VEGETATIVE, REPRODUCTIVE, AND PHYSIOLOGICAL ADAPTATIONS TO ARIDITY OF PITAYO (*STENOCEREUS QUERETAROENSIS*, CACTACEAE)[1]

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Pimienta-Barrios, Eulogio *(Departamento de Ecología, CUCBA, Universidad de Guadalajara, Jalisco, Mexico)* **and Park S. Nobel** *(Department of Biology, University of California, Los Angeles, California 90095-1606).*VEGETATIVE, REPRODUCTIVE, AND PHYSIOLOGICAL ADAPTATIONS TO ARIDITY OF PITAYO (*STENOCEREUS QUERETAROENSIS*, CACTACEAE). *Economic Botany 52(4):401–411. 1998. Pitayos (*Stenocereus spp.*) are columnar cacti that produce attractive edible fruits under both wild and cultivated conditions. Until recently the study of pitayos has been relatively neglected even though they have been a crucial staple for the inhabitants of subtropical semi-arid lands of Mexico since ancient times and this century have become an important fruit crop there. The main objective of this review is to relate seasonal aspects of vegetative and reproductive growth, CO_2 uptake, and carbohydrate resources to abiotic components of the environment. Flower and fruit production occur during the dry season in the late winter and spring, roots grow during the summer wet season, and stem elongation commences in the autumn at the beginning of the dry season. Vegetative growth thus does not coincide with reproductive growth, as it does for other fruit crops in temperate and tropical regions. The time offset of vegetative and reproductive activities reduces competitive sink effects, regulating assimilate partitioning to different organs, which may allow* Stenocereus queretaroensis *to adapt to water-limited environments. Reserve carbohydrates (starch, mucilage) accumulate in the early summer just after reproductive growth and in the early winter just after stem extension. Reducing sugars increase during the middle of the summer before stem elongation begins. The low rates of growth and of photosynthesis for* S. queretaroensis *are associated with low tissue levels of nitrogen, chlorophyll, and some micronutrients (Fe, Mn). Low levels of gibberellic acid may also contribute to its low growth rate. It does not respond morphologically to irrigation during the dry period, indicating a low plasticity for growth. Although* S. queretaroensis *is cultivated, its physiological and phenological activities closely resemble those of wild CAM species and other wild perennial plants, reflecting its rather recent domestication and the fact that selections were based mainly on fruit quality and adaptation to aridity rather than biomass productivity.*

ADAPTACIONES VEGETATIVAS, REPRODUCTIVAS Y FISIOLOGICAS DEL PITAYO (STENOCEREUS QUERETAROENSIS, CACTACEAE) A LA ARIDEZ. *Los pitayos (*Stenocereus spp.*) son cactáceas columnares que producen frutos comestibles de colores atractivos en poblaciones silvestres y cultivadas. Hasta hace poco tiempo el pitayo había sido poco estudiado, no obstante haber sido un alimento importante para los habitantes de las tierras semiáridas subtropicales desde tiempos antiguos y haberse convertido en este siglo en una importante especie frutal. El principal objetivo de esta revisión es relacionar el crecimiento vegetativo y reproductivo, la asimilación de CO_2 y las reservas de carbohidratos con algunos componentes abióticos del ambiente. La producción de flores y frutos ocurre durante la estacion seca del año. Las raíces crecen durante el periodo de lluvias en el verano y la elongación de las ramas comienza en el otoño al inicio de la estación seca. El crecimiento vegetativo no coincide con el crecimiento reproductivo, como ocurre con otras especies frutales de regiones templadas y tropicales. La competencia entre demandas metabólicas se reduce, debido a que no se traslapa el crecimiento vegetativo con el reproductivo, de esta manera se regula la distribución de fotosintetizados a los diferentes órganos de la planta, lo cual permite que* S. queretaroensis *se adapte en ambientes en los que el agua es un factor limitante. Los carbohidratos de reserva (almidón, mucílago) se acumulan al empezar el verano después del crecimiento reproductivo y en el invierno, justo después de la elongación de las ramas. El contenido de azúcares reductores aumenta a mediados del verano, antes del crecimento de las ramas. Las bajas tasas de crecimiento y fotosíntesis registrados en* S. queretaroensis *se asocian con niveles bajos de nitrógeno, clorofila y algunos micronutrientes como Fe y Mn. Probablemente niveles bajos de ácido giberélico también con-*

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tribuyan a la baja tasa de crecimiento de esta planta. S. queretaroensis *no responde morfológicamente al riego durante la estación seca, revelando poca plasticidad en el desarrollo. Aunque* S. queretaroensis *se encuentra en condición cultivada, su comportamiento fenológico y fisiológico presenta semejanza con especies silvestres con metabolismo CAM y otras plantas silvestres perennes. Este comportamiento refleja su relativamente reciente domesticación, así como el hecho de que al hacer la selección de fenotipos sobresalientes de pitayo se prestó una mayor atencion a la calidad del fruto y la adaptación a la aridez, en lugar de la productividad de biomasa.*

Key Words: Adaptation; aridity; cacti; carbohydrates; fruit.

