Ethnobotany, Productivity, and Ecophysiology of Pitaya (Stenocereus queretaroensis)

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ABSTRACT

Pitaya (*Stenocereus queretaroensis*) is a columnar cactus that produces attractively colored edible fruits in both wild and cultivated populations in the subtropical semiarid lands of Mexico. Pitaya is a relatively recently domesticated fruit, which during the last 10 years has emerged as a fruit crop whose cultivation is feasible using relatively low inputs of anthropogenic energy or water and whose fruits ripen during the spring season, before summer when the local markets are flooded with other fresh summer fruits. These agronomic traits have increased the economic viability of small farms in semiarid subtropical lands of Mexico.

This article summarizes the work on agroecological and biological aspects of *Stenocereus queretaroensis* conducted during the last seven years in the subtropical semiarid lands of the Sayula Basin, Jalisco, Mexico. Our work is oriented to the development of basic knowledge of the plant and its environment, which allowed us to define opportunities and needs for basic and applied research, oriented to the domestication of pitaya under the modern precepts of sustainable development.

Keywords: Cacti, Stenocereus, aridity, ethnobotany, ecophysiology.

INTRODUCTION

Pitaya are columnar cacti native to subtropical regions of Mexico that produce attractively colored edible fruit (Bravo, 1978). Pitaya belong to the tribe Pachycereae of the Cactoideae subfamily (Sanchez-Mejorada, 1984). Economically, the most important subtribe is *Stenocereae,* which includes the genus *Stenocereus,* with 24 species distributed from the southwestern United States to Venezuela and Peru (Bravo, 1978). *Stenocereus* have provided valuable additions to the diets of Indian tribes inhabiting tropical semiarid lands in coastal plains along the Gulf of Mexico and the Pacific Ocean as well as subtropical semiarid inland regions of Mexico.

Commercial planting started in the late 19th century and has always been on a small scale. Yet, pitayas were one of the most important fruit crops at the beginning of this century (Aldana, 1986). The first systematic planting of S. *queretaroensis* occurred in Southwestern Jalisco, in a region know as the Sayula Basin (68 km south-southwest of Guadalajara). Efforts to improve this fruit crop are rather recent and have been made primarily by selecting outstanding phenotypes, with emphasis on fruit quality rather than biomass productivity (Nobel and Pimienta-Barrios, 1995). Pitayas require relatively low inputs of water and fertilizer. Such attributes have made these cacti attractive for small-scale farms in Mexico (Pimienta-Barrios and Nobel, 1994).

In this article we attempt to summarize our work conducted in both wild and cultivated populations of *Stenocereus queretaroensis* during the last seven years. As a final remark, we will try to propose the route of domestication of pitayas taking into consideration their economical positions in the economy of the subsistence agriculture in the semiarid lands of Mexico, the actual trends evolution of national and international markets. Pitayas, as an exotic fruit, have the potential to become a fruit for exportation to international markets.

ETHNOBOTANY

The name pitaya originated in the Antilles and meant scaly fruit (Piña, 1977). The ancient Mexicans called the fruit Coapetilla, meaning thick serpent, relating to the appearance of the stems. Since pre-Hispanic times, various species of *Stenocereus* have provided valuable additions to diets of Indian tribes inhabiting tropical semiarid lands on coastal plains along the Gulf of Mexico and the Pacific Ocean as well as subtropical semiarid inland regions of Mexico. For the Seri Indians the pitayas were one of the most important foods, as well as their favorite plant. The fruits commonly were saved after drying; both the seeds and the petals were removed from the dried fruits and eaten (Nobel, 1994).

Chavero (1967) mentions that two kinds of fruits were used as food for the Nahoas Indians, both in the past and at present. He described the fruits produced by the pitaya with different colored flesh: white, red, and yellow. The Nahoas were famous for the ``wine celebrations'' during the harvest time of pitaya, the time of year in which the old people invited the neighboring towns to make war alliances.

The fruits of pitaya were important also for the Californian of Cocachimies tribes, because they used the fruits as a source of food. The seeds were roasted and ground to obtain flan and used as a food during the winter, as ``a second harvest of pitayas'' (López, 1993).

The state of Sinaloa, meaning ``land of pitayas.'' Because their name is derived from the Cahitas, ``Sina'' means pitaya and ``Lobola'', means round (redonda), hence, literally, the meaning of the Sinaloa State is ``pitaya redonda'' or ``round pitaya.'' The Sinaloa name is reminiscent of those columnar cacti. Some traditional pre-Hispanic costumes depict the harvest of fruits to produce candies, persist in some regions of the state of Sinaloa (Lopez, 1993).

PLANT DESCRIPTION

The columnar cacti that produce pitayas belong to tribe Pachycereae of subfamily Cactoideae (Sanchez-Mejorada, 1984). Economically, the most important subtribe is *Stenocereae*, which includes the genus Stenocereus with 24 species distributed from southwestern United States to

Venezuela and Peru (Bravo, 1978). The most important cultivated species are: *S. queretaroensis*, *S. griseus*, *S. stellatus*, and *S. fricii*. However, S. *queretaroensis* is the only species under intensive cultivation in Mexico and thus will be the main point of our discussion.

