Botanical Sciences 104 (2): 394-409. 2026
DOI: 10.17129/botsci.3823

Received: October 16, 2025, Accepted: December 27, 2025
On line first: February 17, 2026

Ecology / Ecología

Evidence of andromonoecy in a northern population of *Guaiacum coulteri* (Zygophyllaceae)

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Abstract

Background: Angiosperms exhibit diverse reproductive systems, and andromonoecy—where individuals produce both hermaphroditic and staminate flowers—is rare, occurring in about 1.7 % of species. The family Zygophyllaceae is common in the Sonoran Desert, yet little is known about the reproductive biology of *Guaiacum coulteri*, a protected species in Mexico. Preliminary observations suggested the occurrence of two floral morphs, possibly indicating andromonoecy.

Questions: What is the breeding system of *G. coulteri*? Is the species self-compatible or self-incompatible?

Studied species: *Guaiacum coulteri*.

Study site and dates: Hermosillo, Sonora, 2022.

Methods: Floral traits were described, flower longevity and pollinators were documented, and controlled pollination treatments were conducted in a northern population from Hermosillo, Sonora.

Results: Two flower morphs were identified: short-gynoecium (SG) and long-gynoecium (LG) flowers. SG flowers did not set fruits, whereas LG flowers produced fruits and lasted longer (two days vs. one). LG flowers exhibited protandry and positive herkogamy. Pollination experiments showed that LG flowers are self-incompatible. Natural and cross-pollination treatments produced very low fruit set (< 4 %), and flowers were mainly visited by native bees.

Conclusions: *G. coulteri* exhibits andromonoecy, with SG flowers functioning as staminate and LG flowers as hermaphroditic. The species is self-incompatible and bee-pollinated. These results represent the first evidence of andromonoecy in *G. coulteri* and provide key insights into the reproductive ecology of this threatened desert tree.

Keywords: Floral dimorphism, pollination ecology, self-incompatibility, Sonoran Desert.

Resumen

Antecedentes: Las angiospermas presentan una gran diversidad de sistemas reproductivos. Los sistemas andromonoicos son poco frecuentes entre las angiospermas (≈ 1.7 %) y están caracterizados por tener individuos que producen flores hermafroditas y estaminadas. La familia Zygophyllaceae es frecuente en el Desierto Sonorense, pero la biología reproductiva de *Guaiacum coulteri*, especie protegida por la legislación mexicana, es poco conocida. Observaciones preliminares indicaron la presencia de dos morfos florales, lo que sugiere un sistema andromonoico.

Preguntas: ¿Cuál es el sistema reproductivo de *G. coulteri*? ¿Es autocompatible o autoincompatible?

Especie de estudio: *Guaiacum coulteri*.

Sitio y años de estudio: Hermosillo, Sonora, 2022.

Métodos: Se describieron los rasgos florales, la longevidad de las flores, los visitantes florales, y se realizaron tratamientos de polinización controlada en una población del norte de Hermosillo, Sonora.

Resultados: Se identificaron dos morfos florales: flores con gineceo corto (SG) y largo (LG). Las SG no desarrollaron frutos, mientras que las LG sí, y mostraron mayor longevidad (dos días frente a uno). Las LG presentaron protandria y hercogamia positiva. Los tratamientos de polinización indicaron autoincompatibilidad, y tanto la polinización natural como la cruzada mostraron baja fructificación (<4%). Las flores fueron visitadas principalmente por abejas nativas.

Conclusiones: *G. coulteri* presenta un sistema andromonoico con flores SG funcionalmente estaminadas y LG hermafroditas. La especie es autoincompatible y dependiente de polinizadores. Estos resultados constituyen la primera evidencia de un sistema andromonoico en *G. coulteri* y aportan información clave sobre su ecología reproductiva.

Palabras clave: Autoincompatibilidad, Desierto Sonorense, dimorfismo floral, ecología de la polinización.

Breeding systems refer to the presence and distribution of fertile floral whorls and their arrangement at different levels, such as within and among individuals and populations (Fernandes-Cardoso *et al.* 2018). Angiosperms exhibit a wide variety of breeding systems, with hermaphroditic or bisexual systems considered as basal, being widespread and representing a high percentage (72 %) of the known species (Yampolsky & Yampolsky 1922, Richards 1997). Other breeding systems that represent a lower percentage among angiosperms include monoecy, andromonoecy, gynomonoecy, dioecy, gynodioecy, and androdioecy, among others (Richards 1997, Charlesworth 2002). Andromonoecy is a rare (≈ 1.7 %) breeding system distributed in few angiosperm families (Yampolsky & Yamplosky 1922, Miller & Diggle 2003). In these families, individuals within populations show hermaphroditic and staminate flowers.

Andromonoecy occurs in at least 33 angiosperm families (Miller & Diggle 2003). Theoretical models suggest that this is the most likely transition from a hermaphroditic to a monoecious breeding system (de Jong *et al.* 2008). This system is considered as a plastic system that allow to adjust allocation to male and female function by producing a variable number of hermaphroditic and staminate flowers in response to resource availability (Miller & Diggle 2003). The flower traits of both morphs in andromonoecious species exhibit a wide spectrum of variation. In some taxa, hermaphroditic and staminate flowers are similar in pistil length, petal length, nectar secretion and pollen production (Luo *et al.* 2017, Casimiro-Soriguer *et al*. 2013, Contreras-Varela *et al.* 2023) whereas in others, staminate flowers are either smaller (Murakami *et al.* 2022, Lucas-García *et al.* 2025) or larger with significantly larger anthers (Huang 2003, Marcelo *et al.* 2021, Lyu *et al.* 2024) and higher pollen production (Huang 2003, Casimiro-Soriguer *et al.* 2013, Lyu *et al.* 2024). Additionally, male flowers may be more successful siring seeds (Dai & Galloway 2012), and seeds sired by male flowers perform better (Lyu *et al.* 2024). Flower morphs may appear in different positions within inflorescences or be intermixed (Vallejo-Marín & Rausher 2007, Ajani & Claßen-Bockoff 2021, Contreras-Varela *et al.* 2023).