The effects of aridity on food production has become a major concern in developing countries, especially in Latin America, because arid and semi-arid regions occupy one third of their area and most of the land available for the expansion of agricultural activities is in or bordering such regions (Izquierdo and Oltremari 1996). One factor limiting the development of agriculture in arid regions is the high sensitivity of most domesticated crops to drought. Recently, interest has increased for cacti that produce edible fruits, especially because such plants are resistant to drought. Important fruits are cactus pear (*Opuntia* spp.), which is presently cultivated in nearly 20 countries, and pitaya (*Stenocereus* spp.) (Mizrahi, Nerd, and Nobel 1997). Genetic resources for such potential fruit crops occur in subsistence agriculture in arid and semi-arid regions of Mexico and other countries.

This article reviews existing and new data on biological and agronomic aspects of *Stenocereus queretaroensis,* a columnar cactus that produces attractively colored edible fruits under both wild and cultivated conditions. *S. queretaroensis* is native to the subtropical semiarid lands of Mexico and it is widely distributed in the central part of Mexico (Bravo 1978: 590–591). Since prehispanic times, *Stenocereus* have provided valuable additions to the diets of Indian tribes inhabiting tropical and subtropical semiarid lands of Mexico. Recently, pitayo has emerged as a fruit crop whose cultivation is feasible using relatively low inputs of anthropogenic energy or water and whose fruits ripen before local markets are supplied with other summer fruits (Pimienta-Barrios and Nobel 1994). These agronomic traits have increased the economic viability of small farms in semi-arid subtropical lands of Mexico.

PHENOLOGY

Shoot growth for *S. queretaroensis* takes place at the branch apices and occurs essentially only in the autumn and early winter (October through December; Fig. 1a). Flower differentiation starts in early February, ending in early April; fruits ripen from early March until the end of May. Thus vegetative and reproductive growth occur in the dry season (Fig. 1b,c; Lomeli and Pimienta 1993; Pimienta-Barrios and

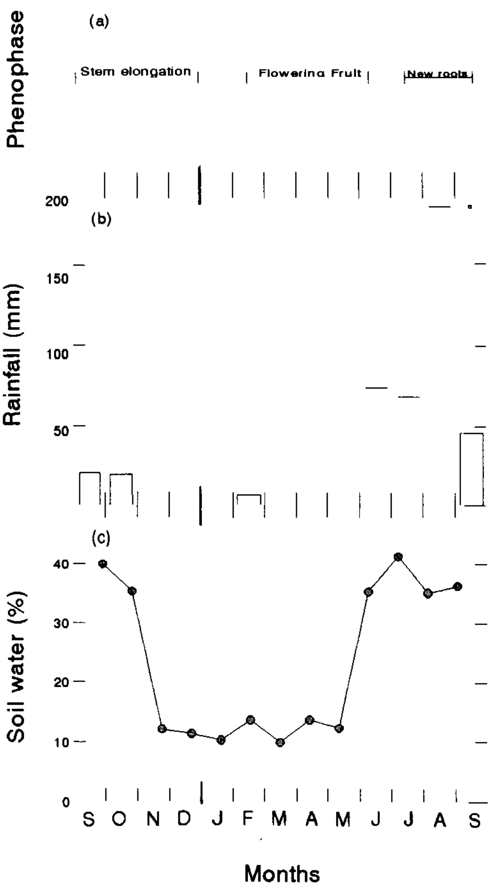

Fig. 1. Occurrence of the main reproductive and vegetative phenophases of *Stenocereus queretaroensis* (a), total monthly rainfall (b), and monthly soil moisture content (c) during 1994–1995 in the Sayula Basin, Jalisco, Mexico. Adapted from Pimienta, et al. (1998).

Nobel 1995). The differentiation of new roots coincides with the start of the summer rainy season, which is the only prominent vegetative event then (Fig. 1a; Arceta 1997). Such phenological behavior contrasts with that of woody perennials growing in temperate climates, whose root growth begins in the early spring when soil temperatures are rising and precedes stem growth, which occurs at the beginning of the spring and during the summer (Kozlowski, Kramer, and Pallardy 1991: 13–15). Moreover, vegetative growth of *S. queretaroensis* does not coincide with reproductive growth, as is does for most conventional crops in temperate and tropical regions (Ryugo 1988: 68–82). The time offset of vegetative and reproductive activities reduces competitive sink effects of different organs, which may help *S. queretaroensis* adapt to water-limited environments (Pimienta-Barrios and Nobel 1995).

Although *S. queretaroensis* is native to subtropical climates, water availability as well as air temperatures may not strongly influence its vegetative growth, as occurs for the majority of perennial species (Larcher 1995: 301–309), because the highest rates of primary growth occur during the middle of the autumn when both soil moisture and temperature can become limiting. Moreover, greater rates of stem extension were recorded in 1995 than in 1994 even though water availability was greater during the autumn of 1994 than of 1995 for *S. queretaroensis* in natural populations (Arceta 1997). Irrigation during the period of reproductive development of *S. queretaroensis* affects some reproductive traits. For instance, it increases flower and fruit size but decreases the number of flowers per plant by 36%. Irrigation decreases the number of ovules by 12%, seed number per fruit by 25%, and final seed set by 15%, although seed size is unaffected (Pimienta-Barrios, Robles-Murguia, and Dominguez de la Torre 1995).

