Chapter 5
Physiological Ecology of Vascular Plants

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Abstract The Yucatán Peninsula has opposing gradients of precipitation and evaporation from north to south: as precipitation increases, evaporation rates decrease. Also, due to bedrock composed primarily of limestone, the area presents high porosity and rainfall infiltrates quickly, resulting in no superficial runoff. Natural disturbances such as hurricanes and fires are also common. The interaction of these factors has created a mosaic of environmental conditions that has given rise to a series of physiological adaptations in the plant species of the area. This chapter focuses mainly on the morphophysiological responses and adaptations of native plant species of the Yucatán to natural conditions, and on how plants respond to environmental factors at the level of the individual, species, population and/or functional groups. In this chapter, species were grouped according to their metabolic pathway (C_3 species or crassulacean acid metabolism species (CAM)), and discussed based on adaptations to limiting resources: water, nutrients, temperature, and light. For C_3 species only trees were included, and studies incorporated in this section spanned from plant establishment, growth, water use and water relations, alternative water sources, and carbon and nutrient flow. For the section on CAM the focus was on the factors that affect CAM plants in the microenvironments in which they occur. Other issues analyzed include plant physiological responses to natural

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disturbances, the potential impact of climate change on plant populations, and gaps in information as well as additional perspectives of study.

Keywords Tropical dry forests • Water stress • Microenvironments • Precipitation gradient • Photosynthesis • Carbon stable isotopes • Light stress • Ecophysiology • Epiphytes • CAM

5.1 Introduction

The floristic composition of the woody vegetation of the Yucatán Peninsula resembles that of other dry forests in the Caribbean and Mesoamerica that have limestone as parent material (White and Hood 2004). In the Yucatán Peninsula, differences in rainfall and temperature play a major role in floristic change, both directly through climate effects on vegetation, and indirectly through climate effects on other factors such as pH, organic matter, and soil depth (White and Hood 2004). Due to lime dissolution, rock fractures, cavities, and soil pockets are sometimes formed in the soil/bedrock profile (Querejeta et al. 2006, 2007). These fractures and soil pockets may modify water retention of different soil layers (Estrada-Medina et al. 2013), which may influence the phenology of the local vegetation (Valdez-Hernández et al. 2010).

Vegetation types found in the Yucatán Peninsula include extensive areas of mangrove, particularly along the West and East coasts (Espejel 1987). One particular type of mangrove forest stands out on the West coast around springs, easily identified as large domes from the air (called 'petenes'; Zaldivar-Jimenez et al. 2010). Trees of up to 6 m in height are found growing in the extreme conditions of coastal sand dunes, with annual rainfall between 300 and 400 mm and average annual temperatures of 30 °C (Torres et al. 2010; Flores Guido et al. 2010). Further inland, parallel to the coast, seasonally dry tropical forests are found, with an annual rainfall from 700 to 1000 mm, a dry season (<100 mm per month) of 4–7 months, and shallow soils (≤30 cm) (Valdez-Hernández et al. 2010; Estrada-Medina et al. 2013). In these seasonally dry tropical forests, trees are taller than those on the sand dunes, reaching about 12 m, and legumes represent the main tree family (Flores Guido et al. 2010; Reyes-García et al. 2012a).

In the central part of the Yucatán Peninsula, plant communities vary in composition according to precipitation and soil depth (See Fig. 5.1 for rainfall patterns). Seasonally dry tropical forests are found in areas with rainfall between 900 and 1100 mm annually, dry seasons of up to 6 months, and shallow soils. Here the canopy reaches between 15 and 25 m, and between 50 and 75 % of the trees are leafless in the dry season. Trees in the Fabaceae, Sapotaceae, and Boraginaceae families are among the most common (Cabrera et al. 1982; Sánchez and Islebe 2002). In areas with an annual rainfall of 1000–1500 mm, where the carbonate rock layer is naturally eroded, communities with a higher proportion of evergreen species are found (50–75 %). Here the canopy also reaches between 15 and 25 m. Common tree families include Fabaceae, Sapotaceae, and Moraceae (Cabrera et al. 1982; Sánchez and Islebe 2002). In the south, where precipitation is higher

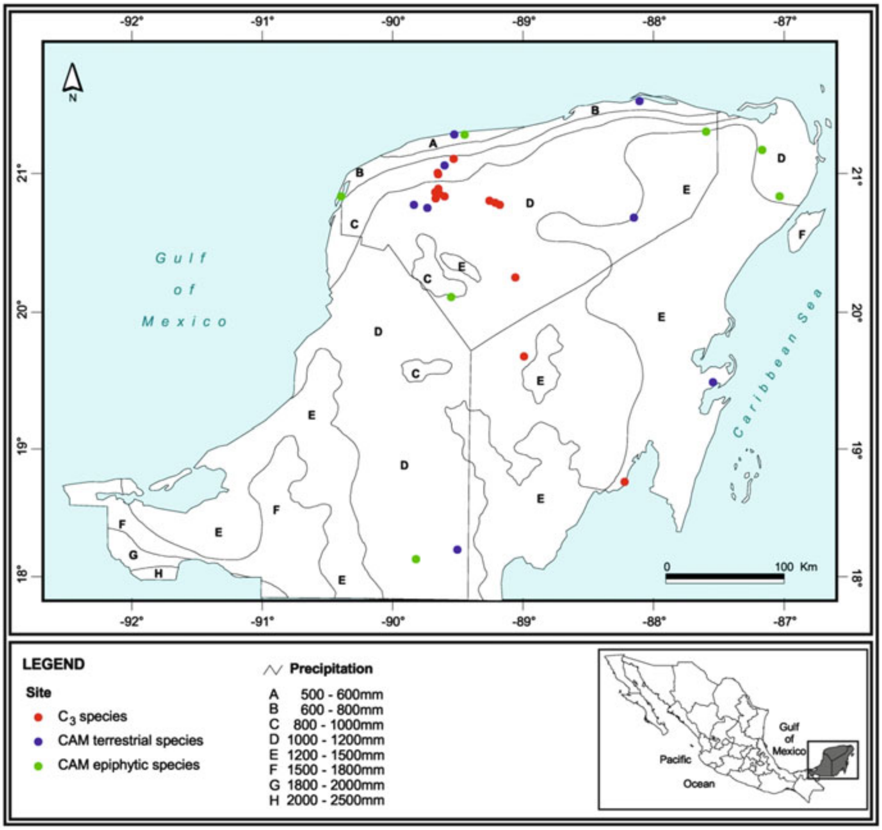


Fig. 5.1 Location of studies on plant physiological ecology in the Yucatán Peninsula (courtesy of H. Weissenberger, El Colegio de la Frontera Sur, Mexico)

(>1500 mm per year), soils are deeper and relatively rich in organic material, and have efficient drainage; the forest is composed mainly of evergreen species (>75 %) and the canopy reaches about 25 m. Common tree families include Sapotaceae, Moraceae and Arecaceae (Cabrera et al. 1982; Sánchez and Islebe 2002).

Hurricanes are a recurring disturbance on the Yucatán Peninsula. Their frequency and intensity varies across the region, but tends to be highest in the northeast tip of the peninsula (Boose et al. 2003). The long history of disturbance, both natural (hurricanes and fires) and anthropogenic (fires, agriculture, and more recently, cattle ranching), has led plants of the Yucatán to have a series of characteristics and adaptations, many of which allow for a rapid recovery after disturbance (Boose et al. 2003; Valdez-Hernández et al. 2014, see Chap. 7).

The particular characteristics of the vegetation of the Yucatán Peninsula, and the continuous disturbances that occur there, makes their native plants an exceptional and remarkable subject for physiological studies under natural conditions. However, only 2 % (50 species) of the total vascular plant species estimated for the peninsula (2400 species; Duno et al. 2011) have been reported in physiological studies. Most of these studies have focused on species with C_3 photosynthesis (mainly trees) and on plants with crassulacean acid metabolism (CAM). Geographically, most of the studies have been in the northern part of the Yucatán Peninsula (Fig. 5.1). In this chapter we will discuss C_3 and CAM species separately. For C_3 species the focus will be on changes in the floristic composition of the woody vegetation across the Yucatán Peninsula and on studies of C_3 tree species native to the peninsula. CAM species will be considered according to their life form, either terrestrial or epiphytic and the focus will also be on studies of species native to Yucatán.

