

# Growth and reproductive characteristics of the columnar cactus *Stenocereus queretaroensis* and their relationships with environmental factors and colonization by arbuscular mycorrhizae

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**Summary** Three natural populations of pitayo (*Stenocereus queretaroensis* (Weber) Buxbaum), a columnar arborescent cactus, were studied in their subtropical environments in western Mexico. All of the sites were characterized by shallow, nutrient-poor soils. Percentage of colonization by arbuscular mycorrhizae (AM) fungi, stem growth, fruit mass, and percentage germination were greater in *S. queretaroensis* at Autlan, Jalisco (AJ) than at Zacoalco de Torres, Jalisco (ZTJ) or Santa Rosa, Zacatecas (SRZ). The onset of root colonization by arbuscular mycorrhizae during the middle of the summer wet period preceded increases in stem extension rate and stem phosphorus concentration. Based on previous studies of effects of environmental factors on photosynthesis, climatic conditions were more favorable for photosynthesis at AJ than at SRZ and ZTJ, as indicated by the amount of summer rainfall, the amount of light, and the moderate air temperatures that prevailed during the fall and winter seasons. There was a significant positive correlation between stem growth and percentage of total root length colonized by arbuscules of AM fungi for *S. queretaroensis* at SRZ and AJ, but not at ZTJ. A negative significant correlation was observed between stem growth and maximal and minimal air temperatures at the three study sites. Stem growth was positively related to rainfall only at SRZ, and light was statistically related to stem growth only at ZTJ. Among sites, *S. queretaroensis* at AJ had the highest carbon gain and greatest AM colonization, creating physiological conditions that led to the highest stem growth, fruit mass and percentage of seed germination.

**Keywords:** AM fungi, fruit, phosphorus, seed quality, subtropical environments.

## Introduction

Wild populations of the arborescent cactus pitayo (*Stenocereus queretaroensis* (Weber) Buxbaum), a species that produces edible, attractively colored fruits, are an integral part of the natural ecosystems of subtropical deciduous forests (Pimienta-Barrios and Nobel 1994). The reproductive structures, flowers and fruits produced by *S. queretaroensis* are a staple of the diet of the inhabitants of these regions. The fruits are also an important source of water and energy for invertebrates (e.g., bees, ants, beetles) and vertebrates (e.g., bats), because the fruits ripen at the end of the dry season when both water and energy sources are scarce in the natural environment (Lomeli and Pimienta 1993, Fleming and Sosa 1994, Petit 1995, Valiente-Banuet et al. 1997). Wild populations of pitayo grow on subtropical, semiarid inland mountains on rocky slopes with shallow soils. Commonly, plants growing in a rocky environment enhance nutrient uptake through mycorrhizal associations (Chapin 1980, Smith and Smith 1996). Cui and Nobel (1992) demonstrated that inoculation of the Crassulacean acid metabolism (CAM) species *Agave deserti* Engelm. and *Ferocactus acanthodes* (Lem.) Britton & Rose with field-collected mycorrhizal spores enhanced water and nutrient uptake. Symbiosis between arbuscular mycorrhizae (AM) fungi and tree species in natural populations is well documented (Klironomos and Kendrick 1993, Merryweather and Fitter 1995, Smith and Read 1997). Although reports on the association of cacti with AM fungi in natural populations are scarce (Rincon et al. 1993, Smith and Read 1997, Pimienta-Barrios and Nobel 1998, Arceta-González et al. 1999), a preliminary survey revealed that *S. queretaroensis* develops a symbiosis with AM fungi (Arceta-González et al. 1999).

The symbiosis between host and AM fungi is generally regarded as mutualistic, with a bidirectional transfer of nutri-

ents. The fungus depends on recent photosynthate supply by the host, and the external mycelium of the fungal symbiont increases the capacity of the plant to obtain resources from the soil (Smith and Read 1997, Lambers et al. 1998). Thus, conditions that favor photosynthesis might play an important role in the functioning of the mycorrhizal symbiosis.

