

TESTING THE BERG HYPOTHESIS IN THE LONG-LIVED ROSETTE PLANT *HESPEROYUCCA WHIPPLEI*

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Abstract

Background: Variation in floral and vegetative traits and their degree of covariation can provide insights into the roles of abiotic and biotic selective forces acting on different plant modules. According to the Berg hypothesis, floral traits in species with specialized pollination systems are expected to exhibit low phenotypic variation and weak correlations with vegetative traits.

Question: We tested if floral traits exhibit lower variability than vegetative traits and if floral and vegetative traits are phenotypically decoupled.

Species: *Hesperoyucca whipplei* (Torr.) Baker ex Trel. (Asparagaceae) is a semelparous monocot with an obligate pollination mutualism.

Study sites and dates: between 2022 and 2024, we visited 16 locations throughout the range of *H. whipplei* in the Baja California Peninsula.

Methods: We measured four vegetative and nine reproductive traits in 202 individuals across 16 locations. Trait variation and covariation were assessed using coefficients of variation and principal component analysis. Pearson correlations were used to test for within- and between-module trait correlations.

Results: Floral traits showed lower coefficients of variation (11-25 %) than vegetative traits (21-31 %), supporting predictions of Berg hypothesis. Principal component and correlation analyses revealed strong within-module correlations and weak correlations between floral and vegetative traits, suggesting phenotypic modularity.

Conclusions: Our results support the Berg hypothesis and suggest that floral and vegetative traits in *H. whipplei* are decoupled. This modularity reflects divergent selective regimes: floral traits shaped by pollinator specialization and vegetative traits shaped by environmental heterogeneity. Such decoupling may promote adaptive flexibility within modules in long-lived species with obligate mutualisms.

Keywords: floral-vegetative decoupling, phenotypic covariation, specialized pollination system

Resumen

Antecedentes: La variación y covariación de rasgos florales y vegetativos puede proporcionar información sobre el papel de fuerzas selectivas bióticas y abióticas que actúan sobre diferentes módulos de la planta. Según la hipótesis de Berg, los rasgos florales en especies con sistemas de polinización especializados presentan baja variación fenotípica y correlaciones débiles con los rasgos vegetativos.

Pregunta: Evaluamos si los rasgos florales presentan menor variabilidad que los vegetativos y si ambos módulos están fenotípicamente desacoplados.

Especie: *Hesperoyucca whipplei* (Torr.) Baker ex Trel. (Asparagaceae) es una monocotiledónea semélpara con un mutualismo de polinización obligado.

Sitios y fechas del estudio: Entre 2022 y 2024 visitamos 16 localidades a lo largo de la distribución de *H. whipplei* en la Península de Baja California.

Métodos: Medimos cuatro caracteres vegetativos y nueve reproductivos en 202 individuos. La variación y covariación de caracteres se evaluaron mediante coeficientes de variación y análisis de componentes principales. Las correlaciones de Pearson se utilizaron para evaluar correlaciones dentro y entre módulos.

Resultados: Los rasgos florales mostraron coeficientes de variación menores (11–25 %) que los vegetativos (21–31 %), respaldando las predicciones de la hipótesis de Berg. Los análisis de componentes principales y de correlación revelaron fuertes correlaciones dentro de los módulos y correlaciones débiles entre rasgos florales y vegetativos, sugiriendo modularidad fenotípica.

Conclusiones: Nuestros resultados respaldan la hipótesis de Berg y sugieren que los rasgos florales y vegetativos en *H. whipplei* están desacoplados. Esta modularidad refleja regímenes selectivos divergentes: los rasgos florales determinados por la especialización de los polinizadores y los vegetativos por la heterogeneidad ambiental.

Palabras clave: disociación floral-vegetativa, covariación fenotípica, sistema de polinización obligado

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Plant phenotypic variation is a ubiquitous component of biodiversity in terrestrial ecosystems and is intimately linked to the evolutionary potential of species (Futuyma 2007). This variation encompasses the wide range of morphological, physiological, and developmental traits observed among individuals within and between populations of the same species (Kalisz & Kramer 2008). In plants, phenotypic variation largely depends on standing genetic variation, the genetic architecture underlying that variation (Mitchell-Olds & Schmitt 2006), and on environmental factors that vary across a species' geographic range (Arteaga *et al.* 2015, Alcántara-Ayala *et al.* 2020, Li *et al.* 2021). The form and function of vegetative organs, such as leaves and stems, are strongly shaped by biotic and abiotic conditions (Wang *et al.* 2022). In contrast, reproductive traits, particularly floral characteristics, are mainly influenced by interactions with pollination vectors, either biotic (animals) or abiotic (wind, water) factors (Elle 2004, Rosas-Guerrero *et al.* 2014, Armbruster & Wege 2019). These functional differences contribute to the evolution of phenotypic modules that respond to distinct selective regimes.

