REVIEW

Highlights for *Agave* Productivity

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Abstract

Agaves can grow in marginal arid and semiarid lands where their special ecological and physiological adaptations to environmental conditions give them the potential to produce substantial biomass. *Agave americana* was the first agave species shown to be a Crassulacean Acid Metabolism plant, with CO_2 uptake occurring primarily at night and with high water-use efficiency (photosynthesis/transpiration). *A. salmiana* and *A. mapisaga* can have high nocturnal net CO_2 uptake rates and high productivities averaging 40 tonnes dry weight ha^{-1} yr^{-1}. Agaves can benefit from the increases in temperature and atmospheric CO_2 levels accompanying global climate change. An Environmental Productivity Index can predict the effects of soil and environmental factors on CO_2 uptake and hence on the regions appropriate for cultivating agaves. In turn, their increased cultivation can support the production of innovative earth-friendly commodities that can be used as new bioenergy feedstocks.

Keywords: Agaves, biomass, CAM, ecophysiology, Environmental Productivity Index, global climate change, Mexico

Introduction

Agave species are part of natural and anthropogenic landscapes in many arid and semiarid regions worldwide but are particularly prominent in Mexico. Indeed, agaves were second only to maize (corn) in the development of agriculture in Mesoamerica. They are used for beverages, food, fiber, shelter, and as ornamentals, for soil stabilization to prevent desertification (Gentry, 1982; Nobel, 2010). They can remove heavy metals from aqueous solutions, as can occur around mines (Romero *et al.*, 2006, 2007). Currently, beverages from the stems of various agave species include the sweet drink aguamiel, the fermented pulque, and the distilled mescal and tequila (Gentry, 1982; Nobel, 1994, 1998). Tequila, made from *Agave tequilana*, is of major importance domestically and for export from Mexico. Recently, the carbohydrates in the stems of agaves as well as lignocelluloses from their leaves have been recognized as possible sources of biofuels (Borland *et al.*, 2009; Nobel, 2010; Somerville *et al.*, 2010), although agaves are not usually listed among feedstocks for bioenergy production. The latter typically focus on conventional

crops like sugarcane; sugar beet; maize; cassava; wheat; oil crops like soybean, rapeseed, jatropha; and lignocellulosic materials from herbaceous woody crops and agricultural residues (PROINBIOS, 2009; Dale *et al.*, 2010; FAO, 2010; e.g. Fig. 1).

In Mexico, energy production in 2008 from biomass (mainly, bagasse and firewood; Gonzalez, 2009) was 0.86% of the total (SENER, 2009). Various crops are considered for potential ethanol or biodiesel production there (Fig. 1b). Also, ethanol can be derived from agave distillates. For example, *A. tequilana* with an average density of 2500 plants ha^{-1} can produce 21 300 L ha^{-1} (Gonzalez, 2009; Frias, 2009). Even higher yields are expected from *A. mapisaga* and *A. salmiana*, which are used for pulque. Moreover, such production can occur in regions with poor soil.

One objective here is to describe carbon capture and sequestration by agaves, which are the crucial initial steps for their production of biofuels. Also, the ecophysiological consideration of agaves will include effects of climate change, especially the increases of the atmospheric CO_2 concentration and the temperature. Both wild and cultivated populations of agave species will be discussed. The intention is to put in perspective the knowledge obtained about their distribution, densities, population structure, and biomass partitioning with

