Physiology / Fisiología

Physiological ecology of Mexican CAM plants: history, progress, and opportunities

Fisiología ecológica de plantas CAM mexicanas: historia, avances y oportunidades

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Abstract

In Mexico, plants with crassulacean acid metabolism (CAM) are part of the Mexican culture, have different uses and are even emblematic. Unfortunately, only a small fraction of the Mexican CAM plants has been studied physiologically. For this review, the following questions were considered: What ecophysiological studies have been conducted with CAM species native to Mexico? What ecophysiological processes in Mexican CAM plants are the most studied? What type of ecophysiological studies with CAM plants are still needed? A database of scientific studies on CAM plant species from Mexico was documented, including field and laboratory works for species widely distributed, and those studies made outside Mexico with Mexican species. Physiological processes were grouped as germination, photosynthesis, and water relations. Most studies were done for CAM species of Cactaceae, Bromeliaceae, Asparagaceae and Orchidaceae, and most ecophysiological studies have been done on germination of cacti. Field and laboratory studies on photosynthesis and water relations were mostly for terrestrial cacti and epiphytic bromeliads. There were few physiological studies with CAM seedlings in Mexico and few studies using stable isotopes of water and carbon of CAM plants in the field. More field and laboratory studies of physiological responses and plasticity of CAM plants to multiple stress factors are required to model plant responses to global climate change. In general, more physiological studies are essential for all CAM species and for species of the genus *Clusia*, with C_3-CAM and CAM members, which can become ecologically important under some climate change scenarios.
Keywords: Asparagaceae, Bromeliaceae, Cactaceae, germination, photosynthesis, water relations.

Resumen

Las plantas con metabolismo ácido de las crasuláceas (CAM) son parte de la cultura mexicana, tienen numerosos usos y son emblemáticas. Desafortunadamente solo una pequeña fracción de especies CAM ha sido estudiada con una perspectiva fisiológica. Para esta revisión consideramos las siguientes preguntas: ¿Qué estudios ecofisiológicos se han realizado con especies CAM nativas de México? ¿Qué procesos ecofisiológicos han sido los más estudiados? ¿Qué tipos de estudios ecofisiológicos con plantas CAM aún faltan? Se construyó una base de datos de artículos científicos sobre CAM en México, incluyendo estudios de campo y laboratorio con especies ampliamente distribuidas, y trabajos fuera de México con especies mexicanas. Los procesos fueron agrupados en fotosíntesis, germinación y relaciones hídricas. La mayoría de los estudios ecofisiológicos se enfocaron en especies CAM de las familias Cactaceae, Bromeliaceae, Asparagaceae y Orchidaceae y la mayoría de ellos abordó la germinación de cactáceas. Casi todos los estudios de campo y laboratorio sobre fotosíntesis y relaciones hídricas han sido realizados con especies terrestres de cactáceas y de bromeliáceas epifitas. Pocos estudios han sido con plántulas de especies CAM y pocos usaron isótopos estables de agua y carbono de CAM en campo. Se requieren más estudios de campo y laboratorio sobre la ecofisiología y plasticidad de plantas CAM en respuesta a múltiples factores para alimentar modelos de respuesta al cambio climático global. Es esencial llevar a cabo más estudios con plantas CAM y especies del género *Clusia*, con miembros C_3-CAM y CAM, ya que pueden llegar a ser ecológicamente importantes en algunos escenarios de cambio climático.
Palabras clave: Asparagaceae, Bromeliaceae, Cactaceae, fotosíntesis, germinación, Orchidaceae, relaciones hídricas.

Plant physiological ecology —or plant ecophysiology— is an experimental science that aims to describe the physiological mechanisms underlying ecological observations. Thus, plant ecophysiology deals with ecological issues that affect plant life-cycle phases, such as germination, growth, and reproduction, as well as survival, abundance, and geographical distribution of plants, as these processes are affected by interactions between plants with their physical, chemical, and biotic environment (Lambers & Oliveira 2019). In addition plant ecophysiologists incorporate knowledge from multiple disciplines such as anatomy (Pérez-Noyola *et al.* 2021), different 'omic' technologies, from genomics to metabolomics (Flexas & Gago 2018), biophysics (Szabó & Zavafer 2021), chemistry (Guerra *et al.* 2019), micrometeorology (Zhao *et al.* 2019), edaphology (Delgado *et al.* 2021) and even the most advanced engineering and computer sciences (Muller & Martre 2019).

This review focuses on Mexican plant species displaying crassulacean acid metabolism (CAM). CAM is one of three metabolic pathways found in the photosynthetic tissues of vascular plants for assimilation of atmospheric CO_2; unlike C_3 and C_4 plants, CAM plants take up CO_2 from the atmosphere predominantly at night, subsequently assimilating this CO_2 to the level of carbohydrate during the following light period (Winter & Smith 1996, Winter *et al.* 2015). Thus, CAM is an ecophysiological modification of photosynthetic carbon acquisition by plants and is one of the classic examples of a metabolic adaptation to environmental stress (Lüttge 2004). CAM plants are distinguished by their succulence, the capacity to fix CO_2 at night via PEP carboxylase, the accumulation of malic acid in the vacuole, and the posterior de-acidification during the day, when CO_2 is released from malic acid and fixed in the Calvin cycle via Rubisco (Lambers & Oliveira 2019, Winter & Smith 2021).

The CAM photosynthetic pathway

The CAM pathway was discovered in the Crassulacean plant *Kalanchoe pinnata* (now known as *Bryophyllum calycinum*) and, in consequence, it was named by this species' family (Kluge & Ting 1978). However, CAM also occurs commonly in over 400 genera in 38 plant families comprising ~6 % of flowering plant species (Niechayev *et al.* 2019), and about 10,000 species (Lambers & Oliveira 2019). CAM photosynthesis has arisen independently at least 35 times in flowering plants (Silvera *et al.* 2010) and there is great plasticity in the expression of this metabolism (Borland *et al.* 2011).

Where CAM plants occur. In families such as the Cactaceae, CAM is most likely existing in all genera with exception of the leaf-bearing cacti of the genus *Pereskia* (Nobel 2003), although one species from Venezuela, *Pereskia guamacho*, exhibited C_3-like patterns of stomatal conductance in the rainy season, but during a prolonged drought, nocturnal stomatal opening and high accumulation of titratable acid in leaves were found (Edwards & Díaz 2006).

In the Asparagaceae, subfam. Agavoideae, *Agave* spp., *Hesperaloe* spp., and *Manfreda* spp. are considered to show CAM, whereas *Beschorneria* and *Polianthes* are genera having C_3-CAM photosynthesis, and *Yucca* has C_3 species and CAM species (Heyduk *et al.* 2016). In the Orchidaceae, more than 10 % of species have CAM (Silvera *et al.* 2009), whereas in the Bromeliaceae 57 % of species exhibit CAM (Crayn *et al.* 2015).

CAM plants occupy unfavorable environments for the growth of plants with C_3 photosynthesis. Most of the CAM species inhabit warm, seasonally dry habitats such as semi-deserts with little, but relatively predictable, seasonal rainfall (Winter *et al.* 2015). The existent richness of CAM species of large stature and other major terrestrial CAM lineages seem to have emerged during the global expansion of arid environments in the late Miocene (Arakaki *et al.* 2011, Horn *et al.* 2014). Among epiphytic lineages, CAM is considered to have facilitated diversification of the more extreme epiphytic life-forms occupying arid microhabitats in forest canopies, remarkably in the tropical Bromeliaceae and Orchidaceae (Crayn *et al.* 2004, 2015, Silvera *et al.* 2009). Thus, while the physiognomy of semi-deserts outside the tropics is often determined by succulent CAM plants, tropical forests house many more CAM plants in terms of biomass and species diversity (Lüttge 2010).

Vascular epiphytes are elements occurring in almost all ecosystems of the world, but they are particularly diverse in evergreen rain forests and cloud forests of tropical and subtropical regions (Silvera & Lasso 2016). Vascular epiphytes

constitute a heterogeneous group that represents approximately 10 % of the tracheophytes, with more than 31,000 species distributed in 79 families, although the vast majority (80 %) belong to the Orchidaceae, Bromeliaceae and Polypodiaceae (Zotz *et al.* 2021). In Mexican flora, the proportion of vascular epiphytes is 7.8 %, with approximately 1,813 species distributed in 37 families, mainly in the Orchidaceae (50 %), Bromeliaceae (13 %) and Polypodiaceae (7 %) and are found with greater diversity in the cloud forest or mesophyllous mountain forest (Espejo-Serna *et al.* 2021).

It has been estimated that most epiphytic species exhibit CAM photosynthesis (Zotz & Hietz 2001, Lüttge 2004, Andrade *et al.* 2007, Silvera & Lasso 2016, Zotz *et al.* 2021). About 50 % of the approximately 30,000 epiphytic species of the Orchidaceae family are CAM (Winter & Smith 1996, Silvera & Lasso 2016). In Bromeliaceae, CAM is common in the Bromelioidae subfamily (90 % of species; Zotz *et al.* 2021), and less common in the Tillandsioidae subfamily (28 % of species; Crayn *et al.* 2015). Also, all epiphytic cacti are CAM (Zotz *et al.* 2021). In Mexico, CAM epiphytic bromeliad species predominate in areas with dry climate or seasonal drought (Andrade *et al.* 2007). Although it has been documented that approximately 19 % of epiphytic species used the CAM mechanism in a dry forest (Zotz 2004), a recent analysis showed that the global proportion of CAM species was similar between epiphytic and terrestrial plants and that most vascular plant families with epiphytic species are not CAM (Zotz *et al.* 2021). However, the facts that CAM epiphytic species are more abundant than C_3 epiphytic species in exposed canopy sites in tropical moist and dry forests (Griffiths & Smith 1983, Zotz & Ziegler 1997, Lüttge 2004, Silvera & Lasso 2016) and that almost all epiphytic species in dry deciduous forests of Mexico use CAM (Reyes-García *et al.* 2012, Valdez-Hernández *et al.* 2015) reveal that it is a highly favorable photosynthetic mechanism for their existence.

CAM plants in Mexico. Mexican CAM plants are distinctive of arid and semiarid regions of Mexico where, sometimes, they are the more conspicuous evergreen component in the Sonoran, Chihuahuan and Tehuacán-Cuicatlán deserts (Valiente-Banuet & Godínez-Álvarez 2002) and even in some endangered and disturbed tropical dry forests (Durán & Olmsted 1999, Arias-Medellín *et al.* 2014). In these natural habitats, CAM plants are essential because during the dry season they provide water and food to animals. Indeed, because of this high-water use efficiency, some native and cultivated CAM terrestrial plants, under irrigated and fertilized conditions, surpass in productivity many C_3 and C_4 crops (Nobel 1991, 1996, Andrade *et al.* 2009). Furthermore, the conspicuousness of many Mexican terrestrial CAM plants, such as the opuntias, agaves and saguaros, and of those that are extensively cultivated, has made these plants emblematic of Mexican culture (Nobel 2002, De la Barrera & Andrade 2005).