A useful framework for understanding phenotypic complexity in plants is through the analysis of variation and covariation within and between functional or developmental units (Berg 1959, 1960). In this context, Berg (1959) proposed that in species with specialized pollination systems, floral traits experience stabilizing selection that reduces their variation (*e.g.*, low coefficients of variation). Based on this idea, Berg (1960) later proposed the *correlation pleiades* hypothesis, which suggests that floral traits animal pollinated plants become developmentally and functionally decoupled from vegetative traits. This decoupling results in strong correlations among floral traits, and weaker correlations between floral and vegetative traits forming quasi-independent modules—defined as sets of traits that covary more strongly within than between groups (Mitteroecker & Bookstein 2007). While floral traits evolve under stabilizing selection that matches pollinator morphology and behavior (Armbruster *et al.* 1999, Reich *et al.* 2020), vegetative traits remain more responsive to environmental heterogeneity and thus exhibit higher levels of phenotypic variation. This modular independence is thought to optimize plant responses to distinct selective pressures acting on different parts of the organism.

Differences in the levels of variation between vegetative and floral modules are expected to depend on pollinator specificity, the type and intensity of selection acting on floral traits, and the capacity of the vegetative phenotype to respond to variable abiotic conditions (Berg 1960). For instance, low variation in floral traits can result in those traits having coevolved with insects that enhances reproductive success by ensuring effective pollen deposition on the stigma (Solís-Montero & Vallejo-Marín 2017, Armbruster & Wege 2019), indicating that pollinators primarily influence patterns of variation and covariation in animal-pollinated flowers (Stebbins 1970, Rosas-Guerrero *et al.* 2011). In contrast, vegetative organs such as leaves, stems, and roots typically exhibit greater phenotypic variability (Conner & Lande 2014).

In addition to the imprinting of selective pressures, differences in phenotypic variation among vegetative, inflorescence, and floral traits may also reflect their distinct functional roles within the plant and their contrasting developmental timing and lifespan (Nobel 1977, 1987, Mitteroecker & Bookstein 2007, Conner & Lande 2014). Vegetative traits, which are primarily involved in resource acquisition and storage, develop over multiple years, and are therefore exposed to interannual environmental variation, which may contribute to increased phenotypic variability. In contrast, inflorescence structures function in the support and display of reproductive organs, while floral traits are directly associated with reproduction and pollination; both develop over shorter time scales and are therefore exposed to more temporally restricted conditions, which may constrain their phenotypic variation.

Although empirical evidence supports the predictions of the Berg hypothesis (Conner & Lande 2014), most studies examined herbaceous plants with relatively short life cycles. In contrast, to our knowledge, no studies have examined semelparous long-lived species with specialized pollination systems. The main objective of this study was to evaluate patterns of phenotypic variation and trait correlations among vegetative, inflorescence, and floral modules in the rosette-forming monocot *Hesperoyucca whipplei* (Torr.) Baker ex Trel. (Asparagaceae), which maintains an obligate mutualism with its pollinator *Tegeticula maculata* (Powell & Mackie 1966). Specifically, we examined whether: (1) floral traits exhibit lower phenotypic variability than vegetative traits, consistent with Berg hypothesis and reduced sensitivity to environmental variation; and (2) floral and vegetative traits are phenotypically decoupled, with weak or

no correlations between modules, allowing independent responses to environmental conditions. Given this specialized interaction, we hypothesized that floral traits would show reduced phenotypic variation relative to vegetative traits, and that correlations between floral and vegetative traits would be weak. Our study contributes to a broader understanding of how phenotypic variation and modularity influence the evolutionary potential of plants.

Material and methods

Study system. *Hesperoyucca whipplei* (Torr.) Baker ex Trel. (Asparagaceae) is a long-lived monocot native to the region extending from the northwest of the Baja California peninsula in Mexico to southwestern and southeastern California, USA (Hodgson 2020a). The genus *Hesperoyucca* comprises two additional species distributed in western North America, *H. newberryi* and *H. peninsularis*, and all the three species exhibit an allopatric distribution (Clary 2001, Hodgson 2020b, Hodgson & Salywon 2022).