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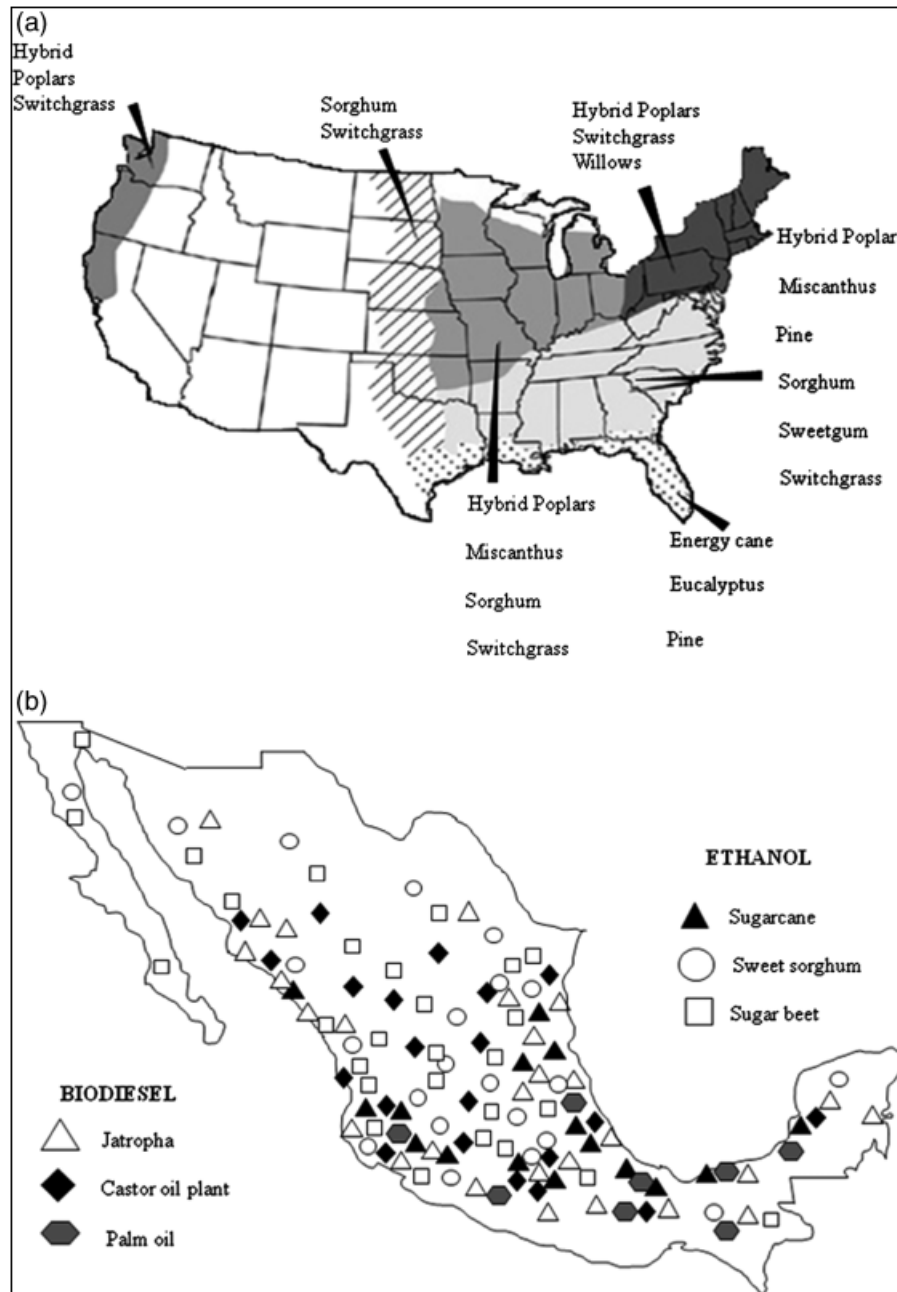
Fig. 1 Potential rainfed crops for the production of biomass for bioenergy in (a) the United States and (b) Mexico (Modified from Dale *et al.*, 2010; PROINBIOS, 2010).

respect to their potential productivity in spite of growing under stressful soil and climatic conditions. Such knowledge can provide alternative options for bioenergy feedstocks as well as new economic opportunities. Such cultivation of agaves for biofuels would be complementary to their use for tequila and mescal. Indeed, leaves left in the field by the beverage industries (Tello & Garcia, 1988) could be used for biofuels.

Distribution and ecology

Production of liquid fuels from plants involves several ecological parameters, such as landscape, biodiversity, and land use (Dale *et al.*, 2010). Hence it is important to know the origin of agaves, their variation as a raw material, current distribution, and ecology.

Origin and richness of Agave species

The group Agave emerged 8–10 million years ago (as evidenced by molecular clock studies and with two different genes that evolve at different rates) and had a peak in speciation rates coincident with an increase in dry conditions in central Mexico (Garcia, 2002, 2007; Good *et al.*, 2006). Indeed, agaves are keystone species of arid and semiarid regions, with Mexico representing the geographic center of origin, although natural populations currently spread from the southwestern United States through Central America, the Caribbean, and into northern South America. The genus *Agave* is the largest one in the family Agavaceae (Garcia, 2002, 2007).

Gentry (1982) described the taxonomy of 122 North American mainland agave taxa (125 taxa according to Garcia, 2002) in subgenus *Agave*, leaving out the agaves of South America and the Caribbean. Mexico has 150 of the 200 known species of *Agave* plus 36 infraspecific categories (Garcia, 2002), and there are 254 taxa worldwide. Mexico, United States, Cuba, and Guatemala have the highest species richness of the genus (Fig. 2), whereas Colombia, Venezuela and the other Caribbean islands have eight species, <3% of the total (Garcia, 2002, 2007).

huan Desert (10 species), and (3) the Jalisco Plateau (21 species; see also CONABIO, 2007). Agaves are native to Desert and Chaparral (52 species), Conifer and Oak Forest (44), Tropical Deciduous Forest (31), Thorn Forest (14), Grassland (12), Cloud Forest (4), Subdeciduous Forest (3), and Tropical Evergreen Forest (1) (Garcia, 2002). For species richness, the Valley of Tehuacan-Cuicatlan (central-southern region of Mexico) is first with 15 species (Garcia, 2002). Second is Sierra Madre Occidental in the north-west plus the border regions of Sonora, Chihuahua, and Sinaloa with nine species, mainly in conifer and oak forests. The third most important area of Mexico corresponds to the Chihuahuan Desert in the north-east bordering San Luis Potosi, Nuevo Leon, and Tamaulipas. The richness centers of *Agave* in Mexico involve virtually all states, except Tabasco and Quintana Roo. Garcia (2002) mentions 129 of 186 species (69%) as endemic to Mexico. The species richness of *Agave* in protected natural areas in Mexican states is listed by Golubov *et al.* (2007) as follows: Oaxaca (52 species), Puebla and Durango (43), Sonora and Jalisco (40), Coahuila (35), Chihuahua (34), San Luis Potosi (33), Nuevo Leon and Zacatecas (29), and Hidalgo (27).

