UNIVERSIDAD DE GUADALAJARA

CENTRO UNIVERSITARIO DE CIENCIAS BIOLÓGICAS Y AGROPECUARIAS

DIVISIÓN DE CIENCIAS BIOLÓGICAS Y AMBIENTALES

B I O L O G Í A

Seasonal Variation of Net CO_2 Uptake for Cactus Pear (*Opuntia ficus-indica*) and Pitayo (*Stenocereus queretaroensis*) in a Semiarid Environment.

ARTÍCULO CIENTÍFICO PUBLICADO

QUE PARA OBTENER EL TÍTULO DE

LICENCIADO EN BIOLOGÍA

P R E S E N T A

ENRICO ARTURO YEPEZ GONZÁLEZ

LAS AGUJAS, ZAPOPAN, JALISCO. DE 1999

UNIVERSIDAD DE GUADALAJARA

CENTRO UNIVERSITARIO DE CIENCIAS BIOLOGICAS Y AGROPECUARIAS

COORDINACION DE CARRERA DE LA LICENCIATURA EN BIOLOGIA

COMITÉ DE TITULACION

C. ENRICO ARTURO YEPEZ GONZALEZ
P R E S E N T E .

Manifestamos a Usted que con esta fecha ha sido aprobado su tema de titulación en la modalidad de ARTICULO PUBLICADO con el título **"SEASONAL VARIATION OF NET CO2 UPTAKE FOR CACTUS PEAR (Opuntia ficus-indica AND PITAYO (Stenocereus** queretaroensis) **IN A SEMIARID ENVIRONMENT"**, para obtener la Licenciatura en Biología.

Al mismo tiempo le informamos que ha sido aceptado como Director de dicho trabajo al **DR. EULOGIO PIMIENTA BARRIOS.**

A T E N T A M E N T E
" PIENSA Y TRABAJA "
LAS AGUJAS, ZAPOPAN, JAL., OCTUBRE 1 DE 1999

COMITE DE TITULACION

DRA. MONICA ELIZABETH RIOJAS LOPEZ
PRESIDENTE DEL COMITE DE TITULACION

LICENCIATURA EN BIOLOGIA

Alma Rosa Villalobos

DRA. ALMA ROSA VILLALOBOS ARAMBULA
SECRETARIO DEL COMITE DE TITULACION

c.c.p. .-DR. EULOGIO PIMIENTA BARRIOS.- Director del Trabajo.
c.c.p. Expediente del alumno.

MERL/ARVA/bacg*

Km. 15.5 Carretera Guadalajara - Nogales
Predio "Las Agujas", Nextipac, C.P. 45110 • AP 39-82
Tels (91-3) 682-0246 682-0374 Fax. 6820120
Zapopan, Jalisco, México

Seasonal Variation of Net CO_2 Uptake for Cactus Pear (*Opuntia ficus-indica*) and Pitayo (*Stenocereus queretaroensis*) in a Semiarid Environment*.

Eulogio Pimienta-Barrios★, Julia Zañudo-Hernandez★, Enrico Yepez-González★, Enrique Pimienta-Barrios† & Park S. Nobel‡

★*Departamento de Ecología, Centro Universitario de Ciencias Biológicas y Ambientales, Universidad de Guadalajara, Zapopan, Jalisco, Mexico.*

†*Departamento de Producción Agrícola, Centro Universitario de Ciencias Biológicas y Ambientales, Universidad de Guadalajara, Zapopan, Jalisco, Mexico.*

‡*Department of Biology-OBEE, University of California, Los Angeles, CA 90095-1606, USA.*

*(Variación Estacional de Asimilación de CO_2 para el Nopal (*Opuntia ficus-indica*) y Pitayo (*Stenocereus queretaroensis*) en un Ambiente Semiarido.

Para ser publicado en:

ACADEMIC PRESS

JOURNAL OF ARID ENVIRONMENTS

ISSN 0140-1963

1999

JOURNAL OF ARID ENVIRONMENTS

Academic Press Editorial Office
10d St Edward's Passage
Cambridge CB2 3PJ, UK
Telephone: +44 (0)1223 329933
Fax: +44 (0)1223 460236
email: jae@harcourtbrace.com

Dr Eulogio Pimienta-Barrios
Cerrada de la maestranza 924
Residencial Guadalupe Jardin, 45030
Zapopan
Jalisco
Mexico

14 July 1999

Dear Dr Pimienta-Barrios

Re: Manuscript Reference Number: JAE 99/025

Title: Seasonal Variation of Net CO2 Uptake for Cactus Pear (Opunita ficus-indica) and Pitayo (Stenocereus queretaroenisis) in a Semiarid Environment

Authors: E Pimienta-Barrios, J Zanudo-Hernandez, E Ypees-Gonzalez, E Pimiento-Barrios, P A Nobel

I am pleased to inform you that the above paper has been accepted for publication in the ***Journal of Arid Environments***.