Hesperoyucca whipplei populations occur between 300 and 2,500 meters above sea level in diverse habitats including chaparral, coastal shrubland, and rosette shrub communities (Udovic 1981, Aker 1982, Clary 2001). Individuals from Baja California populations exhibit a unique rosette composed of numerous rigids, linear or spear-like leaves (Matuda & Piña-Luján 1980). During its vegetative phase, it enlarges by producing new leaves over several years, accumulating substantial leaf biomass prior to reproduction. After several years of growth, the plant produces a single robust inflorescence stalk that can reach 2 to 4 meters in height (Haines 1941). The numerous flowers are arranged in a terminal panicle. Fruits are capsules that remain attached to the floral stalk and disperse seeds by gravity. Individual rosettes die after completing reproduction. *H. whipplei* has a highly specialized pollination system, relying exclusively on the moth *Tegeticula maculata* (Prodoxidae) for fertilization (Segraves & Pellmyr 2001). Female moths insert their eggs into the ovary of open flowers, and then actively deposit pollen in the same flowers to pollinate. The larvae hatch out inside the fruits and consume developing seeds (Powell & Mackie 1966, Aker 1982).

Phenotypic measurements. This study was conducted in 16 localities representing the full distributional range of *Hesperoyucca whipplei* in Baja California, Mexico (Figure 1), and we measured a total of 202 plants. Of these, 115 individuals (57 %) had inflorescences and 97 plants had mature flowers. The other 18 individuals were in bud or had

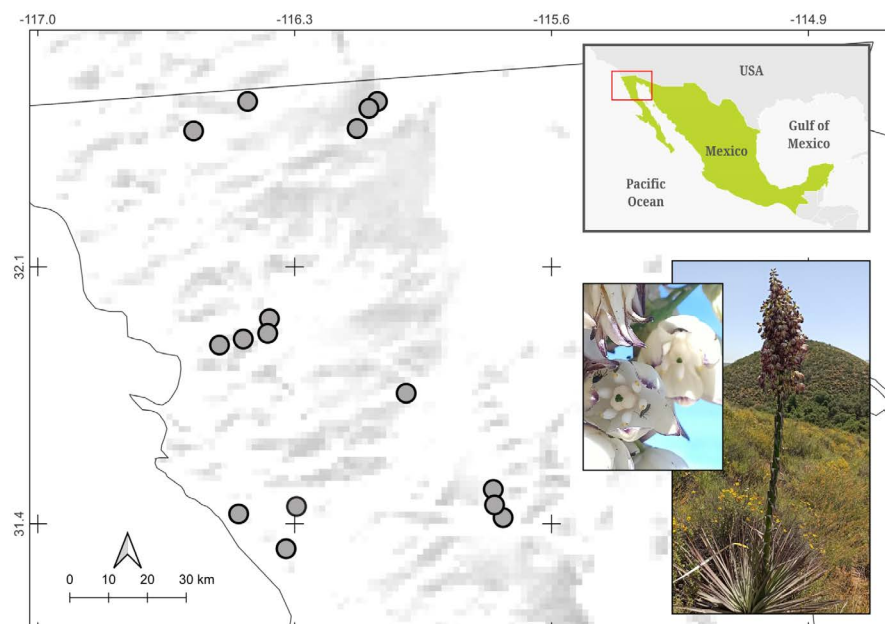


Figure 1. Geographic location of *Hesperoyucca whipplei* sites sampled across the Baja California Peninsula, Mexico.

aborted flowers. The four vegetative traits measured included length and width of one leaf, and diameter and height of the rosette (N = 202). Only non-reproductive plants that matched the size of flowering individuals were included for comparison. Reproductive traits included four features of the single inflorescence (total plant height, stem circumference, panicle width, and panicle height; N = 115) and five floral characteristics (internal and external tepal length and width, pistil length and width, and filament length; N = 97; [Figure 2](#)). Five mature, fully opened flowers per plant were sampled to avoid variation due to floral development, resulting in a total of 392 flowers from 97 plants (mean $\pm$ SD = 4.0 $\pm$ 0.9 flowers per plant). Floral traits were measured using digital calipers ($\pm$ 0.01 mm).