First studies of CAM in Mexico. The first Mexican study on CAM plants was published by Tinoco-Ojanguren & Vázquez-Yanes (1983). These authors found that the epiphytic plant *Epiphyllum crenatum* (Lindley) Don. (Cactaceae) and the tree *Clusia lundellii* Standl. (Clusiaceae) have CAM photosynthesis, and this paper was the first one in showing CAM in a tree. Later, Vazquez-Yanes (1989) and Larqué-Saavedra (1994) in the *Boletín de la Sociedad Botánica de México* (now *Botanical Sciences*) communicated the increase in scientists and studies on plant ecophysiology and plant physiology in Mexico. However, despite the great diversity of plants and ecosystems and the enormous richness of CAM plants in Mexico, physiological studies of native plant species are still incipient (De la Barrera & Andrade 2005, Andrade *et al.* 2007, Valdez-Hernández *et al.* 2015, Tinoco-Ojanguren *et al.* 2018, Briones *et al.* 2020).

In this review, advances on the physiological processes of the Mexican CAM plants (seed germination, photosynthesis, and water relations) are highlighted. Also, ecophysiological responses to plants stress and novel ecophysiological research are considered to increase knowledge of potential responses from Mexican CAM plants to global climate change.

Germination of Mexican CAM plants

The first germination study of a native Mexican CAM species was conducted on the saguaro cactus (*Carnegiea gigantea*) by Alcorn & Kurtz Jr (1959) in Arizona; the saguaro is a CAM plant distributed in the southern United States as well as in northern Mexico. These authors evaluated some factors affecting the seed germination of the saguaro

and found that germination is stimulated by red light and that the optimum temperature for germination was 25 °C. Later, more seed germination experiments on Mexican CAM plants have been done, mainly evaluating soil water potential, hydration memory, light conditions, temperature, mucilage and microbiota, seed bank, and seed ageing.

Soil water potential. In arid and semiarid environments, soil water potential is one of the key factors affecting seed germination (Flores & Briones 2001, Guillén *et al*. 2009, 2011, 2015, Flores *et al*. 2017, Barrios *et al*. 2020). Seed germination of Mexican cacti occurs mainly at water potentials of between 0 to -0.6 MPa, and species differ in the minimum water potential at which germination can occur (Table 1). Thus, cactus seeds adapted to germinate at high soil moisture, but not necessarily at the soil field water capacity, have an advantage in arid environments (Barrios *et al*. 2020). For instance, of the 660 Mexican cactus species (Ortega-Baes & Godínez-Álvarez 2006), the effect of water potential on seed germination has been studied in only 17 species: most of them columnar (12), two globose, two barrel, and one epiphytic (Table 1). Most of these studies have used polyethylene glycol (PEG) 6000 or 8000 to simulate water stress on seeds. These PEG solutions are osmotic media with large molecular weight that cannot penetrate the living cell wall, and they have been used to impose a water potential stress on seeds by decreasing the water potential (Table 1).

Of the 402 Mexican taxa of the family Asparagaceae, subfamily Agavaoideae (García-Mendoza & Galván 1995), the effect of water potential on seed germination has been studied in 17 species, 13 of the stemless rosette-like (all *Agave* species) and four rosette-like with stem (three *Yucca* species and *Beaucarnea gracilis*). Species of the subfamily Agavaoideae appear to be more tolerant to water stress for germination than cacti, because eight of the species (seven *Agave* species plus *Yucca elata*) show germination > 80 % at water potential of -1 MPa (Table 1).

For Bromeliaceae, water potential for germination has been studied in only one species (*Tillandsia recurvata*); seeds from this species increase germination at -0.1 MPa and decrease it at -0.6 MPa (Table 1). Mexican species from this and other families showing CAM still need to be evaluated.

Hydration memory. Desert plants have developed strategies to germinate even in places where available moisture is sporadic (Dubrovsky 1996, Contreras-Quiroz *et al*. 2016a). Seeds of some cactus species have desiccation tolerance of imbibed seeds or "hydration memory," a seed ability to retain some of the physiological changes, like the differential expression of proteins (López-Urrutia *et al*. 2014), induced by hydration-dehydration cycles (Dubrovsky 1996). Reduced germination times have been found after treating the seeds with hydration-dehydration cycles for three cactus species (*Stenocereus thurberi*, *Pachycereus pecten-aboriginum* and *Ferocactus peninsulae*), from the Sonoran Desert in Mexico (Dubrovsky 1996). In addition, higher germination percentage with hydration-dehydration cycles have been found for *Ferocactus pilosus* and *Echinocactus platyacanthus*; however, *Yucca filifera* seeds germinated more with the control than with the hydration-dehydration treatments. Thus, "hydration memory" is not a trait present in all CAM species (Contreras-Quiroz *et al*. 2016a) nor exclusive to CAM species, *e.g.*, several non-CAM species of the Mediterranean region show seed hydration memory (Copete *et al*. 2021).

Contreras-Quiroz *et al*. (2016b) assessed if seed hydration memory depends on climate. These authors studied seven species from the Argentinian Córdoba Mountains (mesic environment): *Gymnocalycium capillense*, *Parodia mammulosa*, *Echinopsis candicans*, *Gymnocalycium bruchii*, *Gymnocalycium mostii*, *Gymnocalycium quehlianumand*, *Gymnocalycium monvillei*, and two species (*Echinocactus platyacanthus* and *Ferocactus pilosus*) from the Mexican Chihuahuan Desert (dry environment). Four hydration (hours)/dehydration (days) treatments were employed: T1 = 24 h/5 days, T2 = three successive cycles of 24 h/5 days, T3 = 72 h/5 days, and T4 = control (untreated seeds). The treatments were carried out in germination chambers at a constant temperature of 25 °C, with 12 h of light and 12 h of darkness, in containers with distilled water. The authors found that the Mexican species respond to at least one hydration-dehydration treatment by increasing their germination (54 % in untreated and 88 % in T3 for *E. platyacanthus*, and 38 % in untreated seeds and 93.8 % for *F. pilosus*). For the Argentinian species, only *G. mostii* increases its germination in a hydration-dehydration treatment (24 % in untreated and 68 % in T2). This species inhabits rocky and hence drier habitats than the other Argentinian species studied. Thus, it appears that seed hydration memory in cacti depends on climate.

Table 1. Effect of water potential on seed germination percentage of Mexican CAM plants. Water potential values were applied with different methods at 25 °C.

Species	Growth-form	Water potential (MPa)														Method	Reference
		0	-0.1	-0.2	-0.3	-0.4	-0.5	-0.6	-0.7	-0.8	-0.9	-1.0	-1.2	-1.5	-2.0		
Asparagaceae																	
Agave americana var. marginata	Stemless rosette-like	87	-	-	-	-	-	-	-	-	-	91	-	-	0	Vermiculite at different soil water potential (Ψw)	Ramírez-Tobías et al. (2014)
Agave asperrima	Stemless rosette-like	90	-	-	-	-	-	-	-	-	-	87	-	-	0	Vermiculite at different soil water potential (Ψw)	Ramírez-Tobías et al. (2014)
Agave colorata	Stemless rosette-like	96	-	-	93	-	83	-	-	80	-	0	-	-	-	PEG 8000	Borbón-Palomares et al. (2018)
Agave cupreata	Stemless rosette-like	95	-	-	-	-	-	-	-	-	-	98	-	-	0	Vermiculite at different soil water potential (Ψw)	Ramírez-Tobías et al. (2014)
Agave duranguensis	Stemless rosette-like	88	-	-	-	-	-	-	-	-	-	92	-	-	0	Vermiculite at different soil water potential (Ψw)	Ramírez-Tobías et al. (2014)
Agave lechuguilla	Stemless rosette-like	95	-	-	-	-	93	-	-	-	-	-	66	-	5	PEG 8000	Campos et al. (2020)
Agave lechuguilla	Stemless rosette-like	74	-	85	-	65	-	6	-	0	-	0	-	-	-	PEG 6000	Flores et al. (2017)
Agave lechuguilla	Stemless rosette-like	98	-	-	-	-	-	-	-	-	-	93	-	-	0	Vermiculite at different soil water potential (Ψw)	Ramírez-Tobías et al. (2014)
Agave parryi	Stemless rosette-like	80	-	-	77	-	63	-	-	-	-	6	-	-	-	Carbowax 4000	Freeman (1975)
Agave salmiana	Stemless rosette-like	63	-	-	-	-	57	-	-	-	-	42	-	-	14	PEG 8000	Campos et al. (2020)
Agave salmiana	Stemless rosette-like	91	-	94	-	95	-	82	-	37	-	0	-	-	-	PEG 6000	Flores et al. (2017)
Agave salmiana	Stemless rosette-like	85	-	-	-	-	-	-	-	-	-	90	-	-	0	Vermiculite at different soil water potential (Ψw)	Ramírez-Tobías et al. (2014)

Species	Growth-form	0	-0.1	-0.2	-0.3	-0.4	-0.5	-0.6	-0.7	-0.8	-0.9	-1.0	-1.2	-1.5	-2.0	Method	Reference
								Water potential (MPa)									
Agave striata	Stemless rosette-like	93	-	-	-	-	-	-	-	-	-	89	-	-	0	Vermiculite at different soil water potential (Ψw)	Ramírez-Tobías *et al.* (2014)
Beaucarnea gracilis	Rosette-like with stem	31	40	74	-	69	-	-	3	-	-	-	-	-	-	Soil at different water potential (Ψw)	Flores & Briones (2001)
Yucca decipiens	Rosette-like with stem	95	-	87	-	9	-	0	-	0	-	0	-	-	-	PEG 6000	Flores *et al.* (2017)
Yucca elata	Rosette-like with stem	90	-	-	-	-	91	-	-	-	-	81	-	13	-	Mannitol	Prado-Tarango *et al.* (2017)
Yucca periculosa	Rosette-like with stem	47	62	82	-	83	-	-	29	-	-	-	-	-	-	Soil at different water potential (Ψw)	Flores & Briones (2001)
Bromeliaceae																	
Tillandsia recurvata	Epiphytic	80	95	-	-	-	-	70	-	20	0	-	-	-	-	PEG 8000	Montes-Recinas *et al.* (2012)
Cactaceae																	
Echinocactus platyacanthus f. *biznaga*	Barreliform	1	-	26	-	38	-	4	-	0	-	0	-	-	-	PEG 6000	Flores *et al.* (2017)
Escontria chiotilla	Columnar	52	-	76	-	74	-	70	-	38	-	-	-	-	-	PEG 8000	Guillén *et al.* (2015)
Ferocactus histrix	Barreliform	99	-	98	-	93	-	10	-	0	-	0	-	-	-	PEG 6000	Flores *et al.* (2017)
Isolatocereus dumortieri	Columnar	50	-	60	-	46	-	28	-	0	-	0	-	-	-	PEG 6000	Flores *et al.* (2017)
Mammillaria gaumeri	Globose	100	-	100	-	94	-	-	-	-	-	67	-	-	-	PEG 8000	Cervera *et al.* (2006)
Mammillaria grahamii	Globose	65	60	59	45	28	-	3	-	0	-	0	-	-	-	PEG 8000	Bracamonte *et al.* (2017)
Myrtillocactus schenckii	Columnar	35	-	50	-	10	-	-	-	-	-	0	-	-	-	PEG 8000	Guillén *et al.* (2009)