5.2 C_3 Species

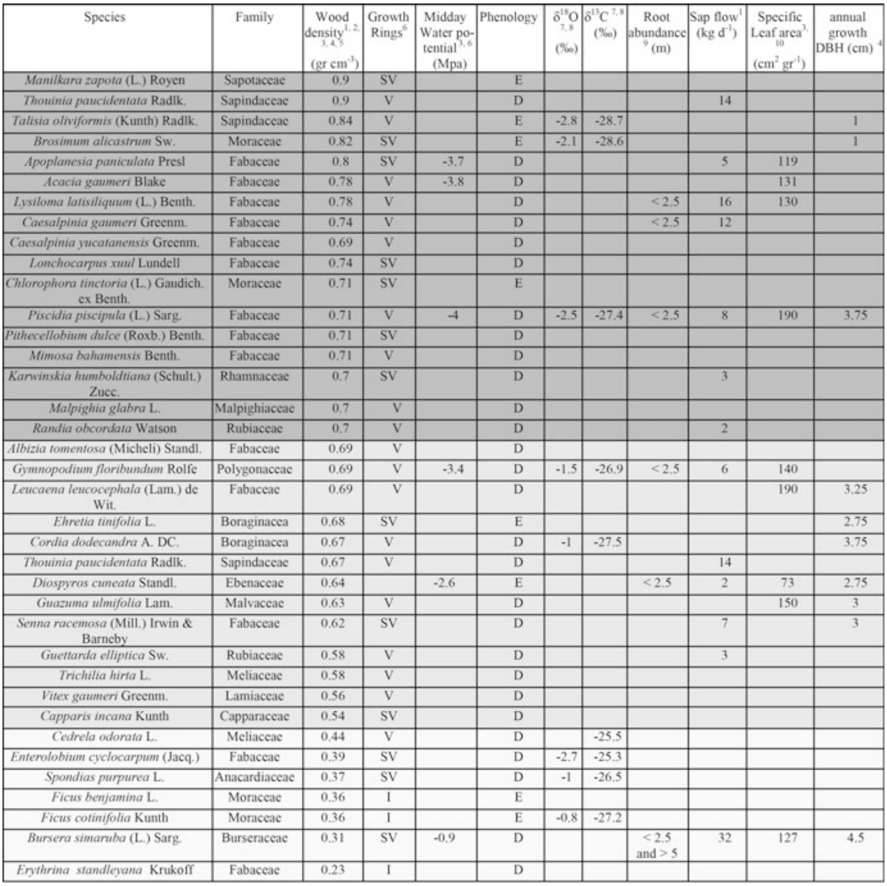
In natural areas of north central Yucatán, important woody species (stems greater than 3 cm main stem diameter) include *Caesalpinia gaumeri*, *Bursera simaruba*, *Gymnopodium floribundum*, *Thouinia paucidentata* and *Piscidia piscipula* (White and Hood 2004). Water availability appears to influence tree species diversity, which increases following increase in water availability from north to south (Flores Guido et al. 2010). Tree richness and stem density are also correlated to nutrient availability (Ceccon et al. 2002); tree diversity also appears to be related to successional age, with older areas generally presenting greater diversity of tree species.

Research on C_3 species in the Yucatán has focused mainly on tree species and of the estimated 500 tree species in the peninsula (Ibarra-Manríquez et al. 1995), only about 15 species (or 3 %) have been studied. These studies have focused mainly on the response of a few morphophysiological parameters (e.g. wood density, water potential, water-use efficiency, among others) to water deficit; on the identification of the source of water used by trees, and on the community level effects of climate change and other disturbances on the ecology of the area. The main features and parameters that have been studied for trees in the Yucatán Peninsula are presented in Table 5.1.

5.2.1 Responses to Water Stress

As might be expected in a tropical dry forest where water is an important determinant of plant success, research on the early stages of development of deciduous species has found that seed germination is highest and seedling mortality lowest during the rainy season (Ceccon et al. 2004). Tamayo-Chim et al. (2012) looked at the effect of drought on seedlings of four legume species and one non-legume over a 2-month period. They found that all species showed detrimental effects of drought (in the form of reduced stem diameter, plant height, leaf area, and biomass), but the

Table 5.1 Select physiological and morphological traits for the most studied tree species of Yucatán



Species	Family	Wood density[1, 2, 3, 4, 5] (gr cm^{-3})	Growth Rings[6]	Midday Water potential[3, 6] (Mpa)	Phenology	$\delta^{18}O$[7, 8] (‰)	$\delta^{13}C$[7, 8] (‰)	Root abundance[9] (m)	Sap flow[1] (kg d^{-1})	Specific Leaf area[3, 10] (cm^2 gr^{-1})	annual growth DBH (cm)[4]
Manilkara zapota (L.) Royen	Sapotaceae	0.9	SV		E						
Thouinia paucidentata Radlk.	Sapindaceae	0.9	V		D				14		
Talisia oliviformis (Kunth) Radlk.	Sapindaceae	0.84	V		E	-2.8	-28.7				1
Brosimum alicastrum Sw.	Moraceae	0.82	SV		E	-2.1	-28.6				1
Apoplanesia paniculata Presl	Fabaceae	0.8	SV	-3.7	D				5	119	
Acacia gaumeri Blake	Fabaceae	0.78	V	-3.8	D					131	
Lysiloma latisiliquum (L.) Benth.	Fabaceae	0.78	V		D			< 2.5	16	130	
Caesalpinia gaumeri Greenm.	Fabaceae	0.74	V		D			< 2.5	12		
Caesalpinia yucatanensis Greenm.	Fabaceae	0.69	V		D						
Lonchocarpus xuul Lundell	Fabaceae	0.74	SV		D						
Chlorophora tinctoria (L.) Gaudich. ex Benth.	Moraceae	0.71	SV		E						
Piscidia piscipula (L.) Sarg.	Fabaceae	0.71	V	-4	D	-2.5	-27.4	< 2.5	8	190	3.75
Pithecellobium dulce (Roxb.) Benth.	Fabaceae	0.71	SV		D						
Mimosa bahamensis Benth.	Fabaceae	0.71	V		D						
Karwinskia humboldtiana (Schult.) Zucc.	Rhamnaceae	0.7	SV		D				3		
Malpighia glabra L.	Malpighiaceae	0.7	V		D						
Randia obcordata Watson	Rubiaceae	0.7	V		D				2		
Albizia tomentosa (Micheli) Standl.	Fabaceae	0.69	V		D						
Gymnopodium floribundum Rolfe	Polygonaceae	0.69	V	-3.4	D	-1.5	-26.9	< 2.5	6	140	
Leucaena leucocephala (Lam.) de Wit.	Fabaceae	0.69	V		D					190	3.25
Ehretia tinifolia L.	Boraginacea	0.68	SV		E						2.75
Cordia dodecandra A. DC.	Boraginacea	0.67	V		D	-1	-27.5				3.75
Thouinia paucidentata Radlk.	Sapindaceae	0.67	V		D				14		
Diospyros cuneata Standl.	Ebenaceae	0.64		-2.6	E			< 2.5	2	73	2.75
Guazuma ulmifolia Lam.	Malvaceae	0.63	V		D					150	3
Senna racemosa (Mill.) Irwin & Barneby	Fabaceae	0.62	SV		D				7		3
Guettarda elliptica Sw.	Rubiaceae	0.58	V		D				3		
Trichilia hirta L.	Meliaceae	0.58	V		D						
Vitex gaumeri Greenm.	Lamiaceae	0.56	V		D						
Capparis incana Kunth	Capparaceae	0.54	SV		D						
Cedrela odorata L.	Meliaceae	0.44	V		D		-25.5				
Enterolobium cyclocarpum (Jacq.)	Fabaceae	0.39	SV		D	-2.7	-25.3				
Spondias purpurea L.	Anacardiaceae	0.37	SV		D	-1	-26.5				
Ficus benjamina L.	Moraceae	0.36	I		E						
Ficus cotinifolia Kunth	Moraceae	0.36	I		E	-0.8	-27.2				
Bursera simaruba (L.) Sarg.	Burseraceae	0.31	SV	-0.9	D			< 2.5 and > 5	32	127	4.5
Erythrina standleyana Krukoff	Fabaceae	0.23	I		D						

Species are listed from higher (dark grey) to lower (light grey) wood density. Letters under growth rings indicate level of visibility of growth rings for a given species, with "V" indicating clearly visible and distinguishable growth rings; "SV" indicating growth rings were semi-visible, or present but not easily distinguished; and "I" indicating growth rings were indistinguishable. Leaf phenology: "D" for deciduous and "E" evergreen. The numbers in superscripts indicate the source of the data [1]Reyes-García et al. (2012a), [2]Chan-Dzul (2010), [3]Valdez-Hernández et al. (2010), [4]Palomo-Kumul (2013), [5]Valdez-Hernández (unpublished data), [6]Roig et al. (2005), [7]Estrada-Medina et al. (2013b), [8]Querejeta et al. (2007), [9]Estrada-Medina et al. (2013), [10]Tamayo-Chim et al. (2012), [11]Reyes-García et al. (unpublished data)

extent of the effect on the seedlings and the extent of water limitation that triggered a response differed among species. The legume species (*Albizia lebbeck*, *Leucaena leucocephala*, *Piscidia piscipula*, and *Lysiloma latisiliquum*) displayed higher drought resistance compared to the non-legume species included in the study (*Guazuma ulmifolia*, Malvaceae). A different study, also looked at responses to water stress with deciduous species, including *L. leucocephala, P. piscipula,* and *Cordia dodecandra*, but determined the effect of water stress at the time the seedlings showed the first signs of wilt, such that the duration of each treatment differed among species, and no effect on growth (height, root length and biomass) or on water-use efficiency (ratio of carbon gained to water loss, Lambers et al. 1998) was found (Luna-Flores et al. 2012). The main effects of water stress in all three species were related to the water status of the plants, which under stress presented lower water potentials (20 % more negative), low evapotranspiration, low relative water content, and for legumes, lower leaf areas (Luna-Flores et al. 2012). Studies on the effect of drought on seedlings of evergreen species appear scarce and were not found in the literature.