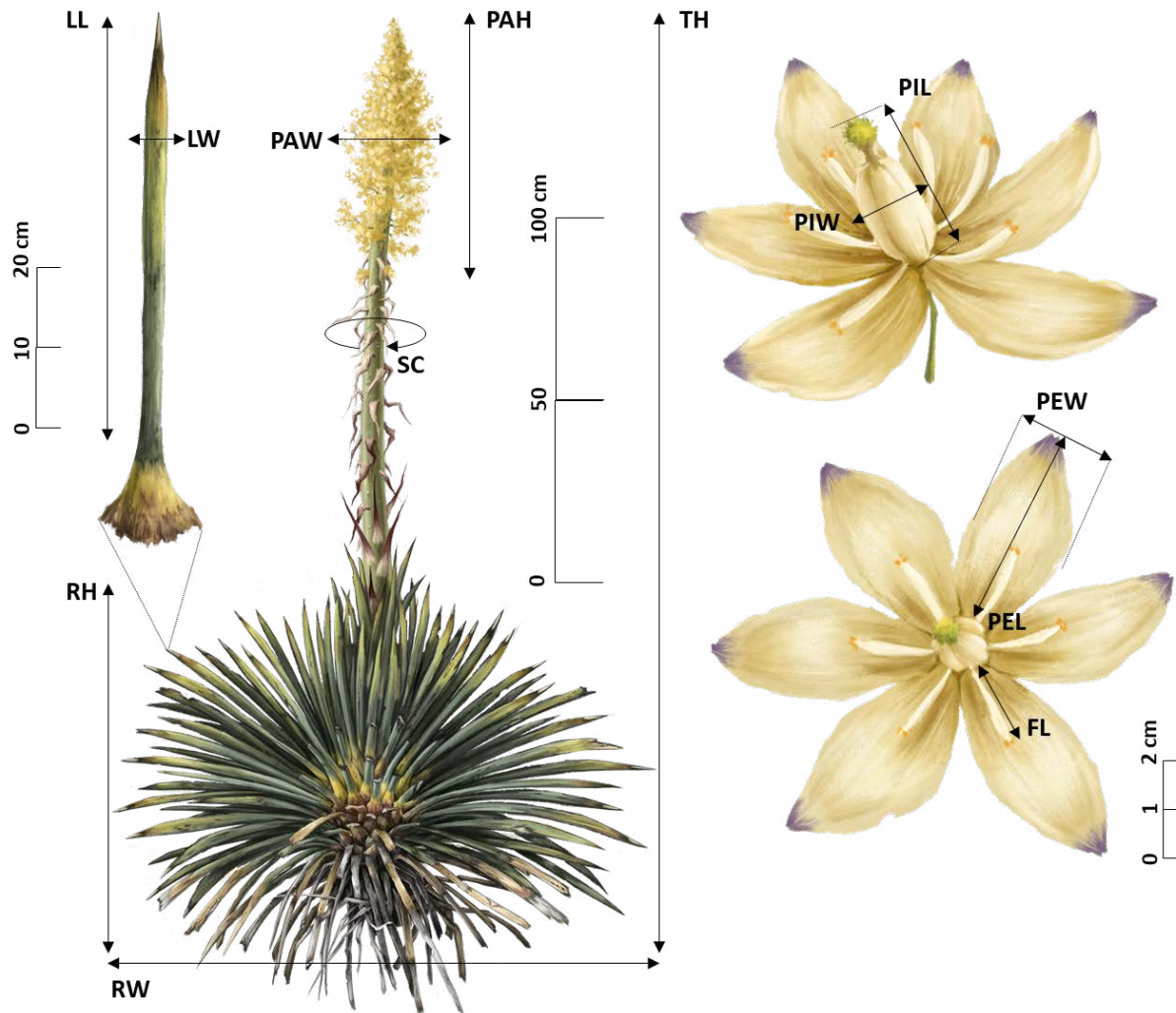


Figure 2. Diagram of vegetative and reproductive traits measured in *Hesperoyucca whipplei*. Vegetative traits: leaf length (LL), leaf width (LW), rosette height (RH), and rosette width (RW). Inflorescence traits: total plant height (TH), panicle height (PAH), panicle width (PAW), and stem circumference (SC). Floral traits: petal width (PEW), petal length (PEL), filament length (FL), pistil length (PIL), and pistil width (PIW). Illustration by Cullen Townsend (2020).

