Climate and microenvironmental parameters affecting anthesis and nectar secretion for *Polaskia chende* and *P. chichipe*, endemic columnar cacti from the Tehuacán Valley, Puebla

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Abstract

Anthesis is a process of paramount ecological importance because it allows access of pollinators to floral structures enabling fertilization and an eventual fruit development. Anthesis is regulated by endogenous and exogenous factors, so changes in the environment can have effects on this process. In the present study, the climate of Acatepec, Puebla was obtained for determining possible climate change scenarios. Also, some microenvironmental factors were measured simultaneously with observations of anthesis and nectar secretion for the columnar cacti *Polaskia chende* and *P. chichipe* in order to shed some light on our understanding of the environmental control of anthesis for these species. Climate change scenarios estimated an increase in January minimum temperature of 1.12 °C for the year 2020, 2.16 °C for the year 2050, and 3.24 °C for the year 2080. A decrease in annual mean precipitation was also estimated; in particular, reductions of 15.23, 18.34, and 23.62 % were respectively estimated for the same years. Nectar production for *P. chende* fluctuated throughout the day while for *P. chichipe* the production was constant. Sugar concentrations were 33.0 ± 1.2 and 27.6 ± 2.2 °Brix, respectively. Both species had diurnal anthesis and their flowering occurred in the winter. In this case, floral evocation can be induced by periods of low temperatures. Therefore, if, at is it expected, winters are increasingly warmer, reproductive development for these species could be reduced owing to an insufficient accumulation of chill units or a decoupling between anthesis and pollinator activity may occur (Cleland *et al*., 2007). Under a scenario of imminent increase in winter temperatures and a reduction in rainfall, a better understanding of the costly process of reproduction can contribute to an assessment of vulnerability of these species.

Key words: climate change, drought, energy balance, photosynthetic photon flux, temperature.

Resumen

La antesis es un proceso de gran importancia ecológica ya que permite el acceso de los polinizadores para llevar a cabo la fecundación permitiendo el posterior desarrollo del fruto. Está regulada por factores internos y externos, por lo que los cambios ambientales pueden tener repercusiones en la antesis. En este estudio se obtuvo la climatología de Acatepec, Puebla, para determinar posibles escenarios de cambio climático. Asimismo, se determinaron algunos factores microambientales de manera simultánea con el seguimiento de la antesis y la secreción de néctar en las cactáceas columnares *Polaskia chende* y *P. chichipe*, a fin de avanzar en el entendimiento del control de la antesis en estas especies. Los escenarios de cambio climático estimaron un aumento de 1.12 °C de la temperatura mínima en el año 2020 de 2.16 °C para el 2050, y de 3.24 °C para el 2080. También se estimó una disminución en la precipitación media anual de 15.23, 18.34 y 23.62 % para los años 2020, 2050 y 2080, respectivamente. La producción de néctar de *P. chende* fluctuó durante todo el día; mientras que la producción de *P. chichipe* fue constante. La concentración de azucares fue de 33 ± 1.2 y 27.6 ± 2.2 °Brix, respectivamente. Las dos especies consideradas en este estudio presentaron flores diurnas de invierno. En tales casos, la evocación floral puede ser inducida por períodos de bajas temperaturas. Por lo tanto, si los inviernos son cada vez menos fríos, es posible que el desarrollo reproductivo pueda ser reducido debido a una acumulación insuficiente de unidades de frío o incluso que se provoque un desfase entre la antesis y la llegada de los polinizadores. Con los supuestos de un inminente aumento de las temperaturas de invierno y disminución de las precipitaciones, la comprensión del costoso proceso de reproducción contribuirá a la evaluación de la vulnerabilidad de estas especies.

Palabras clave: balance de energía, cambio climático, flujo de fotones para fotosíntesis, temperatura, sequía.

Introduction

Anthesis is a process of great ecological significance as it allows access of pollinators to plant reproductive structures for carrying out fertilization and enabling subsequent fruit development (Ollerton and Lack, 1998; van Doorn and van Meeteren, 2003; Fleming, 2006). Anthesis is regulated by internal factors such as hormonal regulation that leads to the expansion of the cell wall and the metabolism of carbohydrates in response to external factors such as light and temperature (Ichimura and Suto, 1998; Bieleski *et al.*, 2000; Taiz and Zeiger, 2002; van Doorn and van Meeteren, 2003; Jaeger *et al*., 2006; van Dijk and Hautekéete, 2007).

