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**Photosynthetically active radiation and carbon gain drives the southern orientation of
Myrtillocactus geometrizans fruits**

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Abstract

- The equatorial orientation of reproductive structures is known in some columnar cacti from extratropical deserts. It has been hypothesized that photosynthetically active radiation (PAR) interception is the main reason for this orientation, due its key effect on nocturnal CO₂ uptake. However, there are no studies addressing, both, the effect of PAR and its consequence, carbon gain, on fruit orientation. Accordingly, we tested whether PAR and carbon gain could explain the southern fruits orientation of *Myrtillocactus geometrizans*, an intertropical columnar cactus.
- We studied three populations of *M. geometrizans* in Mexico. For each population, azimuth of fruits, total daily PAR, nocturnal acid accumulation (NAA), and fruit production were measured. The relationships between rib orientation and number of fruits, as well as total daily PAR, were evaluated using periodic regressions. The effect of total daily PAR and NAA on number of fruits was assessed using generalized linear models.
- During the springtime, mean fruit orientation had a south azimuth for three populations. Likewise, rib orientation had a significant effect on fruit production, with the south-facing ribs having the maximum number of fruits. Total daily PAR was highest in the south-facing ribs, at least for those in the northern and central populations. Furthermore, during springtime, there was a significant positive effect of total daily PAR and NAA on fruit production.
- Our results provide strong evidence that the higher carbon gain in equatorial ribs, due to a highest interception of PAR, would be the responsible factors for the equatorial orientation of fruits in an intertropical columnar cactus.

Keywords: columnar cactus; fruit orientation; nocturnal acid accumulation; photosynthetically active radiation

INTRODUCTION

Among the environmental factors affecting plant performance, light may be the most spatially and temporally heterogeneous (Percy 2007), in terms of both quantity and quality (Valladares 2003). In arid and semiarid ecosystems, light cannot be a limiting factor for desert plant species (Nobel 1980; Gibson & Nobel 1986); however, this is not the case for some succulent plants, such as cacti. In addition to plant shading, clouds, and landscape features (Geller & Nobel 1987), several characteristics of cacti (e.g. spines, vertical and opaque photosynthetic surfaces, and very low surface-volume ratios) could reduce the availability of photosynthetically active radiation (PAR), which in turn, limits CO₂ uptake (Nobel 1980, 1985, 1988; Gibson & Nobel 1986; Zavala-Hurtado *et al.* 1998; Sortibrán *et al.* 2005; Herce *et al.* 2014). Moreover, since cacti display crassulacean acid metabolism, in which CO₂ uptake occurs at night, cacti depend more on the total daily PAR than on the instantaneous rate (Geller & Nobel 1987). Therefore, total daily PAR could be a major limiting factor for CO₂ uptake among cacti (García de Cortázar *et al.* 1985; Geller & Nobel 1986). Therefore, the orientation of photosynthetic tissues is critical in cacti, since such features affect the interception of PAR and CO₂ uptake (Nobel 1981; Geller & Nobel 1987).

In addition to the aforementioned constraints and sources of variability affecting PAR interception, the sun's trajectory can result in an uneven distribution of PAR over the photosynthetic surfaces of a cactus (Geller & Nobel 1986, 1987). These micro-environmental differences may set extrinsic gradients of within-plant variation related to orientation and light intensity (see Herrera 2009). Depending on the orientation of these surfaces, such heterogeneity in the lighting environment

produces within-plant variability (Herrera 2009), with ribs or branches receiving more PAR than other tissues (Nobel 1980; Geller & Nobel 1987). Therefore, there is a differential net carbon gain among ribs or branches at the within-plant level (Pimienta-Barrios & Nobel 1998). In this regard, equatorial orientation of reproductive structures in columnar cacti should reflect this phenomenon.

The equatorial orientation of reproductive structures (i.e. floral buds, flowers, and fruits) is known in some columnar cacti from extratropical deserts, growing in the northern and southern hemispheres.