Stenocereus queretaroensis is arborescent, up to 8 m tall, with a well-defined trunk and numerous branches. The cylindrical stems generally have about eight prominent ribs and a diameter of 13 to 18 cm when mature. The flowers grow from areoles along the upper half of a branch, are 10 to 14 cm long, and are reddish with a whitish interior. The fruit varies from globose to ovoid, is 6 to 8 cm long, and matures from late April to June (Salcedo and Arreola, 1991). The seeds are numerous, small, black, fragile, and readily swallowed.

PHYSICAL ENVIRONMENT

Stenocereus queretaroensis is widely distributed in semiarid regions of Mexico as both wild and under cultivation in Jalisco, Colima, Michoacán, Queretaro, and Zacatecas. Its most important production center is in the Sayula Basin approximately 80 km southwest of Guadalajara, where about 1000 ha are currently cultivated (Pimienta and Tomas, 1993). In the states of Jalisco, Colima and Zacatecas, wild populations grow on rocky slopes in shallow soils at elevations of 1300 to 1600 m above sea level. Cultivated populations in the Sayula Basin are grown between 1000 and 1400 m. The Sayula Basin, where *S. queretaroensis* grows, has moderate temperatures. Monthly averages of daily air temperatures range from 8°C to 18°C at night, and 24°C to 34°C during the day. From the coldest to the warmest month, minimum and maximum temperatures each varies only 8°C. Subzero air temperatures are rare. The annual average rainfall is nearly 700 mm, mostly in summer; 64% of the total annual precipitation is from June through August, and 10% is from January through May.

The soils are classified as Cambisol cromic, including feozem haplic and acrisol ortico. Those soils have a sandy-loam texture and slightly acidic pH (6.0 to 6.8) (Pimienta-Barrios and Nobel, 1994; Huerta, 1995).

ESTABLISHING AND MANAGING PLANTATION

Cultivated *S. queretaroensis* plants thrive in deep, slightly acidic, sandy-loam soils but can grow satisfactorily in stony, infertile soils that are unsuitable for conventional crops. In fact, the cultivation of pitaya has helped convert marginal lands into productive ones in the Sayula Basin (Salcedo and Arreola 1991) (Figure 1).

Orchards are established by planting terminal stem segments that are 80 to 120 cm in length and 4 to 5 years in age. These segments are excised before flowering from branches that have produced fruit for at least 2 years.

Although flowers and fruit production start one year after planting, 10 years are required to reach commercial profitability. Productivity of *S. queretaroensis* in the Sayula Basin can last more than 100 years, whereas the useful productivity of *S. stellatus* cultivated in Puebla is less than 30 years (Cruz, 1984).

Because irrigation increases plant vigor, flower production, and fruit size, some orchards in the Sayula Basin are irrigated during exceptionally dry periods. Fertilizers are rarely applied, in part to avoid ``burning'' the roots. On the other hand, application of manure enhances the growth of *S. griseus* in Puebla and Oaxaca (Cruz, 1984). Pruning can control plant height and

branch length, which facilitates fruit harvesting, but most plants are not pruned. To provide fruit diversity, some plants in home gardens are grafted with up to five varieties (Pimienta-Barrios and Nobel, 1994).

Relatively few pests and diseases affect *S. Queretaroensis*. Spring frosts occasionally damage its buds in their early stages of formation. Flowers that abscise after anthesis often have underdeveloped ovules, possibly indicating early senescence or lack of fertilization (Lomeli and Pimienta, 1993). Beetle larvae attack the pericarp of developing fruits and cause abscission. Ants can also cause young fruits to abscise and are sometimes controlled by pesticides.

FRUIT QUALITY AND FRUIT YIELDS

The most important cultivated variety of pitaya (*S. queretaroensis*) in the Sayula, Basin is termed "Mamey," which represents 80% of the total fruit production. For plants of medium age, the annual harvest varies from 45 to 98 fruits per plant; average fresh weight per fruit ranges from 120 g to 165 g. Compared with cactus pear, a larger fraction of the pitaya fruit is eaten. The peel, which is removed to exposed the edible pulp, generally represents 40% to 45% of the fresh weight for cactus pear, but only 18% to 24% for fruits of *S. queretaroensis* (Pimienta and Tomas, 1993f). Moreover, the relatively large, indigestible seeds of cactus pear represent nearly 4% of their fresh weight, whereas the small seeds of pitayas are readily chewed and digested.

The fruits must be eaten within a few hours of being purchased, as they have a short shelf life. Indeed, fruits are often harvested with the peel split open, which exposes the colorful pulp. This natural dehiscence at the time of ripening is one of the main factors limiting the commercialization of pitayas. With the pulp exposed, the harvested fruits over ripen in 1 to 2 days without refrigeration (Figure 2).

The pitaya is an acidic fruit. The pH varies from 3.9 to 5.0; the malic acid content varies from 0.14% to 0.50%. Sugars compose 10% to 11% of the fresh weight and are nearly all reducing sugars, which are more readily digested than nonreducing sugars. The sugar content of the pitaya pulp is somewhat low compared with other fruits, such as apples, apricots, cherries, oranges, and cactus pears. The pulp has an extremely low protein content, as is typical of fruits, although the seeds contain nearly 1 g of protein per kilogram of fresh weight.

Yields of pitaya increase with plant age, reflecting the increase in both the numbers and the length of the stems along which the fruits are borne. At about 20 years of age, the fresh weight of harvested fruits can be approximately 16 metric tons/ha. Thereafter, fruit production increases by approximately 25% to reach a maximum at about 40 years of age. Plants of *S. queretaroensis* in the Sayula Basin that are 100 years old can still produce fruit, but at a diminishing rate as parts of the older stems become senescent (Pimienta-Barrios and Nobel, 1994).

