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Floral orientation in *Eulychnia acida*, an arborescent cactus of the Atacama Desert, and implications for cacti globally

STEVEN D. WARREN,[1,]† LORGIO E. AGUILERA,[2] L. SCOTT BAGGETT,[3] AND MAURICIO ZUÑIGA[2]

[1]*Rocky Mountain Research Station, Shrub Sciences Laboratory, U.S. Forest Service, 735 North 500 East, Provo, Utah 84606 USA*
[2]*Departamento de Biología, Universidad de La Serena, La Serena, Chile*
[3]*Rocky Mountain Research Station, U.S. Forest Service, 240 West Prospect Road, Fort Collins, Colorado 80526 USA*

Citation: Warren, S. D., L. E. Aguilera, L. S. Baggett, and M. Zuñiga. 2017. Floral orientation in *Eulychnia acida*, an arborescent cactus of the Atacama Desert, and implications for cacti globally. Ecosphere 8(10):e01937. 10.1002/ecs2.1937

Abstract. The hyperarid Atacama Desert of northern Chile may be the driest place on Earth. Plants surviving there have adapted a number of unique strategies to cope with the harsh conditions. Many cacti in arid areas tend to produce reproductive organs in positions that maximize incidence of solar radiation. We sought to determine whether *Eulychnia acida*, an endemic cactus with an arborescent growth form, follows the same pattern. We conducted a study in two populations of the cactus. One population occurs where average annual precipitation (AAP) is 113 mm; AAP at the other site is 50 mm. We randomly sampled 10 plants at each location, and 300 reproductive structures on those plants. On each plant, we recorded the position of all reproductive organs relative to the center of the plant, and relative to the center of the stems on which they were located. The results of the two populations did not differ significantly, so results of the two populations were combined. Both populations lie south of the Tropic of Capricorn, beyond the point where the sun reaches its southernmost zenith. Hence, the sun is located at to the north all year long. We discovered that the reproductive tissue emerges predominantly on stems found the equatorial (north) side of the plant and on the equatorial (north) side of those stems. As reproduction is energetically expensive, the generation of reproductive organs from vegetative tissue that receives high levels of direct solar radiation minimizes the cost of translocating photosynthates from photosynthetic tissue to non-photosynthetic reproductive tissue, thus begetting energetic efficiency. The strategy appears to be common among many cacti and in some other plants of arid regions worldwide and is especially prevalent at extra-tropical latitudes. In addition to nectar rewards, the strategy may also benefit pollinators by offering a thermal reward, especially on overcast or otherwise cool days, thus improving the odds of successful pollination.

Key words: copao; energetic efficiency; equatorial orientation; *Eulychnia acida;* flowers; hyperaridity.

Received 12 July 2017; accepted 17 July 2017. Corresponding Editor: Eric Ribbens.
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† **E-mail:** swarren02@fs.fed.us

INTRODUCTION

The Atacama Desert comprises a relatively narrow strip of land along the Pacific coast of northern Chile. It stretches some 1500 km northward from the city of La Serena (~30° S latitude) to near the city of Arica and the border with Peru (~18° S latitude). The width of the desert is variable, averaging <100 km, and extends eastward from the Pacific coast to an elevation of approximately 1500 m where the arid zone reaches the foothills of the Andes Mountains (Börgel 1973). Average annual precipitation (AAP) ranges from approximately 70 mm in the south to <1 mm in the north, making it one of the driest places on Earth (Cereceda et al. 2008). The Atacama is the oldest continuously arid region on Earth (Hartley et al. 2005, Clarke 2006). Aridity is thought to have existed for at least 34 million years, and hyperaridity has persisted for the last 15–25 million

years (Dunai et al. 2005, Rech et al. 2006). Various factors contribute to the hyperaridity: (1) the Andes Mountains create an effective rain shadow from the prevailing southeasterly trade winds, (2) the atmospheric Hadley and Ferrel cells converge and descend at about 30° S latitude, creating a high-pressure zone characterized by a large mass of descending dry air that carries little moisture, and (3) the oceanic Humboldt Current, coming from Antarctica, flows northward along the Pacific coast, thus cooling the air and reducing available atmospheric moisture.