Species	Growth-form	Water potential (MPa)														Method	Reference
		0	-0.1	-0.2	-0.3	-0.4	-0.5	-0.6	-0.7	-0.8	-0.9	-1.0	-1.2	-1.5	-2.0		
Neobuxbaumia macrocephala	Columnar	79	76.3	-	-	57.5	-	-	-	-	-	0	-	-	-	PEG 8000	Ramírez-Padilla & Valverde (2005)
Neobuxbaumia mezcalaensis	Columnar	71	59	-	-	-	-	-	-	-	-	0	-	-	-	PEG 8000	Ramírez-Padilla & Valverde (2005)
Neobuxbaumia tetetzo	Columnar	7	15	47	-	70	-	-	78	-	-	-	-	-	-	Soil at different water potential (Ψ_w)	Flores & Briones (2001)
Pachycereus hollianus	Columnar	0	3	50	-	94	-	-	62	-	-	-	-	-	-	Soil at different water potential (Ψ_w)	Flores & Briones (2001)
Polaskia chende	Columnar	100	-	100	-	100	-	67	-	64	-	29	-	-	-	PEG 8000	Guillén *et al.* (2015)
Polaskia chichipe	Columnar	68	-	92	-	90	-	60	-	13	-	-	-	-	-	PEG 8000	Guillén *et al.* (2015)
Rhipsalis baccifera	Epiphytic	88	-	74	-	-	-	7	-	-	-	0	-	-	-	PEG 8000	de la Rosa-Manzano & Briones (2010)
Stenocereus pruinosus	Columnar	93	-	45	-	14	-	9	-	0	-	-	-	-	-	PEG 8000	Guillén *et al.* (2015)
Stenocereus queretaroensis	Columnar	75	62	-	-	-	-	-	-	-	-	50	-	-	-	PEG 8000	De la Barrera & Nobel (2003)
Stenocereus stellatus	Columnar	69	-	30	-	14	-	-	5	-	-	1	-	-	-	PEG 8000	Guillén *et al.* (2015)

Soil temperature. Besides water, soil temperature may also be important in seed germination in arid and semiarid environments (Rojas-Aréchiga & Vázquez-Yanes 2000, Barrios *et al.* 2020). There are CAM species in which optimum germination temperatures coincide with the mean germination season temperatures of their local habitats (Flores & Briones 2001). However, when temperature is close to the seed germination optimum, water potential becomes less restrictive (Flores *et al.* 2017).

Seed germination of Mexican CAM species (Asparagaceae and Cactaceae) takes place at constant temperatures between 20 and 30 °C, and species differ in the minimum and maximum temperature at which germination can occur (Table 2). The effect of constant temperature on seed germination has been studied in 31 CAM species (22 Cactaceae, 8 Asparagaceae, and 1 Bromeliaceae). Twelve species are barrel, seven are columnar, six are stemless rosette-like, three species are rosette-like with stem, two are globose, and one is epiphytic (Table 2).

Alternating temperature effects on seed germination of CAM species are not very clear, *e.g.*, for cacti, in most studies only constant temperatures have been used, and some experiments that included alternating temperatures did not reveal any significantly different effects on germination compared to constant temperatures, or simply do not favor germination (Rojas-Aréchiga & Vázquez-Yanes 2000). However, for *Mamillaria gaumeri* the highest germination occurs at diurnal/nocturnal temperatures of 30/20 °C and lowering or raising the diurnal/nocturnal temperature by 5 °C reduces germination by 10 % (Cervera *et al.* 2006).

Because seeds of CAM plants on the surface of desert soils would be subjected to elevated temperatures, exposure of seeds to high temperatures has often been explored as a pre-treatment to promote germination of desert CAM plants. For instance, for the Cactaceae, seeds of *Pachycereus pringlei* have higher germination at 40 °C for 7 d and lower at 70 °C for 21 d (Cancino *et al.* 1993). For *Mammillaria magnimamma*, 90 °C for 4 and 12 h do not influence germination percentage (Ruedas *et al.* 2000). For *Ferocactus histrix*, germination is constant at 40 and 70 °C for 7 d and 21 d; also, seeds of *Isolatocereus dumortieri* show higher germination after exposure to 40 °C for 14 d and lower at 70 °C for 7 d, and *Echinocactus platyacanthus* has the highest germination after exposure to 70 °C for 14 d and the lowest with no exposure to heat (Pérez-Sánchez *et al.* 2011). Among the Agavoideae members, germination for *Agave salmiana* is consistent at 40 and 70 °C for 7 d and 21 d, and for both *Agave lechuguilla* and *Yucca decipiens*, seed exposure to 70 °C results in the lowest germination percentage both at 7 and 14 d (Pérez-Sánchez *et al.* 2011). Thus, it appears that high temperature pretreatments as a means of increasing germination percentages are not so good for members of Agavoidae, but they are good for some cacti. In addition, hot temperature pretreatments are not exclusive to CAM species, because high temperature also promotes seed germination or breaks seed dormancy in fire-prone habitats with non-CAM species (Luna *et al.* 2019).

Light environment. Light is another important environmental signal to which the life cycle of a plant may respond to in any environment (Gutterman 1993). The promoting effect of light on seed germination was documented by Caspary in 1860 (Shinomura 1997). Of the various photoreceptor systems in the seeds, phytochrome plays an especially important role in seed germination (Shinomura 1997). Phytochrome is a blue protein pigment with a molecular mass of about 125 kDa (Taiz *et al.* 2015). Borthwick *et al.* (1952) discovered the red/far-red photoreversible effect on seed germination. Absorption of red light converts the inactive P_r form of phytochrome (which inhibits germination) to the active P_{fr} form (which promotes germination); the absorption of far-red light converts P_{fr} to P_r (Shinomura 1997). Thus, in many species if seeds are exposed to red light they germinate, but if they are exposed to far-red light they do not germinate. However, in some seeds, far-red light can promote germination (Baskin & Baskin 2014); thus, the active form of phytochrome stimulates germination in darkness in some species (Shinomura 1997).

In terms of their responses to light for germination, plants can be classified as follows: (i) those that require light to germinate (positive photoblastic), (ii) those that require darkness to germinate (negative photoblastic), and (iii) those that have a large percentage of seeds neutral to light (neutral photoblastic, Flores *et al.* 2016). Positively photoblastic seeds may detect through the phytochrome a transference from a dark to an illuminated environment when buried seeds are exhumed. Such seeds may also detect the change in the red (655–665 nm): far red (725–735 nm) ratio (R:FR) of the light (Vázquez-Yanes & Orozco-Segovia 1996).

Table 2. Effect of temperature on seed germination percentage of Mexican CAM plants. All temperatures were constant in all experiments.

Species	Growth-form	Temperature (°C)																			Reference
		10	11	12	15	16	17	18	20	22	24	25	26	27	28	30	32	35	36	40	
Asparagaceae																					
Agave americana	Stemless rosette-like	-	2	-	-	25	-	50	-	75	75	-	70	-	-	-	72	-	60	2	Pritchard & Miller (1995)
Agave angustifólia subsp. *tequilana*	Stemless rosette-like	-	-	-	0	-	-	-	7	-	-	28	-	-	-	33	-	21	-	1	Ramírez Tobías *et al.* (2016)
Agave lechuguilla	Stemless rosette-like	-	-	-	-	-	-	81	-	-	-	74	-	-	-	-	30	-	7	-	Flores *et al.* (2017)
Agave mapisaga	Stemless rosette-like	-	-	-	65	-	-	-	63	-	-	80	-	-	-	72	-	68	-	2	Ramírez Tobías *et al.* (2016)
Agave salmiana	Stemless rosette-like	-	-	-	-	-	-	91	-	-	-	91	-	-	-	-	93	-	74	-	Flores *et al.* (2017)
Beaucarnea gracilis	Rosette-like with stem	-	-	0	-	-	-	-	-	-	-	-	2	-	-	-	95	-	-	-	Flores & Briones (2001)
Yucca decipiens	Rosette-like with stem	-	-	-	-	-	-	98	-	-	-	95	-	-	-	-	56	-	34	-	Flores *et al.* (2017)
Yucca periculosa	Rosette-like with stem	-	-	0	-	-	-	-	-	-	-	-	72	-	-	-	94	-	-	-	Flores & Briones (2001)
Bromeliaceae																					
Tillandsia recurvata (Mexico City Ecological Park)	Epiphytic	-	-	-	55	-	-	-	55	-	-	60	-	-	-	55	-	45	-	-	Montes-Recinas *et al.* (2012)
Tillandsia recurvata (Zapotitlán de las Salinas Valley)	Epiphytic	-	-	-	88	-	-	-	90	-	-	90	-	-	-	88	-	85	-	-	Montes-Recinas *et al.* (2012)
Cactaceae																					
Astrophytum capricorne	Globose	-	-	-	-	-	-	-	30	-	-	-	-	-	46	-	-	-	-	-	De la Rosa-Ibarra & García (1994)
Astrophytum myriostigma	Globose	-	-	-	-	-	-	-	18	-	-	-	-	-	64	-	-	-	-	-	De la Rosa-Ibarra & García (1994)

Species	Growth-form	10	11	12	15	16	17	18	20	22	24	25	26	27	28	30	32	35	36	40	Reference
Carnegiea gigantea	Columnar	-	-	-	0	-	-	-	21	-	-	38	-	-	-	24	-	2	-	-	Alcorn & Kurtz Jr (1959)
Cephalocereus chrysacanthus	Columnar	42	-	-	60	-	-	-	64	-	-	62	-	-	-	75	-	55	-	35	Rojas-Aréchiga *et al.* (1998)
Echinocactus grusonii	Barreliform	-	-	-	-	-	-	-	16	-	-	-	-	-	16	-	-	-	-	-	De la Rosa-Ibarra & García (1994)
Echinocactus platyacanthus f. *grandis*	Barreliform	0	-	-	43	-	-	-	47	-	-	63	-	-	-	47	-	47	-	17	Rojas-Aréchiga *et al* (1998)
Echinocactus platyacanthus f. *visnaga*	Barreliform	-	-	-	-	-	-	0	-	-	-	1	-	-	-	-	12	-	0	-	Flores *et al.* (2017)
Echinocactus platyacanthus f. *visnaga*	Barreliform	-	-	-	-	-	-	-	18	-	-	-	-	-	16	-	-	-	-	-	De la Rosa-Ibarra & García (1994)
Ferocactus flavovirens	Barreliform	0	-	-	62	-	-	-	65	-	-	63	-	-	-	45	-	45	-	17	Rojas-Aréchiga *et al.* (1998)
Ferocactus glaucescens	Barreliform	0	-	-	100	-	-	-	100	-	-	100	-	-	-	100	-	78	-	-	Zimmer (1998)
Ferocactus histrix	Barreliform	-	-	-	-	-	-	93	-	-	-	99	-	-	-	-	92	-	89	-	Flores *et al.* (2017)
Ferocactus histrix	Barreliform	55.4	-	-	100	-	-	-	100	-	-	100	-	-	-	100	-	72.8	-	-	Zimmer (1998)
Ferocactus latispinus	Barreliform	0	-	-	0	-	-	-	100	-	-	100	-	-	-	100	-	95	-	-	Zimmer (1998)
Ferocactus peninsulae	Barreliform	0	-	-	0	-	-	-	100	-	-	100	-	-	-	100	-	100	-	-	Zimmer (1998)
Ferocactus recurvus	Barreliform	0	-	-	33	-	-	-	55	-	-	55	-	-	-	70	-	50	-	17	Rojas-Aréchiga *et al.* (1998)
Ferocactus robustus	Barreliform	0	-	-	35	-	-	-	55	-	-	65	-	-	-	24	-	20	-	0	Rojas-Aréchiga *et al.* (1998)
Ferocactus setispinus	Barreliform	1.2	-	-	70	-	-	-	100	-	-	100	-	-	-	91.2	-	67.4	-	-	Zimmer (1998)
Ferocactus stainesii var. pringlei	Barreliform	1.6	-	-	94.3	-	-	-	100	-	-	100	-	-	-	97.6	-	89.2	-	-	Zimmer (1998)
Ferocactus wislizenii	Barreliform	0	-	-	0.6	-	-	-	83.9	-	-	100	-	-	-	91.8	-	85.2	-	-	Zimmer (1998)

