Flower orientation in *Pachycereus pringlei*

Clara Tinoco-Ojanguren and Francisco Molina-Freaner

Abstract: The orientation of flowers in columnar cacti has been a subject of great interest to plant biologists. The interpretation of this pattern has invoked warmer temperatures as the underlying factor. In this paper, we describe flower orientation in two populations of *Pachycereus pringlei* (S. Watson) Britton & Rose and propose a hypothesis of the underlying mechanism. Stems from the two populations showed a significant mean direction of their flowers, with most flowers (70–77%) present between 90° and 270°. Photosynthetic photon flux density interception and stem temperature reached maximum values on south-facing ribs, showing concordance with flower orientation. We suggest that PFD interception, through its influence on CO₂ uptake and stem temperature, is the major factor underlying the observed orientation of flowers in *P. pringlei*.

Key words: columnar cacti, flower orientation, *Pachycereus pringlei*, PFD interception.

Résumé : L’orientation des fleurs chez les cactus columnaires a toujours été d’un grand intérêt pour les botanistes. Pour interpréter ce patron, on a évoqué comme facteur sous-jacent des températures plus chaudes. Les auteurs décrivent ici l’orientation des fleurs dans deux populations du *Pachycereus pringlei* (S. Watson) Britton & Rose et proposent une hypothèse à propos du mécanisme sous-jacent. Les tiges des deux populations montrent une direction moyenne significative de leurs fleurs, la plupart de celles-ci (70–77 %) se retrouvant entre 90° et 270°. L’interception de la densité du flux de photons photosynthétiques et la température de la tige atteignent des valeurs maximales sur les arêtes tournées vers le sud, montrant ainsi une concordance avec l’orientation des fleurs. Les auteurs suggèrent que l’interception du flux de photons photosynthétiques, par son influence sur l’absorption du CO₂ et sur la température de la tige, constitue le facteur majeur responsable de l’orientation des fleurs chez *P. pringlei*.

Mots clés : cactus columnaires, orientation des fleurs, *Pachycereus pringlei*, interception du PFD.

[Traduit par la Rédaction]

Introduction

The orientation of vegetative and reproductive structures in cacti has been a subject of considerable interest to plant biologists. Plant structures that show a significant mean direction in cacti include cladodes in platyopuntias (Nobel 1982), stems (tilting) in barrel cacti (Ehleringer et al. 1980; Nobel 1988), and flowers in columnar cacti (Rundel 1974; Zavala-Hurtado et al. 1998).

The orientation of cladodes has been interpreted as a response that allows platyopuntias to maximize photosynthetic photon flux density (PFD) interception and CO₂ uptake (Nobel 1988). The underlying mechanism involves a phototropic response of daughter cladodes under an interaction between development, morphology, and physiology (Nobel 1988). In contrast, tilting of the longitudinal stem axis toward the equator in barrel cacti generally leads to less PFD incident on their stems and, therefore, does not appear to be advantageous for enhancing PFD interception and CO₂ uptake. Rather, equatorial tilting has been interpreted as an adaptation to increase apical temperatures during springtime that favors the development of reproductive structures (Ehleringer et al. 1980).

Flowers of different species of columnar cacti are produced in a wide variety of positions. Flower-bearing areoles can be apical, subapical, or lateral, and thus, some species have apical flowering, some have lateral flowering, and some have flower clusters as in species that produce a cephalium or a pseudocephalium (Gibson and Nobel 1986). In *Cephalocereus columna-trajani*, a species endemic to the intertropical desert of Tehuacán in Mexico, the pseudocephalium is oriented away from the equator, presumably to avoid direct solar radiation and predation (Zavala-Hurtado et al. 1998). In contrast, some columnar cacti from extratropical deserts have flowers oriented toward the equator (Johnson 1924; Moran 1968; Rundel 1974). In species with apical flowering, such as *Carnegia gigantea*, flowers are produced on east and southeast ribs around the apex (Johnson 1924). In species with subapical to lateral flowering, flowers are present mainly on the warmer side of the stems, i.e., flowers face the east, south, and west sides in *Pachycereus pringlei* (S. Watson) Britton & Rose in North America (Moran 1968) and flowers facing north in *Trichocereus chilensis* in South America (Rundel 1974). However, although it is known that flowers are not randomly distributed in these species, flower orientation and its underlying mechanism have not been measured and studied in quantitative terms. Based on observations concerning the position and development of flowers and temperature measurements on different...
ribbs, Johnson (1924) proposed that flowers of *C. gigantea* develop mainly on the eastern and southeastern sides of the apex, because they experience more hours with temperature suitable for flower development than on the west side. However, this hypothesis has not been empirically tested. In this paper, we measure flower orientation, light interception, and temperature in ribs of the columnar cactus *P. pringlei*. Based on their relationships we propose a testable hypothesis that attempts to explain the pattern of circular distribution of the flowers of this species. This paper develops the basis of this hypothesis that will be tested in future studies.

