

PART OF A SPECIAL ISSUE ON CAM AT THE CROSSROADS

CAM plants: their importance in epiphyte communities and prospects with global change

Gerhard Zotz^{1,2,*}, José Luis Andrade³ and Helena J. R. Einzmann¹

¹Functional Ecology Group, Institute of Biology and Environmental Sciences, Carl von Ossietzky University Oldenburg, Box 5634, D-26046 Oldenburg, Germany, ²Smithsonian Tropical Research Institute, Box 0843-03092, Panama, Republic of Panama, and ³Unidad de Recursos Naturales, Centro de Investigación Científica de Yucatán, Calle 43 No. 130, Chuburná de Hidalgo, Mérida, Yucatán, Mexico

* For correspondence. E-mail gerhard.zotz@uol.de

Received: 7 October 2022 Returned for revision: 8 December 2022 Editorial decision: 14 December 2022 Accepted: 15 December 2022

• **Background and Scope** The epiphytic life form characterizes almost 10 % of all vascular plants. Defined by structural dependence throughout their life and their non-parasitic relationship with the host, the term epiphyte describes a heterogeneous and taxonomically diverse group of plants. This article reviews the importance of crassulacean acid metabolism (CAM) among epiphytes in current climatic conditions and explores the prospects under global change.

• **Results and Conclusions** We question the view of a disproportionate importance of CAM among epiphytes and its role as a ‘key innovation’ for epiphytism but do identify ecological conditions in which epiphytic existence seems to be contingent on the presence of this photosynthetic pathway. Possibly divergent responses of CAM and C₃ epiphytes to future changes in climate and land use are discussed with the help of experimental evidence, current distributional patterns and the results of several long-term descriptive community studies. The results and their interpretation aim to stimulate a fruitful discussion on the role of CAM in epiphytes in current climatic conditions and in altered climatic conditions in the future.

Key words: Carbon isotopes, crassulacean acid metabolism, disturbance, dry forest, epiphytes, functional traits, germination, global change, key innovation, plant–water relationships.

A BRIEF HISTORY OF OUR VIEW OF CAM IN EPIPHYTES

Vascular epiphytes differ from ground-rooted terrestrial autotrophs by their structural dependence on a host, typically a tree. They germinate, grow and reproduce on a host tree without establishing contact to the soil at any stage of their life cycle, which sets them apart from other structurally dependent forms, such as climbers or hemiepiphytes (Zotz, 2016). Importantly, in contrast to co-occurring mistletoes, they do not tap the host directly for resources. The epiphytic lifestyle is common; the most recent tally of the number of vascular plant species that primarily occur epiphytically reported >30 000 species, i.e. ~10 % of the global flora (Zotz *et al.*, 2021b). A rather precarious supply of water is typically seen as a major consequence of epiphytic growth in trees.

Considering that a key benefit of crassulacean acid metabolism (CAM) is the economical use of water (Winter, 2019), it is unsurprising that researchers investigated the possibility that CAM might be used by vascular epiphytes. [‘CAM plants’ obtain the majority of their carbon through the CAM pathway throughout their lives, typically deduced from a $\delta^{13}\text{C}$ value of leaf tissue > -20 ‰ (Winter, 2019).] This was shown, for the first time, ~60 years ago (Nuernbergk, 1961, 1963). From the 1960s until the early 1980s, it was possible to publish reports with the basic discovery that an epiphyte was capable

of nocturnal CO₂ uptake, e.g. ‘Algumas informações sobre a capacidade rítmica diária da fixação e acumulação de CO₂ no escuro em epífitas e erbáceas terrestres da mata pluvial’ by Coutinho (1964), ‘Two types of carbon fixation in tropical orchids’ by Neales and Hew (1975), or ‘Water relations of tropical epiphytes. III. Evidence for CAM’ by Sinclair (1984). Starting out as a curiosity, more and more studies documented the occurrence of CAM among epiphytes not only in dry forests, but also in moist habitats (Winter *et al.*, 1983; Earnshaw *et al.*, 1987; Holthe *et al.*, 1992; Kluge *et al.*, 1995; Zotz and Ziegler, 1997). A pattern that was noted early on (Nuernbergk, 1961, 1963) was a correlation between leaf thickness and the presence of CAM. Once C₄ is excluded by way of inspection of leaf anatomy, species with thin leaves are typically C₃ and those with thicker leaves are associated with CAM. Although later studies largely confirmed this general pattern (e.g. Teeri *et al.*, 1981; Winter *et al.*, 1983; Earnshaw *et al.*, 1987; Zotz and Ziegler, 1997), there are also obvious deviations from this rule, e.g. in the case of species with thin leaves and with a carbon isotope ratio indicative of CAM (Zotz and Ziegler, 1997; Herrera, 2020). Hence, leaf thickness is a rough, but not totally reliable proxy for the photosynthetic pathway of epiphytes.

Summarizing the knowledge on CAM among epiphytes after more than three decades of research, Winter and Smith (1996) came up with the following calculation: with a then known number of 20 000 orchid species, more than two-thirds of

which are epiphytes and an estimated 50 % of which were considered likely to use the CAM metabolic pathway (Winter and Smith, 1996), there could be as many as 7000 epiphytic orchid species with CAM. The number of CAM taxa in the global flora apart from orchids was estimated as 9000 species by the same authors (Smith and Winter, 1996; Winter and Smith, 1996). Given that many of these CAM species are also epiphytic, most importantly in Bromeliaceae (e.g. in genera such as *Aechmea* and *Tillandsia*), Cactaceae (e.g. in *Rhipsalis* and *Epiphyllum*) or Apocynaceae (e.g. in *Hoya* and *Dischidia*), epiphytic species would thus account for the majority of an estimated 16 000 CAM species globally, exceeding by far the number of terrestrial CAM taxa.

During the last two decades it has become increasingly clear that the bimodal distribution of $\delta^{13}\text{C}$ values commonly found in screening studies (e.g. Winter, 1979; Winter et al., 1983; Earnshaw et al., 1987; Zotz and Ziegler, 1997) with a ‘gap’ at $\sim -20\text{‰}$ does not delineate two distinct groups with and without the capacity for nocturnal acidification. Rather, there is a linear relationship between the proportion of nocturnally fixed carbon and $\delta^{13}\text{C}$ values (Winter and Holtum, 2002), with a value of -20‰ being indicative of $\sim 50\%$ nocturnal uptake. Not surprisingly then, there is an ongoing debate over whether CAM should be seen as a discrete or a continuous trait (e.g. Zotz, 2002; Winter et al., 2015; Messerschmid et al., 2021; Winter and Smith, 2022). However, such a conceptual debate is by no means idiosyncratic for this photosynthetic pathway. ‘Halophyte’ vs. ‘glycophyte’ is another example of seemingly binary categories that will probably remain an issue of rather arbitrary delimitations (Grigore et al., 2014), as is the case for ‘succulent’ (‘Succulence is not a binary trait’; Ogburn and Edwards 2010) or ‘pseudobulb’ vs. ‘normal’ stem in Orchidaceae (Göbel et al., 2020). In the following treatise, we do not ignore cases with rather modest nocturnal activity, frequently called ‘weak CAM’ (Winter, 2019), but reserve the term ‘CAM species’ or ‘CAM plant’ for those cases in which the majority of carbon uptake occurs nocturnally (Winter, 2019).

RECENT INSIGHTS: HOW IMPORTANT IS CAM IN EPIPHYTES?

Regular water shortage is usually seen as one of the few challenges that most epiphytes share. Considering that the water-use efficiency of CAM plants is much higher than that of C_3 plants (Winter, 2019), suggesting a high proportion of epiphyte species with CAM seems very reasonable, but has the estimate of Winter and Smith (1996) stood the test of time? The answer is clearly no.

Further exploration in the following decades until today has led to a strong decrease in our current estimate of the numbers of epiphytes using CAM. In one of the most ambitious studies to date, covering >1000 orchid species from Panama and Costa Rica, Silvera et al. (2010) detected $\delta^{13}\text{C}$ values indicative of CAM ($\delta^{13}\text{C} > -20\text{‰}$) in only $\sim 10\%$ of all epiphytic species. Although the proportion of CAM species is much lower among terrestrial orchids (4 of 121 species, i.e. 3 %), this proportion among epiphytes falls short by far of the 50 % estimate of Winter and Smith (1996). Another, similarly extensive survey among Colombian orchids by Torres-Morales et al.

(2020) reported a comparable figure for epiphytic CAM species (9.5 %, or 76 of 805 species), but relatively more CAM species among terrestrials (7.3 %, or 19 of 260 species).

A recent, comprehensive analysis of numerous functional traits of vascular epiphytes by Hietz et al. (2022) revealed that CAM is found in $\sim 10\%$ of the studied epiphyte species. This proportion is similar to the global estimate of 6–7 % for all vascular plants (Winter and Smith, 1996), particularly when considering that the latter group includes >70 000 species of trees (Gatti et al., 2022), all of which are C_3 (with the rare exception of a few CAM trees in the genus *Clusia*; Luján et al., 2021) and a strong taxonomic and geographical bias in the epiphyte data (details in the study by Hietz et al., 2022). Note that bromeliads are excluded from this calculation because this family stands out with a much higher proportion of CAM species (Crayn et al., 2015). In the subfamily Bromelioideae, CAM is highly dominant ($\sim 90\%$), but this high proportion is not related to life form; epiphytic and terrestrial taxa do not differ in that regard. In the subfamily Tillandsioideae, which is dominated by epiphytes, CAM is also common; 28 % of all species show CAM, but again without a life form bias. Hietz et al. (2022) pointed out that many, if not most, aspects of the functional ecology of vascular epiphytes are understudied, hampering generalizations. However, this is not true for CAM; there is a solid database available. Thus, we can dismiss with considerable certainty previous assertions that CAM is ‘common’ among epiphytes (e.g. Zotz and Hietz, 2001) or speculations that the majority of all CAM taxa globally are epiphytic (e.g. Winter and Smith, 1996; Lüttge, 2004), and as discussed below, we conclude that the large majority of epiphytes are not CAM plants. This statement does not ignore that in some taxonomic groups CAM species can be very common (e.g. in Bromeliaceae) or even ubiquitous (e.g. in Cactaceae). However, these are family characteristics irrespective of terrestrial or epiphytic growth. Neither is this a statement about the occurrence of limited nocturnal acidification in epiphytes. There are simply not enough data to conclude whether such ‘weak’ CAM is particularly common among epiphytic compared with terrestrial plants.

In the following, we quantify the relative importance of CAM in epiphyte communities with data from three published studies (Einzmann et al., 2015; Einzmann and Zotz, 2017; Wagner et al., 2021). When possible, we perform a separate analysis for epiphytes in tree crowns, excluding trunk epiphytes. In the first of these studies, in emergent trees on Barro Colorado Island (BCI), the number of epiphyte individuals with CAM is clearly highest on drought-deciduous tree species, such as *Cavanillesia platanifolia* (Table 1), whereas such a trend is not observed with regard to species numbers. As expected, the proportion of CAM species is higher in tree crowns compared with that on the trunk or that of the epiphyte community of the entire tree (Wilcoxon signed rank tests, $P < 0.01$).

The relative importance of CAM in the epiphyte communities of four evergreen emergents in the moister forest of the San Lorenzo crane site in Panama is similar in terms of both individual numbers and species (Table 2). However, in this case the differences between the proportion of CAM species in tree crowns vs. tree trunks or that of the epiphyte community of the entire tree are not significant (Wilcoxon signed rank test, $P > 0.2$).

