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RESEARCH ARTICLE

Patterns of phenotypic variation in *Gossypium turneri*: a wild cotton with a restricted distribution in Sonora, Mexico

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Abstract Crop wild relatives (CWR) represent important genetic resources for crop improvement. *Gossypium turneri*, a wild cotton species with a restricted distribution in the Sonoran Desert of northwestern Mexico, has been identified as a potential breeding resource for cotton improvement. While several agronomically important traits have been previously identified through limited observations from only one location within its range, phenotypic variation in this xerophytic species has not been thoroughly studied. This study aimed to describe the pattern of phenotypic variation in floral and leaf traits along the three known populations of *G. turneri* and identify traits of agronomic interest. Leaves and flowers through its distribution range were collected and quantitative and qualitative attributes were analyzed. Phenotypic variation in flowers and leaves was predominantly found among individuals within populations, with a smaller proportion occurring between populations, likely due to the species' restricted distribution. Interpopulation variation in leaf traits was probably influenced by differences in local rainfall, whereas flower traits exhibited minimal interpopulation variation, likely due to similarities in pollinator composition. Some traits of interest for cotton improvement were identified, such as polymorphic bracts and production of anthers without pollen among flowers. This desert-adapted wild cotton offers valuable traits with potential for adaptation of cultivated cotton to water- and heat-stressed environments.

Keywords Crop Wild Relatives (CWR) · Flower traits · Leaf traits · Quantitative attributes · Qualitative attributes

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Introduction

Phenotypic variation refers to the expression of different morphological, physiological, biochemical, behavioral, and developmental traits among individuals within and between populations of the same species (Kalisz and Kramer 2008; Schreiber et al. 2011). This variation is driven by genetic, epigenetic and environmental factors, that act both within and among populations across the

species' geographic range (Arteaga et al. 2015; Alcántara-Ayala et al. 2020; Li et al. 2021). In response to diverse environmental conditions across the distribution range, individuals may express phenotypic variation, influenced in part by the genetic variation within and between populations (Lopez et al. 2015; Opedal et al. 2022).

Species with a wide geographic distribution tend to exhibit greater phenotypic variation among populations due to increased environmental heterogeneity, which drives trait differentiation as populations adapt to diverse conditions (Domínguez et al. 1998; Gratani 2014). In contrast, phenotypic variation in species with a narrow distribution have been less studied, and consequently, little is known about the patterns of variation within and among populations. In such species, phenotypic variation may be limited for ecologically important quantitative traits, making them potentially more sensitive to environmental changes (Oakley 2015).

Crop wild relatives (CWR) are progenitors or closely related wild species of domesticated crops (Cockel et al. 2022; Kapazoglou et al. 2023). Unlike their domesticated counterparts, CWR often exhibits high genetic and phenotypic variability due to their adaptation to diverse natural habitats, making them valuable resources for breeding programs (Viruel et al. 2021; Kapazoglou et al. 2023). These relatives carry traits and genes that confer resistance to biotic and abiotic stresses-traits that are often absent in modern crops. Incorporating such traits into cultivated species is therefore crucial for strengthening food security (Kapazoglou et al. 2023). The extent of phenotypic variation in CWR can depend on factors such as their distribution range, with wider-ranging species often displaying more variation (Renzi et al. 2022).

To effectively utilize CWR in crop improvement, understanding their cross-compatibility with domesticated species is crucial (Viruel et al. 2021). CWR are classified into three categories based on their compatibility with cultivated species: primary, secondary, and tertiary gene pools (Viruel et al. 2021). The primary gene pool includes CWR that can easily interbreed with cultivated species, allowing straightforward gene transfer. The secondary gene pool consists of CWR that can interbreed but face reproductive or genetic barriers, making gene transfer more challenging yet still feasible. The tertiary gene pool comprises CWR for which gene transfer to cultivated species is not possible (Viruel et al. 2021). Given their value as genetic resources, conserving and studying CWR is crucial for ensuring crop sustainability. Research on phenotypic variation in CWR offers insights into their genetic diversity and helps identify traits of agronomic interest, especially in species within the primary and secondary gene pools where interbreeding is viable (Dong et al. 2020; Karam et al. 2023).

Cotton (genus *Gossypium*) is one of the most important agricultural crops as it is the most widely used source of natural textile fiber globally (Mammadov et al. 2018; Viot and Wendel 2023). The genus *Gossypium* comprises 52 species (7 tetraploids and 45 diploids), of which only four have been domesticated and are currently cultivated: *G. hirsutum*, *G. barbadense*, *G. herbaceum*, and *G. arboreum*. The remaining species are wild and considered crop wild relatives (CWR) (Shim et al. 2018; Viot and Wendel 2023). Among these wild relatives, *Gossypium turneri* is a species endemic to the state of Sonora in northwestern Mexico, with a restricted distribution along the coastal area of the Guaymas municipality (Fig. 1) (Ulloa 2014; Wegier et al. 2018; Yescas-Romo et al. 2024). Like other CWR of the secondary pool (Chen et al. 2018), *G. turneri* possesses traits of interest for cotton improvement. This wild species is classified within the subsection Caducibracteolata of the subgenus Houzingenia (Chen et al. 2018; Viot and Wendel 2023). Members of this subsection exhibit deciduous bracts at anthesis, a trait of economic importance since the bracts fall before fiber formation and exposure, reducing the need for fiber cleaning treatments in cultivated cotton (Chen et al. 2018; Hu et al. 2021). Additionally, *G. turneri* shows tolerance to salinity, presumably associated with its coastal desert habitat, and has reduced leaves with a thick cuticle and a double palisade layer, which helps minimize water loss (Ulloa 2014; Hu et al. 2021). These traits have been identified using limited observations from one location within its distribution range (Fryxell 1978). Despite the identification of these traits, phenotypic variation has yet to be thoroughly studied in this xerophytic species. Therefore, investigating the floral and leaf traits of *G. turneri* is crucial for uncovering agronomically relevant attributes. This study aims to analyze the phenotypic variation in *G. turneri* through floral and foliar traits. The objectives