Previous studies with the columnar cacti *Polaskia chende* and *P. chichipe*, endemic to the Tehuacán Valley, Mexico (Cruz and Casas, 2002; Otero–Arnaiz *et al*., 2003), suggest that these species may be interesting for studying environmental factors controlling anthesis. Flowering for these sympatric species occurs throughout the winter and the beginning of the spring. However, their reproductive patterns are different. *P. chende* has a gradual increase in flower production that peaks in winter, whereas *P. chichipe* has two flowering peaks, one in winter and the other in spring (Cruz and Casas, 2002; Otero–Arnaiz *et al*., 2003). East–facing flowers of a given individual plant of both species open earlier than their west–facing counterparts. For both species, anthesis occurs well after dawn, 8:00 h for *P. chende* in winter and 9:00 h for *P. chichipe* in winter and spring; therefore, increasing temperature or photosynthetic photon flux have been suggested as plausible environmental cues that trigger anthesis (Cruz and Casas, 2002; Otero–Arnaiz *et al*., 2003).

The Tehuacán Valley is an arid zone in which an astounding diversity of columnar cacti has evolved (Valiente–Banuet *et al*., 1996; Valiente–Banuet and Arizmendi, 1997; Valiente–Banuet *et al*., 1997; Valiente–Banuet *et al*., 2004). As it is the case for most arid regions, a very marked seasonality determines plant phenology. In particular, low temperatures during winter induce flowering when milder temperatures occur toward the spring (Byrne and Bacon, 1992), while the water accumulation in succulent stems of plants during the summer allows the development of their massive flowers and fruits during the dry spring of the following year (Gibson and Nobel, 1986; de la Barrera *et al*., 2009).

Climate change has affected the ecological dynamics of many species and is expected to impose natural selection on various ecologically important traits. Droughts and other anticipated changes in precipitation may be particularly relevant selective factors, especially in arid regions (Franks *et al*., 2007). The effects of global warming in the 20th century, caused by human activity, have been marked by a rise in the average surface temperature (Houghton *et al.*, 1995; Abu–Asab *et al*., 2001). It has been shown that climate change can pose a threat to biodiversity at high–latitudes due to a shortening of low temperatures or by a reduction in precipitation in more tropical regions, but the possible effects of climate change in tropical arid environments has seldom been investigated (Bowers, 2007; Téllez–Valdés and Dávila–Aranda, 2003).

In this study, anthesis and nectar secretion of the columnar cacti *P. chende* and *P. chichipe* were investigated for sympatric populations from San Luis Atolotitlán, Puebla, Mexico. The plants were simultaneously monitored in the field, with the prevailing air temperature, relative humidity, and the incident photosynthetic photon flux, in order to identify possible environmental cues that trigger flower opening and nectar secretion. In addition, inter–annual variations of climate at the study site were used to simulate possible climate change scenarios, in order to assess the vulnerability of Tehuacán plants species to such human–caused climatic perturbation.

Materials and methods

Field site and species

From 26 February to 5 March 2010, anthesis was studied for wild populations of the columnar cacti *Polaskia chende* and *P. chichipe* at San Luis Atolotitlán (18° 10' 43" N; 97° 26', 38" W), Puebla, Mexico, within the Tehuacán–Cuicatlán Biosphere Reserve, where the mean annual temperature is 18 °C and precipitation averages is 546 mm (García, 1981). The Tehuacán Valley has an astounding diversity of cacti. In addition, most of its nearly twenty species of columnar cacti are consumed by humans and eight of them are cultivated (MacNeish, 1967; Casas *et al*., 1999; Casas *et al*., 2001; Casas and Barbera, 2002). The species considered this study constitute the sole two members of an endemic genus from Tehuacán–Cuicatlán.

Climate for San Luis Atolotitlán

Climate data for San Luis Atolotitlán were obtained from the nearest weather station (Comisión Nacional del Agua, 2010) located in Acatepec (18º 15' 24” N, 97º 35' 15” W), Puebla, at a distance of 18 km from the study site. Climate records from 1954 to 2008 were used to determine the baseline climate. The precipitation precipitation was estimated for 49 years (1954–2008), whereas the temperature baseline was estimated for 30 years (1974–2008).

The Regional Analysis Tool, developed by the Pacific Climate Impacts Consortium of the University of Victoria (2010), was used to generate climate change scenarios for the study site. In particular, scenarios were generated utilizing the Canadian Climatic Change Model for an A2 emissions scenario, projecting the mean air temperature and precipitation anomalies for three future times (2020, 2050, and 2080).

Air and plant temperatures

Air temperature, photosynthetic photon flux (PPF, solar radiation with wavelengths between 400 and 700 nm), and relative humidity were measured in the field at 15 minute intervals with a HOBO weather station (Onset Computer Corporation Bourne, MA). Tissue temperature for plant structures (stem, flower bud, flower anthesis) were measured every hour with type T thermocouples and read with a digital thermometer (HH–25KC, Omega Engineering, Inc. Stamford, Ct). The thermocouples were were inserted at a depth of 5 mm on north–facing stems.

