

Variation on Floral Traits of *Agave gentryi* (Asparagaceae) along an Elevational Gradient in Tamaulipas, México

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Abstract

Spatio-temporal variation in flower traits was analyzed along an elevational gradient in *Agave gentryi*. Flower measurements were made during the flowering season (May-June) at three sites (2238; 2469; 2618 m.a.s.l.) located in Mi-quihuana, Tamaulipas, México. We hypothesize that a variation pattern is present that is correlated with changes in pollinator composition along the distributional elevation gradient of *Agave gentryi*. We investigated whether differences exist between the elevation gradient between day/night periods in terms of nectar volume and sugar concentration, stamen and pistil length, and corolla diameter. The data were analyzed using discriminant analysis. Floral traits showed significant differences along elevation and just for one side, between day/night periods. As elevation increases, corolla diameter increases, stamen length and nectar volume decrease. *Agave gentryi* shows significant differences in flower traits along this elevational gradient.

Keywords

Agave, Elevation Gradient, Flower Morphology, Sierra Madre Oriental

1. Introduction

Environmental gradients are excellent systems to explore how species and biotic

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communities respond to gradual changes in abiotic factors. Environmental gradients include latitudinal, elevational or aridity gradients. Elevational gradients are considered natural experiments for testing ecological and evolutionary responses of organisms to variation in geophysical factors. Along with elevational gradients, atmospheric pressure, temperature and clear-sky turbidity decrease, and species exhibit a diverse range of physiological and morphological responses [1].

Biotic communities usually exhibit changes along elevational gradients. Plant species richness and diversity usually decline with elevation due to the decreasing importance of herbs, vines and shrubs [2].

Elevation profoundly affects floral traits, forcing plants to adapt to extreme conditions. Altitudinal gradients constitute a robust framework to analyze the variation of functional traits in plants, since they represent consistent climatic contrasts. As the elevation increases there is a decrease in mean temperature and atmospheric pressure and the growing seasons are shorter; these changes in climatic conditions directly affect the morphology, phenology and physiology of species [1] [3]. These patterns make it possible to distinguish the effects of altitude from local site or habitat influences, which are usually more linked to edaphic or microclimatic conditions [4]. Empirical evidence shows that seedling phenology and plasticity in temperature adaptation are predictably adjusted along altitudinal gradients, reinforcing the idea that functional traits respond mainly to large-scale climatic variables [5]. At higher altitudes, flowers tend to be smaller in overall size, but with specific morphological and chromatic adaptations to survive and attract scarce pollinators [6].

For several plant species, elevational changes in flower morphology have been documented as result of changes in abiotic and biotic factors, like temperature and plant-animal interactions [7]. For instance, Devoto *et al.* [8] found that along elevation gradients, pollinators changed from hymenoptera to diptera and from specialist to generalist [9]. When pollinator composition changes along elevation, pollinator services are also modified and flowers respond to these changes [10].

Plants respond to elevational gradients through morphological or physiological changes that allow them to persist in a particular habitat, maximizing their fitness [3] [11]. For reproductive structures, several studies have documented positive responses in flower longevity, flowering time and floral traits while other traits like total number of flowers decline with elevation. In *Phacelia secunda* [12], *Aritolochia chilensis* [13], *Campanula sp.* [14] [15], *Oxalis compacta* [16], and *Rosmarinus officinalis* [17], flower longevity, flowering time and flower size increase with elevation. In contrast, the total number of flowers of *Stylidium armeria* [18] and *Campanula rotundifolia* [15] decreases with elevation. Most of these studies have been carried out in iteroparous plant species with periodic reproduction while very few have been conducted on semelparous species that invest in large floral displays in one final reproductive event [19] [20]. This is the case of rosette plants with semelparous reproduction, which exhibit a reproductive strategy often associated with bat pollination that often produces large inflorescences and flowers that secrete large quantities of nectar and attract a large pollination guild [19].

The genus *Agave* consists of semelparous rosette species endemic to the American continent, and it is represented by approximately 166 species [21]. México is the center of diversity, where nearly 150 species are distributed in its territory, representing around 90% of the genus [22]. Many species produce flowers that open at night and nectar secretion is primarily nocturnal [23]-[27]. Very few species of *Agave* have been studied among environmental gradients. For instance, Silvano-Montellano and Eguiarte [28] studied how flower traits and pollinators change along a latitudinal gradient in northern Mexico. They found that flowers were longer and showed smaller diameters in southern sites and shorter and greater diameters in northern sites. However, no previous study has explored how flower traits vary along elevation in the genus *Agave*. One of the members of this genus is *Agave gentryi*, with a distribution in the Sierra Madre Oriental in México, from 1800 to 3200 meters above sea level. *A. gentryi* represents an excellent system to study how flowers respond to spatial changes along an elevational gradient. In this study, we describe patterns of variation of flower traits in three populations inhabiting an elevation gradient. Particularly, we measure nectar volume, sugar concentration, corolla diameter and lengths of the stamens and pistils.