Among angiosperm families, the Zygophyllaceae family comprises 22 genera and 230-240 species distributed mainly in dry regions of Europe, Asia, Australia, Africa and America, with few species extending into mesic regions (Sheahan 2007, Wang *et al.* 2016). The pollination biology of this family has only been studied in a few species. Most species have hermaphrodite flowers and are pollinated by insects, mainly bees, although insects of other orders also participate (Mamut *et al.* 2014, Chen *et al.* 2015, Naghiloo & Claßen-Bockhoff 2020, Abid *et al.* 2022). Only one species has documented evidence of male sterility and a gynodioecious breeding system (Cuevas García *et al.* 2005). To date, only one study has described floral sexuality and evaluated the self-compatibility of a small number of plants of *Guaiacum coulteri* in Chamela, Jalisco, Mexico (Bullock 1985). Flowers of *G. coulteri* were characterized as hermaphrodite and self-compatible (Bullock 1985). Nevertheless, no study has examined the pollination biology of *G. coulteri* in Sonora or throughout its distribution in Mexico. Research on the closely related *G. sanctum* provides valuable context. In Costa Rica and Puerto Rico, *G. sanctum* has hermaphroditic flowers, with 5 blue to purple petals, 10 anthers, and an ovary with 8 to 10 ovules (Fumero-Cabán *et al.* 2022). Flower anthesis begins in the morning and the flowers remain open for two days. During this time, the petals change color from blue to white. The fruit is a capsule with several ellipsoid seeds 1 cm long covered with a red aril (Fumero-Cabán *et al.* 2022). In Puerto Rico, the main floral visitors were bees, including both native species and *Apis mellifera*. Eight species of visitors were recorded in one location in Puerto Rico, while 17 insect species were recorded on a small island (Fumero-Cabán *et al.* 2022). Pollination treatments indicate that in *G. sanctum*, cross-pollination produces twice as many fruits and seeds of self-pollinated flowers (Fumero-Cabán *et al.* 2022). Although they produce fewer seeds, flowers of this species are self-compatible. Evidence obtained in both Puerto Rico and Costa Rica indicates that *G. sanctum* has a mixed mating system, in which cross-pollination predominates (Fuchs & Hamrick 2011, Fumero-Cabán *et al.* 2022). This species requires a vector to achieve efficient pollination and reproduction (Fumero-Cabán *et al.* 2022). In contrast, knowledge about the reproductive ecology of *G. coulteri* in the Sonoran Desert is limited.

In a preliminary study of flower longevity, two morphs were detected within individuals of *G. coulteri* in a peri-urban area of Hermosillo, Sonora. Building on this observation, the present study describes the different flower morphs found in a northern population of *G. coulteri* and several aspects of the pollination ecology of this species.

The objectives are to: a) characterize the different flower morphs and describe their respective longevity; b) assess whether the species is self-compatible or self-incompatible; c) document floral visitors; and d) describe the breeding system of *G. coulteri*.

Materials and methods

Study area. The studied population is located in an area known as El Bachoco, in the northern margin of the city of Hermosillo, Sonora, within the Sonoran Desert scrub vegetation. The local vascular flora comprises approximately 167 plant species, with Fabaceae, Asteraceae, Euphorbiaceae, Cactaceae, Boraginaceae, Poaceae, Acanthaceae, Convolvulaceae, Solanaceae, and Malvaceae as the most species-rich families (Sánchez-Escalante & Van Devender 2021).

Average monthly temperatures in Hermosillo range from 17.1 and 32.5 °C, with July being the hottest month (mean maximum: 39.8 °C) and January reaching the coldest temperatures (mean minimum: 9.8 °C) (Supplementary material, Figure S1A). The mean annual temperature is 24.9 °C. Rainfall (1966-2023) occurs mainly between July and September (73 % of annual), with an annual precipitation of 355.9 mm (Servicio Meteorológico Nacional 2024) (Figure S1B). During the study period (2022), annual rainfall was 552.7 mm (Servicio Meteorológico Nacional 2024) (Supplementary material, Figure S1B).

The nearby Sierra Espinazo Prieto is primarily composed of granitic rocks, featuring NW-SE oriented dike systems (Rodríguez-Castañeda 1981). Local soils are predominantly young, including Cambisols, Regosols, Calcisols and Luvisols (INEGI 2007).

Study species. Guaiacum coulteri (A.Gray, 1854) was originally described in 1854 by Botanist Asa Gray, based on a specimen collected in October 1851 by George Thurber in the hills between Ures and Rayón, in the state of Sonora (Gray 1854). The genus consists of six species of trees or shrubs distributed in dry environments in the tropical region of America (Axelrod 2002). *G. coulteri* is distributed from Sonora (Turner *et al.* 1995) to Oaxaca (Gordon *et al.* 2005). This species belongs to the Zygophyllaceae family, one of the most prominent families in the vegetation of the Sonoran Desert (Felger *et al.* 2001). It is a shrub or tree that grows up to 12 m tall (Figure 1A) (López-Toledo *et al.* 2011). The leaves are pinnate with 3-5 short, dark green, evergreen or tardily deciduous (under extreme drought conditions) leaflets. The flowers are grouped in small axillary clusters on thin pedicels; each flower is composed of 5 green sepals at the base with brown to blue-violet tips and margins, 5 separate petals 10-15 mm long, each twisted at the base, bright blue-violet in color, fading after anthesis. It has 10 blue filaments and yellow anthers; the ovary is superior and green with a short stalk. The fruit is dehiscent, semi-fleshy, obovate-shaped, yellow to yellow-orange in color, and develops 1 or 2 seeds, generally 1 cm long, wrapped in a thin, bright red aril (Figure 1D) (Felger *et al.* 2001, Turner *et al.* 1995). Flowering peaks in May, June, and July; however, flowers can be found from April to November. New leaves appear in early spring and fall in October (Turner *et al.* 1995). This species grows on slopes, plains, and streams, reaching its northern distribution limit in northern Sonora, indicating sensitivity to frost and a requirement for summer rainfall (Turner *et al.* 1995).

G. coulteri is a protected species under NOM-059-SEMARNAT-2010, the Mexican Norm for Endangered Species, in category A of threatened species (SEMARNAT 2010). Due to overexploitation for timber extraction (Gordon *et al.* 2005), it is also on the International Union for Conservation of Nature's Red List of Threatened Species (Rivers 2017). Furthermore, in 2016, it was included in the list of species of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (Sánchez-Soto *et al.* 2017).

Flower longevity and fruit development. To study several aspects of the reproductive ecology of *G. coulteri*, 10 individuals distributed along a stream were tagged. Five tagged plants from the study area were selected to evaluate flower longevity and fruit development in a sample of 25 flowers (five flowers/plant) through systematic observations made during June 2022. Flower longevity was documented by recording the time from the opening of the flower bud to the closing of the flower. For flower longevity, changes in flower development were checked every four hours

for two days (not including the night), taking photos of the different stages. For fruit development, observations were made from the closing of the flower to the formation of the ripe fruit; the marked fruits were checked weekly until they opened and exposed the seeds. During the observations, the different phases of the flower and fruit were recorded, as well as the events of flower opening, pollen dehiscence in the anthers, flower closing, and fruit development. Each phase was documented with photographs.