Anthesis and nectar secretion and concentration

The onset and duration of anthesis was observed for flower buds that had been covered the night before flower opening with translucent cloth bags for preventing the access of pollinators to flowers. An east–facing and a west facing bud were selected from each of eight individuals for each species. Starting at 5:00 h, approximately 1.5 hours before dawn, the flowers were monitored every two hours. The time of the onset of anthesis, of full opening, and of flower closing was recorded throughout the day. In addition, the secreted nectar solution was collected with a micropipette at the time of each observation to determine its volume and concentration measured with a Brix50 Refractometer (Reichert, Inc. New York, N.Y).

Laboratory observations with detached stems

North–facing apical stems of both species bearing multiple flower buds were collected at San Luis Atolotitlán and transported to a laboratory at the Centro de Investigaciones en Ecosistemas of the Universidad Nacional Autónoma de Mexico (CIEco, UNAM) for careful observation of anthesis and nectar production. Plant apical stems were exposed during the day to direct sunlight (19.4 mol m^{-2} day^{-1}; air temperature ranged from 18 to 25.7°C) and enclosed in a growth chamber (air temperature of 23°C) at night to avoid floral exposure to light. In general, a photoperiod of 10/14 day/night hours was used to mimic the day length observed at the field site. In the morning, when the apical stems were exposed to light, the time and duration of anthesis, as well as nectar secretion and concentration were recorded as described above for plants in the field.

Results

Climate

Acatepec had an average annual temperature of 16.4 ± 0.14ºC and annual precipitation of 558 ± 13.49 mm. The lowest annual temperatures occurred during December and January (Figure 1), averaging 13.6 ± 0.12°C, whereas the highest temperatures occurred in May with an average of 19.2 ± 0.98°C.

Precipitation was seasonally distributed (Figure 2), with 45% of the annual rainfall occurring from June to September, which represents two peaks of maximum precipitation. In contrast, the driest period occurred from November to March accumulating only 4.6% of the annual precipitation.

Historical records showed significant changes in the annual rainfall regime in contrast with a relative stability in the temperature (Figure 2). During the period from 1955 to 1981 the average annual precipitation was 639.53 mm, but in 1982 the annual precipitation was only 128.6 mm. After this year, all annual precipitations have remained below the historical average.

The average annual minimum air temperature was 6.22 ± 0.22ºC over 26 years (Figure 3). The year with the lowest average minimum temperature in January was 1996 with a temperature of 4.32°C. However, the climate change scenarios estimated an increase of 1.12°C for this month in the year 2020 of 2.16°C the year 2050, and of 3.24 for 2080 (Figure 3).

Climate change scenarios also estimated a decrease in the average annual precipitation of 15.23, 18.34 and 23.62% for the years 2020, 2050, and 2080, respectively (Figure 3).

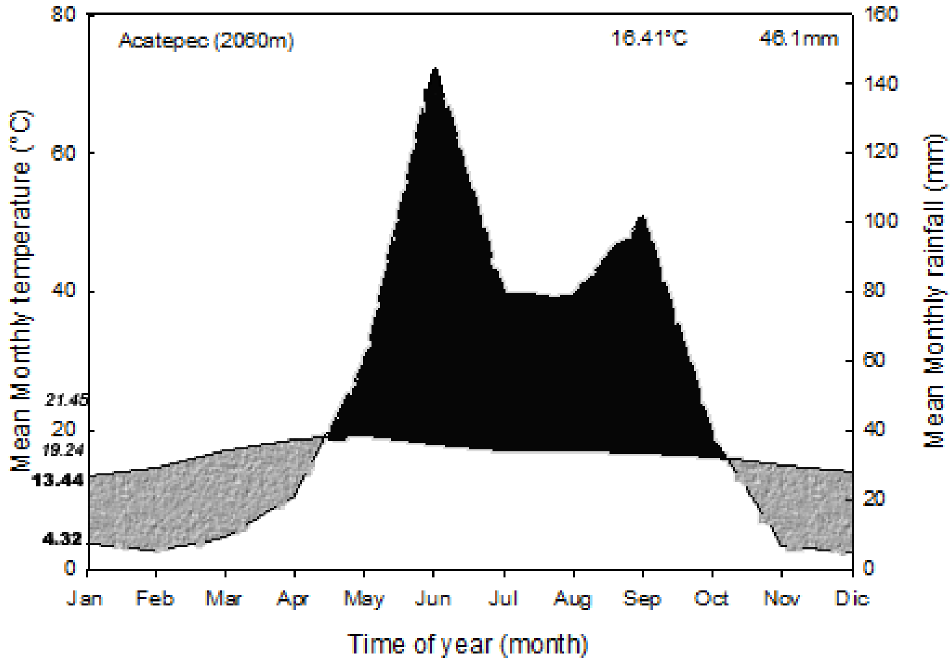

Figure 1. Climate for Acatepec, Puebla; location far away 18 km from the study site. The solid line indicates the monthly mean air temperature and the dashed line indicates the average precipitation for each month. The black polygon formed where the precipitation line is higher than the temperature line indicates the time of the time of the year with water surplus, while the regions with the gray shading represent the times of relative drought. The temperatures in bold–face on the ordinate indicate the average temperature of the coldest month and the absolute lowest monthly temperature, respectively. Similarly, the temperatures in italics indicate the corresponding high temperatures.