In the Yucatán Peninsula, nutrient and water limitation interact with each other in several ways. For example, in moist soils, seed germination and seedling establishment are limited by nutrient availability: mainly phosphorous (P), potassium (K), nitrogen (N) and manganese (Mn); and in dry soils, certain nutrients (mostly P) may be more limiting than others (des Grades 2006). It has been found that seedlings of deciduous trees such as *Piscidia piscipula*, *Lysiloma latisiliquum*, *Phyllostylon brasiliense* and *Bursera simaruba* have higher growth and survival rates with the addition of P and N (Salinas-Peba et al. 2013; Ceccon et al. 2004). The effect of nutrient addition (N and P) however, may differ depending on forest age, with the addition of N aiding seedling density in younger forests (~10 years), and addition of P decreasing diversity in older forest stands (~60 years, Ceccon et al. 2004).

Re-sprouting is also important to regeneration. Trees capable of basal re-sprouting or of producing suckers are abundant throughout the Yucatán Peninsula. Furthermore, although in the understory of the dry forest areas regeneration through seeds appears to be more prevalent (Ceccon et al. 2004), seedlings regenerated through sprouts appear to survive longer than those regenerated from seed. Given the high incidence of disturbance, this mode of regeneration appears to be a faster and more successful mechanism (in terms of either establishing or maintaining a presence) in the peninsula (Valdez-Hernández et al. 2014).

Wood density can be one of the main indicators and predictors of physiology in tropical trees (Borchert 1994). Valdez-Hernández et al. (2010) found that based on wood density and phenology trees could be placed into three functional groups: deciduous hardwood, deciduous softwood, or leaf-exchanging species. They also found that proximity to an underground water source (*cenote*) could affect species differently depending on the functional group. For example, in deciduous hardwood species (*Acacia gaumeri* and *Apoplanesia paniculata*) the timing of leaf abscission differed among trees growing close (water table at ca. 2 m depth) or far (water table at ca. 10 m depth) from the *cenote*, with individuals retaining their leaves longer at sites near the *cenote*. In contrast, for the leaf- exchanging species (*Gymnopodium floribundum* and *Diospyros cuneata*), distance to the *cenote* did not seem to have a major effect on leaf production and leaf fall, but did influence the production of reproductive structures. Leaf-exchanging species had a higher proportion of flower and fruit production near the *cenote*. For the three functional groups, differences in nutrient availability (higher phosphorous at the site near the *cenote*) may have interacted with water availability in its effect on phenology. Valdez-Hernández et al. (2010) also found that functional groups differed in their water storage capacity and their minimum water potentials. Deciduous hardwood species tolerated lower leaf water potentials (less than −3.0 MPa) compared to the other two groups (deciduous softwood and leaf exchanging species); whereas deciduous softwood species (*Bursera simaruba*) presented high leaf water potentials (0 to −1 MPa), and had the capacity to store water in their stems. This water storage capacity allowed deciduous softwood trees to flower during the dry season (February–April) and produce fruit and seed in the more favorable rainy season. The leaf-exchanging species had leaf water potentials below −2.0 MPa, exhibited a high percent of leaf loss during the dry season (50–70 %) and a fast recovery with rainfall (Valdez-Hernández et al. 2010).

Studies in different parts of northern Yucatán have used isotopic signatures (in the dry season) to identify the source of water used by tree species. These studies have found a diversity of patterns of soil water use that do not appear to conform to patterns of leaf phenology. For example, evergreen species (*Brosimum alicastrum* and *Talisia oliviformis*) and the deciduous species (*Enterolobium cyclocarpum*) appeared to access water stored to depths of within 0.5–3 m of the soil-bedrock profile (Querejeta et al. 2006, 2007). However, for other evergreen species (*Ficus cotinifolia*) and deciduous species (*Cordia dodecandra* and *Spondias purpurea*) water uptake during the dry season appeared to be largely restricted to the upper soil layers (to ~20 cm deep; Querejeta et al. 2007). This shows a distribution of soil water uptake that may decrease interspecific competition. Partitioning of soil water resources has also been found in the savanna ecosystems of Brazil (Jackson et al. 1999) and used to explain maintenance of high species diversity in those ecosystems. Other deciduous species of Yucatán (e.g. *B. simaruba* and *Neomillspaughia emarginata*) were found to distribute their roots in three layers of the soil-bedrock profile (from shallow to deep: *laja*, *sascab* and *coquina*). More than 20 % of their roots reached more than 5 m deep, thus ensuring access to more reliable water sources (Estrada-Medina et al. 2013). The distribution of roots may change with season, as in the dry season the amount of roots in the *sascab* layer (2.5–5.0 m) increases, whereas in the rainy season many roots occur in the *laja* layer (0.3–2.5 m; Estrada-Medina et al. 2013). Also, differential biomass allocation to roots and stems across the peninsula follows the precipitation gradient, with plants showing a higher biomass allocation to stems in areas with higher water availability (Estrada-Medina et al. 2013). However, biomass allocation to roots does not seem to proportionally follow the stem allocation pattern with water gradient, suggesting a greater overall allocation to stem biomass in the seasonally dry tropical forests of Yucatán (Roa-Fuentes et al. 2012).

In addition to leaf loss and the use of different water sources, trees of the Yucatán present a series of other mechanisms to deal with the low water availability and high temperatures of the area. Dominant species, such as those in the legume family, typically have compound leaves with small leaf areas that lose heat quickly through convection; leaves frequently can modify their angle through pulvini. In general, these species present a low ratio of leaf area to total plant biomass (Tamayo-Chim et al. 2012), fast growth, high water use efficiency, and mainly early-seral stage colonization (Hasselquist et al. 2010a; Reyes-García et al. 2012a; Estrada-Medina et al. 2013).

Reyes-García et al. (2012a) studying sap flow in trees, found potential water conservation in legume trees through the development of heartwood in stems greater than 5 cm DBH. In that study, smaller legumes did not present notable heartwood, and volume of water moved was similar to that of other trees of similar diameter. Presence of heartwood in larger trees however, brought about notable differences, with large legumes utilizing less water compared to trees of similar diameter in other species. This apparent development of heartwood could be a potential mechanism that legumes use to add to their success in tropical dry forests.

5.2.2 Tree Growth Rings

The study of growth rings may contribute to understanding the effect environmental stressors have on the physiological response of a given tree, and to reconstruct the environment under which the tree grew and the rings were formed (Roig et al. 2005). In the Yucatán Peninsula, out of 52 tree species characterized, 35 % presented growth rings that could be clearly distinguished. In 52 % of the species growth rings could be identified with some difficulty, and only in 13 % of the species were growth rings not visible (Roig et al. 2005).

The presence of growth rings appears to be related to wood density (Fig. 5.2), with rings more clearly distinguished in trees with higher wood density (wood density > 0.6 g cm^{-3}; $p < 0.05$). For example, the evergreen species *Talisia oliviformis* and *Brosimum alicastrum* that have high wood density (~0.8 g cm^{-3}) present well defined growth rings. In deciduous species such as *Cedrela odorata* and *Bursera simaruba* that have lower wood density (~0.4 g cm^{-3}) growth rings, although identifiable, were not as clearly visible. In the evergreen species *Erythrina standleyana* and *Ficus cotinifolia*, which have still lower wood density (<0.3 g cm^{-3}), growth rings were not visible. So, in addition to seasonality of rainfall, the formation of clearly defined growth rings for tropical tree species may depend on additional factors, many of which are interrelated. Tree wood density has been found to be related to the water status of a plant (Borchert 1994), which is also related to leaf flush and leaf fall. Furthermore, the timing of leaf production and loss will affect whether a tree exhibits continual or seasonal growth, since the presence of leaves in the dry season generates the continuous activity of meristematic tissue (Roig et al. 2005), and hence will influence the presence of growth rings.