Statistical analyses. Statistical analyses were conducted pooling data of plants from all localities because the objective was to obtain estimates at species level. In addition, the reduced and unbalanced number of plants per locality does not allow estimate and compare correlations amongst localities. To quantify phenotypic variation the coefficient of variation ($CV = SD/mean \times 100$) for each trait was estimated. Coefficients of variation (CV) were calculated

separately for each trait using all available individuals per trait category, including vegetative traits ($N = 202$), inflorescence traits ($N = 115$), and floral traits ($N = 97$). For traits measured multiple times per individual (e.g., floral organs), mean values were calculated to represent each plant. For correlation and multivariate analyses (i.e., PCA), only individuals with complete measurements for all trait categories were included ($N = 97$).

To evaluate potential scale effects on relative variation, we assessed whether CV covaried with trait mean across traits using linear regression. No significant relationship was detected ($R^2 = 0.12$, $P = 0.24$). Standard deviations scaled linearly with trait means ($R^2 = 0.96$, $P < 0.0001$). These results support the use of CV as a size-standardized descriptor of phenotypic variation (Pélabon *et al.* 2020). In addition, CV was preferred because it captures relative standing variation within traits and allows comparison among traits differing in magnitude, consistent with classical and contemporary applications in studies of the Berg hypothesis (Berg 1959, 1960, *see* Conner & Lande 2014). Coefficients of variation were not subjected to statistical comparison because a single CV value was calculated per trait, and therefore no replication was available to estimate variance for inferential testing.

Principal component analysis (PCA) was conducted using standardized variables (mean = 0, variance = 1), equivalent to a correlation-based PCA. This approach ensures that variables measured on different scales contribute equally to the analysis. Principal components were extracted from the correlation matrix, and the first two components were retained based on explained variance. For visualization, two complementary approaches were used. The main figure presents a correlation-based loading plot, where variable loadings correspond to correlations between traits, and principal components, constrained within the range of -1 to 1. This representation facilitates interpretation of trait–component relationships. Trait relationships were evaluated using Pearson correlation coefficients. All statistical analyses were conducted in JMP 17 (SAS Institute Inc.).

Results

Vegetative and reproductive traits exhibited different coefficients of variation. Vegetative traits ranged from 20–30 %, inflorescence traits from 23–36 %, and floral traits from 11–25 %. Pistil length had the lowest coefficient of variation (11 %), whereas the highest values were observed in inflorescence traits, reaching up to 36 % (Table 1).

The PC1 accounted for 39.5 % of the variance and was primarily associated with vegetative and inflorescence traits, with high positive loadings for rosette height (RH), rosette width (RW), total height (TH), and stem circumference (SC). PC2 explained 20.3 % of the variance and was mainly driven by floral traits, including petal length (PEL), petal width (PEW), and pistil length (PIL), which showed strong positive loadings, whereas vegetative traits exhibited negative loadings on this axis (Table 2). This pattern is consistent with the separation of two modules, one composed by vegetative/inflorescence traits and other with floral features, which is observed in the PCA ordination (Figure 3).

Pearson phenotypic correlation coefficients were generally high and positive among traits within both modules (Figure 4). Vegetative and inflorescence traits showed strong positive correlations ($r = 0.53$ – 0.94), particularly among rosette and leaf traits (e.g., RW–LL, $r = 0.94$; RH–LL, $r = 0.92$) and among inflorescence traits (e.g., TH–PAW, $r = 0.90$; TH–SC, $r = 0.88$). Floral traits also exhibited strong intercorrelations, especially between petal dimensions (PEL–PEW, $r = 0.95$) and between pistil traits (PIW–PIL, $r = 0.72$), as well as between pistil and petal traits (e.g., PIL–PEL, $r = 0.89$; PIL–PEW, $r = 0.83$) (Table 3). In contrast, correlations between vegetative and floral traits were generally weak or negative and non-statistically significant ($r = -0.36$ to 0.17), supporting the modular decoupling hypothesis (Figure 4). Associations between inflorescence and vegetative traits were consistently positive and moderate to strong, whereas their correlations with floral traits were weaker and more variable, indicating that the flower stalk is developmentally and functionally more closely associated with the vegetative module than with the floral module.