For example, in a study on two populations of *Pachycereus pringlei* (S. Watson) Britton & Rose in the Sonoran Desert in Mexico (above 28° latitude N), Tinoco-Ojanguren & Molina-Freaner (2000) reported that flowers were orientated in a southern direction (190.70° and 197.45°). On the other hand, *Eulychnia breviflora* Phil. in the Atacama Desert in northern Chile (27° latitude S), floral buds and flowers were located, mainly, on the northern side of the plant and the stems (Warren *et al.* 2016).

To explain the pattern of equatorial orientation of reproductive structures in *P. pringlei*, Tinoco-Ojanguren & Molina-Freaner (2000) hypothesized that PAR interception is a major factor, due to its effect on CO₂ uptake and stem temperature. In fact, they report that PAR was highest on south-facing ribs measured on a single-stem plant. They suggested that if the induction of areoles to produce floral buds relies on the accumulation of carbohydrates, and no translocation of photosynthates among ribs occurs, then only the regions of the stem that receive higher PAR (i.e. the south-eastern and west ribs for cacti found in the northern hemisphere) will be capable of obtaining sufficient resources to produce floral buds. Besides the study of Tinoco-Ojanguren & Molina-Freaner (2000), only the studies of Figueroa-Castro & Valverde (2011) on *P. weberi* (J.M. Coult.) Backeb., an intertropical columnar cactus, and Aguilar-Gastélum & Molina-Freaner (2015) on *P. pecten-aboriginum* (Engelm.) Britton & Rose, an extratropical columnar species, have reported that the southern patterns of reproductive structures' orientation are associated to the maximum PAR received, recorded on a single branch. However, to our knowledge, there are no studies addressing, both, the effect of PAR and its consequence, carbon gain, in the equatorial orientation of fruits of columnar cacti. In addition, the Tinoco-Ojanguren & Molina-Freaner (2000) hypothesis explains the non-random circular

distribution of reproductive structures for columnar cacti in high latitudes, where ribs or branches facing towards the equator receive PAR all year long. Unlike cacti from extratropical regions, in species from intertropical deserts, the amount of PAR received on the ribs or branches facing towards the equator vary depending on the season (Nobel 1985; Herce *et al.* 2014). Consequently, it is necessary to explore whether this also explains the pattern of orientation of reproductive structures among cacti from tropical deserts.

A previous study on two populations of *Myrtillocactus geometrizans* (Mart. ex Pfeiff.) Console in central Mexico (20° latitude N) revealed that fruits were mainly produced in the southern ribs (Rosas-García 2010). Therefore, the observed pattern of orientation in *M. geometrizans* could be because southern ribs receive higher PAR and may have a higher availability of resources to produce more fruits (Tinoco-Ojanguren & Molina-Freaner 2000; Figueroa-Castro & Valverde 2011). Thus, it is expected that the southern orientated ribs, producing most of the fruits, should receive the highest PAR and, consequently, the highest carbon gain during springtime (reproductive season). In crassulacean acid metabolism plants, such as cacti, nocturnal CO₂ uptake leads to nocturnal acid accumulation (NAA) in tissues (Nobel 1988). In this way, by measuring changes in tissue acidity, we could assess the amount of CO₂ uptake (Gibson & Nobel 1986; Nobel 1988). To test this hypothesis, we addressed the following questions in three populations of *M. geometrizans*: (1) Does the southern pattern of fruit orientation occurs across its distributional range and along the fruiting season; (2) Are the production of fruits and total daily PAR dependent on the orientation of ribs; and (3) Is there an effect of total daily PAR and CO₂ uptake on fruit production in ribs with different orientations?

MATERIALS AND METHODS

Plant species

M. geometrizans is an endemic arborescent columnar cactus, with a wide distribution in Mexico (Guzmán *et al.* 2003). Although found in northeastern Mexico, above the tropic of Cancer, this species is much more common in the tropical arid and semiarid regions of central and southern

Mexico. Individual plants (up to 6 m in height) have a short trunk, from which sprouts a fairly large cup of numerous branches, each with 5 to 6 ribs (Fig. 1, Bravo-Hollis 1978). Flowers and fruits are produced along the stems, mainly in the areoles of the upper two-thirds of the branches. Fruits are small (1 to 2 cm in diameter), globose to ellipsoid, purple, and spineless (Bravo-Hollis 1978). The flowering season spans from February to April (Arias *et al.* 1997), while fruiting begins in March and continues until September (Palacios 1999; Pérez-Villafaña & Valiente-Banuet 2009).