Because little information is available on the factors that affect growth and reproduction of columnar cacti such as *Stenocereus* spp. and on the association of AM fungi with CAM plants, we investigated relationships among growth, reproductive components, root colonization by AM fungi, and climatic factors in three wild populations of *S. queretaroensis* growing in subtropical localities in western Mexico. These localities differ in climatic variables that affect growth, reproductive components and photosynthesis of perennial plants in general (Kozłowski et al. 1991) and CAM plants such as *S. queretaroensis* in particular (e.g., temperature, light, and rainfall; Nobel and Pimienta-Barrios 1995, Pimienta-Barrios and Nobel 1998, Pimienta-Barrios et al. 2000).

## Materials and methods

*Stenocereus queretaroensis* is a leafless, arborescent cactus growing up to 8 m in height with a short trunk and numerous, mostly vertical branches. The study was conducted from May 1998 to May 1999 with three wild populations located at Autlan in southern Jalisco (AJ; 19°46' N, 104°21' W, 879 m a.s.l.), Zacoalco de Torres in southern Jalisco (ZTJ; 20°14' N, 103°34' W, 1360 m a.s.l.), Santa Rosa in southwestern Zacatecas (SRZ; 21°16' N, 103°10' W, 1065 m a.s.l.). Daily air temperatures and rainfall were obtained from official weather stations (Comision Nacional del Agua) near the study localities. Photosynthetic photon flux (PPF; 400–700 nm) was measured hourly once per month with an LI-190S quantum sensor (Li-Cor, Lincoln, NE) in an open field at each study site. Texture, pH, mineral content (Walsh 1971) and number of arbuscular mycorrhizae (AM) fungal spores were determined from the rhizosphere at 1.2 m radially outward from the base of the main stem of 10 plants, at a soil depth of about 20 cm (each sample was 5 kg). Spores were extracted by wet sieving and separated by sucrose density gradient centrifugation (Daniels and Skipper 1982). A 100-g sample was passed through nested 250, 149 and 45  $\mu\text{m}$  sieves using a forced water spray. The contents of the 250, 149 and 45  $\mu\text{m}$  sieves were layered onto a 20/60% sucrose gradient and centrifuged at 900  $g$  for 2 min. The supernatant was poured onto the 45  $\mu\text{m}$  sieve and carefully washed to remove the sucrose, and transferred to a glass petri dish. All spores were examined with a Zeiss stereomicroscope, and spores of each distinct morphotype were counted. Spores of each morphotype were mounted in polyvinyl alcohol-lactic acid-glycerin (PVLG; Koske and Tessier 1983) and PVLG mixed 1:1 (v/v) with Melzer's reagent. Whole and broken spores were examined with a Leitz light microscope. Species identification of spores was based on subcellular characteristics, as described by Schenck and Perez (1990) and Morton et al. (1993).

The times of initiation and termination of the main vegeta-

tive and reproductive phenophases as well as stem extension were determined monthly for 10 mature plants at each study site. Stem length was measured for four peripheral branches in the four cardinal directions from May 1998 to February 1999. A calibrated ruler was placed against the stem and aligned with reference marks on the branches. Stem phosphorus (P) concentration was determined monthly from August 1998 to December 1998 according to Jackson (1976).

Fine roots that are commonly associated with AM fungi were collected from July to September 1998 at the three study sites. After fixing in FAA (formaldehyde:acetic acid:ethanol 2:1:17, v/v/v), the roots were cleared in 10% KOH (w/v) and then stained with trypan blue to reveal the fungal components (Phillips and Hayman 1970). Twenty replicates of root segments (each 1 cm in length) were mounted on slides and examined with a Leitz light microscope. Mycorrhizal colonization was estimated as the percentage of root length containing hyphae, vesicles and arbuscules.