Discussion

The Berg hypothesis predicts reduced phenotypic variation in floral traits in species with specialized pollination systems, along with their decoupling from vegetative traits (Berg 1959, 1960). Both attributes, reduced variation,

and decoupling, are commonly interpreted as reflecting the influence of different selective pressures on floral morphology imposed by pollinators, and environmentally driven variation in vegetative traits. As a result, floral and vegetative structures may differ not only in the level of variation, but also in the strength of internal trait correlations, forming phenotypic modules that may be influenced by a combination of selection, developmental processes, and environmental covariance (Murren 2002, Pigliucci 2003).

Table 1. Summary statistics for vegetative, inflorescence, and floral traits measured in *Hesperoyucca whipplei*. N = sample size; Max = maximum value; Min = minimum value; Mean $\pm$ SD = mean $\pm$ standard deviation; CV = coefficient of variation (%). Trait abbreviations and units: RH = rosette height (cm), RW = rosette width (cm), LL = leaf length (cm), LW = leaf width (cm), TH = total height (cm), SC = stalk circumference (cm), PAH = panicle height (cm), PAW = panicle width (cm), PEL = petal length (cm), PEW = petal width (cm), PIW = pistil width (cm), PIL = pistil length (cm), FL = filament length (cm).

		Traits	N	Max	Min	$\bar{x} \pm SE$	CV (%)
Vegetative traits	RH	Rosette height	202	145.5	26	67.47 $\pm$ 1.42	29.96
	RW	Rosette width	202	239	37	116.66 $\pm$ 2.47	30.13
	LL	Leaf length	202	97	24	52.58 $\pm$ 0.99	26.95
	LW	Leaf width	202	3	0.8	1.58 $\pm$ 0.02	20.75
Inflorescence traits	TH	Total height	115	434	152	258.4 $\pm$ 5.59	23.22
	PAH	Panicle height	115	261	32	115.06 $\pm$ 3.9	36.41
	PAW	Panicle width	115	54	17	29.85 $\pm$ 0.78	28.08
	SC	Stem circumference	115	38.5	4.5	17.41 $\pm$ 0.55	34.75
Floral traits	PEL	Petal length	97	6.66	1.82	4.05 $\pm$ 0.10	25.33
	PEW	Petal width	97	2.64	0.72	1.60 $\pm$ 0.03	24.22
	PIW	Pistil width	97	0.97	0.5	0.73 $\pm$ 0.009	12.93
	PIL	Pistil length	97	1.49	0.89	1.18 $\pm$ 0.01	11.31
	FL	Filament length	97	1.6	0.82	1.22 $\pm$ 0.01	14.52

Table 2. Principal component analysis (PCA) of vegetative, inflorescence, and floral traits of *Hesperoyucca whipplei*. Values represent trait loadings (correlation coefficients) on the first two principal components (PC1 and PC2). The percentage of variance explained by each component was PC1 = 39.5 % and PC2 = 20.3 %.

	Trait	PC 1	PC 2
TH	Total height	0.836	-0.49
PAH	Panicle height	0.729	-0.623
PAW	Panicle width	0.777	-0.627
SC	Stem circumference	0.921	-0.278
RH	Rosette height	0.795	-0.658
RW	Rosette width	0.698	-0.484
LL	Leaf length	0.689	-0.518
LW	Leaf width	0.716	-0.660
PEL	Petal length	0.19	0.888
PEW	Petal width	0.286	0.793
PIW	Pistil width	0.575	0.443
PIL	Pistil length	0.225	0.836
FL	Filament length	0.389	0.497

Hesperoyucca whipplei a long-lived plant with obligate pollination by *Tegeticula maculata*, is an ideal model system to test the predictions related with Berg hypothesis, because the co-dependence of plant and pollinator imposes a selective regime that may reduce variation of the traits implicated in the interaction. Consistent with the hypothesis, floral traits involved in pollen transfer (*e.g.*, pistil length and petal size) exhibited lower coefficients of variation (11–25 %) than vegetative traits (21–31 %), supporting the idea that pollinator-mediated selection favors reduced variability (Armbruster *et al.* 1999, Joussetin & Kjellberg 2001). In contrast, vegetative traits such as rosette height and leaf length showed higher variability, likely reflecting plasticity in response to environmental variation. However, this pattern also indicates that functional role alone does not fully explain variation among modules, because inflorescence traits, although associated with reproduction, exhibited higher coefficients of variation than floral traits and were more closely associated with the vegetative module. A more sophisticated study could be designed to examine the interannual variation in morpho-functional traits.