Temperature (°C)

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Species	Growth-form	Temperature (°C)																			Reference
		10	11	12	15	16	17	18	20	22	24	25	26	27	28	30	32	35	36	40	
Isolatocereus dumortieri	Columnar	-	-	-	-	-	-	4	-	-	-	50	-	-	-	-	18	-	7	-	Flores *et al.* (2017)
Leuchtenbergia principis	Stemless rosette-like	-	-	-	-	-	-	-	40	-	-	-	-	-	42	-	-	-	-	-	De la Rosa-Ibarra & García (1994)
Neobuxbaumia macrocephala	Columnar	-	-	-	-	-	73.8	-	-	-	-	-	-	80	-	-	-	-	-	-	Ramírez-Padilla & Valverde (2005)
Neobuxbaumia mezcalensis	Columnar	-	-	-	-	-	96.3	-	-	-	-	-	-	93.8	-	-	-	-	-	-	Ramírez-Padilla & Valverde (2005)
Neobuxbaumia tetetzo	Columnar	-	-	5	-	-	-	-	-	-	-	-	11	-	-	-	100	-	-	-	Flores & Briones (2001)
Neobuxbaumia tetetzo	Columnar	27	-	-	27	-	-	-	43	-	-	65	-	-	-	67	-	44	-	35	Rojas-Aréchiga *et al.* (1998)
Neobuxbaumia tetetzo	Columnar	-	-	-	-	-	95	-	-	-	-	-	-	98.8	-	-	-	-	-	-	Ramírez-Padilla & Valverde (2005)
Pachycereus hollianus	Columnar	-	-	15	-	-	-	-	-	-	-	-	76	-	-	-	86	-	-	-	Flores & Briones (2001)
Pachycereus hollianus	Columnar	20	-	-	43	-	-	-	80	-	-	55	-	-	-	53	-	30	-	15	Rojas-Aréchiga *et al.* (1998)

Light requirements and small seed mass have coevolved as an adaptation to ensure germination in desert plants (Fenner & Thompson 2005). Flores *et al.* (2006) investigated the effect of light on seed germination of 28 cactus species from the Chihuahuan Desert. Only 11 of the species have non-dormant seeds, germinating ≥ 70 % in the light; these species are positively photoblastic, and all of them have small seeds. Ungerminated seeds in darkness do not germinate to a significantly higher percentage when the same set of seeds is transferred from dark to light, suggesting that darkness triggers a secondary dormancy type named skotodormancy, as an adaptive strategy in xeric environments when conditions are not optimal for germination. Similarly, Rojas-Aréchiga & Mandujano-Sánchez (2017) found that *Mammillaria compressa* and *Turbinicarpus gielsdorfianus* develop skotodormancy after darkness incubation for one month. However, skotodormancy is not exclusive to CAM species, because it has also been found in cultivated plants (Bewley 1980).

For cactus species belonging to all tribes (including many Mexican species), lower light requirement is found for seeds from taller than for shorter taxa, and lower for taxa with heavier seeds than for taxa with lighter seeds (Flores *et al.* 2011). However, for 54 Mexican cactus species belonging to the tribe Cacteae, no relationship between the requirement of light for germination and seed mass is found (Rojas-Aréchiga *et al.* 2013). These results could be explained by the generally small seed mass in cacti from tribe Cacteae (seed mass from the studied species belonging to 15 genera ranged from 0.025 mg to 3.95 mg; Rojas-Aréchiga *et al.* 2013). Seed mass in other taxa is bigger, *e.g.*, from 0.46 mg to 9.6 mg for Pachycereeae, and from 6.99 mg to 16 mg for Opuntioideae (Flores *et al.* 2011).

Thirteen members of the Agavoideae are neutral photoblastic: *Agave americana*, *A. angustifolia*, *A. asperrima*, *A. gentry*, *A. filifera*, *A. lechuguilla*, *A. salmiana*, *A. striata*, *Yucca carnerosana*, *Y. elata*, *Y. filifera*, *Y. potosina*, and *Y. queretaroensis* (Jiménez-Aguilar & Flores 2010, Flores *et al.* 2016). These findings are not surprising since these species have big seeds; however, more studies are necessary to better know the photoblastic responses of species of the Agavoideae and of the other CAM families.

There are cactus species having small seeds and neutral photoblastism, *e.g.*, *Mammillaria compressa* and *Coryphantha clavata* (Flores *et al.* 2016). In addition, these authors found that seedlings from these two species under darkness conditions were columnar and those exposed to light were cylindrical, on the basis that the cylindrical growth-form has a stem < 2 times higher in length than in diameter, and the columnar one has a stem 2–5 times higher in length than in diameter (Vázquez-Sánchez *et al.* 2012). It is possible that seeds from this species can germinate in the dark because they produce columnar seedlings with the ability to emerge from greater soil depths where sunlight cannot penetrate.

Mucilage and microbiota. Adaptive traits have been found in some cactus species to germinate in arid and semiarid environments, *e.g.*, seeds from some species have a secretory layer (mucilage) that absorbs water and distributes it over the seed surface; this mucilage surrounds the ripe seed and improves germination under relatively dry conditions (Bregman & Graven 1997, Mascot-Gómez *et al.* 2020). The production of seed mucilage is known as myxospermy (Western 2012), and seeds from five Mexican cactus species (*Coryphanta maiz-tablasensis*, *Echinocactus platyacanthus*, *Ferocactus latispinus*, *F. pilosus* and *Stenocereus queretaroensis*) from the Chihuahuan Desert have been found to have mucilage (Mascot-Gómez *et al.* 2020). This mucilage results in higher germination percentage in three species: *E. platyacanthus* (88.5 *vs.* 21.1 % without mucilage), *F. latispinus* (88.5 *vs.* 48.2 %) and *S. queretaroensis* (96.0 *vs.* 1.0 %), and a lower germination time for *E. platyacanthus* (10.0 *vs.* 19.5 d without mucilage), *F. pilosus* (14.1 *vs.* 16.4 d) and *F. latispinus* (7.8 *vs.* 14.0 d) (Mascot-Gómez *et al.* 2020). Mucilage in seeds has not been investigated for other Mexican CAM species; however, it is not a trait exclusive to CAM species because it occurs also in a broad range of species, from the Acanthaceae to the Brassicaceae to the Linaceae to the Plantaginaceae (Western 2012).

Besides mucilage, some cactus seeds have a microbiota comprising potential pathogens and beneficial microorganisms that could influence the germination percentage. For example, *Echinocactus platyacanthus* seeds having episeminal microbial communities have better germination percentage and are less susceptible to colonization by fungi than washed seeds (Mascot-Gómez *et al.* 2021). For *Opuntia* spp. seeds, fungi attack the testa, eroding or cracking the hard/stony endocarp, and thus reduce the mechanical resistance to germination in dormant seeds

(Delgado-Sánchez *et al.* 2010, 2011, Sánchez-Coronado *et al.* 2011). However, the positive effect of fungi on *Opuntia* seeds depends on the light condition; Delgado-Sánchez *et al.* (2013a) found that the fungi *Phoma medicaginis*, *Trichoderma harzianum*, *T. koningii*, and *Penicillium chrysogenum* erod the funicular envelope and promote seed germination for *O. leucotricha* and *O. streptacantha* but this is more so in light than in darkness. The effects of microorganisms on seed germination for other cacti and other CAM species remain to be investigated.

Seed bank. The seed bank is constituted by the viable seeds available for potential germination and recruitment of new plants (Montiel & Montaña 2003). Species that form seed banks show small seed mass and several ecophysiological features that permit them to persist in the soil for some time, including light requirement for germination (positive photoblastism), some dormancy mechanisms, a period of post maturation for germination, and high ecological longevity (Bowers 2000; Rojas-Aréchiga & Batis 2001). Also, differences in nurse plant availability and in rodent density can explain the differences between seed bank dynamics in desert ecosystems (Montiel & Montaña 2003).

The information in the reviewed literature about the seed bank of Mexican CAM species is scarce, and most of them is about cacti. For *O. rastrera*, about 15,000 seeds/ha in *nopaleras* (*Opuntia*-dominated stands) and 2,500 seeds/ha in grasslands remain stored in the soil and are able to germinate as soon as environmental conditions are suitable (Montiel & Montaña 2003). The seeds of *Ferocactus wislizeni* can persist in the soil for at least 18 months or up to 3 years and, if not consumed by predators, can form a between-year seed bank (Bowers 2000, 2005). *Mammillaria grahamii* seeds survive in or on the soil as long as six years, forming a long-term persistent seed bank, and also a between-year seed bank (Bowers 2005). *Opuntia tomentosa* seeds also can persist in the soil for at least 18 months (Olvera-Carrillo *et al.* 2009). One more species forming long-term persistent soil seed banks is *Polaskia chende*, whose seeds survive in the soil over a 5-year period (Ordoñez-Salanueva *et al.* 2017).

Other group of CAM species has the potential to form a short-term persistent seed bank, such as the columnar cacti *Carnegiea gigantea* (Bowers 2005) and *Stenocereus stellatus* (Álvarez-Espino *et al.* 2014). Recently dispersed *S. stellatus* seeds do not germinate because they have primary dormancy; however, this dormancy is broken after 6 months of burial in the soil. Seeds buried for 10 months enter secondary dormancy and they are not viable at 24 months, probably because of pathogen attack (Álvarez-Espino *et al.* 2014). Similarly, germination of buried seeds from two Asparagaceae (*Agave striata* and *Yucca filifera*) is high in spring and summer, but no seeds remain viable to test for germination in the other seasons (Aragón-Gastélum *et al.* 2018). Epiphyte seeds are non-dormant and do not build seed banks (Benzing 1990). However, there is evidence of germination from aged *Tillandsia caput-medusae* seeds (Flores-Palacios *et al.* 2015). Thus, more research on aerial seed bank is needed.

Seed ageing. Some CAM species show lower germination in fresh seeds than in old seeds, *e.g., Ferocactus* spp. (Zimmer 1980, Bowers 2000), *Opuntia* spp. (Potter *et al.* 1984, Mandujano *et al.* 1997), *Mammillaria heyderi* (Trejo-Hernández & Garza-Castillo 1993), *Stenocereus stellatus* (Rojas-Aréchiga *et al.* 2001), *S. queretaroensis* (De la Barrera & Nobel 2003), *Turbinicarpus lophophoroides* and *T. pseudopectinatus* (Flores *et al.* 2005), and *Ferocactus peninsulae* (Rojas-Aréchiga & García-Morales 2022). Therefore, these species are likely adapted to germinate only after heavy rainfall events, forming soil seed banks. These species could have a post-maturation period (after ripening), which is associated with seed bank formation and permanence (Rojas-Aréchiga & Batis 2001). It has been suggested that seed banks result from evolution of dormancy mechanisms as a response to unpredictable environments such as deserts and semi-deserts (Jurado & Flores 2005).