Yours sincerely

Anne Marquess
(on behalf of Professor Whitford)

REPORTE DE ANOMALIAS

CUCBA

A LA TESIS:

LCUCBA00523

Autor:

Yepez Gonzalez Enrico Arturo

Tipo de Anomalía:

Errores de Origen: No cuenta con indice de contenido
La tesis no esta foliada

The objective of this work was to evaluate the effects of seasonal variation in temperature, irradiation and soil moisture content on the photosynthetic rates of *Opuntia ficus-indica* and *Stenocereus queretaroensis*. The lowest values of positive daily net CO_2 uptake were recorded during the summer rainy season and the highest values during autumn and winter. These highest values were likely the result of a prolonged period of CO_2 assimilation caused by decreased cloudiness, and high rates of nocturnal CO_2 assimilation due to moderate day/night air temperatures. In spring, when drought was exacerbated, daily net CO_2 uptake was negative for both *O. ficus-indica* and *S. queretaroensis* . Stem photosynthesis allowed both *O. ficus-indica* and *S. queretaroensis* to obtain carbon during the fall and winter, when the soil water was lowest.

Key words: *Opuntia*; *Stenocereus*; air temperature; drought; gas exchange; phenology; photosynthetic photon flux; stress

Introduction

Cactus pear (*Opuntia* spp.) and pitayo (*Stenocereus* spp.) are fruit crops used for subsistence agriculture in Mexico (Pimienta, 1994; Pimienta-Barrios & Nobel, 1994). Cactus pear is also cultivated worldwide on just over 1,000,000 ha (Nobel, 1994, 1999), mostly for forage and fodder. In Mexico, it is an important fruit crop in semiarid temperate lands, where it has been cultivated for centuries and now occupies about 60,000 ha (Nobel, 1994; Flores, 1995). In contrast, pitayo is a relatively recent fruit crop, and cultivation of *S. queretaroensis* is restricted to the Sayula Basin in Jalisco, Mexico, on an area of about 1,000 ha (Pimienta & Tomas, 1993). In other regions of central and southern Mexico, fresh fruits of other pitayos are harvested from plantations, backyards of rural homes, and wild populations (Pimienta-Barrios & Nobel, 1994).

Cactus pear evolved in a semiarid temperate environment with relatively cool nights and moderate daytime temperatures (Pimienta, 1990, 1994). In contrast, pitayo evolved in a subtropical environment with warm nights and high daytime temperatures (Pimienta *et al.*, 1998). Although differences occur in the day/night air temperatures in the main localities where cactus pear and pitayo are cultivated, large variations in soil water availability and long drought periods occur where both are native (Gibson & Nobel, 1986; Pimienta-Barrios & Nobel, 1994). For instance, the dry season can be 6 to 8 months long and is interrupted by rains during the summer season. This study examined the influence of seasonal variations in day/night air temperatures, soil moisture content, and photon flux density on the daily patterns of gas exchange for both *O. ficus-indica* and *S. queretaroensis* in a region where the latter is native. We tested the hypothesis that environmental conditions in the study site adversely affect the photosynthetic activity of *O. ficus-indica* relative to *S. queretaroensis* because of the relatively warm day/night air temperatures.

Materials and methods

The study was conducted from July 1997 to May 1998 at a commercial plantation in Techaluta, Jalisco, Mexico, in the Sayula Basin of southern Jalisco at 20° 5' North latitude, 103° 32' West longitude, and 1,380 m above sea level. The Sayula Basin, where pitayo [*Stenocereus queretaroensis* (Weber) Buxbaum] occurs in the wild and also is extensively cultivated, has average daily extreme temperatures that range from 10 °C to 34 °C, with an annual average of 22 °C. The average annual rainfall is nearly 700 mm, most of which occurs in the summer (Pimienta & Nobel, 1994). Pitayo de Queretaro (*S. queretaroensis*) is an arborescent cactus growing up to 8 m in height with a well-defined short trunk and numerous, mostly vertical branches. Thirty-year-old plants of the most cultivated variety, Mamey, were used in this study.