2. Materials and Methods

2.1. Study Area

The study area is in the northwest region of the Sierra Madre Oriental, in the municipality of Miquihuana, in the state of Tamaulipas, México. In this region, there are mountains with an altitudinal range of 1500 to 3400 meters above sea level [29].

2.2. Sampling Sites

In the Sierra Madre Oriental within the municipality of Miquihuana, Tam., three sampling sites were selected at three altitudinal levels. Site 1 was in a Pinyon Pine Forest (PPF) at coordinates 23°34'45"N & 99°42'50.8"W at an elevation of 2238 m.a.s.l., presenting a temperate semi-dry climate with scarce rainfall all year round (BS1k(x) according to the modified Köppen classification for México), with an average annual temperature of 12°C to 18°C. The second site is in an Oak-Pine Forest (OPF) at 2469 m.a.s.l., at coordinates 23°36'10.6"N & 99°42'37.3"W, this site is in transition zone from temperate semi-dry to temperate sub-humid climates (C(wo)) typical of mixed forests of the Tamaulipas mountain ranges. Site 3 was in a Pine Forest (PF) at an elevation of 2618 m.a.s.l. At coordinates 23°40'44.67" & 99°48'49.69"W, the climate in this site is temperate sub-humid with rainfall in summer (C(wo)) with average annual temperature between 12°C and 18°C, with dry winters and receiving rainfall between April and October [30].

2.3. Experimental Units

In each sampling site, five *gentryi* agaves in bloom were selected, with a separation distance between the individuals of 200 m, then five flower buds were isolated

from the central part of the inflorescence with a nylon bag. *A. gentryi* blooms in June and July [31].

2.4. Study Variables

The attributes that were measured in the flowers were stamen length, pistil length and corolla diameter (Figure 1); nectar volume and concentration of sugars in the nectar. Measurements were made every three hours during the entire anthesis period. A vernier (Autotec, range from 1 to 200 mm) was used for length and diameter measurements. To obtain the nectar, it was extracted from the flower with a syringe of 1 ml volume with graduations every 0.02 ml; all nectar extractions were placed in a glass vial and conserved at ambient temperature. The concentration of sugars in the nectar was measured in °Brix using a field refractometer (Vee Gee model ABT-32).

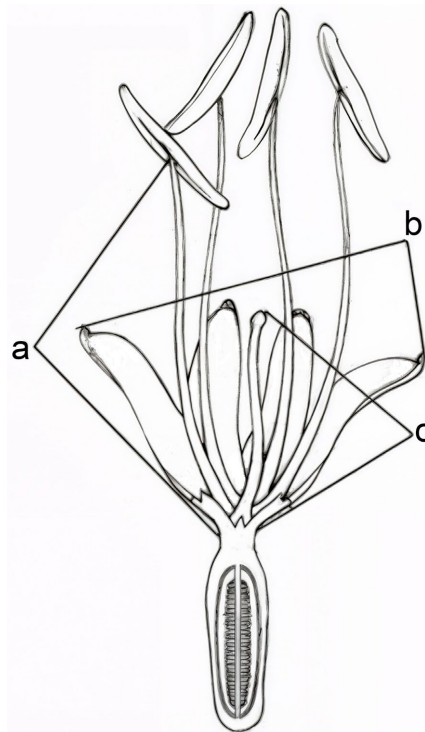


Figure 1. Morphometric floral traits measured (in mm.) in *Agave gentryi* along an elevational gradient: a) stamen length, b) pistil length, c) corolla diameter. Modified from Silva-Montellano and Eguiarte (2003).

2.5. Data Analysis

The mean values and standard deviations for each of the study variables were obtained for the total data and for the day/night periods for each population. The variation between sites and between day/night periods was evaluated by discriminant analysis which maximizes variation between groups and minimizes variation within groups by creating new variables that discriminate groups and identify variables associated with such variation [32]. The data analysis was done using the

statistical software STATISTICA 12 [33] with an alpha value of 0.05, reporting significant roots (successive chi square analysis), eigenvalues, centroid plots of each group as well as the value of Wilk's lambda, if this value are close to 0.0 represent a accurate classification and values close to 1.0 correspond to a erroneous classification.