TABLE 1. Occurrence (abundance and species) of epiphytes with crassulacean acid metabolism (CAM) on five emergent tree species of varying phenology on Barro Colorado Island, Panama. Of each tree species, five individuals were studied, except *Brosimum alicastrum* with only four individuals. The 'Total' column gives the number of all individuals and species, respectively, across all 24 studied trees (or crowns, respectively) and the proportion of individuals/species with CAM. Percentage data for the individual tree species are given as the mean \pm s.d. Data are from Einzmann et al. (2015). Barro Colorado Island is located in the Panamanian lowlands and experiences a pronounced 4-month dry season and ~ 2700 mm yr⁻¹ rainfall

Epiphyte	Total	Host tree species				
		<i>Anacardium excelsum</i>	<i>Brosimum alicastrum</i>	<i>Ceiba pentandra</i>	<i>Pseudobombax septenatum</i>	<i>Cavanillesia platanifolia</i>
Individuals	25 592	10 963	3432	8826	2296	75
Species	87	65	49	50	20	7
CAM individuals (%)	4.9	1.2 \pm 1.1	9.3 \pm 6.4	8.1 \pm 4.6	15.3 \pm 19.7	24.6 \pm 33.9
CAM species (%)	16	7.1 \pm 5.5	17.0 \pm 10.0	21.3 \pm 9.7	21.4 \pm 8.0	16.7 \pm 23.6
Crown individuals	24 420	10 458	2755	8290	1763	14
Crown species	79	60	43	47	7	7
Crown CAM individuals (%)	4.6	1.2 \pm 1.1	8.3 \pm 8.1	8.0 \pm 5.3	15.7 \pm 20.5	16.7 \pm 33.3
Crown CAM species (%)	15.2	6.6 \pm 5.5	18.5 \pm 15.7	22.6 \pm 12.0	31.3 \pm 6.4	8.3 \pm 16.7

TABLE 2. Occurrence (abundance and species) of epiphytes with crassulacean acid metabolism (CAM) on four tree species in the forest of San Lorenzo, Panama. Eight emergent trees of *Aspidosperma spruceanum*, three trees of *Brosimum utile*, eight trees of *Calophyllum longifolium* and four trees of *Manilkara bidentata* were studied. Only species for which $\delta^{13}\text{C}$ information was available were included. Hemiepiphytes were excluded. The 'Total' column gives the number of all individuals and species, respectively, across all 24 studied trees (or crowns, respectively) and the proportion of individuals/species with CAM. Percentage data for the individual tree species are given as the mean \pm s.d. Data are from Wagner et al. (2021). The forest is tropical moist lowland forest that experiences a 3- to 4-month-long dry season each year and ~ 3300 mm yr⁻¹ of rainfall

Epiphyte	Total	Host tree species			
		<i>Aspidosperma spruceanum</i>	<i>Brosimum utile</i>	<i>Calophyllum longifolium</i>	<i>Manilkara bidentata</i>
Individuals	4655	824	807	1516	1508
Species	66	39	39	53	33
CAM individuals (%)	3.0	10.1 \pm 12.6	1.6 \pm 1.9	5.1 \pm 7.0	1.6 \pm 1.3
CAM species (%)	11.9	10.3 \pm 10.7	5.1 \pm 4.5	8.7 \pm 5.6	7.7 \pm 6.2
Crown individuals	4080	672	713	1307	1388
Crown species	57	32	33	46	29
Crown CAM individuals (%)	2.8	10.3 \pm 15.1	1.9 \pm 2.0	4.8 \pm 9.6	6.1 \pm 9.4
Crown CAM species (%)	15.1	11.1 \pm 13.9	7.1 \pm 6.3	6.5 \pm 5.3	13.7 \pm 14.1

The third data set represents epiphytes on pasture trees along a rainfall gradient in western Panama (Table 3). Here, CAM species account for a remarkable 57 % of all individuals (and 33 % of the species) even at the wet end, where rainfall is similar to that received by the forest in San Lorenzo. This reinforces the notion that the spatial context of host trees is highly important, and not only large-scale climatic conditions; the microclimate in the crowns of widely spaced trees differs substantially from those in tree crowns in a closed forest. At the dry end of the gradient, with <1500 mm yr⁻¹ of rain, almost all epiphytes use CAM (Einmann and Zotz, 2017).

The last observation is fully in line with reports from dry tropical forest habitats. There, CAM seems to be (almost) indispensable for epiphytic existence. Relevant studies from dry tropical forests in Mexico consistently show that the proportion of epiphytes with CAM reaches 100 % (Mooney et al., 1989;

Reyes-García et al., 2008; Cach-Pérez et al., 2018), whereas the results of a study from Brazil (Fontoura and Reinert, 2009) are more in line with observations by Einmann and Zotz (2017) in pasture trees in lowland Panama (Table 3). In both cases, CAM is clearly dominant, but there is a considerable proportion of species that use C₃.

The previous comparisons of species numbers assessed the relative importance of CAM primarily in a biodiversity context. To evaluate the importance of CAM in an ecosystem context, carbon flux or biomass is the more appropriate currency. Using this rationale, Zotz (2004) compared the relative contribution of CAM epiphytes to the total species count, total number of individuals and total biomass in a moist lowland forest. Given that CAM species tended to be rarer and smaller than C₃ species, the relative importance of CAM at the community level was much smaller when expressed on an individual and on a

TABLE 3. Occurrence of crassulacean acid metabolism (CAM) in epiphytes on 425 pasture trees with epiphytes in Panama, 2013. Only species for which $\delta^{13}\text{C}$ information was available were included, excluding five species. CAM was much more prominent at the dry end of the rainfall gradient of this study (Einzmann and Zotz, 2017). The study was conducted in the south-western Panamanian lowlands, spanning a rainfall gradient from ~1100 to 4200 mm yr⁻¹. The region experiences a 3- to 4-month dry season each year

Epiphyte	Census 2013	Gradient dry end, 1100–1500 mm yr ⁻¹	Gradient wet end, >3500 mm yr ⁻¹
Individuals	60 878	2576	21 282
Species	81	9	57
CAM individuals (%)	53.2	99.6	57.2
CAM species (%)	34.6	66.7	33.3

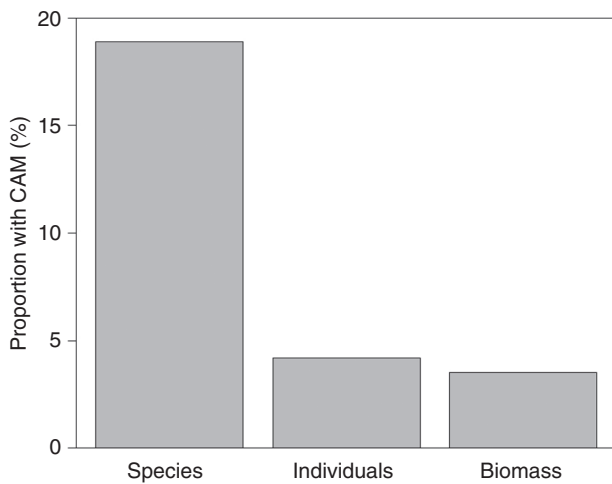


FIG. 1. Relative importance of crassulacean acid metabolism (CAM) in a vascular epiphyte community in the lowland forest of San Lorenzo (Panama) expressed as the proportion of species with CAM, the proportion of individuals with CAM and the contribution of these individuals to total biomass. For details, see Zotz (2004).

biomass basis (Fig. 1). Whether this is a general pattern remains to be assessed in future studies.

Along elevational gradients, such as the one that Hietz *et al.* (1999) studied, from dry premontane forest to montane cloud forest, the proportion of CAM in epiphyte communities declines. In humid upper montane forests with particularly lush epiphyte vegetation, the proportion of CAM species is low (Earnshaw *et al.*, 1987; Hietz *et al.*, 1999; Torres-Morales *et al.*, 2020; Guzmán-Jacob *et al.*, 2022) and CAM biomass may account for only 2–3 % of the total epiphyte biomass (Hietz *et al.*, 1999). Thus, although the global database is still rather limited and future studies might lead to some adjustments of these figures, current evidence from studies of elevational patterns does not support the notion that CAM is particularly common in these epiphyte-rich habitats.

Finally, Zotz (2016) compiled biomass data for epiphytic and terrestrial CAM plants at a global scale. Available data suggest that the biomass of CAM epiphytes in tropical lowland forests

is typically <10 kg ha⁻¹, with much higher values for so-called ‘atmospheric’ epiphytic bromeliads in semi-desert environments (>100 kg ha⁻¹; Flores-Palacios *et al.*, 2015). Terrestrial CAM biomass in arid systems in southern Peru, North America or Southern Africa can exceed 1000 kg ha⁻¹ (Zotz, 2016). Thus, CAM in epiphytes does not rival the importance of CAM in terrestrial plants from an ecosystem perspective either.

To summarize, CAM is not (as frequently claimed) generally predominant in the epiphytic habitat, whether analysed as a proportion of species or individuals or as the contribution of CAM species to total biomass. However, at least in two Neotropical families (Cactaceae and Bromeliaceae), the presence of CAM has been called a key factor for the evolutionary radiation of plant lineages into tree crowns (e.g. Benzings, 1989; Givnish *et al.*, 2014). Is this a valid argument?

CAM AND THE EVOLUTION OF EPIPHYTISM

A key evolutionary innovation is a morphological or physiological change in an individual trait that leads to an increase in diversification rate (Hunter, 1998). CAM is an excellent candidate for the study of such a potential key innovation because both the adaptive advantages and the metabolic costs of CAM are well characterized and because this trait has arisen multiple times, which allows the comparative study of the ecological and evolutionary implications of a transition from C₃ to CAM and vice versa in many independent plant groups. Another aspect of considerable interest in the context of this review is the possible correlation of the evolution of CAM with other aspects of the biology of a plant group, such as particular morphological features (e.g. a tank in bromeliads or a pseudobulb in orchids) or habitat preferences, i.e. a possible link between epiphytism and CAM.

There are a number of studies that suggest increased diversification rates in CAM clades compared with C₃ lineages, e.g. in Euphorbiaceae (Horn *et al.*, 2014), Bromeliaceae (Givnish *et al.*, 2014; Silvestro *et al.*, 2014) or Orchidaceae (Silvera *et al.*, 2009; Givnish *et al.*, 2015), irrespective of a preference for terrestrial or epiphytic growing sites. In contrast, other studies have found no such differences. For example, diversification rates of CAM and C₃ species of Afro-Malagasy Eulophiinae orchids did not differ (Bone *et al.*, 2015), and a recent study with >100 *Bulbophyllum* species (Hu *et al.*, 2022) suggested that a stimulation of speciation processes by CAM did happen initially, but was only temporary (i.e. during a low-CO₂ period in the Miocene). In the long run, CAM lineages in that genus had ten times higher extinction rates than C₃ lineages.

The empirical support for a link between CAM and epiphytism is also mixed. There is, for example, a study with the genus *Cymbidium*, in which CAM is restricted to epiphytic and lithophytic taxa, whereas all terrestrial *Cymbidium* species use C₃ photosynthesis (Motomura *et al.*, 2008b). Givnish *et al.* (2014) reported a very strong link between the evolution of epiphytism and both the possession of a water-impounding tank and entangling seeds in Bromeliaceae, but they were unable to detect a correlated evolution between the epiphytic habit and CAM. They observed, however, that CAM photosynthesis evolved more frequently overall in epiphytic than in terrestrial

clades. An earlier analysis of the same family had found the opposite trend; transitions to CAM photosynthesis were much more common in terrestrial clades (Quezada and Gianoli, 2011). Even if there are methodological reasons for such disparate results for the same family, neither study provides strong support for a link between CAM and epiphytism.

In summary, evidence that CAM is a key innovation that leads to higher diversification in plants in general is mixed. Likewise, evidence for correlated evolution of CAM and epiphytism is also varied, which is not very surprising, given that previous estimates of a disproportionate number of CAM species among epiphytes seem to be exaggerated.