Air and plant temperatures

At the time of measurement, the air temperature ranged from 8.5°C at 6:00 h to 23.3°C at 15:00. At such times the relative humidity extremes were also recorded, ranging from 22% to 85% (Figure 4A). The photosynthetic flux density peaked at 12:00 h when it amounted to 1866 µmol m^{-2} s^{-1}. During a day length of 13 h a net photon flux of 20.45 µmol m^{-2} d^{-1} was recorded (Figure 4B).

The tissue temperature of the various organs of *Polaskia chende* gradually increased throughout the day, presenting the highest temperatures at 15:00 h (Figure 5A). A similar pattern was observed for *P. chichipe* whose highest tissue temperature was also recorded at 15:00 h (Figure 5B). For both species, the structure that presented the highest temperature was the stem; where as flower buds and flowers at anthesis had similar temperatures.

Anthesis and nectar secretion and concentration in the field

The anthesis of *P. chende* and *P. chichipe* was diurnal. However, the flowers of *P. chichipe* opened very early in the morning, approximately at 5:00 h. Nectar production of *P. chende* fluctuated throughout the day (Figure 6A). Before anthesis, only a small amount of nectar could be measured (9.42 ± 0.58 µL day^{-1}), and it increased substantially at 11:00 h. The average solute concentration of the nectar solution was 33 ± 1.2°Brix. In turn, nectar production for *P. chichipe* was continuous and the maximum production occurred between 13:00–15:00 h (Figure 6B). The average solute concentration of the nectar solution was 27.6 ± 2.2°Brix.

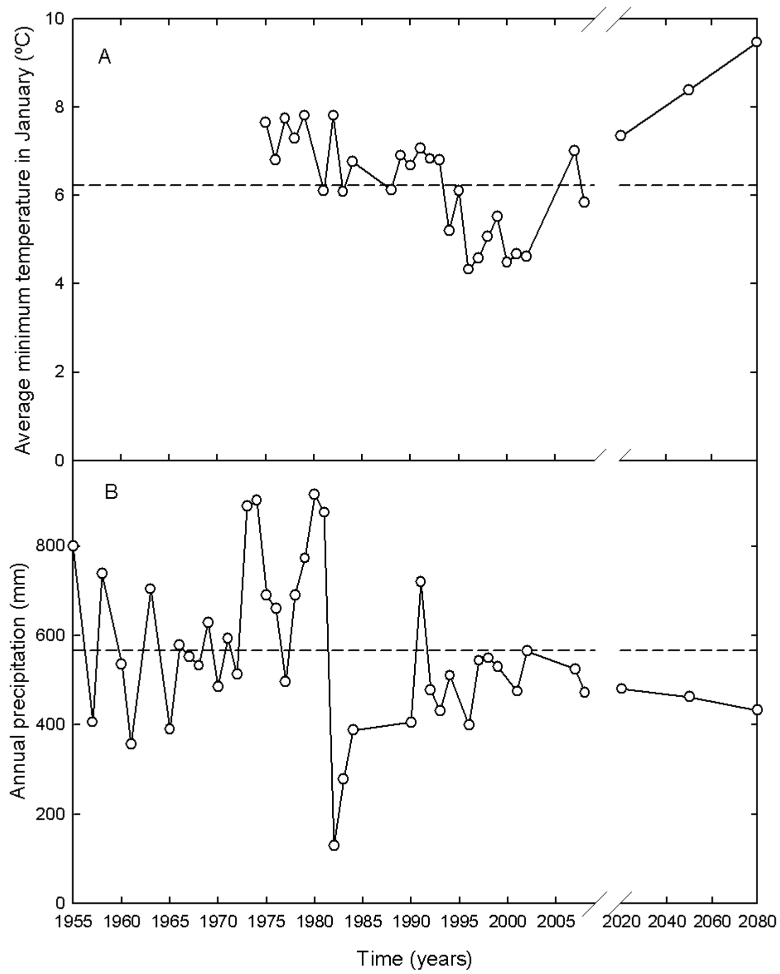

Figure 2. Average minimum temperature in January (A) and cumulative annual precipitation (B) at Acatepec, Puebla. Temperatures are shown from 1975 to 2008 and precipitation spans from 1955 to 2008. For each panel the horizontal line indicates the historial averages of 13.63 ± 0.58 ºC and 566.9 ± 28.2 mm. The projected temperature and precipitation scenarios for the years 2020, 2050, and 2080 are shown after the break for each panel.