Opuntia ficus-indica (L.) Miller var. Pelón-Liso is a variety of cactus pear introduced into the Sayula Basin from the semiarid temperate highlands of San Luis Potosi, Mexico, where it is cultivated as a fruit crop. Cuttings planted in Techaluta in 1990 were collected at about 23° 05' North, 102° 32' West, and 2,000 to 2,200 m above sea level. The collection site has about 400 mm of precipitation in summer, winter rains occur in some years, and the average annual temperature is 17 °C (Pimienta, 1994). *O. ficus-indica* is an arborescent, 2-3 m tall cactus, with a poorly defined trunk, wide crown, and flat obovate segments (cladodes).

Times of initiation and termination of the main vegetative and reproductive phenophases (stem elongation, flowering and fruit development, and new root growth) new root formtation) were determined monthly for six mature plants of *O. ficus-indica* and six mature plants of *S. queretaroensis*. The times of initiation and termination of stem elongation, flowering and fruit development were determined from monthly observations, and root formation was determined by careful excavations of the rhizosphere in order to distinguish between existing roots and new ones. Daily maximum and minimum air temperatures and rainfall were obtained from an official weather station maintained by the Comision Nacional del Agua, Delegacion Jalisco, at Atoyac (20° 1' North, 103° 32' West, 1,373 m above sea level). The photosynthetic photon flux (PPF; wavelengths of 400-700 nm) for each measurement time was measured from approximately 2 h after sunrise to 2 h before sunset with a Li-Cor 190S quantum sensor (Li-Cor, Lincoln, NE.). For each measurement time, soil water content was determined for 10 soil samples from the center of the root zone (a depth of 15 cm). Soils were dried at 80 °C until no further mass change occurred (generally within 72 h); data are expressed as percent water content (fresh mass - dry mass)/dry mass (Torres, 1984).

Net CO_2 uptake, stomatal conductance, and intercellular CO_2 mole fraction for *O. ficus-indica* and *S. queretaroensis* were measured every 2 h over 24-h periods during 25-26 July 1997, 7-8 November 1997, 17-18 December 1997, 12-13 February 1998, and 9-10 May 1998 with a Li-Cor LI-6200 portable photosynthesis system. A Li-Cor 250-cm^3 leaf chamber was modified by replacing the distal half-cylinder with a narrowed opening (1 cm × 3 cm) that was lined with a foam-rubber gasket, which was firmly pressed against east-facing stems during measurement..

Results

Flower development for *O. ficus-indica* started in early March and ended in late April; fruit development lasted from mid April to late August (Fig. 1a). Its stem growth occurred from April through July. Flowering for *S. queretaroensis* started in early February and ended in early April; fruit development lasted from early March until late May (Fig. 1b). Its stem extension occurred from mid September through December. For both species, the differentiation and growth of fine roots coincided with the summer rainy season, July through September (Fig.1).

Monthly means of daily air temperature extremes at Techaluta, Jalisco, varied from 8 to 15 °C at night and from 27 to 35 °C during the daytime (Fig. 2a). The warmest months were April and May, just before the rainy season. The lowest average day/night air temperatures during the 24-h periods of gas exchange measurement were in December (26/16 °C) and February (29/15 °C) The highest were in November (32/24 °C) and May (36/23 °C), and July was intermediate (30/17°C). Total rainfall in the study year under was 447 mm, 75% occurring from June to September (Fig. 2b). Soil water content ranged from 2% in May to 41% in July (Fig. 2c) and was over 30% from June through October. Photosynthetic photon flux (PPF) was lowest during the summer rainy season, increased gradually during autumn and winter and reached its highest values in spring (Fig. 2d). Photosynthetic photon flux averaged 1,050 μmol m^{-2} s^{-1} from early morning to late afternoon. With the exception of May 1998, net CO_2 uptake patterns for *O. ficus-indica* (Fig. 3) and *S. queretaroensis* (Fig. 4) were typical of CAM plants. Most assimilation occurred at night, and the highest rates were near midnight. Diurnal assimilation was observed for *O. ficus-indica* in the early morning in July 1997, in the late afternoon in November 1997 and December 1997, and at both times in February 1998 (Fig. 3a-d). For *S. queretaroensis*, diurnal assimilation was observed mainly in the early morning (Fig. 4a-d). In May 1998 the instantaneous rates of net CO_2 uptake were mainly negative for both species (Figs. 3e and 4e).