3. Results

Agave gentryi has an anthesis period that lasts from 4 to 6 days, with protandrous flowers, where stamens grow from 50.5 to 81.2 mm and pistils grow from 44.9 to 70.2 mm. Nectar secretion takes place during both the male and female phases and during the night and the day. The accumulated volume of nectar per flower varies from 1.16 to 2.22 mL (Table 1).

Table 1. Mean (\pm sd) of morphometric and nectar traits along the elevational gradient.

Trait	PPF	OPF	PF
Pistil length (mm)	70.29 \pm 20.38	58.02 \pm 10.9	44.9 \pm 23.6
Stamen length (mm)	81.26 \pm 7.96	68.83 \pm 8.64	50.5 \pm 13.8
Corolla diameter (mm)	11.61 \pm 0.90	10.05 \pm 1.21	13.1 \pm 1.0
Nectar volume (mL)	0.16 \pm 0.12	0.13 \pm 0.05	0.04 \pm 0.02
Sugar concentration ($^{\circ}$ Brix)	13.06 \pm 5.28	15.32 \pm 3.67	5.90 \pm 2.02
Accumulated nectar volume (mL)	2.22 \pm 0.04	1.52 \pm 0.03	1.16 \pm 0.06
Flower longevity (day)	5.6	5.1	4.8

Discriminant analysis of floral traits between sites showed significant differences along the elevation gradient (Wilks' $\lambda = 0.009$, $p < 0.001$). The first root managed to explain 95.4 % of the data, with the variable length of the stamen being the ones that contribute the most to these differences and the second root diameter explains the 4.4 % of the differences with corolla diameter being the ones that contribute the most to these differences (Table 2). The length of the stamen tends to decrease with altitude, while the diameter of the corolla increases.

Table 2. Results from the discriminant function analysis.

Function	Roots 1	Roots 2
Eigenvalues	35.72009	1.638574
Variability (%)	95.38654	4.375631
Variable	Standardized coefficient	
Pistil length	-0.09	-0.37
Stamen length	-0.24	-0.66

Continued

Corolla diameter	0.11	-0.62
Nectar volume	-0.08	-0.18
Sugar concentration	-0.11	0.06

Figure 2 shows the centroids of the six groups. We can see that there are no differences between day and night except for the case of the PPF site ($p = 0.03$), the growth of the corolla and the length of the stamens were greater during the night than during the day at this site.

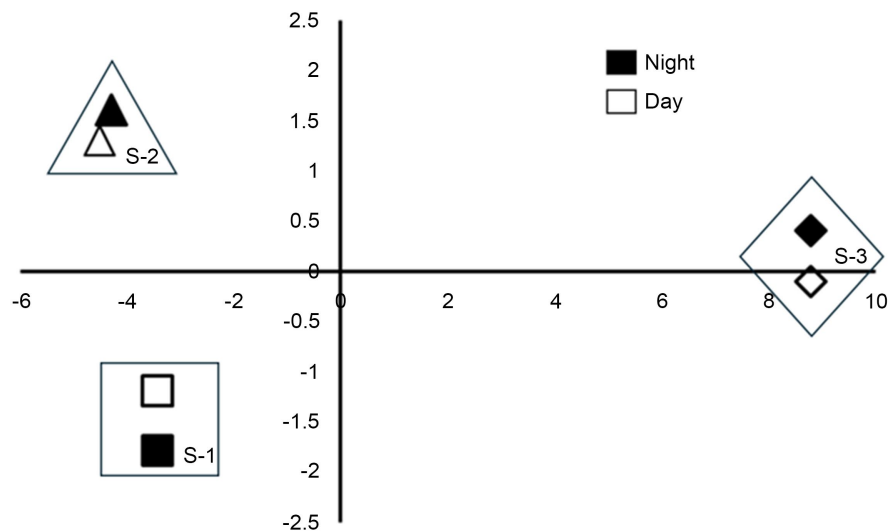


Figure 2. Chart showing centroids of the six groups: square: pinyon pine forest (low elevation site); triangle: oak-pine forest (middle elevation site); diamond: pine forest (high elevation site). Open figures correspond to diurnal and closed figures correspond to night values.

4. Discussion

Studies of elevational gradients have contributed to our understanding of how organisms respond to gradual changes in abiotic factors [1]. Along altitudinal gradients, biotic interactions can also be important for generating local adaptation [34]. The magnitude of the changes observed in altitude, species diversity, functional diversity, and network structure, when they occur simultaneously, indicates that environmental factors influence the functional and phylogenetic diversity of plants and pollinators, thus impacting the configuration of the ecological network [35].

In this study we have shown that *A. gentryi* exhibits significant differences in flower traits along an elevational gradient in the Sierra Madre Oriental in México. In this gradient, stamen length and nectar volume decrease, and corolla diameter increases with elevation (**Figure 3**).