Laboratory observations with detached stems

Similar to plants in the field, the flowers of *P. chichipe* observed in the laboratory were diurnal. Their anthesis was triggered after 192.14±32.5 (n=7) minutes of exposure to sunlight. For *P. chende* only two flowers underwent anthesis during the laboratory experiment and required f250-300 minutes of exposure to sunlight to trigger anthesis.

The very small number of flowers of *P. chende* prevented the measurement of nectar secretion in the laboratory, while nectar secretion for *P. chichipe*, which amounted to 12.8±0.7 µl day^{-1}, was similar to that of flowers in the field (Fig. 5B). In this case, a solute concentration of the nectar solution of 25.9±2.2°Brix was also similar to the concentrations measured in the field.

Discussion

Despite a relatively stable temperature throughout the year, the rather pronounced seasonality of precipitation in the Tehuacán Valley, along with its soil particularities, explains why a high richness of cactus species can be found in this arid region of south–central Mexico (Arias *et al*., 1997; Casas *et al*., 2001; Davila *et al*., 2002; Valiente–Banuet *et al*., 2009). For these plants, a very large water storage capacity allows survival even under prolonged droughts, as it occurs for *Polaskia chende* and *P. chichipe* from San Luis Atolotitlán, where the annual precipitation is just below the upper threshold for semiarid zones (Wilsie, 1962; Food and Agriculture Organization, 1993). In turn, such a water capacitance can enable the presence of other associated species of plants and animals, as is the case for the pollinators of these species at a time of the year when drought is at its peak (Gibson and Nobel, 1986; Cruz and Casas, 2002; Otero–Arnaiz *et al*., 2003; de la Barrera *et al*., 2009).