**Materials and methods**

**Study species**

*Pachycereus pringlei* is a columnar cactus endemic to the Sonoran desert. This cactus is the most massive one in the region, reaching heights of 15–20 m and producing stems with 10–15 ribs and basal diameters up to 1.5 m (Turner et al. 1995). Plants are single-stemmed until they reach sexual maturity, when branches start to emerge from the major axis. This species is widespread throughout most of Baja California and on most of the islands of the Gulf of California. In mainland Sonora, it is distributed along the gulf coast between Guaymas and Caborca (Turner et al. 1995).

Flower buds start to appear and enlarge in February, and the flowering season lasts from late March through early June (Fleming et al. 1994, 1996). Flowers are produced mainly on the upper stems, mostly within 1–2 m of the apex. The large (8.7–10.2 cm) white flowers open shortly after sunset and close around noon the next day. At night they are visited by the nectarivorous bat *Leptonycteris curasoae*, and after sunrise, by several species of birds and bees (Fleming et al. 1994, 1996).

**Populations studied**

The study was carried out in two populations of *P. pringlei* located along the coast of the state of Sonora in Mexico. One population is located at Rancho El Sacrificio (29°05.82N, 112°08.00W) and the other at San Nicolas (28°49.78N, 111°48.37W). Both sites are located within the central Gulf Coast vegetational subdivision of the Sonoran desert (Shreve 1964). At Rancho El Sacrificio, the population density is 58.0 ± 10.8 plants/ha (mean ± SD). Individual plants in this population range from 0.01 to 1.02 m in basal diameter and from 0.09 to 12.62 m in height. At San Nicolas, the population density is 39.5 ± 5.4 plants/ha. Individual plants in this population range from 0.01 to 1.48 m in basal diameter and from 0.03 to 13.76 m in height.

**Orientation of flowers**

All orientation measurements were made on 10 adult plants of each population. Measured plants were a random sample of the size variation present in each population. The length of the major axis of each plant was measured with a telescopic measuring pole equipped with a device that sits on the apex of the stem. Branch length was measured as the distance between the apex and the point of insertion of the branch in the major axis. The azimuth of each branch was determined using a Brunton compass corrected for declination. The azimuth of all ribs on every branch or major axis of each plant was measured using the same compass. For each rib, we counted the number of flower buds, flowers or fruits present at the beginning of the flowering season: 28–29 March 1996 at San Nicolas and 3–4 April 1997 at El Sacrificio. The azimuth of reproductive structures (buds, flowers, and fruits) and branches was analyzed using circular statistics (Zar 1999). Descriptive statistics and the Rayleigh’s test for circular uniformity were employed according to Zar (1999).

**Characterization of the light environment and temperature of ribs with different orientation**

An isolated, unobstructed single-stem plant (height 3.85 m, basal diameter 0.22 m) was selected at El Sacrificio for measurements of PFD and rib temperature during the phase in which flower buds start to enlarge. We measured the diurnal courses of PFD and stem temperature experienced by flower buds present on ribs with different orientation. Measurements were made for two typical sunny days when the flower buds started to develop (14–15 February 1998). PFD was measured with small gallium-arsenide phosphide (GaAsP) photodiodes (Hamamatsu model G1118). GaAsP photodiodes were calibrated against a LI-COR quantum sensor 190SB. The light sensors were placed on the crest of the rib, on the top of flower buds, and 30 cm below the stem apex. Stem and air temperature were measured with copper–constantan thermocouples. Temperature sensors were inserted 1–2 mm below the cuticle of the stem in a place close to the light sensors. Data were taken every 5 s and averaged every 5 min; means were stored in a datalogger (Campbell 21X).

**Results**

**Orientation of flowers**

Most reproductive structures (70–77%) were present on ribs facing azimuths between 90° and 270° (Fig. 1). Based on the Rayleigh test the two populations showed a significant mean direction of their flowers (Table 1). The mean direction and the circular standard deviation were 197.45° ± 81.20° for El Sacrificio and 190.70° ± 73.78° for San Nicolas. In contrast, branches showed a uniform circular distribution around the major stem. According to the Rayleigh test of uniformity, branches at San Nicolas (p = 0.72, n = 55) and El Sacrificio (p = 0.63, n = 66) were uniformly distributed.