Total daily net CO_2 uptake obtained by integrating the instantaneous rates over 24-h periods was about 270 mmol m^{-2} d^{-1} for *O. ficus-indica* and *S. queretaroensis* in July 1997 (Table 1). Values increased for both species in November, became highest in December 1997, decreased in February 1998, and became negative in May. The highest total daily net CO_2 uptake in December 1997 for *O. ficus-indica* (618 mmol m^{-2} d^{-1}) and *S. queretaroensis* (767 mmol m^{-2} d^{-1}) were due both to prolonged periods of assimilation (19 and 21 h, respectively) and to the highest maximal instantaneous rates (24 μmol m^{-2} s^{-1} for both species; Figs. 3c and 4c). Averaged over the five measurements dates, total daily net CO_2 uptake was 393 mmol m^{-2} d^{-1} for *O. ficus-indica* and 367 mmol m^{-2} d^{-1} for *S. queretaroensis* (Table 1), which correspond to annual CO_2 uptake values of 144 mol m^{-2} and 134 mol m^{-2}, respectively. Total daily net CO_2 uptake in December 1997 for *O. ficus-indica* was statistically similar to November 1997 and February 1998, but those months were statistically higher than July 1997 and May 1998. On the other hand, in *S.*

queretaroensis December was statistically higher than the rest of the months; November 1997 and February 1998 were statistically similar, but higher than July 1997 and May 1998 (Table 1).

The average nighttime stomatal conductance decreased gradually from July 1997 to February 1998 for both *O. ficus-indica* and *S. queretaroensis* and then increased in May 1998 (Table 1). The average intercellular CO_2 mole fraction during the night for both *O. ficus-indica* and *S. queretaroensis* decreased gradually from the beginning of the summer (July 1997) to the middle of the winter (February 1998), when the values were the lowest (Table 1). The intercellular CO_2 mole fraction at night substantially increased in May 1998 for both species (Table 1).

Discussion

The subtropical climate that prevails in the study site, which is the native habitat of *Stenocereus queretaroensis*, was expected to affect adversely the photosynthetic activity of *Opuntia ficus-indica* because the day/night air temperatures of the Sayula Basin are significantly higher than those where the *Opuntia* is native. However, total daily net CO_2 uptake was often higher in *O. ficus-indica* than in *S. queretaroensis*. The latter has an unusual growth phenology, as its vegetative growth does not coincide with its reproductive growth (Pimienta *et al.*, 1998). By contrast, both vegetative and reproductive growth overlap at the end of winter and during spring in *O. ficus-indica* (Pimienta, 1990). Sink strength commonly affects source strength or the rate of photosynthesis (Salisbury & Ross, 1992), but in both *O. ficus-indica* and *S. queretaroensis*, the highest daily net CO_2 uptake was recorded in December, a time of year when the stem extension had ended in *S. queretaroensis* and had not yet begun in *O. ficus-indica*.

The lowest positive daily net CO_2 uptake over 24 h occurred at the beginning of the rainy season, July 1997, when plants began their recovery from the drought and PPF was reduced because of cloudiness. Light limits photosynthesis for both *O. ficus-indica* and *S. queretaroensis*, as net CO_2 uptake increases more-or-less linearly with total daily PPF up to 20 mmol m^{-2} d^{-1} (Nobel & Hartsock, 1984; Nobel & Pimienta-Barrios, 1995). For instance, recent gas exchange observations in the field during the summer reveal that exposed stems of *S. queretaroensis* (PPF of 16 mol m^{-2} d^{-1}) have longer periods of net CO_2 uptake, higher maximal rates, and greater daily net CO_2 uptake than do shaded stems (PPF of 3 mol m^{-2} d^{-1}; Pimienta-Barrios & Nobel, 1998).

The highest maximal instantaneous rates and highest total daily net CO_2 uptake for both species occurred in December 1997, reflecting the moderate day/night air temperatures (26/16 °C) and the increase in PPF because of reduced cloudiness. Moderate night temperatures favor PEPCase activity and CO_2 uptake by CAM succulents (Hanscom & Ting, 1978; Israel & Nobel, 1995; Kluge & Ting 1978; Nobel, 1988). In particular, the mean day/night air temperatures in December 1997 (26/16 °C) and February 1998 (29/15 °C) were close to those optimal for net CO_2 uptake by *O. ficus-indica* under controlled environmental conditions (25/15 °C; Israel & Nobel, 1995; Nobel & Hartsock, 1984). Maximal daily net CO_2 uptake for *S. queretaroensis* in the laboratory occurs under day/night temperatures averaging 32/16 °C (Nobel & Pimienta-Barrios, 1995).