PHENOLOGY AND REPRODUCTIVE BIOLOGY

Primary growth for *S. queretaroensis* takes place at the branch apices and occurs essentially only in the autumn and early winter (October through December). Floral differentiation starts in early February and ends in early April; fruits ripen from early March until the end of May. Thus, vegetative and reproductive growth coincide with the dry season (Lomeli and Pimienta, 1993; Pimienta-Barrios and Nobel, 1995). The differentiation of new roots coincides with the

start of the summer rainy season, which is the only prominent vegetative event that occurs then (Arceta, 1997) (Figure 3). 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 end of spring and during summer (Kozlowski et al., 1991). Moreover, vegetative growth of S. queretaroensis does not coincide with reproductive growth, as it does for most conventional crops in temperate and tropical regions (Ryugo, 1988).

VEGETATIVE AND REPRODUCTIVE GROWTH

The major rates of stem extension for *S. queretaroensis* occur in the autumn when minimum air temperatures are lower and soil water is less available (Figure 4). For instance, for mature cultivated plants 85% of the annual growth rate is from December to January, when the daily rate is 0.26 cm day (Pimienta-Barrios and Nobel, 1995). Thus *S. queretaroensis* is a slowly-^{1} growing plant similar to other columnar cacti producing edible fruit (Nerd et al., 1993), but unlike young cladodes of Opuntia under similar conditions (Robles, 1994) or other herbaceous and woody plants (Grime and Hunt, 1975), which have higher growth rates (Table 1). Thus, it behaves like wild perennial plants growing in infertile soils that 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), but tend to be less plastic than plants with higher growth rates (Grime and Hunt, 1975). Low plasticity is a common feature of cultivated S. queretaroensis, because irrigation does not markedly affect stem extension, even when other environmental factors like temperature and irradiance are favorable for photosynthesis and growth (Pimienta-Barrios and Nobel, 1995).

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 one month (Pimienta-Barrios et al., 1998, in press).

Table 1. Stem Growth Rates Between Selected Cam Plants
and Woody and Herbaceous Plants
(Adapted from Nobel and Pimienta-Barrios, 1995).

Specie	Annual growth rates (meters day Annual growth rates (meters day^{-1})
Pitaya (Stenocereus queretaroensis)	0.0018 m^{-2} day^{-1}
Cactus pear (Opuntia ficus-indica)	0.09 - 0.014 m^{-2} d^{-1}
Herbaceous and woody species	0.03 - 0.32 m^{-2} day^{-1}

The rate of flower growth is 0.31 cm day^{-1} ; 22 days elapse from the emergence of flowers buds to anthesis. After abscission of the perianth, the developing fruit is about 15% longer for irrigated plants than those under natural rainfall conditions (Pimienta-Barrios et al., 1995). Fruit length reaches more than 90% of its final size in about 40 days. The overall development

period from anthesis to maturity is about 90 days, resulting in larger flowers (Figure 5). 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. The time to reach maturity for fruits of S. *queretaroensis* is relatively short compared with other cacti (e.g., *Opuntia*), peach, plum, apple, and avocado (Barbera et al., 1992; Lee and Young, 1983; Ryugo, 1988).

STEM ANATOMY

S. queretaroensis has a low stomatal density (10 to 40 mm^2) and thick cuticle (13 to 17 Fm). A thick cuticle and low stomatal density represents an important adaptation to aridity, leading to the ability to withstand long periods of drought (Nobel, 1994). Calcium oxalate crystals (druses) are not present in the stem cortex of *S. queretaroensis* consistent with the observation that its calcium content is relatively low (Nobel and Pimienta-Barrios, 1995), but in contrast to other cacti (Nobel, 1983).

A distinctive feature of stem anatomy of *S. queretaroensis* is the presence of aerenchyma in the hypodermis. Aerenchyma tissue 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; Salisbury and Ross, 1992). The aerenchyma tissue is located on the adaxial side of the stem and the chlorenchyma in the abaxial side, suggesting a homology with the anatomy of bifacial or dorsiventral mesophytic leaves for which the aerenchyma resembles spongy parenchyma (Mauseth, 1991). The abundance of intercellular air spaces may be an important adaptation to facilitate gas exchange and photosynthesis (Sajeva and Mauseth, 1991).

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). This behavior favors the ecological success of cacti in arid environments because less water is lost than for species having stomatal opening during the daytime (Nobel, 1995).

As was true for laboratory studies (Nobel and Pimienta-Barrios, 1995), gas exchange measurements in the field revealed that nearly all of the net CO_2 uptake occurs at night. Young plants (three to four years old) had a higher rate of CO_2 uptake (11 Fmol m^{-2} s^{-2}) than adult plants (7.6 Fmol m^{-2} s^{-2}). The total daily net CO_2 uptake, obtained by integrating the net CO_2 uptake rates over 24-hour periods, was 30 mmol m^{-2} day^{-1} for the old plants and 409 mmol m^{-2} day^{-1} for the young plants (Figure 6). Such young plants showed higher rates of net CO_2 uptake than for *S. queretaroensis* in a glass house but did not exhibit as much net CO_2 uptake in the early morning and late afternoon (Nobel and Pimienta-Barrios, 1995), possibly indicating a lower soil water potential in the field.