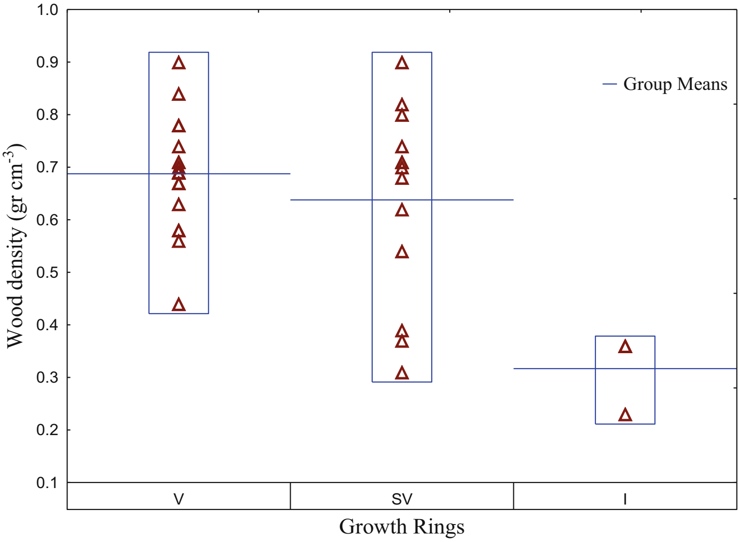


Fig. 5.2 Relationship of growth rings and wood density for 36 tree species found in the Yucatán Peninsula. *Letters* under growth rings indicate level of visibility of growth rings for a given species: "V" indicating clearly visible and distinguishable growth rings, "SV" indicates growth rings were semi-visible or present but not easily distinguished, and "I" indicates that growth rings were indistinguishable. Growth ring data were obtained from Roig et al. (2005) and wood density was obtained from Chán-Dzul (2010), Valdez-Hernández et al. (2010), Palomo-Kumul (2013) and Valdez-Hernández (unpublished data)

5.2.3 Climate Change and Disturbances

Climate change predictions include a potential increase in the frequency and or severity of hurricanes (IPCC 2013). In general, recovery of aboveground forest structure after hurricane disturbance is expected to be relatively fast (Chazdon 2003), but because the Yucatán Peninsula is also subject to frequent fires and other disturbances, the ability of a given site to recover after a hurricane may differ depending on the history of the site (Hasselquist et al. 2010a, b; Vargas et al. 2010). Hasselquist et al. (2010b), studying the response to a large hurricane disturbance in Yucatán at forest sites that differed in time since a fire, found that early and mid-stage seral sites appeared to be more resilient to the hurricane disturbance when compared to the more advanced seral stages. They also found that below-ground processes (fine root density, colonization of arbuscular mycorrhizae (AM) and ectomycorrhizae, and soil nitrogen availability) had the potential to exert strong feedback influences on above ground processes (Hasselquist et al. 2010b). Vargas et al. (2010) also found below ground effects after a hurricane. In that study, the effects after a hurricane differed among thinned and control plots, with both plots exhibiting lower frequency of spore production by AM fungi and increased AM root colonization, which was comparatively greater in the thinned plots than the control plots.

Hurricane frequency and severity can also have an effect on carbon pools both below and aboveground, with large soil carbon discharges reported following hurricane Wilma, where soil CO_2 flux was 18 % higher 1 year after the hurricane (Vargas and Allen 2008). Also, 1 year post-hurricane gross primary productivity was reduced by approximately 15 %, although the pre-hurricane values were reset after 2 years (Vargas 2012). Following a severe disturbance like a hurricane, trees of the region have the capacity to re-mobilize older reserves of carbon for the production of fine roots; an ability that increases with age, size, and volume of the tree (Vargas et al. 2009). In the Yucatán Peninsula, however, the apparent higher biomass allocation to stems together with the higher vulnerability of aboveground biomass to disturbances (Roa-Fuentes et al. 2012) may mean that these forests face greater potential vulnerability to carbon loss.

In addition to the effect of climate change on hurricane frequency and precipitation; changes in the carbon (C), nitrogen (N) and phosphorus (P) cycles are also expected. For tropical forests in general, increases in temperature are expected to stimulate the activity of soil microorganisms (Powers et al. 2009), causing an increased flow of C and N, high CO_2 emissions, and lower net primary productivity (Saxe et al. 2001). Studies that have analyzed the effect of CO_2 and nitrogen fertilization in this region have shown that the ecosystem level response to these treatments can be highly variable. In native palms, under controlled conditions of CO_2 (360 ppm and 750 ppm), CO_2 assimilation, plant growth, and the amount of pigments produced, did not show differences between CO_2 levels (Orellana et al. 2011). Also studies on litter decomposition in *Gymnopodium floribundum* and *Piscidia piscipula* under two scenarios of increased nitrogen deposition found that in moist sites with N enrichment, litter decomposition of *G. floribundum* increased, whereas litter decomposition of *P. piscipula* decreased. Dry sites showed no significant effect of N enrichment on decomposition rates (Bejarano-Castillo 2012).

5.3 CAM Species

Crassulacean acid metabolism (CAM) is an adaptation that some plants have to concentrate carbon dioxide within their cells (Cushman 2001; Dodd et al. 2002; Lüttge 2004). It is common in plants living in environments with long periods without water, but also exists in aquatic plants that inhabit places where CO_2 becomes scarce during the day (Keeley and Rundel 2003). Also, because in non-aquatic species the CO_2 assimilation of CAM occurs at night, when air temperature is lower and relative humidity is higher than during the day, it allows less water loss by transpiration and permits high water use efficiency. In fact, CAM plants have greater water use efficiency than C_3 and C_4 plants under similar conditions (Drennan and Nobel 2000; Winter et al. 2005). Consequently, CAM plants are distinctive of arid and semiarid regions and of forest canopies, as epiphytes, and represent about 6 % of vascular plant species (Winter and Smith 1996).

In the Yucatán Peninsula CAM plants are distributed according to the precipitation gradient which, as mentioned previously, increases from north to south. In the north, with short-statured communities such as dunes and dry deciduous forests, terrestrial CAM plants dominate (Ricalde et al. 2013). In the south, where taller forests exist, CAM plants are predominantly epiphytes or hemiepipytes. In fact, in the northern area, large plantations of a CAM plant, *Agave fourcroydes* (henequen) from which fiber was extracted, constituted the main economic activity of the peninsula for a century (1880s–1970s; García-Quintanilla 1986). These plantations had a large ecological impact on local vegetation, as large areas of forest were destroyed for their creation (González-Iturbe et al. 2002).

This section will focus on CAM plants and the environmental factors that affect their performance. Specifically, their responses to water availability, light, and temperature, will be considered, but also their response to some of the ecological factors that affect their microhabitats such as, deciduousness of host trees, and the distribution of neighbors. Table 5.2 summarizes all physiological studies done for the CAM species of the Yucatán Peninsula.

5.3.1 CAM Terrestrial Species

5.3.1.1 Water Relations

Terrestrial CAM plants have massive succulent stems or leaves that store substantial amounts of water, so negligible changes in photosynthesis occur in these plants during the first days of drought. Specialized storage tissues and the high water use efficiency of the CAM cycle allow continuous CO_2 uptake, since water can be transported from storage tissues to maintain turgor in the photosynthetic tissues (Barcikowski and Nobel 1984; Goldstein et al. 1991; Lüttge 2004; Andrade et al. 2009). Indeed, average relative capacitance, which is the capacity of the tissues to maintain their water potentials when the water content decreases, is more than two times higher for terrestrial CAM plants than that of epiphytic CAM species (Andrade et al. 2009).

In terrestrial Bromeliaceae (a family with many CAM species), plant size, tissue relative capacitance, leaf anatomy, and clonal reproduction all confer drought resistance. For instance, *Bromelia karatas*, which does not have a high organic acid production (González-Salvatierra et al. 2013), is ecologically one of the most important species in dry deciduous forests (Ricalde et al. 2013). Additionally, about half of the plants of the large epiphyte *Aechmea bracteata*, also a bromeliad, live and reproduce on the soil in a dry deciduous forest (Chávez-Sahagún 2014). Yet, the small volume to surface area ratio of terrestrial CAM seedlings makes them too vulnerable to drought and most of them die when the dry season starts (Nobel

Table 5.2 Published physiological studies on CAM terrestrial and epiphytic plants from the Yucatán Peninsula

Species	Family	Physiological responses studied	Reference
Terrestrial CAM			
Agave angustifolia Haw.	Agavaceae	Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
		Growth and water relations	Ricalde-Pérez (2010)
Bromelia karatas L.	Bromeliaceae	Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
		Photoprotective mechanisms	González-Salvatierra et al. (2010)
		Water relations, photosynthesis and leaf morphology	González-Salvatierra et al. (2013)
Acanthocereus tetragonus (L.) Hummelinck	Cactaceae	Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
Hylocereus undatus (Haworth) Britton & Rose		Photosynthesis, growth and establishment	Andrade et al. (2006)
Mammillaria gaumeri (Britton & Rose) Orcutt		Germination and establishment	Cervera et al. (2006)
		Photosynthesis and growth	Cervera et al. (2007)
		Pollinators	Giovanetti et al. (2007)
Nopalea inaperta Schott ex Griffiths		Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
Opuntia dillenii (Ker Gawl.) Haw.		Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
Pereskiopsis scandens Britton & Rose		Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
Pilosocereus gaumeri (Britton & Rose) Backeb.		Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
Selenicereus donkelaarii (Salm-Dyck) Britton & Rose		Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
Stenocereus eichlamii (Britton & Rose) Buxb		Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
Clusia chanekiana Lundell	Clusiaceae	Type of photosynthesis	Vargas-Soto et al. (2009) Vargas-Soto (2010)
Clusia guatemalensis Hemsl.		Type of photosynthesis	Vargas-Soto et al. (2009) Vargas-Soto (2010)

(continued)

Table 5.2 (continued)