The number of reproductive structures produced by individual branches was a function of stem length. Branches less than 1 m in length did not produce flowers in either population (Fig. 2). On branches longer than 1 m, flower production was dependent on branch length (Fig. 2).

**Microclimatic conditions**

Although we measured microclimatic parameters during two consecutive days, we report data only from the sunniest day. As expected, PFD interception by ribs on different azimuths differed during the day (Fig. 3a). East-facing ribs intercepted more light during the morning, and west-facing ribs intercepted more light during the afternoon. North-facing ribs received less than 300 mol·m⁻²·s⁻¹, while south-facing ribs received the highest PFD intensities during the day (Fig. 3a). Stem temperatures followed similar diurnal courses (Fig. 3b). North-facing ribs experienced the lowest temperature and closely followed the air temperature during the day. East- and west-facing ribs experienced the highest temperature during the morning and afternoon, respectively, reaching temperatures 5–8°C above air temperature. South-facing ribs experienced the highest temperatures during most of the day (Fig. 3b).

Total daily PFD intercepted by the stem varied from 6.19 mol·m⁻² on north-facing ribs to 38.15 mol·m⁻² on south-facing ribs (Fig. 4a). As expected, mean and maximum temperature experienced by the stem varied according to rib azimuth (Fig. 4b). Diurnal mean temperature reached a maximum on south-facing ribs, while maximum temperature values were
Fig. 1. Frequency distribution of the number of flowers per rib in two populations of *Pachycereus pringlei*. Values are means of the number of observed flowers on ribs of different azimuths for San Nicolas (a) and El Sacrificio (b). Error bars are SD.

![Graph of flower distribution](image1)

**Table 1.** Summary of circular statistics for flower orientation in two populations of *Pachycereus pringlei*.

<table>
<thead>
<tr>
<th></th>
<th>El Sacrificio</th>
<th>San Nicolas</th>
</tr>
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<tbody>
<tr>
<td>Mean vector (°)</td>
<td>197.45</td>
<td>190.70</td>
</tr>
<tr>
<td>Length of mean vector (°)</td>
<td>0.37</td>
<td>0.44</td>
</tr>
<tr>
<td>Circular standard deviation (°)</td>
<td>81.20</td>
<td>73.78</td>
</tr>
<tr>
<td>95% confidence interval (°)</td>
<td>192.5–202.4</td>
<td>188.2–193.2</td>
</tr>
<tr>
<td>Sample size (no. of flowers)</td>
<td>1788</td>
<td>4867</td>
</tr>
<tr>
<td>Rayleigh test of uniformity (p)</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Fig. 2. Number of flowers (F) as a function of stem length (SL) for San Nicolas (a) and El Sacrificio (b). Linear regression analysis showed: *F* = 2.06 + 20.42 (SL); *r*² = 0.40, *F* = 43.56, *p* < 0.001, for San Nicolas and *F* = 14.36 + 15.18 (SL); *r*² = 0.62, *F* = 124.03, *p* < 0.001 for El Sacrificio.

![Graph of flower distribution](image2)

**Discussion**

In this paper we have shown that flowers of *P. pringlei* are produced mainly on east-, south-, and west-facing ribs (Fig. 1). Furthermore, flower orientation shows concordance with PFD interception and maximum values of mean daily temperature across ribs (Fig. 4). Previous hypotheses to explain the orientation of flowers in columnar cacti from extratropical deserts have invoked optimum temperatures for flower development.
as the underlying mechanism (Johnson 1924). For the particular case of *P. pringlei*, we suggest that PFD interception, through its influence on CO₂ uptake and stem temperature, is the major factor underlying the orientation of flowers. This hypothesis assumes that areole induction depends on carbohydrate accumulation and optimum temperature in the surrounding tissue and that there is no translocation between ribs.

The factors that induce the formation of new organs in cacti are poorly understood. In platyopuntias, at least four factors are known to induce new organs: (i) dry matter accumulation, (ii) environmental factors such as radiation and thermoperiod, (iii) hormonal action, and (iv) osmotic factors (Nobel 1996; Nobel and Castañeda 1998). In columnar cacti, however, little is known about the factors that induce fertile areoles to produce flowers.