Mexico's Agave regions and habitats

Gentry (1982) cites three areas where agaves congregate: (1) Central Mexico (30 species), (2) the Chihua-

Density and demography of wild Agaves

Few estimates of the density (number of plants per unit area) of various agave species occur for Mexico, except
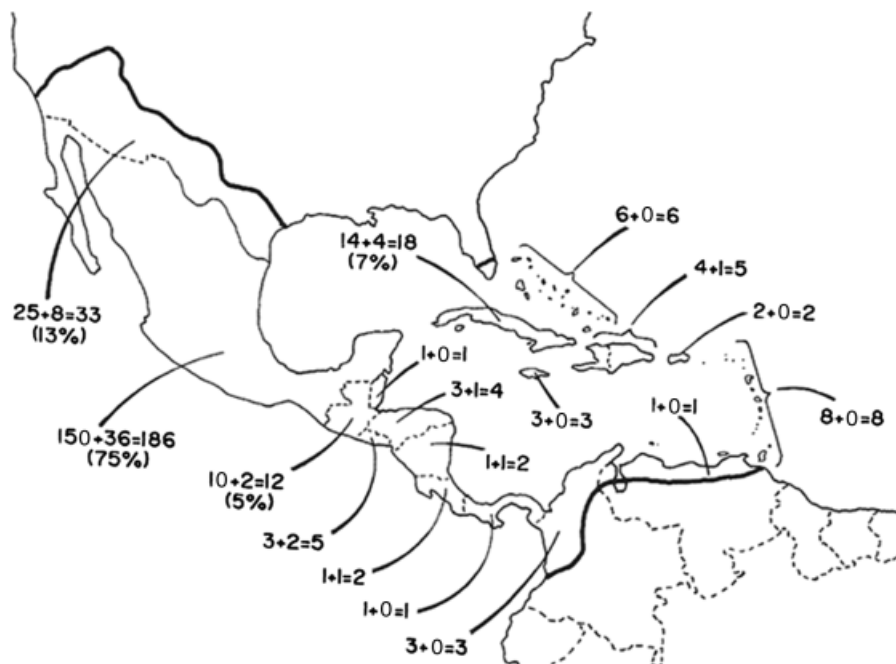

Fig. 2 Distribution of *Agave* in North America, South America, and the Caribbean including the number of species for each country. The quantities are: Species + Intraspecific Categories = Total Taxa (%). *Agave* has 200 species and 247 taxa (Garcia, 2002).

those in the San Luis Potosi and Zacatecas Plateau by Martinez (1985), Garcia (1988), Tello et al. (1991), and Medina et al. (2003) for the mescal maguey [Agave salmiana Otto ex. Salm. ssp. crassispina (Trel.) Gentry]. For this region, and considering the cited references for wild populations of agave, the estimate is 0.924 ± 0.948 agaves m^{-2} (mean $\pm$ SE), or 9240 agaves ha^{-1}. Zacatecas is nationally the second highest producer state for cultivated mescal agave (60 000 tonnes fresh weight), the first being Oaxaca (100 000 tonnes); others producer states are Guerrero (50 000 tonnes), San Luis Potosi (40 000 tonnes), Tamaulipas (35 000 tonnes), Durango (25 000 tonnes), and Guanajuato (20 000 tonnes; Comite Sistema Producto Maguey Mezcal, 2006; Valdez, 2007).

The agro-ecological characterization of A. salmiana indicates that its biomass productivity is influenced by the soil particle size distribution (i.e., percent clay, silt, and sand) and the consequent water infiltration rate, where faster is better (Reyes, 1987; Garcia, 1988; Martinez et al., 2005). Survival and productivity of agaves are better on calcareous than on igneous substrates. Standing biomass of A. salmiana with 1430 plants ha^{-1} can be 71 tonnes ha^{-1} compared with 153 tonnes ha^{-1} for A. tequilana with 2500–3000 plants ha^{-1} (Medina et al., 2003). In Zacatecas A. salmiana occurs over approximately 60 000 ha; about 2% of the area has a high density (over 3000 plants ha^{-1}) and 12% has a low density (<700 ha^{-1}; Martinez et al., 2005). In the Valley of Tehuacan, Puebla, A. marmorata Roezl., used for aguamiel, has 900–1100 plants ha^{-1}; its survival is better with nurse plants, similar to other species from dry environments (Nobel, 1988; Godinez et al., 2008).

A threat to various species of agaves is foraging by livestock on the leaves and the inflorescences (Martinez et al., 1995; Golubov et al., 2007; Baraza & Estrella, 2008).

Martinez (1985) characterized the structural distribution of dry matter of A. salmiana based on size classes. Small plants, about 1.5 kg in dry weight and 0.3 m in height, had approximately 16% of their total dry weight belowground (roots and rhizomes), 14% in the stem, 60% in unfolded leaves, and 10% in leaves still folded about the central spike. Large plants, about 35 kg in dry weight and 1.2 m in height, had 9% of their dry weight belowground, 8% in the stem, 80% in unfolded leaves, and 4% in folded leaves. Similar data have been collected for Agave salmiana and for A. mapisaga from Tequesquinahuac, Mexico (Table 1). The biomass for the first species increases exponentially with height (aerial $y = 10.874e^{0.7702x}$, $r^2 = 0.9475$; total $y = 11.244e^{0.7653x}$, $r^2 = 0.9541$), whereas the increase is more linear with height (aerial $y = 93.565x - 65.32$, $r^2 = 1$; total $y = 95.51x - 67.243$, $r^2 = 0.9998$) for the second species.