In February 1998 total daily net CO_2 uptake was 15% less for *O. ficus-indica* and 46% less for *S. queretaroensis* than in December 1997 but higher than in July and November 1997. The reduction paralleled decreases in soil water availability and water stored in the cladodes of *O. ficus-indica* and the columnar stems of *S. queretaroensis* but did not parallel day/night air temperatures, which were moderate (29/15 °C), and PPF, which reached higher levels than in preceding months. Nevertheless, the water stored in the stems still sustained stomatal opening, thereby keeping the photosynthetic tissue active during the initial period of drought (Barcikowski & Nobel, 1984; Goldstein *et al.*, 1991). Prolonged drought decreased stomatal conductance, thereby reducing transpirational water losses, as previously demonstrated for *O. ficus-indica* (Acevedo *et al.*, 1983; Kluge & Ting, 1978).

Negative daily net CO_2 uptake in May 1998 for both species reflected the prolonged drought, as soil moisture was extremely low (<5%) and day/night air temperatures were high (36/23 °C). Such conditions affect both stomatal opening and activity of photosynthetic enzymes, (Nobel, 1994). The prolonged drought reduced both the instantaneous rate and the daily period of net CO_2 uptake. The stress exacerbated by high day/night temperatures and drought apparently increased respiration and reduced enzymatic activity, because the gas exchange measurements in May 1998 revealed an increase in the internal CO_2 mole fraction at night, consistent with responses to drought in other CAM plants, such as *Kalanchoe daigremontiana* (Maxwell *et al.*, 1997).

The ecological and agronomical success of cacti such as *Opuntia* and *Stenocereus* in semiarid environments depends on various adaptive characteristics, such as stem succulence and nocturnal carbon assimilation (Nobel, 1988, 1995). These allow cacti to tolerate prolonged drought by extending carbon gain during periods of low soil water availability, as stem succulence acts as an important buffer to maintain turgescence in the photosynthetic tissue (Nilsen *et al.*, 1989, 1990; Nobel, 1995). Stem photosynthesis allowed *O. ficus-indica* and *S. queretaroensis* to obtain carbon three months after the soil water content was below 5%, so the plants could store energy that will support reproductive growth before new resources become available.

Acknowledgment

We thank Lucila Méndez-Morán, Joanna Acosta- Velásquez, Alejandro Valenzuela Martínez, Marcela López-Coreas, and Alejandro Domínguez de la Torre for field assistance. We thank Arnulfo Torres Padilla for access to the pitayo plantation and the Pitayo Growers Association of Techaluta, Jalisco, for their support. This project was financially supported by the Universidad de Guadalajara, CONACyT grant 0568P-B9506, and the UCLA Council on Research.

References

Acevedo, E., Badilla, I. & Nobel P. S. (1983). Water relations, diurnal acidity changes, and productivity of a cultivated cactus, *Opuntia ficus-indica*. *Plant Physiology*, **72**: 775-780.

Barcikowski, W. & Nobel P. S. (1984). Water relations of cacti during dessication: distribution of water in tissue. *Botanical Gazzette*, **145**: 110-115.

Flores, V. C. (1995). Factores economicos que afectan la produccion de nopal en México. In: Pimienta-Barrios, E., Neri-Luna, C., Muñoz-Urias, A. & Huerta-Martinez, M.(Eds.). *6to. Congreso Nacional y 4to. Internacional sobre el conocimiento y aprovechamiento del Nopal*, pp. 228-234. México: Universidad de Guadalajara. 308 pp

Gibson, A. C. & Nobel P. S. (1986). *The cactus primer*. Cambridge, MA: Harvard University Press. 286 pp.

Goldstein, G., Andrade J. & Nobel, P. (1991). Differences in water relations parameters for the chlorenchyma and the parenchyma of *Opuntia ficus-indica* under wet versus dry conditions. *Australian Journal of Plant Physiology*, **18**: 95-107.

Hanscom, Z. & Ting I. P. (1978). Irrigation magnifies CAM-photosynthesis in *Opuntia basilaris* (Cactaceae). *Oecologia*, **33**: 1-15.

Israel, A. A. & Nobel P. S. (1995). Growth temperature versus CO_2 uptake, Rubisco and PEPCase activities, and enzyme high temperature sensitivities for a CAM plant. Plant Physiology and Biochemistry, **33**: 345-351.