Twenty fruits were collected from each study site, weighed, and peeled. After squeezing through cheesecloth, the seeds were counted and weighed. The pH of the pulp was measured, and the total soluble solids were determined with a Reitter-Jung 10432 refractometer (Cambridge Instruments, Buffalo, NY) with temperature compensation. Pulp protein was extracted according to Choe and Thimann (1975) and assayed by the method of Lowry et al. (1951). Groups of seeds (0.2 g) were oven-dried at 70 °C until they reached constant weight, ground to a fine powder with sand, and then extracted three times with 5 ml of chloroform:methanol (2:1, v/v). After centrifugation, the supernatant was dried at 50 °C to yield the lipid fraction (Harborne 1984). The pellet was extracted three times with 10 ml of methanol:chloroform:water (12:5:3, v/v/v) and then twice with 10 ml of distilled water and the extracts used for determination of starch. After centrifugation, the insoluble fraction was boiled for 2 h in 2 ml of distilled water; 4 ml of 50 mM sodium acetate (pH 4.5) containing 50 U of amyloglucosidase was added to hydrolyze the starch before glucose determination (Haissig and Dickson 1979). Seed protein was determined as for pulp protein. To test for germination, five replicates of 100 seeds from each study site were placed on two layers of Whatman no. 1 filter paper at 20 °C in a 9-cm-diameter petri dish containing 8 ml of distilled water. A PPF of 100  $\mu\text{mol m}^{-2} \text{s}^{-1}$  was provided for 12 h daily by incandescent lamps. Germination, scored when the radicle was > 1 mm length, was recorded every 5 days.

Data were subjected to ANOVA and where significant differences existed, means were separated by a least significant difference (LSD) test. Correlation analysis was used to test correlations between stem extension and environmental variables including air temperature, light and rainfall, and percentage root colonized by arbuscules (Little and Hill 1975). Data are presented as means  $\pm$  SE ( $n$  = number of measurements).

## Results

Daily minimum air temperatures averaged over a month from May 1998 to May 1999 were 14.3 °C at Autlan, Jalisco (AJ),

9.6 °C at Santa Rosa, Zacatecas (SRZ) and 13.1 °C at Zacoalco de Torres, Jalisco (ZTJ) (Figures 1a–c). Monthly means of daily air temperature extremes varied from 8 to 20 °C at night and from 18 to 36 °C during the daytime at AJ. The corresponding values at the other sites were 2 to 18 °C at night and 21 to 36 °C during the daytime at SRZ, and 8 to 18 °C at night and 25 to 33 °C during the daytime at ZTJ (Figures 1a–c). During the fall and winter (October–March) when *S. queretaroensis* has the highest rates of net CO<sub>2</sub> uptake (Pimienta-Barrios et al. 2000), monthly means of daily air temperature extremes varied from 8 to 18 °C at night and from 18 to 33 °C during the daytime at AJ. The corresponding values at the other sites were 2 to 14 °C at night and 21 to 31 °C during the daytime at SRZ, and 8 to 16 °C at night and 24 to 28 °C during the daytime at ZTJ.

Rainfall for May 1998 to May 1999 totaled 1206 mm at AJ, 672 mm at SRZ and 215 mm at ZTJ (Figures 1a–c). Most rainfall occurred from June to September: 65% at AJ, 80% at SRZ, and 83% at ZTJ. From 0800 to 1600 h, PPF averaged 960  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at AJ, 770  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at SRZ and 803  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at ZTJ. *Stenocereus queretaroensis* grew on rocky slopes in shallow soils classified as feozems with a sandy loam texture (Table 1). Soils were neutral at AJ and slightly acidic at the other sites (Table 1). Among sites, soil nitrogen (N) and P concentra-

tions were lowest at AJ, and potassium (K) concentration was intermediate.

A relatively high number of AM fungi were identified (Table 2). *Glomus* was the most frequently occurring genus at all three sites. Spore numbers were similar at AJ and ZTJ ( $450 \pm 81$  and  $490 \pm 32$  per 100 g of soil, respectively) but higher than at SRZ ( $336 \pm 114$  per 100 g of soil).