Species	Family	Physiological responses studied	Reference
Clusia flava Jacq.		Type of photosynthesis	Vargas-Soto et al. (2009)
		Photosynthesis of seedlings in a common garden	Vargas-Soto (2010)
Clusia rosea Jacq.		Type of photosynthesis	Vargas-Soto et al. (2009)
		Photosynthesis of seedlings in a common garden	Vargas-Soto (2010)
Epiphytic CAM			
Tillandsia balbisiana Schult & Schult F.	Bromeliaceae	Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
		Light stratification	Chilpa-Galván et al. (2013)
		Seasonal C assimilation (stable isotopic composition)	Goodeet al. (2010)
		Distribution across occupied phorophytes	Zimmerman and Olmsted (1992)
Aechmea bracteata (Sw.) Griseb		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
		Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
		Light stratification	Chilpa-Galván et al. (2013)
		Photosynthesis and water relations in two microenvironments	Chávez-Sahagún (2014)
		Light stratification	Zimmerman and Olmsted (1992)
Tillandsia brachycaulos Schltdl.		Plant characteristics and water relations	Andrade (2003)
		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
		Light microhabitats, growth and photosynthesis	Cervantes et al. (2005)
		Light stratification	Chilpa-Galván et al. (2013)
		Photoprotective mechanisms and photosynthesis	González-Salvatierra (2009)
		Photoprotective mechanisms	González-Salvatierra et al. (2010)

(continued)

Table 5.2 (continued)

Species	Family	Physiological responses studied	Reference
		Seasonal C assimilation (stable isotopic composition)	Goode et al. (2010)
		Stratification for photoprotective mechanisms and drought tolerance	Graham and Andrade (2004)
Tillandsia dasyliriifolia Baker		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
		Seasonal C assimilation (stable isotopic composition)	Goode et al. (2010)
		Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
		Light stratification	Zimmerman and Olmsted (1992)
Tillandsia elongata Kunth var. subimbricata (Baker) L. B. Sm.		Plant characteristics and water relations	Andrade (2003)
		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
		Light stratification	Chilpa-Galván et al. (2013)
Tillandsia fasciculata Sw.		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
		Light stratification	Chilpa-Galván et al. (2013)
		Seasonal C assimilation (stable isotopiccomposition)	Goode et al. (2010)
Tillandsia juncea (Ruiz and Pav.) Poir.		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
Tillandsia polystachia (L.) L.		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
Tillandsia pseudobaileyi CS Gardner		Light stratification	Zimmerman and Olmsted (1992)
Tillandsia recurvata (L.) L.		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
		Light stratification	Chilpa-Galván et al. (2013)

(continued)

Table 5.2 (continued)

Species	Family	Physiological responses studied	Reference
Tillandsia schiedeana Steud.		Light stratification	Chilpa-Galván et al. (2013)
		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
Tillandsia streptophylla Scheidw.		Light stratification	Zimmerman and Olmsted (1992)
Tillandsia usneoides (L.) L.		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
Tillandsia utriculata L.		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
Tillandsia variabilis Schltdl.		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
Tillandsia yucatana Baker		Distribution gradients related to seasonal microclimates	Cach-Pérez et al. (2013)
		Light stratification	Chilpa-Galván et al. (2013)
Brassavola nodosa (L.) Lindl.	Orchidaceae	Light stratification	Zimmerman and Olmsted (1992)
Catasetum integerrimum Hook.		Light stratification	Zimmerman and Olmsted (1992)
Cohniella ascendens (Lindley) Christenson		Drought responses	de la Rosa et al. (2014b)
		Vertical distribution in microclimatic conditions	de la Rosa et al. (2014a)
Cohniella yucatanensis Cetzal and Carnevali		Drought responses	de la Rosa et al. (2014b)
		Vertical distribution in microclimatic conditions	de la Rosa et al. (2014a)
Encyclia alata (Bateman) Schltr.		Climate change	Goode and Allen (2008)
Encyclia belizensis (Reich. f.) Schlechter		Light stratification	Zimmerman and Olmsted (1992)
Encyclia boothiana (Lindl.) Luer		Light stratification	Zimmerman and Olmsted (1992)
Encyclia nematocaulon (BC Rich.) Acuña		Drought responses	de la Rosa et al. (2014b)
		Vertical distribution in microclimatic conditions	de la Rosa et al. (2014a)

(continued)

Table 5.2 (continued)

Species	Family	Physiological responses studied	Reference
Laelia rubescens Lindley		Drought responses	de la Rosa et al. (2014b)
		Vertical distribution in microclimatic conditions	de la Rosa et al. (2014a)
Lophiaris oerstedii (Rchb. f.) A. Jimenez, Carnevali and Dressler		Drought responses	de la Rosa et al. (2014b)
		Vertical distribution in microclimatic conditions	de la Rosa et al. (2014a)
Myrmecophila christinae Carnevali & Gómez-Juárez		Photosynthesis over a rainfall gradient	Ricalde et al. (2013)
Polystachya cerea Lindl.		Light stratification	Zimmerman and Olmsted (1992)
Rhyncholaelia digbyana (Lindl.) Schlechter		Light stratification	Zimmerman and Olmsted (1992)
Schomburgkia tibicinis (Batem.) Batem		Light stratification	Zimmerman and Olmsted (1992)

1988). Consequently, for seedlings of terrestrial CAM plants, there is a higher probability of survival under the canopy of nurse plants (Esparza-Olguín et al. 2002; Flores et al. 2004; Cervera et al. 2006). For instance, seedlings of the rare cactus *Mammilaria gaumeri* growing in a coastal sand dune of northern Yucatán show a two-fold higher volume to surface area ratio when they are growing under the canopy of a local shrub than when they grow receiving 50 % of ambient light (Cervera et al. 2006).

5.3.1.2 Water and CO_2 Uptake

Although CAM photosynthesis can occur during drought, there is a substantial difference in the amount of carbon fixed when compared to the photosynthesis that occurs when water is available. Studies in the Yucatán Peninsula reveal that the greatest tissue acid accumulation (a proxy for CO_2 uptake) of terrestrial CAM plants occurs during the rainy season (Andrade et al. 2006; Cervera et al. 2007; Ricalde et al. 2013; Vargas-Soto 2010; González-Salvatierra et al. 2013; Chávez-Sahagún 2014), when there are lower air temperatures and vapor pressure deficits than during the rest of the year.

Also, because the enzyme that fixes CO_2 at night in CAM plants, phosphoenolpyruvate carboxylase (PEPc), does not discriminate against $^{13}CO_2$ whereas the one that fixes carbon during the day, ribulose bisphosphate carboxylase (RuBisCO), does and favors ^{12}C fixation, investigations of carbon isotopic composition ($\delta^{13}C$) can provide information on the proportion of CO_2 fixed during the night or day (Griffiths 1992). Terrestrial CAM species from northern Yucatán show $\delta^{13}C$ values between −15 and −20 ‰, which indicates strong CAM performance (Ricalde et al. 2013). CAM plants with CO_2 uptake exclusively at night, by PEPc, would be expected to have $\delta^{13}C$ values around −11 ‰ (close to atmospheric values), whereas if all CO_2 is fixed by RuBisCO the values of $\delta^{13}C$ would be approximately −27 ‰ (O'Leary 1988). In northern Yucatán Peninsula, tissue $\delta^{13}C$ values for terrestrial CAM plants of the coastal dunes are 2 ‰ higher than CAM plants from the dry tropical deciduous forests (Ricalde et al. 2013), indicating greater CO_2 fixation through the CAM pathway with decreasing water availability.

One group of plants that shows an interesting array of growth forms and physiological plasticity is the genus *Clusia*, with species exhibiting C_3, C_3/CAM and CAM pathways (Winter and Smith 1996; Winter et al. 2005; Lüttge 2006). In Mexico, there is a preponderance of C_3/CAM *Clusia* species, but in the Yucatán Peninsula the majority of the genus have CAM metabolism (five out of six species, Vargas-Soto et al. 2009). *Clusia rosea* is the only C_3/CAM species found in the peninsula that can change from C_3 to CAM as drought progresses, even at the seedling stage (Vargas-Soto 2010).

5.3.1.3 Plant Responses to Light and Temperature

Depending on their habitat, CAM plants in the Yucatán Peninsula may experience large changes in light environment in different seasons (Graham and Andrade 2004; Cervantes et al. 2005). In dry forests, most of the trees lose their leaves during the dry season, and understory plants may receive up to nine times more light than in the wet season (Graham and Andrade 2004). However, even in the evergreen canopies, changes between seasons, cloud cover, and sunflecks create a highly variable light environment. The physiological adaptations of CAM plants, particularly the ability to tolerate water and light stress, are decisive in their distribution (Graham and Andrade 2004; Reyes-García et al. 2012b). Because physiological responses to these parameters are correlated, it is very difficult to independently analyze the effects of water availability, light, and temperature on CAM plants.

A combination of lack of water and high temperatures can affect growth and reproduction of CAM plants (Andrade et al. 2009). The optimal diurnal/nocturnal temperature for CO_2 uptake of two co-occurring species in the seasonal dry forest of Yucatán, *Agave fourcroydes* and *Hylocereus undatus*, are 30/20 °C (Nobel 1985; Nobel and de la Barrera 2002). Temperatures above or below the optimal, especially nocturnal ones, reduce growth and reproduction in CAM plants (Andrade et al. 2007).