Kluge, M. & Ting I. P. (1978). Crassulacean acid metabolism. Analysis of an ecological adaptation. Springer-Verlag, Berlin. 209 pp

Maxwell K., Von caemmerer S., & Evans J.R, (1997) Is a low internal conductance to CO2 diffusion a consequence of succulence in plants with crassulacean acid metabolism *Australian Journal of Plant Physiology*, **24**: 777-786.

Nilsen, E., Meinzer F. C., & Rundel P.W. (1989). Stem photosynthesis in *Psorothamnus spinosus* (smoke tree) in the Sonoran Desert of California. *Oecologia*, **79**: 193-197.

Nilsen, E., Sharifi M., Rundel P., Forseth I.. & Ehleringer J. (1990). Water relations of stem succulent trees in north-central Baja California. *Oecologia*, **82**: 299-303.

Nobel, P. S. (1988). *Environmental biology of agaves and cacti.*, New York, NY: Cambridge University Press. 270 pp.

Nobel P.S. (1994). *Remarkable agaves and cacti.* New York, NY: Oxford University Press. 166 pp

Nobel P.S. (1995). Environmental biology. Agro-ecology, cultivation and uses of cactus pear, pp. 36-48. In: G. Barbera, Inglese P. & Pimienta-Barrios, E. (Eds.). FAO Plant Production and Protection Paper 132, Rome. 216 pp.

Nobel P.S. (1999). *CAM crops.* In: K. R. Reddy and H. F. Hodges (Eds.). Climate change and global crop productivity. England, Wallingford: CAB International. in press.

Nobel P.S. &. Hartsock T. L. (1984). Physiological responses of *Opuntia ficus-indica* to growth temperature. *Physiologia Plantarum*, **60**: 98-105.

Nobel P.S. & E. Pimienta-Barrios. (1995). Monthly stem elongation for *Stenocereus queretaroensis*: Relationships to environmental conditions, net CO_2 uptake, and seasonal variations in sugar content. *Environmental and Experimental Botany*, **35**: 17-42.

Pimienta, B. E. (1990). *El nopal tunero.* Guadalajara, Jalisco, México: Universidad de Guadalajara. 246 pp.

Pimienta B.E. & M.L. Tomas V. (1993). Caracterizacion de la variacion en el peso y la composición quimica del fruto en variedades de pitayo (*Stenocereus queretaroensis*). *Revista Sociedad Mexicana Cactologia*, **38**: 82-88.

Pimienta-Barrios, E. (1994). Prickly pear (*Opuntia* spp.): A valuable fruit crop for the semi-arid lands of México. *Journal of Arid Environments*, **28**: 1-11.

Pimienta-Barrios, E. & Nobel P. S. (1994). Pitaya (*Stenocereus* spp., Cactaceae). An ancient and modern fruit crop of México. *Economic Botany*, **48**: 76-83.

Pimienta-Barrios, E. & Nobel P. S. (1998). Vegetative, reproductive, and physiological adaptations to aridity of pitayo [*Stenocereus queretaroensis* (Weber) Buxbaum]. *Economic Botany*,. **52**: 391-401.

Pimienta-Barrios, E., Hernandez, G., Dominguez, A. & Nobel P. (1998). Growth and development of the arborescent cactus *Stenocereus queretaroensis* in a subtropical semiarid environment, including effects of gibberellic acid. *Tree Physiology*, **18**: 59-64.

Salisbury, B. F. & Ross, C. W. (1992). *Plant physiology* (4th Edn). Belmont, CA: Grupo Editorial Interamericana (México). 279 pp.

Torres, R. E. (1984). *Manual de conservacion de suelos agricolas.* México: Diana. 180 pp.

Table 1. Seasonal variations in daily net CO_2 uptake, mean nighttime stomatal conductance, and mean nighttime intercellular CO_2 mole fraction over 24-h periods for *Opuntia ficus-indica (O. f.-i.)* and *Stenocereus queretaroensis (S. q.)*. Data are means ± SE (n = 6 plants).

Date	Total daily net CO_2 uptake (mmol m^{-2} d^{-1})		Mean nighttime stomatal conductance (mol m^{-2} s^{-1})		Mean nighttime intercellular CO_2 mole fraction (μmol mol^{-1})	
	O. f.-i.	*S. q.*	*O. f.-i.*	*S. q.*	*O. f.-i.*	*S. q.*
25-26 July 1997	269b	273 c	1.90 a	1.23 a	334 b	349b
7-8 November 1997	597a	443 b	0.89 ab	1.01 ab	354 b	362 a
17-18 December 1997	618a	767 a	0.15 b	0.17 b	301 c	288 bc
12-13 February 1998	523 a	414 b	0.21 b	0.14 b	231 d	230 c
9-10 May 1998	-40 c	-76 d	0.84 ab	0.83 ab	399 a	424 a

Mean values within a column that are followed by different letters are significantly different at $P < 0.05$ by LSD's multiple test.