Stem extension growth of *S. queretaroensis* began in August at AJ, in September at SRZ and in July at ZTJ (Figure 2a). In the linear phase, mean daily growth rate was 0.13 cm day<sup>-1</sup> at AJ, 0.11 cm day<sup>-1</sup> at SRZ and 0.06 cm day<sup>-1</sup> at ZTJ. Stem extension ceased in November at ZTJ and in December at the other two sites (Figure 2a). The overall increase in stem length was 19.5 cm at AJ, 12.9 cm at SRZ and 9.2 cm at ZTJ. The differentiation of new fine roots coincided with the start of the summer rainy season at the three sites (data not shown). Flowering started in February and ended in April and fruit ripening occurred from March to June.

Stem P concentration (Figure 2b), which was lowest in *S. queretaroensis* at AJ, tended to decrease in trees at AJ, but not in trees at SRZ and ZTJ during the period of maximal stem extension (Figure 2a). Colonization of fine roots by mycorrhizal fungi tended to increase during the summer rainy season. The percentage of root length colonized by hyphae increased by an average of 70%, peaking in September at AJ and ZTJ and in August at SRZ. Arbuscules were first observed in the middle of the summer (August) at AJ and ZTJ but were not observed until September at SRZ. In midsummer, the percentage of root colonized by arbuscules of mycorrhizal fungi was higher at AJ than at the other sites. At the end of the summer (September), arbuscules were common at the three sites, but the percentage of root colonized by arbuscules was only 5% at SRZ. From August to September, the percentage of root colonized by arbuscules decreased by 20 and 90% at AJ and ZTJ, respectively. Vesicles were common on roots at the three sites, and were higher in August and September at AJ than at SRZ and ZTJ. At the end of the summer, similar numbers of vesicles were observed at AJ and ZTJ, whereas lower numbers of vesicles were found at SRZ (Table 3).

Fruits of *S. queretaroensis* at ZTJ had lower total mass and pulp mass and a lower quotient of pulp mass/fruit mass than at the other sites (0.61 compared with 0.76 at AJ and SRZ; Table 4). Fruits at SRZ were the least acidic, but total soluble solids did not differ among sites. Fruits from *S. queretaroensis* at ZTJ had lower protein concentrations than fruits at the other sites. Fruits of *S. queretaroensis* at SRZ had more seeds and higher seed protein concentrations than fruits at the other sites (Table 5). The seed lipid concentration was slightly higher than the protein concentration and did not vary among sites. Mean seed starch concentration was only 0.2% and was similar at all sites (Table 5).

Correlation analysis between stem growth rate and the percentage of root length colonized by arbuscules revealed a significant positive relationship between total root length colonized by arbuscules and stem growth for *S. queretaroensis* at AJ and SRZ but not at ZTJ (Table 6). A significant negative relationship was also observed between stem growth and sum-