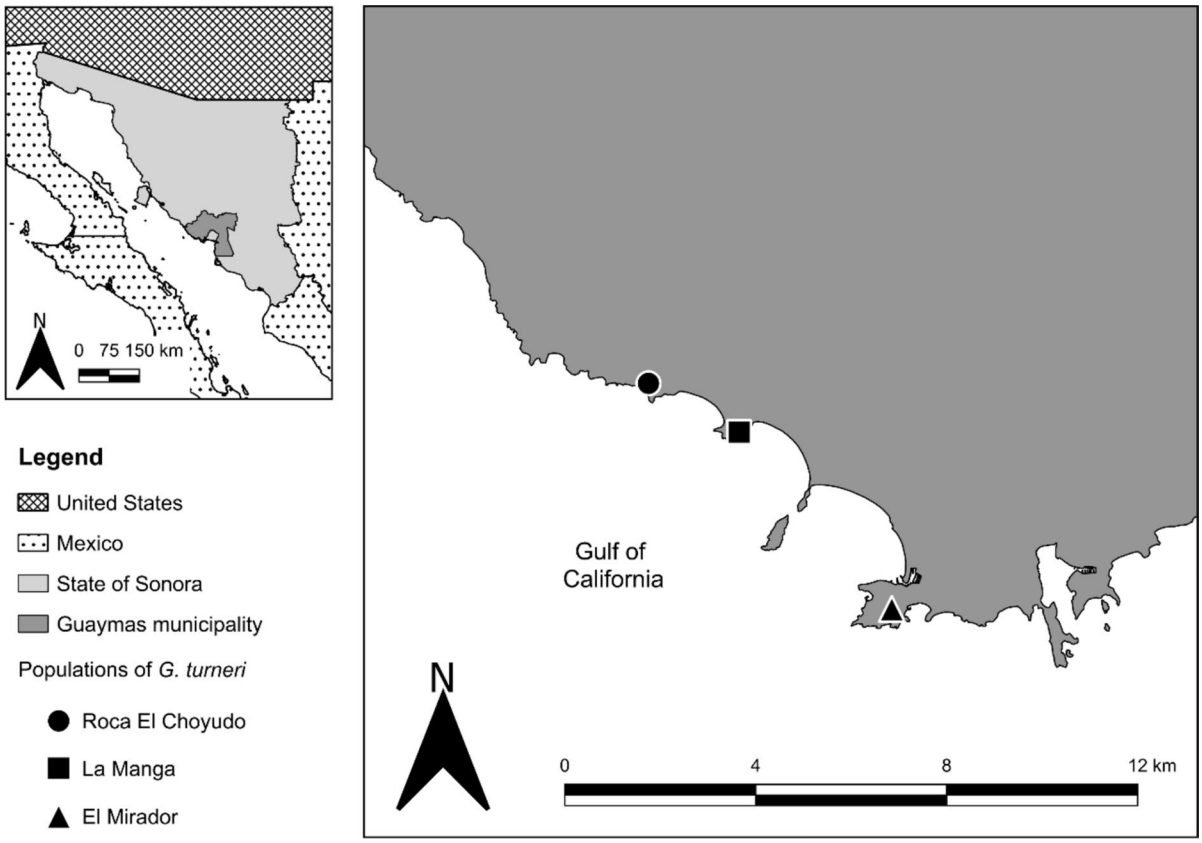


Fig. 1 Populations of *Gossypium turneri* in the municipality of Guaymas, Sonora

are to: a) describe patterns of phenotypic variation in flowers and leaves, b) examine phenotypic variation within and between populations, and c) identify traits of agronomic interest for cotton improvement.

Materials and methods

Study area and sample collection.

The wild cotton species *Gossypium turneri* is native to the state of Sonora in northwestern Mexico, with its natural distribution limited to a small area along the coast of San Carlos in the municipality of Guaymas (Wegier et al. 2018) (Fig. 1). Within this range, individuals of *G. turneri* have been significantly affected by tourism-driven coastal development in San Carlos, leading to habitat fragmentation and a decline in their distribution (Wegier et al. 2018; Yescas-Romo et al. 2024). Currently, only three distinct and accessible populations of this wild cotton have been identified: El Mirador, La Manga, and Roca El Choyudo (Fig. 1). The geographic coordinates of these populations have been excluded from consideration due to the classification of *G. turneri* as an endangered species under Mexican legislation (DOF 2019) and its listing as critically endangered on the International Union for Conservation of Nature (IUCN) Red List (Wegier et al. 2018).

No climatological data is available for the populations of *G. turneri*. The nearest meteorological station is located in Guaymas, approximately 21 km east of El Mirador. A historical record of 56 years (1967 to 2023) indicates an average annual precipitation of 264.53 mm, with interannual variation from 51.76 to 502.01 mm (CESAVE-SIAFESON 2024a; SMN 2024). The mean monthly temperature oscillates between 16.8 and 31.2 °C, from the coldest month (January) to the warmest month (August), respectively (SMN 2024). The climate of Guaymas

is classified as hot desert (BW, INEGI 2008; Brito-Castillo et al. 2010), while the soil type varies across the municipality. Among these, regosol is one of the primary soil types (INEGI 2007). The vegetation of the area is desert scrub, located within the Central Gulf Coast subdivision of the Sonoran Desert (Shreve 1964).

In each population, three fully open flowers (Yescas-Romo et al. 2024) and three mature leaves were collected from each of 20 individuals, resulting in a total of 180 flowers and 180 leaves. The collected flowers and leaves were immediately stored in a cold icebox and transported to the laboratory. Upon arrival, the flowers were dissected and, together with the leaves, were photographed with a millimetric scale on the same day of collection to facilitate measurements of flower and leaf traits. All samples were collected under a permit (09/K5-1337/11/21) issued by SEMARNAT-Wildlife Direction.