For the commercial hemiepiphytic cactus *H. undatus*, growth is reduced when young plants are exposed or deeply shaded (Andrade et al. 2006). Also, seedlings of the rare cactus *Mammillaria gaumeri* cannot survive under more than 20 % of ambient light, but adults increase growth under 40–80 % of ambient light, indicating that low-magnitude disturbances can be beneficial for populations of this species (Cervera et al. 2006, 2007). However, large disturbances that increase light can be harmful for CAM terrestrial plants. For instance, tissues of

H. undatus and *M. gaumeri* cannot tolerate temperatures above 50 °C (Nobel and de la Barrera 2002; Cervera et al. 2006). Exposure to high temperatures increases respiratory rates and plant tissues must invest photosynthetic products to repair the photosynthetic apparatus from photoinhibitory damage, which leads to lower investment against pathogens and predators (Andrade et al. 2009).

5.3.2 CAM Epiphytic Species

5.3.2.1 Water Relations

Epiphytes represent a main group of interest for ecophysiological studies in the Yucatán Peninsula. Because the epiphytes are disconnected from the stored moisture in the ground and must obtain water during precipitation pulses the epiphytic habitat in itself is water limited. Nutrients are also obtained mainly by precipitation, yet water has been reported as the main limiting factor for epiphyte growth (Laube and Zotz 2003).

In the water limited habitats of Yucatán, vascular epiphytes are not as diverse or important in number or in biomass as in the wet forests. Nevertheless, the species show interesting adaptations to deal with the lack of water, excess light, and high temperatures. Studies have focused on the families Bromeliaceae and Orchidaceae, and have found the prevalence of CAM photosynthesis, which is an important water saving mechanism, with only one Bromeliaceae species using C_3 photosynthesis (*Catopsis nutans*, Benzing and Renfrow 1971). This species is found in the wetter, southern region of the peninsula (Cach-Pérez et al. 2013). The isotopic signature of carbon ($\delta^{13}C$) shown in the species of Yucatán denote tight diurnal stomatal closure and the predominance of carbon fixed in the night by the enzyme PEPc (see Sect. 5.3.1.2), as compared to epiphytic CAM species from Trinidad (Griffiths and Smith 1983), distributed over a larger precipitation gradient that may show higher fluctuation in $\delta^{13}C$ values (Fig. 5.3). This low variation in carbon isotope signatures is also evidenced in C_3 trees, which show relatively high $\delta^{13}C$ values, suggesting that RuBisCO is not able to fully discriminate against the heavier isotope, as stomatal closure to conserve water is frequent in the tree species, increasing $\delta^{13}C$ (Hasselquist et al. 2010a; Cach-Pérez 2013; Martin 1994; Fig. 5.3).

The CAM epiphytes exhibit a morphology and physiology modified to tolerate water scarcity and high light incidence (Benzing 1990; Zotz and Hietz 2001; Andrade 2003). Epiphytic bromeliads may store water in succulent tissues or in water-storing tanks, and may absorb water and nutrients through modified leaf trichomes (Reyes-García et al. 2012b). Leaves in bromeliads form a rosette, which, in the case of tank species, has wide leaf bases that form a water impounding reservoir (Fig. 5.4). Thus, the morphology of the leaves in 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. 2012b).

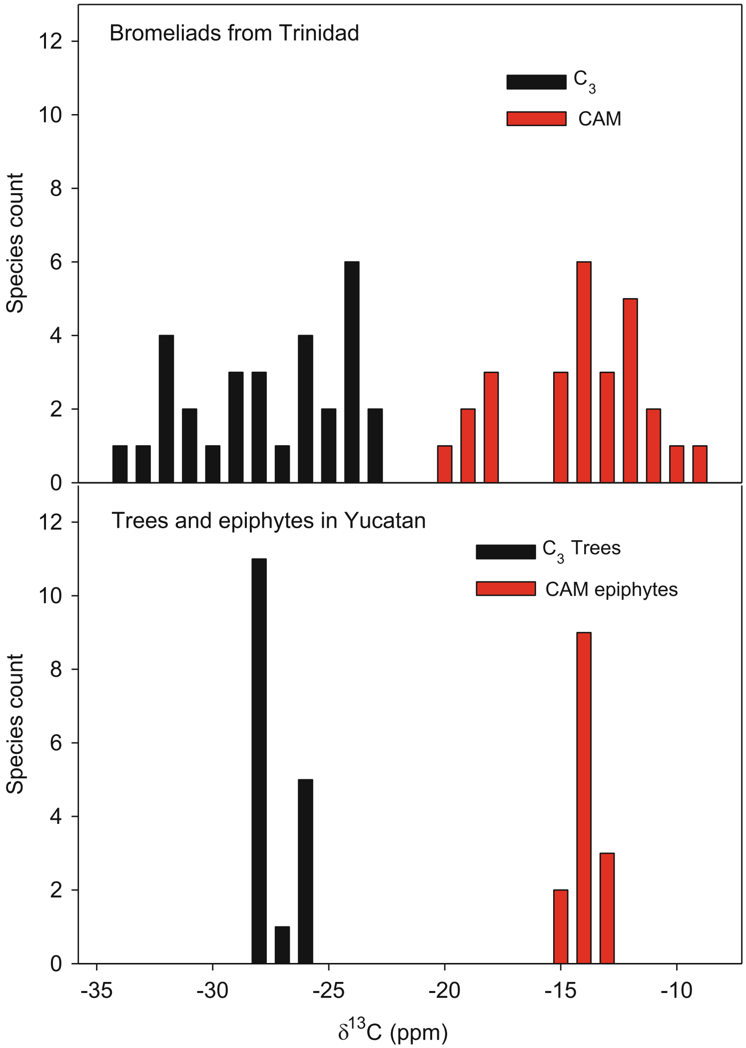


Fig. 5.3 Frequency values of the carbon isotopic signal of Bromeliads from Trinidad (*top panel*) growing in a precipitation gradient of 1000–3000 mm per year (Redrawn from Griffiths and Smith 1983) and C_3 trees and shrubs from Yucatán (*bottom panel*) in a precipitation gradient of 800–1650 mm per year and CAM epiphytic bromeliads in a gradient of 500–1500 mm per year (Hasselquist et al. 2010a, b; Cach-Pérez 2013). No isotopic data are available for *Catopsis nutans*, which is reported to be C_3 (Benzing and Renfrow 1971) and is present in the wetter southern edge of the peninsula (Cach-Pérez et al. 2013)

Alternatively, atmospheric bromeliads lack tanks (Pittendrigh 1948) and may either have succulent leaves or nebulophyte morphology. Nebulophytes are characterized by having very long and thin leaves that have a small boundary layer, allowing for the small fog droplets to be intercepted (Reyes-García et al. 2012b). In the southern region of the Yucatán, where fog formation is frequent, the bromeliad nebulophytes, *Tillandsia festucoides* and *Tillandsia juncea* are common (Cach-Pérez et al. 2013; Ramírez Morillo et al. 2004). The atmospheric *Tillandsia usneoides* shares this environment; this highly modified bromeliad has a tiny succulent stem, but clones of the same individual grow interlinked and can extend for meters and hang as a mesh from trees (Billings 1904), functioning as an effective fog trap.

The different morphologies described in the Bromeliaceae contribute to different interactions with the local microclimate. The more succulent species, which are less in number (representing both tank and atmospheric types), are present in the northern part of the peninsula, while the southern, wetter regions have more diverse epiphytic communities (Cach-Pérez et al. 2013). Life forms of the Orchideaceae have not been defined as well as for the Bromeliaceae, but the morphologies found in the Yucatán suggest a mixture of species that rely on succulence and nebulophytic forms (Fig. 5.4). Orchidaceae species also may show large water storage capacity in their stems or pseudobulbs and have specialized roots with the highly absorptive velamen (de la Rosa et al. 2014b). The lack of water during the prolonged dry seasons in the Yucatán Peninsula, induces partial or total stomatal closure in the evergreen epiphytes (Graham and Andrade 2004). Consequently the

Fig. 5.4 (**a**) *Aechmea bracteata* (bromeliad, tank species), (**b**) *Encyclia nematocaulon* (orchid nebulophyte), (**c**) *Tillandsia juncea* (bromeliad, nebulophyte atmospheric species), (**d**) *Cohniella yucatanensis* (orchid, succulent atmospheric). *Scale bar* shows 5 cm in all images (courtesy of E. de la Rosa, Centro de Investigación Científica de Yucatán, Mexico)

potential of photoinhibition is greatest in epiphytes that grow on more exposed sites or in the upper canopy strata (see Section on photoinhibition 5.3.2.2). The stress induced by reduced CO_2 uptake may be overcome in some CAM species by enhancing CO_2 release from organic acids during the hours of higher light incidence and by using recycled respired CO_2 for carbon fixation (Griffiths et al. 1986).