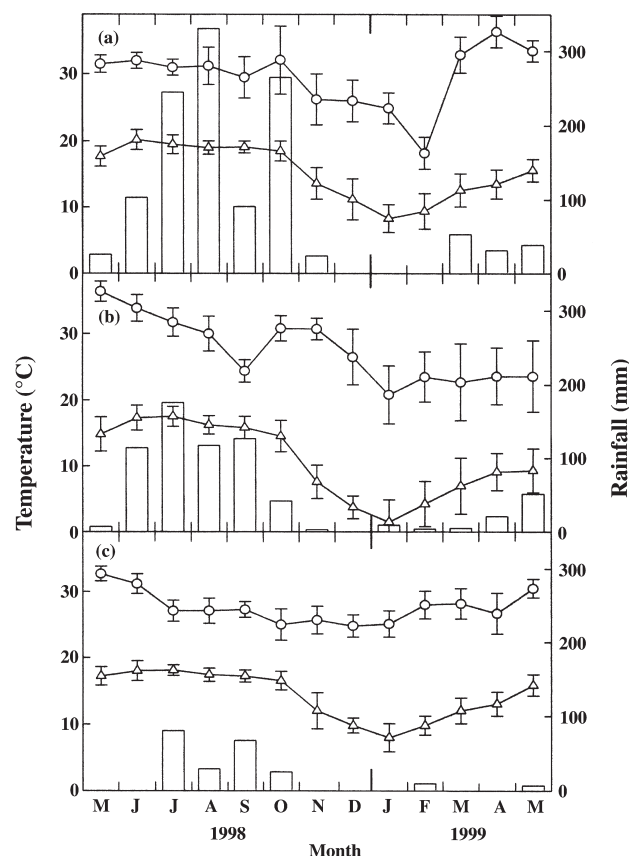


Figure 1. Maximum (○) and minimum (△) air temperatures averaged over a month and total rainfall (bars) at (a) Autlan, Jalisco (AJ), (b) Santa Rosa, Zacatecas (SRZ) and (c) Zacoalco de Torres, Jalisco (ZTJ).

Table 1. Chemical and physical properties of the sandy loam soils at Autlan, Jalisco (AJ), Santa Rosa, Zacatecas (SRZ) and Zacoalco de Torres, Jalisco (ZTJ). Values are means of 10 soil samples per study site.

Study site	pH	Organic matter (% of dry mass)	Mineral concentration (mg g <sup>-1</sup> )					
			N	P	K	Mg	Na	Ca
AJ	6.8	0.5	2.2	2.0	2.2	4.1	0.14	22
SRZ	6.0	1.5	4.7	3.0	2.7	3.4	0.16	46
ZTJ	5.9	1.5	4.5	3.0	5.5	4.1	0.18	34

Table 2. Spores identified at Autlan, Jalisco (AJ), Santa Rosa, Zacatecas (SRZ) and Zacoalco de Torres, Jalisco (ZTJ).

Study site	Species
AJ	<i>Glomus fasciculatum</i> Thaxter, <i>G. deserticola</i> Trappe, Bloss & Menge, <i>G. macrocarpum</i> Tulasne & Tulasne, <i>Glomus</i> sp., <i>Scutellospora arenicola</i> Koske & Halvorson
SRZ	<i>Acaulospora</i> sp., <i>A. foveata</i> Trappe & Janos, <i>Gigaspora gigantea</i> Nicolson & Gerdemann, <i>Glomus versiforme</i> Karsten, <i>G. constrictum</i> Trappe, <i>G. fasciculatum</i> Thaxter, <i>G. deserticola</i> Trappe, Bloss & Menge, <i>Scutellospora</i> sp.
ZTJ	<i>Gigaspora margarita</i> Bercker & Hall, <i>Glomus fasciculatum</i> Thaxter, <i>G. constrictum</i> Trappe, <i>G. caledonium</i> Nicolson & Gerdemann, <i>G. tortuosum</i> Schenck & Smith, <i>G. clarum</i> Nicolson & Schenck, <i>Sclerocystis microcarpa</i> Iqbal & Bushra, <i>Scutellospora</i> sp. Walker & Sanders, <i>S. calospora</i> Nicolson & Gerdemann