Historical research on the physiological ecology of Agave

CAM photosynthesis and water-use efficiency (WUE)

Approximately, 7% of vascular plants exhibit Crassulacean Acid Metabolism (CAM; Andrade et al., 2007; Nobel, 2010). Agave is a leaf succulent taxon having the CAM photosynthetic mode, fixing CO_2 mainly at night (Phase I, solar times of approximately 19–7); it then produces malic and other organic acids that accu-

Table 1 Morphological characteristics of Agave salmiana and A. mapisaga from Tequesquinahuac, Mexico vs. height

Characteristics	Agave salmiana			Agave mapisaga		
Height (m)	1.00	1.30	1.60	1.42	1.82	2.18
Stem DW (kg)	0.939	1.277	2.511	0.617	3.361	3.422
Number of unfolded leaves	19	16	32	20	26	26
Unfolded leaves DW (kg)	6.473	6.405	23.605	7.027	21.909	32.526
Number of folded leaves	15	21	28	16	24	29
Folded leaves DW (kg)	0.381	0.948	1.727	0.429	2.062	4.026
Number of death leaves	13	13	15	13	19	16
Dead leaves DW (kg)	4.433	5.200	11.07	4.563	16.017	20.016
Roots DW (kg plant^{-1})	0.55	1.65	1.35	0.43	1.64	5.40
Average leaf area both sides (cm^2)	2954	4653	6438	3738	6398	8261
Average leaf length (m)	1.03	1.34	1.65	1.46	1.84	2.16
Average DW (kg) unfolded leaves	0.341	0.400	0.738	0.351	0.843	1.251
Aerial DW (kg plant^{-1})	17.560	32.790	85.542	19.071	86.674	172.718
Belowground DW (kg plant^{-1})	0.55	1.65	1.35	0.43	1.64	5.40
Total DW (kg plant^{-1})	18.11	34.440	86.89	19.501	88.314	180.118

Aerial DW = Stem DW + (Folded leaves DW × number of folded leaves) + (unfolded leaves DW) + (Dead leaves DW).

DW, dry weight, FW, fresh weight ($n = 1$ per height per species). E. Garcia Moya, unpublished results.

mulate in the central vacuoles of mesophyll cells. At dawn (Phase II, approximately 7–9), CO_2 fixation transitions from PEP carboxylase to Rubisco. As the day progresses (Phase III) and stomata are closed, decarboxylation of malic acid occurs, the internal CO_2 levels rise, and CO_2 is fixed by Rubisco. Late in the afternoon (Phase IV), PEP carboxylase is reactivated (Pimienta *et al.*, 2006; Nobel, 2010).

CAM plants are characterized by a high WUE, measured as the amount of CO_2 fixed by photosynthesis relative to the amount of water lost through transpiration. Opening the stomata at night, when the temperatures are lower and closing them during the daytime results in a high WUE. Specifically, the WUE (photosynthesis/transpiration) of CAM plants is 10–40 g CO_2 kg^{-1} H_2O compared with 1–3 for C_3 plants and 2–5 g CO_2 kg^{-1} H_2O for C_4 plants (Nobel, 2009).

Gas exchange

Early studies on gas exchange for *Agave* began in the late 1960s with Neales *et al.* (1968), Ehrler (1969), and Kristen (1969). Neales *et al.* (1968) provided the first report on the night opening of agave stomata. Their measurements of photosynthesis and transpiration for *A. americana* clearly demonstrated the CAM nature of this species (Fig. 3a), with 75% of net CO_2 uptake and most water loss taking place at night. Net CO_2 uptake was extremely low for solar times from 7 to 15 but became high again at the end of the daytime. Other *Agave* species with gas exchange patterns characteristic of CAM are *A. deserti*, *A. fourcroydes*, and *A. tequilana* (Fig. 3b) plus *A. angustifolia*, *A. lechuguilla*, *A. lurida*, *A. murpheyi*, *A. parryi*, *A. salmiana*, *A. scabra*, *A. schottii*, *A. shawii*, *A. sisalana*, *A. utahensis*, *A. vilmoriniana*, *A. virginica*, and *A. weberii* (cited in Nobel, 1988).