Measurement of quantitative and qualitative attributes.

To describe the patterns of phenotypic variation in *G. turneri*, a total of 22 attributes were evaluated in flowers and leaves, comprising 10 quantitative and 12 qualitative traits. For flowers, seven quantitative attributes were measured (Table 1, Fig. 2) and 10 qualitative traits were evaluated (Table 1, Fig. S1). In contrast, three quantitative and two qualitative traits were measured in leaves (Table 1, Fig. 3, Fig. S2). Color attributes of flowers and leaves were evaluated using the Royal Horticultural Society (RHS) Color Chart (RHS 2020). The software ImageJ (https://imagej.nih.gov/) was used to measure the quantitative attributes

Table 1 Quantitative and qualitative attributes evaluated in flowers and leaves of *Gossypium turneri*

Plant organ	Attributes	Attribute abbreviation	Unit of measurement/ Coding key
	Quantitative traits		
	Petal length	PL	cm
	Petal width	PW	cm
	Gynoecium length	GL	cm
	Style length	SL	cm
	Length of staminal column	LSC	cm
	Width of staminal column	WSC	cm
	Herkogamy	H	cm
	Qualitative traits		
Flower	Petal color	PC	1–8
	Spot on the petal	SP	1–2
	Spot color	SC	1–19
	Gossypol glands in petal	GGP	1–2
	Bracts	B	1–2
	Nectaries below bracts	NB	1–2
	Style position	S	1–4
	Pollen in anthers	PA	1–2
	Gossypol glands in style	GGS	1–2
	Gossypol glands in calix	GGC	1–2
Leaf	Quantitative traits		
	Leaf length	LL	cm
	Leaf width	LW	cm
	Leaf area	LA	cm^2
	Qualitative traits		
	Leaf color	LC	1 – 9
	Nectaries on leaf	NL	1 – 2

cm: centimeters, cm^2: square centimeters

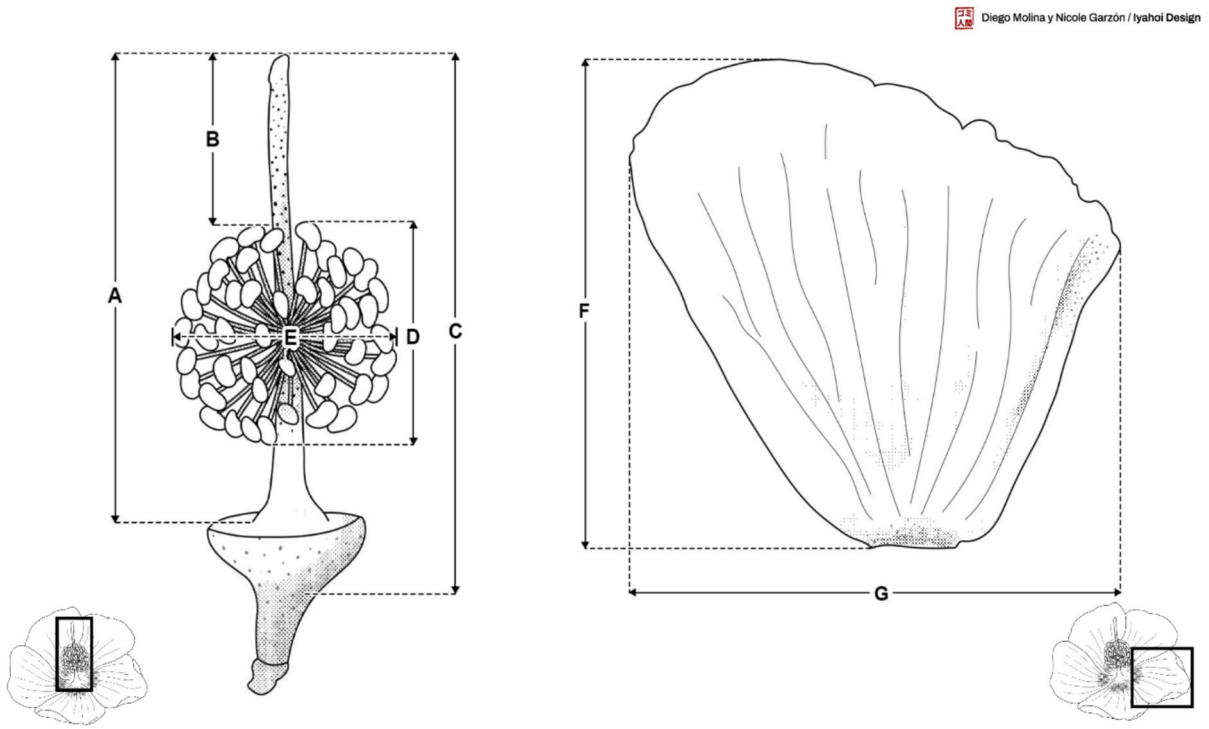


Fig. 2 Quantitative attributes measured in flowers of *Gossypium turneri*: A) style length (SL), B) herkogamy (H), C) gynoecium length (GL), D) length of staminal column (LSC), E) width of staminal column width (WSC), F) petal length (PL) and G) petal width (PW). Illustrations made by Diego Molina Tinoco and Nicole Garzón