VEGETATIVE AND REPRODUCTIVE GROWTH

Shoot elongation in temperate perennial species, especially trees, is more rapid during the long days of late spring and early summer than during the autumn or winter (Salisbury and Ross 1992: 341–342). However, the major stem extension for *S. queretaroensis* occurs in the autumn when minimum air temperatures are lower and soil water is less available (Figs. 1, 2). For mature cultivated plants, 85% of the annual growth is from December to January, when the daily rate averages 0.26 cm day^{-1} (Fig. 2; Pimienta-Barrios and Nobel 1995). Thus *S. queretaroensis* is a slowly growing plant similar to other columnar cacti producing edible fruits (Nerd, Raveh, and Mizrahi 1993), but unlike young cladodes of *Opuntia* spp. under similar conditions (Nobel 1988: 184–186; Robles 1994) or other herbaceous and woody plants (Grime and Hunt 1975), which have higher growth rates. It thus behaves as do wild perennial plants growing in infertile soils that commonly tend to be long-lived with slow growth and low capacity for photosynthesis and nutrient absorption (Chapin 1980). Such plants often maintain growth and reproduction even during periods of low water availability (Grime 1979: 45–50) but tend to be less plastic than plants with higher growth rates (Grime and Hunt 1975). Low plasticity is indeed a feature of cultivated *S. quere-*

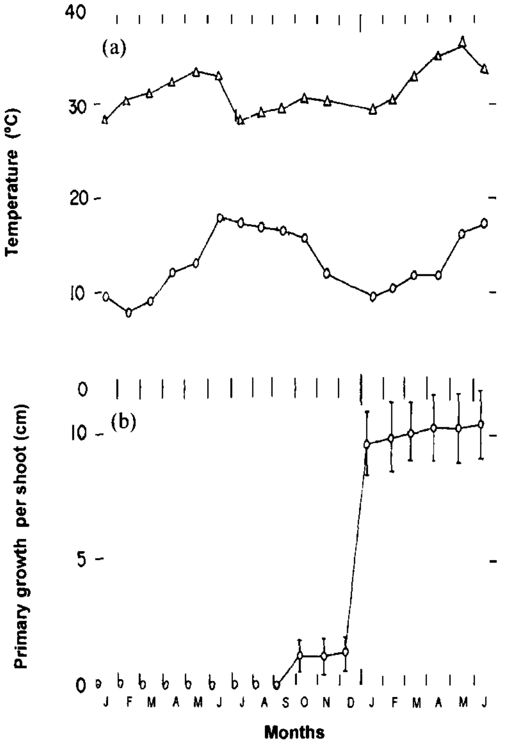

Fig. 2. Daily minimum (O) and maximum (D) air temperatures averaged over a month (a) and cumulative monthly stem extension for *S. queretaroensis* (b) in the Sayula Basin, Jalisco, Mexico in 1993–1994. Extension data are means ± SE, except when the error bars are smaller than the symbols (n = 24 stems). Adapted from Pimienta-Barrios and Nobel (1995).

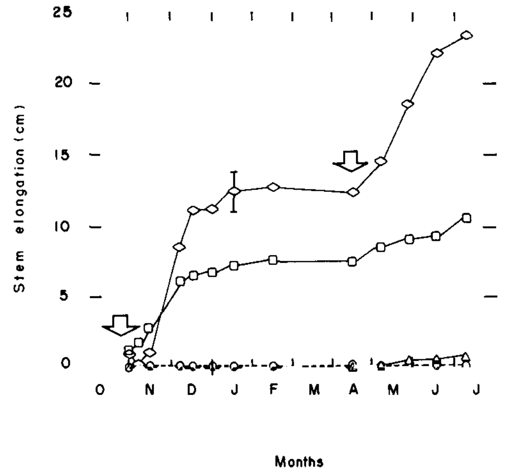

Fig. 3. Cumulative monthly stem extension for *S. queretaroensis* approximately 100 years old injected with 0 (○), 10^{-5} (△), 10^{-4} (□), or 10^{-3} (◇) M GA_3 on the two dates indicated by arrows. Data from 1994–1995 are means ± SE ($n = 7$ plants). Adapted from Pimienta, et al. (1998).