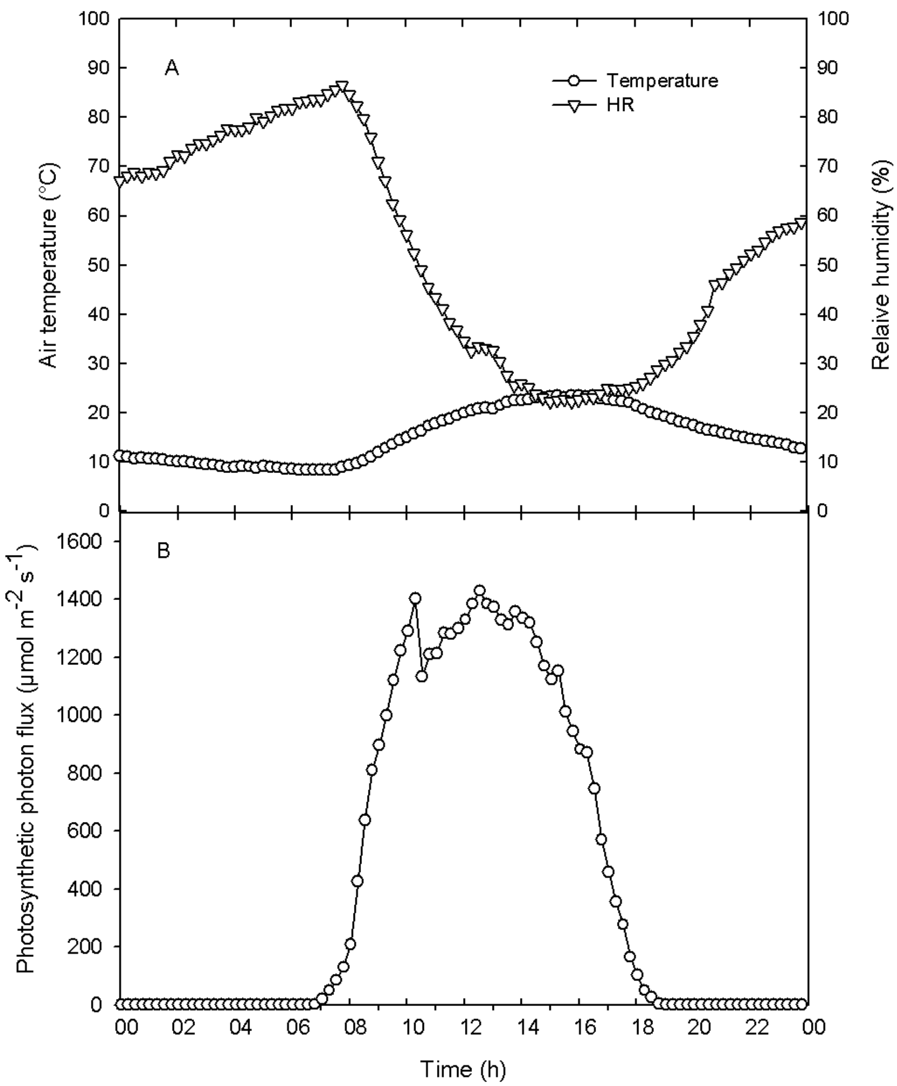

Figure 3. Environmental conditions at Cerro el Tocotín, San Luis Atolotitlán, Puebla, where the prevailing air temperature, relative humidity (A), and photosynthetic photon flux (B) were recorded. Data shown are instantaneous measurements.

Both species considered in this study have winter flowering that extends into the early spring, as is the case for other fruit bearing trees (Cruz and Casas, 2002; Otero–Arnaiz *et al*., 2003; de la Barrera *et al*., 2009). In such cases, floral evocation can be induced by periods of low air temperature, i.e., by the accumulation of so called chill units at temperatures between 0 and 14 °C, and eventually triggered by warm spring temperatures (Byrne and Bacon, 1992; Larcher, 2002). If winters are increasingly mild as projected by climate change scenarios, tree reproductive development can be reduced, or even inhibited, due to an insufficient accumulation of chill units, a phenomenon that has already been observed for some plants from high latitudes of the northern hemisphere (Abu–Asab *et al*., 2001; Cotton, 2003; Primack *et al*., 2004; Bowers, 2007). Indeed, the temperature increase projected for the study site would lead to the reduction of the potentially available chill units.

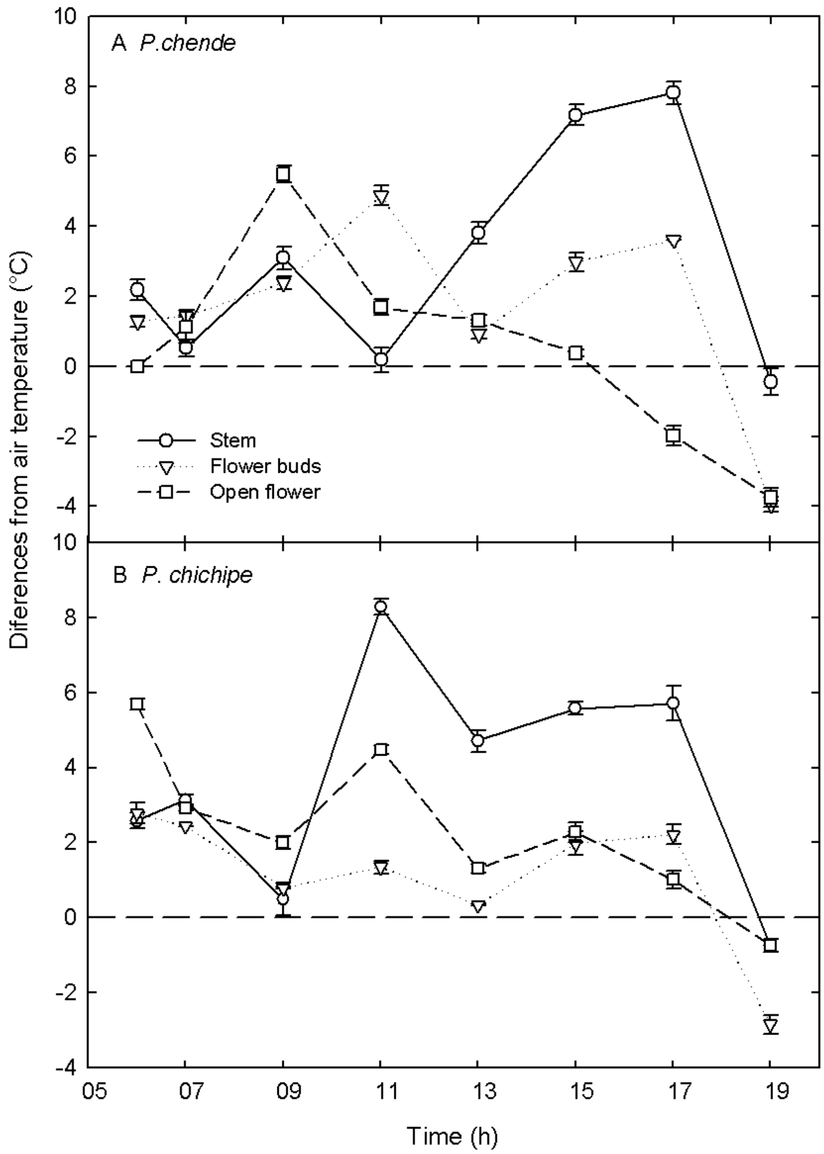

Figure 4. Temperature differences between the air and the stems, flower buds, and open flowers for *Polaskia chende* (A) and *P. chichipe* (B). Data are shown as mean ± standard error (n = 15).

