Revista Chilena de
Historia Natural

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Directional orientation of reproductive tissue of *Eulychnia breviflora* (Cactaceae) in the hyperarid Atacama Desert

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Abstract

Background: Many barrel or columnar cacti, including some in the Atacama Desert, produce their reproductive tissue at or near the terminal apices of solitary or minimally branched stems that lean toward the equator, reportedly to maximize exposure to photosynthetically active radiation (PAR). Those with lateral reproductive tissue, often produce the tissue on the equatorial side of the stems. An examination of the multi-stemmed, arbuscular cactus, *Eulychnia breviflora*, was made to determine if it follows the same general strategy.

Methods: Individuals of the species were evaluated along a 100 km transect in the Atacama Desert. The position of all floral buds and open flowers was documented relative to the center of the plants and relative to the center of the individual stems on which they were located.

Results: A highly significant majority of the reproductive tissue was located on the equatorial (north) side of the plant and on the equatorial (north) side of the stems on which it was found.

Conclusion: Our explanation of the phenomenon differs from other researchers. Inasmuch as reproductive tissue contains little or no chlorophyll, we suggest that the flowers emerge from areas of the stems that receive abundant PAR, not because the reproductive tissue itself requires exposure to PAR. Because the translocation of photosynthates in cacti is difficult and energetically expensive, positioning of reproductive tissue in zones of the stems with high photosynthetic capacity is more energetically efficient. In addition, the Atacama Desert is not particularly warm. Exposure of flowers to solar radiation may produce a thermal reward for pollinators, in addition to any nectar rewards received.

Keywords: *Eulychnia breviflora*, Energetic efficiency, Equatorial orientation, Flowers, Photosynthetically active radiation (PAR)

Background

The Atacama Desert covers a strip approximately 1000 km long in northern Chile, extending southward from the city of Arica, near the border with Peru at approximately 18° 24' S Latitude, to near the city of La Serena at approximately 29° 55' S Latitude. The desert extends eastward, beginning at the Pacific coast, to an elevation of approximately 1500 m near the base of the Andes Mountains [4]. The width of the desert varies, but averages less than 100 km. Average annual precipitation ranges from less than 1 mm near Arica to approximately 70 mm near La Serena, making it one of the driest places on Earth [7]. Various factors contribute to the aridity: (1) the Atacama Desert is characterized by a significant rain shadow effect created as the easterly winds rise to cross the Andes Mountains in the east, (2) the desert lies in the high pressure zone where the descending cool, dry air masses of the atmospheric Hadley and Ferrel cells converge, and (3) the surface of the adjacent Pacific Ocean is characterized by cool temperatures brought by the Humboldt Current from Antarctica [26, 31]. As a consequence, aridity in the region has existed for some 34 Ma, and hyperaridity has prevailed for 15–25 Ma [12, 32, 37]. Despite the extreme aridity, a fog zone exists in the

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narrow strip near where the desert reaches the coast. Semi-regular fog banks, known locally as *camanchaca*, roll in from the Pacific Ocean. Many of the plants that persist in the western Atacama Desert derive the bulk of the moisture needed for survival and reproduction from condensation of the *camanchaca* [6, 38, 41]. Although the *camanchaca* may occur in any season and at any time of day, it is most prevalent at night during the winter months in the north [8], but in the springtime in the south [20]. It is generally limited to an elevational range between 650 and 1200 m above sea level, and frequently leads to the formation of unique fog oases, known as *lomas*, that are characterized by unusually high vegetative diversity and endemism [7, 41, 47].

While visiting the Parque Nacional Pan de Azúcar (Sugarloaf National Park) in the Atacama Desert, we observed an unusual growth form in some cacti of the region. Ehleringer et al. [14] previously described the columnar or barrel cacti of the genus *Copiapoa* as leaning to the north (equatorially) in the Atacama Desert. Because the area lies south of the Tropic of Capricorn, the point at which the sun reaches its southernmost zenith, the sun is present at various distances to the north all year long. Hence, by leaning to the north, the cacti ensure that their reproductive tissue, located at the apices of the stems, maximizes direct exposure to sunlight. While in the National Park for an unrelated project, we observed several shorter species of *Copiapoa* that exhibited that trait. On our return southward toward La Serena, the southernmost city of the Atacama Desert, we saw what we first assumed to be a much taller species of *Copiapoa*. On closer inspection, we determined that it was *Eulychnia breviflora* Phil., an endemic multi-stemmed, arbuscular or shrub-like species of cactus known locally as *copao*. The flowers and flower buds were located predominantly along the sides of the stems rather than at the apices. Based on our observations, we hypothesized that the species was able to maximize exposure of its reproductive tissue to direct solar radiation, not by leaning toward the equator, but by producing floral structures on stems that grew on the equatorial side of the plants, and on the equatorial side of those stems. Here, we report the findings of a subsequent visit during which we collected field data from a large number of plants over a wider geographic area.