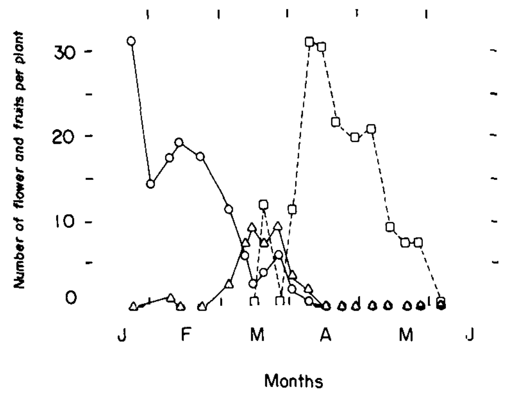

Fig. 4. Reproductive development for *S. queretaroensis* under natural conditions. Number of emerging flower buds (○), open flowers (△), and nearly ripe fruits (□). The decline in number toward the end of the season was the result of periodic fruit harvesting. Data from 1994 are means ± SE ($n = 6$ to 7 plants). Adapted from Pimienta-Barrios and Nobel (1995).

taroensis, because irrigation does not markedly affect stem extension, even when other environmental factors such as temperature and irradiance are favorable for photosynthesis and growth (Pimienta-Barrios and Nobel 1995). The slow growth rates of *S. queretaroensis* have limited its domestication, as 8 to 10 years are required to obtain a large enough production for commercial profitability, even when stem cuttings are used as the starting material for propagation (Pimienta-Barrios and Nobel 1994).

The low growth rates for cultivated *S. queretaroensis* are associated with low tissue levels of nitrogen, chlorophyll, and some micronutrients (Fe, Mn), even in deep alluvial soils (Nobel and Pimienta-Barrios 1995). In addition, low levels of hormones such as gibberellic acid may also contribute to the low growth rates. For instance, injecting gibberellic acid into stems of 100-year-old plants that have stopped growing, causes stem elongation to resume within 1 month (Pimienta-Barrios, et al. 1998; Fig. 3).

The rate of flower extension growth for *S. queretaroensis,* which is pollinated primarily by bats, is 0.31 cm day^{-1}, and 22 days elapse from the emergence of flower buds to anthesis. After abscission of the perianth, the developing fruit is about 15% longer for irrigated plants compared with those under natural rainfall conditions (Pimienta-Barrios, Robles-Murguia, and Dominguez de la Torre 1995). Fruit length attains over 90% of its final size in about 40 days, and the overall development period from anthesis to maturity is about 90 days, resulting in larger flowers under irrigation. The length enhancements resulting from irrigation during the last stages of flower and fruit growth suggest that such growth occurs by cell elongation, as for other fleshy fruits (Coombe 1976; Zanchin, et al. 1994). The time to reach maturity for fruits of *S. queretaroensis* is relatively short compared with other cacti (e.g., *Opuntia* spp.) and other fruit crops (peach, plum, apple, and avocado) (Barbera, Carimi, and Inglese 1992; Lee and Young 1983; Ryugo 1988: 107–111).

REPRODUCTIVE BIOLOGY

Reproductive development of *S. queretaroensis* is asynchronous, as flowers in early stages of differentiation, flowers in anthesis, and young developing fruits occur simultaneously (Fig. 4). Asynchronous growth, which may be advantageous ecologically as well as commercially, is not affected by irrigation. The time between flower bud initiation and anthesis is relatively short for *S. queretaroensis,* about 40–50 days, as in other columnar cacti that produce edible fruits (Nerd and Mizrahi 1997; Pimienta-Barrios and Nobel 1994). This behavior is similar to that for other tropical and subtropical fruit crops, such as orange, avocado, mango, and cactus pear (Pimienta 1990; Osuna and Pimienta 1992), but it contrasts with that of temperate fruit crops (e.g., apple, peach and pear), whose flower bud initiation usually occurs 1 year before flowering (Faust 1989).

The occurrence of fruit ripening at the end of the spring may be optimal for *S. queretaroensis.* In particular, seed maturation occurs just before the start of the summer rainy season, which favors seed germination and establishment because of favorable soil moisture and shading by surrounding natural vegetation. As for other cacti (Nobel 1988: 87, 135–137; Nobel 1994: 104–106), nurse plants are necessary for the survival of *Stenocereus* seedlings. In contrast, seed development for *Opuntia* spp. in the same regions occurs near the middle or the end of the rainy season, so its seed maturation and dispersal coincide with the beginning of the dry season (Perez 1993). To avoid drought stress, the seeds of *Opuntia* spp. have a dormancy period of 7 to 8 months; its seed germination is initiated at the start of the next rainy season (Perez 1993).

The seeds of *S. queretaroensis* are smaller (2.6 mg) than those of *Opuntia ficus-indica* (23 mg), which is advantageous from a commercial point of view. They contain a relatively large amount of lipid and germinate in response to light. Seeds of many wild species that respond to light are also small and rich in lipids. Because of their small size and light requirements, such seeds must be near the soil surface for successful germination (Salisbury and Ross 1992: 451), whereas seeds of *O. ficus-indica* are not light-requiring and can germinate even when buried in the soil. The germination rate is higher for *S. queretaroensis* receiving irrigation). Seeds of S. queretaroensis are thus similar to those of wild species (Salisbury and Ross 1992: 451), reflecting its relatively recent domestication for its fruits.