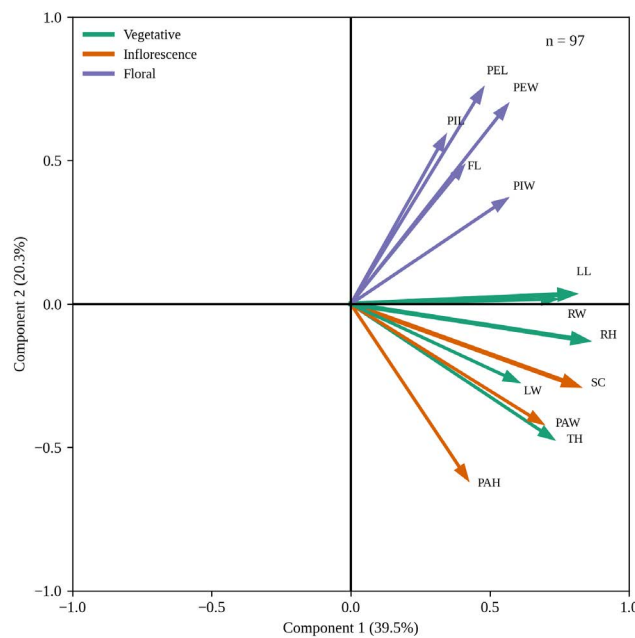


Figure 3. The PCA plot summarizing the major axes of phenotypic variation across *Hesperoyucca whipplei* individuals based on vegetative and reproductive traits. Principal component analysis (PCA) is based on standardized variables (correlation matrix). Vectors represent correlations between traits. Colors indicate trait categories: vegetative (green), inflorescence (orange), and floral (purple). Line thickness is proportional to the magnitude of the loading. Only variables are shown (no individual scores). Sample size: $n = 97$. Vegetative traits: leaf length (LL), leaf width (LW), rosette height (RH), and rosette width (RW). Inflorescence traits: total plant height (TH), panicle height (PAH), panicle width (PAW), and stem circumference (SC). Floral traits: petal width (PEW), petal length (PEL), filament length (FL), pistil length (PIL), and pistil width (PIW).

Phenotypic variation and modularity are associated with evolutionary potential in plants and may contribute to differential responses to selective pressures (Feng *et al.* 2019, Damián *et al.* 2020). In *Hesperoyucca whipplei*, floral and vegetative traits each formed highly correlated modules that may facilitate coordinated responses to specific functional and environmental conditions (Lande & Arnold 1983). Moreover, the correlations between modules were weak, supporting the relative developmental independence of floral and vegetative phenotypes. This pattern is consistent with previous studies reporting low correlations between vegetative and floral modules, particularly in animal pollinated plants (Armbruster *et al.* 1999, Conner & Sterling 1996, Conner & Lande 2014). Although small modifications in floral traits have been documented within the Yucca clade (*e.g.*, Smith *et al.* 2009), these traits may

maintain relatively low levels of phenotypic variation under consistent interactions with their obligate pollinators. In contrast, the vegetative module appears to show greater functional flexibility in response to environmental variation (E-Vojtkó *et al.* 2022). Thus, our results are consistent with Berg's view of reduced correlations between floral and vegetative modules.

Considering the floral module, our results agree with previous studies that report strong correlations among floral traits in species with specialized pollination systems (Rosas-Guerrero *et al.* 2011, Fornoni *et al.* 2016), such as *Hesperoyucca whipplei*. Moreover, in our study, the strongest correlations within the floral module were observed between pistil length and petal size, which may reflect the strength and specificity of the obligate antagonistic and mutualistic interactions with *Tegeticula maculata* (Smith *et al.* 2009). These patterns are consistent with the idea that such interactions may contribute to coordinated variation in floral traits potentially favoring floral sub-modularity, as has been reported in other plants (Diggle 2014).