Figure Legends

Figure 1. Phenological stages of *Opuntia ficus-indica* (a) and *Stenocereus queretaroensis* (b) at Techaluta, Jalisco, Mexico.

Figure 2. Daily minimum (∇) and maximum (Δ) air temperatures averaged over a month (a), total monthly rainfall (b), soil water content (c), and mean photosynthetic photon flux (PPF) from early morning to late afternoon (d) at Techaluta, Jalisco, Mexico. Data are means ± SE, except when error bars are smaller than the symbol (n = 10).

Figure 3. Net CO_2 uptake rates over 24-h periods for *O. ficus-indica* on 25-26 July 1997 (a), 7-8 November 1997 (b), 17-18 December 1997 (c), 12-13 February 1998 (d), and 9-10 May 1998 (e) at Techaluta, Jalisco, Mexico. Data are means ± SE (n = 6 plants).

Figure 4. Net CO_2 uptake rates over 24-h periods for *S. queretaroensis* on 25-26 July 1997 (a), 7-8 November 1997 (b), 17-18 December 1997 (c), 12-13 February 1998 (d), and 9-10 May 1998 (e) at Techaluta, Jalisco, Mexico. Data are means ± SE (n = 6 plants).

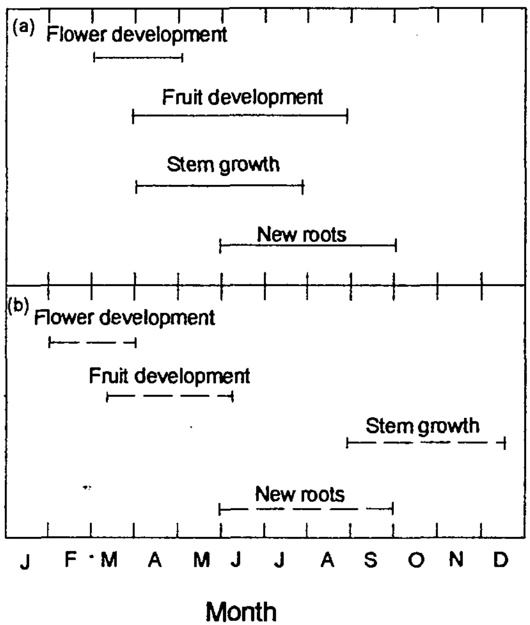

Figure 1. Phenological stages of *Opuntia ficus-indica* (a) and *Stenocereus queretaroensis* (b) at Techaluta, Jalisco, Mexico.

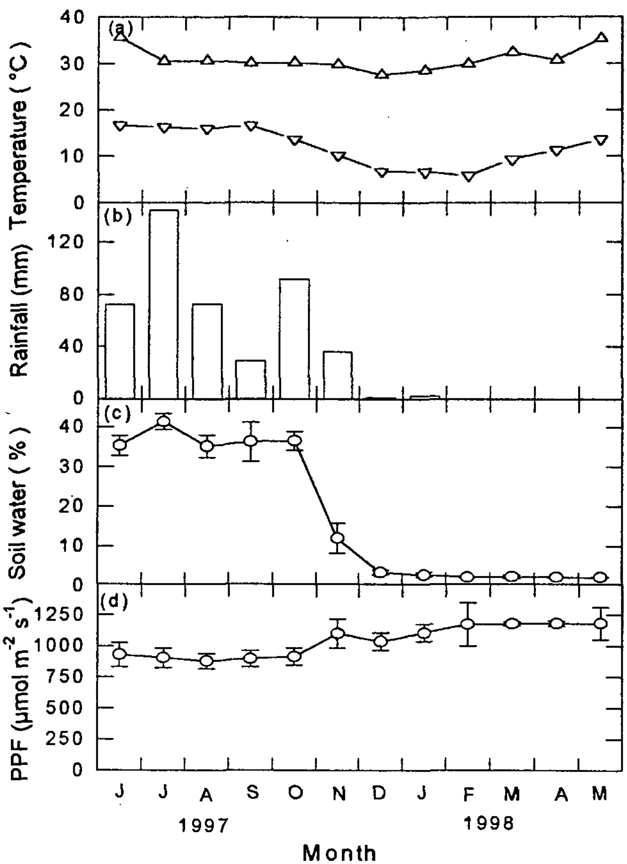

Figure 2. Daily minimum (∇) and maximum (Δ) air temperatures averaged over a month (a), total monthly rainfall (b), soil water content (c), and mean photosynthetic photon flux (PPF) from early morning to late afternoon (d) at Techaluta, Jalisco, Mexico. Data are means ± SE, except when error bars are smaller than the symbol (n = 10).