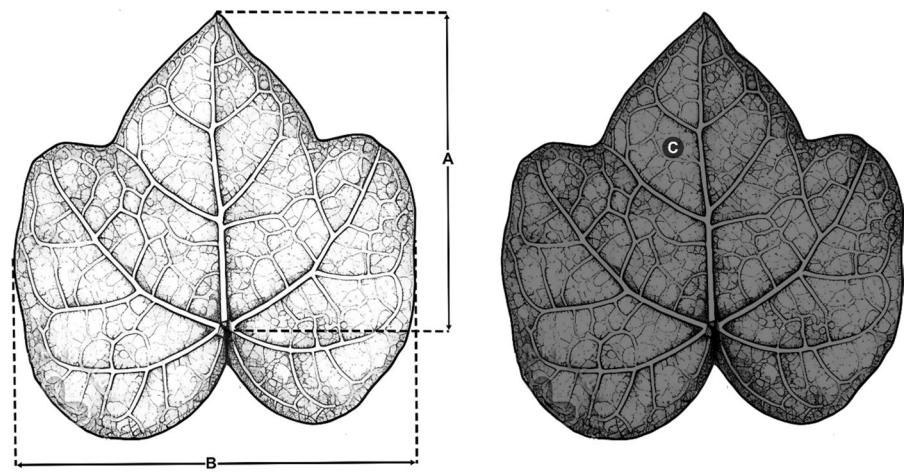


Fig. 3 Quantitative attributes measured in leaves of *Gossypium turneri*: A) leaf length (LL), B) leaf width (LW) and C) leaf area (LA)

in both flowers and leaves based on the photographs taken with a millimeter scale. During this process, qualitative attributes were also assessed and coded as binary or multistate (Table 1, Table S1).

Statistical analysis

Descriptive statistics, including the mean, standard deviation, and coefficient of variation (CV in %), were calculated for each quantitative and qualitative attribute globally (across all samples) and for

each population (Javid et al. 2024) to describe phenotypic variation in flowers and leaves. To assess whether there is significant phenotypic variation among populations, generalized linear models (GLM) were executed with gamma distribution and inverse link function (Limón et al. 2016). For H attribute, where negative values were obtained, a constant value was added to the original data to perform the GLM. For PL trait, where one measurement per petal was obtained (five petals per flower), the average per flower was calculated in order to perform the GLM. For each GLM, Type III analysis of variance (ANOVA) was used to determine statistical differences among population. In instances where statistically significant differences were detected, Tukey's post hoc test were conducted (Limón et al. 2016; Gutiérrez-Lozano et al. 2021). These analyses were performed using the glm2 v. 1.2.1 (Marschner 2011), car v. 3.1–2 (Fox and Weisberg 2019) and multcomp v. 1.4–26 (Hothorn et al. 2008) packages in R Core Team v. 4.4.1 (R Core Team 2024).

To determine the association between quantitative traits of flowers and leaves, a correlation analysis was conducted using Spearman's correlation coefficient in the R package correlation v. 0.8.5 (Makowski et al. 2020; Javid et al. 2024). Furthermore, a principal factor analysis was conducted on the quantitative traits of flowers and leaves using JMP Pro 18.0.2 (https://www.jmp.com/es_mx/home.html) with the aim of reducing dimensionality. The factors were obtained through the maximum likelihood algorithm and the number of retained factors was determined by $\chi 2$ tests (Domínguez et al. 1988). Nested ANOVAs were performed on the factor scores retained from the principal factor analysis to partition the total variation of flowers and leaves. The factor scores were divided into levels: differences between populations, differences between individuals within populations, and differences between flowers/leaves within individuals (with this last level used as the error term) (Domínguez et al. 1988). Population and individual variables were randomly assigned in nested ANOVAs (Domínguez et al. 1988). These analyses were performed in JMP Pro 18.0.2.

Soil measurements: pH and electrical conductivity (EC).

Soil salinity negatively impacts cotton growth and yield; therefore, salinity tolerance could be advantageous for cultivated cotton (Mammadov et al. 2018). To determine whether *G. turneri* plants grow in saline soils and are likely tolerant to salinity, soil samples were collected from each population for analysis of pH and electrical conductivity. Five soil samples per population were collected at a depth of 20 cm under the canopy of five randomly selected plants. The samples were sieved through 2 mm, 1 mm, and 500 µm sieves to separate and measure soil fractions. Subsequently, 3 g of the fine fraction soil sample (particles smaller than 500 µm in diameter) was weighed into 50 mL Falcon tubes, and 50 mL of distilled water was added. The samples were shaken for 18 h, followed by a 1-h resting period and centrifugation at 2000 rpm for 1 min (Hernández Quiroz 2012). The pH and electrical conductivity (EC) were then measured using a Laqua pH/ION/COND meter F-74BW (HORIBA Scientific) to assess the salinity of the soil.

Results

Phenotypic variation of flowers and leaves

The CV revealed a considerable degree of variability in the evaluated traits for *G. turneri*, ranging from 0.00% to 40.31% for flowers (Table S2) and 0.00% to 55.33% for leaves (Table S3). Among the quantitative attributes in flowers, H exhibited the greatest variability (CV = 40.07%), whereas GL showed the lowest variability (CV = 15.35%) (Fig. 4a). In contrast, for qualitative traits in flowers, attributes related to color (PC and SC) exhibited the greatest variability (Fig. 4b, Table S2). Moreover, PC color codes (Table S1) identified in the RHS Color Chart indicate that flower petals exhibited tones of yellow, while SC color codes (Table S1) show that petal spots displayed tones of orange. Traits associated with gossypol glands in different flower structures (GGP, GGS, and GGC) showed the lowest variability, with CV values below 10% (Fig. 4b, Table S2). Flower bracts (B) and pollen in anthers (PA) at anthesis showed CV values of 35.09% and 13.46% respectively, indicating that plants of *G. turneri* exhibit flowers with and without bracts and anthers with and without pollen.