Methods

As we traveled southward from the Parque Nacional Pan de Azucar on a subsequent visit, we observed large numbers of individuals of *Eulychnia breviflora* beginning at approximately 27° 43' 668" S Latitude, 70° 58' 634" W Longitude, not far from the town of Bahía Inglesa. We continued on a marginally improved road for approximately 100 km, stopping periodically when we observed healthy individuals of *E. breviflora*, thus creating a 100 km transect. We recorded all flower buds or open flowers present on randomly selected plants. On each plant, we recorded the position of the reproductive organs relative to the center of the plant, and relative to the center of the individual stems on which they were located.
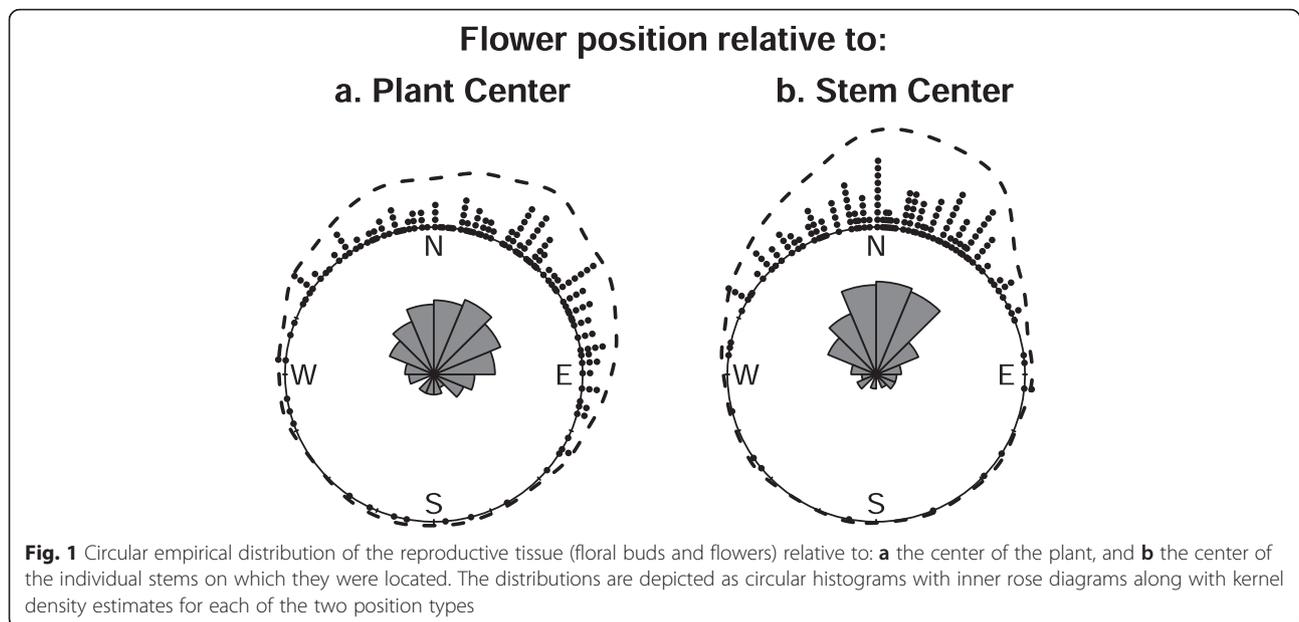
Statistical analyses were subsequently completed using R [36], and the R package 'circular' [2]. To evaluate the research hypothesis, a Rayleigh test for unimodal departures from uniformity was conducted [28]. Next, a Watson's test for Goodness of Fit for a von Mises distribution was conducted for both responses. The von Mises distribution is described in [28] and is given by $f(\theta) = e^{\kappa \cos(\theta - \mu)}/2\pi I_0(\kappa)$ where $\theta, \mu \in [0, 2\pi]$ and $\kappa > 0$. This distribution is commonly used to assess unimodal circular distributions because of its tractability and analogous relationship to the linear normal distribution [17]. The von Mises distribution has two parameters, a location parameter μ and a dispersion or concentration parameter κ that can be considered analogous to the standard error in a linear normal distribution. This distribution function contains a modified Bessel function of the first kind $I_0(\kappa)$ that requires the likelihood to be evaluated by numerical integration.