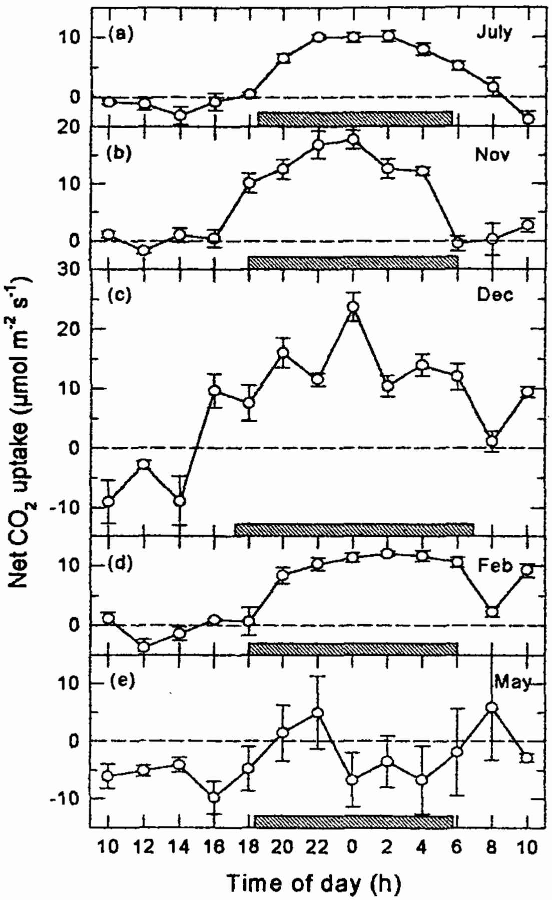

Figure 3. Net CO_2 uptake rates over 24-h periods for *O. ficus-indica* on 25-26 July 1997 (a), 7-8 November 1997 (b), 17-18 December 1997 (c), 12-13 February 1998 (d), and 9-10 May 1998 (e) at Techaluta, Jalisco, Mexico. Data are means ± SE (n = 6 plants).

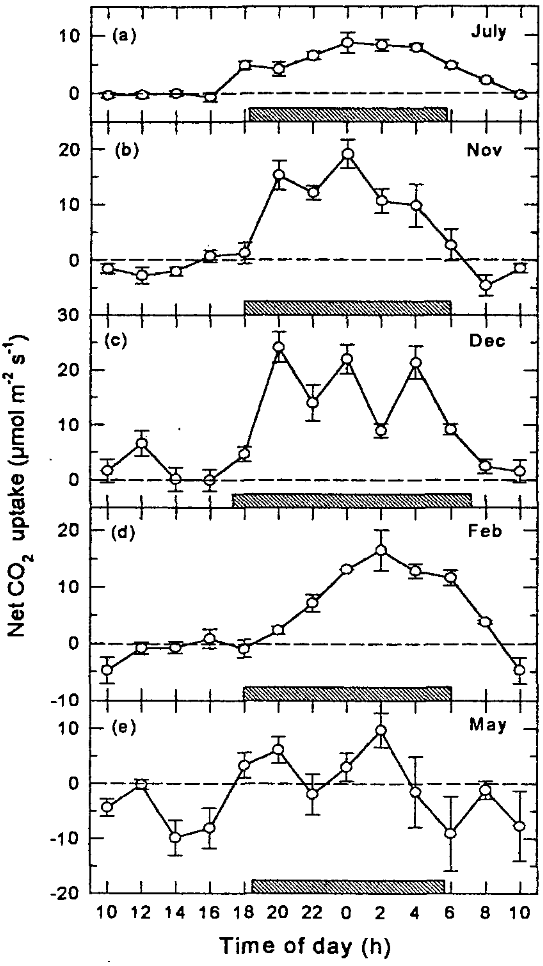

Figure 4. Net CO_2 uptake rates over 24-h periods for *S. queretaroensis* on 25-26 July 1997 (a), 7-8 November 1997 (b), 17-18 December 1997 (c), 12-13 February 1998 (d), and 9-10 May 1998 (e) at Techaluta, Jalisco, Mexico. Data are means ± SE (n = 6 plants).