For the quantitative attributes evaluated in leaves, LA showed the greatest variability (CV = 55.33%), whereas LW showed the lowest variability (CV = 28.12%) (Fig. 4a). Regarding qualitative traits

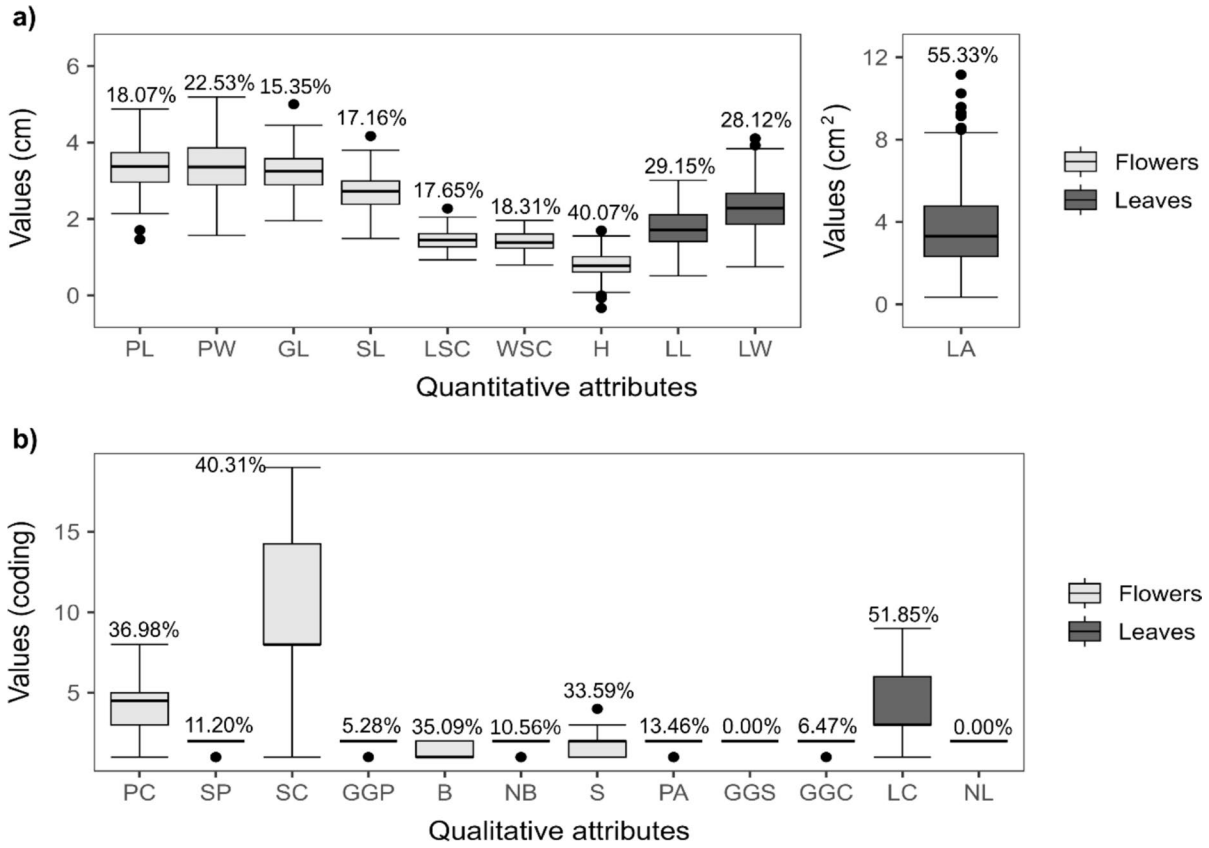


Fig. 4 Box plots of measured attributes in flowers and leaves of *Gossypium turneri*: **a** quantitative traits and **b** qualitative traits. The coefficient of variation (CV in %) is displayed above each attribute. The abbreviations used for the traits are provided in Table 1

in leaves, LC exhibited greater variability, while NL showed less variability as indicated by their respective CV values (Fig. 4b, Table S3). For LC, color codes from the RHS Color Chart (Table S1) show that leaves exhibited green tones. As for leaf nectaries (NL), all evaluated leaves had a nectary located along the primary vein on the adaxial side.

Phenotypic variation among population.

The results of the GLMs and ANOVAs revealed highly significant differences for all quantitative attributes, except for PL and LSC, among the populations ($\chi 2 = 3.70$ to 104.77, $p < 0.02$) (Fig. 5) indicating a consistent inter-population variation in phenotypic traits of flowers and leaves of *G. turneri*.

Descriptive statistics and multiple comparisons among populations revealed that the El Mirador population exhibited the greatest values for PW, GL, SL, and H (Fig. 5b, 5c, 5d, 5g), followed by La Manga and Roca El Choyudo (Table S2). This suggests that flowers of El Mirador were larger, while in Roca El Choyudo, flowers were smaller. Similarly, LL, LW, and LA values (Fig. 5h, 5i, 5j) were higher in El Mirador, followed by La Manga and Roca El Choyudo (Table S3), indicating that leaves from El Mirador were larger, and smaller at Roca El Choyudo.

Although La Manga population did not show significant differences in quantitative attributes compared to El Mirador, a distinct latitudinal pattern was observed when the data were analyzed along with the descriptive statistics (Table S2, Table S3). This pattern suggests a consistent decline in the size of flowers and leaves, with the southernmost population (El Mirador) displaying the largest flowers and leaves and the northernmost population (Roca El Choyudo) exhibiting the smallest.