Before a test of difference in location between the two position types could be conducted, the difference in concentration between each was assessed. This is comparable to a two sample *t*-test where one must consider an alternate form of the test when the variance estimates between the two samples are different. Fisher's test of common concentration was used to assess differences in κ since the position types are both from von Mises distributions [17]. The test statistic is distributed as F with *g*-1, *N*-*g* degrees of freedom, where *g* = 2 is the number of groups and *N* = 359 is the total sample size of all groups.

To test for differences in common mean direction between the two position types, a Watson's large sample nonparametric test was used [17]. This test is potentially less powerful than the Watson-Williams Test for homogenous directions between two von Mises distributions [46]. However, the former was used because the concentrations between the two types are different, whereas the latter assumes equal concentrations. The test statistic is distributed as χ^2 with *g*-1 degrees of freedom.

Results

By the time we completed the 100 km transect, we had documented the location of 180 flowers or flower buds on 40 different plants of *E. breviflora*. Figure 1 suggests unimodal symmetric distributions of the reproductive organs relative to the center of the plants and relative to the center of the stems on which they were growing. The vast majority of the buds and/or flowers were located on the north (equatorial) side of the plants (Fig. 1a). They were also largely located on the north (equatorial)

Flower position relative to:

a. Plant Center   b. Stem Center

Fig. 1 Circular empirical distribution of the reproductive tissue (floral buds and flowers) relative to: **a** the center of the plant, and **b** the center of the individual stems on which they were located. The distributions are depicted as circular histograms with inner rose diagrams along with kernel density estimates for each of the two position types

side of the stems on which they were found (Fig. 1b). Rayleigh tests for the two position categories indicate non-uniform distributions ($p < 0.01$) for both. Watson's Goodness of Fit tests indicate that both samples were drawn from von Mises distributions ($p > 0.05$ for both). Von Mises maximum likelihood estimates for both samples are shown in Table 1.

The Fisher test indicated a significant difference in concentration parameters between the two position types at $\alpha = 0.05$ ($F_{1,357} = 14.06$, $p = 0.0002$). Watson's test indicated that mean directions were significantly different at $\alpha = 0.05$ ($\chi^2_1 = 4.38$, $p = 0.036$). The average position of the reproductive tissue relative to the center of the stems on which they grew (5°) was not significantly different from north. The position of the reproductive structures relative to the center of the plants was centered slightly but significantly east of north at approximately 24°.

Discussion

Reproduction is energetically expensive [23], and the amount of energy that plants can afford to devote to reproduction is limited [3]. This can be especially critical in arid areas where water is a scarce resource [39]. Plants have evolved a variety of strategies to cope with aridity [16]. Average annual precipitation at Bahía Inglesa, where we began the transect, averages only 58 mm, falling

primarily during the winter months of June–August (Climate-Data.org/location/498309/). While the Atacama Desert is classified as hyperarid, it is also considered to be a cool desert. Temperatures at Bahia Inglesa range from approximately 13 °C in the winter to about 20 °C in the summer.

Various cacti have reportedly evolved structural and morphological strategies to maximize the exposure of their reproductive tissue to photosynthetically active radiation (PAR). Many columnar and barrel cacti are known to produce flowers in cephalia or pseudocephalia at or near the terminal apices of solitary or minimally branched stems that lean toward the equator [13, 14, 21, 33, 43, 44, 48]. Other columnar cacti produce their flowers and fruits along the sides of the stems that face the equator, thus accomplishing the same effect of maximizing exposure to PAR [1, 10, 15, 29, 42]. Although Ehleringer et al. [14] noted equatorial tilting of stems of the columnar cactus genus *Copiapoa* in the Atacama Desert, presumably as a mechanism to orient the cephalia toward the equator in order to maximize exposure to PAR, very few researchers have explored the phenomenon for non-columnar cacti. Notably, the stems of the arbuscular *Eulychnia breviflora* do not tilt notably; this species produces reproductive tissue primarily on the sides of stems located on the equatorial side of the plant, and on the equatorial side of those stems.