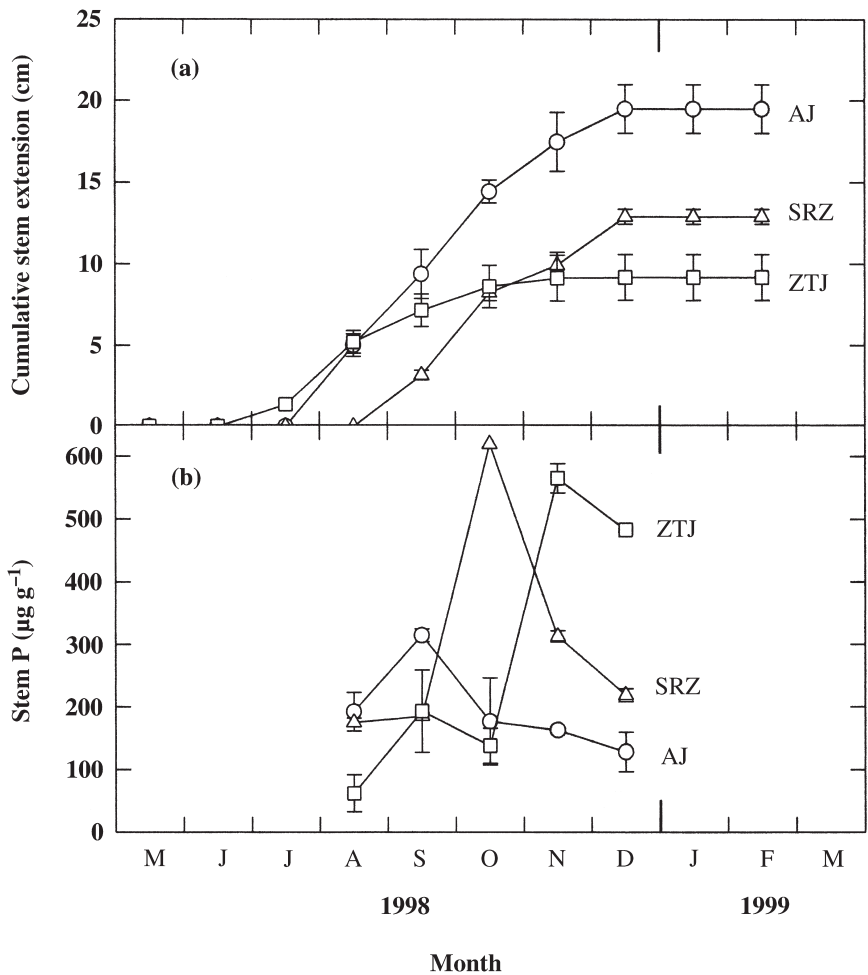


Figure 2. Monthly variation in (a) cumulative stem extension and (b) stem phosphorus concentration of *S. quere-taroensis* at Autlan, Jalisco (AJ; ○), Santa Rosa, Zacatecas (SRZ; △) and Zacoalco de Torres, Jalisco (ZTJ; □).



Table 3. Percent of root length of *Stenocereus queretaroensis* colonized by hyphae, arbuscules and vesicles at Autlan, Jalisco (AJ), Santa Rosa, Zacatecas (SRZ) and Zacoalco de Torres, Jalisco (ZTJ) during summer 1998. Values within a column followed by different letters are significantly different at  $P < 0.01$  by the LSD multiple test. Values are means of 10 roots per study site.

Study site	Root length infected (% of total)								
	Hyphae			Arbuscules			Vesicles		
	July	Aug	Sept	July	Aug	Sept	July	Aug	Sept
AJ	59 a	66 c	88 a	0 a	52 a	42 a	22 a	53 a	50 a
SRZ	51 a	87 a	85 a	0 a	0 c	5 b	6 b	16 c	6 b
ZTJ	43 a	70 b	84 a	0 a	19 b	2 b	4 b	26 b	46 a

Table 4. Fruit characteristics of *S. queretaroensis* at Autlan, Jalisco (AJ), Santa Rosa, Zacatecas (SRZ) and Zacoalco de Torres, Jalisco (ZTJ). Values within a column followed by different letters are significantly different at  $P < 0.01$  by the LSD multiple test. Values are means of 10 roots per study site.

Study site	Fruit mass (g)	Pulp mass (g)	pH	Total soluble solids (% of fresh mass)	Protein ( $\text{mg g}^{-1}$ )
AJ	98.5 a	74.6 a	4.0 b	11.2 a	4.0 a
SRZ	87.5 b	66.4 a	4.5 a	11.4 a	3.2 a
ZTJ	53.0 c	32.3 b	4.0 b	12.2 a	1.5 b

Table 5. Seed characteristics of *S. queretaroensis* at Autlan, Jalisco (AJ), Santa Rosa, Zacatecas (SRZ) and Zacoalco de Torres, Jalisco (ZTJ). Values within a column followed by different letters are significantly different at  $P < 0.01$  by the LSD multiple test. Values are means ( $n = 15\text{--}20$  fruits for seed number and mass,  $n = 500$  seeds for seed germination, and  $n = 10$  samples protein, lipid and starch analyses).