PARTICULAR ASPECTS OF CAM IN EPIPHYTES

Epiphytes might still be special in the use of CAM because this photosynthetic pathway can be found in any vegetative and reproductive organ, particularly noteworthy in roots. Roots of terrestrial plants typically grow underground, which precludes any photosynthetic activity, but at least the roots of bark epiphytes are exposed to sunlight. In some cases, such as many species in the genera *Campylocentrum*, *Dendrophylax* or *Chiloschista*, roots even serve as the only photosynthetically active organ (Benzing and Ott, 1981). All the tested leafless orchids have roots that use CAM (Benzing and Ott, 1981; Cockburn et al., 1985; Winter et al., 1985). In most other studied epiphytic orchids, however, roots fix carbon via the C₃ pathway, even in species in which leaves engage in CAM (Motomura et al., 2008a; Moreira et al., 2009; Martin et al., 2010). In most cases, the contribution of roots to the carbon budget of the entire plant is probably moderate; Benzing and Ott (1981) found constant release of CO₂ during both day and night in eight of nine tested species. No data are available about possible photosynthetic activity of roots of non-orchid epiphytes.

CAM is found in the stems of all epiphytic (as in terrestrial) cacti, and there is also evidence for CAM in pseudobulbs of many Orchidaceae (Rodrigues et al., 2013; Tay et al., 2019). There are a few leafless orchids, such as *Bulbophyllum minutissimum*, in which the pseudobulb is even the primary photosynthetic organ. Unlike most other pseudobulbs (Göbel et al., 2020), these organs possess not only a well-developed succulent chlorenchyma, but also stomata, and a δ¹³C value of -17 ‰, which is clear evidence for CAM (Winter et al., 1983). CAM activity has also been documented in reproductive organs. Nocturnal CO₂ fixation in petals was already reported >50 years ago by Dueker and Arditti (1968) for two *Cymbidium* hybrids, and CAM in the fruits of two orchid species has been reported decades later (Zotz et al., 2003).

In most of the cases described, CAM activity in non-foliar organs does not seem to lead to a net uptake of CO₂ but rather allows the recovery of some otherwise lost respiratory CO₂ and an increase in water retention across the entire plant body. This might be highly relevant in epiphytes that can invest up to 30 % of plant biomass into reproductive structures. As in foliar organs, CAM can be constitutive or inducible (*sensu* Winter, 2019). For example, no CAM activity was detected in leaves, pseudobulbs and roots of well-watered *Oncidium* sp., but under drought stress the pseudobulbs and roots switched to CAM (Rodrigues et al., 2013).

All these observations lead to the conclusion that the photosynthetic pathways of different plant organs can be independent. Thus, a ‘CAM plant’, typically identified by the analysis of the photosynthetic pathway of its primary photosynthetically active organ, can have roots with C₃ photosynthesis, such as in a *Paphiopedilum* cultivar (Martin et al., 2010), whereas a ‘C₃ plant’, such as *Dimerandra emarginata* (Zotz and Tyree, 1996), can have fruits that engage in CAM (Zotz et al., 2003).

CAM AND EPIPHYTES IN THE FUTURE

Human activities have led to unprecedented changes in the biosphere and continue to do so (IPCC, 2021). At a global level, CO₂ concentrations and air temperatures are on the rise, climatic extremes are increasing in frequency and severity, and all these changes are accompanied by changes in land use and increased nutrient depositions (Sala et al., 2000). In the following, we review experiments and other evidence that shed light on the effects of several aspects of global change: elevated CO₂, increased temperature, altered water supply and extreme weather events, always with particular emphasis on epiphytes with CAM. We note from the start that the data basis is generally thin, and conclusions must therefore be considered preliminary.

Effects of elevated CO₂

Numerous gas exchange studies have investigated the effect of varying CO₂ concentrations on plants. Generally, an increase in atmospheric CO₂ concentration stimulates leaf photosynthesis, water-use efficiency and growth in C₃ and C₄ plants (Drake et al., 1997; Ward et al., 1999; Winter et al., 2001; Cernusak et al., 2013). Although CAM plants use phosphoenolpyruvate carboxylase (PEPCase) for the initial CO₂ fixation at night, in well-watered conditions they can assimilate CO₂ directly by ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO) during the daytime (phases II and IV of CAM; Nobel and Bobich, 2002; Winter and Smith, 2022). Then, the response of net CO₂ uptake to increasing atmospheric CO₂ concentrations of CAM species resembles that of C₃ species and exceeds that of C₄ species (Drennan and Nobel, 2000). Terrestrial CAM plants generally have higher maximal instantaneous rates of net CO₂ uptake (3–18 μmol m⁻² s⁻¹) than epiphytic CAM plants (2–3 μmol m⁻² s⁻¹) (Nobel and Bobich, 2002). Does this translate into relative differences in the responses to increasing atmospheric CO₂ concentrations?

Few studies have investigated the effect of elevated CO₂ on vascular epiphytes, and most of them have used *in vitro* plantlets (Gouk et al., 1997, 1999) or ornamental plants (Li et al., 2002a; Croonenborghs et al., 2009; Monteiro et al., 2009). Furthermore, some results from studies with epiphytic bromeliads are inconsistent (Monteiro et al., 2009; Zotz et al., 2010). Among the expected physiological responses of C₃ and CAM epiphytes to elevated CO₂ are increases in photosynthesis, growth and dark respiration, as observed in gametophytes of the C₃ fern *Pyrrosia piloselloides* (Ong et al., 1998), reduced stomatal conductance in phase I of CAM, that led to a reduction of ~20% in water loss in *Tillandsia brachycaulos*, but an increase in stomatal conductance and water loss by ~130% in the C₃ fern *Phlebodium aureum* in low-light conditions (Batke

et al., 2018). However, there are also unexpected growth responses (Croonenborghs *et al.*, 2009; Monteiro *et al.*, 2009). For example, Croonenborghs *et al.* (2009) found that elevated CO₂ treatments had adverse effects on the ornamental value of three bromeliads, producing shorter plants with paler green leaves than control plants.

Laboratory studies on the effect of doubled CO₂ concentrations on C₃ and CAM epiphytes report an average increase in relative growth rate of ~20 %, with little difference in growth stimulation between C₃ species and CAM species (Table 4). The median increase of ~16 % in CAM epiphytes is less than half of the reported increase in terrestrial CAM plants. There, increases in shoot dry mass average 35 % under similar CO₂ enrichment (Drennan and Nobel, 2000).

In several CAM epiphytes, an increase of photosynthetic and sugar production enzymes, titratable acidity (Li *et al.*, 2002b) and exceptional root growth (Gouk *et al.*, 1999; Li *et al.*, 2002b) have been found. Such increased root growth in elevated CO₂ conditions has also been described in terrestrial CAM species (Cui *et al.*, 1993; Zhu *et al.*, 1997).

What is the physiological basis of increased growth? Higher carbon gain during the light period under elevated CO₂, compared with current CO₂ conditions (mostly in phase IV of CAM), has been reported for terrestrial CAM plants (Graham and Nobel, 1996; Winter *et al.*, 2014). Indeed, many CAM plants will take up substantial amounts of CO₂ during the daytime given favourable environmental conditions (Nobel, 2003). This is also true for CAM epiphytes. For instance, two epiphytic bromeliad species took up ~20 % of the daily total CO₂ during the light period, mostly in phase IV, in well-watered conditions (Graham and Andrade, 2004). Further evidence that an increase in nocturnal CO₂ uptake might play hardly any role in a growth stimulation of epiphytic CAM plants comes from an experimental study with three *Aechmea* species (Wagner and Zotz, 2018): doubling CO₂ from 400 to 800 µL L⁻¹ increased their relative growth rate by 61 % in well-watered conditions, but nocturnal acidification remained unchanged. Thus, this increase in growth resulted entirely from higher assimilation during the light period.

TABLE 4. The effect of elevated CO₂ on growth of vascular epiphyte species in five published studies. Given are the average relative growth rates (RGR, in mg g⁻¹ d⁻¹) at low and high CO₂, the absolute (in mg g⁻¹ d⁻¹) and relative effect size (as a %). CO₂ concentrations were 280/560 µL L⁻¹ (Monteiro *et al.*, 2009), 350/700 µL L⁻¹ (Zotz *et al.*, 2010), 380/760 µL L⁻¹ (Li *et al.*, 2002a; Croonenborghs *et al.*, 2009) and 400/800 µL L⁻¹ (Wagner and Zotz, 2018). The median absolute and relative effect sizes are 0.4 mg g⁻¹ d⁻¹ and 19 %, respectively, with no differences between CAM and C₃ plants (Wilcoxon test, P > 0.5)

Species	Family	C ₃ /CAM	RGR low	RGR high	Effect size (absolute)	Effect size (relative)	Source
<i>Aechmea bracteata</i>	Bromeliaceae	CAM	1.1	3.9	2.8	250	Wagner and Zotz (2018)
<i>Aechmea fasciata</i>	Bromeliaceae	CAM	11.8	10.6	-1.2	-10.2	Croonenborghs <i>et al.</i> (2009)
<i>Aechmea fasciata</i>	Bromeliaceae	CAM	2.1	2.9	0.7	33.6	Monteiro <i>et al.</i> (2009)
<i>Aechmea</i> 'Maya'	Bromeliaceae	CAM	3.6	3.2	-0.3	-8.7	Croonenborghs <i>et al.</i> (2009)
<i>Aechmea mexicana</i>	Bromeliaceae	CAM	7.1	10	2.9	43	Wagner and Zotz (2018)
<i>Aechmea veitchii</i>	Bromeliaceae	CAM	5.9	7.0	1.1	19	Wagner and Zotz (2018)
<i>Catopsis juncifolia</i>	Bromeliaceae	C ₃	3.8	4.3	0.5	11.8	Monteiro <i>et al.</i> (2009)
<i>Catopsis nitida</i>	Bromeliaceae	C ₃	6.5	6.1	-0.5	-7.1	Zotz <i>et al.</i> (2010)
<i>Guzmania</i> 'Hilda'	Bromeliaceae	C ₃	10.5	12.9	2.4	23.1	Croonenborghs <i>et al.</i> (2009)
<i>Guzmania monostachya</i>	Bromeliaceae	C ₃	1.4	2.0	0.6	39.0	Zotz <i>et al.</i> (2010)
<i>Racinea contorta</i>	Bromeliaceae	C ₃	0.4	2.0	1.6	440	Zotz <i>et al.</i> (2010)
<i>Tillandsia elongata</i>	Bromeliaceae	CAM	3.6	4.0	0.4	11.1	Zotz <i>et al.</i> (2010)
<i>Tillandsia fasciculata</i>	Bromeliaceae	CAM	2.8	2.4	-0.4	-14.2	Monteiro <i>et al.</i> (2009)
<i>Tillandsia fasciculata</i>	Bromeliaceae	CAM	2.0	2.3	0.3	14.0	Zotz <i>et al.</i> (2010)
<i>Tillandsia heterophylla</i>	Bromeliaceae	C ₃	0.1	2.2	2.2	4300	Zotz <i>et al.</i> (2010)
<i>Tillandsia juncea</i>	Bromeliaceae	C ₃	2.3	2.7	0.5	20.7	Zotz <i>et al.</i> (2010)
<i>Tillandsia subulifera</i>	Bromeliaceae	CAM	1.8	1.0	-0.8	-44.6	Zotz <i>et al.</i> (2010)
<i>Tillandsia viridiflora</i>	Bromeliaceae	C ₃	0.4	0.8	0.4	88.6	Zotz <i>et al.</i> (2010)
<i>Vriesea</i> 'Splendret'	Bromeliaceae	C ₃	4.4	4.6	0.2	3.8	Monteiro <i>et al.</i> (2009)
<i>Werauhia laxa</i>	Bromeliaceae	C ₃	8.6	8.7	0.1	1.3	Zotz <i>et al.</i> (2010)
<i>Werauhia sanguinolenta</i>	Bromeliaceae	C ₃	4.2	5.5	1.4	32.8	Zotz <i>et al.</i> (2010)
<i>Bulbophyllum longissimum</i>	Orchidaceae	CAM	0.9	1.0	0.2	20.0	Monteiro <i>et al.</i> (2009)
<i>Mokara</i> 'Yellow'	Orchidaceae	CAM	6.8	8.5	1.7	25.3	Li <i>et al.</i> (2002a)
<i>Oncidium enderianum</i>	Orchidaceae	C ₃	1.2	1.1	-0.1	-8.2	Monteiro <i>et al.</i> (2009)