STEM ANATOMY

For both *S. queretaroensis* and *Opuntia* spp., the stomatal frequency is low (10–40 per mm^2; Pimienta, Loera, and Lopez 1993), which is generally considered to be an adaptation to arid environments. Cuticular thickness of the stems varies from 13 to 17 μm for *S. queretaroensis* and from 10 to 50 μm for *Opuntia* spp. (Jimenez-Lopez, Pimienta-Barrios, and Muñoz-Urias 1995; Pimienta-Barrios, Robles-Murguia, and Dominguez de la Torre 1995). Thus the cuticle of *S. queretaroensis* is relatively thick compared with that of mesophytic plants (Nobel 1994: 92) but thinner than for various species of *Opuntia.* A thick cuticle represents an important adaptation to aridity, leading to the ability to withstand long droughts (Nobel 1994: 92). Calcium oxalate crystal (druses) are not present in the stem cortex of *S. queretaroensis* consistent with its low calcium content (Nobel and Pimienta-Barrios 1995) but in contrast to other cacti (Gibson and Nobel 1986: 52; Nobel 1983).

A distinctive feature of stem anatomy of *S. queretaroensis* is the presence of aerenchyma in its hypodermis. Aerenchyma, characterized by continuous gas spaces in shoots and roots, is often an adaptation to low oxygen levels and is a distinctive feature of many wetland species (Esau 1977: 259; Salisbury and Ross 1992: 285–286). The aerenchyma is located on the adaxial side of the stem and the chlorenchyma on the abaxial side, suggesting an homology with the anatomy of bifacial or dorsiventral mesophytic leaves for which the aerenchyma resembles spongy parenchyma (Mauseth 1991: 146–147). The abundance of intercellular air spaces may be an important adaptation to facilitate gas exchange and photosynthesis (Sajeva and Mauseth 1991). However, for *S. queretaroensis* the tissue may have evolved in response to the conditions of shade that occur during early stages of development in natural populations, as occurs for other species (Sifton 1957).

PHYSIOLOGY

Net CO_2 uptake by *S. queretaroensis* occurs primarily at night (Nobel and Pimienta-Barrios 1995), as is characteristic of Crassulacean acid metabolism (CAM) plants (Nobel 1988: 51–57). This behavior favors the ecological success of cacti in arid environments because less water is lost than for the species having stomatal opening during the daytime (Nobel 1995). Indeed, CAM is an extremely important adaptation that allows plants to successfully compete in environments with limited water or CO_2 availability (Cushman and Bohnert 1997).

As for laboratory studies (Nobel and Pimienta-Barrios 1995), gas exchange measurements in the field revealed that nearly all of the net CO_2 uptake for *S. queretaroensis* occurs at night. Young plants (three to four years old) had a higher maximum rate of CO_2 uptake (11.2 μmol m^{-2} s^{-1}) than adult plants (7.6 μmol m^{-2} s^{-1}). The total daily net CO_2 uptake, obtained by integrating the net CO_2 uptake rates over 24-h pe-

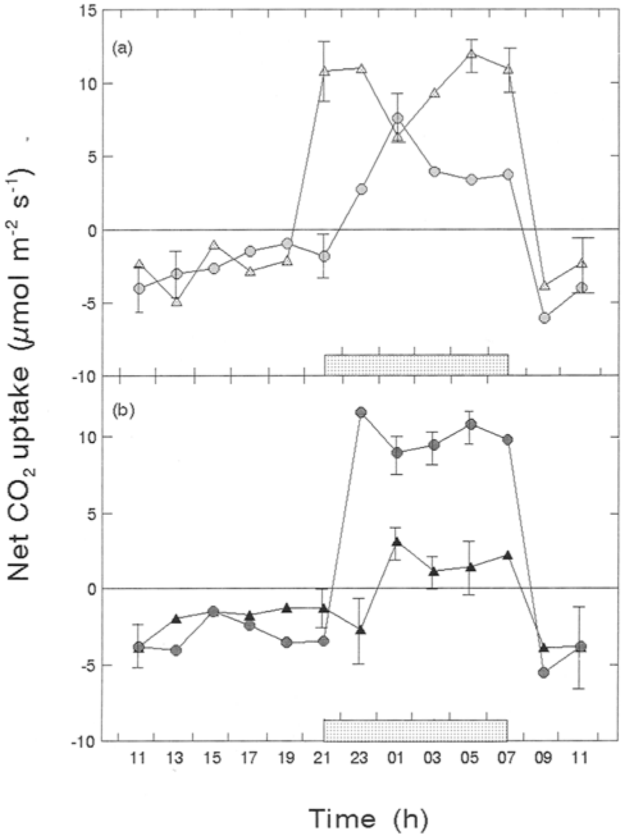

Fig. 5. Net CO_2 uptake by *S. queretaroensis* for young plants (△) and old plants (○; a), and light exposed stems (●) and shaded stems (▲; b) in the Sayula Basin, Jalisco, Mexico. Data are means ± SE ($n = 12$ stems). Previously unpublished data were obtained on 29–30 June 1997.

riods, was 30 mmol m^{-2} day^{-1} for the old plants and 303 mmol m^{-2} day^{-1} for the young plants (Fig. 5a). The young plants in the field had similar net CO_2 uptake as for *S. queretaroensis* of about the same age in a glasshouse (Nobel and Pimienta-Barrios 1995).