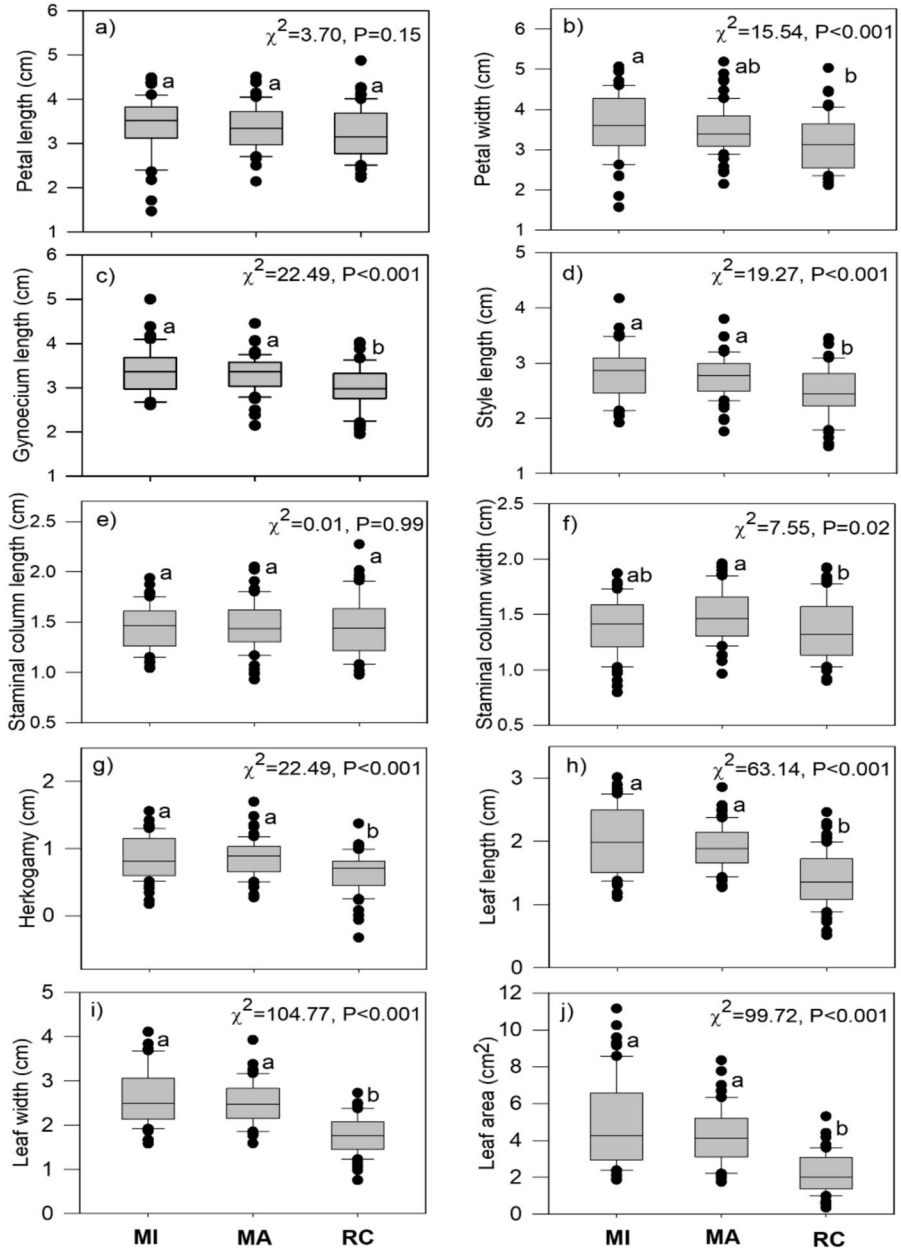


Fig. 5 Box plots of quantitative attributes evaluated in flowers and leaves of *Gossypium turneri* in the three populations (MI: El Mirador, MA: La Manga, and RC: Roca El Choyudo): **a** petal length, **b** petal width, **c** gynoecium length, **d** style length, **e** staminal column length, **f** staminal column width, **g** herkogamy, **h** leaf length, **i** leaf width and **j** leaf area. Likelihood ratio chi-square test results are in the upper right corner of each box plot. Box plots with different letters indicate significant differences using Tukey Contrasts tests

Correlation between attributes.

A positive and significant correlation was observed among all quantitative traits evaluated in flowers and leaves of *G. turneri* (Fig. 6), with correlation coefficients ranging from r = 0.15 to 1.00 ($p < 0.001$). Higher correlations were observed within flower and leaf traits than between flower and leaf attributes (Fig. 6). Correlations among leaf traits (LL, LW, and LA) ranged from 0.92 to 0.99, while correlations among flower traits (PL, PW, GL, SL, LSC, and WSC) ranged from 0.60 to 0.99. In contrast, correlations between flower and leaf traits were lower (r = 0.31 to 0.40) (Fig. 6). For H, correlations varied from 0.15 (LSC) to 0.77 (SL).

The phenotypic variation observed in flowers and leaves of *G. turneri* was attributed to three factors ($\chi 2 = 67.69$, $p < 0.001$), collectively accounting for 85.9% of the cumulative variance. The first factor accounted for 29.03% of the variance, followed by