Physiological dormancy is the type of dormancy found in the Cactaceae (Rojas-Aréchiga & Vázquez-Yanes 2000; Barrios *et al.* 2020). Seeds with physiological dormancy can cycle through a gradation of dormancy 'states' in response to environmental cues, during which the range of conditions under which the seeds are able to germinate expand and contract (Long *et al.* 2015). Dormancy cycling, which indicates that the ungerminated seeds are viable seeds in the soil seed bank, has been found for *Polaskia chende* from the Tehuacán Valley (Ordóñez-Salanueva *et al.* 2017), as well as for *Echinocactus platyacanthus* seeds from the Southern Chihuahuan Desert (Aragón-Gastélum *et*

al. 2018). Seeds of *E. platyacanthus* acquired secondary dormancy in the rainy season (summer and autumn), which was alleviated at the end of the subsequent dry season (winter), possibly because of the high variation recorded in mean and minimum soil temperature at the end of winter.

Other CAM species do not show significant differences between fresh and aged seeds, *e.g.*, *Echinocereus* spp. and *Ferocactus* spp. (Fearn 1977, 1981), as well as *Turbinicarpus knuthianus* (Flores *et al.* 2005). For *Tillandsia caput-medusae* seeds, fresh seeds have 99.5 % germination success and after more than one year they only decline to 81.7 %, which indicates that seeds of this species can germinate in at least two consecutive rainy periods (Flores-Palacios *et al.* 2015). These results can be interpreted as a strategy to produce both seeds for immediate propagation and seeds for securing the medium and/or long-term survival of the species; thus, these species could form seedbanks under natural conditions, but this remains to be investigated.

Some CAM species show higher germination in fresh seeds than in old seeds, *e.g.*, *Cephalocereus senilis*, *Echinocereus reichenbachii*, *Escobaria tuberculosa*, *Ferocactus acanthodes* (*Ferocactus cylindraceus*) (Fearn 1977), *Tillandsia recurvata* (Fernández *et al.* 1989; Flores-Palacios *et al.* 2015), *Agave americana* (Pritchard & Miller 1995), *Opuntia tomentosa* Salm-Dick (Olvera-Carrillo *et al.* 2003), *Turbinicarpus swobodae* and *T. valdezianus* (Flores *et al.* 2005), *Mammillaria huitzilopochtli* (Flores-Martínez *et al.* 2008), *Rhipsalis baccifera* (de la Rosa-Manzano & Briones 2010), *Tillandsia* a*chyrostachys*, *T. circinnatioides*, *T. hubertiana*, and *T. schiedeana* (Flores-Palacios *et al.* 2015), as well as *Lophophora williamsii* (Mandujano *et al.* 2020). All these species are CAM plants, but there is no information about the photosynthetic pathway of *T. hubertiana* (Crayn *et al.* 2015). These species might not have the ability to form seed banks in the soil. A higher germination in fresh seeds would appear to represent a special form of adaptation to their desert habitat, which is characterized by short and irregular rainfall periods. In such a climate, seeds must germinate as soon as rainfall occurs (Flores *et al.* 2004).

Photosynthesis of terrestrial Mexican CAM plants

Environmental conditions in the natural habitats where terrestrial CAM plants occur affect CAM photosynthesis. This is particularly severe during the dry season because drought is accompanied by elevated temperatures and high photosynthetic photon fluxes (PPF); also, during drought, some CAM phases can be reduced or lost as drought evolves (Nobel 2003, Lüttge 2004, Andrade *et al.* 2007). In Mexico, most studies on CAM photosynthesis have been done with plants found in arid or semiarid places (Nobel 2003). However, tropical dry deciduous forests of Mexico are rich in terrestrial CAM plants (Ricalde *et al.* 2010, Valdez-Hernández *et al.* 2015, Tinoco-Ojanguren *et al.* 2018).

Light microenvironments. Light varies seasonally for terrestrial CAM plants because the rainy season is cloudier than the dry season. Furthermore, in tropical forests, the light environment is low but extremely variable for the understory terrestrial CAM plants, where CAM provides a more rapid response to sunflecks than for other nearby C_3 shade adapted plants (Skillman *et al.* 1999). In contrast, in tropical dry deciduous forests, the tree deciduousness makes light environment to change more dramatically (Graham & Andrade 2004, Andrade *et al.* 2006, González-Salvatierra *et al.* 2013), favoring CAM terrestrial plants over C_3 plants in some sites (Ricalde *et al.* 2010, Valdez-Hernández *et al.* 2015). However, it is not easy to separate the light changes effect on CAM from the lack of water or temperature changes, since all these variables usually correlate (Andrade *et al.* 2009).

The maintenance of the electron transport during the day as well as the photorespiration confer photoprotection for CAM plants (Niewiadomska & Borland 2008). Also, the xanthophyll cycle helps protecting the photosynthetic apparatus from photoinhibitory damage, particularly during drought (Lu *et al.* 2003). Acclimation to high light during the dry season also involves the biosynthesis of antioxidant metabolites to neutralize reactive oxygen species (González-Salvatierra *et al.* 2010, González-Salvatierra & Flores 2019).

Excess light reduces photosynthesis in tropical CAM plants. For instance, the hemiepiphytic cactus *Hylocereus undatus* has a maximal net CO_2 uptake at a PPF of 20 mol m^{-2} d^{-1}, above which photoinhibition reduces CO_2 uptake (Nobel & De la Barrera 2004). For desert CAM plants, although water stress usually increases the negative high

radiation effects, light effects are more pronounced for young CAM plants (Flores *et al.* 2004, Andrade *et al.* 2006, Cervera *et al.* 2006, 2007, Gallardo-Vásquez & De la Barrera 2007). However, when water is available, seedlings of several species of cacti can survive high light levels using CAM (Hernández-González & Briones Villareal 2007). Likewise, one of the adaptations for survival of CAM seedlings, in open areas in well-watered conditions, is the chloroplast movement to avoid high PPF (Delgado-Sánchez *et al.* 2013b).

Leaves and stems of CAM terrestrial plants are massive and mature plants cannot easily orient their leaves or stems to get more PPF or to avoid it. Because of this, PPF levels influence leaves or stems arrangement and the production of new photosynthetic surfaces. For instance, opuntias living between the 27° latitudes north and south from the equator tend to develop cladodes facing east-west, which maximizes PPF incidence on cladode surfaces (Nobel 2003). Comparably, ribs of the columnar cactus *Myrtillocactus geometrizans* facing south produce more fruits than ribs facing other directions (Ponce-Bautista *et al.* 2017).

Water, CO_2 uptake and chlorophyll fluorescence. When there is enough water in the soil, CO_2 uptake occurs mostly at night for terrestrial CAM plants. For instance, in *Agave fourcroydes*, a cultivated agave from Yucatan (henequen), 91 % of the CO_2 fixed in a 24-h period is at night (Nobel 1985). For *A. lechuguilla*, in the Chihuahuan desert, 85 % of the daily CO_2 uptake occurs at night (Nobel & Quero 1986). After a slight drought, total net CO_2 uptake for *A. fourcroydes* decreases to about 22 % and to less than 1 % after a 30-day drought, but fully recovers after 7 d of watering (Nobel 1985). *Agave lechuguilla* is more sensitive to drought than *A. fourcroydes* since after 13 d of drought, its daily CO_2 uptake decreases to 0.8 % of the total daily CO_2 uptake for well-irrigated plants (Nobel & Quero 1986).

When soil water is at field capacity and temperatures are moderate (day/night air temperatures of 25/20 °C), many members of the genera *Opuntia* and *Agave* have net CO_2 uptake at the beginning of the light period (Cui & Nobel 1994, Nobel 2003, Andrade *et al.* 2009). This CO_2 uptake during the early morning or late afternoon via C_3 makes CAM crops, such as *Opuntia ficus-indica* or *A. angustifolia*, highly productive compared to C_3 or C_4 crops (Acevedo *et al.* 1983, Nobel 1991, 1996, José Jacinto & García Moya 1995).

Another way to evaluate the photosynthetic performance of CAM plants is using chlorophyll fluorescence. For instance for *Agave salmiana*, drought causes a direct effect on photosystem II (PSII) photochemistry in light-acclimated leaves, as indicated by a decrease in the photosynthetic electron transport rate. Additionally, down-regulation of photochemical activity occurs mainly through the inactivation of PSII reaction centers and an increased non-photochemical quenching (NPQ, thermal dissipation capacity) of the leaves. These results suggest that the thermal dissipation of excess energy can be an important acclimation mechanism to protect the photosynthetic apparatus from over-excitation in droughted *Agave* plants (Campos *et al.* 2014).

Similarly, González-Salvatierra & Flores (2019) report several mechanisms that enable *Yucca filifera* saplings to endure water shortage. These authors showed that maximum quantum efficiency and effective quantum yield of photosystem II values, as well as titratable acid and chlorophyll *a/b* ratio, are strongly affected by water shortage, and their values reverted after rewatering. They also revealed higher proline content, antioxidant activity, and high NPQ during the water-shortage treatment, which represent mechanisms for preventing photodamage. The high ability of *Y. filifera* saplings to withstand stress caused by water shortage indicates that this species can be a key species for conservation and restoration of degraded arid ecosystems.

Temperature and CAM photosynthesis. Daytime air and leaf or stem temperatures are no critical for the net daily CO_2 uptake (Nobel 2003). Because the initial CO_2 fixation by PEP carboxylase is at night, the nocturnal temperature becomes more important for CAM photosynthesis. As nocturnal temperature increases, stomata conductance decreases, which indicates that stomata close at higher nighttime temperatures for desert CAM plants (Nobel 2003). The optimal average nocturnal temperature for CO_2 uptake of *O. ficus-indica* is 15 °C but significant net CO_2 uptake occurs at 0 °C (Cui & Nobel 1994, Nobel & Bobich 2002). Optimal temperatures for CO_2 uptake in tropical CAM terrestrial plants are higher than those for desert ones. For instance, for *Agave fourcroydes* and *Hylocereus undatus*, these optimal diurnal/nocturnal temperatures are 30/20 °C (Nobel 1985, Nobel & De la Bar-

rera 2004). Similarly, desert and cultivated cacti can tolerate temperatures as high as 70 °C (Nobel 2002, 2003) but tropical *H. undatus* and *Mammillaria gaumeri* cannot tolerate temperatures above 50 °C (Nobel *et al.* 2002, Cervera *et al.* 2006).

Low temperatures are more critical for the distribution or cultivation of CAM plants than are high ones. For instance, stem temperatures of -7 to -10 °C are lethal for *Carnegiea gigantea*, *Opuntia ficus-indica* and *Stenocereus queretaroensis* (Nobel 2002, 2003). Then, global climate warming would favor northward expansion for Mexican CAM terrestrial plants. Indeed, induce warming experiments on seedlings of two CAM species indicate that they acclimate by increasing photosynthetic pigments and NPQ (Aragón-Gastélum *et al.* 2014, 2020). More physiological research at the cell level for this high-temperature tolerance, and energy balance at the whole individual level would be necessary for restoration and conservation of arid zones under global climate warming scenarios.