During systematic observations of flowers, it was noted that all tagged flowers with short gynoecium failed to set fruit. To assess whether these flowers were capable of setting fruits, five flowers from each of the ten plants in the study area were tagged in June 2022, for a total of 50 flowers. The fruit set was recorded five days after tagging.

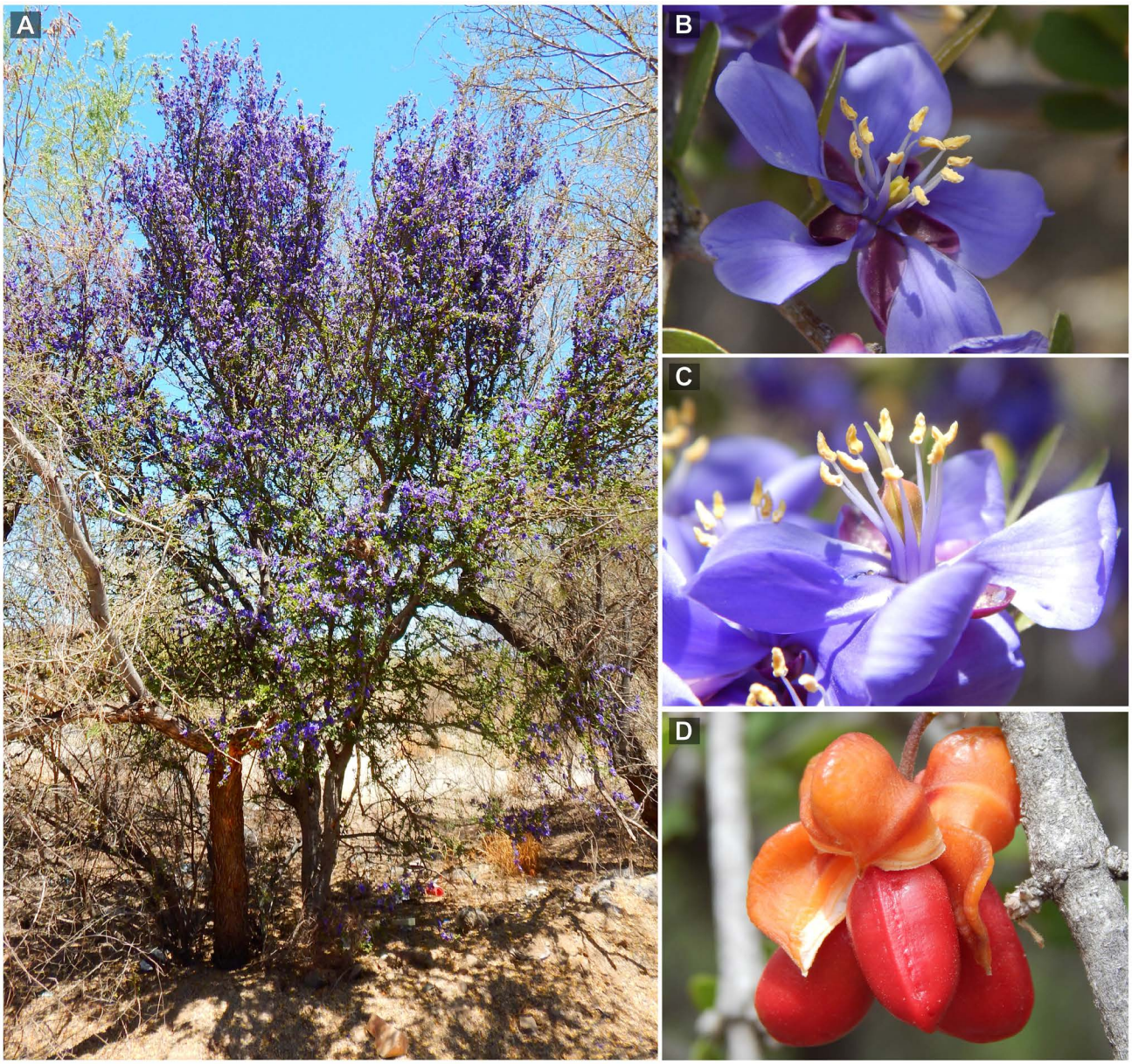

Figure 1. Guayacan (*Guaiacum coulteri*). A) Flowering individual of *G. coulteri.* B) Flower of *G. coulteri* with short gynoecium. C) Flower of *G. coulteri* with long gynoecium. D) Fruit of *G. coulteri*.

Flower types. During the study of flower longevity, flowers with marked morphological differences were noticed and subsequently described in detail. Two types of flowers were recorded differing in gynoecium length: flowers with reduced (short) gynoecium (hereafter SG, Figure 1B) and flowers with a more elongated (long) gynoecium (hereafter LG, Figure 1C). Six tagged plants from the study area were used to characterize the two flower morphs found within individuals. From each plant, a sample of 4-6 SG and LG flowers were collected. Flowers from each individual were stored in plastic containers within an ice box and immediately transported to the Lab where they were dissected and photographed alongside a millimeter scale to enable the measurement of six floral traits in centimeters: petal length (PL), petal width (PW), length of the stamen filament (LSF), length of the stamen anther (LSA), stamen length (SL), gynoecium length (GL) (Figure 2). The software ImageJ v. 1.54p (imagej.net/ij/) was used to measure floral traits from the photographs.

Pollination treatments. Given that only LG flowers were capable of setting fruits (see results), during July 2022, an experiment with controlled pollination treatments in these flowers was established to evaluate whether *G. coulteri* is self-compatible or self-incompatible. Based on previous observations of flower longevity, the experimental treatments were: a) manual cross-pollination. In this instance, flower buds were isolated in mesh bags; once open and with the stigma receptive (second day, see results), external pollen from both flower types collected from at least three nearby individuals was transferred to the stigma of the experimental flower; b) manual self-pollination. For this, flowers previously isolated with mesh bags were pollinated when the stigma was receptive using pollen from anthers of the same individual; c) automatic self-pollination. Flower buds were isolated with mesh bags and remained closed and inaccessible to any floral visitor throughout the entire period; d) control treatment or natural pollination. In this case, flower buds were marked and left exposed to all floral visitors to determine natural fruit set. For these experimental treatments, 10 plants were used to treat a total of 50 to 62 flowers per treatment. Each week, the experimental flowers were observed, recording those that aborted and those setting fruits until the fruits ripened. At the end of the reproductive cycle, fruit set was estimated as the percentage of the fruits produced among the flowers included in each treatment and seed production as the average number of seeds per fruit per treatment.