Despite the extreme aridity, a fog zone exists in the narrow strip of land near where the desert reaches the Pacific coast. Semi-regular fog banks, known locally as *camanchaca*, roll in from the Pacific Ocean. Many plants persisting along the western edge of the Atacama Desert derive the bulk of the moisture needed for survival and reproduction from condensation and drip from the *camanchaca* (Rundel and Mahu 1976, Cáceres et al. 2007). 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 (Rundel et al. 1997, Cereceda et al. 2008), but in the springtime in the south (Garreaud et al. 2008). It is generally limited to an elevational range between 650 and 1200 m above sea level and facilitates the frequent formation of unique fog-dependent oases, known as *lomas*, that are characterized by unusually high vegetative diversity and endemism (Rundel et al. 1991, Marquet et al. 1998, Cereceda et al. 2008).

Given the hyperarid climate that characterizes the Atacama, it is reasonable to assume that organisms persisting there have evolved unique strategies to cope. Ehleringer et al. (1980) previously described columnar or barrel cacti of the genus *Copiapoa* as leaning to the north. Because much of Atacama lies south of the Tropic of Capricorn, the point at which the sun reaches its southernmost zenith, the sun is present during most or all of the year at various distances to the north. By leaning or tilting equatorially (to the north), their reproductive tissue tends to emerge from near the apices of the stems where direct exposure to sunlight is maximized. However, Warren et al. (2016*a*) noted that individuals of the cactus species *Eulychnia breviflora*, with a multi-stemmed arbuscular growth form, do not produce their flowers at the apices of the stems and do not lean toward the north. Rather, they generate reproductive tissue along the sides of stems that grow on the north side of the plant, and on the north side of those stems. The net effect ensures that reproductive tissue arises from vegetative tissue that is oriented in positions that maximize exposure to direct sunlight. The strategy minimizes the energetic cost of translocating photosynthates from tissue with high levels of photosynthesis to reproductive tissue with great energetic requirements.

Eulychnia acida, known locally as *copao*, occurs near the southern end of the Atacama Desert where AAP ranges from 50 to 115 mm. It is neither columnar nor arbuscular; it has an arborescent growth form with a single trunk-like stem and multiple columnar branches. *E. acida* can grow to a height of 6 m. Its spines can be up to 20 cm long. The fruit, also known as *copao* or *rumpa*, is consumed by locals and has antioxidant (Jiménez-Aspee et al. 2014) and anti-inflammatory (Jiménez-Aspee et al. 2015) properties. It is a good source of soluble dietary fiber, vitamin C, and the minerals Ca, K, Mg, and P (Masson et al. 2011). Soil beneath *E. acida* tends to accumulate N, P, K, water, and soluble salts compared to soil outside the influence of the canopy, thus facilitating invasion by *Mesembryanthemum crystallinum*, a prostrate, succulent, exotic plant (Madrigal-González et al. 2013).

Here, we report on a visit to the Atacama Desert during which we identified two distinct populations of *E. acida*. We evaluated the populations to test our research hypothesis that despite its arborescent growth form, *E. acida* produces its reproductive tissue in positions that maximize the reception of solar radiation.

Methods

We identified two populations of *Eulychnia acida* near the southern end of the Atacama Desert. The first population was located near the community of Los Choros (29.20° S latitude) where AAP is approximately 50 mm. A second population was found northeast of the Parque Nacional Fray Jorge (30.37° S latitude) where annual precipitation reaches 113 mm (http://www.chile365.cl/es-parques-nacionales-region-4-parque-nacionalfray-jorge.php). We randomly sampled 10 plants from each population. On each plant, we recorded the position of all

reproductive organs relative to the center of the plant, and relative to the center of the individual stems on which they were located. By summing the sampled flowers and/or floral buds at both locations, we sampled a total of 300 reproductive structures on 20 *E. acida* plants. While the Atacama Desert is hyperarid, it is not especially warm; in fact, it is considered a cool desert. Temperatures range from an average low of 8°C in the winter to an average high of 26°C in the summer at Los Choros; the average low temperature ranges from 7°C in the winter to 23°C in the summer at the Parque Nacional Fray Jorge.