Study populations

We studied three populations of *M. geometrizzans* located in the northern, central, and southern regions of its distributional range (Fig. 2). The climate in these regions is semiarid, with summer rainfall (Rzedowski 1988). The northern population, ‘La Mantequilla’, is located in the State of San Luis Potosí (22°25′38.60″N, 100°52′57.60″W, 1861 m a.s.l.). Vegetation is a sclerophyllous scrub (Aragón-Gastélum *et al.* 2017) with *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C. Johnst., *Cylindropuntia leptocaulis* (DC.) F.M. Knuth, *Opuntia robusta* H.L.Wendl. ex Pfeiff., *O. ficus-indica* (L.) Mill., and *Acacia farnesiana* (L.) Willd. The mean annual precipitation is 341 mm, and the mean annual temperature is 17.8 °C (Medina-García *et al.* 2005). The central population, ‘La Casita’, is located in the Barranca de Metztitlán Biosphere Reserve in the State of Hidalgo (20°26′44.94″N, 98°40′28.85″W, 1611 m a.s.l.). Vegetation is crassicaulous scrub, accompanied by *P. laevigata* and *Senna wislizeni* (A. Gray) H.S. Irwin & Barneby (Jiménez-Sierra & Jiménez-González 2003). The mean annual precipitation is 427 mm, and the mean annual temperature is 22 °C (SEMARNAP 1999). Finally, the southern population, ‘Barranca del Conejo’, is located in Zapotitlán in the Tehuacán-Cuicatlán Biosphere Reserve in the State of Puebla (18°19′09.71″N, 97°27′05.61″W, 1445 m a.s.l.). At this site, the vegetation is a xerophyllous shrub with *P. laevigata*, *Mimosa luisana* Brandegees, and *Castela tortuosa* Liebm. The mean annual precipitation is 380 mm, and the mean annual temperature is 21 °C. The study was carried out during the fruiting season of *M. geometrizzans* (March-July 2014).

Although the three populations of *M. geometrizzans* had similar fruiting seasons, they experienced different light and thermal environments because of their differences in latitude and longitude.

Orientation of fruits

In order to evaluate if the southern pattern of fruit orientation occurs across its distributional range and along the fruiting season, 30 cacti were randomly selected from each *M. geometrizzans* population. For simplicity, we divided the canopy of each individual plant into two sections, north and south, and selected the two most external northern or southern branches, respectively. The orientation of all ribs of each branch was measured using a Brunton compass. For each rib, we counted the total number of fruits in the first ten areoles from the top at late March-early April, late May-early June, and late June-early July. We used rib orientation as a surrogate of fruit orientation. Angular mean and circular standard errors of the azimuth of the fruits for each population were analysed using circular statistics (Batschelet 1981; Zar 1999). Watson-Williams multisample *F* test for circular data was performed to evaluate the differences in fruit orientation among populations. These analyses were performed using ORIANA for Windows v. 4.02 (Kovach 2013).

PAR, nocturnal acid accumulation (NAA), and fruit production

The PAR and NAA measurements, as well as the first fruit count, were conducted on two consecutive sunny days: 29-30 March 2014 for 'La Casita' (hereafter referred to as Metztlán), 2-3 April for 'Barranca del Conejo' (Zapotitlán), and 11-12 April for 'La Mantequilla' (San Luis Potosí). For each population, we selected the more exposed rib from 16 unobstructed branches, each from 16 different individuals. The sample ribs were distributed evenly from 0 to 360° under the hypothesis that PAR

and NAA vary with orientation. As much as possible, we tried to replicate the same rib orientation in the three populations. In fact, the circular distributions of the orientation of the 16 selected ribs in each population were not different from uniformity (Rayleigh's test for circular uniformity: $0.442 \leq z \leq 0.502$, $p \geq 0.612$).