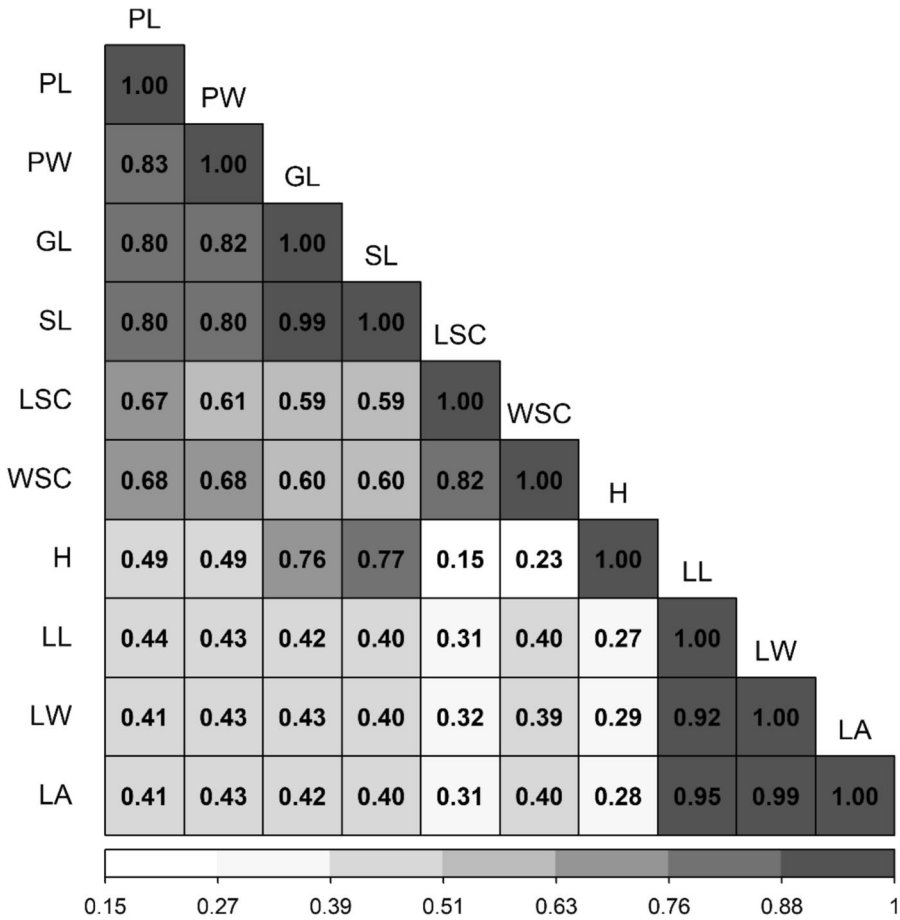


Fig. 6 Spearman's correlations between quantitative attributes of flowers and leaves of *Gossypium turneri*. The abbreviations used for the traits are provided in Table 1

the second factor with 28.91%, and the third factor with 27.96%. All factor loadings, which represent the correlation between the traits and the factors, were positive. Traits evaluated on leaves, LL, LA and LW, exhibited high factor loadings on factor 1. Likewise, attributes measured on flowers, LSC, WSC, PL and PW, showed high correlation on factor 2. While H, SL and GL, had high factor loadings on factor 3 (Table 2).

Table 2 Factor loadings of the quantitative traits evaluated in flowers and leaves of *Gossypium turneri* for each factor derived from the principal factor analysis

Attributes	Factor 1	Factor 2	Factor 3
LW	0.96	0.16	0.15
LA	0.96	0.17	0.14
LL	0.88	0.21	0.17
LSC	0.12	0.86	0.13
WSC	0.21	0.82	0.16
PL	0.19	0.67	0.49
PW	0.24	0.62	0.51
H	0.12	0.02	0.87
SL	0.18	0.50	0.84
GL	0.21	0.49	0.82

Attribute abbreviations are detailed in Table 1

Principal factor analysis

The nested ANOVAs, based on the scores for each factor, indicated that the population and/or individual levels account for a significant proportion of the total variation in flower and leaf traits of *G. turneri* (Table 3). For factor 1, the greatest proportion of variance was explained by differences among individuals within populations, followed by the differences between populations (Table 3). Regarding factor 2, the difference among individuals within populations was found to account for a

Table 3 Percentage of variation exhibited at the population and individual level for each factor for the traits evaluated in flowers and leaves of *Gossypium turneri*

Source of variation	Variance component (%)	F	*p* value
Factor 1			
Population	37.86	16.20	< 0.001
Individual (Population)	43.57	8.00	< 0.001
Flower/leaf (Individual, Population)	18.56		
Total	100		
Factor 2			
Population	-2.58	0.27	0.760
Individual (Population)	55.36	4.49	< 0.001
Flower/leaf (Individual, Population)	47.21		
Total	100		
Factor 3			
Population	9.85	4.14	0.020
Individual (Population)	48.64	4.49	< 0.001
Flower/leaf (Individual, Population)	41.50		
Total	100		

The percentages of variation were calculated based on the scores of factors 1, 2, and 3, as identified through principal factor analysis

significant proportion of the variance, amounting to 55.36%. However, the difference between populations did not explain a significant proportion of the variance for factor 2. Similarly, for factor 3, a greater portion of the variance was accounted by differences among individuals within populations and only a small proportion between populations (Table 3).

Soil salinity

Soil fraction measurements indicate that individuals of *G. turneri* from El Mirador are found in soils with a greater fraction of particles larger than 2 mm (Table 4). In contrast, individuals of La Manga and Roca El Choyudo are found in soils with finer particles (Table 4). The pH and EC values exhibited a range from 7.07 ± 0.24 to 7.39 ± 0.56 and 0.15 ± 0.03 to 0.27 ± 0.09, respectively, among populations of *G. turneri*.

Discussion

Patterns of phenotypic variation within and among populations.

Factor analysis of phenotypic variation in *G. turneri* shows that most leaf and flower trait variation occur within populations, with only a small portion between populations (Table 3). This pattern aligns with the species' restricted distribution, spanning a coastal area of less than 15 km, where abiotic factors like rainfall and temperature likely exhibit minimal variation. Additionally, this pattern of phenotypic variation is consistent with the moderate genetic differentiation (F_{ST}) observed among populations based on 46,770 SNPs (Yescas-Romo et al. submitted).

Leaf traits showed a strong correlation with factor 1, with individual and population levels accounting for a significant proportion of the variation (Table 3). Leaf traits (LL, LW and LA) showed a consistent spatial decline in size along populations (Fig. 5h, 5i, 5j), most likely due to differences in seasonal rainfall. Data from a network of meteorological stations (CESAVE-SIAFESON 2024b, Fig. S3) indicate a

Table 4 Soil parameters (particle size, pH and EC) in samples of *Gossypium turneri* from the three populations

Soil parameters	Population		
	El Mirador	La Manga	Roca El Choyudo
	Mean ± SD	Mean ± SD	Mean ± SD
Particles greater than 2 mm diameter (%)	60.00 ± 13.66	27.82 ± 7.14	17.87 ± 7.18
Particles greater than 1 mm diameter (%)	12.69 ± 3.71	21.08 ± 1.23	23.02 ± 2.96
Particles greater than 500 µm diameter (%)	10.31 ± 2.46	19.40 ± 3.45	27.15 ± 3.26
Particles less than 500 µm diameter (%)	18.30 ± 7.11	31.21 ± 3.29	32.51 ± 7.63
pH	7.07 ± 0.24	7.39 ± 0.56	7.27 ± 0.36
EC (dS/m)	0.27 ± 0.09	0.15 ± 0.03	0.16 ± 0.06

SD: standard deviation, mm: millimeter, %: percentage, EC: electrical conductivity, dS/m: deciSiemens per meter

decrease in rainfall along the distribution range of the studied populations during the previous month when leaves were collected. Thus, it is possible that such interpopulation differences in leaf size are due to variation in rainfall among populations. Unfortunately, reliable rainfall records for the three populations are not available for the purpose of evaluating the correlation with foliar traits, which limits the ability to make robust inferences. However, this decline in leaf size is consistent with what is known about population divergence for leaf traits: phenotypic variation is more dependent on variation on the abiotic environment (Opedal et al. 2022). In the Sonoran Desert, leaf size depends among other factors on rainfall (Molina-Freaner et al. 2004). Therefore, the observed differences in leaf traits among *G. turneri* populations probably reflect a response to rainfall variation across their range.