The rate of net CO_2 uptake depends on light level, hence varies with the orientation of the stems and their rib surfaces. Field observation showed that net CO_2 uptake increases more-or-less linearly with photosynthetic photon flux (PPF). Exposed stems receiving PPF averaging 745 Fmol m^{-2} s^{-1} during a partially cloudy summer day had 8 hours of nocturnal CO_2 assimilation and high rate of net CO_2 uptake (11.5 Fmol m^{-2} day^{-1}), whereas shaded stems receiving a PPF averaging 326 Fmol m^{-2} s^{-1} had 5 hours of nocturnal CO assimilation and a

lower maximal rate (3.1 Fmol m^{-2} s^{-1}). Net CO_2 uptake during 24 hours was 300 mmol m^{-2} day^{-1} for the exposed stems and -32 mol m^{-2} day^{-1} for the shaded stems (Figure 5).

Temperature and drought duration affect net CO_2 uptake for greenhouse-grown plants under moderate total daily PPF (Nobel and Pimienta-Barrios, 1995). The total daily net CO_2 uptake was unchanged as the minimal nighttime temperature was reduced from 18°C to 13°C. However, the CO_2 uptake decreased 25% when the minimal temperature was reduced to 80°C. Drought lasting 14 days did not significantly affect total daily net CO_2 uptake, but uptake, but was 33% lower after 27 days of drought, 69% lower after 41 days, and 89% lower after 56 days (Nobel and Pimienta-Barrios, 1995).

Table 2. Shows total daily net CO_2 uptake for S. queretaroensis under various environmental conditions in a temperature-controlled greenhouse. Day/night temperatures are the mean maximal/minimal air temperatures under which the plants were maintained for at least 7 days. Drought was defined as commencing when weekly watering ceased; soil water potential in the root zone then decreased below -0.5 Mpa, becoming -1.9 Mpa after 2 weeks of drought and £5.0 Mpa after 3 weeks. The total daily PPF incident on the rib surfaces considered was 14±3 mol m^{-2} day^{-1}. Data are means ±S.E. (n=5 plants) (Nobel and Pimienta-Barrios, 1995).

Table 2. Total Daily Net CO_2 Uptake for *S. queretaroensis* Under Various Environmental Conditions in a Temperature-controlled Greenhouse

Day/night temperatures (°C/°C)	Drought Length (days)	CO Uptake (mmol m^{-2} day^{-1})
32/18	0	230 ±11
32/13	0	235 ±14
32/8	0	177 ±9
32/18	14	222 ±14
32/18	27	167 ±15
32/18	41	71 ±17
32/18	56	26 ±6

Daily net CO_2 uptake for *S. queretaroensis* was 340 mmol m^{-2} day^{-1} under wet conditions during the summer. Under similar conditions, the daily net CO_2 uptake ranged from 158 to 285 mmol m^{-2} day^{-1} for four perennial CAM species native to the Chihuahuan or Sonoran deserts and from 760 to 1170 mol m^{-2} day^{-1} for five highly productive cultivated CAM species (Nobel, 1988). 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 biomass productivity (Nobel and Pimienta-Barrios, 1995).

The absence of reproductive growth and very slow vegetative growth during the wet summer season for *S. queretaroensis*, coupled with the favorable environmental conditions for photosynthesis that prevail then, allows its photosynthetic stems to replenish and to store carbohydrates and to extend its root system to absorb water and mineral nutrients from the soil. This seasonal storage of carbohydrates, minerals, and water in photosynthetic tissue during the summer is essential to 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 with scarcity of water.

Similar, to some conifers (Salisbury and Ross, 1992), juvenile plants of *S. queretaroensis* are sensitive to high levels of light. 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 evident for *S. queretaroensis*. This sensitivity to light is revealed also at the level of pigment stability. For instance, chlorophyll in S. queretaroensis is more sensitive to photo oxidation (De Luna, 1996), than that of *Opuntia* (Neri-Luna et al., 1993).

Maximal rates and daily uptake by *S. queretaroensis* are hiqher under doubled atmospheric CO_2 concentrations of 720 Fmol mol , expected by the end of the 21st century. Net CO_2 exchange becomes positive in mid-afternoon under the doubled concentration. The total daily net CO_2 uptake is 360%, for the doubled concentrations, than the current ambient atmospheric CO_2 concentrations, *S. queretaroensis* will likely respond favorably as the atmospheric CO, concentrations increases in the future, as for other CAM plants, expanding the regions where they may be cultivated profitably (Nobel, 1996).

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 et al., 1981) that supplies carbon for malic acid synthesis during dark CO_2 fixation (Nobel, 1994). However, the role of mucilage in CAM plants is unclear. Some authors 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 et al., 1992). Mucilage may serve both as a form of carbon storage and as a high molecular weight polymer that facilitates adaptation to drought and 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 et al. 1990). For *S. queretaroensis* both mucilage and starch tend to increase in the stems at the beginning of the summer wet season, decreasing at the end of the summer and early fall (Figure 7). 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. 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 sole morphological change then.