For all selected ribs, we measured the diurnal courses of PAR using a portable MINIPAM fluorometer (Walz, Effeltrich, Germany). The sensor (Leaf-Clip Holder 2030B with a Distance Leaf-Clip 2010A; Walz, Effeltrich, Germany) was placed on each of the two rib sides, at approximately the midway point between the first and tenth areole. Measurements were recorded hourly from 0500 (predawn) to 1900 (dusk). The total daily incident PAR for each rib was calculated as the average of the total daily PAR (value integrated over the daytime; Nobel 1980, 1985) for both sides of the rib (expressed as $\text{mol m}^{-2} \text{d}^{-1}$). During this time (i.e. late March-early April), the total number of fruits in the first 10 areoles of each of the 16 ribs was counted, and the count was repeated in late May-early June and late June-early July.

In each population, for the same selected ribs, we determined the NAA by measuring tissue acidity in a sample collected at dusk (1900) and one collected at predawn (0500). The two tissue samples were removed (1 cm^2 cork borer) from the right side of the ribs (1 cm apart), where PAR had been measured. Each sample was placed in a vial containing 70 % ethanol. Tissue acids were extracted by boiling samples in distilled H_2O . For each sample extract, acid equivalents were determined by titration with 0.01 N NaOH to an endpoint of pH 7.0 (Osmond *et al.* 1994; Baker & Adams III 1997; Andrade *et al.* 2007). Tissue acidity was expressed on an area basis ($\text{mmol H}^+ \text{m}^{-2}$). The NAA was calculated as the difference between the values of malic acid at predawn and dusk (Nobel 1988).

The effect of rib orientation on number of fruits and total daily PAR (late March-early April) for each population was analysed using periodic regressions (Batschelet 1981) and performed with PAST v.

2.17 (Hammer *et al.* 2001). In order to evaluate the effect of total daily PAR and NAA on the number of fruits for ribs with different orientations, we performed a generalized linear model with a Poisson distribution and a log link function. Similarly, in order to test if the total daily PAR and NAA measured in late March-early April had an effect on the number of fruits counted at late May-early June and late June-early July, we performed a generalized linear model for each date (assumed a Poisson distribution and a log link function). Because there were significant differences in the number of fruits among populations, we also performed generalized linear models to evaluate the effect of total daily PAR and NAA on the number of fruits in each population (assuming a Poisson distribution and a log link function). All generalized linear models were carried out using JMP software v. 9.0.0 (SAS Institute Inc. 2010).

RESULTS

Orientation of fruits

The fruits for the three populations at each of the three dates showed a significant angular mean (Raleigh's test; Table 1, Fig. 3). During late March-early April and late May-early June, the average orientation was southern, between 136.44° and 206.88° (Table 1, Fig. 3). However, during late June-early July (Table 1, Fig. 3), the average orientation was southern for San Luis Potosí (194.36°) and Metztlán (149.81°), but Zapotitlán had an eastern orientation (108.18° ; Table 1, Fig. 3). There were significant differences among populations for each of the three dates (Williams-Watson multisample F test: $F_{2,16560} = 121.4, p < 0.0001$; $F_{2,18597} = 394.45, p < 0.0001$; and $F_{2,11339} = 277.9, p < 0.0001$, respectively).