Study site	Number of seeds per fruit	Seed dry mass (mg)	Germination (%)	Protein (% by dry mass)	Lipids (% by dry mass)	Starch (% by dry mass)
AJ	1034 b	2.2 a	98 a	14 b	17 a	0.21 a
SRZ	1327 a	2.0 ab	90 b	18 a	22 a	0.19 a
ZTJ	1124 b	1.8 b	94 ab	12 b	17 a	0.08 a

Table 6. Correlation analysis between stem growth and arbuscular colonization, minimal air temperatures, maximal air temperatures, photosynthetic photon flux (PPF) and rainfall at Autlan, Jalisco (AJ), Santa Rosa, Zacatecas (SRZ) and Zacoalco de Torres, Jalisco (ZTJ). Asterisks indicate significance of correlation coefficients ( $r$ ): \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ; and ns = not significant.

Study site	Percentage arbuscular colonization	Air temperature		Rainfall	PPF
		Maximal	Minimal		
AJ	0.610*	-0.751*	-0.834**	-0.472 ns	0.008 ns
SRZ	0.690***	-0.701*	-0.929***	-0.749*	-0.062 ns
ZTJ	0.410 ns	-0.821**	-0.740*	-0.185 ns	-0.714*

mer rainfall at SRZ, but not at AJ and ZTJ. In contrast, there were significant negative relationships between stem growth and maximal and minimal air temperatures at all three sites. There was a statistically significant negative relationship between stem growth and light only at ZTJ (Table 6).

## Discussion

The natural population of *Stenocereus queretaroensis* at AJ differed markedly in stem length, fruit mass, percentage of

seed germination and percentage of root colonization by arbuscules of AM fungi from the natural populations at ZTJ and SRZ. Among the characteristics measured, stem extension showed the greatest difference among study sites. One of the main climatic differences among study sites was the amount of rainfall, which is the ecological factor that most restricts both vegetative and reproductive growth (Coombe 1976, Zanchin et al. 1994, Larcher 1995, Lambers et al. 1998). At ZTJ, which received only 18% as much rainfall as AJ and 32% as much as SRZ, *S. queretaroensis* had the lowest values of fruit mass,

pulp mass and stem extension. Irrigation of *S. queretaroensis* increases final fruit weight, seed weight, germination rate, and the final germination percentage, but not chemical components (e.g., pH, sugars, and protein concentration) compared with plants that receive only rainfall (Nobel and Pimienta-Barrios 1995). Moderate air temperatures also enhance growth and photosynthesis in *S. queretaroensis* (Pimienta-Barrios et al. 2000), as reported for other CAM plants (Hanscom and Ting 1978, Kluge and Ting 1978, Israel and Nobel 1995, Pimienta-Barrios et al. 2002).

Although photosynthesis was not measured for the wild populations of *S. queretaroensis*, previous studies of effects of environmental conditions on photosynthesis of *S. queretaroensis* under controlled conditions (Nobel and Pimienta-Barrios 1995, Nobel 1996) and in the field (Pimienta-Barrios and Nobel 1998, Pimienta-Barrios et al. 2000) together with the climatic data obtained at the present study sites allowed prediction of photosynthetic responses. Based on this information, we conclude that plants at AJ had a more favorable environment for photosynthesis, particularly with respect to rainfall, air temperature and light availability, than plants at ZTJ and SRZ. Rainfall at AJ was above average for subtropical semiarid environments in Mexico (Medina-García et al. 1998), and air temperatures were close to optimal for net CO<sub>2</sub> uptake (Nobel and Pimienta-Barrios 1995, Nobel 1996, Pimienta-Barrios and Nobel 1998, Pimienta-Barrios et al. 2000).

Pimienta-Barrios et al. (2002) observed that wild platyopuntia subjected to a prolonged drought (annual precipitation of 200 mm) had significantly reduced photosynthesis, root formation, and root colonization by AM fungi. In arid environments of Baja California Sur, with a mean annual precipitation of 180 mm, the columnar cacti *Machaerocereus gummosus* (Engelm.) Britton & Rose, *Pachycereus pringlei* (S. Watson) Britton & Rose and *Stenocereus thurberi* (Engelm.) Buxbaum show only traces of root colonization by AM fungi (Carrillo-García et al. 1999). Our finding of a lower percentage of root length colonized by arbuscules at ZTJ and SRZ than at AJ corroborate these studies and provide further evidence that the capacity for symbiosis with AM fungi is associated with favorable conditions for photosynthesis by the host plant (DeMars and Boerner 1995, Smith and Smith 1996).