The rate of net CO_2 uptake depends on light level and hence varies with the orientation of the stems and their rib surfaces. Net CO_2 uptake increases more-or-less linearly with photosynthetic photon flux (PPF, wavelengths of 400 to 700 nm). Daily net CO_2 uptake over a 24-h period is 80 mmol m^{-2} d^{-1} for a north-facing surface (with a total daily PPF of 3.5 mol m^{-2} day^{-1}), 148 mmol m^{-2} day^{-1} for one facing northeast (PPF of 9.2 mol m^{-2} day^{-1}), 213 mmol m^{-2} day^{-1} for one facing south (PPF of 13.9 mol m^{-2} day^{-1}), and 317 mmol m^{-2} day^{-1} for one facing west (PPF of 19.2 mol m^{-2} day^{-1}; Nobel and Pimienta-Barrios 1995).

Similar tendencies for responses to PPF were observed in the field. Exposed stems receiving a total daily PPF of 16 mol m^{-2} day^{-1} during a partially cloudy summer day had 8 h of nocturnal CO_2 assimilation and a high maximal rate of net CO_2 uptake (11.5 μmol m^{-2} day^{-1}), whereas shaded stems receiving a PPF of 3 mol m^{-2} day^{-1} had 5 h of nocturnal CO_2 assimilation and a lower maximal rate (3.1 μmol m^{-2} s^{-1}; Fig. 5b). Net CO_2 uptake over 24 h was 300 mmol m^{-2} day^{-1} for the exposed stems and −32 mol m^{-2} day^{-1} for the shaded stems (Fig. 5b).

Temperature and drought duration affect net CO_2 uptake for glasshouse-grown plants under moderate total daily PPF (Nobel and Pimienta-Barrios 1995). The total daily net CO_2 uptake is unchanged as the minimal nighttime temperatures is reduced from 18°C to 13°C but decreases 25% when the minimal temperature is reduced to 8°C. Drought lasting 14 days does not significantly affect total daily net CO_2 uptake, but uptake is 33% lower after 27 days of drought, 69% lower after 41 days, and 89% lower after 56 days (Nobel and Pimienta-Barrios 1995).

Daily net CO_2 uptake for *S. queretaroensis* can be 340 mmol m^{-2} day^{-1} under wet conditions during the summer. Under similar conditions, daily net CO_2 uptake ranges from 158 to 285 mmol m^{-2} day^{-1} for four perennial CAM species native to the Chihuahuan or the Sonoran deserts and from 760 to 1170 mmol m^{-2} day^{-1} for five, highly-productive, cultivated, CAM species (Nobel 1988: 94–99). Thus even though *S. queretaroensis* is cultivated, its net CO_2 uptake more closely resembles that of wild perennial CAM species, probably reflecting its rather recent domestication and the fact that selections made by growers were based on fruit quality, phenologies, and suitability to adverse conditions rather than on biomass productivity (Nobel and Pimienta-Barrios 1995).

The absence of reproductive growth and the low vegetative growth during the wet summer for *S. queretaroensis,* coupled with the favorable environmental conditions for photosynthesis that prevail then, allows its photosynthetic stems to replenish and store carbohydrates and its root system to extend in order to absorb more water and mineral nutrients from the soil. This seasonal storage of carbohydrates, minerals, and water in its stems during the summer is essential for the ecological success of *S. queretaroensis.* Vegetative growth during the autumn and reproductive growth in the spring are supported by such reserves, enabling it to grow when soil water is scarce.

Similar to some conifers (Salisbury and Ross 1992: 258–259), juvenile plants of *S. queretaroensis* are sensitive to high light levels. When seedlings and cuttings are established in open fields, they usually become chlorotic and die. In contrast, both seedlings and cuttings of *Opuntia* spp. perform satisfactorily in the open, and they do not show the symptoms of high light damage that are evident for *S. queretaroensis.* This sensitivity to light is also revealed at the level of pigment stability. For instance, chlorophyll in *S. queretaroensis* is more sensitive to photooxidation (De Luna 1996) than that of *Opuntia* spp. (Neri-Luna, Pimienta-Barrios, and Robles-Murguia 1993).

Maximal rates and daily net CO_2 uptake by *S. queretaroensis* are higher under a doubled atmospheric CO_2 concentration of 720 μmol mol^{-1}, expected by the end of the twenty-first century, than under the current ambient atmospheric CO_2 concentration (Nobel 1996). Net CO_2 exchange becomes positive in midafternoon under the doubled CO_2 concentration. Because the total daily net CO_2 uptake is 36% higher for the doubled than the current atmospheric CO_2 concentration, *S. queretaroensis* will likely respond favorably as the atmospheric CO_2 concentration increases in the future, as for other CAM plants, expanding the regions where they may be profitably cultivated (Nobel 1996).

