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Short Communication

Flower orientation in *Pachycereus weberi* (Cactaceae): Effects on ovule production, seed production and seed weight

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ABSTRACT

Few studies have determined the importance of orientation on flower reproductive success. Flower orientation may affect reproduction of Cactaceae; the interception of photosynthetic active radiation (PAR) differs along the different sides of cacti stems, and translocation of resources between cacti ribs does not appear to occur. Therefore, PAR received by each cacti stem face may determine the resources available for reproduction. We examined the reproductive success of *Pachycereus weberi* flowers with contrasting orientations. Ovule production per ovary, number of seeds per fruit, seed set per fruit and seed weight were used as indicators of reproductive success for flowers facing southeast and northeast. PAR received on opposite stem sides was recorded as an estimator of resource availability for each side. Results showed that flowers facing southwards produced more ovules and seeds and produced heavier seeds. Seed set was not significantly different between flowers with contrasting orientations. The southern stem faces received more PAR than the northern faces. Reproductive success was different for flowers with contrasting orientations, suggesting that there is an association between PAR received on different *P. weberi* stem faces and floral reproductive success.

1. Introduction

Capture of photosynthetic active radiation (PAR) by plants is associated with CO_2 uptake and plant productivity (Lajtha et al., 1997; Nobel and Quero, 1986; Nobel et al., 1991). PAR interception is particularly important for cacti (Niklas, 2002) because they require an optimal capture of PAR without over-heating the stems. Tilting of the stems is a strategy that allows cacti to overcome this conflict (Lajtha et al., 1997; Zavala-Hurtado et al., 1998). Thus, cacti tilt toward the equator to optimize PAR capture and prevent stem over-heating (Gibson and Nobel, 1986).

Cacti stem orientation may determine resource availability for diverse physiological processes taking place on the stem (e.g., Drezner, 2003). This is particularly important because carbohydrates do not appear to transfer among ribs in columnar cacti (Tinoco-Ojanguren and Molina-Freaner, 2000). Thus, the amount of PAR received on a particular region of the stem determines productivity on that region of the stem (Geller and Nobel, 1986; Lajtha et al., 1997; Nobel et al., 1991). Moreover, it has been shown that PAR received on different sides of the stem is significantly different (Nobel and Quero, 1986; Nobel et al., 1991).

It is possible that PAR received on different regions of the stem may also determine flower reproductive success. In some Cactaceae species, reproductive structures are not evenly distributed around the stem (e.g., Johnson, 1924; Tinoco-Ojanguren and Molina-Freaner, 2000; Valverde et al., 2007). For example, species from the northern hemisphere, such as *Pachycereus pringlei* (Tinoco-Ojanguren and Molina-Freaner, 2000) and *Pachycereus weberi* (Córdova-Acosta et al., 2007), have most of their reproductive structures on their south-southeastern stem sides, where higher PAR is received.

Tinoco-Ojanguren and Molina-Freaner (2000) have suggested that the region of the stem that receives higher PAR (i.e., the southern face for species found in the northern hemisphere) may have higher photosynthetic rates than the region of the stem that receives lower PAR. Consequently, the region of the stem that receives higher PAR may have a higher availability of resources and thus may develop more reproductive structures than the region of the stem that receives lower PAR (Tinoco-Ojanguren and Molina-Freaner, 2000). Therefore, it is expected that a plant from the northern hemisphere will produce more reproductive structures and more seeds and have heavier seeds on their southern stem sides than on their northern stem sides.

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We examined the aforementioned hypotheses in *P. weberi* (J.M. Coulter) Backeb. This species produces floral buds on all sides of the stems; however, flowers and fruits are produced predominantly facing south-southeast (Córdova-Acosta et al., 2007). We aim to determine the role of flower orientation on flower reproductive success. Particularly we examine whether reproductive structures facing southwards are more successful at producing ovules and seeds, filling seeds and producing heavier seeds than structures facing northwards. In addition, we corroborate that different PAR is received on the northern and southern stem faces of *P. weberi*.

2. Study species

P. weberi is an arborescent cactus (10–15 m in height). The main stem branches out into numerous vertical branches each with 9–11 ribs (Arias et al., 1997). Flowers are 7–11 cm in length and 4.9 cm in diameter and grow apically in the stem (Arias et al., 1997; Valiente-Banuet et al., 1997). Fruits are ellipsoidal, fleshy, red, 3.5–7 cm in length and 3–6 cm in width. Seeds are 2.5–3.5 mm in length. *P. weberi* flowers from November to February and fructifies from February to May (Valiente-Banuet et al., 1997). *P. weberi* is self-incompatible, has nocturnal anthesis and is pollinated by bats (Valiente-Banuet et al., 1997). *P. weberi* is endemic to Mexico and grows in arid and semi-arid environments in Central and South Mexico (Guzmán et al., 2003).

3. Study site

This study was conducted on the southwest border of the Tehuacán-Cuicatlán Biosphere Reserve where *P. weberi* dominates the landscape. The study site is close to San José Chichihualtepec (18°11′35″N, 97°48′20″W) and is around 1589 m above sea level. Vegetation in the study site is xerophytic shrubland. The climate is semi-arid, with a rainy season during the summer. The average annual temperature is 18–22 °C, and the mean annual precipitation is 400 mm (Zavala-Hurtado and Hernández-Cárdenas, 1998).