PAR, NAA, and fruit production

There was a significant effect of rib orientation on the number of fruits, with all three populations having the highest number of fruits for south-facing ribs (Fig. 4a). Periodic regressions showed that the number of fruits increased significantly towards 184.5° at San Luis Potosí ($x^2 = 979.69$, $p = 0.0127$, $r^2 = 0.37$), 182.5° at Metztitlán ($x^2 = 394.79$, $p = 0.0229$, $r^2 = 0.26$), and 161° at Zapotitlán ($x^2 = 658.02$, $p = 0.0009$, $r^2 = 0.47$). These results were consistent with the aforementioned southern orientation for the three populations. Furthermore, the periodic regressions revealed that the relationship between the orientation of the ribs and the total daily PAR intercepted was significant for Metztitlán ($x^2 = 112.7$, $p = 0.0008$, $r^2 = 0.47$, Fig. 4b) and marginally significant for San Luis Potosí ($x^2 = 866$, $p = 0.0526$, $r^2 = 0.21$, Fig. 4b). The total daily PAR increased significantly towards 182.5° for Metztitlán and 184.5° for San Luis Potosí. However, this relationship was not significant for Zapotitlán ($x^2 = 271.59$, $p = 0.1236$, $r^2 = 0.14$).

In late March-early April, the number of fruits was significantly different among populations ($x^2 = 54.00$, $df = 2$, $p < 0.0001$). Metztitlán had the lowest number of fruits (mean \pm SE: 5.81 ± 1.49) compared to San Luis Potosí (11.71 ± 2.41) and Zapotitlán (12.81 ± 2.27). At this date, both total daily PAR and NAA had a significant positive effect on the number of fruits ($x^2 = 21.08$, $df = 1$, $p < 0.0001$ and $x^2 = 33.30$, $df = 1$, $p < 0.0001$, respectively). At the population level, we found a significant positive effect of total daily PAR on the number of fruits at San Luis Potosí ($x^2 = 13.74$, $df = 1$, $p = 0.0002$), Metztitlán ($x^2 = 17.36$, $df = 1$, $p < 0.0001$), and Zapotitlán ($x^2 = 4.33$, $df = 1$, $p = 0.0374$). In addition, there were significant positive effects of NAA on the number of fruits for San Luis Potosí ($x^2 = 19.91$, $df = 1$, $p < 0.0001$) and Zapotitlán ($x^2 = 34.41$, $df = 1$, $p < 0.0001$). However, for Metztitlán, this relationship was not detected ($x^2 = 1.19$, $df = 1$, $p = 0.2751$) probably because this population showed the lesser production of fruits during the study.

In late May-early June, there were no significant differences among populations for the number of fruits ($x^2 = 1.64$, $df = 2$, $p = 0.4387$). There was a significant positive relationship between the total daily PAR intercepted during late March-early April and the number of fruits ($x^2 = 14.05$, $df = 1$, $p = 0.0002$). In contrast, the effect of NAA on number of fruits was not statistically significant ($x^2 = 0.61$, $df = 1$, $p = 0.4328$). In late June-early July, there were no significant differences among populations for the number of fruits ($x^2 = 2.53$, $df = 2$, $p = 0.2822$), and no significant effect of total daily PAR or NAA on number of fruits ($x^2 = 2.5$, $df = 1$, $p = 0.0912$ and $x^2 = 0.08$, $df = 1$, $p = 0.7704$).

DISCUSSION

The explanation for equatorial orientation of reproductive structures for extratropical columnar cacti suggested by Tinoco-Ojanguren & Molina-Freaner (2000) states that the highest amount of PAR, received by equatorial-facing ribs and branches, results in the highest carbon gain. Thus, in the northern hemisphere, a high interception of total daily PAR on southern ribs and branches would result in more available resources for fruit production (Figueroa-Castro & Valverde 2011). In this study, we found evidence suggesting that these factors are responsible for the southern pattern of fruit orientation observed in populations of *M. geometrizans*, an intertropical columnar cactus. Further evidence could be provided by infrared gas analyzer (IRGA) documenting patterns of gas exchange among ribs with different orientation

Although the mean direction varied among populations of *M. geometrizans*, the mean fruit orientation showed a consistent south azimuth (136.44°-206.88°), at least during springtime (i.e. late March-early April and late May-early June). However, at the end of the fruiting season (i.e. late June-early July), the southernmost population, Zapotitlán, exhibited an eastern orientation (108.18°). This is likely

because in the Zapotitlán population (18° latitude N), east- and west-facing ribs intercept the highest PAR at the beginning of the summer (Nobel 1985; Gibson & Nobel 1986; Nobel 1988).