Flower visitors. To document the main flower visitors, systematic observations of three individuals were made for one day (June 16, 2022) during the flowering period. Three independent observers recorded the number of visits by floral visitors, as well as their identity, during 20 min periods throughout the day. The observers stood approximately one meter away from each individual to have good visibility of the visitors. The type of contact with the flower (whether it touched the anthers and/or stigma) and the identification of the type of visitor (bee, butterfly, etc.) were recorded. The observations covered the period of flower anthesis from morning to sunset. Using the evidence obtained on pollen release detected during the flower longevity study, the first observation began at 9:00 a.m., the second was made around 12:00 p.m., and the third at 5:00 p.m.; that is, three 20 min observation periods by three observers for a total of three effective hours of observation during a single day.

Bee sampling. Bee sampling was conducted using pan traps and active netting, following the guidelines of the Bee Inventory (BI) Plot method (Lebuhn *et al*. 2003). Two parallel transects were established along the plants of *G. coulteri* marked for this study. A total of 18 sets of three pan traps painted with fluorescent yellow, white, and blue were deployed within the plant canopies of *G. coulteri* along the transects. Pan traps consisted of plastic bowls partially filled with a soapy water solution, with a small partially submerged stone placed in each trap to facilitate insect contact with the solution. Traps were set at 9:00 a.m. and remained active for a continuous 24 h period.

Complementary active sampling was conducted along the same transects using entomological nets to increase sampling effort and record species not captured by passive traps. This activity was carried out by four collectors during the peak foraging period, between 9:00 a.m. to 12:00 p.m. Collected specimens were pinned and identified to the lowest possible taxonomic level by one coauthor based on morphological characters, using dichotomous keys (Michener *et al.* 1994, Michener 2007) and online resources available through Discover Life (www.discoverlife.org). Species

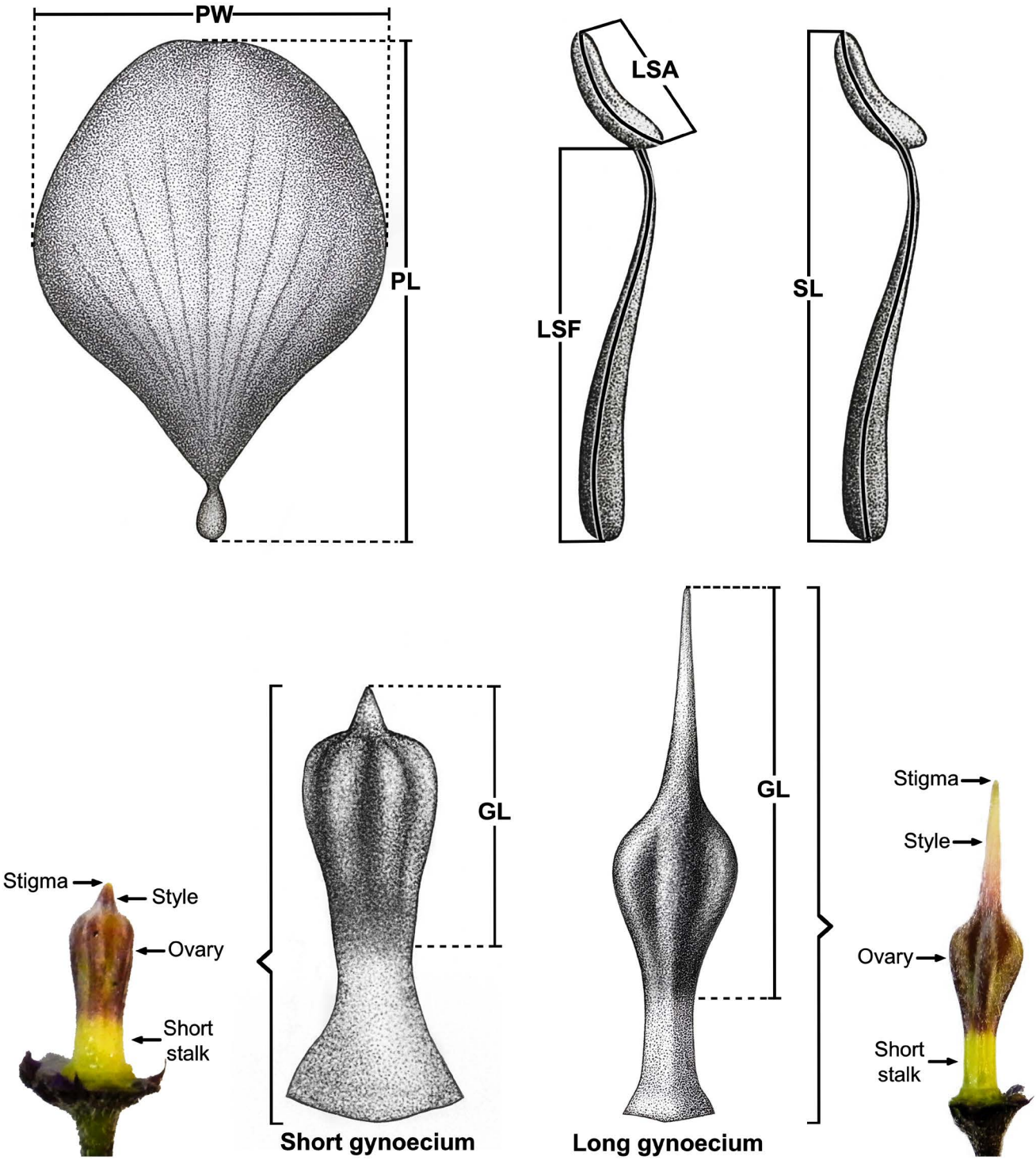

Figure 2. Floral traits measured in flowers of *Guaiacum coulteri*: petal length (PL), petal width (PW), length of the stamen filament (LSF), length of the stamen anther (LSA), stamen length (SL), gynoecium length (GL). For LSF and LSA, measurements were taken following the shape of each part of the stamen (black line inside the filament and anther). Similarly, SL was measured along the entire stamen (black line in the center). For GL, measurements were taken from the base of the ovary, where a change in color from green to brown can be observed in the short stalk, to the stigma.

determinations were supported by historical records for the state of Sonora obtained from reference collections and databases, including the Colección Nacional de Insectos (UNAM) accessed through IBDATA (www.ibdata.abaco2.org) and the Madrean Discovery Expedition (MDE) Fauna databases (https://flora.madreandiscovery.org/collections/search/index.php). Specimens are deposited in the bee collection of the Herbarium (USON) of the University of Sonora, in Hermosillo, Sonora, México. All bee collection activities were conducted under permit SGPA/DGVS/10355/21, issued by the Mexican Ministry of the Environment, SEMARNAT.