Statistical analyses were completed using R (R Core Team 2013) and the R package circular (Agostinelli and Lund 2011). To test for similarity in the directional orientation of reproductive tissue relative to the center of the plants and relative to center if the stems, we performed a Rayleigh test for unimodal departures from uniformity (Mardia and Jupp 2000). 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 Mardia and Jupp (2000) and is given by $f(\theta) = e^{\kappa \cos(\theta-\mu)}/2\pi I_0(\kappa)$, where $\theta, \mu \in [0, 2\pi]$ and $\kappa > 0$. The distribution is commonly used to assess unimodal circular distributions because of its tractability and analogous relationship to the linear normal distribution (Fisher 1993). The von Mises distribution has two parameters, a location parameter μ and 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 (Fisher 1993). The test statistic is distributed as *F* with g-1, N-g degrees of freedom, where g is the number of groups and N 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 (Fisher 1993). This test is potentially less powerful than the Watson–Williams test for homogenous directions between two von Mises distributions (Watson and Williams 1956). 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

There was no significant difference in directional orientation between the two populations. With populations combined, Fig. 1 illustrates the unimodal symmetric distribution of the reproductive organs relative to the center of the plants and relative to the individual stems on which they were located. There was a clear and overwhelming predilection for the north (equatorial) side of the plants (Fig. 1a) and for the north (equatorial) side of the individual stems on which they grew (Fig. 1b). Rayleigh tests for the two position types indicated non-uniform distribution ($P < 0.05$) for both. Watson's goodness-of-fit tests indicated that both samples were drawn from von Mises distributions ($P < 0.05$). 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 ($F_{1, 300} = 56.41$, $P < 0.0001$). Watson's test indicated that mean directions were not significantly different ($\chi^2_1 = 0.05, P = 0.815$). The average position of the reproductive organs relative to the center of the stems on which they grew was slightly east of north at about 8°. The average position of the reproductive organs relative to the center of the plants was centered to the northeast at approximately 26°.

Discussion

The research hypothesis was supported; that is, the vast majority of reproductive organs of *Eulychnia acida* occurred on the north (equatorial) side of the plant (Fig. 1a). However, a few did not. The reason for the variance, however small, seems clear. It happened when stems on the

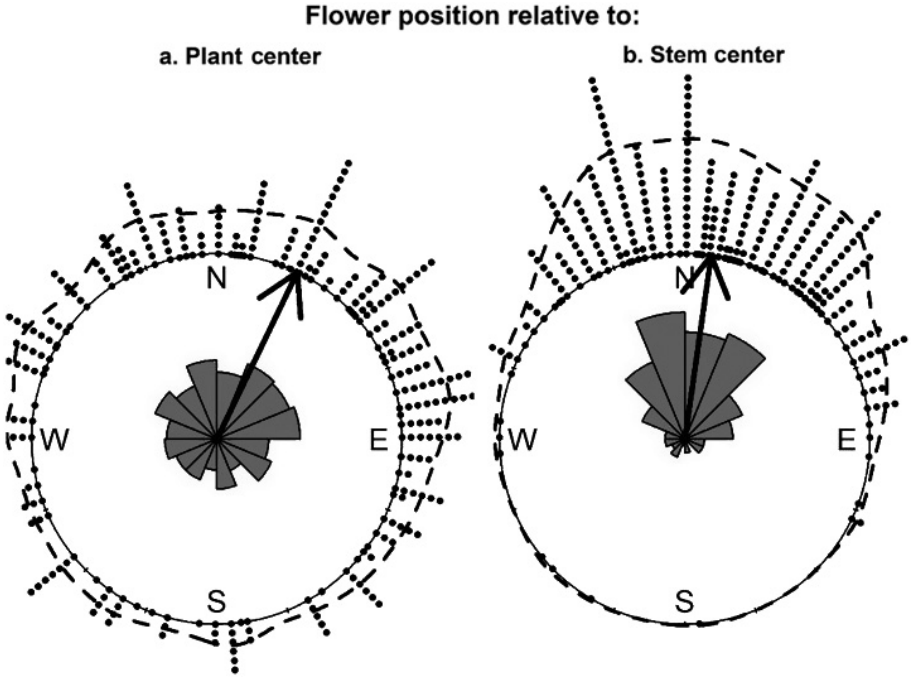


Fig. 1. Circular empirical distributions of the reproductive tissue (open flowers and flower buds) of two combined populations of *Eulychnia acida* in the Atacama Desert relative to (a) the center of the plant, and (b) the center of individual stems on which they were found. The distributions are depicted as circular histograms with inner rose diagrams, along with kernel density estimates for each of the position types. In each graph, the single arrows represent the mean orientation of all floral tissue relative to the plant or stem center, respectively.