4. Methods

We measured PAR to corroborate that its interception is different between opposite branch faces of *P. weberi*. PAR was measured on one *P. weberi* individual using a Li-Cor LI-189 (Li-Cor Instruments, Lincoln, NE). Radiation sensors facing south, north and toward the sky were attached apically (where reproductive structures are produced) to a single branch of the cactus. Sensors were fixed to the stem with an adhesive Velcro® belt and wire. From 1000 h on April 6 to 1000 h on April 7, 2009, PAR was recorded every 5 min on a 24 h cycle. The average hourly PAR interception and total daily PAR for each orientation were estimated.

Ovule production, seed number, seed set and mean seed weight per fruit were calculated to estimate reproductive success on flowers with contrasting orientations. Buds, flowers and fruits were collected, and their orientation in the field was determined with a Brunton© compass. Buds and flowers were stored in formaldehyde–acetic acid–ethyl alcohol (FAA), whereas fruits were stored in paper bags. Reproductive structures were brought to the laboratory for posterior analysis. All reproductive structures were collected from individual plants growing on a flat surface; thus, the effect of slope on PAR interception is absent.

Sixty-seven buds and flowers (from 18 individuals; 1–13 structures from each plant) and 118 fruits (from 20 individuals; 1–17 fruits from each plant) with contrasting orientations were selected randomly. While we wanted to compare the reproductive success between reproductive structures facing north (270–89°) versus those facing south (90–269°), all of the reproductive structures collected were oriented toward the northeast (buds and flowers faced 0–89°; fruits faced 3–86°) and the southeast (buds and flowers faced 95–170°; fruits faced 95–178°) stem faces. Thus, for all of the traits analyzed we compared the reproductive success of reproductive structures facing northeast versus those facing southeast.

Sixty-seven buds and flowers were dissected to determine ovule production (35 faced northeast while 32 faced southeast). The number of ovules was quantified on a quarter of the ovary and then multiplied times four to estimate the total number of ovules per ovary.

Fruits were dried at room temperature, and the number of seeds per fruit was counted. Seed set was estimated as the percentage of matured seeds from the mean number of ovules per fruit in each plant (as was previously determined). Mean seed weight per fruit was estimated as the total seed weight per fruit divided by the total number of seeds per fruit. Seeds were weighed on a Sartorius BL610 scale at 0.01 g.

The effect of orientation on ovule and seed production, seed set and seed weight was analyzed with *t*-tests. Fruits with no seed production were excluded from the analysis for seed weight. To fit data normality, number of ovules and number of seeds were transformed as $\sqrt{x} + 0.5$, whereas seed set was transformed as arcsin $\sqrt{x}$. Analyses were conducted in SAS 9.0.

5. Results

The southern stem faces of *P. weberi* received more PAR than the northern faces for at least 6 h a day (from 0900 to 1500 h; half of the time that the plants are exposed to light; Fig. 1). Maximum PAR received on the southern and northern stem faces were 272.97 μmol m^{-2} s^{-1} and 193.12 μmol m^{-2} s^{-1}, respectively. The maximum PAR received by the sensor facing toward the sky was 2183.9 μmol m^{-2} s^{-1}. Total daily PAR was 7.08 mol m^{-2} and 5.99 mol m^{-2}, for the southern and northern stem faces, respectively.

Reproductive structures facing toward the southeast produced significantly more ovules per flower (mean ± 1 SE: 1376.5 ± 87.96) than reproductive structures facing toward the northeast (1016.77 ± 73.68; $t = 3.34$, d$f = 65$, $P < 0.01$; Fig. 2a). Likewise, the number of seeds per fruit was significantly higher in fruits oriented toward the southeast (895.92 ± 48.55) than in fruits oriented toward the northeast (712.82 ± 52.03; $t = 2.70$, d$f = 116$, $P < 0.01$; Fig. 2b). In

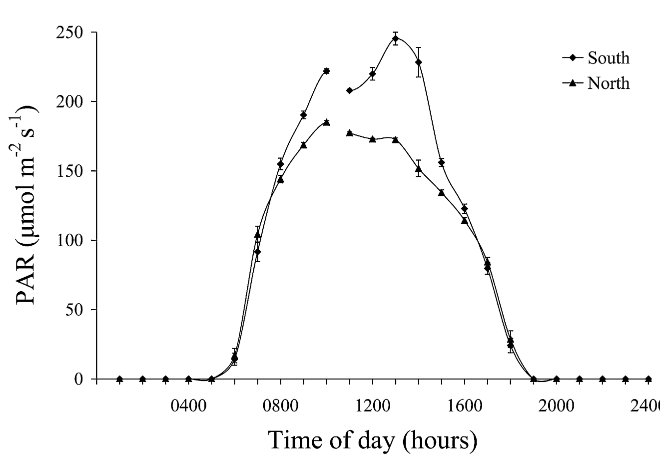

Fig. 1. Photosynthetically active radiation (PAR, μmol m^{-2} s^{-1} ± 1 SE) received on opposite sides of the stems of *Pachycereus weberi*. Only measurements from the northern and southern faces of the stem are shown. The sensor oriented toward the sky had a maximum PAR interception of 2183.9 μmol m^{-2} s^{-1}. Measurements were recorded on a 24 h period, April 6–7, 2009.