Seed production. To determine seed production per fruit, five fruits were randomly collected from ten different individuals in the studied population. The fruits were kept in paper bags and then taken to the laboratory where the number of seeds was counted to estimate the average number of seeds per fruit.

Statistical analysis. To evaluate the effect of different pollination treatments on fruit set, generalized linear models (GLMs) with a binomial distribution (0 = aborted; 1 = fruit) and log link function were used (McCullagh & Nelder 1989). To describe any difference between flower types, descriptive statistics, including the mean, standard deviation (SD), and coefficient of variation (CV), were estimated for each floral trait. To test for significant differences in trait values between flower types, GLMs with a gamma distribution and inverse link function were executed (McCullagh & Nelder 1989). All GLMs were performed using the glm2 v. 1.2.1 (Marschner 2011) packages in R v. 4.5.0 (R Core Team 2025).

Results

Flower longevity. During the monitoring of 25 marked flowers on five plants, distinct morphological differences in gynoecium length were observed, leading to the identification of two flower types: LG and SG flowers (Figure 1B and 1C). Based on this morphological trait, flower longevity was characterized separately by each flower type.

The longevity of the LG flowers was recorded to last two days (Figure 3). Flower opening occurred between 7:00 and 8:00 a.m. Early in the morning, the anthers were bright yellow but had not released pollen yet. Pollen dehiscence began gradually around 9:00 a.m., but no pollen adhered to the stigma on the first day. Pollen remained visible in the anthers until around 5:00 p.m., after which the anthers turned pale yellow and appeared nearly depleted of pollen (Figure 3). On the second day, the anthers no longer contained pollen, and pollen was observed deposited on the stigma (Figure 3). The pistil shifted from green to light purple, and the petals became lighter in color. After the second day, petal abscission began while the gynoecium-initiated fruit development. During systematic observation, it was observed that LG flowers were capable of developing fruit. These flowers exhibited protandry, with pollen release occurring on the first day (the male phase) and, based on pollen deposition, stigma receptivity was observed on the second day (the female phase). Positive herkogamy was also recorded, as the stigma was positioned above the anthers (Figure 3).

The SG flowers had a duration of only one day (Figure 4). Flower opening occurred between 7:00 and 7:30 a.m., and pollen dehiscence began around 9:00 a.m. (Figure 4). The anthers remained visibly loaded with pollen until around 5:00 p.m. By the following day, some flowers had lost their stamens (Figure 4), while others retained a few. During systematic observations, it was observed that SG flowers did not set fruits: none of the 50 SG flowers tagged to assess their fruit set produced fruit. In these flowers, the gynoecium remained consistently positioned below the anthers, indicating reverse or negative herkogamy (Figure 4).

Flower types. A total of 29 SG and 30 LG flowers were analyzed. Both types of flowers had between 4 and 5 petals, with those with LG flowers showing larger petal length (PL) and petal width (PW) (Table 1, Figures 5A and 5B). SG flowers had between 8 and 10 stamens with a stamen length (SL) of 0.91 ± 0.20 cm, while LG flowers had between 7 and 10 stamens with an SL of 0.89 ± 0.13 cm (Table 1). Regarding gynoecium length (GL), LG flowers had a significantly greater GL than SG flowers (Figure 5C), with values of 0.77 ± 0.14 cm and 0.27 ± 0.07 cm, respectively (Table 1).

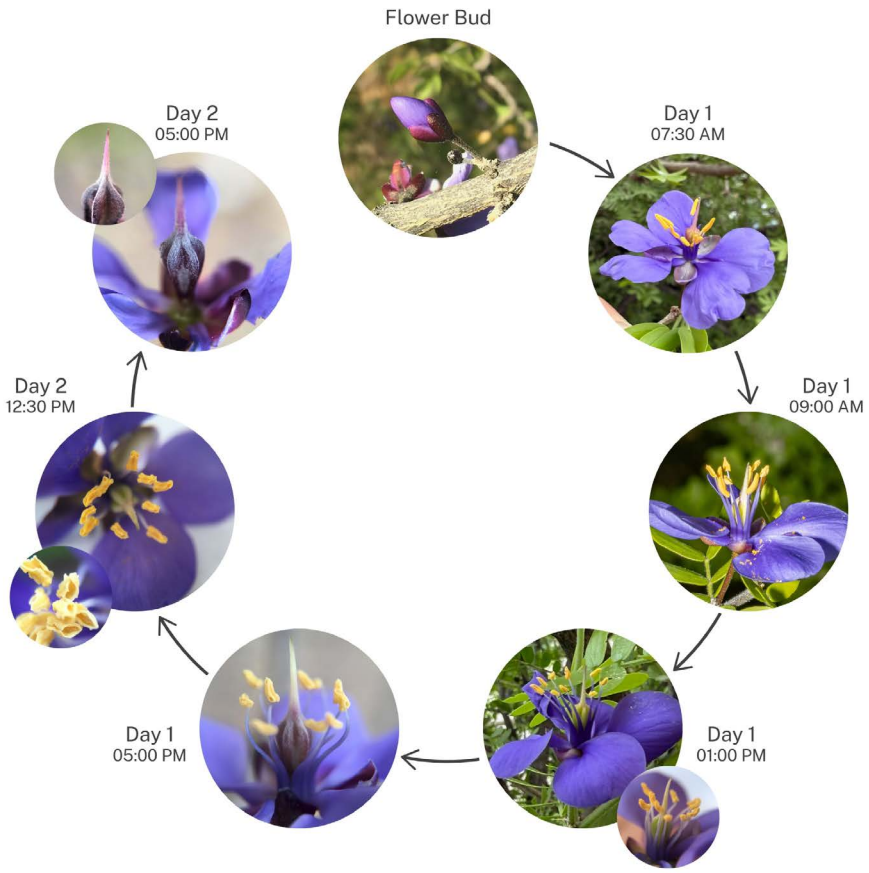

Figure 3. Floral longevity of LG flowers of *Guaiacum coulteri.*

Among the floral traits evaluated in both types of flowers, the traits with the highest CV values were length of the stamen filament (LSF) and GL (Table 1). Conversely, the traits with the lowest CV values were PW for SG flowers and SL for LG flowers (Table 1). In general, SG flowers showed higher CV values in floral traits (Table 1).