The expected mitigating effect of elevated CO₂ under low water supply was not found in a study with several epiphytic bromeliad species (Zotz *et al.*, 2010); however, it was noted that species from the lowlands were more drought tolerant than those from montane areas. Likewise, Wagner and Zotz (2018), studying three *Aechmea* species, found that elevated CO₂ did not compensate for the negative effect of low water supply. In contrast, Batke *et al.* (2018) reported a strong reduction in 24 h water loss for *Tillandsia brachycaulos* in high-light and elevated CO₂ conditions, but no changes in water relationships between CO₂ treatments. Yet, in this last study, the high-light treatment (650 mmol m⁻² s⁻¹) was unrealistic, because *in situ* such light conditions occur only during the dry season in the driest forest habitat of this species (González-Salvatierra *et al.*, 2021), whereas the experiment was conducted with well-watered plants. Moreover, although *T. brachycaulos* inhabits forests where high light and low water availability are usually accompanied by high vapour pressure deficits and high temperature, this species shows modest seasonal changes in leaf water relationships within the forest canopy (Hernández-Robinson *et al.*, 2020).

Increased temperature

Temperature affects all aspects of the biology of plants, from germination to growth and reproduction. In a study with a focus on epiphytic bromeliads, Müller *et al.* (2017) observed that the expected temperature increase in tropical latitudes of 3 °C by the end of this century would stimulate germination in most cases. This positive effect warns against sweeping predictions of generally negative effects of climate change. However, conditions in nature are complex, and any positive temperature effect in laboratory conditions might be irrelevant ecologically if *in situ* low and more erratic water availability precludes germination. Using the data of Müller *et al.* (2017), we tested whether a temperature rise of 3 °C would affect germination in C₃ and CAM species differently. Specifically, we analysed whether the experimentally determined optimal temperature for germination would fall within the predicted mean annual temperature ranges of each species at the end of this century. This is the case for a majority of C₃ species (14 of 20 species), but for only eight of the 21 CAM species in that particular study. However, this difference was not significant ($\chi^2 = 2.6$, $P = 0.11$). If anything, the trend indicates an advantage of C₃ species.

At a leaf physiological level, the main problem for CAM plants should be an increase in nocturnal temperatures, because daytime temperatures hardly affect net CO₂ uptake in terrestrial CAM plants (Nobel, 2003). In contrast, there is evidence for many terrestrial CAM plants that high night-time temperatures (>30 °C) affect stomatal aperture and reduce net CO₂ uptake (Nobel, 2003). Certainly, the optimal mean nocturnal temperature for most of these terrestrial CAM plants is relatively low, ~15 °C (Nobel and Bobich, 2002; Nobel, 2003), because PEPCase and NAD(P)-malate dehydrogenase have optimal mean temperatures reflecting the conditions of cooler nights (Yamori *et al.*, 2014). Indeed, substantial net CO₂ uptake occurs at a nocturnal temperature of as low as 0 °C for *Opuntia ficus-indica* (Cui *et al.*, 1993). In tropical lowland areas, CAM epiphytes grow at higher mean nocturnal temperatures for most of

the year, and their PEPCase activity can acclimatize to higher stem temperatures. Thus, CAM epiphytes can be expected to have an optimal night temperature for CO₂ uptake like that of the hemiepiphytic cactus *Hylocereus undatus*, which is ~20–25 °C (Raveh *et al.*, 1995; Nobel and de la Barrera, 2004).

Owing to the lack of experimental data for temperature optima in CAM epiphytes in fully controlled laboratory conditions, we focus on data from field studies. Epiphytic CAM orchids growing in the open in Singapore experience a nocturnal minimum night temperature of ~22 °C (Neales and Hew, 1975). The epiphytic CAM bromeliad *Tillandsia usneoides* shows an optimum CO₂ assimilation between temperatures of 15 and 20 °C (Medina, 1987). Epiphytic orchids from dry forests have higher increases in titratable tissue acidity (ΔH^+) during the early dry season, when leaf nocturnal temperatures are ~22 °C or less, compared with those of the rainy and late dry seasons (de la Rosa-Manzano *et al.*, 2014). Also, some *Tillandsia* spp. increase ΔH^+ in cooler months in a tropical dry forest of the Pacific coast of Mexico (e.g. *T. eistetteri* and *T. ionantha*; Reyes-García *et al.*, 2008). However, in another tropical dry forest in Yucatan, Mexico, plants of *T. brachycaulos* have greater ΔH^+ during the warmer nights of the rainy season than during the cooler early dry season nights (González-Salvatierra *et al.*, 2021).

High temperatures have relatively little influence on growth and survival of terrestrial CAM plants; apparently, daytime air and leaf or stem temperatures are not critical for photosynthesis, with the tolerated temperature extreme reaching 68 °C (Nobel and Bobich, 2002). In general, however, tolerance limits are certainly lower for tropical CAM plants. For example, hemiepiphytic *H. undatus* and terrestrial *Mammillaria gaumeri* cannot tolerate temperatures >50 °C (Nobel *et al.*, 2002; Cervera *et al.*, 2006). *Tillandsia* species from tropical dry forests tolerate air temperatures of ≤42 °C (Cervantes *et al.*, 2005; Hernández-Robinson *et al.*, 2020; Rosado-Calderón *et al.*, 2020). Furthermore, a study applying different day/night temperature regimes found that most of the 17 tested species of epiphytic bromeliads (C₃ and CAM) performed well at temperatures predicted for the end of this century (Müller *et al.*, 2018). More field and laboratory studies are clearly required, with information on the abiotic conditions of epiphytic microhabitats, to understand the effect of high temperatures on growth and survival of CAM epiphytes and of epiphytes in general.

Climatic extremes

Apart from changing long-term averages in temperature and precipitation, an increased likelihood of extreme events in the future is a major concern (Castillo *et al.*, 2021). For example, climate change might lead to more and stronger cyclonic storms (Landsea *et al.*, 2006; Elsner *et al.*, 2008; Sobel *et al.*, 2016). In combination with the ongoing fragmentation of tropical forests, strong wind (of increased intensity or otherwise) will affect epiphyte communities in addition to the habitat loss they experience. Fragmented forests are more vulnerable to wind disturbance (Laurance *et al.*, 1997; Laurance and Curran, 2008), with the epiphytic component in the upper strata of the forest being particularly vulnerable (Tay *et al.*, 2021; Einzmann

et al., 2022a). However, CAM epiphytes might be less affected if such disturbance leads mainly to increased exposure, but overall, the photosynthetic pathway used by epiphytes is likely to be largely irrelevant in the context of such disturbance.

As another consequence of global change, there seems to be an increase in the frequency of Central Pacific El Niño events in recent decades (Freund *et al.*, 2019). For one such event in 2015–16, the effect on an epiphyte community in small-statured *Annona glabra* trees growing along the shoreline of BCI has been documented (Einzmann *et al.*, 2022b). During this very strong El Niño event, annual rainfall in central Panama was reduced from the average 2600 mm yr⁻¹ to only 1800 mm yr⁻¹ (Paton, 2022), following 2 years with already markedly below-average rainfall. *Annona glabra* has a relatively open crown, and growth along the shore means that epiphytes experience conditions resembling the upper crown in the forest despite the small stature of the host tree. If CAM were of major advantage, C₃ species should be much more affected than CAM species. However, no difference in their change in abundance was found (Einzmann *et al.*, 2022b). In the reference period, 2002–15, both CAM and C₃ species growing on the very same trees consistently increased in abundance, while individual numbers decreased in similar proportion irrespective of photosynthetic pathway from 2015 to 2016 (Table 5).

Long-term variation in the proportion of CAM species

Gradual changes in climate could affect C₃ and CAM species differentially. Increasing temperatures and changes in precipitation could lead to a drier climate, in which the CAM species among epiphytes might be favoured. We searched for possible evidence in long-term studies of epiphyte assemblages. We found only three data sets that cover a longer time period, from 8 years (Einzmann and Zotz, 2017) and ~11 years (Mendieta-Leiva *et al.*, 2022) to a maximum of 21 years (Einzmann *et al.*, 2021). Given that all these studies were performed in Panama, where neither annual precipitation nor dry season length has changed over the last decades (Paton, 2022), and where changes in precipitation are not predicted for the future (Kusunoki *et al.*, 2019), one would not expect any directional change in

TABLE 5. Proportions of epiphytes with crassulacean acid metabolism (CAM) and C₃ growing on the *Annona glabra* trees along the shoreline of Barro Colorado Island (BCI), Panama. About 50 % of the trees growing around BCI form the basis for a long-term study that encompasses three censuses: 1994, 2002 and 2015. Included here is a subset of 145 trees that were studied before and after a very strong El Niño event (Einzmann *et al.*, 2022b)

Epiphyte	2002	2015	2016
Individuals	4298	8074	7895
Species	42	52	52
CAM individuals	2032	3457	3340
CAM species	11	14	14
CAM individuals (%)	47.3	42.8	42.3
CAM species (%)	26.2	26.9	26.9

community composition. However, we consider it important to document these unique time series of ‘normal’ fluctuations as essential background information for future studies designed to detect any directional changes in the proportion of CAM species elsewhere.

Over 21 years and three censuses, epiphytes growing on *Annona glabra* around BCI did not show a consistent pattern regarding CAM species (Table 6; Einzmann *et al.*, 2021). In a first census interval (1994–2002), there was a relative decrease in abundance of CAM species, whereas in the second census interval (2002–15) there was a relative increase in CAM species. Overall, in the long-term data set the proportion of CAM species varied little (~20–26 %), with a similarly constant contribution of ~47 % of CAM individuals to total epiphyte abundance (Table 6). Compared with the proportion of CAM species and individuals from forest trees (Tables 1 and 2), CAM species were of much greater importance in *Annona glabra*.

There were no larger changes in the proportion of CAM epiphytes in the other two studies either (Fig. 2). The maximum difference was observed in epiphytes in pasture trees, with a decrease in abundance of CAM species of ~10 % over 8 years.

Land use change

The process euphemistically termed ‘land use change’ is still the largest threat for tropical epiphytes compared with other drivers of global change identified by Sala *et al.* (2000), such as direct effects of CO₂, altered rainfall patterns or climatic extremes. Although the photosynthetic pathway is clearly irrelevant in the case of complete deforestation, it seems to play a role given more moderate conversions, e.g. to secondary forests or agricultural landscapes with pasture trees. In the case of more isolated trees and more fragmented forest patches, the microclimate is typically drier, which should favour CAM species. Indeed, the proportion of CAM species is much higher in pasture trees (Table 3) than in forest trees (Table 2) under otherwise comparable precipitation regimes. The same is true for the number of individuals.