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. Its seasonal cycles in carbohydrate accumulation are like those of a deciduous plant (Chapin et al., 1990; Kozlowski et al., 1991) but contrast with woody perennials, in which total carbohydrates in branches reaches a maximum in autumn, decreasing rapidly in early spring (Haddad et al., 1995). The latter differences evidently result from both vegetative and reproductive phenophases in woody perennials occurring during spring and summer (Kozlowski et al., 1991), while for S. queretaroensis vegetative development and reproductive development do not coincide as stem extension occurs during late summer and autumn but reproductive growth occurs during late winter and spring (Pimienta-Barrios and Nobel, 1995).

MINERAL NUTRITION

S. queretaroensis grows satisfactorily in both alluvial soils in a relatively rich nutrient environment and in infertile shallow stony soils. As a matter of fact, 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, because *S. queretaroensis* evolved in a low-nutrient environment. Plants growing in infertile habitats often enhance nutrient intake through a high root-to-shoot ratio and mycorrhizal associations (Chapin, 1980). Although S. queretaroensis does not have a high root-to-shoot ratio, it has mycorrhizal associations (Arceta, 1997). Mycorrhizae allows 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-to-shoot ratio.

For *S. queretaroensis* the mutualistic association between the fungi and the roots is temporal, because it is restricted to the rainy summer, when fine roots (rain roots) develop on main roots. The rain 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 mycorrhizas (VAM) of the genus Glomus and Gigaspora facilitates absorption of water and minerals, even with low amounts of rainfall. Even light rains of only 6 mm to 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 were not differentiated 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 values observed for other species of cacti (Nobel, 1988; 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 species considered (average of 16.7 mg g^{-1}). Also, the macronutrient Ca has a mean of only 6 mg g^{-1} 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. 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 uptake rates observed for *S. queretaroensis*, compared with highly productive cultivated CAM species (Nobel and Pimienta-Barrios, 1995).

OPPORTUNITIES AND NEEDS FOR BASIC AND APPLIED RESEARCH

The main factors that limit the domestication of pitaya are the low metabolic activities in the vegetative sinks and the photosynthetic sources, as indicated by the low rates of growth and photosynthesis. In fact, the low rates of stem growth have limited their domestication because 10 years are required to obtain a large enough production for commercial profitability. Therefore, a priority should be placed on understanding the physiological and genetical controls of growth in order to overcome this limitation of pitaya domestication.

Experimental work revealed that pitaya does not respond to traditonal management (i.e., watering and fertilization), which is perhaps due to their symbiotic association with mycorrhizae (VAM), enabling the plants to grow suscessfully in low-quality soils. The understanding of the physiological, genetical and environmental factors that control this mutualistic cooperation will be valuable in developing production systems that require low imputs of anthropogenic energy.

Finally, we also must try to evaluate the importance of pitaya as a component of low deciduous forest and their relation with the ecosystems, because they provide food for several species of animals (especially bats and birds) during the dry season when other sources of food are scarce. We must pay particular attention to the deforestation of the low deciduous forest, due to changes in use of the soil.

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LITERATURE CITED

Aldana, R. M. 1986. El campo jaliscience durante el porfiriato. Instituto de Estudios Sociales. Universidad de Guadalajara. Guadalajara, Jalisco.

Arceta, E. G. I. 1997. Caracterizacion fisiológica de una poblacion silvestre de pitayo (Stenocereus aueretaroensis (Weber) Buxbaum) asociada con micorrizas vesiculo arbuscular. Bachelor's Thesis. Universidad de Guadalajara, Mexico.

Barbera, G. F., F. Carimi and P. Inglese. 1992. Physical, morphological and chemical changes during fruit development and ripening in three cultivars of prickly pear, Opuntia ficus-indica (L.) Miller. J. of Hort. Sci. 67:307-312.

Bradford, J. K. 1994. Water stress and the water relations of seed development: A critical review. Crop Science 34:1-11.

Bravo, H. 1978. Las Cactáceas de México, UNAM. México. Chavero, A. 1967. México a través de los siglos. Tomo I. Edit. Cumbre, México. 6a. Ed. Esau, 1977. The anatomy of seed plants. 2d. John Wiley Sons. New York, New York.

Chapin, S. F. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematic 21:423-447.

Chapin, S.F., E. D. Schulze, and H. A. Mooney. 1990. The ecology and economics of storage in plants. Annual Review of Ecology and Systematic 21:423-447.

Coombe, B.G. 1976. The development of fleshy fruits. Annual Review of Plant Physiology 27:507- 528.

Cruz, H.P. 1984. Caracterizacion del fruto de cuatro tipos de pitaya (Stenocereus stellatus Riccobono). Tesis de Maestria. Colegio de Postgraduados. Chapingo, Mex.

De Luna, F. A. 1996. Efecto de la aplicación de inhibidores de la expresion genetica sobre la senescencia de segmentos de tallo de pitayo (Stenocereus queretaroensis). Bachelor's Thesis. Universidad de Guadalajara, Mexico.

Grime, P. J. 1979. Plant strategies and vegetation processes. Wiley, New York.

Grime, P.J., and R. Hunt. 1975. Relative growth rate: its range and adaptative significance in local flora. Journal of Ecology 63:393-422.

Haddad, Y., D. Clair-Maczulajtys, and G. Bory. 1995. Effects of curtain-like pruning on distribution and seasonal patterns of carbohydrate reserves in plane (Platanus acerifolia Wild) trees. Tree Physiology 15:135-140.