Pollination treatments. The results of the experimental pollination treatments showed that flowers subjected to self-pollination (both manual and automatic) did not produce any fruit, suggesting that these flowers are self-incompatible. Cross-pollination and control or natural pollination treatments were the only ones that produced fruits, both with very low fruit set. Out of 54 cross-pollinated flowers, only two produced fruit (3.70 %), each containing a single seed. Similarly, the control pollination treatment yielded two fruits (4 %) containing one and two seeds, respectively, with an average of 1.5 seeds per fruit. Regarding GLMs, no significant differences in fruit set were detected between pollination treatments ($z = 0.005$, $P = 0.996$).

Flower visitors. During the day when floral visitors were observed, only insects were recorded. A total of 83 visits to the flowers were detected during the day, of which 74 (89 %) were legitimate visits, i.e., visits that touched the stigma and/or anthers. Of the observed time periods, the highest number of visits was recorded between 9:00 and 9:20 a.m. (Figure 6A), with 45.9 % of the day's visits. In descending order, this was followed by the period between 12:00 and 12:20 p.m., with 43.2 % of visits, and finally, the period between 5:00 and 5:20 p.m., with 10.8 % of visits (Figure 6A). In terms of the frequency of legitimate visits to the flowers, Hymenoptera exhibited the highest frequency (87.8 %), with eight morphospecies identified. This was followed by Diptera (9.4 %), with two morphospecies documented, and Lepidoptera (2.7 %), with a single morphospecies identified. The species with the highest frequency

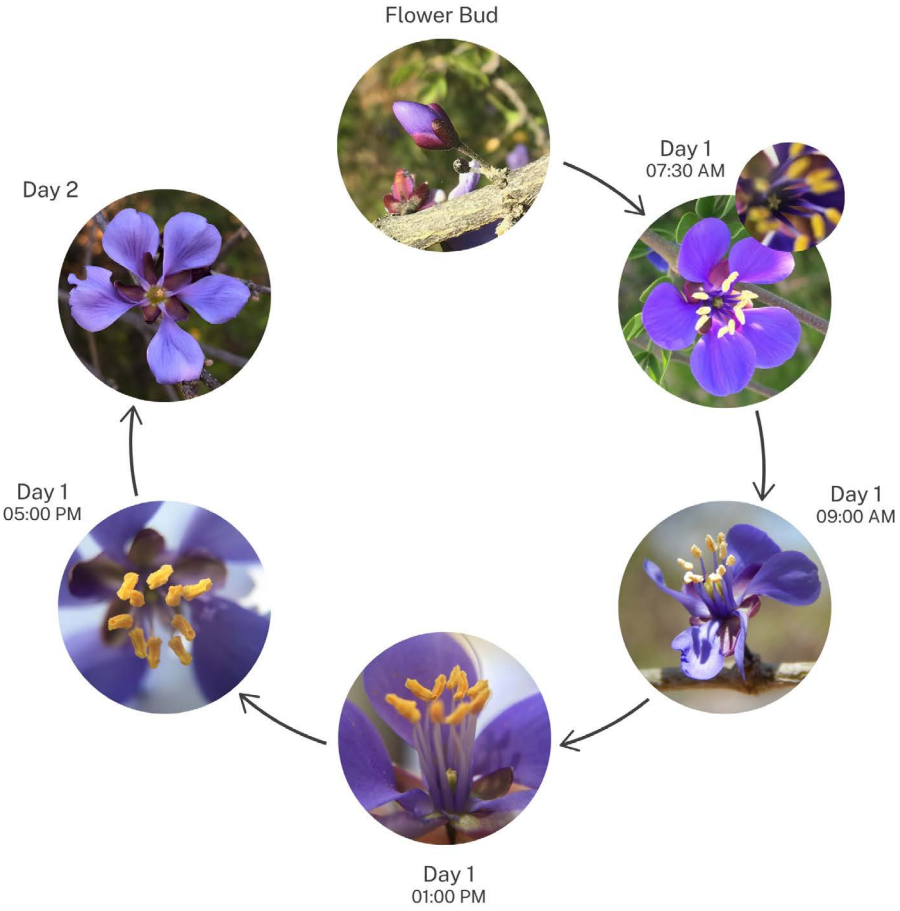

Figure 4. Floral longevity of SG flowers of *Guaiacum coulteri.*

of visits to flowers was a native bee of the genus *Centris* (Figure 6B), which accounted for 28.4 % of all visits. On average, a flower receives 24.5 visits per day, of which about 22 are legitimate visits.

Bee diversity. Of the 64 bee specimens collected using pan traps and hand netting (Table 2), representatives of four families, 15 genera and 19 taxa were identified; four taxa remained as morphospecies. Most species belonged to Apidae, which accounted for 47 specimens (73.4 %). Within this family, the tribe Eucerini was the most frequent, with 22 (34.3 %), followed by *Centris* with eight (12.5 %) and *Ceratina* with six specimens (10.9 %). Three specimens each (4.6 %) were recorded in *Diadasia*, the cleptoparasitic *Leiopodus singularis* (Emphorini), and the introduced honeybee *Apis mellifera*.

Megachilidae was represented by six (9.4 %), including three *Ashmeadiella* and one specimen each of *Diadanthium* and *Megachile*, as well as two unidentified morphospecies. Halictidae comprised five (7.8 %), represented by four of *Augochloropsis* and one of *Nomia*. Andrenidae was represented by a single unidentified specimen (1.6 %).

Fruit development. In LG flowers, fruits have a ripening process of approximately four months (Figure 7). One week after pollination, the ovary turns dark purple, almost brown, and the locules become visible (Figure 7). By week four, the fruit undergoes another color change, turning green with a slight change in size (Figure 7). By week eight, the fruit changes color again, this time from green to brown, and the seeds inside the locules are visible. By week 12, the color changes again to violet-brown, and the seeds are more clearly visible. By week 15, the fruit is fully ripe and yellow, exposing the seed surrounded by a bright red aril.

Table 1. Descriptive statistics of floral traits measured in flowers of *Guaiacum coulteri*. Significant differences in floral traits are indicated by values marked with '***', as determined by a t-test at $P < 0.001$ in GLMs.