However, historically, epiphytic CAM species might have suffered much more from previous human activities than C₃ species, because tropical dry forests, in which CAM epiphytes dominate, have been transformed to a larger degree than any other type of tropical forest for hundreds of years (Portillo-Quintero *et al.*, 2015; Sunderland *et al.*, 2015;

TABLE 6. Epiphytes growing on *Annona glabra* trees along the shoreline of Barro Colorado Island, Panama, were followed over 21 years (Einzmann *et al.*, 2021)

Epiphyte	1994	2002	2015
Individuals	14 920	23 674	30 734
Species	58	69	72
CAM individuals	6913	11 497	14 419
CAM species	15	14	17
CAM individuals (%)	46.3	48.6	46.9
CAM species (%)	25.9	20.3	23.6

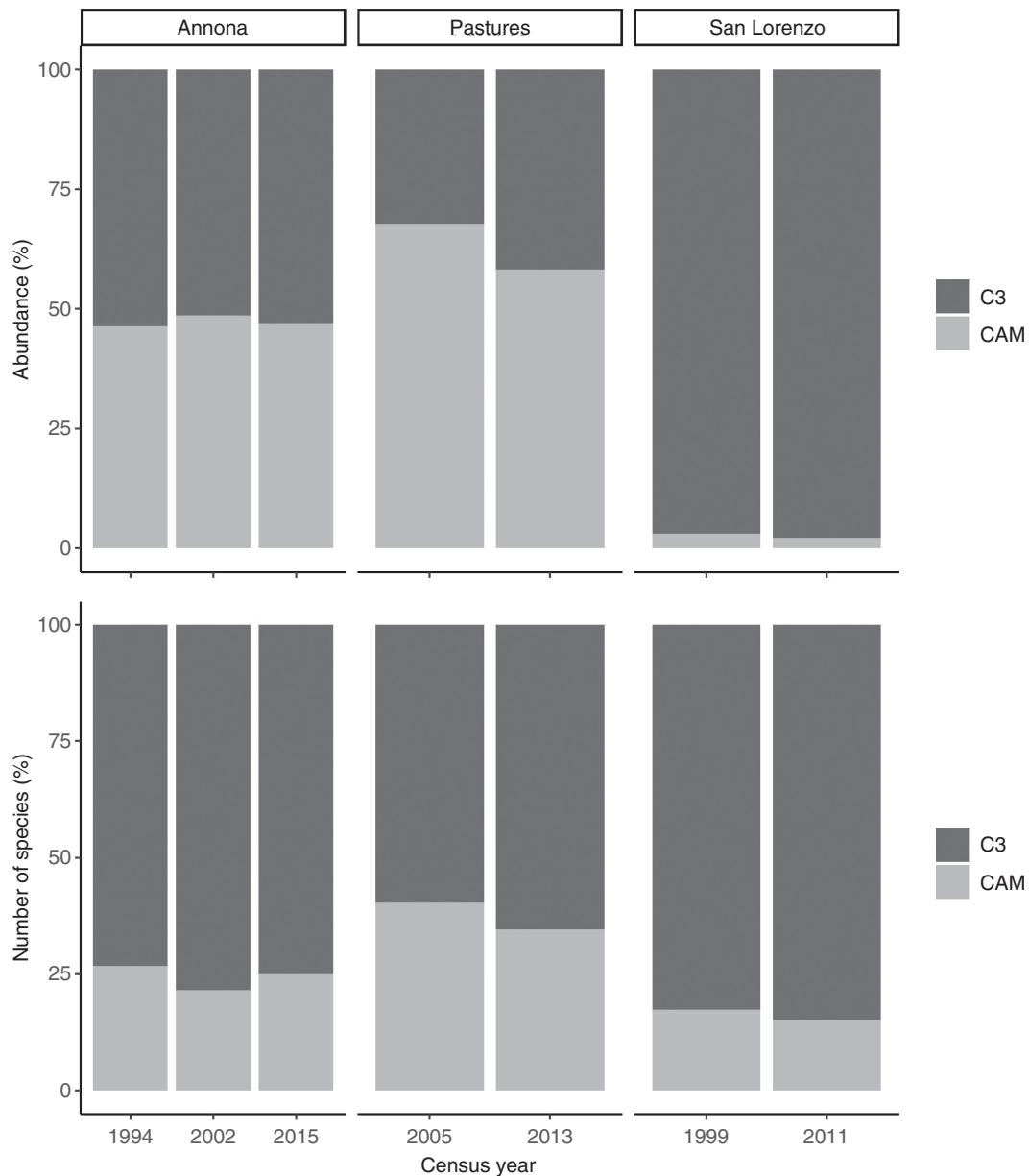


FIG. 2. Temporal changes in the percentage of abundance and number of species of epiphytic C_3 species and species with crassulacean acid metabolism (CAM) in three different systems. *Annona*, epiphyte assemblages censused three times on *Annona glabra* trees growing along the shoreline of Barro Colorado Island (Einzmann *et al.*, 2021); Pastures, epiphyte assemblages censused twice on pasture trees growing along a rainfall gradient in western Panama (Einzmann and Zotz, 2017); San Lorenzo, epiphyte assemblages censused twice on all trees within the San Lorenzo crane site (Mendieta-Leiva *et al.*, 2022).

Siyum, 2020). Some attention has been paid to dry forest recovery. For instance, the long history of the transformation of tropical dry deciduous forest of northern Yucatan has resulted in the impoverishment of tree species, because succession has favoured species that sprout after perturbation (González-Iturbe *et al.*, 2002). In other areas with less perturbation and with remnants of old forest, recovery of canopy height, plant density and crown cover occurred in ~20 years, but species richness and biomass continue to increase after >80 years (Lebrija-Trejos *et al.*, 2008; Dupuy *et al.*, 2012; Guerra-Martínez *et al.*, 2021). Nevertheless,

the recovery of epiphyte assemblages has been almost entirely ignored in successional studies of tropical dry forests and tropical forests in general. In one of the few exceptional studies with a focus on epiphytes, Woods and DeWalt (2013) argued that it takes almost two centuries for epiphyte species composition in secondary lowland forests of central Panama to recover. Comparing this number with the estimated 120 years for secondary tropical forest to recover other forest attributes (Poorter *et al.*, 2021), epiphytes might take particularly long to recover from such disturbances.

WHY IS CAM NOT MORE COMMON AMONG VASCULAR EPIPHYTES?

Although CAM is key at the dry end of current epiphytic existence (Mooney *et al.*, 1989; Reyes-García *et al.*, 2008; Fontoura and Reinert, 2009; Cach-Pérez *et al.*, 2018), current evidence does not suggest that, compared with vascular plants in general, this metabolic pathway is disproportionately common among epiphytes. If water scarcity is genuinely the defining feature of the epiphytic habitat, as often suggested (e.g. Benzing, 1990; Zotz and Hietz, 2001; Lüttge, 2008), this is somewhat surprising. So, what did we miss?

We see a number of explanations for this seeming discrepancy. We know that at the regional scale the epiphytic life form responds more strongly than others (e.g. trees or climbers) to differences in water supply, as demonstrated in the classic study by Gentry and Dodson (1987). However, by far the highest numbers of species and the highest abundances are found at the wet end, where epiphytes are not much affected by water scarcity. In such ecosystems, CAM would primarily incur a metabolic cost, while possible benefits would be restricted to rare drought events. The impact of such occasional periods of water scarcity on cloud forest epiphytes has been studied in detail by Gotsch and collaborators (e.g. Gotsch *et al.*, 2015, 2018; Williams *et al.*, 2020). These authors highlighted the importance of water storage. The need to develop a more differentiated view of the importance of the factor water for epiphytes was also emphasized by Zotz *et al.* (2021a) in a recent review of epiphyte ecophysiology. Here are a few observations that contradict the arguably simplistic view that epiphytes, as a group, are generally more affected by water stress than ground-rooted plants. First, $\delta^{13}\text{C}$ values of C_3 epiphytes do not differ from those of terrestrial herbs in the TRY database (Kattge *et al.*, 2020), which suggests similar broad-scale stomatal limitations (Hietz *et al.*, 2022). Second, water content per dry mass or leaf area is substantially lower in epiphytic bromeliads compared with terrestrials, in both C_3 and CAM species (Males and Griffiths, 2017). As the samples for that study came from well-watered collections in botanical gardens, this finding should primarily reflect genetic differences, which makes it even more surprising. Finally, in forests at Mount Kilimanjaro, tree leaves stored three times as much water as foliage of co-occurring epiphytes (Schellenberger Costa *et al.*, 2018). Taken together, epiphytes might be less special in terms of their water relationships than previously thought, which should also lead to an adjustment of our expectation about the prevalence of CAM among epiphytes.

Following Winter (2019), we reserved the term ‘CAM plant’ to those species that ‘throughout their lives, obtain the majority of their carbon through the CAM pathway’, which is typically deduced from a $\delta^{13}\text{C}$ value of leaf tissue higher than -20‰ , which is indicative of $\geq 50\%$ nocturnal CO_2 uptake. This approach ignores the possibility that CAM might affect whole plant carbon budgets via reducing carbon losses by other organs (petals, fruit, stems and roots; see above) and also ignores the possible importance of limited nocturnal acidification without uptake of external CO_2 , i.e. ‘weak CAM’ *sensu* Winter (2019), as found in the leaves of many orchids, bromeliads and ferns (Zotz and Tyree, 1996; Holtum and Winter, 1999; Schmidt and Zotz, 2001; Silvera *et al.*, 2005). Naturally, all species estimates

would change if all taxa that show small but detectable nocturnal acidification at least occasionally were to be included as ‘ C_3 -CAM plants’ or ‘weak CAM plants’. Given that most of the relevant studies were performed with epiphytes, there is a largely unknown number of terrestrial equivalents, which does not allow us to provide a reasonable estimate for the relative occurrence of this phenomenon among epiphytic vs. terrestrial taxa. However, we would argue that rather than juggling with the number of species with ‘weak CAM’, it is more important to study the ecological relevance of such small nocturnal acidification in either life form. The few detailed analyses of such ‘weak CAM’ activity in vascular epiphytes suggest a rather moderate contribution to water and carbon budgets. In the tank bromeliad *Werauhia sanguinolenta* (Schmidt and Zotz, 2001) and the orchid *Dimerandra emarginata* (Zotz and Tyree, 1996) maximum nocturnal acidification under drought amounted to the equivalent of net CO_2 fixation rates of, respectively, 0.1 and 0.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the night. This is less than what one would expect from the complete recycling of respiratory CO_2 . Currently, it is unclear whether such weak ‘CAM activity’ in C_3 plants is ecologically important and/or more or less idiosyncratic for epiphytes; we would need information on the frequency of ‘weak CAM’ in epiphytic vs. terrestrial taxa to address this question.

It is important to emphasize that CAM is not the only option for plants to deal with drought. Sinclair (1984), for example, stated that the most important drought-related strategy in the studied ferns is the tolerance to very large reductions in leaf relative water content rather than CAM. Other ways to bridge periods of water scarcity among epiphytic taxa include internal water storage in leaves, roots and shoots (Gessner, 1956; Yang *et al.*, 2016; Hernández-Robinson *et al.*, 2020), external water storage in phytotelmata (Zotz and Thomas, 1999; Zotz *et al.*, 2020), strongly reduced cuticular water loss (Benzing and Burt, 1970; Helbsing *et al.*, 2000), drought-deciduousness (Benzing *et al.*, 1982; Mehltreter, 2008) and desiccation tolerance (Stuart, 1968; Proctor, 2012), while highly effective water uptake via roots (Biebl, 1964; Zotz and Winkler, 2013; Leroy *et al.*, 2019) and leaves (Gotsch *et al.*, 2015; Darby *et al.*, 2016) allows epiphytes to replenish stores fast as part of a general recovery after stress events. Interestingly, the C_4 pathway, which is common in many arid terrestrial biomes (Sage *et al.*, 2018), is apparently not used by any epiphyte (Zotz, 2016).