The inter–annual variation of precipitation had a relatively large oscillation around the average, even exceeding 900 mm $year^{-1}$ in extremely wet years. A severe drought in 1982, when only 23 % of the average precipitation was recorded coincided with an El Niño event that spanned from April 1981 to July 1982 (National Weather Service, 2010). After this event, the annual precipitation has reached or exceeded the historical average only twice, including during the 1992–1993 and 2002–2003 El Niño events. For the other 13 years with sufficient data, the annual precipitation did not reach the historical average. The possible causes for this reduction in the amplitude of the inter–annual variation in rainfall are beyond the scope of this manuscript and should be investigated. However, it is noteworthy that the mean annual rainfall has decreased by 14.4 % over the last 28 years.

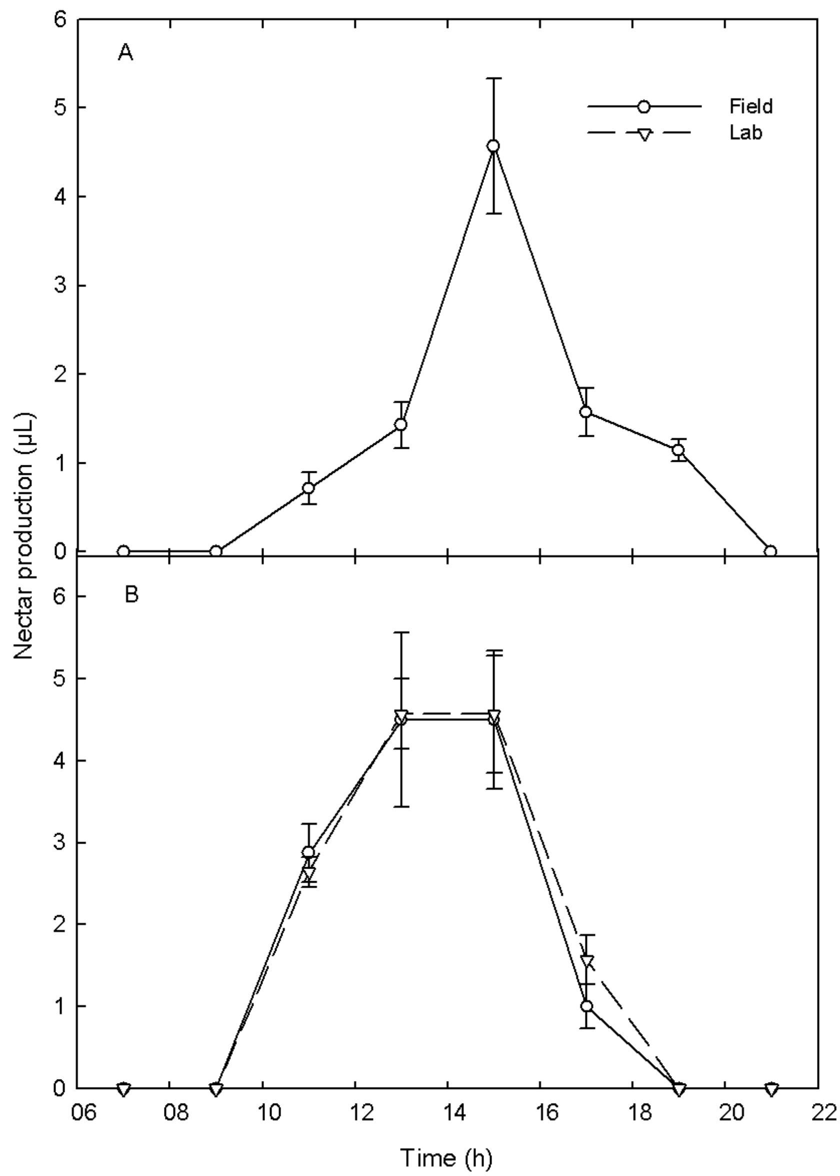

Figure 5. Nectar production for *P. chende* (A) in the field and *P. chichipe* (B) in field and the laboratory. Data are shown as mean ± standard eror (n = 30).