Ehrler (1969) found that water loss by transpiration for seedlings of *A. americana* over 70 days was accompanied by a 71-fold increase in dry weight, evidence of the high WUE of this species. Also, *A. deserti* and *A. mapisaga* have WUEs of 0.0165 and 0.0051, respectively, much higher than the 0.0009 for the six most productive cultivated C_3 species (Nobel, 1994). The maximal nocturnal rates of net CO_2 uptake by *A. fourcroydes* and *A. tequilana* can be 10 μmol m^{-2} s^{-1} (Fig. 3b). As the physiological ecology of agaves became better understood, conditions for even higher maximal rates were determined. For instance, *A. tequilana* can have a maximal rate of 16 μmol m^{-2} s^{-1} (Nobel, 2010). *A. angustifolia* can have a maximal rate of 22 μmol m^{-2} s^{-1} (Fig. 4). Even higher maximal nocturnal net CO_2 uptake rates of 29 and 31 μmol m^{-2} s^{-1} have been reported for *A. salmiana* and *A. mapisaga*, respectively (Nobel *et al.*, 1992). Clearly, these CAM species can have high net CO_2
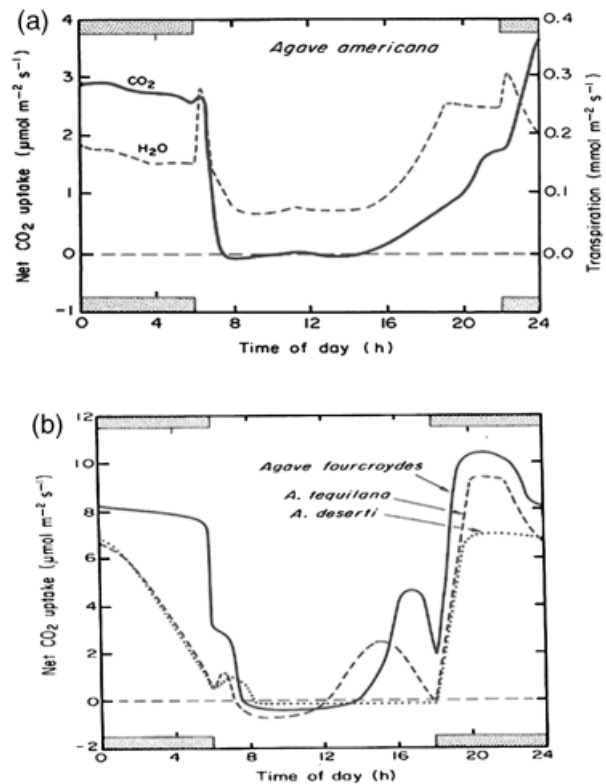

Fig. 3 Gas exchange by *Agave americana* (a) and net CO_2 uptake (b) by *Agave deserti*, *A. fourcroydes*, and *A. tequilana*. [Panel (a) was modified by Nobel (1988) from Neales *et al.* (1968); panel (b) is from Nobel (1984, 1985) and Nobel & Valenzuela (1987)].
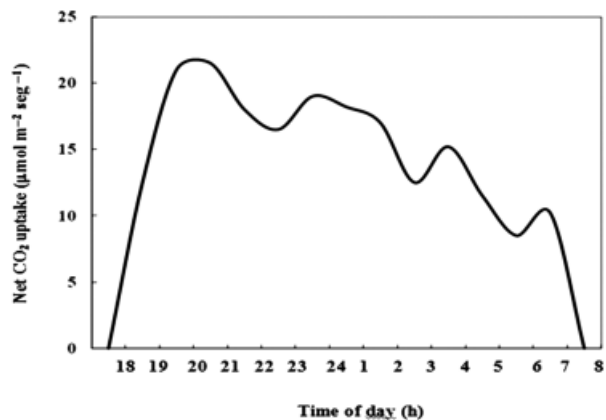

Fig. 4 Net CO_2 exchange under field conditions for 8-year-old *Agave angustifolia* from Santiago Matatlan, Oaxaca, Mexico (n = 8 plants) (Jose & Garcia, 1995).

uptake rates (Nobel, 2009), which augurs well for their potentially high biomass productivity.

The morphology of agave leaves, which are crescent-shaped in cross-section, also affects their gas exchange. Their Leaf Area Index (LAI), which is the total leaf area (both sides) per unit ground area, affects light absorption and hence productivity (Nobel, 2010). The LAI for

mature *A. fourcroydes* under cultivation varies from 3.8 to 8.4 (Nobel, 1985). Plantations of *A. angustifolia* can have an LAI of 3.2 (Jose, 1995). Maximal productivity for *A. fourcroydes* and other agaves occurs at an LAI of 6–8 (Nobel & Garcia de Cortazar, 1987; Nobel, 1988, 2010).

Unfolding of new leaves

The number of new leaves unfolding from the central spike of folded leaves of agaves is a morphological indicator of biomass productivity, as first shown for *A. deserti* and *A. fourcroydes* in the 1980s (Nobel, 1985, 2010). Moreover, clipping the dead tip of unfolded leaves is an easy way to monitor the number of new leaves unfolding subsequently. Such unfolding varies with plant age, shading, and season (Fig. 5). The total number of leaves unfolding per plant over a 1-year observation period was 19.6 for plants initially 3 years old and 24.9 for those initially 6 years old ($P < 0.05$). Shading by 30% reduced the number of leaves unfolding in both cases by 35% ($P < 0.01$). The rate of leaf unfolding was greater during the wet summer season vs. the dry winter season (Fig. 5).