Notably, while flowers of *E. breviflora* were generally oriented toward the equator, the equatorial orientation was stronger relative to the center of the stems than relative to the center of the plants. Indeed, relative to the center of the plants, orientation averaged somewhat east of north. Flowers of *E. breviflora* may emerge from any stem, depending on the level of exposure of the

Table 1 Parameter estimates of von Mises distributions for each sample. 95 % confidence intervals are indicated in parentheses

Position of the flower bud	$\hat{\mu}$ (degrees)	$\hat{\kappa}$ (degrees)
Relative to the center of the plant	24.39 (16.04, 32.74)	1.61 (1.30, 1.92)
Relative to the center of the stem	5.06 (−0.78, 10.90)	2.64 (2.17, 3.11)

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equatorial side of the stem to direct sunlight. Because of the somewhat open structure of the canopy, even the north side of stems located on the south side of the plant may receive sufficient PAR to produce occasional flowers. We have noted a similar slightly eastward orientation of some non-cactus desert plants in North America (unpublished data).

Reproductive tissue is not known to contain chlorophyll or to be involved in photosynthesis to any notable degree. Therefore, the question reasonably arises as to why the reproductive tissue needs to be exposed to large quantities of PAR. In short, we suggest that it does not. It is known that the translocation of photosynthates laterally between regions of a single cactus stem is difficult, energetically costly, and uncommon [15, 18, 42]. We suggest, therefore, that the reproductive tissue arises from regions of the stems that receive adequate direct exposure to PAR, and where the cost of translocating the photosynthates is minimized by close proximity to the reproductive tissue. Higher levels of PAR interception in photosynthetic regions of the stem is almost assuredly associated with more resources available for reproduction in nearby reproductive tissue, whether it translates into more flowers or seeds, or greater seed viability. Nocturnal CO_2 uptake is also correlated with greater stomatal conductance in regions of cactus plants that receive high PAR [19, 42].

Another potential benefit of producing flowers in positions that maximize exposure to direct sunlight, relates to potential thermal rewards for pollinators [9], in addition to any nectar rewards. Flowers of *E. breviflora* are known to be visited, in descending order of frequency, by bee, fly and beetle pollinators [40]. Bees are able to regulate their internal temperature by vibrating their wings, while beetles and flies depend mostly on radiant or reflected solar energy [45]. Although the climate of the Atacama Desert is relatively cool, the predominant pollinator group (bees) is less dependent on a thermal reward for their pollinating activity than the less frequent pollinators (flies and beetles), which depend on direct, reflected or re-radiated solar energy.

While there may be abundant pollinators, there is still the risk of inadequacy of other resources. Among the likely resource deficiencies that may lead to flower or fruit abortion in a hyperarid desert is water [5, 11]. By aborting reproductive structures early, the plants avoid the unnecessary cost of maintaining structures that will not benefit the plant in the long term [27, 34]. Other potential factors that may lead to the abortion of reproductive structures in some cacti include inadequate or incompatible pollen [24, 35], and insect damage [25, 30]. While we chose to record only healthy flower buds that exhibited the promise of maturing to the flower stage, we did note that approximately 5–10 % of the buds present

had been aborted or were in the process of being aborted. The abortion of buds and flowers is not necessarily negative, inasmuch as the overall fecundity of the plant may be enhanced [22].

Conclusions

Our research hypothesis was confirmed, i.e., reproductive tissue (flower buds and open flowers) of *Eulychnia breviflora*, an endemic, arbuscular cactus of the hyperarid Atacama Desert, was present nearly always on the equatorial (north) side of the plants and on the equatorial side of the individual stems on which they were located. Such orientation of the reproductive tissue, places it adjacent to areas of the stems that receive maximum exposure to PAR, thus minimizing the energetic cost of translocating photosynthates. In addition to nectar, pollinating insects in this cool desert may also be attracted to the flowers of this species due to the potential thermal reward from flowers that receive abundant solar radiation.

Authors' contributions
SDW and LEA conceptualized the study and performed all field work. LSB performed statistical analyses. All authors participated in writing and revising the manuscript.

Competing interest
The authors declare that there are no competing interests.

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