MINERAL NUTRITION

Under conditions of cultivation *S. queretaroensis* thrives in alluvial soils is in a relatively rich nutrient environment. Indeed, growers claim that cultivated plants show a negative response to the application of fertilizer, possibly due to low absorption rates (Pimienta-Barrios and Nobel 1994). Such responses to minerals may reflect its ecological origin, inasmuch as *S. queretaroensis* evolved in a low-nutrient environment. Plants growing in infertile habitats often enhance nutrient intake through a high root: shoot ratio and mycorrhizal associations (Chapin 1980). Although *S. queretaroensis* does not have a high root:shoot ratio, it has mycorrhizal associations (Arceta 1997). Mycorrhizae allow plants to expend less energy in foraging for soil resources, because it is energetically less costly to support the mycorrhizal fungi than to develop a high root:shoot ratio.

For *S. queretaroensis* the mutualistic association between the fungi and the roots is temporal, restricted to the rainy summer when fine roots (rain roots) develop on main roots. The fine roots become suberized and develop into permanent roots at the beginning of the autumn, when the mutualistic cooperation disappears. Thus the absorption of water and mineral nutrients occurs more readily during the summer wet season (Arceta 1997). The fine roots are superficial, and their association with mycorrhizae facilitates the absorption of water and minerals, even with low amounts of rainfall. For instance, light rains of only 6–7 mm on dry soils are enough for the absorption of water by roots of cacti (Jordan and Nobel 1982). However, the development of fine roots by *S. queretaroensis* is not strictly rain-induced, because they did not develop during the abnormally wet spring of 1997.

The levels of most elements in the chlorenchyma and the water-storage parenchyma of *S. queretaroensis* are similar to levels observed for other species of cacti (Nobel 1988: 176–180; Nobel and Pimienta-Barrios 1995). However, the N content in its chlorenchyma is only 7.8 mg g^{-1} dry weight, which is less than for any of the other 11 cactus species considered (average of 16.7 mg g^{-1}). Also, the macronutrient Ca averages only 6 mg g^{-1} in *S. queretaroensis* compared with 44 mg g^{-1} in the chlorenchyma of the other species, many of which contain prominent calcium oxalate crystals. The contents of the micronutrients Fe and Mn in the chlorenchyma of *S. queretaroensis* average 54% lower than the average for the other 11 species of cacti (Nobel 1988: 176–180). The relatively low contents of these two micronutrients and the extremely low content of nitrogen are consistent with the relatively low growth rates and low CO_2 uptakes rates for *S. queretaroensis* compared with highly productive cultivated CAM species (Nobel 1988; Nobel and Pimienta-Barrios 1995).

SEASONAL VARIATION IN CARBOHYDRATE CONTENT

Although seasonal variations of carbon accumulation and distribution have received little attention for CAM plants, it is widely accepted that starch is the major storage polysaccharide (Sutton, Ting, and Sutton 1981) that supplies carbon for malic acid synthesis during dark CO_2 fixation (Nobel 1994: 108–114). However, the role of mucilage in CAM plants is unclear. Some have discounted the role of mucilage in the water economy of cacti (Ting 1994), while others have demonstrated that the relative capacitance of the water-storage parenchyma is related to the mucilage content (Nobel, Cavalier, and Andrade 1992). Mucilage may serve both as a form of carbon storage and as a high molecular weight polymer that facilitates adaptation to drought and to low temperatures (Zañudo 1998).

Compounds with multiple physiological roles are common in plants, and the extent to which a compound serves a storage role depends on the environment (Chapin, Schulze, and Mooney 1990). For *S. queretaroensis* both starch and mucilage tend to increase in the stems at the beginning of the summer wet season, decreasing at the end of the summer and early fall (Fig. 6a,b). On the other hand, the content of reducing sugars in its stems is low at the beginning of the summer, increasing from August to September when both mucilage and starch decrease (Fig.6c). The storage of carbohydrates in *S. queretaroensis* during early summer coincides with favorable environmental conditions for photosynthesis, when carbon gains exceed demands for growth. In particular, root formation is the prominent morphological change then (Fig. 1a).

The seasonal variations in reserve carbohydrates and reducing sugars in the stems of *S. queretaroensis* are closely related to the beginning of the main vegetative and reproductive phenophases (Fig. 1a). Its seasonal cycles in carbohydrate accumulation are like those of deciduous plants (Chapin, Schulze, and Mooney 1990; Kozlowski, Kramer, and Pallardy 1991: 57) but contrast with woody perennials, in which carbohydrate content in branches reaches a maximum in autumn, decreasing rapidly in early spring (Haddad, Clair-Maczulajtys, and Bory 1995). The latter difference evidently results from both vegetative and reproductive phenophases in woody perennials occurring during spring and summer (Kozlowski, Kramer, and Pallardy 1991: 13–15), whereas for *S. queretaroensis* vegetative development and reproductive development do not coincide, as its stem extension occurs during late summer and autumn but reproductive growth occurs during late winter and spring (Pimienta-Barrios and Nobel 1995).