Table 1. Parameter estimates of von Mises distributions for combined populations of *Eulychnia acida* in the Atacama Desert.

Category	$\hat{\mu}$ (degrees)	$\hat{\kappa}$ (degrees)
Plant center	25.79 (11.62, 39.96)	0.66 (0.49, 0.84)
Stem center	8.14 (3.89, 12.40)	2.90 (2.50, 3.30)

Note: 95% confidence intervals are indicated in parentheses.

south side of the plant were positioned in such a way that their north (equatorial) sides were able to access direct sunlight through gaps in the canopy. Hence, the flowers were found almost ubiquitously on the north sides of the stems on which they were located. The net result was that a clear preponderance of all flowers occurred on the north (equatorial) side of the stems, regardless of the location of the stem with respect to the center of the plant (Fig. 1b).

Reproduction is an energetically costly proposition (Kunz and Orrell 2004), and the amount of energy that plants can afford to expend on reproduction is limited, especially in hyperarid environments where water is limited (Bell 1980). Consequently, plants have adapted a suite of unique strategies to cope with water scarcity (Fischer and Turner 1978). Cacti have variable growth forms, varying from columnar or barrel-shaped with a single unbranched or minimally branched trunk-like stem ranging from very short to quite tall, arbuscular with many stems arising from beneath the soil surface, or arborescent with a single trunk-like stem and many branches arising from the trunk at points above the soil surface. Numerous cacti, and some other arid zone plants, have been shown to generate their reproductive tissue from photosynthetic tissue at or near positions that maximize the interception of solar radiation. However, the specific orientation strategies can vary considerably. Shorter, non-branching columnar or barrel cacti often generate their reproductive tissue in cephalia located at the apices of the stems. Cephalia have no photosynthetic tissue, and epidermal cells contain modified

leaves, represented by hairs, bristles, or spines that are also non-photosynthetic (Gorelick 2013). Such cacti, if sufficiently tall, may tilt equatorially, thus maximizing the exposure of the photosynthetic tissue surrounding the cephalia to direct sunlight (Ehleringer et al. 1980, Ehleringer and House 1984, Vázquez-Sánchez et al. 2007, Herce et al. 2014).

Columnar cacti without cephalia may generate reproductive tissue in pseudocephalia located near, but not at, the apices of the stems. Pseudocephalia also have hairs, bristles, and spines, but originate from photosynthetic epidermal tissue (Gorelick 2013). Directional orientation of the pseudocephalia may depend on whether plants are intra- or extra-tropical, that is, inside or outside the Tropics of Cancer and Capricorn. The location of pseudocephalia of intra-tropical cacti may vary according to the position of the sun during the season when the plants produce flowers, with some pseudocephalia oriented away from the equator because the sun is located in that direction during the season of flower production (Zavala-Hurtado et al. 1998, Valverde et al. 2007), whereas pseudocephalia of extra-tropical cacti are almost always oriented equatorially (Méndez 2015) because solar radiation comes from that direction all year long.

Other cacti with columnar stems produce neither cephalia nor pseudocephalia, but generate their reproductive tissue along the equatorial side of the stems, thus accomplishing the same objective of orienting vegetative tissue that gives rise to reproductive organs in a cardinal direction that maximizes exposure to direct sunlight (Tinoco-Ojanguren and Molina-Freaner 2000, Vázquez-Sánchez et al. 2007, Figueroa-Castro and Valverde 2011, Córdova-Acosta et al. 2012, Aguilar-Gastellum and Molina-Freaner 2015, Warren et al. 2016*a*, Ponce-Bautista et al. 2017). *Eulychnia acida*, evaluated in the present study, falls in the latter group of cacti.