We suggest that PFD interception, through its influence on CO₂ uptake and stem temperature, is the leading factor responsible for the observed orientation of flowers in *P. pringlei*. It is well known that the vertical stems of columnar cacti intercept less PFD than horizontal surfaces (Nobel 1986). Furthermore, for the latitude of the studied populations, south-facing surfaces are expected to receive more PFD between the winter solstice and the vernal equinox (Nobel 1986), the interval in which flower development occurs. On the other hand, the relationship between nocturnal CO₂ uptake and total daily PFD for several cacti shows that compensation points occur at 3–4 mol·m⁻²·day⁻¹ and saturation at 30 mol·m⁻²·day⁻¹, whereas the PFD level leading to 90% of maximum CO₂ uptake occurs at 23 mol·m⁻²·day⁻¹ (Nobel 1986). The response of CO₂ uptake to total daily PFD received by the ribs of...
of these cacti, P. pringlei is unknown. However, if we assume that the response is similar to other columnar cacti that have been studied, PFD received on north-facing ribs (6.19 mol·m⁻²·day⁻¹) would be very close to the compensation point, whereas that on south-facing ribs (38.15 mol·m⁻²·day⁻¹) would be above saturation. Under this radiation regime, north-facing ribs are likely to be limited in PFD exposure, and carbon gain would be minimal. In contrast, east-, south-, and west-facing ribs receive enough PFD to attain maximum rates of carbon gain, if there is no limitation by temperature and (or) water stress. Differences in carbon gain by ribs of different orientation are known to occur in columnar cacti (Nobel and Pimiento-Barrios 1995). Therefore, if the induction of areoles to produce flowers depends on the accumulation of carbohydrates, and if there is no translocation between ribs, then east-, south-, and west-facing ribs of P. pringlei may be the only ones capable of accumulating sufficient carbohydrates to allow flower production. Detailed studies on carbon gain, carbohydrate accumulation, and translocation on ribs with different orientation would be required to test the above hypothesis.

The differential interception of PFD by ribs resulted in differences in stem temperature among ribs. East-, south-, and west-facing ribs experienced temperatures 5–8°C above ambient temperature while north-facing ribs maintained a temperature close to ambient. South-facing ribs kept a temperature above 25°C most of the day. In Opuntia ficus-indica, in addition to carbohydrate accumulation, thermoperiod has been found to influence the formation of new organs (Nobel and Castañeda 1998). However, in columnar cacti it is unknown if thermoperiod has an influence on the induction of areoles and whether there is an optimum temperature for flower development. For P. pringlei, we suggest that the differential PFD interception leads to major differences in carbon gain and stem temperature among ribs that results in a significant mean direction of their flowers. However, further studies are necessary to elucidate the relative importance of carbon gain and stem temperature in flower orientation.

Several experiments could shed light into the mechanism(s) involved in flower orientation in P. pringlei; the artificial illumination of north-facing ribs or shading treatments on south-facing ribs could reveal if PFD interception is, in fact, the leading factor. Experimental additions of carbohydrates into north-facing ribs through injected solutions (e.g., sucrose, Nobel 1996), could elucidate if stem temperature is really a critical factor.

In contrast with previous reports (e.g., Geller and Nobel 1986), branches of P. pringlei were uniformly distributed. Giant columnar cacti usually do not tilt, even when grown under unidirectional radiation (Geller and Nobel 1987), presumably because gravity would exert a considerable bending moment on their massive stems (Nobel 1988). Columnar cacti that exhibit stem tilting (Zavala-Hurtado et al. 1998) often show mechanical failure (Zavala-Hurtado and Díaz-Solis 1995). The distribution of branches around the major axis could significantly affect the structural stability of branched plants like P. pringlei. Although a significant branch orientation could lead to slightly greater PFD interception and CO₂ uptake (Geller and Nobel 1986), we argue that the mechanical stability of P. pringlei plants requires a uniform distribution of branches. Although the number of sampled plants was limited in each of the studied populations, our field observations through coastal Sonora suggest that branches of P. pringlei are uniformly distributed around the major axis.

The study of the orientation of reproductive structures in columnar cacti has received little attention. Although scarce, information on this topic indicates that some extratropical species produce flowers with an equatorial orientation, whereas some intratropical species have flowers oriented away from the equator. The study of the orientation of reproductive structures in columnar cacti from different latitudes offers an excellent opportunity to learn how frequent and general this phenomenon is and also how it is influenced by changes in solar radiation due to latitudinal effects. Studies of species with wide latitudinal distribution (e.g., Pachycereus pecten-aboriginum) or comparative studies with columnar cacti from North and South America could reveal if PFD interception is really a significant factor driving flower orientation.

Acknowledgements

We thank Ezequiel Ezcurre, Park S. Nobel, and Alfonso Valiente for comments on a previous version of the manuscript and Ricardo Clark, Mabeth Burgos, and Conrado Valenzuela for field assistance. Field work was supported by funds from the operating budget of the Instituto de Ecología, Universidad Nacional Autonoma de México, to both authors and a Consejo Nacional de Ciencia y Tecnología grant (3274P-N9607).

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