Arbuscular mycorrhizal fungi influence plant growth by promoting absorption of nutrients, particularly P (Fitter and Nichols 1988, Merryweather and Fitter 1996, Jakobsen et al. 2001, Wilson et al. 2001). Fine roots form on cacti after the first rains (Nobel 1994, Pimienta-Barrios et al. 1998), and shortly thereafter the roots are colonized by AM fungi (Arceta-González et al. 1999). In August, fine roots of *S. queretaroensis* showed vesicles and hyphae at all three study sites, but arbuscules were observed only at AJ and ZTJ and their appearance coincided with the onset of stem extension. In contrast, arbuscules were not observed at SRZ until September; however, their appearance also coincided with the initial stages of stem growth, as indicated by correlation analysis. The presence of arbuscules preceded the maximal rate of stem extension and the increase in stem P concentration at AJ and SRZ, but not at ZTJ. Arbuscules may be essential for nutritionally

efficient mycorrhizae. For instance, soil P, Ca and Mg absorbed by the extraradical hyphae are exchanged with the host across the interface with arbuscules (Smith and Smith 1996). The highest percentage of root colonization by arbuscules on *S. queretaroensis* at AJ was associated with high rates of annual stem extension (20 cm) and a low concentration of stem P. This high stem extension rate approached that of *S. queretaroensis* growing in more fertile, deep, alluvial soils with more water holding capacity (22 cm year<sup>-1</sup>; Pimienta-Barrios et al. 1998). Thus, the beneficial effect of AM fungi on plant growth may be associated with improved P nutrition of the mycorrhizal plants (Jeffries 1987, Boswell et al. 1998).

Photosynthesis is highly dependent on P availability (Terry and Rao 1991, Halsted and Lynch 1996, Kielsen et al. 1998). The decreasing concentration of stem P in *S. queretaroensis* at AJ during summer and fall may be a result of high sink strength caused by high stem extension rates and increased net CO<sub>2</sub> uptake, which commonly occurs during fall and winter when air temperatures are moderate (Pimienta-Barrios et al. 2000). A stepwise decline in stem P concentration in the populations at AJ and SRZ coincided with the major increase in monthly stem extension.

The number of spores and species diversity of AM fungi for the three wild populations of *S. queretaroensis* suggest that it is an obligatory mycorrhizal species that does not become established until the population of AM has built up (Titus and Del Moral 1998). Although the number of AM fungus species recorded was higher than the number recorded in other studies in arid regions (Bethlenfalvay et al. 1984, Stutz and Morton 1996, Picone 2000, Stutz et al. 2000), as found in other regions, *Glomus* was the most important genus for *S. queretaroensis*.

A low root/shoot ratio often predisposes plants to mycorrhizal colonization (Koide 1991). Plants such as *S. queretaroensis* that have low root/shoot ratios with thick roots that have little branching and few or no root hairs (Arceta-González et al. 1999) tend to show greater mycorrhizal colonization and growth responses to environmental variables than plants with fine, highly branched roots and numerous root hairs (Hetrick 1991). It may be energetically less costly to support mycorrhizal fungi than to develop a high root/shoot ratio. The symbiotic association between AM fungi and *S. queretaroensis* roots is temporal, being restricted to the rainy summer when fine roots develop on the main roots. The symbiotic association disappears at the beginning of fall when fine roots become suberized and develop into permanent roots (Pimienta-Barrios and Nobel 1998, Arceta-González et al. 1999). Consequently, the absorption of water and mineral nutrients by *S. queretaroensis* occurs more readily during the summer wet season than during the winter dry season (Arceta-González et al. 1999).

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