Floral trait	Flower type			
	SG flower		LG flower	
	Mean ± SD	CV (%)	Mean ± SD	CV (%)
PL (cm)	1.08 ± 0.20***	18.93	1.16 ± 0.20***	17.18
PW (cm)	0.80 ± 0.12***	15.61	0.87 ± 0.14***	16.48
LSF (cm)	0.66 ± 0.18	28.10	0.64 ± 0.11	18.28
LSA (cm)	0.25 ± 0.04	17.38	0.24 ± 0.03	15.74
SL (cm)	0.91 ± 0.20	22.14	0.89 ± 0.13	14.78
GL (cm)	0.27 ± 0.07***	26.71	0.77 ± 0.14***	19.17

SG: short gynoecium, LG: long gynoecium, PL: petal length, PW: petal width, LSF: length of the stamen filament, LSA: length of the stamen anther, SL: stamen length, GL: gynoecium length, SD: standard deviation, CV: coefficient of variation

Seed production. The number of seeds per fruit ranged from 1-5 (Figure S2), with a mean number (± SD) of 2.12 ± 0.74 seeds per fruit.

Discussion

During the initial survey, two types of flowers differing in gynoecium length were observed within individual plants of *G. coulteri* (Figure S3). These flowers differ in gynoecium and petal length as well as petal width (Figure 5) but are similar in other traits such as length of stamen filament and length of the stamen anther. Although not quantified, observations in the field suggest that plants had different frequencies of both type of flowers, as in some plants it was difficult to find flowers with short gynoecium, whereas in others it was quite easy. These types of flower morphs that differ in size of several traits and frequency among individuals have been recorded in other species with andromonoecious breeding systems (Medan & D´Ambrogio 1998, Miller & Diggle 2003, Casimiro-Soriguer *et al.* 2013). Both flower morphs have been observed in other populations of *G. coulteri* in the Sonoran Desert (K. Yescas, unpublished data). The variation in the frequency of staminate flowers might be a plastic response to resource availability as these flowers are less costly as they do not produce seeds (Murakami *et al.* 2022).

Both flower morphs showed clear differences in longevity and fruit set. SG flowers lasted only one day, and the available evidence suggest that they do not set fruits. In contrast, LG flowers last two days, show positive herkogamy, and although with low values, are capable of setting fruits. As SG flowers have a reduced gynoecium, do not set fruits and produce apparently viable pollen, they are likely phenotypically staminate flowers. In contrast, LG flowers have an apparently normal gynoecium, produce apparently viable pollen and set fruits. Therefore, it is likely that they are phenotypically hermaphrodite flowers. A similar pattern of flower longevity has been observed in other species with an andromonoecious breeding system (Medan & D´Ambrogio 1998, Vallejo-Marín & Rausher 2007).

The evidence from the pollination treatment revealed that LG flowers are self-incompatible. This finding contrasts with evidence on self-compatibility in *G. coulteri* from Chamela (Bullock 1985) and *G. sanctum* (Fumero-Cabán *et al.* 2022). Thus, the available evidence suggests that Sonoran populations of *G. coulteri* are self-incompatible. In addition, control and cross-pollination treatments in *G. coulteri* reveal that fruit set is quite low compared to *G. sanctum* (Fumero-Cabán *et al.* 2022). Such pattern of low fruit set values is typical of Sonoran Desert trees with massive flowering, such as *Olneya tesota*, *Neltuma velutina* and *N. glandulosa* that exhibit low fruit set values (Sutherland & Delph 1984). Given the evidence of interpopulation variation on incompatibility and the low values of fruit set, future studies should employ larger sample sizes to verify whether there is geographic variation in the incompatibility system of *G. coulteri*.

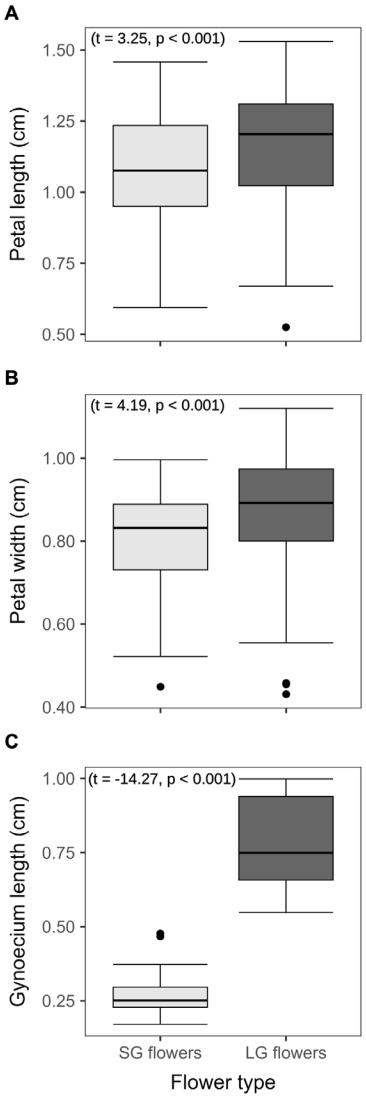

Figure 5. Floral traits with significant differences between flower types of *Guaiacum coulteri.* A) Petal length (PL). B) Petal width (PW). C) Gynoecium length (GL).

As in other members of the Zygophyllaceae, floral visitors to *G. coulteri* were insects. This pattern is common in most species of this family that have been previously studied (Minckley *et al.* 1999, Chen *et al.* 2015, Fumero-Cabán *et al*. 2022). Although butterflies and flies were recorded, most visitors were wild bees. Interestingly, although the study area is in a peri-urban location, honeybees were rarely recorded visiting flowers and captured in pan traps (Table 2). In contrast, in Puerto Rico, honeybees were the most frequent flower visitor in *G. sanctum* (Fumero-Cabán *et al.* 2022). Among the wild bees, one of the most frequent visitors was a species from the genus *Centris* (Figure 6B), a pattern like the records of flower visitors for *G. sanctum* (Zygophyllaceae) in Mona Island (Fumero-Cabán *et al.* 2022). However, more extensive sampling is necessary to identify the most important pollinators of *G. coulteri*.

Fruit development took approximately four months from flower anthesis to fruit ripening. Such longevity is shorter than the time reported for *G. sanctum* (6 months: Fumero-Cabán *et al.* 2022). Open pollinated flowers of *G. coulteri* had on average 2.1 seeds per fruit whereas for *G. sanctum,* the average was 3.5 (Fumero-Cabán *et al.* 2022). Seeds of *G. coulteri* are surrounded by a red aril that most likely serves as a reward to seed dispersers, as in *G. sanctum* in Guatemala (Wendelken & Martin 1987).