Carbon isotope ratios. Nocturnal acidification is restricted to CAM plants (Winter & Smith 2021) but is not necessarily associated to CO_2 uptake, because during drought and/or higher temperatures stomata close and CO_2 released internally by respiration is also fixed (Nobel 2003). A powerful technique for indicating whether a plant species uses the CAM pathway is the use of carbon isotope ratios. This is because CAM plants with CO_2 uptake at night by PEP carboxylase would have $\delta^{13}C$ values from -11 to -18 ‰ (like values for C_4 species), whereas if all CO_2 is fixed by Rubisco $\delta^{13}C$ values would range from -25 to -30 ‰ (Nobel 2003, Santiago *et al.* 2005). The use of stable isotopes is particularly convenient in broad surveys in a particular location (Vargas-Soto *et al.* 2009, Santiago *et al.* 2017) or for investigating photosynthetic pathway evolution in some plant families (Winter & Smith 2021).

In the coastal dune of northern Yucatán, tissue $\delta^{13}C$ values for terrestrial CAM plants are 2 ‰ higher than for CAM plants from the tropical dry deciduous forests (Ricalde *et al.* 2010), which indicates greater CO_2 fixation through the CAM pathway in sites with less water. Also, using tissue $\delta^{13}C$ values of specimens of the genus *Clusia* from herbaria in Mexico, it was possible to find out that *Clusia* species are CAM in tropical dry forests but in the rest of the country there is a preponderance of species with C_3 and C_3-CAM photosynthesis (Vargas-Soto *et al.* 2009).

Long-lived succulents contain a record of past variation in growth and photosynthesis coupled to climatic conditions. Using the spines of *Carnegiea gigantea*, it was revealed that their signatures of stable isotopes of carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) are coupled to environmental variation (English *et al.* 2007, 2010). In fact, working with several saguaro populations, Hultine *et al.* (2018) demonstrated that stem growth and photosynthetic physiology recorded by $\delta^{13}C$ are coupled to a complex set of environmental conditions from the previous summer and winter.

Photosynthesis of Mexican epiphytic CAM plants

CO_2 uptake. Under greenhouse conditions, plants of the hemiepiphytic cactus *Hylocereus undatus* increased the nocturnal CO_2 uptake from 3.9 to 4.7 µmol CO_2 m^{-2} s^{-1} when well-watered but decreased it from 4.3 to 2.9 µmol CO_2 m^{-2} s^{-1} when water is withheld (Ortiz Hernández *et al.* 1999). Similarly, measurements of the instantaneous flux of CO_2 (with 20, 40, 50 and 65 % of PPF) show that the plants of the epiphytic cactus *R. baccifera* have CO_2 uptake during the day and the night period, restricting daytime stomatal opening after a month without irrigation (de la Rosa Manzano 2008). Likewise, gas exchange measurements for two *Tillandsia* species from a tropical dry deciduous forest show that for *T. brachycaulos* 12 % of the total carbon gain is fixed during daytime, whereas for *T. elongata*, 25 % of the carbon is fixed in the late afternoon via C_3 photosynthesis; also, for both species, after six days of drought, daytime net CO_2 uptake stops, and nighttime CO_2 uptake is reduced as drought progressed (Graham & Andrade 2004).

The reaction norm of a transplant experiment of *T. utricularia* plants from populations of a coastal scrub to an evergreen forest and from an evergreen forest to a coastal scrub, shows that CO_2 exchange rates are higher under conditions of high light and irrigation in the plants from both provenances, reaching a maximum mean of 2.29 µmol CO_2 m^{-2} s^{-1} in the individuals of the forest population and the lowest values (0.64 µmol CO_2 m^{-2} s^{-1}) when they grew in the scrub under drought; by contrast, individuals from the scrub population have less variation in carbon exchange in both environments (Rosado-Calderón *et al.* 2018).

Tissue acidity. Measurements of foliar or stem acidity show that, in epiphytic CAM plants, the effect of stress depends on the acclimatization capacity of each species to face the diurnal and seasonal environmental changes. For instance, in four CAM epiphytic bromeliads (*Aechmea bracteata*, *Tillandsia brachycaulos*, *T. dasyliriifolia*, and *T. streptophylla*) the values of nocturnal acidification are higher in the rainy season, compared to those in the dry season in the tropical dry deciduous forest, coastal dune scrub and mangrove forest in the Yucatan Peninsula (Cach-Pérez 2008, González-Salvatierra *et al.* 2010, Ricalde *et al.* 2010, Cach-Pérez *et al.* 2014). While the diurnal variation in tissue acidity (ΔH^+) of *T. dasyliriifolia* in a mangrove decreases to about 30 %, and that of *T. brachycaulos* in the tropical dry deciduous forest to 78 %, compared to ΔH^+ of the rainy season (Cach-Pérez *et al.* 2014).

In general, CAM terrestrial plants show high nocturnal accumulation of organic acids with high incidence of PPF (Nobel 2003). For instance, *T. usneoides*, a CAM epiphytic plant widely distributed in the Americas, shows high nocturnal accumulation at high PPF under laboratory conditions (Martin *et al.* 1985). However, this high PPF must be accompanied by water in the substrate. For instance, in a transplant experiment with the obligate CAM epiphyte *T. utricularia*, the titratable acidity gradually decreases from a maximum of 431.9 mmol H^+ m^{-2} to almost zero as the relative water content decreases over time in a drought treatment for a native population of a Yucatán coastal scrub, while tissue acidity decreases even more as the water content decreases, with a maximum of 925.2 mmol H^+ m^{-2} to almost zero, in samples from an evergreen forest in Chiapas (Rosado-Calderón *et al.* 2018). Similarly, tissue acidity showed that the epiphytic cactus *R. baccifera* achieves the highest photosynthesis under the highest PPF (65 %) when grown under irrigation but when growing under drought the highest photosynthesis is under moderate PPF (40 %) (de la Rosa Manzano 2008).

Temperature and tissue acidity. The epiphytic CAM *T. usneoides* shows an optimum carbon dioxide assimilation between temperatures of 15 and 20 °C, but assimilation decreases at temperatures outside this range (Medina 1987). In response to high air temperature at night, which is above 23 °C in the dry and wet seasons in the tropical dry deciduous forest were *T. brachycaulos* inhabits (Hernández-Robinson *et al.* 2020), individuals reduce CAM activity, as measured by change in tissue acidity, during the dry season, but increased it by opening stomata in the II and IV phases of CAM during the rainy season in Yucatán, Mexico (González-Salvatierra *et al.* 2021).

The epiphytic orchid *Encyclia nematocaulon* increases the leaf ΔH^+ to 0.2 mol H^+ m^{-2} during the early dry season and decreases it 90 % in the dry season, but contrary to expectations, it shows intermediate acidity values during the rainy season in a tropical dry deciduous forest with a mean annual rainfall of 770 mm in Yucatán (de la Rosa-Manzano *et al.* 2014). Similarly, the epiphytic orchids *Cohniella yucatanensis* and *Laelia rubescens*, in the same tropical dry deciduous forest, show the highest acidity values during the early dry season and decrease them during the rainy and dry seasons. However, the epiphytic orchids *E. nematocaulon*, *C. ascendens* and *Lophiaris oerstedii* show slight variation in foliar acidity and relative water content in the three seasons in a semi-deciduous tropical forest also located in Yucatán, but with a two-fold mean annual rainfall that of the tropical dry deciduous forest (de la Rosa-Manzano *et al.* 2014). The lower nocturnal temperature in the early dry season, as well as the low vapor pressure deficit, which increases the probability of dew deposition, can favor CAM in these tropical forests (Andrade 2003, de la Rosa-Manzano *et al.* 2014, Chávez-Sahagún *et al.* 2019).

Light, tissue acidity an electron transport rate. Under three light regimes of 20, 50 and 70 % of total daily radiation, the epiphytic orchid *Stanhopea tigrina* shows a strong reduction in nocturnal acidity under drought and high radiation, but the orchid *Prosthechea cochleata* has similar photosynthetic responses to the different PPF conditions during the dry period in a subtropical cloud forest (Guevara-Pérez *et al.* 2019).

The quantum yield (Φ_{PSII}) of plants of the epiphytic cactus *R. baccifera* from the cloud forest under irrigation and low light (20 % of sunlight, 1.81 mol m^{-2} d^{-1} PPF) was maximum (Φ_{PSII} pre-dawn = 0.8, Φ_{PSII} noon = 0.7) and decreased (Φ_{PSII} pre-dawn = 0.7, Φ_{PSII} noon = 0.3) at high light (65 % of sunlight, 9.8 mol m^{-2} d^{-1} PPF); the electron transport rate (ETR) increases linearly with the increase of light (maximum values of ETR at low light with irrigation = 160-180 µmol m^{-2} s^{-1}, ETR after one month without irrigation = 120-140 µmol m^{-2} s^{-1}), and at high light it reaches satura-

tion (ETR with irrigation = 138.9 µmol m^{-2} s^{-1}, ETR after one month without irrigation = 126.6 µmol m^{-2} s^{-1}) (de la Rosa Manzano 2008). In the bromeliad *T. brachycaulos*, Φ_{PSII} values differ between shaded and exposed plants and between the dry and the rainy seasons; the lowest average of Φ_{PSII} (0.57) is in the leaves of exposed *T. brachycaulos* plants during the dry season and the highest value of Φ_{PSII} (0.80) is in leaves of shaded plants during the rainy season (González-Salvatierra *et al.* 2021). Additionally, the maximum ETR of this epiphytic bromeliad is higher during the rainy season, with values of 23 and 32 µmol m^{-2} s^{-1} in exposed and shaded plants, respectively, and the light saturation point of 800 µmol m^{-2} s^{-1} in both light conditions; in contrast, during the dry season the maximum rate of electron transport is 12 and 18 µmol m^{-2} s^{-1} in exposed and shaded plants, respectively, and the light saturation point decreases to less than 465 µmol m^{-2} s^{-1} in both light conditions (González-Salvatierra *et al.* 2021). On the other hand, individuals of the epiphytic *T. utriculata* under a similar light environment (a coastal scrub) have a higher electron transport rate than those individuals of the same species from a population of a broadleaf forest transplanted to a coastal scrub site; after 20 d without irrigation, plants from the coastal scrub reduce ETR to 30 %, while those from the forest reduce ETR to 50 % (Rosado-Calderón *et al.* 2018). Under the reduced light conditions of the forest site, ETR values do not differ between individuals from both populations. The effect of the drought is more evident in the coastal scrub site, where the maximum ETR values of the individuals of both populations decrease after 20 days without water, while in the forest site the maximum ETR values remain unchanged in the individuals of both populations during the same period (Rosado-Calderón *et al.* 2018).