Huerta M. F, 1995. Aspectos ecológicos del pitayo y cardón en la cuenca de Sayula, Jalisco. México, Tesis de Maestria. Colegio de Postgraduados Chapingo. México.

Jordan, P.W., and P.S. Nobel. 1982. Height distribution of two species of cacti in relation to rainfall, seedling establishment, and growth. Botanical Gazette 143:511-517.

Kozlowski, R.T, P.J. Kramer and S.G. Pallardy. 1991. The physiological ecology of woody plants. Academic Press, San Diego.

Lee, S. K., and R.E. Young. 1983. Growth measurements as an indication of avocado maturity . J.the Amer. Assoc. for Hort. Sci. 108:395-397.

Lomeli, M.E., and E. Pimienta. 1993. Demografia reproductiva del pitayo (Stenocereus queretaroensis (Weber) Buxbaum). Rev. Cact. y Suc. Mexicanas 38:13-19.

López, P., J. 1993. Caracterización Agroecológica y Social del Pitayo Stenocereus queretaroensis, en la Subcuenca de '17'(1 Sayula, Jalisco, México. Tesis de Maestria, Universidad de Guadalajara.

Mauseth, J.D. 1991. Botany: an introduction to plant biology. Saunders College Publishing. Nerd, A., E. Raveh and Y. Mizrahi. 1993. Adaptation of five columnar species to various conditions in the Negev Desert of Israel. Econ. Bot. 47:304-311.

Neri-Luna, C., E. Pimienta-Barrios, and C. Robles-Murguia. 1993. Cambios fisiologicos durante el proceso de senescencia en cladodios jovenes de nopal (Opuntia ficus-indica (L.) Miller). Agrociencia 4:7-18.

Nobel, P. S. 1983. Nutrient levels in cacti-relation to nocturnal acid accumulation and growth. Amer. J. of Bot. 70(8):1244-1253.

Nobel, P.S. 1988. Environmental biology of agaves and cacti. Cambridge University Press, New York.

Nobel, P. S., J. Cavalier, and J. L. Andrade. 1992. Mucilage in cacti: its apoplastic capacitance, associated solutes, and influences of tissue water relations. J. Expe. Bot. 43(250):641-648.

Nobel, P.S. 1994. Remarkable agaves and cacti. Oxford University Press, New York.

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

Nobel, P. S. 1996. Response of some North American CAM plants to freezing temperatures and doubled CO_2 concentrations: implications for global climate change for extending cultivation. J. of Arid Envir. 34:187-196.

Nobel, P.S., and E. Pimienta-Barrios. 1995. Monthly stem elongation for Stenocereus queretaroenesis: relationships to environmental conditions, net CO_2 uptake, and seasonal variations in sugar content. Envir. and Experimental Bot. 35:17-42.

Pimienta-Barrios, E. y M.V. Tomas. 1993. Caracterización de la variación en el peso y la composición quimica del fruto en variedades de pitayo (Stenocereus queretaroensis (Weber) Buxbaum). Cact. Suc. Mex. 38:82-88.

Pimienta-Barrios, E., and P.S. Nobel. 1994. Pitaya (Stenocereus spp., Cactaceae): An ancient and modern fruit crop of Mexico. Econ. Bot. 48:76-83.

Pimienta-Barrios, E., and P.S. Nobel. 1995. Reproductive characteristics of pitayo (Stenocereus queretaroensis) and their relationships with soluble sugars and irrigation. J. of Amer. Soc. for Hort. Sci. 120(6):1082-1086.

Pimienta-Barrios, E., C. Robles-Murguia and A. Dominguez de la Torre. 1995. Estrategias fisiologicas y reproductivas de adaptacion del pitayo a la aridez. Ciencia 46:339-349.

Pimienta, E., G. Hernandez, A. Dominguez and Nobel. 1988. Growth and development of the columnar cactus Stenocereus queretaroensis (Weber) Buxbaum in a subtropical environment. Tree Physiology (in press).

Robles, M.C. 1994. Estudio anatomico-fisiologico comparativo entre el nopal (Opuntia ficus-indica (L.)Miller) y el pitayo (Stenocereus queretaroensis (Weber) Buxbaum). Bachelor's Thesis. Universidad de Guadalajara, Mexico.

Salisbury, B.F., and C. W. Ross. 1992. Plant physiology. 4d. Wadsworth. Belmont, California.

Ryugo, K. 1988. Fruit culture. Wiley, New York.

Sajeva, M., and J.D. Mauseth. 1991. Leaf-like structure in the photosynthetic, succulent stems of cacti. Annals of Botany 68:405-411.

Sutton, B.G., I.P. Ting and R. Sutton. 1981. Carbohydrate metabolism of cactus in a desert environment. Plant Physiol. 68:784-787.

Ting, I. P. 1994. Carbohydrate metabolism in cacti: gums and mucilage. Felker, P. (ed.). Proceedings of 5th Annual Texas Prickly Pear Council. Kingsville, TX. pp. 7-12.

Zanchin, A.C., C. Bonghi., G. Casadoro., A. Ramina, and N. Rascio. 1994. Cell enlargement and cell separation during peach fruit development. Internat. J. of P. Sci. 155:4956.

Zañudo, H. J. 1997. Relacion entre factores climaticos, desarrollo y la variacion estacional de carbohidratos de reserva y azucares reductores en pitayo (Stenocereus queretaroensis (Weber) Buxbaum). Bachelor's Thesis. Universidad de Guadalajara, Mexico.