Although not widely recognized, some other plants surviving in arid zones have also adapted strategies with a similar objective of limiting the growth of reproductive tissue to areas of the plants that have maximum direct exposure to solar radiation. For example, the iconic Joshua tree, an arborescent member of the *Yucca* genus, produces the bulk of its reproductive organs on leafy rosettes at the ends of branches on the equatorial side of the plant (Warren et al. 2016*b*). The authors documented that in both *Yucca brevifolia* (an arborescent non-cactus of the Mojave Desert, USA) and *Eulychnia breviflora* (an arbuscular cactus of the hyperarid Atacama Desert, Chile; Warren et al. 2016*a*), the orientation of reproductive tissue is a few degrees east of an equatorial direction. A possible explanation may have first been articulated by Johnson (1924), who suggested that the east side of the stem of the giant saguaro cactus (*Carnegiea gigantea*) of North America is the first to be warmed by the morning sun to an optimal temperature for flower development and that it maintains the optimal temperature for longer than the west side. Johnson (1924) suggested, but did not experimentally quantify, that initiation of flowering occurs more rapidly on the southeastern region of the stem than on the southwestern region, possibly due to a combination of insolation and optimal tissue temperature.

Lateral transfer of photosynthates between adjacent regions of a cactus stem has been shown to be difficult, uncommon, and energetically expensive (Geller and Nobel 1986, Tinoco-Ojanguren and Molina-Freaner 2000). Therefore, it seems reasonable for reproductive tissue to arise primarily from regions of the stem that receive high levels of solar radiation, thus minimizing the cost of photosynthate translocation. Nocturnal CO_2 uptake is also correlated with greater stomatal conductance in regions of cacti plants that are exposed to high levels of solar radiation (Geller and Nobel 1987, Tinoco-Ojanguren and Molina-Freaner 2000), thus increasing growth in those regions of cacti and in some members of the *Yucca* genus that receive high insolation (Nobel and Hartsock 1981). Whether the trait is common in related species of the same yucca genus and in other non-cactus desert plant taxa is, as of yet, not well explored.

Cacti are primarily pollinated by insects, birds, and bats (Schlumpberger 2012). The pollination ecology of the *Eulychnia* genus of the Atacama Desert has received little specific attention. Bees, flies, and beetles have been reported as insect pollinators of flowers of *E. acida* (Smith-Ramírez and Yañez Ramírez 2010). The congeneric *Eulychnia iquiquensis* is known to also be pollinated by hummingbirds (Pinto 2007). Because the Atacama is known to be generally cool, particularly in the spring and early summer when flowering of

E. acida takes place, generation of reproductive tissue in positions oriented toward the equator helps ensure that the flowers receive abundant solar radiation. The resulting elevated temperature of the flowers may serve as a temperature reward for pollinators, in addition to any nectar rewards received. Warmth may be a significant reward for pollinators on cool days and during cool seasons, thus encouraging pollinators to spend a greater amount of time engaged in foraging and pollinating behavior (Cooley 1995, Rands and Whitney 2008). This may be especially important for hymenopterans, dipterans, and coleopterans that are unable to thermoregulate internally (Warren et al. 1988). Moths have only recently been reported as pollinators of cacti in the Atacama Desert (Schlumpberger and Badano 2005) although, to date, they have not yet been reported as pollinators on *Eulychnia.* Because both moths and bats tend to emerge near or shortly after sundown, these pollinators could also benefit from residual warmth as a thermal reward. Whatever the reason, equatorially oriented cactus flowers have been shown to attract a greater abundance of insect pollinators than non-equatorially oriented flowers (Figueroa-Castro et al. 2014).

Conclusions

Cacti and some other plants of arid environments have evolved structural and physiological adaptations that assist them in coping with aridity. One reported adaptation consists of producing reproductive tissue in locations that maximize exposure to direct solar radiation. Among cacti, the adaptation has been reported in plants of both the Northern Hemisphere and the Southern Hemisphere. In extra-tropical environments, reproductive tissue generally emerges in positions with equatorial orientation, as incident solar radiation comes from that direction all year long. In intra-tropical environments, the orientation depends on the position of the sun during the season when reproductive tissue is formed. Reproductive tissue may have polar orientation if the sun has surpassed a vertical zenith during the time when the reproductive tissue is formed. We evaluated the directional orientation of floral structures of *Eulychnia acida*, an endemic extra-tropical cactus of the Atacama Desert of northern Chile. The species has a decidedly arborescent growth form. Reproductive structures exhibited a marked equatorial orientation, strengthening the hypothesis of directional orientation of flowers and fruits of members of the Cactaceae family in arid environments. Such orientation may also provide a thermal reward for some pollinators that depend on external sources of warmth on cool or overcast days, seasons, or times of day when they are active.

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