Although our view of the importance of CAM among epiphytes has possibly been exaggerated in the past, there are recurring patterns in epiphyte community structure that demonstrate an important role of CAM, not only at the very dry end of forest habitats. Similar to the results shown for epiphytes on emergent trees in central Panama (Table 1), a number of studies have found a clear stratification, with CAM species typically being dominant or at least relatively abundant in the upper parts of moist tropical forests (Griffiths and Smith, 1983; Zotz and Ziegler, 1997; Zotz, 2004). Again, such a pattern should not be confused with the notion that CAM is indispensable in the most exposed growing sites. Numerous C_3 species can be found there, with well-studied examples in the upper crown of large, drought-deciduous emergents in the lowland forest of BCI being *Dimerandra emarginata* (Einzmann *et al.*, 2015), *Niphidium crassifolium* and *Catasetum viridiflavum* (Zotz and Winter, 1994).

Likewise, Fontoura and Reinert (2009), studying epiphytic bromeliads in a dry forest in Southeastern Brazil, found that most species used CAM, but at the most exposed microsites a C₃ bromeliad (*Vriesea procera*) dominated, and not a CAM species. A similar pattern was described by Zotz (1997); the large C₃ tank bromeliad *Werauhia sanguinolenta* was more common in the exposed parts of *Annona glabra* crowns than a co-occurring CAM (*Tillandsia fasciculata*) and a C₃-CAM species (*Guzmania monostachia*). This again highlights that CAM can be important among epiphytes, but is still but one of several functional options allowing growth in demanding epiphytic situations.

CONCLUSION

This paper reviews the importance of CAM among epiphytes in general in current climatic conditions and explores future prospects under global change. We aimed to stimulate a discussion by questioning the frequently expressed view of a disproportionate importance of CAM among vascular epiphytes compared with ground-rooted plants. Although there is little doubt that at the dry end of the ecological spectrum, epiphytic growth is often difficult or impossible for C₃ plants, in general CAM species are not overly common among epiphytes. Thus, we should also reconsider claims that CAM is a key innovation for epiphytism as such and narrow any evolutionary importance down to specific ecological scenarios, such as growth in dry forests. An answer to the question regarding whether global change might lead to a shift in the relative importance of CAM among epiphytes is again facing complexity. Historically, the almost complete destruction of tropical dry forests has probably affected CAM epiphytes more than C₃ species, but depending on the particular driver (temperature, precipitation, CO₂ or disturbance), future effects of human activities might be neutral with regard to photosynthetic pathway, or CAM species might possibly be less affected, e.g. by drought, and thus benefit relatively, as long as trees are available as hosts.

ACKNOWLEDGEMENTS

G.Z. wants to thank his former PhD advisor for many stimulating conversations on CAM and other topics over more than three decades.

LITERATURE CITED

- Batke SP, Holohan A, Hayden R, Fricke W, Porter AS, Evans-FitzGerald CM. 2018. The pressure is on – epiphyte water-relations altered under elevated CO₂. *Frontiers in Plant Science* 9: 1758.
- Benzing DH. 1989. The evolution of epiphytism. In: Lüttge U, ed. *Vascular plants as epiphytes: evolution and ecophysiology*. Heidelberg: Springer, 15–41.
- Benzing DH. 1990. *Vascular epiphytes. General biology and related biota*. Cambridge: Cambridge University Press.
- Benzing DH, Bent A, Moscow D, Peterson G, Renfrow A. 1982. Functional correlates of deciduousness in *Catasetum integerrimum* (Orchidaceae). *Selbyana* 7: 1–9.
- Benzing DH, Burt KM. 1970. Foliar permeability among twenty species of the Bromeliaceae. *Bulletin of the Torrey Botanical Club* 97: 269–279. doi:10.2307/2483646.
- Benzing DH, Ott DW. 1981. Vegetative reduction in epiphytic Bromeliaceae and Orchidaceae: its origin and significance. *Biotropica* 13: 131–140. doi:10.2307/2387715.
- Biebl R. 1964. Zum Wasserhaushalt von *Tillandsia recurvata* L. und *Tillandsia usneoides* L. auf Puerto Rico. *Protoplasma* 58: 345–368. doi:10.1007/bf01253007.
- Bone RE, Smith JAC, Arrigo N, Buerki S. 2015. A macro-ecological perspective on crassulacean acid metabolism (CAM) photosynthesis evolution in Afro-Madagascan drylands: Eulophiinae orchids as a case study. *New Phytologist* 208: 469–481. doi:10.1111/nph.13572.
- Cach-Pérez MJ, Andrade JL, Reyes-García C. 2018. Morphophysiological plasticity in epiphytic bromeliads across a precipitation gradient in the Yucatan peninsula, Mexico. *Tropical Conservation Science* 11: 1940082918781926. doi:10.1177/1940082918781926.
- Castillo F, Wehner M, Stone DA. 2021. *Extreme events and climate change: a multidisciplinary approach*. New York: John Wiley & Sons.
- Cernusak LA, Winter K, Dalling JW, et al. 2013. Tropical forest responses to increasing atmospheric CO₂: current knowledge and opportunities for future research. *Functional Plant Biology* 40: 531–551. doi:10.1071/fp.12309.
- Cervantes SE, Graham EA, Andrade JL. 2005. Light microhabitats, growth and photosynthesis of an epiphytic bromeliad in a tropical dry forest. *Plant Ecology* 179: 107–118. doi:10.1007/s11258-004-5802-3.
- Cervera JC, Andrade JL, Simá JL, Graham EA. 2006. Microhabitats, germination, and establishment for *Mammillaria gauderi* (Cactaceae), a rare species from Yucatan. *International Journal of Plant Sciences* 167: 311–319. doi:10.1086/498650.
- Cockburn W, Goh CJ, Avadhani PN. 1985. Photosynthetic carbon assimilation in a shootless orchid, *Chiloschista usneoides* (DON) LDL: a variant on crassulacean acid metabolism. *Plant Physiology* 77: 83–86. doi:10.1104/pp.77.1.83.
- Coutinho LM. 1964. Algumas informações sobre a capacidade rítmica diária da fixação e acumulação de CO₂ no escuro em epífitas e erbáceas terrestres da mata pluvial. *Botânica* 21: 397–408.
- Crayn DM, Winter K, Schulte K, Smith JAC. 2015. Photosynthetic pathways in Bromeliaceae: phylogenetic and ecological significance of CAM and C₃ based on carbon isotope ratios for 1893 species. *Botanical Journal of the Linnean Society* 178: 169–221.
- Croonenborghs S, Ceusters J, Londers E, De Proft MP. 2009. Effects of elevated CO₂ on growth and morphological characteristics of ornamental bromeliads. *Scientia Horticulturae* 121: 192–198. doi:10.1016/j.scienta.2009.01.018.
- Cui M, Miller PM, Nobel PS. 1993. CO₂ exchange and growth of the crassulacean acid metabolism plant *Opuntia ficus-indica* under elevated CO₂ in open-top chambers. *Plant Physiology* 103: 519–524. doi:10.1104/pp.103.2.519.
- Darby A, Draguljić D, Glunk A, Gotsch SG. 2016. Habitat moisture is an important driver of patterns of sap flow and water balance in tropical montane cloud forest epiphytes. *Oecologia* 182: 357–371.
- Drake BG, González-Meler MA, Long SP. 1997. More efficient plants: a consequence of rising atmospheric CO₂? *Annual Review of Plant Physiology and Plant Molecular Biology* 48: 609–639. doi:10.1146/annurev.arplant.48.1.609.
- Drennan PM, Nobel PS. 2000. Responses of CAM species to increasing atmospheric CO₂ concentrations. *Plant, Cell & Environment* 23: 767–781.
- Dueker J, Arditti J. 1968. Photosynthetic ¹⁴C fixation by green *Cymbidium* (Orchidaceae) flowers. *Plant Physiology* 43: 130–132. doi:10.1104/pp.43.1.130.
- Dupuy JM, Hernández-Stefanoni JL, Hernández-Juárez RA, et al. 2012. Patterns and correlates of tropical dry forest structure and composition in a highly replicated chronosequence in Yucatan, Mexico. *Biotropica* 44: 151–162.
- Earnshaw MJ, Winter K, Ziegler H, et al. 1987. Altitudinal changes in the incidence of crassulacean acid metabolism in vascular epiphytes and related life forms in Papua New Guinea. *Oecologia* 73: 566–572. doi:10.1007/bf00379417.
- Einmann HJR, Beyschlag J, Hofhansl F, Wanek W, Zotz G. 2015. Host tree phenology affects vascular epiphytes at the physiological, demographic and community level. *AoB Plants* 7: plu073.
- Einmann HJR, Tay J, Zotz G. 2022a. What happens to epiphytic bromeliads in a windy spot? *Journal of Tropical Ecology* 38: 158–163.
- Einmann HJR, Weichgrebe L, Zotz G. 2021. Long-term community dynamics in vascular epiphytes on *Annona glabra* along the shoreline of