The 27% higher rate of leaf unfolding for the initially 6-year-old plants of *A. angustifolia* compared with 3-year-old plants (Fig. 5) is consistent with data on other agave species (Table 2). For instance, the rate is 19% higher for 6- compared with 4-year-old plants of *A. fourcroydes*; 62% and 82% higher for 10- compared with 5-year-old plants of *A. mapisaga* and *A. salmiana*, respectively; and 32% higher for 6- compared with 3-year-old plants of *A. tequilana*. For approximately 6-year-old cultivated plants, the annual number of leaves unfolding per plant is about 25 for *A. angustifolia*, 27 for *A. fourcroydes*, five for *A. mapisaga* and *A. salmiana*, and 46 for *A. tequilana*. The two species observed in natural populations, *A. deserti* and *A. lechuguilla*, had five and seven annually unfolding leaves per plant, respectively (Table 2).

Biomass productivity

In the early 1990s, the optimal biomass yields of five C_3, five C_4, and five CAM species were compiled (Table 3; Nobel, 1991). *A. mapisaga* and *A. salmiana* compared well against the most productive C_3 and C_4 agricultural and forest species, both deciduous and evergreen. Other agaves had lower productivities than the mean value of 40 tonnes dry weight $ha^{-1} yr^{-1}$ for *A. mapisaga* and *A. salmiana* (Table 4). However, optimal conditions for productivity for agaves had not been established up through the 1980s, and even today the maximal productivity of various species is a topic of much debate.
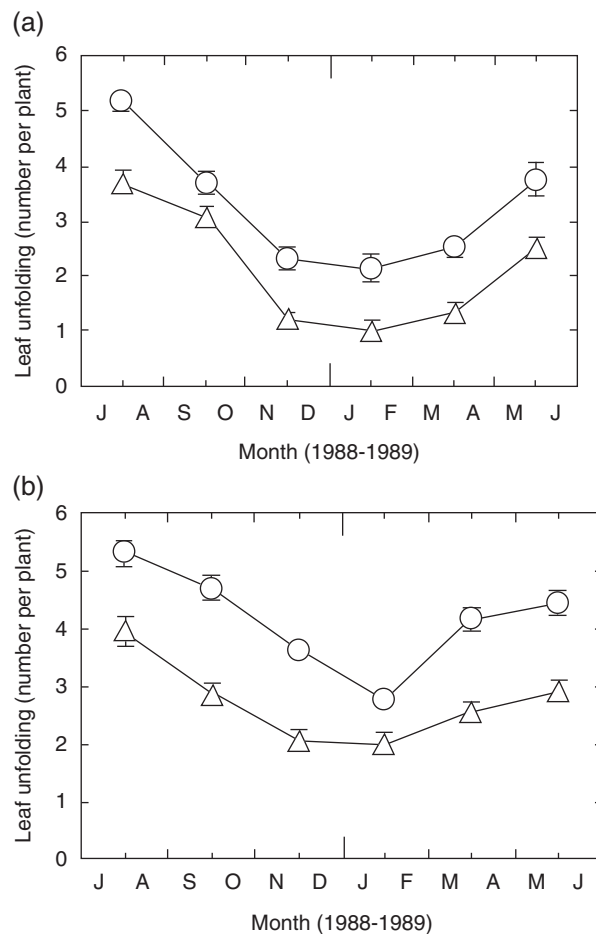
(a)

(b)

Fig. 5 Unfolding of leaves for *Agave angustifolia* plants that were 3 years old (a) or 6 years old (b). Data are means + SE ($n = 20$ plants), obtained at 2-month intervals for unshaded plants (○) or plants shaded 30% by trees (△). Measurements were taken on the field conditions in Santiago Matatlan, Oaxaca, Mexico. E. Garcia Moya & P. S. Nobel, unpublished results.

To provide an analytical framework for evaluating environmental and edaphic factors on net CO_2 uptake and hence productivity of CAM species, an Environmental Productivity Index (EPI) was developed as a powerful quantitative tool (Nobel, 1988, 2009). It can be used to predict productivity over wide geographical areas and under new environmental conditions to help evaluate the agronomic potential of *Agave*. In particular, EPI equals the fraction of maximal net CO_2 uptake over a 24 h period, as is appropriate to consider for a CAM species (Fig. 3), based on a Light Index × a Temperature Index × a Water Index. As a refinement, EPI can represented as: Light Index × Temperature Index × Water Index × Nutrient Index × CO_2 Index (Nobel, 2010).

Individual indices generally vary from 0.00, indicating complete inhibition of net CO_2 uptake by that factor, to 1.00, which indicates that that factor is optimal.

Table 2 Annual leaf unfolding for native and cultivated agaves

Species	Description	Age (years)	Number of plants considered	Leaves unfolding per year per plant	Reference
Agave angustifolia	Plantation in Oaxaca, Mexico	3	20	19.6	This article
		6	20	24.9	
A. deserti	Native plants in southern California, USA	–	50	5.2	Nobel (1987)
A. fourcroydes	Plantation in Yucatan, Mexico	4	20	22.5	Nobel (1985)
		6	20	26.8	
A. lechuguilla	Native plants in Coahuila, Mexico	–	52	6.8	Nobel & Quero (1986)
A mapisaga	Planted single rows in the Valley of Mexico and Tlaxcala	10	120	6.9–9.9	Garcia & Nobel (1990)
	Planted single rows in Tequesquinahuac, Mexico	5	40	5.2	Nobel *et al.* (1992)
A. salmiana	Native plants in San Luis Potosí, Mexico	–	73	4.4	Nobel & Meyer (1985)
	Plantations in Hidago, Mexico, and in Tlaxcala, Mexico	10	120	7.2–10.7	Garcia & Nobel (1990)
	Planted single rows in Mexico, Mexico	5	40	4.9	Nobel *et al.* (1992)
A. tequilana	Plantation in Jalisco, Mexico	3	20	34.7	Nobel & Valenzuela (1987)
		6	20	45.7	