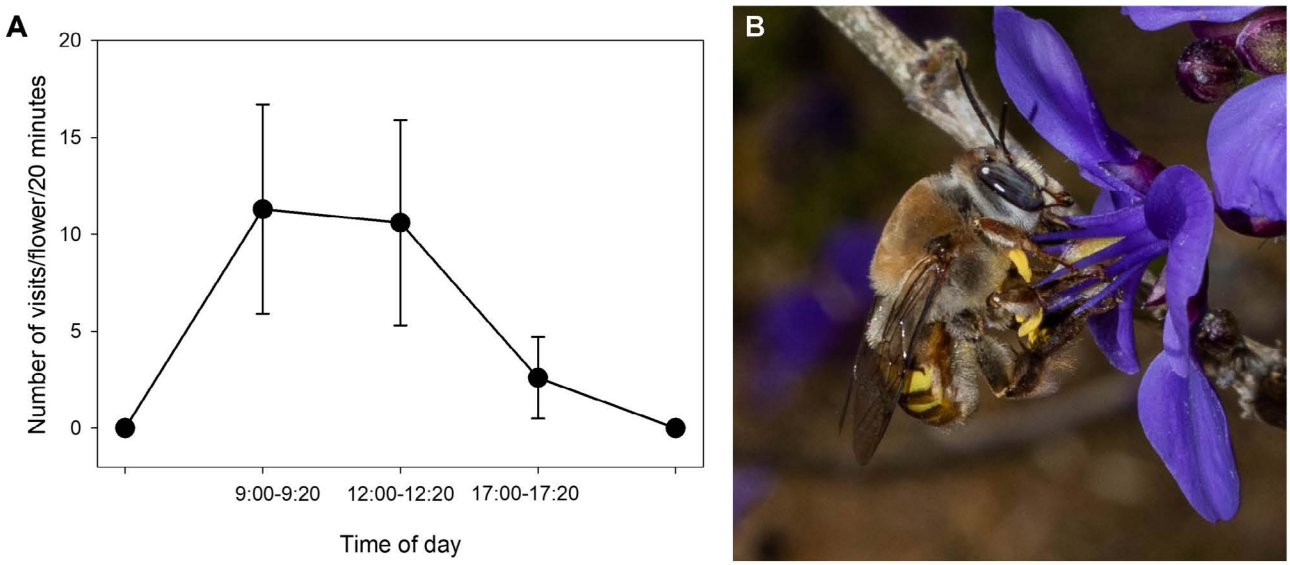

Figure 6. Floral visitors of *Guaiacum coulteri*. A) Number of visits to flowers at different times of the day. B) *Centris* sp., species with the highest frequency of visits to flowers.

Table 2. List of bee species recorded in pan traps and entomological nets among individuals of *Guaiacum coulteri*.

Family	Tribe or genus	Specimen count
Andrenidae		
	sp. *1*	1
Apidae		
	Apis mellifera	4
	Centris caesalpiniae	1
	Centris sp.1	3
	Centris sp.2	4
	Ceratina sp.1	2
	Ceratina sp. 2	4
	Diadasia sp.1	3
	Eucerini	22
	Leiopodus singularis	3
	Melissodes sp.1	1
Megachilidae		
	Ashmeadiella sp.1	3
	Dianthidium sp.1	1
	Megachile sp. 1	1
	sp. 2	1
	sp. 3	3
	sp. 4	1
Halictidae	*Augochloropsis* sp.1	4
	Nomia sp.1	1
Total specimens		64
Total taxa		19

Overall, the evidence shown here suggests that the studied population of *G. coulteri* has an andromonoecious breeding system. SG flowers are most likely male flowers, whereas LG flowers are hermaphrodite. Given the extensive distribution range along the Pacific coast of Mexico (López-Toledo *et al.* 2011), future studies on *G. coulteri* should document whether there is variation in the breeding system or if it is andromonoecious along its range. It is also suggested to describe flower development of male flowers to identify the proximal process that prevents the formation of seeds in male flowers (Luo *et al.* 2017). Similarly, it is suggested to study the development of anthers and pollen grains in hermaphrodite flowers to assess whether these flowers are functionally hermaphrodite or female (Luo *et al.* 2017).

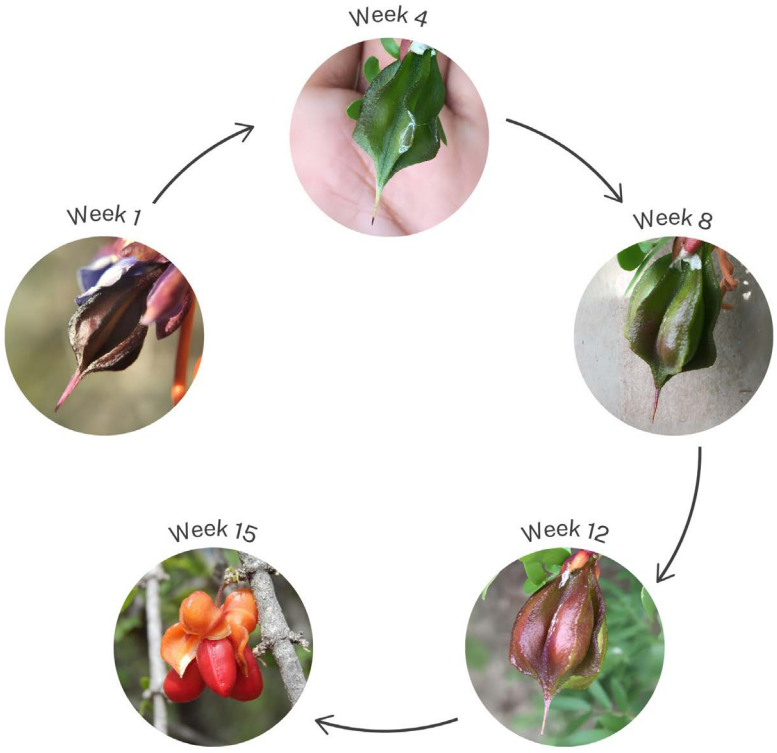

Figure 7. Fruit development and maturation of *Guaiacum coulteri.*

Supplementary material

Supplemental data for this article can be accessed here: https://doi.org/10.17129/botsci.3823

Acknowledgements

We thank Benjamín Bustamante and José F. Martínez for field assistance. We also thank Benjamín Bustamante for the photographs of a *G. coulteri* flower (Figure 3) and a *Centris* bee (Figure 6), and Tania Molina for diagrams in Figures 2, 3, 4 and 7.

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Associate editor: Pedro Luis Valverde

Author contributions: SYHL, field work, laboratory work, data compilation, data analysis, LGBV, field work, laboratory work, data analysis, writing-review & editing; FMF, conceptualization, supervision, field work, laboratory work, data analysis, writing-review & editing; KFYR, field work, laboratory work, data analysis, writing-review & editing.

Supporting Agencies: Instituto de Ecología, Universidad Nacional Autónoma de México.

Conflict of interest: The authors declare that there is no conflict of interest, financial or personal, in the information, presentation of data and results of this article.