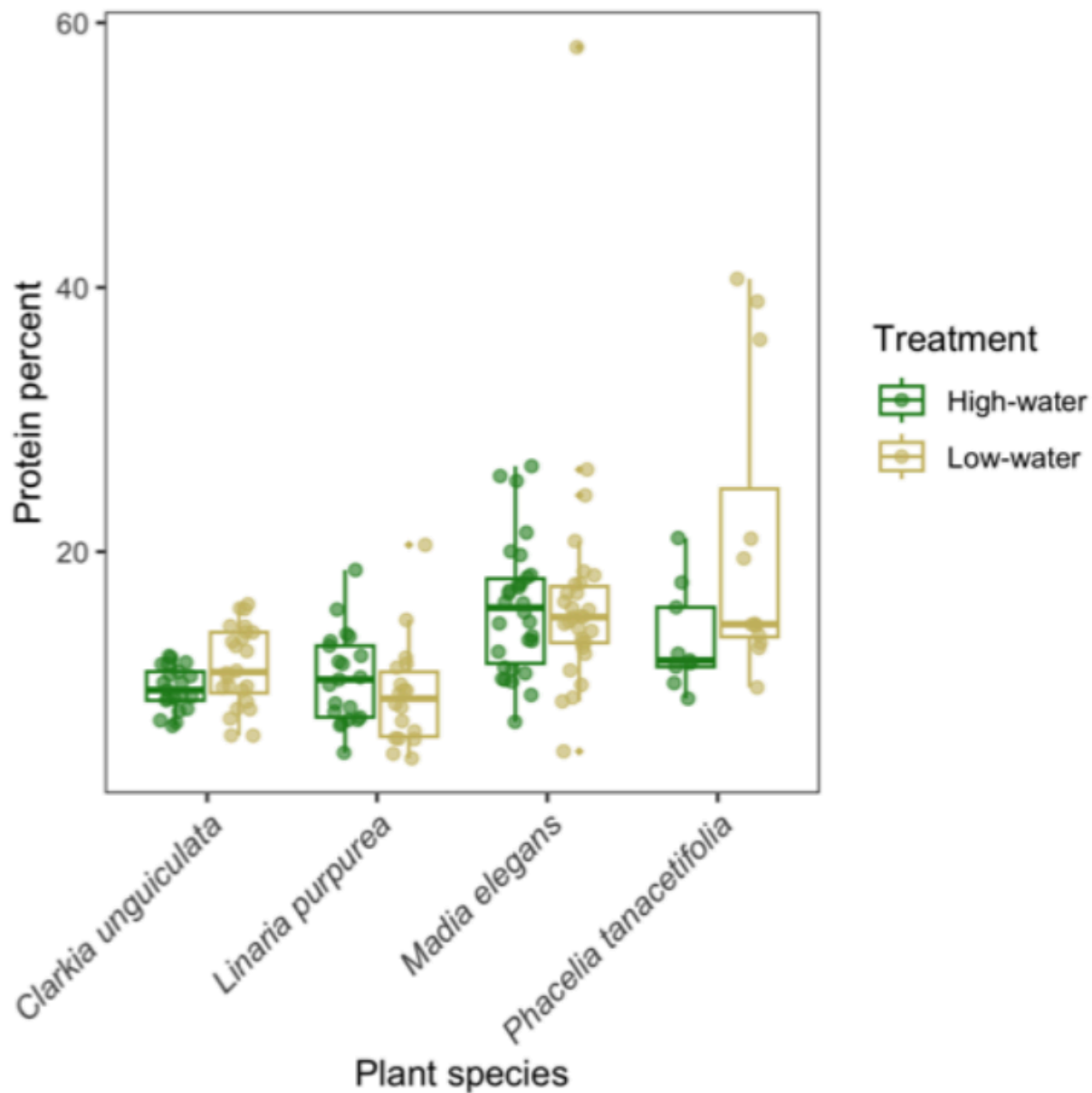


Figure 3

The percent protein found in pollen volume of plant species commonly planted to support pollinators and grown in a greenhouse common garden under high and low-water conditions. Colors reflect treatment, with green representing high-water and tan representing low water. Plots are boxplots with outliers designated by diamonds. Points are actual data points that represent technical replicates for plant individuals, that are jittered for clarity, and for which darker colors represent overlapping points. All species are annuals except *Linaria purpurea*, which is a perennial.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Gregor2025DataSupplementary.docx](#)