In the three studied populations of *M. geometrizans*, periodic regression models predict a maximum fruits production for orientations towards 184.5°, 182.5°, and 161° at San Luis Potosí, Metztitlán and Zapotitlán, respectively. In similar way, southern ribs also received the highest total daily PAR, reaching maximum values towards 184.5° and 182.5°, at San Luis Potosí and Metztitlán, respectively. However, such pattern was not statistically supported at Zapotitlán, the southernmost population, likely because at lower latitudes of the Northern Hemisphere, the incidence of light on the southern ribs would be less marked than in higher latitudes due to the angle of incidence of incoming radiation (Nobel 1985). Broadly, these results suggest that in *M. geometrizans*, south-facing ribs receive the highest total daily PAR and produce the most fruit. For extratropical species, similar results were noted for *P. pringlei* (Tinoco-Ojanguren & Molina-Freaner 2000) and *P. pecten-aboriginum* (Aguilar-Gastelum & Molina-Freaner 2015) in the Sonoran Desert. Both studies reported that south-facing ribs receive the highest PAR and have the most reproductive structures. Similarly, in *P. weberi*, an intertropical species, flowers and fruits are produced mainly on ribs facing south-southeast (Córdova-Acosta 2011), which also receives more total daily PAR (Figueroa-Castro & Valverde 2011).

Our analyses during the fruiting season revealed that total daily PAR has a significant positive effect on fruit production for ribs varying in orientation. This suggests that ribs intercepting more PAR (i.e. southern orientated ribs) produce more fruits. Moreover, we found similar results for the effect of NAA on the number of fruits. In cacti, NAA has been used as a measure of carbon gain (Nobel & Harstock 1983; Gibson & Nobel 1986; Sortibrán *et al.* 2005), and therefore, those ribs that experience more carbon gain produce more fruits. The positive effect of high total daily PAR and NAA values on fruit production provides the strongest evidence in support of our hypothesis. The positive relationship between PAR and productivity has been documented in some cacti species (Gibson &

Nobel 1986; Nobel 1988). For example, during the reproductive season (mid-spring), the *P. weberi* south-facing flowers, compared to the north-facing flowers, received 18.19 % more total daily PAR (Figueroa-Castro & Valverde 2011), were bigger (Córdova-Acosta 2011), and contained a higher number of ovules per ovary (Figueroa-Castro & Valverde 2011) and pollen grains per floral bud (Aguilar-García 2012). Furthermore, Figueroa-Castro & Valverde (2011) noted more and heavier seeds for south-facing fruits than for north-facing fruits. Because the incident PAR and CO₂ uptake depend on the orientation of the ribs (Nobel & Pimienta-Barrios 1995), highly irradiated south-facing ribs, or branches, appear to be more capable of obtaining sufficient resources to produce fruits within a plant (Tinoco-Ojanguren & Molina-Freaner 2000; Figueroa-Castro & Valverde 2011). Our study provides new evidence suggesting that a differential net carbon gain among ribs or branches, as a consequence of the heterogeneity in the lighting environment at the within-plant level, could be accountable for the southern orientation pattern of *M. geometrizzans* fruits, among and within populations.

Notwithstanding the evidence regarding the non-random circular distribution of fruits in columnar cacti could be traced since Johnson (1924) on flower orientation of the *Carnegiea gigantea* (Engelm.) Britton & Rose, a species native of the Sonoran Desert, this evidence has been scarce and limited to extratropical species (Tinoco-Ojanguren & Molina-Freaner, 2000; Aguilar-Gastelum & Molina-Freaner, 2015; Warren *et al.*, 2016). For extratropical species of columnar cacti, ribs or branches facing towards the equator receive PAR all year long. However, for intertropical species, the amount of PAR received by equatorial-facing ribs or branches varies between seasons. For example, at low latitudes in the northern hemisphere (0° to 20° N), east-, north-, and west-facing ribs experience similar PAR interception during the summer solstice, while south-facing ribs receive their lowest PAR (Nobel 1985; Gibson & Nobel 1986). Our results suggest that *M. geometrizzans* has a similar pattern of fruit orientation as extratropical columnar cacti. To our knowledge, this is the first study that tests the hypothesis that the higher carbon gain on equatorial ribs, due to a highest interception of

PAR (Tinoco-Ojanguren & Molina-Freaner, 2000), would be the main responsible factor for the equatorial orientation pattern of reproductive structures in an intertropical columnar cactus species.