Clouds or shading of plants reduces the Light Index below 1.00 and drought reduces the Water Index below 1.00. The CO_2 Index can exceed 1.00, such as 1.35 for a doubling of the current atmospheric CO_2 level, which increases net CO_2 uptake over a 24 h period by many CAM species by 35% (Drennan & Nobel, 2000; Nobel, 2010). In the case of the Nutrient Index, fertilizer applications can increase net CO_2 uptake and productivity: for example, a 50% increase in soil nitrogen can raise net CO_2 uptake by 20% for CAM species, a 50% increase in soil phosphorus can raise it by 10%, whereas 1/5 of the salt concentration in sea water can inhibit net CO_2 uptake and growth of CAM species by about 50% (Nobel, 1989).

EPI closely predicted the monthly number of leaves of *A. fourcroydes* unfolding, a nondestructive method correlated with productivity, during a 1-year study period (Nobel, 1985). Likewise productivity of *Agave lechuguilla* was predictable using EPI ($r^2 = 0.83$; Nobel & Quero, 1986) (Fig. 6), as is also the case for *A. deserti* (Nobel, 1984; Nobel & Hartsock, 1986; Nobel, 2010). For *A. lechuguilla*, an EPI of 0.28 was equivalent to 6.8 tonnes of carbohydrate made $ha^{-1} yr^{-1}$, much of which is used to build and maintain folded leaves, stems, and roots. Indeed, the net productivity of *A. lechuguilla* was 3.8 tonnes $ha^{-1} yr^{-1}$ (Nobel & Quero, 1986), which is much less than for agricultural crops but much larger than the average productivity of desert ecosystems. Such early ecophysiological research on agaves, summarized in Nobel (1994), was translated into Spanish by Edmundo Garcia Moya (Nobel, 1998).

Recent research on the ecophysiology of *Agave*

Recently, ecophysiological research on *A. tequilana* has been summarized in Spanish by Eulogio Pimienta *et al.* (2006). This book highlights both greenhouse and field data for selecting optimal climatic areas for its cultivation and comments on its response to global climate change. *A. tequilana* is a typical CAM plant, tolerant of drought, with considerable photosynthetic plasticity in response to changes in temperature, light, and water status (Pimienta *et al.*, 2001). Extreme temperatures, $<4\,°C$ or $>40\,°C$, considerably lower daily net CO_2 uptake. Interestingly, *A. tequilana* is physiologically dependent on mycorrhizal symbiosis in the early stages of development. This species can help mitigate the high concentrations of CO_2 generated by anthropogenic activities because of its great ability to sequester carbon. Currently, the latest word is Nobel (2010), a book that reminds us of the uses of agaves and has scientific information on CAM, plant tolerances, and the crop improvements based on EPI; it broadly addresses the implications of climate change produced by increasing

Table 3 The five highest, aboveground, annual productivities for each photosynthetic pathway*

Photosynthetic pathway*	Species	Location	Productivity ($Mg\,ha^{-1}\,yr^{-1}$)
C_3	*Cryptomeria japonica*	Japan	44
	Elaeis guineensis	Malaysia	40
	Eucalyptus globulus	Portugal	40
	Eucalyptus grandis	South Africa	41
	Pinus radiata	New Zealand	38
C_4	*Cynodon plectostachyus*	United States	37
	Pennisetum purpureum	El Salvador, United States	70
	Saccharum officinarum	Australia, United States	64–67
	Sorghum bicolor	United States	47
	Zea mays	Italy, United States	36–40
CAM	*Agave mapisaga*	Tequexquinahuac, Mexico	38
	Agave salmiana	Tequexquinahuac, Mexico	42
	Ananas comosus	Hawaii, United States	35
	Opuntia amyclea	Saltillo, Coahuila, Mexico	45
	O. ficus-indica	Saltillo, Coahuila, Mexico; Santiago, Chile	47

*Data for C_3 and C_4 were obtained up to 1990, and were recompiled from various authors cited by Nobel (1991). Annual aboveground dry-weight biomass productivities of CAM data are from Nobel (1991) and Nobel *et al.* (1992). More recently, higher productivities have been found for some of these species, for example, $70\,Mg\,ha^{-1}\,yr^{-1}$ for *Saccharum officinarum* in Mexico and 110–$120\,Mg\,ha^{-1}\,yr^{-1}$ in Peru (www.caneros.org.mx) using harvest data for 2009.
CAM, Crassulacean acid metabolism.

Table 4 Biomass productivity of other *Agave* species ($Mg\,ha^{-1}\,yr^{-1}$)

Species	Productivity ($Mg\,ha^{-1}\,yr^{-1}$)	Location	Reference
Agave deserti	7	Sonoran Desert, California, United States	Nobel & Hartsock (1986)
A. fourcroydes	15	Yucatan, Mexico	Nobel (1985)
	20–30		Nobel & Garcia de Cortazar (1987)
A. lechuguilla	4	Chihuahuan Desert	Nobel & Quero (1986)
A. sisalana	5	Tanzania (conditions were not optimal)	Lock (1962)
A. tequilana	25	Jalisco, Mexico	Nobel & Valenzuela (1987)

atmospheric CO_2 levels, increasing of temperatures, and variable rainfall patterns.