- Barro Colorado Island, Panama. *Journal of Ecology* **109**: 1931–1946. doi:10.1111/1365-2745.13618.
- Einzmann HJR, Weichgrebe L, Zotz G. 2022b. The impact of a severe El Niño event on vascular epiphytes in lowland Panama. *Diversity* **14**: 325. doi:10.3390/d14050325.
- Einzmann HJR, Zotz G. 2017. ‘No signs of saturation’: long-term dynamics of vascular epiphyte communities in a human-modified landscape. *Biodiversity and Conservation* **26**: 1393–1410. doi:10.1007/s10531-017-1306-z.
- Elsner JB, Kossin JP, Jagger TH. 2008. The increasing intensity of the strongest tropical cyclones. *Nature* **455**: 92–95. doi:10.1038/nature07234.
- Flores-Palacios A, García-Franco JG, Capistrán-Barradas A. 2015. Biomass, phorophyte specificity and distribution of *Tillandsia recurvata* in a tropical semi-desert environment (Chihuahuan Desert, Mexico). *Plant Ecology and Evolution* **148**: 68–75.
- Foutoura T, Reinert F. 2009. Habitat utilization and CAM occurrence among epiphytic bromeliads in a dry forest from southeastern Brazil. *Revista Brasileira de Botânica* **32**: 521–530.
- Freund MB, Henley BJ, Karoly DJ, McGregor HV, Abram NJ, Dommegen D. 2019. Higher frequency of Central Pacific El Niño events in recent decades relative to past centuries. *Nature Geoscience* **12**: 450–455. doi:10.1038/s41561-019-0353-3.
- Gatti RC, Reich PB, Gamarra JGP, et al. 2022. The number of tree species on Earth. *Proceedings of the National Academy of Sciences of the United States of America* **119**: e2115329119.
- Gentry AH, Dodson CH. 1987. Diversity and biogeography of Neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden* **74**: 205–233. doi:10.2307/2399395.
- Gessner F. 1956. Der Wasserhaushalt der Epiphyten und Lianen. In: Stocker O, ed. *Pflanze und Wasser*. Berlin: Springer, 915–950.
- Givnish TJ, Barfuss MHJ, Van Ee B, et al. 2014. Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. *Molecular Phylogenetics and Evolution* **71**: 55–78.
- Givnish TJ, Spalink D, Ames M, et al. 2015. Orchid phylogenomics and multiple drivers of their extraordinary diversification. *Proceedings of the Royal Society B: Biological Sciences* **282**: 20151553.
- Göbel CY, Schlumpberger BO, Zotz G. 2020. What is a pseudobulb? Toward a quantitative definition. *International Journal of Plant Sciences* **181**: 686–696.
- González-Iturbe JA, Olmsted I, Tun-Dzul F. 2002. Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico. *Forest Ecology and Management* **167**: 67–82. doi:10.1016/S0378-1127(01)00689-2.
- González-Salvatierra C, Peña-Rodríguez LM, Reyes-García C, de la Barrera E, Andrade JL. 2021. Seasonal changes in photosynthesis for the epiphytic bromeliad *Tillandsia brachycaulos* in a tropical dry deciduous forest. *Botanical Sciences* **99**: 850–862.
- Gotsch SG, Dawson TE, Draguljić D. 2018. Variation in the resilience of cloud forest vascular epiphytes to severe drought. *New Phytologist* **219**: 900–913.
- Gotsch SG, Nadkarni NM, Darby A, et al. 2015. Life in the treetops: ecophysiological strategies of canopy epiphytes in a tropical montane cloud forest. *Ecological Monographs* **85**: 393–412. doi:10.1890/14-1076.1.
- Gouk SS, He J, Hew CS. 1999. Changes in photosynthetic capability and carbohydrate production in an epiphytic CAM orchid plantlet exposed to super-elevated CO₂. *Environmental and Experimental Botany* **41**: 219–230. doi:10.1016/S0098-8472(99)00006-4.
- Gouk SS, Yong JWH, Hew CS. 1997. Effects of super-elevated CO₂ on the growth and carboxylating enzymes in an epiphytic CAM orchid plantlet. *Journal of Plant Physiology* **151**: 129–136. doi:10.1016/S0176-1617(97)80144-7.
- Graham EA, Andrade JL. 2004. Drought tolerance associated with vertical stratification of two co-occurring epiphytic bromeliads in a tropical dry forest. *American Journal of Botany* **91**: 699–706. doi:10.3732/ajb.91.5.699.
- Graham EA, Nobel PS. 1996. Long-term effects of a doubled atmospheric CO₂ concentration on the CAM species *Agave deserti*. *Journal of Experimental Botany* **47**: 61–69. doi:10.1093/jxb/47.1.61.
- Griffiths H, Smith JAC. 1983. Photosynthetic pathways in the Bromeliaceae of Trinidad: relations between life-forms, habitat preference and the occurrence of CAM. *Oecologia* **60**: 176–184. doi:10.1007/bf00379519.
- Grigore M-N, Ivanescu L, Toma C. 2014. *Halophytes: an integrative anatomical study*. Switzerland: Springer International Publishing.
- Guerra-Martínez F, García-Romero A, Martínez-Morales MA, López-García J. 2021. Resiliencia ecológica del bosque tropical seco: recuperación de su estructura, composición y diversidad en Tehuantepec, Oaxaca. *Revista Mexicana de Biodiversidad* **92**: 923422. doi:10.22201/ib.20078706e.2021.92.3422.
- Guzmán-Jacob V, Guerrero Ramirez N, Craven D, et al. 2022. Broad- and small-scale environmental gradients drive variation in chemical, but not morphological, leaf traits of vascular epiphytes. *Functional Ecology* **36**: 1858–1872. doi:10.1111/1365-2435.14084. in press.
- Helbsing S, Riederer M, Zotz G. 2000. Cuticles of vascular epiphytes: efficient barriers for water loss after stomatal closure? *Annals of Botany* **86**: 765–769.
- Hernández-Robinson S, Graham EA, Hernández-González O, et al. 2020. Hot but not dry: Modest changes in water relations for an epiphytic bromeliad in a tropical dry deciduous forest. *International Journal of Plant Sciences* **181**: 945–954.
- Herrera A. 2020. Are thick leaves, large mesophyll cells and small intercellular air spaces requisites for CAM? *Annals of Botany* **125**: 859–868. doi:10.1093/aob/mcaa008.
- Hietz P, Wagner K, Nunes Ramos F, et al. 2022. Putting vascular epiphytes on the traits map. *Journal of Ecology* **110**: 340–358.
- Hietz P, Wanek W, Popp M. 1999. Stable isotopic composition of carbon and nitrogen, and nitrogen content in vascular epiphytes along an altitudinal transect. *Plant, Cell & Environment* **22**: 1435–1443.
- Holthe PA, Patel A, Ting IP. 1992. The occurrence of CAM in *Peperomia. Selbyana* **13**: 77–87.
- Holtum JAM, Winter K. 1999. Degrees of crassulacean acid metabolism in tropical epiphytic and lithophytic ferns. *Australian Journal of Plant Physiology* **26**: 749–757.
- Horn JW, Xi Z, Riina R, et al. 2014. Evolutionary bursts in *Euphorbia* (Euphorbiaceae) are linked with photosynthetic pathway. *Evolution* **68**: 3485–3504. doi:10.1111/evo.12534.
- Hu AQ, Gale SW, Liu ZJ, Fischer GA, Saunders RMK. 2022. Diversification slowdown in the *Cirrhopetalum* alliance (*Bulbophyllum*, Orchidaceae): insights from the evolutionary dynamics of crassulacean acid metabolism. *Frontiers in Plant Science* **13**: 794171.
- Hunter JP. 1998. Key innovations and the ecology of macroevolution. *Trends in Ecology & Evolution* **13**: 31–36.
- IPCC. 2021. *Climate change 2021: the physical science basis. contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge: Cambridge University Press.
- Kattge J, Bönsch G, Díaz S, et al. 2020. TRY plant trait database – enhanced coverage and open access. *Global Change Biology* **26**: 119–188.
- Kluge M, Bruffert J, Rauh W, Ravelomanana D, Ziegler H. 1995. Ecophysiological studies on the vegetation of Madagascar: a $\delta^{13}\text{C}$ and δD survey for incidence of crassulacean acid metabolism (CAM) among orchids from montane forests and succulents from the xerophytic thorn-bush. *Isotopes in Environmental and Health Studies* **31**: 191–210. doi:10.1080/10256019508234018.
- Kusunoki S, Nakaegawa T, Pinzón R, Sanchez-Galan JE, Fábrega JR. 2019. Future precipitation changes over Panama projected with the atmospheric global model MRI-AGCM3.2. *Climate Dynamics* **53**: 5019–5034.
- Landsea CW, Harper BA, Hoarau K, Knaff JA. 2006. Can we detect trends in extreme tropical cyclones? *Science* **313**: 452–454. doi:10.1126/science.1128448.
- Laurance WF, Curran TJ. 2008. Impacts of wind disturbance on fragmented tropical forests: a review and synthesis. *Australian Ecology* **33**: 399–408.
- Laurance WF, Laurance SG, Ferreira LV, Rankin de Merona JM, Gascon C, Lovejoy TE. 1997. Biomass collapse in Amazonian forest fragments. *Science* **278**: 1117–1118.
- Lebrija-Trejos E, Bongers F, Pérez-García EA, Meave JA. 2008. Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. *Biotropica* **40**: 422–431. doi:10.1111/j.1744-7429.2008.00398.x.
- Leroy C, Gril E, Si Ouali L, et al. 2019. Water and nutrient uptake capacity of leaf-absorbing trichomes vs. roots in epiphytic tank bromeliads. *Environmental and Experimental Botany* **163**: 112–123.
- Li CR, Gan LJ, Xia K, Zhou X, Hew CS. 2002a. Responses of carboxylating enzymes, sucrose metabolizing enzymes and plant hormones in a tropical epiphytic CAM orchid to CO₂ enrichment. *Plant, Cell & Environment* **25**: 369–377.
- Li CR, Liang YH, Hew CS. 2002b. Responses of Rubisco and sucrose-metabolizing enzymes to different CO₂ in a C₃ tropical epiphytic