Other studies have documented similar patterns. For instance, Malo and Baonza [36] detected that in *Cytisus scoparius*, flower size increases with elevation. Simi-

larly, in *Campanula rotundifolia*, Maad *et al.* [15] recorded that corolla diameter increases with elevation. For the case of the genus *Agave*, previous studies have documented significant differences in flower traits along latitudinal but not along elevational gradients. In *A. lechuguilla*, corolla diameter increases but flower size decreases with latitude [28]. Lebron-Liriano *et al.* [37] mention that a part of the morphological diversity observed in *Agave* individuals within the Sierra de Bahoruco National Park is determined by the influence of environmental factors. Abiotic conditions show great variation along altitude gradients; factors such as temperature, solar radiation, humidity and the availability of nutrients in the soil depend mostly on altitude and have direct effects on plant activity [38].

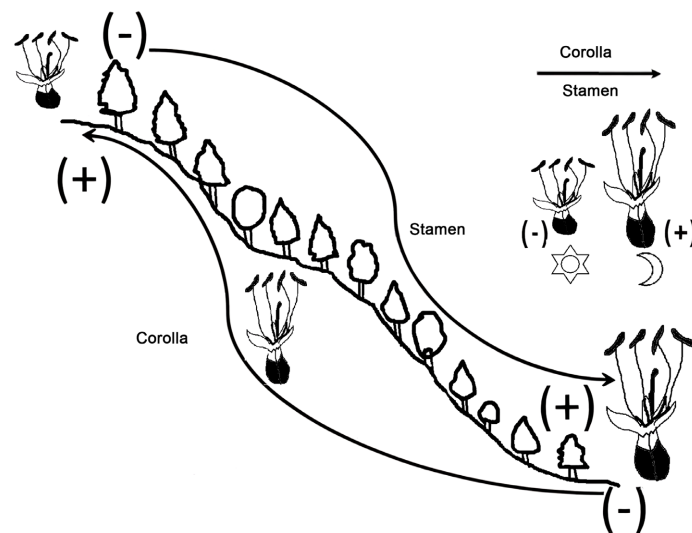


Figure 3. Changes in the morphology of *Agave gentry* flowers (a) along an elevation gradient and (b) during the day and night periods.

The observed changes in flower morphology in the studied gradient also might be associated with changes in pollinator composition and abundance. Therefore, the observed changes in the characteristics of the flowers in the elevation gradient could be due to the changes in the available pollinators [39]. For instance, in *Trollius ranunculooides*, flower diameter changes with altitude due to changes in pollinator composition, with flies in high elevation sites and bees in lower elevation sites [40]. In *Cytisus scoparius*, flower size increases with elevation because of changes in the size of available pollinators [36]. In temperate systems, this pollinator-led selection has been shown to generate variations in floral characteristics along altitudinal gradients. Populations of different plant species can develop specific adaptations to their local pollinators, leading to divergences in floral traits. These traits are subject to natural selection processes mediated by pollinators, aimed at optimizing the reproductive success of plants [41].

In our case, we hypothesize that changes in pollinator composition may be the underlying cause of the observed changes in flower traits. Bats may be the major pollinators in low elevation sites while bumblebees, bees and hummingbirds might

be the major pollinators at high elevation sites. This hypothesis requires an evaluation of the composition and abundance of pollinators in our study sites.

Significant changes in corolla diameter and stamen length between day/night periods were detected just for the pinyon pine forest at the low elevation site. In this site, during the flowering season maximum temperatures reach 26°C while minimum temperatures reach 1°C, values that are on average 2°C - 3°C greater than in the other sites [42]. Greater nocturnal elongation of flowers may be associated with heat stress during the day in the lower elevation site. This elongation pattern may be a strategy to reduce transpiration and water loss during the day. Other studies have documented that Agave flowers tend to secrete nectar and anther dehiscence mainly during the night [26]. In *A. gentryi*, however, no significant differences were detected for nectar secretion between day and night. This species has a wide latitudinal distribution along the Sierra Madre Oriental from Queretaro to Coahuila and might exhibit a similar pattern of variation of flower traits as in our elevational gradient, as reported to *A. lechuguilla* [28].

5. Conclusion

Our study shows clear differences in flower traits along an elevational gradient. Further studies are needed on the pollinators, fruit and seed set, clonal growth and sugar composition in nectar along the elevational gradient to have a better understanding of the environmental factors that influence reproduction in *Agave gentryi*. Future studies should consider an evaluation of fruit and seed sets and the relative importance of sexual and asexual reproduction in this Agave. Finally, we would like to suggest that this species should be studied along a latitudinal gradient to explore how flowers respond to both types of gradients.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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