CONCLUSIONS

Stenocereus queretaroensis has various strategies of adaptation to aridity and at various levels—development, structure, and physiology. Reproductive development is asynchronous and does not overlap with vegetative development. Seeds mature at the end of the spring, favoring seed germination at the beginning of the summer rainy season, which leads to seedling establishment under advantageous soil moisture conditions when natural vegetation can act as nurse plants. Stem succulence allows the accumulation of water and carbohydrate reserves. Also, the photosynthetic stems have a low stomatal density and thick cuticle, restricting water loss. However, the most crucial adaptive trait to aridity is CAM, which greatly reduces water loss during CO_2 fixation.

The nocturnal fixation of CO_2 and the storage

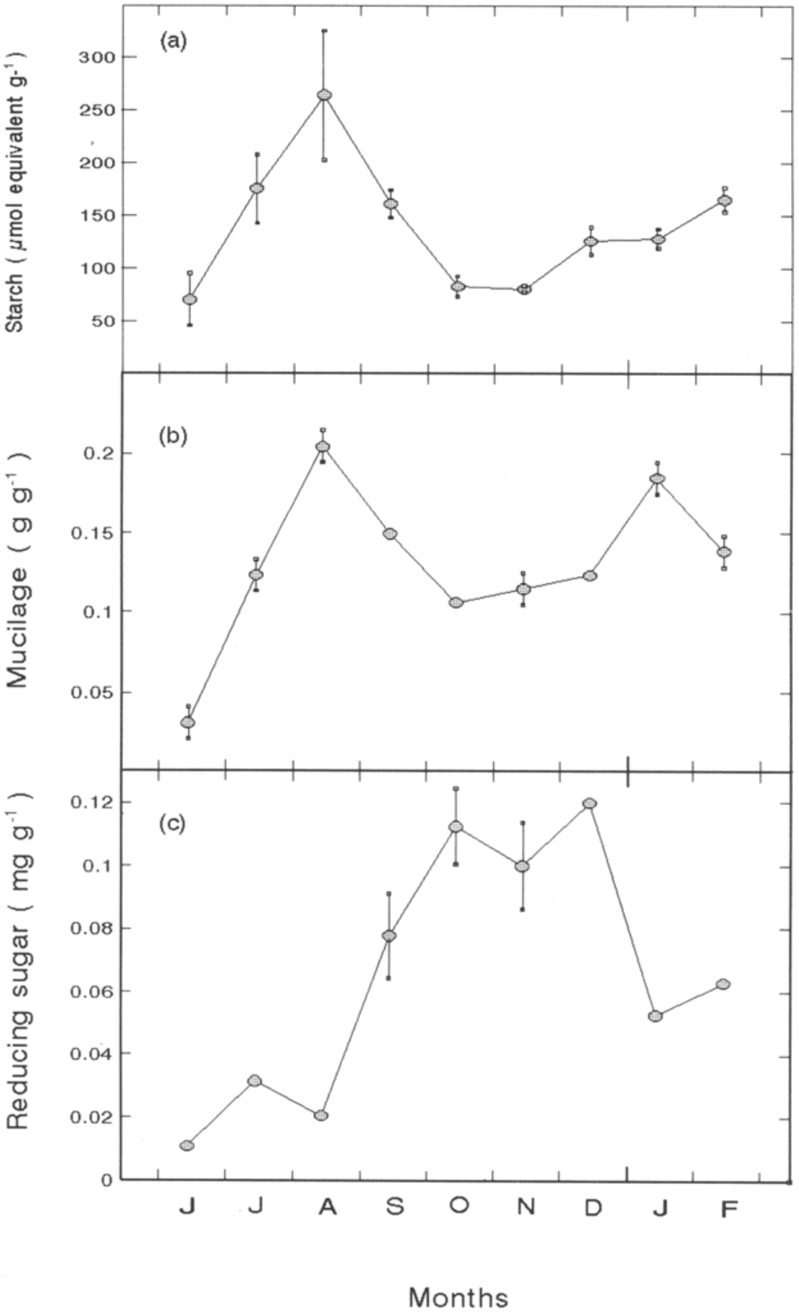

Fig. 6. Monthly levels of starch (a), mucilage (b), and reducing sugars (c) for *S. queretaroensis* in the Sayula Basin, Jalisco, Mexico. Data are on a dry weight basis and are means ± SE (n = 17 plants). Previously unpublished data were obtained during 1996–1997.

of carbohydrates, water, and minerals in the stems of *S. queretaroensis* during the summer, favored by the absence of reproductive growth and the relatively low stem extension then, is essential for its success in a subtropical semi-arid environment. The low rates of growth and photosynthesis for cultivated *S. queretaroensis* are associated with low tissue levels of nitrogen, chlorophyll, and some micronutrients (Fe, Mn), and perhaps low levels of gibberellic acid. Slow growth allows the plants to persist in arid and semi-arid environments, in which adverse environmental conditions must periodically be overcome.

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