Thus, precipitation influences epiphytic species diversity, but the density of the individuals is inversely related to vapor pressure deficit (VPD, Cach-Pérez et al. 2013). At low values of VPD, the rate of water loss between rain events is diminished and there is a higher chance of dew condensation (Chilpa-Galván et al. 2013; de la Rosa et al. 2014a); low VPD also stimulates germination in epiphytic bromeliads (Goode and Allen 2009). In the Yucatán Peninsula, the water table depth may be very shallow at some locations, where trees will be able to tap the permanent water source and increase transpiration and tree leaf area, lowering VPD values locally, creating islands of increased epiphyte density (Chilpa-Galván et al. 2013).

5.3.2.2 Plant Responses to Light and Temperature

In general, studies have found that epiphytes show high plasticity in the use of light, but the differential physiological adaptations of each species will influence its distribution within the canopy strata. This is particularly true of the ability to endure water and light stress, which may vary in intensity from the top to the bottom of the canopy (Graham and Andrade 2004; Chilpa-Galván et al. 2013). In the dry forest in Yucatán, the vertical distribution of two epiphytic bromeliads, the atmospheric species *Tillandsia brachycaulos* and the tank species *Tillandsia elongata*, showed that the distribution of the tank species was limited to the top canopy because this environment provided higher precipitation interception and higher dew condensation, compared to the more sheltered lower canopy (Graham and Andrade 2004). Further studies indicated that for *T. brachycaulos* and other atmospheric species that have higher drought tolerance, excess light limits their distribution to the mid to lower canopy strata (Chilpa-Galván et al. 2013; Cervantes et al. 2005). Cervantes et al. (2005) found that individuals of *T. brachycaulos* under full sunlight had lower growth rates and less flower production than those under moderate shade.

During the dry season, concomitant with increased light incidence, as mentioned previously, drought causes stomatal closure preventing the entrance of the CO_2 supply for photosynthesis. Consequently, the potential for photoinhibition is greatest in epiphytes that grow on exposed branches, already receiving high amounts of light, under higher temperatures, and subject to the desiccating action of winds. The interaction of these factors results in a potential increase in photo-oxidative stress and a consequent decrease in the quantum efficiency of photosystem II (ΦPSII; see Fig. 5.5). To prevent long term damage to the photosynthetic apparatus, plants dissipate excess energy as heat (non-photochemical dissipation, NPQ) or re-emit it as electromagnetic radiation in a process known as chlorophyll

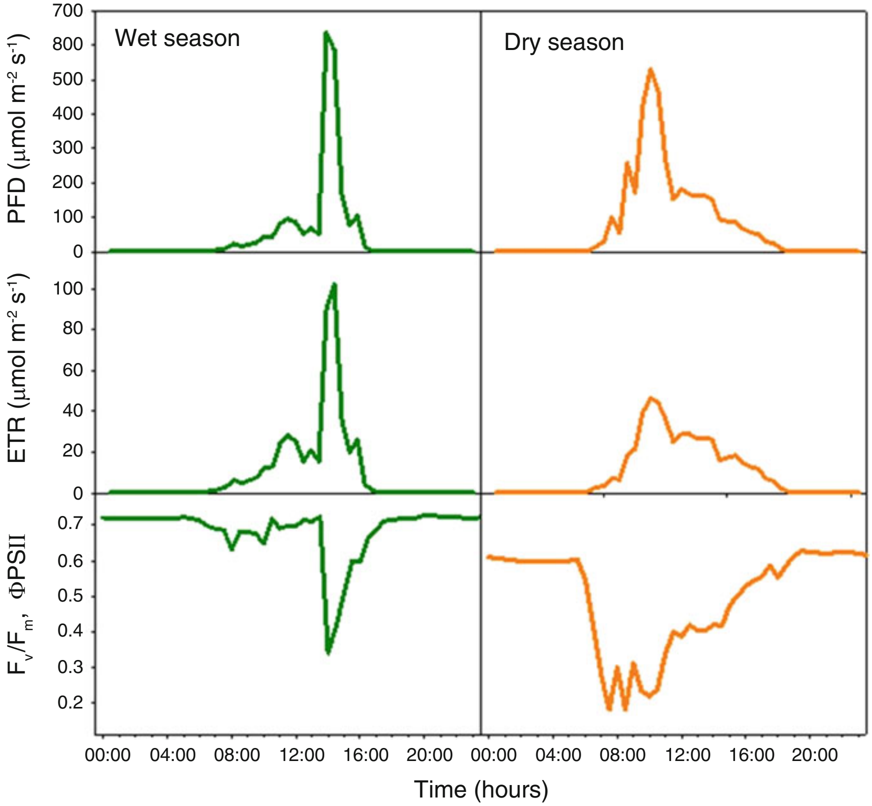


Fig. 5.5 *PFD* Photon flux density, *ETR* electron transport rate and maximum fluorescence (F_v/F_m, under dark conditions) or quantum yield (ΦPSII, in the presence of light) of *Tillandsia utriculata*, an epiphytic bromeliad in a coastal sand dune, during the rainy (*left panels*) and dry (*right panels*) seasons. Measurements were made every 20 m, for 24 h under natural conditions. *T. utriculata* is usually found in the shaded understory, which buffers seasonal changes in incident light. The species undergoes a 6 month dry season (A. Rosado-Calderón and C. Reyes-García, unpublished data)

fluorescence (Maxwell and Johnson 2000). It has been reported that epiphytes showing CAM prevent the production of the harmful reactive oxygen species, controlling photoinhibition and oxidative stress (Niewiadomska and Borland 2008). CAM is advantageous to cope with the desiccating conditions typical of the dry forest (Winter and Smith 1996), because daytime fixation of CO_2 by RuBisCo occurs with closed stomata. This causes high CO_2 concentrations in the cytosol and chloroplasts, favoring RuBisCo's carboxylation activity over its oxygenase activity, providing additional photoprotection through maintenance of electron transport and preventing damage to photosystems (Niewiadomska and Borland 2008).

Usually, excess photons are quickly dissipated as heat and fluorescence (Niyogi 2000), but when the absorption of light energy exceeds the capacity for photosynthesis and the photoprotection mechanisms have been oversaturated, photoinhibition occurs (Takahashi and Murata 2008). Photoinhibition has been defined as a decrease in the photosynthetic efficiency that results from excess light and leads to a partial loss of photochemical capacity and, consequently, diminished growth (Björkman and Demmig 1987; Long et al. 1994; Baker 2008). Therefore, every organism that conducts photosynthesis is potentially vulnerable to injury due to light influences, but the level of susceptibility depends on both environmental factors and physiological limits (Benzing 2000).

In the dry forest, epiphytes, already subjected to stress during the dry season, showed a decrease in photosynthetic efficiency, an increase in antioxidant compounds, and low values of maximum fluorescence (Fig. 5.6), which indicated photoinhibition due to over-excitation of photosystem II (PSII) (Fv/Fm ~0.6; Graham and Andrade 2004; Cervantes et al. 2005; González-Salvatierra et al. 2010). Among the mechanisms of defense against light stress, *T. brachycaulos* increased the production of flavonoids. The production of different types of flavonoids have been reported in a number of species of Bromeliaceae (Saito and Harborne 1983) as a response to high light and other stressful conditions (Benzing 2000). For *T. brachycaulos*, anthocyanins (a type of flavonoid) were located in a single layer under the epidermis on both leaf faces, with higher anthocyanin concentrations in exposed plants during the dry season, confirming their sunscreen role (González-Salvatierra et al. 2010). The strong correlation between incident daily high light and total anthocyanin content suggests that these molecules are involved in photoprotection as a part of a short-term defense to diminish light-derived reactions

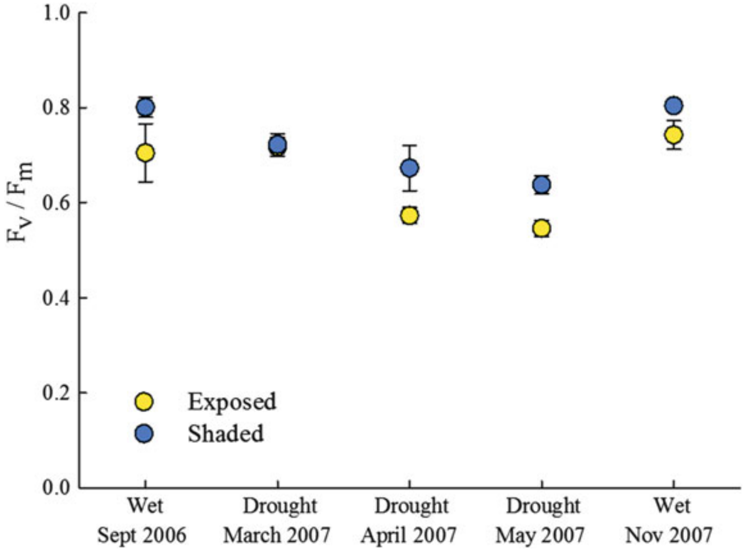


Fig. 5.6 Maximum fluorescence of photosystem II (F_v/F_m) of *T. brachycaulos* under exposed and shaded conditions during sunrise in the dry forest of Dzibilchaltún, Yucatán. Values are mean ± SE, n = 3 (A. Rosado-Calderón and C. Reyes-García, unpublished data)

and prevent the over-energization and over-reduction in the photosynthetic electron transport, protecting the photosynthetic apparatus from the effects of photoxidative stress (Gould et al. 2000; Steyn et al. 2002).