In the epiphytic orchids *E. nematocaulon*, *C. yucatanensis*, and *L. rubescens*, the maximum foliar Φ_{PSII} is high (0.8 on average) during the rainy and early dry seasons in a tropical dry deciduous forest of Yucatán, but it strongly decreases (Φ_{PSII} = 0.46) in the three species during drought, indicating possible photoinhibition because it coincides with the increase in the amount of light and the decrease in foliar acidity; in contrast, also in Yucatán, the maximum foliar Φ_{PSII} of *E. nematocaulon*, *C. ascendens* and *L. oerstedii* remains relatively high (0.7 on average) during the drought and high (0.8 on average) in the rainy and early dry seasons in a semideciduous forest (de la Rosa-Manzano *et al.* 2014). The epiphytic orchids of the low deciduous forest show the highest maximum foliar ETR values (between 18 and 10 µmol m^{-2} s^{-1} on average) during the rainy and early dry seasons and the lowest during the dry season (between 10 and 4 µmol m^{-2} s^{-1}); in contrast, epiphytic orchids from the semideciduous forest show the lowest values of maximum ETR during the rainy season (between 7 and 11 µmol m^{-2} s^{-1} on average) and the highest during the early dry season (between 33 and 13 µmol m^{-2} s^{-1} on average) (de la Rosa-Manzano *et al.* 2014). The increase in foliage density and cloudiness during the rainy season causes a decrease in the amount of light throughout the day and with it, the energy available to capture CO_2.

The epiphytic orchids *Prosthechea cochleata* and *Stanhopea tigrina* from a cloud forest show low foliar Φ_{PSII} predawn values (< 0.6) under 20, 50, and 70 % of the total daily radiation under experimental conditions but are remarkably lower (< 0.1) in *S. tigrina* in the highest light treatment (Guevara-Pérez *et al.* 2019). Also, plants of *P. cochleata* have slightly higher Φ predawn values (0.63) under 50 % than those under 20 and 70 % total daily light (Y predawn = 0.46 and 0.57, respectively). No differences in ETR$_{max}$ (14 µmol m^{-2} s^{-1}) are observed for *P. cochleata* at the three PPF treatments under drought conditions, while *S. tigrina* has a significant decrease in ETR$_{max}$ (< 10 µmol m^{-2} s^{-1}) at the 70 % of total daily PPF compared to the other light treatments (Guevara-Pérez *et al.* 2019).

Non-photochemical energy dissipation (NPQ). Excess light causes photoinhibition due to the production of toxic chemical species and damage to molecules of the light reactions of the photosynthetic apparatus (Taiz *et al.* 2015). Furthermore, NPQ is a mechanism through which leaves avoid damage by dissipating excess energy as heat. In various environments, photoinhibition of photosynthesis has been observed in various CAM species because the process of energy dissipation with the xanthophyll cycle is a competitor of the photosynthetic process (Adams III & Demmig-Adams 1996). However, in epiphytic plants the production of antioxidant compounds and flavonoids in response to high light and other stressful conditions are photoprotectors that prevent photodamage and cause low NPQ values (Saito & Harborne 1983, González-Salvatierra *et al.* 2010).

The CAM epiphytes *T. makoyana*, *T. rothii* and *T. eistetteri* that inhabit the upper canopy stratum in a tropical dry forest with high daily PPF show lower NPQ values (1.5–1.8 on average) compared to the epiphytes *T. ionantha*

and *T. intermedia* (NPQ = 2.4–3.2 on average) preferring the lower canopy stratum with a more shaded environment under experimental conditions of drought, re-wetting and high dew exposure (Reyes-García & Griffiths 2009). Individuals of the epiphyte *T. utriculata* from a coastal scrub population maintain relatively high NPQ values (around 1.5 on average) under experimental conditions of irrigation or drought and with high and low PPF, while individuals from a forest population had higher values (2.4 on average) with irrigation and high PPF and showed values between 1 and 1.5 with drought and high or low PPF conditions (Rosado-Calderón *et al.* 2018). During the rainy and dry seasons, NPQ values in *T. brachycaulos* are consistently low (< 1) in a shaded environment; however, in an exposed environment during the rainy season, NPQ values increase close to 2 during the morning, decreasing to low levels during the day in a tropical dry deciduous forest (González-Salvatierra *et al.* 2021). Plants of the epiphytic cactus *R. baccifera* that grow with constant irrigation or after one month without irrigation increase two-fold the NPQ (about 2.8) when exposed to 65 % compared to 20 % of total PPF (de la Rosa Manzano 2008).

Photoprotective pigments. Flavonoid production has been reported in several species of Bromeliaceae as a response to high PPF and other stressful conditions (Saito & Harborne 1983, Benzing 2000). For *T. brachycaulos*, anthocyanins (a type of flavonoid) are in a single layer under the epidermis on both leaf faces, and anthocyanin concentrations are higher in exposed plants during the dry season, compared to shaded plants (González-Salvatierra *et al.* 2010). Also, there is a strong correlation between incident daily high light and total anthocyanin content, which suggests that these molecules are involved in photoprotection. Epiphytic orchids show mechanisms to avoid excess light and heat, including a reduction in leaf area to increase heat flux by conduction and convection, carotenoid production, and photosystem II heat dissipation of absorbed energy (Adams III & Demmig-Adams 1996, de la Rosa-Manzano *et al.* 2014, 2015). These epiphytic orchids produce more carotenoids during the dry season than during the wet and early dry seasons, and their concentrations are higher in leaves of orchids from a tropical dry deciduous forest than those from a tropical semi-deciduous forest (de la Rosa-Manzano *et al.* 2015). Moreover, orchid leaves from the former forest have higher zeaxanthin retention and lower values of maximum quantum efficiency of photosystem II during the dry season than orchids from the latter forest (de la Rosa-Manzano *et al.* 2015). These changes are related to high incident light and the prolonged dry period that occur in the tropical dry deciduous forests when all trees shed their leaves.

Water relations of terrestrial CAM plants

Specialized tissues. Leaves or stems of terrestrial CAM plants have succulent tissues with specialized functions. The outer cortex, or palisade cortex, is characterized by multiple layers of green photosynthetic palisade parenchyma cells and the inner cortex is a water storage parenchyma (Barcikowski & Nobel 1984, Goldstein *et al.* 1991a, Terrazas Salgado & Mauseth 2002, Nobel 2003). These succulent tissues, especially the water storage parenchyma, undergo successive cycles or filling and emptying and, together with the high-water use efficiency of the CAM cycle, allow continuous CO_2 uptake, since water from storage tissues maintains turgor in the photosynthetic tissues (Goldstein *et al.* 1991a, Lüttge 2004, Andrade *et al.* 2009).

Cell walls of the water storage parenchyma in *Opuntia ficus-indica* are thinner (0.16 ± 0.01 mm) than those of the chlorenchyma (0.32 ± 0.02 mm), and unlignified (Goldstein *et al.* 1991a), which allows a high flexibility for changing in volume without a notable change in water potential (Goldstein *et al.* 1991a, Terrazas Salgado & Mauseth 2002). Moreover, in well-watered plants of this species, the bulk modulus of elasticity is about 0.35 MPa for the water storage parenchyma and 0.85 MPa for the chlorenchyma, which changes to 0.97 MPa under drought, indicating rigid cell walls in the latter tissue (Goldstein *et al.* 1991a).

Water redistribution in tissues. Water storage in the inner cortex allows succulent plants to survive drought and, in CAM terrestrial plants, to continue having photosynthesis through CAM. In *O. ficus-indica* the lower bulk modulus

of elasticity of the water storage parenchyma than that of the chlorenchyma allows the former tissue to maintain turgor and facilitate continuous water movement to the latter. Uprooted CAM terrestrial plants usually survive for years, even losing more than 80 % of the leaf or stem water (Barcikowski & Nobel 1984, Goldstein *et al.* 1991a, Andrade *et al.* 2009).

The water storage capability of leaves and stems of CAM terrestrial plants can be quantified by the volume-to-surface area ratio (V/A). Leaves of agaves and stems of cacti have a mean V/A of about 1 cm and stems of barrel and columnar cacti can have V/A higher than 5 cm (Nobel 1994, 2003). For seedlings of terrestrial CAM plants, the V/A can indicate survival. For instance, a small cactus of about 0.18 of V/A can tolerate a drought of 3.5 months or more if the seedling is under a nurse plant (Nobel 1994). Similarly, seedlings of *Mammillaria gaumeri* in a coastal sand dune have a V/A two-fold higher when growing at 20 % of ambient PPF (under a nurse plant) than those receiving 50 % of ambient PPF (Cervera *et al.* 2006).

Developing organs require water from mature organs. For this to occur, water moves, via xylem, from sites with high water potentials to sites with low water potentials. However, in *O. ficus-indica*, fruits have a higher water potential than underlying cladodes and water movement to fruits must occur via phloem (Nobel *et al.* 1994).

Mucilage and relative capacitance. Mucilage, which is a complex polysaccharide with a high water-binding capacity, is common in many terrestrial CAM plants (Sáenz-Hernández *et al.* 2002). In *O. ficus-indica*, mucilage content is higher in the water storage parenchyma than in the chlorenchyma (Goldstein *et al.* 1991a). Additionally, in other cactus species, mucilage content is positively related to tissue relative capacitance (Nobel *et al.* 1992). Tissue relative capacitance is the capacity of the tissue to maintain its water potentials when the water content decreases, and it is related to succulence, V/A, and other water relation properties; this helps desert CAM plants because they face dry periods of several months (Andrade *et al.* 2009).

Changes in the water potential components. For *O. ficus-indica*, under well-watered conditions, acidity increases in the chlorenchyma account for about a 0.28 MPa decrease in osmotic potential in the morning, but osmotic potential in the water storage parenchyma do not change significantly in a 24-h period (Goldstein *et al.* 1991b). After a 3-month drought, although there is a loss of water in the tissues (27 % in the chlorenchyma and 61 % in the parenchyma), osmotic potential does not change significantly (Goldstein *et al.* 1991b). Diel changes in turgor pressure in the chlorenchyma were similar for well-watered than for droughted *O. ficus-indica* plants, indicating that this species maintains high water turgor in the photosynthetic tissue during extended periods of drought (Goldstein *et al.* 1991b). Also, to compensate for the decrease in turgor pressure in the water storage parenchyma during drought, polymerization of solutes occurs (Barcikowski & Nobel 1984, Goldstein *et al.* 1991a).

A drought of more than 30 d for individuals of *O. rastrera* show no change in their tissue osmotic potential (Briones *et al.* 1998). However, seedlings of *O. streptacantha* have a decrease in osmotic potential as drought progresses at high light, because of their low V/A, compared to those in the shade (Delgado-Sánchez *et al.* 2013b). In other study, seedlings of *Agave salmiana*, with higher V/A than seedlings of *A. striata*, do not change water potential after a drought of 6 months (Ramírez-Tobías *et al.* 2021), not only for the higher succulence of the former species but also for a higher proline production in their tissues than the latter species (Ramírez-Tobías *et al.* 2014).

Root properties. Roots of CAM plants have evolved characteristics that allow them to take water rapidly when soil is wet but reduce water loss during drought (Nobel 1994). This rectifier-like property begins when roots start shrinking, leading to a root-soil air gap that reduces the hydraulic conductivity in the root-soil system (Nobel & Cui 1992). After rewetting, initiation of new roots and the increase of root radial conductivity allows a rapid water uptake (North & Nobel 1996). For most CAM plants, the low root-to-shoot ratio reduces carbon costs, and the efficient root water uptake, coupled to the high stem or leaves water use efficiency, leads to competitive advantage in the locations where they occur (Briones *et al.* 1998, Andrade *et al.* 2009).