Plants are modular organisms that produce multiple repeated structures (Diggle 2003). As an inevitable consequence of plant modularity, is the emergence of variation in the characteristics of the copies of the same organ as flower, fruits, and seeds, produced not only in different branches but also within the same branch of a plant (Herrera 2009, p. 3). Such variation could be explained by extrinsic gradients, which are defined as variation in some environmental parameters, largely independent of the plant architecture (Herrera (2009). Orientation and light intensity are examples of such parameters. Herrera (2009) points out that evidence on such extrinsic gradients in traits of reiterated structures, other than leaves, are uncommon for wild plants. Our results, however, seem to be a remarkable example of these extrinsic gradients of within-individual plant variation. Although in this study, we address the underlying mechanism for the southern orientation pattern of fruit in *M. geometrizans*, a fundamental question remains to be answered: what are the effects of the southern orientation pattern of fruit on plant fitness? In this respect, few studies have addressed the effect of orientation of reproductive structures in components of fitness in cacti species (Córdova-Acosta 2011; Figueroa-Castro & Valverde 2011). Future studies should attempt to examine, for example, if the fruits produced in the south ribs are of better quality and if they are more attractive to fruit dispersers.

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FIGURE CAPTIONS

Fig. 1. Mature individual of *Myrtillocactus geometrizans* in Zapotitlán (southern population). This individual is approximately 5.5 m height.

Fig. 2. Mexico's map showing the three studied populations of *Myrtillocactus geometrizans*. Contours of Mexican states San Luis Potosí, Hidalgo, and Puebla, are shown.

Fig. 3. Circular frequency distributions of fruit orientations for the three studied populations of *Myrtillocactus geometrizans* at three different dates. Angular mean and 95% confidence interval of angular mean are indicated for each distribution.

Fig. 4. Periodic regressions between (a) ribs orientation and number of fruits, and (b) ribs orientation and total daily PAR for the studied populations of *Myrtillocactus geometrizans* at late March-early April. Only significant models, and their observed data, are shown.

Table 1. Summary of circular statistics for fruit orientation in three populations of *Myrtillocactus geometrizans* at three different dates. $\bar{\alpha}$ = angular mean, κ = concentration parameter, SD_{circular} = circular standard deviation, SE_{circular} = standard error of $\bar{\alpha}$, 95% C. I. = lower and upper 95% confidence limits of $\bar{\alpha}$.

Population/date	Number of fruits	$\bar{\alpha}$	κ	SD_{circular}	SE_{circular}	95% C. I.	Rayleigh test of uniformity (p)
San Luis Potosí							
late March-early April	6019	182.19°	0.446	100.06°	2.36°	177.54°–186.83°	< 0.0001
late May-early June	8050	206.88°	0.184	125.26°	4.91°	197.24°–216.52°	< 0.0001
late June-early July	4657	194.36°	0.104	139.28°	11.39°	172.03°–216.69°	< 0.0001
Metztlán							
late March-early April	2849	150.22°	0.636	88.54°	2.44°	145.43°–155.22°	< 0.0001
late May-early June	4401	154.79°	0.417	102.10°	2.95°	148.99°–160.59°	< 0.0001
late June-early July	2860	149.81°	0.307	111.28°	4.96°	140.08°–159.55°	< 0.0001

Zapotitlán

late March-early April	7695	155.50°	0.229	119.50°	4.05°	147.55°–163.44°	< 0.0001
late May-early June	6149	136.44°	0.184	125.20°	5.61°	125.44°–147.44°	< 0.0001
late June-early July	3825	108.18°	0.233	118.97°	5.63°	97.13°–119.23°	< 0.0001