LITERATURA CITADA

Aldana, R. M. 1986. El campo jaliscience durante el porfiriato. Instituto de Estudios Sociales. Universidad de Guadalajara. Guadalajara, Jalisco. Ayon, 1989

Chavero, A. 1967. México a través de los siglos. Tomo I. Edit. Cumbre, México. 6a. Ed.

Clavijero, F. J. 1975. Historia de la antigua o Baja California. 2a. Ed. Colección Sepan Cuantos. Editorial Porrua. México.

Bárcena, M. 1983. Ensayo Estadístico de Jalisco. Guadalajara, Jalisco, México.

Del Barco (1988).

Del Campo, 1957.

Castillo, 1984.

Del Barco, 1988.

Gates, E.H., 1957. Distribución de las cactáceas de Baja California. Cact. Suc. Mex. 2(4): 69-75.

Gates, E. H., 1958. The dwarf pithaya dulce of Baja California. Cact. Succ. J. (Los Angeles) 30(4):114-115.

Martinez, 1983.

Munguía, F. 1988. La Provincia de Avalos. Depto. de Bellas Artes. Gobierno del Estado de Jalisco. 2a. Ed. Jalisco, México.

Nobel, P.S. 1994. Remarkable agaves and cacti. Oxford University Press, New York.

López, P. J. 1993. Caracterización agroecológica y social del pitayo (Stenocereus queretaroensis) en la subcuenca de Sayula, Jalisco, México.

Piña, I. J. 1977. Pitayas y otras cactáceas afines del estado de Oaxaca. Revista de la Sociedad Mexicana de Cactología 38:84-91.

Sánchez-Mejorada, R.H. 1982. Algunos usos prehispánicos de las cactáceas entre los indigenas de México. Secretaria de Desarrollo Agropecuario. Gobierno del Estado de México. Toluca, México.

Figure 1. *Stenocereus queretaroensis*, approximately 20 years old, growing in stony infertile soils, showing numerous fruits

Figure 2. Ripe fruits of *Stenocereus queretaroensis* showing natural dehiscene at the time of ripening

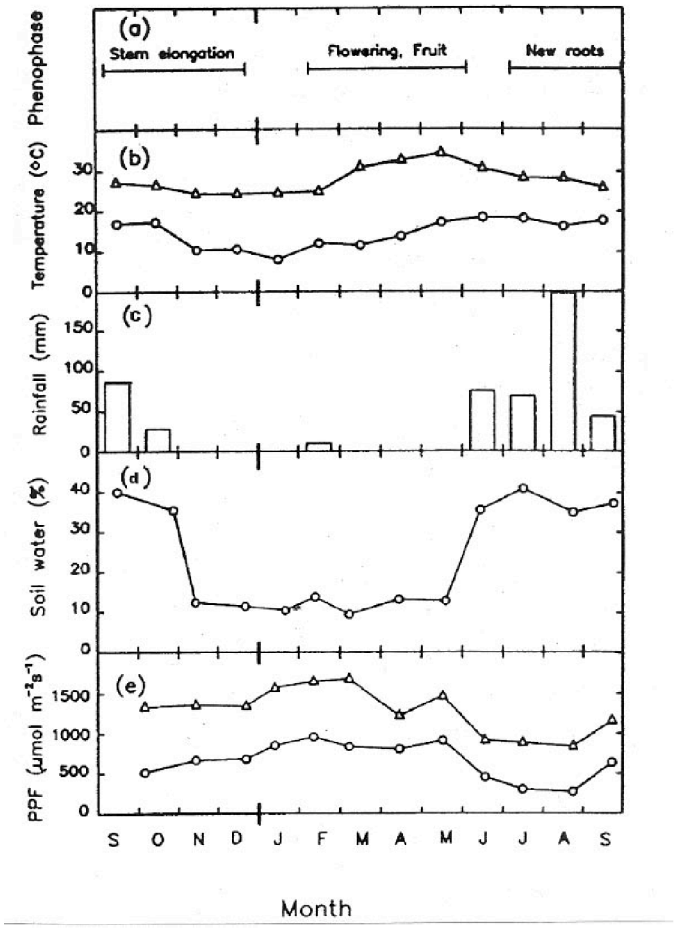

Figure 3. (a) Phenological stages of Stenocereus queretaroensis; (b) daily minimum (o) and maximum ([a]) air temperatures averaged over a months); (c) total monthly rainfall; (d) soil water content; (e) average photosynthetic photon flux in an open field ([a]) and in the plant (o) at the Sayula Basin, Jalisco, Mexico

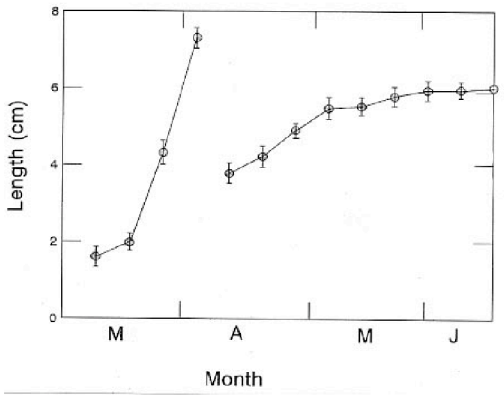

Figure 4. Daily minimum (0) and maximum ([a]) air temperatures averaged over a month and total monthly rainfall (bars) (a); and monthly stem extension for Stenocereus queretaoensis (b); in the Sayula Basin, Jalisco, Mexico. Extension data are means + SE (n=24 stems).