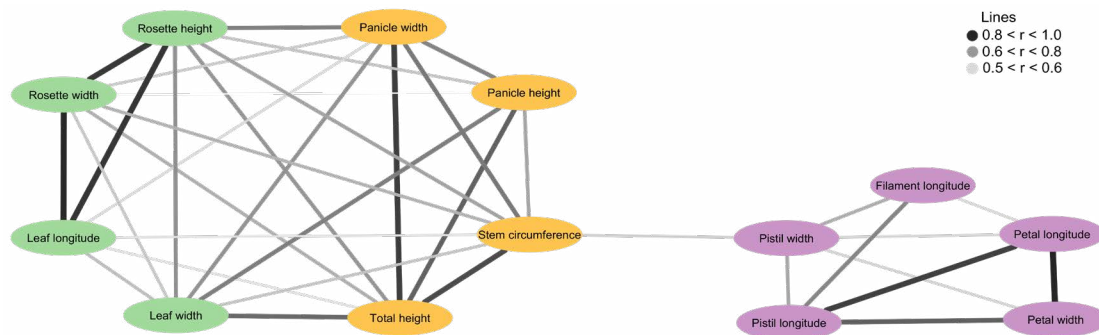


Figure 4. Correlation network among vegetative and reproductive traits in *Hesperoyucca whipplei*. The lines represented only significant correlations ($P < 0.05$) and the thickness represents the magnitude of the correlation coefficients (r), whereas node colors denote trait categories: vegetative, inflorescence and floral.

Table 3. Pearson correlation coefficients (r) among vegetative, inflorescence, and floral traits of *Hesperoyucca whipplei*. Bold values indicate statistically significant correlations ($P < 0.05$) based on pairwise comparisons. Sample size: $n = 97$. Trait abbreviations: TH = total height, SC = stalk circumference, PAH = panicle height, PAW = panicle width, RH = rosette height, RW = rosette width, LL = leaf length, LW = leaf width, PEL = petal length, PEW = petal width, PIW = pistil width, PIL = pistil length, FL = filament length. Significant correlations are visualized in [Figure 4](#).

Trait	TH	SC	PAH	PAW	RH	RW	LL	LW	PEL	PEW	PIW	PIL	FL
TH	1												
SC	0.88	1											
PAH	0.83	0.71	1										
PAW	0.90	0.79	0.77	1									
RH	0.74	0.71	0.65	0.78	1								
RW	0.69	0.68	0.53	0.64	0.92	1							
LL	0.60	0.59	0.46	0.61	0.92	0.94	1						
LW	0.82	0.65	0.79	0.74	0.75	0.64	0.66	1					
PEL	-0.13	0.09	-0.31	-0.27	-0.31	-0.17	-0.23	-0.36	1				
PEW	-0.07	0.13	-0.18	-0.21	-0.23	-0.11	-0.13	-0.21	0.95	1			
PIW	0.40	0.63	0.25	0.12	0.13	0.17	0.06	0.21	0.62	0.63	1		
PIL	0.00	0.21	-0.16	-0.17	-0.33	-0.22	-0.28	-0.34	0.89	0.83	0.72	1	
FL	0.28	0.43	0.14	0.22	-0.02	-0.12	-0.14	0.02	0.60	0.49	0.67	0.77	1

Among the reproductive traits, we included both floral characteristics and inflorescence features. The inflorescence stalk is tightly linked to flowering and is commonly considered reproductive in function, but it may also perform vegetative roles, complicating the distinction (Bazzaz & Reekie 1985). Our results grouped the inflorescence stalk with vegetative traits, a pattern previously reported in other species (Berg 1960). In *Hesperoyucca whipplei*, the stalk originates from the apical meristem and develops from vegetative tissues during the final phase of its life cycle. Studies in other semelparous, long-lived rosette plants have found that stalk elongation is dependent on water and carbon reserves accumulated over the plant's lifetime, as well as on current photosynthesis (Nobel 1977, 1987, McLaughlin *et al.* 2000). This dependence on long-term resource accumulation, together with its structural development from vegetative tissues, may explain the grouping of the stalk within the vegetative module.

Overall, our results agree with the explicit predictions of the Berg hypothesis for plants with specialized pollination systems. Floral traits of *Hesperoyucca whipplei* were less variable and showed strong correlations among traits, forming the floral module. In contrast, vegetative and inflorescence traits were more variable and strongly correlated among themselves. The weak relationship between floral and vegetative traits indicates a modular decoupling, which is consistent with divergent selective regimes acting on both modules (Feng *et al.* 2019). Our study estimates phenotypic correlations and modularity at the species level and does not allow us to partition genetic and environmental components. Given that floral and vegetative traits are known to have genetic bases environmental covariance may nevertheless influence the magnitude of the observed correlations (Winn 2004). A long-term study integrating different genetic families would be necessary to distinguish the influence of genetics from environmental effects. A challenge now is to develop a strategy to demonstrate that vegetative variability is advantageous in this long-lived plant (Villellas *et al.* 2021), to understand the pace of a plastic response in slow-growing plants.

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