The variation of 14.8°C in temperature and of 63% in relative humidity throughout the day resulted in an amplitude of the vapor pressure deficit (VPD, the difference in vapor pressure between the plant, which is assumed to be at saturation, and the air) of 2.3 kPa, ranging from 0.2 kPa at 6:00 h to 2.5 kPa at15:00 h (Lambers *et al*., 1998; Nobel, 2009). It has been well documented, especially for the massive flowers of cacti, that flowering is a process that is water costly and that anthesis, in particular, requires a substantial input of water to the floral structures in order to enable the anatomical and physiological changes involved, such as cell elongation and nectar secretion (de la Barrera and Nobel, 2004ab; de la Barrera *et al*., 2009). The fact that both anthesis and pollinator activity peaks coincide with the time of highest temperature (Cruz and Casas, 2002; Otero–Arnaiz *et al*., 2003) suggests that the plants are indeed relying on an elevated VPD to mobilize the stored water for conducting their reproductive cycle.

Both *P. chende* and *P. chichipe* produce large amounts of flowers whose development requires, in addition to large volumes of water, a substantial translocation of photosynthates. While the photosynthetic metabolism of these species has not been studied, it is most plausible that they display the Crasssulacean Acid Metabolism (Gibson and Nobel, 1986), for which the amount of carbon fixed during at night is directly related to the total photosynthetic photon flux intercepted by the plants during the previous day (Gibson and Nobel, 1986). The carbon fixation that resulted from the 20 mol m^{-2} day^{-1} that these plants received at the time of measurement requires further investigation under controlled environmental conditions.

For both species, stems, flower buds, and open flowers tended to have a tissue temperature higher than that of the surrounding air. This reflects the high water content of their succulent tissues. Not surprisingly, the stems were able to accumulate greater amounts of heat during the day, their temperatures reaching 8°C above air temperature. With respect to floral buds and open flowers a contrasting pattern was observed between the species considered. For *P. chende*, floral buds can measure 2.75 ± 0.06 cm and weigh 4.75 ± 0.09 g, whereas their longer corollas can reach 5.9 ± 0.06 cm (unpublished observations). In this case, bud temperature peaked at 4.49°C above air temperature at 11:00 h and remained warm throughout the day, while the flower temperature peaked at 5.45°C at 9:00 h and then decreased its temperature, suggesting that the latent heat lost through transpiration was enough to reduce the organ's temperature even reaching 4.49°C below air temperature. On the other hand, the smaller floral buds of *P. chichipe* can measure 1.75 ± 0.50 cm and weigh 1.4 ± 0.04 g, while their corollas measure a mere 1.50 ± 0.14 cm (unpublished observations). For this species, bud and flower temperatures were similar throughout the day, suggesting that their transpiration rates are lower. The water and energy balances for these species should be investigated, considering the decreasing annual precipitation at San Luis Atolotitlan, in order to determine whether stored water will continue to be sufficient to support plant reproduction (de la Barrera and Nobel, 2004a; de la Barrera *et al*., 2009).

This study confirmed that anthesis for both species considered was diurnal. However, the onset of flower opening occurred earlier than previously reported. In particular, the anthesis of *P. chende* started 1.5 h before 8:00h (Cruz and Casas, 2002) and the anthesis of *P. chichipe* ocurred 4 hours before 9:00 h (Otero–Arnaiz *et al*., 2003). However, the time of the maximum rate of nectar secretion coincided with previous observations for both species, at the time of the highest vapor pressure difference as stated above (Cruz and Casas, 2002; Otero–Arnaiz *et al*., 2003).

Observations of flower opening on detached stems confirmed that such stem segments are an adequate model for studying cactus physiology, as has been the case for *O. ficus–indica*, *Hylocereus undatus*, and *Stenocereus queretaroensis* (Nobel and Castañeda, 1998; Nobel and de la Barrera, 2002; Nobel and Pimienta, 1995). The flowers transported to the laboratory were insufficient to conduct proper experiments; and at least for the case of *P. chende*, such manipulation did not significantly affect the floral performance of either species. Therefore, a future experiment under controlled environmental conditions will consider the specific effects of temperature and photosynthetic photon flux on anthesis of these columnar cacti.

Anthesis is a process of paramount importance in plant reproduction, as it enables pollinator access to the reproductive structures. Considering that flowering is a process of great water expenditure (de la Barrera and Nobel, 2004a; de la Barrera et al., 2009), understanding its particularities is important, especially in semi–arid environments such as San Luis Atolotitlán where the fruits of *Polaskia chende* and *P. chichipe* are either cultivated or collected from the field. Both air temperature and light seemed to contribute to the onset of anthesis and nectar production. While it seemed that the higher vapor pressure deficit that occurs during the daytime is a driver of nectar secretion, the mechanisms by which light and temperature mediate anthesis need further investigation. Under an impending scenario of increasing winter temperatures and decreasing rainfall, understanding the use of water for the costly process of reproduction, and the possible impacts of a reduced accumulation of chill units on the triggering and the timing of reproductive development will contribute to the assessment of the vulnerability for these species.

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