The orchids of the dry forests of Yucatán show similar distribution patterns to those found in bromeliads. In a study with orchids from two dry forests, de la Rosa et al. (2014a) show that species are more frequent in the mid-canopy stratum, and are rarely found in the lower stratum. Light measurements indicate that the lower stratum of the wettest forest received low light during the wet season (only ~2 % of incident total light), which may be too low to maintain photosynthetic rates in orchids (Ter Steege and Cornelissen 1989). Also, de la Rosa et al. (2014a) found that even though vertical canopy strata show environmental differences, the orchids had higher physiological variation between seasons than between strata. At the beginning of the dry season, the maximum quantum efficiency (F_v/F_m) of the orchids was close to the theoretical optimum (0.8–0.83; Björkman and Demmig 1987), indicating that the plants were not under environmental stress (Horton et al. 1996; Demmig-Adams et al. 2012). However, by the end of the dry season, when environmental conditions such as light, VPD and leaf temperature increased, most species show a decrease in photosynthetic activity, with values of F_v/F_m between 0.4 and 0.7 indicating moderate photoinhibition (de la Rosa et al. 2014a).

The high temperatures exhibited in the Yucatán Peninsula are another stress factor for the native epiphytic species. CAM photosynthesis should alleviate part of the stress, as the high CO_2 concentrations within the mesophyll abolish the temperature dependent process of photorespiration (Winter and Smith 1996). Yet, the metabolic sensitivity to temperature has not been directly studied. An example from the coastal sand dune scrub of the northern region of the peninsula shows the photoinhibition of the epiphyte *Tillandsia utriculata* in the dry season (Fig. 5.5; Rosado-Calderón and Reyes unpublished data). In this case, the epiphyte receives similar light in the dry and wet seasons, but photoinhibition results from the combination of water stress, as the relative water content has diminished from 80 % in the wet season to 40 % in the dry season, and from temperature stress, as maximum temperatures escalate from 23 °C in the wet season to 38.7 °C in the dry season. This results in a diminished day (ΦPSII) and night (F_v/F_m) quantum yield of PSII (Fig. 5.5) that lowers the electron transport rates during the day. Further studies are needed to separate the effects that temperature and water can have on the photosynthetic apparatus.

Studies have dealt with leaf heat dissipation, which is an important issue in CAM plants that cannot transpire to cool off during the day. There is a tradeoff between having large volumes of water storage tissue to survive during drought and reducing leaf area, which allows higher heat dissipation through convection by having a small boundary layer (de la Rosa 2014a). High leaf temperatures and excess light are avoided by the epiphytes of the Yucatán by limiting their distribution mostly to the more shaded mid-canopy stratum (Cach-Pérez et al. 2014). Conversely, in sites with highly reflective karstic soils, the lower canopy stratum is subjected to intense heat with low leaf heat dissipation that has been shown to induce mortality in epiphytes (Cervantes et al. 2005; Mondragón et al. 2004).

5.4 Concluding Remarks and Gaps in Knowledge

Despite the increase in research on the ecology and physiology of vascular plants of the Yucatán, many gaps in knowledge continue to exist. As mentioned in Sect. 5.1, physiological adaptations have been studied in only about 2 % of the total vascular plants of the Yucatán, and even these have not been completely characterized, since studies focus on specific variables (Tables 5.1 and 5.2). This suggests a large gap in information on the basic ecophysiology of many of the species of the area. Among the species studied, most of the information obtained has been for adults and gaps in information exist for seedlings (mainly on their physiology and factors that affect their survivorship). Although studies on below ground processes have started to increase, due in part to the difficulty of such studies, large gaps of information continue to exist regarding below ground processes (e.g. interactions between nutrients and microbes, the effects of soil microbial communities on the mobilization of nutrients or on nutrient sequestration, and potential relationships between levels of mycorrhizal colonization and successional stage; Hasselquist et al. 2010b). But also relationships between levels of mycorrhizal colonization and species (Ceccon et al. 2004), and species type (e.g. pioneer, versus late succession species; Ceccon et al. 2003) also merit further examination. Additional studies are needed to look at the synergistic effects of above and below ground processes, including the relationship of the effects of mycorrhizal colonization with succession and disturbance.

To follow on findings by Reyes-García et al. (2012a), whereby larger legumes presented more heartwood, developmental studies in legumes are needed in order to elucidate if there is an active process whereby drier conditions lead to more heartwood development in larger plants. Also, general ecological surveys, perhaps by collecting wood samples, would be needed to determine potential differences in the extent of heartwood in legumes across precipitation gradients. Active responses of plants to drought, potentially through cell signaling in laying down heartwood but also in growth, total canopy leaf area and osmotic response to drought are also needed in order to elucidate the extent to which responses to drought are dynamic or set (phylogenetic).

Since the main limiting factor in Yucatán is water, studies have focused on characterizing the water relations of tree species. However it is also necessary to study carbon assimilation directly and determine photosynthetic rates of species under different conditions. Due to the technical difficulties involved, the study of photosynthesis in trees has been relegated. However, novel techniques such as eddy covariance are being implemented in the Yucatán Peninsula to study the exchange of carbon, water and energy between the atmosphere and the forest.

The coastal dune scrubland on the north of the peninsula is a narrow area of endemism with several species adapted to arid environments (Espadas et al. 2003). Unfortunately, at present, this area is under considerable pressure due to human activities and several populations of the rare cactus *Mammillaria gaumeri* have been lost (Ferrer et al. 2011). Despite the fact that the dry tropical deciduous forests have been subject to natural disturbances and centuries of human use, CAM terrestrial plants in these forests still possess ecological importance (González-Iturbe et al. 2002; Ricalde et al. 2013). For conservation purposes, additional physiological studies, including all life stages along with demographic studies, should be applied to CAM terrestrial species of these communities to determine sites for the reintroduction of threatened species (de la Barrera and Andrade 2005; Reyes-García and Andrade 2009).

The genus *Clusia* deserves special attention. There is evidence that more than six species occur on the peninsula, but they have not been described (Vargas-Soto 2010). Under climate change scenarios for the region, *Clusia* species could become ecologically important, and should be included in reforestation programs, so more physiological and ecological studies on these species are needed.

CAM plants are good models for biophysical studies. Succulence does not allow leaves and stems to move under normal wind conditions, and energy balance and water relations can be modeled and then more easily predicted (Niklas and Hammond 2013). Also, for photosynthesis, an environmental productivity index has been tested for many CAM species, mainly crops (Nobel 1988, 1996; Andrade et al. 2009). This index can help predict plant photosynthesis and growth under different environmental scenarios, which can allow us to model plant productivity responses to global climate change.

Even though the epiphytes are among the best studied groups of plants in the Yucatán, some topics have not been addressed, such as limitation by nutrients, and how this can change across the different environments found in the peninsula. Differential growth rates, germination rates and seed production among species are other relevant topics that lack study. It is difficult to predict the response of the epiphytic species to climate change. Temperatures in the peninsula are expected to increase with global warming (Orellana et al. 2009), but the temperature limits of the different species have not been tested, so there is little information on how this will affect them. Predictions are uncertain on whether the peninsula will get drier or wetter, but changes in seasonal weather patterns have already been observed, prolonging the dry season, or the wet season in different years. This affects perennial epiphytes by modifying the whole microenvironment as trees lose or conserve their leaves for longer periods. These changes in leaf cover have been shown to affect both productivity, and induce stress, but there has been no attempt to integrate how these changes will affect annual survival rate. If the favorable, wet growing season is too short, the epiphyte may not have enough reservoirs to survive a prolonged drought, when photosynthesis drops and photoinhibition is induced (Reyes-García and Griffiths 2009). In contrast, some of the epiphytic species have high drought tolerance conveyed by traits that may be unfavorable under wetter conditions. For example, stomata are blocked by the water retained on the surface on species with very high trichome density, and these species may have local extinctions under a wetter climate. Furthermore, epiphytes have been seen to be very sensitive to changes in climate (Cach-Pérez et al. 2014) and should be among the first life form to respond to climate change and land use change.

Environmental instability as a result of the effects of climate change on the Yucatán Peninsula generates the following questions: How will plant communities under conditions of climate change be distributed? Will climate change modify the floristic composition of plant associations? Which species will dominate and what are the strategies that will allow them a better adaptation to environmental change? How are C_4 plants reacting in the peninsula? What are the physiological strategies of invasive species? How can we link the plant physiology with conservation strategies? These questions can be answered by modeling plant physiological parameters and environmental variables. However, to achieve an understanding on how plant communities respond to climate change the number of species studied must be increased. With this, well-characterized functional groups may be identified allowing for the potential modeling of C_3 and CAM plants.

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