Flower traits showed a high correlation with factors 2 and 3, with most of the phenotypic variation attributed to differences among individuals, while differences between populations were either non-significant or contributed only a small fraction of the variation (Table 3). The divergence of floral traits among populations likely depends on the degree to which pollinators vary across the species' distribution (Opedal et al. 2022). Pollinators of *G. turneri* include native bees and butterflies (Yescas-Romo et al. 2024), which, despite their limited mobility, have similar composition across populations (Yescas-Romo, personal observation). Therefore, the limited phenotypic variation in flower traits is likely due to the similarity in pollinators among populations. Nevertheless, subsequent research should employ quantitative analysis to evaluate whether pollinator composition exhibits minimal variation among populations that could explain the slight interpopulation variation in flower traits.

Traits of agronomic interest.

A key trait in *G. turneri* with potential relevance for the improvement of cultivated cotton is the presence of deciduous bracts at anthesis (Chen et al. 2018; Shim et al. 2018). This trait is shared by other species in the subsection Caducibracteolata, such as *G. harknessii* and *G. armourianum*, both members of the subgenus Houzingenia like *G. turneri* (Fryxel 1978; Fryxell 1992; Hu et al. 2021). However, during this study, it was observed that out of 180 flowers analyzed, 103 had bracts at anthesis, while 77 lacked bracts. The presence of persistent bracts in open flowers is inconsistent with the current classification of *G. turneri* within Caducibracteolata, suggesting that this trait may be polymorphic in the species. Given the polymorphic nature of this trait, *G. turneri* might represent an important genetic resource where the underlying genetic basis responsible for this polymorphism could be identified, offering an opportunity for cotton crop improvement.

Moreover, 13 of the analyzed flowers were found to lack pollen in their anthers (Fig. S1f). Most flowers without pollen belonged to the same individual where they were collected, suggesting that those plants may exhibit male sterility. Male sterility is important in crop improvement because it prevents self-pollination in self-fertilizing plants while allowing intercrossing with male-fertile plants. This enables heterosis, leading to the production of hybrid seeds (Farinati et al. 2023). Heterosis can be expressed in various ways as increased plant growth, yield, and resistance to biotic and abiotic stressors, all critical traits for crop improvement (Islam et al. 2014). In the genus *Gossypium*, male sterility has been documented in species like *G. harknessii* (Meyer 1975), the sister species of *G. turneri* (Grover et al. 2019). Although this study suggests possible male sterility in *G. turneri*, further research is necessary to determine if this trait is heritable and whether it could be leveraged for the improvement of cultivated cotton.

Leaf size of *G. turneri* (Fig. 5h, 5i, 5j), together with other desert species of the subsection Caducibracteolata (Alaves et al. 2023) is probably the smallest among members of the genus *Gossypium*. Although small leaf size is not necessarily a desired trait in cotton improvement, the physiological mechanisms (Kaur et al. 2023, Lei et al. 2023) that enable xeromorphic wild cottons to withstand water and heat stress could be highly valuable for adapting cultivated cotton to future climate change scenarios (Verma et al. 2024). Leaf traits such as a thick cuticle and a double palisade layer (Hu et al. 2021), along with other attributes that may be adaptive in arid environments, could prove critical in species like *G. turneri*. Therefore, future research should focus on evaluating the traits and mechanisms that enable *G. turneri* to tolerate water and heat stress, assessing its potential role in the improvement of cultivated cotton.

Another trait of interest for cotton crop improvement is salinity tolerance. In cotton, it has

been documented that salinity negatively affects different growth stages such as germination, seedling stage, flowering and bud development, among others; therefore, salinity tolerance is important in this crop (Dong et al. 2020; Sharif et al. 2019). Soil salinity is one of the major threats to crop productivity, expected to impact a significant portion of arable land, characterized by an accumulation of excess ions with an EC higher than 4 dS/m (Butcher et al. 2016). Soil salinization can be attributed to either natural or anthropogenic causes, a process that can be common in drylands (Stavi et al. 2021). *G. turneri*, adapted to the coastal environment of Guaymas, has been previously considered salt-tolerant (Ulloa 2014). However, soil samples collected along its distribution range revealed EC values between 0.15 and 0.27 dS/m, indicating that the soil is not saline. While *G. turneri* does not grow in saline soils, individuals have been observed near the ocean in coastal areas (Fig. S4), raising the possibility of exposure to coastal salt spray (Yescas-Romo, personal observation). Therefore, it remains plausible that *G. turneri* is salinity tolerant. Further investigations with experimental trials are needed to determine its true salinity tolerance (Dong et al. 2020).

Conclusion

Phenotypic variation in leaf and flower traits of *G. turneri* was primarily distributed among individuals within populations, with a smaller portion occurring between populations, most likely due to the species' restricted distribution. Interpopulation differences in leaf traits were probably due to local variations in rainfall whereas the limited interpopulation variation in flower traits was likely due to the similarity in pollinator composition. Several traits of agronomic interest for cotton improvement were identified, such as polymorphisms in flower bracts and anthers with and without pollen. This desert-adapted wild cotton exhibits small leaves that could be valuable for the adaptation of cultivated cotton to arid environments.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflicts of interest The authors declare no competing interests.

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