Effects of global climate change on *Agave* productivity

Agaves are a resource used ancestrally that will continue being an alternative for intensive use in the face of climatic change (Altieri & Nicholls, 2008). CAM plants can have annual productivities close to those found in the most productive C_3 or C_4 agronomic systems (Table 3; Nobel, 1988, 1991). Pimienta *et al.* (2006) argue that ecological sustainability and global climate change with an impending increase in temperature and atmospheric CO_2 levels are challenges that necessitate the search for alternatives to generate energy efficiently. There is a need for the design of agricultural and forestry systems that allow production of carbohydrates convertible to

alcohol as well as the sequestration of large amounts of atmospheric CO_2 (Nobel, 2010). Agaves, well adapted to water-deficient areas, are prime candidates to address these challenges. Shrinkage of the root cortex, even at modest soil water deficits (–0.1 MPa), and cavitation of the root xylem, helps to protect any reverse flux of water from agave storage tissues to a drying soil (Nobel, 1988; North *et al.* 2004). Their efficiency in producing biomass under water deficit, based on their capacity to assimilate and transform CO_2, are features that combined with genetic diversity will enable a better response to global climate change.

Increasing atmospheric CO_2 levels modify the morphology and anatomy of CAM plants. In particular, the chlorenchyma becomes thicker, root systems expand, and shoot development occurs more rapidly (Nobel, 2010). The atmospheric CO_2 level is currently increasing
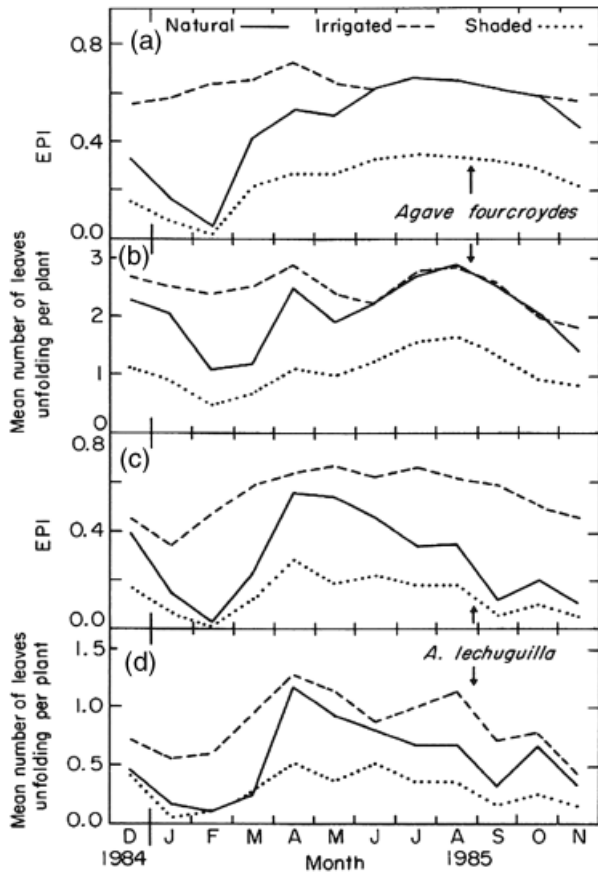
Fig. 6 Monthly variations in Environmental Productivity Index (EPI) (a, c) and leaf unfolding (b, d) for *Agave fourcroydes* (a, b) and *A. lechuguilla* (c, d). Twenty plants were maintained under natural conditions (—), watered weekly so that the soil in the root zone was continuously moist (- - - -), or shaded by screening such that the PAR level was reduced 60% (. . . .). Figure taken from Nobel (1988).

- CAM species have high WUE (photosynthesis/tran-spiration).
- In the 1980s, leaf unfolding was shown to be a convenient, nondestructive morphological trait correlated with biomass productivity using *A. deserti* and *A. fourcroydes*.
- In 1992, *A. mapisaga* and *A. salmiana* were shown to produce 40 tonnes dry weight $ha^{-1}yr^{-1}$ (18 tonnes $acre^{-1}yr^{-1}$).
- An EPI (Light Index × Temperature Index × Water Index × Nutrient Index × CO_2 Index) can predict net CO_2 uptake in various regions and for various climates, both current and expected in the future.
- Global climate change can benefit *Agave* plants.

The best is yet to come!

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at $2 + ppm\,yr^{-1}$. In that regard, the net CO_2 uptake ability of CAM plants increases about 1% per 10 ppm increase in CO_2 level (Drennan & Nobel, 2000). Temperature is increasing at about 0.19 °C per decade. This is also good news for most agaves, as freezing temperatures are a threat in many localities (Nobel, 1988). Also, with acclimation many agave species can tolerate tissue temperatures of 60 °C, so the survival of agaves is not threatened by high temperatures. Rainfall will probably be more variable in the future. This is not problem for most agaves, in part because of their high WUE.

Conclusions

- In the late 1960s, *A. americana* was shown to be a CAM species.

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