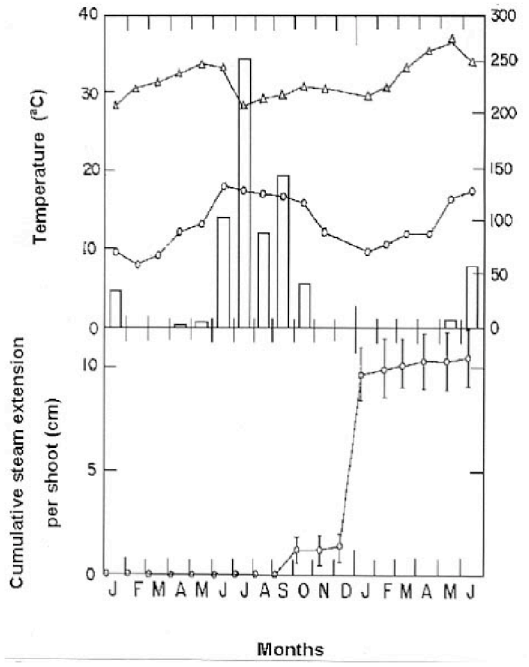

Figure 5. Length of flower buds (receptacle plus perianth; 0), and the subsequently developing fruits (0) for Stenocereus queretaroensis undernatural conditions. Data are means ±SE (n=50 flowers or fruit).

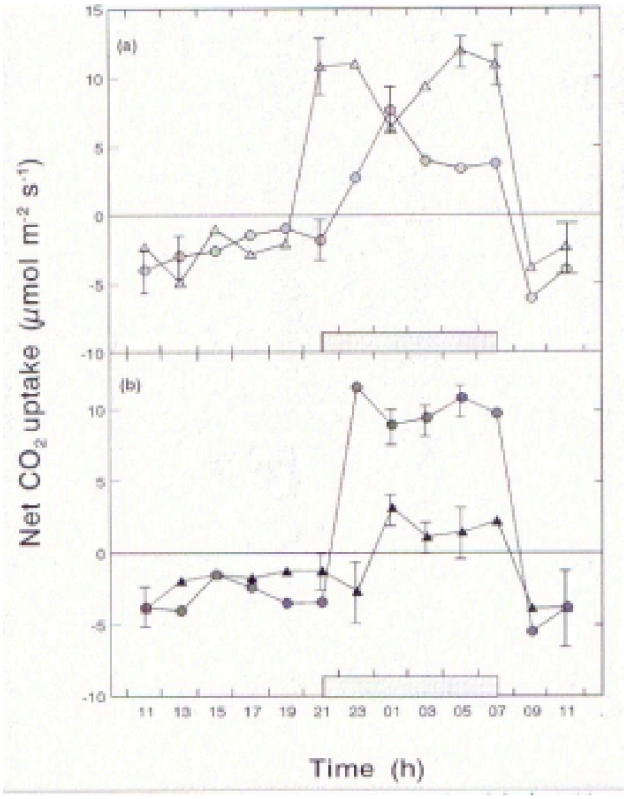

Figure 6. Net CO_2 uptake by Stenocereus queretaroensis by adult plants ([a]), and young plants (0) (a), and light-exposed stems (.) and shaded stems (?) in the Sayula Basin, Jalisco, Mexico. Data are means ±SE (n=12 stems). Data were obtained on 29-30 June 1997.

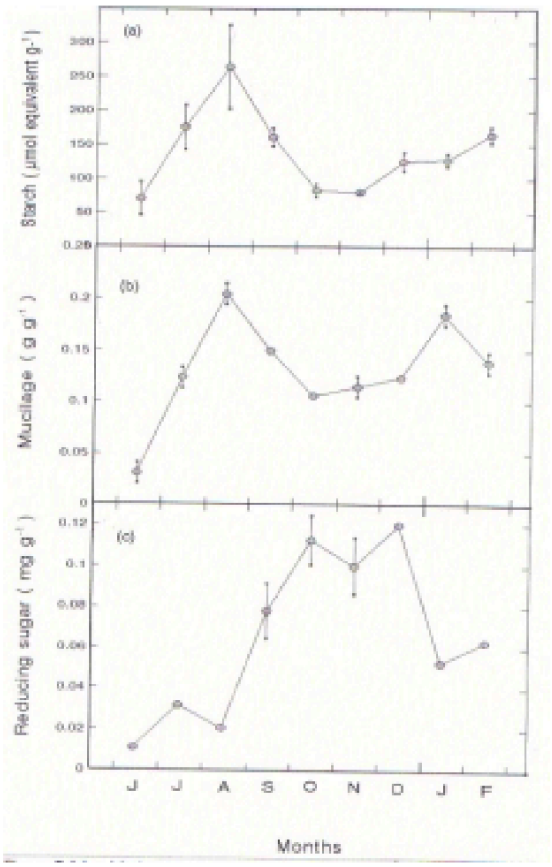

Figure 7. Monthly levels of starch (a), mucilage (b) and reducing sugars (c) for S. queretaroensis in the Sayula Basin, Jalisco, Mexico. Data are on a fresh weight basis and are means ±SE, except when the errors are smaller than the symbol (n=17 plants).