Water relations of epiphytic CAM plants

Humidity and light are the main factors that determine the abundance of epiphytic plants. In relation to light, epiphytes have been grouped as exposed (total or almost total exposure to the sun), sun (partial shade) and shade tolerant (Pittendrigh 1948, Benzing 1990). With respect to humidity, epiphytic species have been grouped as poikilohydric and homohydric, mesophytic and xerophytic hygrophytes (Benzing 1990). Particularly, epiphytic bromeliads have been classified into tank and atmospheric types based on the strategy of acquiring water and mineral nutrients (Pittendrigh 1948). Tank-type bromeliads are mainly C_3 plants of the Bromeloideae subfamily, with succulent rosette leaves in which they store water and trichomes with the ability to absorb water and nutrients at the base of the leaf blade. Atmospheric type bromeliads are CAM and have a poorly developed or absent tank and absorbent trichomes over the entire leaf (Benzing 2000, Reyes-García & Griffiths 2009). Atmospheric species from dry forests of Mexico show succulent leaves, are adapted to use water from rainfall pulses, and can maintain photosynthetic activity with low water content (Reyes-García *et al.* 2012).

Drought tolerance. Plants resist the decrease in water availability by temporarily reducing its impact, with phenological mechanisms, or tolerating it with morphological and physiological mechanisms. CAM epiphytes can tolerate drought by preventing dehydration by maintaining cell turgor and high-water potentials by internally storing water in succulent pseudobulbs and spongy velamen in orchids (Benzing 1990), succulent rhizomes in ferns (Hietz & Briones 1998), succulent stem parenchyma (hydrenchyma) in cacti and succulent leaves of bromeliads, orchids, and ferns (Benzing 1990, Andrade & Nobel 1997, Nobel & De la Barrera 2004, de la Rosa Manzano 2008). Tissue dehydration can also be prevented by reducing the conductance of waxy roots and leaves through diurnal closure of stomata, cuticular thickening, and increased boundary layer of air in contact with the atmosphere. However, CAM epiphytes can also tolerate drought at low water potentials, maintaining turgor by increasing cell elasticity. The accumulation of acids by CAM or solutes compatible with the cytoplasm to reduce the osmotic potential are mechanisms used by terrestrial desert species and could be advantageous for epiphytes with access to aerial soil. For instance, during the dry season, water potential values of *T. brachycaulos* were not significantly different between dawn and noon, but pre-dawn water potential values were lower than midday water potential ones during the rainy season in a tropical dry deciduous forest of Yucatán, Mexico (González-Salvatierra *et al.* 2021). However, osmotic potential changes are subtle because the water obtained by epiphytes is water with high water potentials (Hernández-Robinson *et al.* 2020).

Water absorption. Fluctuations in the availability of rainwater, mist or dew are high in the vertical gradient of the canopy and plants that inhabit it have developed a series of morphological and physiological adaptations to capture atmospheric water rapidly. Epiphytic bromeliads possess hygroscopic peltate trichomes, specialized to condense moisture and absorb liquid water through the leaf surface (Smith 1989, Cach-Pérez *et al.* 2014). Epiphytic orchids accomplish the same thing through the velamen, a tissue consisting of a spongy epidermis with multiple layers at the roots (Goh & Kluge 1989). In Bromeliaceae, leaf morphology in some tank species allow a decrease in leaf temperature, which is usually below air temperature in the early morning, promoting dew condensation, contributing to maintain a high-water balance (Andrade 2003, Reyes-García *et al.* 2012, Chávez-Sahagún *et al.* 2019). Also, nebulophyte morphology, characterized by long and thin leaves with a small boundary layer, allow for the small fog droplets to be intercepted (Martorell & Ezcurra 2002, 2007, Reyes-García *et al.* 2012).

Air humidity benefits epiphyte growth. In the Yucatan Peninsula in Mexico, individual density of epiphytic species is inversely related to vapor pressure deficit (VPD, Cach-Pérez *et al.* 2014). Additionally, in locations where trees tap the permanent water table, tree leaf area and transpiration increase, lowering VPD values, which create low-VPD canopy islands of high epiphyte density (Chilpa-Galván *et al.* 2013). It has been reported that after drought epiphytes recover physiological processes fast (Andrade & Nobel 1996, 1997, Andrade *et al.* 2009). Roots of the epiphytic cacti *Epiphyllum phyllanthus* and *R. baccifera* have sheaths composed of soil particles, root hairs and mucilage, which reduce water loss and helps taking advantage of episodic rainfalls (North & Nobel 1994).

Water storage. Many epiphytic CAM plants can store water in parenchymal tissues located in the roots, stems, and leaves (Benzing 1990). For instance, in El Cielo Biosphere Reserve, Tamaulipas, Mexico, the most important organ for storing water in the epiphytic CAM orchids *Prosthechea cochleata* and *Stanophea tigrina* is the pseudobulb, compared to roots and leaves; the former species, which grows in dry and humid habitats, shows greater succulence in pseudobulbs and leaves and is less sensitive to drought compared to *S. tigrina*, which only colonizes humid places (Guevara-Pérez *et al.* 2019). Another example is the stems of *R. baccifera*, which can withstand one month without irrigation with a little change in succulence (Andrade & Nobel 1997, de la Rosa Manzano 2008). This allows this species and another epiphytic cactus, *Epipyllum phyllanthus*, to occupy more exposed sites in the canopy than other epiphytes in a dry forest in Panama (Andrade & Nobel 1997).

Relative capacitance (change in relative water content per unit change in water potential) of epiphytic cacti is high (0.50 MPa^{-1}) compared to that of epiphytic ferns (0.16 MPa^{-1}), which allows to maintain transpiration longer for the cacti than for the ferns (Andrade & Nobel 1997). In general, relative capacitance for epiphytic CAM species is in average about half of that of terrestrial CAM species (Andrade *et al.* 2009).

Internal transport of water. Elastic cell walls possibly allow *T. ionantha*, a Mesoamerican atmospheric bromeliad that grows in xeric and mesic tropical environments in Mexico, to transport the water stored in the hydrenchyma (spongy tissue of the parenchyma that stores water) to maintain turgidity and high water potential in the leaf chlorenchyma and thus be able to capture or internally recycle CO_2 and remain metabolically active during experimental drought (Nowak & Martin 1997). Similarly, plants of *T. brachycaulos*, an atmospheric CAM, have the highest capacitance and bulk modulus of elasticity values in the wet season, compared to the dry season in a tropical dry deciduous forest (Hernández-Robinson *et al.* 2020). Also, the considerable size of the pseudobulb of the orchid *Laelia rubescens* and the presence of a specialized hypodermis to store water in the orchids *Cohniella yucatanensis* and *C. ascendens*, allow the transport of water to the foliar mesophyll to keep the relative water content constant to carry out photosynthesis during all seasons in a tropical dry deciduous forest of Yucatán (de la Rosa-Manzano *et al.* 2014).

Potential ecophysiological responses of CAM plants to global change

Global environmental change includes both systemic changes that operate globally through the major systems of the geosphere-biosphere, and cumulative changes that represent the global accumulation of localized changes (Turner II *et al.* 1990). The way CAM plants will cope in the face of global environmental change is crucial for their survivorship. Temperatures, carbon dioxide, and other trace gases are up at an unusual rate (IPCC 2021). In addition, habitat disturbance and urbanization, with its expanding and destructive human footprint, continues to affect through and impact all ecosystems (Schmidt *et al.* 2020; Shen *et al.* 2020). Climatic extremes like droughts, frosts, hurricane-associated floods, and warming are now quite common (Altwegg *et al.* 2017; Montiel-González *et al.* 2021). These are World's 'new normal' and plant ecophysiology provides and will provide some of the most critical evidence and fundamental understanding about how the diversity of plant adaptations (including CAM species) will enable plants to operate the conditions of the Anthropocene (Lambers & Oliveira 2019). However, studies on physiological responses of CAM plants to the environment are far from being complete. Most studies have been done in few species from few families. Environmental physiology of growth and reproduction of CAM plants, as well as of seedlings following germination should be given more attention (Andrade *et al.* 2009).

Desert CAM plants are expected to expand their distribution ranges because of climate change, as these species can quickly adapt to water shortage and high temperatures (Aragón-Gastélum *et al.* 2014, 2020, 2021, González-Salvatierra & Flores 2019). However, some studies have indicated the negative effects of induced warming on the survival rate of desert CAM plants during early life cycles (Aragón-Gastélum *et al.* 2017; Pérez-Noyola *et al.* 2020, which may prevent the persistence of their populations in future climate scenarios. It appears that seedling tolerance of warming may increase with age in CAM plants (Aragón-Gastélum *et al.* 2017), although further studies are needed to evaluate this.

CAM plants are excellent plant biosystems for biophysical studies and many of their physiological processes can be modeled. The environmental productivity index has already been analyzed for many CAM species and can be used to model plant productivity in response to global climate change (Nobel 2003, Andrade *et al.* 2009). Also, to feed more robust models, it would be necessary to study multiple stress factors for CAM plants and their plasticity to environmental changes to help predicting plant responses to future climate change (de la Rosa-Manzano *et al.* 2017, Cach-Pérez *et al.* 2018). Such information would be vital for conservation, and restoration programs.

Paradoxically, the first CAM species studied in Mexico was *Clusia lundellii* (Tinoco-Ojanguren & Vázquez-Yanes 1983) and no more significant studies have been done with this remarkable genus with different growth forms and high physiological plasticity (Vargas-Soto *et al.* 2009). Under climate change scenarios, *Clusia* C$_3$-CAM and CAM species could become more ecologically important, and can even been proposed for restoration programs, but more physiological and ecological studies are needed.

The future of epiphytes is uncertain in this changing world (Zotz 2016, Zotz *et al.* 2021), new research that highlights the potential of these species as ornamentals or biological indicators is extremely important. Epiphytes are probably among the first life forms to respond to global change because some bromeliad species are very sensitive to environmental changes (Cach-Pérez *et al.* 2014). If the favorable wet growing season becomes too short, the epiphyte plant cannot have enough reservoirs to survive a prolonged drought when photosynthesis drops and photoinhibition is induced (Reyes-García & Griffiths 2009). In contrast, some of the epiphytic species that have high drought tolerance can be in disadvantage under wetter conditions. The most dramatic concern for Mexican CAM epiphytes is the change of land use of the tropical dry deciduous forests. For hundreds of years these forests have been deforested worldwide and transformed to agricultural lands and towns (Portillo-Quintero *et al.* 2015, Siyum 2020).

Predicted temperature rise due to global change can be the main problem for the physiology of CAM plants. This is because the optimal mean nocturnal temperature for CAM terrestrial plants is relatively low (15 °C, but between 20-25 °C for tropical CAM epiphytes and hemiepiphytes) (Nobel 2003, Nobel & Bobich 2002). However, high diurnal temperatures have little influence in the growth and survival of CAM plants. It seems that daytime air and leaf or stem temperatures are not critical for CO$_2$ uptake and terrestrial CAM plants can tolerate temperatures as high as 68 °C (Nobel 2003, Nobel & Bobich, 2002). However, tropical CAM terrestrial and hemiepiphytes cannot tolerate temperatures above 50 °C (Nobel *et al.* 2002, Cervera *et al.* 2006). Certainly, we will see many CAM species migrating to the northern and southern hemispheres. More field and laboratory studies are required to understand the effect of temperature in the photosynthesis, growth, and survival of CAM species.

Acknowledgments

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