- orchid *Oncidium Goldiana*. *Plant Science* **163**: 313–320. doi:10.1016/S0168-9452(02)00100-0.
- Luján M, Oleas NH, Winter K. 2021. Evolutionary history of CAM photosynthesis in Neotropical *Clusia*: insights from genomics, anatomy, physiology and climate. *Botanical Journal of the Linnean Society* **199**: 538–556. doi:10.1093/botlinnean/boab075.
- Lüttge U. 2004. Ecophysiology of crassulacean acid metabolism (CAM). *Annals of Botany* **93**: 629–652.
- Lüttge U. 2008. *Physiological ecology of tropical plants*. Berlin: Springer.
- Males J, Griffiths H. 2017. Functional types in the Bromeliaceae: relationships with drought resistance traits and bioclimatic distributions. *Functional Ecology* **31**: 1868–1880. doi:10.1111/1365-2435.12900.
- Martin CE, Mas EJ, Lu C, Ong BL. 2010. The photosynthetic pathway of the roots of twelve epiphytic orchids with CAM leaves. *Photosynthetica* **48**: 42–50. doi:10.1007/s11099-010-0007-6.
- Medina E. 1987. Aspectos ecofisiológicos de plantas CAM en los trópicos. *Revista de Biología Tropical* **35**(Suppl. 1): 55–70.
- Mehlreiter K. 2008. Phenology and habitat specificity of tropical ferns. In: Ranker TA, Haufler CH, eds. *Biology and evolution of ferns and lycophytes*. New York: Cambridge University Press, 201–221.
- Mendieta-Leiva G, Buckley HL, Zotz G. 2022. Directional changes over time in the species composition of tropical vascular epiphyte assemblages. *Journal of Ecology* **110**: 553–568.
- Messerschmid TFE, Wehling J, Bobon N, et al. 2021. Carbon isotope composition of plant photosynthetic tissues reflects a Crassulacean Acid Metabolism (CAM) continuum in the majority of CAM lineages. *Perspectives in Plant Ecology, Evolution and Systematics* **51**: 125619.
- Monteiro JAF, Zotz G, Körner C. 2009. Tropical epiphytes in a CO₂-rich atmosphere. *Acta Oecologica* **35**: 60–68. doi:10.1016/j.actao.2008.08.001.
- Mooney HA, Bullock SH, Ehleringer JR. 1989. Carbon isotope ratios of plants of a tropical forest in Mexico. *Functional Ecology* **3**: 137–142. doi:10.2307/2389294.
- Moreira ASP, de Lemos Filho JP, Zotz G, Isaias RMS. 2009. Anatomy and photosynthetic parameters of roots and leaves of two shade adapted orchids, *Dichaea cogniauxiana* Schltr. and *Epidendrum secundum* Jacq. *Flora – Morphology, Distribution, Functional Ecology of Plants* **204**: 604–611.
- Motomura H, Ueno O, Kagawa A, Yukawa T. 2008a. Carbon isotope ratios and the variation in the diurnal pattern of malate accumulation in aerial roots of CAM species of *Phalaenopsis* (Orchidaceae). *Photosynthetica* **46**: 531–536.
- Motomura H, Yukawa T, Ueno O, Kagawa A. 2008b. The occurrence of crassulacean acid metabolism in *Cymbidium* (Orchidaceae) and its ecological and evolutionary implications. *Journal of Plant Research* **121**: 163–177. doi:10.1007/s10265-007-0144-6.
- Müller L-LB, Albach D, Zotz G. 2017. ‘Are 3°C too much?’: thermal niche breadth in Bromeliaceae and global warming. *Journal of Ecology* **105**: 507–516.
- Müller L-LB, Albach D, Zotz G. 2018. Growth responses to elevated temperatures and the importance of ontogenetic niche shifts in Bromeliaceae. *New Phytologist* **217**: 127–139.
- Neales TF, Hew CS. 1975. Two types of carbon fixation in tropical orchids. *Planta* **123**: 303–306. doi:10.1007/bf00390710.
- Nobel PS. 2003. *Environmental biology of agaves and cacti*. New York: Cambridge University Press.
- Nobel PS, de la Barrera E, Beilman DW, Doherty JH, Zutta BR. 2002. Temperature limitations for cultivation of edible cacti in California. *Madroño* **49**: 228–236.
- Nobel PS, Bobich EG. 2002. Environmental biology. In: Nobel PS, ed. *Cacti: biology and uses*. Berkeley: University of California Press, 57–74.
- Nobel PS, de la Barrera E. 2004. CO₂ uptake by the cultivated hemiepiphytic cactus, *Hylocereus undatus*. *Annals of Applied Biology* **144**: 1–8.
- Nuernbergk EL. 1961. Endogener Rhythmus und CO₂-Stoffwechsel bei Pflanzen mit diurnalem Säurerhythmus. *Planta* **56**: 28–70.
- Nuernbergk EL. 1963. On the CO₂ metabolism of orchids and its ecological aspects. *Proceedings of 4th World Orchid Conference, Singapore*. Singapore: Straits Times Press, 158–169.
- Ogburn RM, Edwards EJ. 2010. The ecological water-use strategies of succulent plants. In: Kader JC, Delseny M, eds. *Advances in Botanical Research*, Vol. 55. Burlington: Academic Press, 179–225.
- Ong BL, Koh CK-K, Wee YC. 1998. Effects of CO₂ on growth and photosynthesis of *Pyrosia piloselloides* (L.) price gametophytes. *Photosynthetica* **35**: 21–27.
- Paton S. 2022. *Yearly reports Barro Colorado Island*. Smithsonian Tropical Research Institute. Data set. <https://doi.org/10.25573/data.11799111.v3> (18 March 2022, date last accessed).
- Poorter L, Craven D, Jakovac CC, et al. 2021. Multidimensional tropical forest recovery. *Science* **374**: 1370–1376.
- Portillo-Quintero C, Sanchez-Azofeifa A, Calvo-Alvarado J, Quesada M, do Espírito Santo MM. 2015. The role of tropical dry forests for biodiversity, carbon and water conservation in the neotropics: lessons learned and opportunities for its sustainable management. *Regional Environmental Change* **15**: 1039–1049.
- Proctor MCF. 2012. Light and desiccation responses of some Hymenophyllaceae (filmy ferns) from Trinidad, Venezuela and New Zealand: poikilohydry in a light-limited but low evaporation ecological niche. *Annals of Botany* **109**: 1019–1026. doi:10.1093/aob/mcs012.
- Quezada IM, Gianoli E. 2011. Crassulacean acid metabolism photosynthesis in Bromeliaceae: an evolutionary key innovation. *Biological Journal of the Linnean Society* **104**: 480–486. doi:10.1111/j.1095-8312.2011.01713.x.
- Raveh E, Gersani M, Nobel PS. 1995. CO₂ uptake and fluorescence responses for a shade-tolerant cactus *Hylocereus undatus* under current and doubled CO₂ concentrations. *Physiologia Plantarum* **93**: 505–511. doi:10.1111/j.1399-3054.1995.tb06850.x.
- Reyes-García C, Griffiths H, Rincón E, Huante P. 2008. Niche differentiation in tank and atmospheric epiphytic bromeliads of a seasonally dry forest. *Biotropica* **40**: 168–175.
- Rodrigues MA, Matiz A, Cruz AB, et al. 2013. Spatial patterns of photosynthesis in thin- and thick-leaved epiphytic orchids: unravelling C₃-CAM plasticity in an organ-compartmented way. *Annals of Botany* **112**: 17–29. doi:10.1093/aob/mct090.
- de la Rosa-Manzano E, Andrade JL, Zotz G, Reyes-García C. 2014. Respuestas fisiológicas a la sequía de cinco especies de orquídeas epífitas en dos selvas secas de la península de Yucatán. *Botanical Sciences* **92**: 607–616. doi:10.17129/botsci.139.
- Rosado-Calderón AT, Tamayo-Chim M, de la Barrera E, et al. 2020. High resilience to extreme climatic changes in the CAM epiphyte *Tillandsia utriculata* L. (Bromeliaceae). *Physiologia Plantarum* **168**: 547–562.
- Sage RF, Monson RK, Ehleringer JR, Adachi S, Percy RW. 2018. Some like it hot: the physiological ecology of C₂ plant evolution. *Oecologia* **187**: 941–966. doi:10.1007/s00442-018-4191-6.
- Sala OE, Chapin FS 3rd, Armesto JJ, et al. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**: 1770–1774.
- Schellenberger Costa D, Zotz G, Hemp A, Kleyer M. 2018. Trait patterns of epiphytes compared to other plant life forms along a tropical elevation gradient. *Functional Ecology* **32**: 2073–2084.
- Schmidt G, Zotz G. 2001. Ecophysiological consequences of differences in plant size: *in situ* carbon gain and water relations of the epiphytic bromeliad, *Vriesea sanguinolenta*. *Plant, Cell & Environment* **24**: 101–112.
- Silvera K, Santiago LS, Cushman JC, Winter K. 2009. Crassulacean acid metabolism and epiphytism linked to adaptive radiations in the Orchidaceae. *Plant Physiology* **149**: 1838–1847. doi:10.1104/pp.108.132555.
- Silvera K, Santiago LS, Cushman JC, Winter K. 2010. The incidence of crassulacean acid metabolism in Orchidaceae derived from carbon isotope ratios: a checklist of the flora of Panama and Costa Rica. *Botanical Journal of the Linnean Society* **163**: 194–222. doi:10.1111/j.1095-8339.2010.01058.x.
- Silvera K, Santiago LS, Winter K. 2005. Distribution of crassulacean acid metabolism in orchids of Panama: evidence of selection for weak and strong modes. *Functional Plant Biology* **32**: 397–407. doi:10.1071/fp04179.
- Silvestro D, Zizka G, Schulte K. 2014. Disentangling the effects of key innovations on the diversification of Bromelioideae (Bromeliaceae). *Evolution* **68**: 163–175.
- Sinclair R. 1984. Water relations of tropical epiphytes. III. Evidence for CAM. *Journal of Experimental Botany* **35**: 1–7. doi:10.1093/jxb/35.1.1.
- Siyum ZG. 2020. Tropical dry forest dynamics in the context of climate change: syntheses of drivers, gaps, and management perspectives. *Ecological Processes* **9**: 25.
- Smith JAC, Winter K. 1996. Taxonomic distribution of crassulacean acid metabolism. In: Winter K, Smith JAC, eds. *Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution*. Berlin: Springer, 427–436.
- Sobel AH, Camargo SJ, Hall TM, Lee C-Y, Tippett MK, Wing AA. 2016. Human influence on tropical cyclone intensity. *Science* **353**: 242–246. doi:10.1126/science.aaf6574.

- Stuart TS. 1968. The revival and respiration and photosynthesis in dried leaves of *Polypodium polypodioides*. *Planta* **83**: 185–206. doi:10.1007/bf00385023.
- Sunderland TCH, Apgaua D, Baldauf C, et al. 2015. Global dry forests: a prologue. *International Forestry Review* **17**: 1–9. doi:10.1505/146554815815834813.
- Tay S, He J, Yam TW. 2019. CAM plasticity in epiphytic tropical orchid species responding to environmental stress. *Botanical Studies* **60**: 7.
- Tay J, Zotz G, Puszczylowski J, Einzmann HJR. 2021. Go with the flow: the extent of drag reduction as epiphytes reorient in wind. *PLoS One* **16**: e0252790.
- Teeri JA, Tonsor SJ, Turner M. 1981. Leaf thickness and carbon isotope composition in the Crassulaceae. *Oecologia* **50**: 367–369. doi:10.1007/bf00344977.
- Torres-Morales G, Lasso E, Silvera K, Turner BL, Winter K. 2020. Occurrence of crassulacean acid metabolism in Colombian orchids determined by leaf carbon isotope ratios. *Botanical Journal of the Linnean Society* **193**: 431–477. doi:10.1093/botlinnean/boaa027.
- Wagner K, Wanek W, Zotz G. 2021. Functional traits of a rainforest vascular epiphyte community: trait covariation and indications for host specificity. *Diversity* **13**: 97. doi:10.3390/d13020097.
- Wagner K, Zotz G. 2018. Epiphytic bromeliads in a changing world: the effect of elevated CO₂ and varying water supply on growth and nutrient relations. *Plant Biology* **20**: 636–640. doi:10.1111/plb.12708.
- Ward JK, Tissue DT, Thomas RB, Strain BR. 1999. Comparative responses of model C₃ and C₄ plants to drought in low and elevated CO₂. *Global Change Biology* **5**: 857–867.
- Williams CB, Murray JG, Glunk A, Dawson TE, Nadkarni NM, Gotsch SG. 2020. Vascular epiphytes show low physiological resistance and high recovery capacity to episodic, short-term drought in Monteverde, Costa Rica. *Functional Ecology* **34**: 1537–1550. doi:10.1111/1365-2435.13613.
- Winter K. 1979. δ¹³C values of some succulent plants from Madagascar. *Oecologia* **40**: 103–112. doi:10.1007/bf00388814.
- Winter K. 2019. Ecophysiology of constitutive and facultative CAM photosynthesis. *Journal of Experimental Botany* **70**: 6495–6508. doi:10.1093/jxb/erz002.
- Winter K, Aranda J, García M, Virgo A, Paton SR. 2001. Effect of elevated CO₂ and soil fertilization on whole-plant growth and water use in seedlings of a tropical pioneer tree, *Ficus insipida* Willd. *Flora* **196**: 458–464. doi:10.1016/s0367-2530(17)30087-7.
- Winter K, García M, Holtum JAM. 2014. Nocturnal versus diurnal CO₂ uptake: how flexible is *Agave angustifolia*? *Journal of Experimental Botany* **65**: 3695–3703. doi:10.1093/jxb/eru097.
- Winter K, Holtum JAM. 2002. How closely do the δ¹³C values of crassulacean acid metabolism plants reflect the proportion of CO₂ fixed during day and night? *Plant Physiology* **129**: 1843–1851.
- Winter K, Holtum JAM, Smith JAC. 2015. Crassulacean acid metabolism: a continuous or discrete trait? *New Phytologist* **208**: 73–78. doi:10.1111/nph.13446.
- Winter K, Medina E, García V, Mayoral ML, Muniz R. 1985. Crassulacean acid metabolism in roots of the leafless orchid, *Campylocentrum tyrridion* Garay & Dunsterv. *Journal of Plant Physiology* **118**: 73–78.
- Winter K, Smith JAC. 1996. An introduction to crassulacean acid metabolism: biochemical principles and biological diversity. In: Winter K, Smith JAC, eds. *Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution*. Berlin: Springer, 1–13.
- Winter K, Smith JAC. 2022. CAM photosynthesis: the acid test. *New Phytologist* **233**: 599–609.
- Winter K, Wallace BJ, Stocker GC, Roksandic Z. 1983. Crassulacean acid metabolism in Australian vascular epiphytes and some related species. *Oecologia* **57**: 129–141. doi:10.1007/bf00379570.
- Woods CL, DeWalt SJ. 2013. The conservation value of secondary forests for vascular epiphytes in Central Panama. *Biotropica* **45**: 119–127.
- Yamori W, Hikosaka K, Way DA. 2014. Temperature response of photosynthesis in C₃, C₄, and CAM plants: temperature acclimation and temperature adaptation. *Photosynthesis Research* **119**: 101–117.
- Yang S-J, Sun M, Yang Q-Y, Ma R-Y, Zhang J-L, Zhang S-B. 2016. Two strategies by epiphytic orchids for maintaining water balance: thick cuticles in leaves and water storage in pseudobulbs. *AoB Plants* **8**: plw046.
- Zhu J, Bartholomew DP, Goldstein G. 1997. Effect of elevated carbon dioxide on the growth and physiological responses of pineapple, a species with crassulacean acid metabolism. *Journal of the American Society of Horticultural Science* **122**: 233–237.
- Zotz G. 1997. Substrate use of three epiphytic bromeliads. *Ecography* **20**: 264–270. doi:10.1111/j.1600-0587.1997.tb00370.x.
- Zotz G. 2002. Categories and CAM—blurring divisions, increasing understanding? *New Phytologist* **156**: 4–6. doi:10.1046/j.1469-8137.2002.00511.x.
- Zotz G. 2004. How prevalent is crassulacean acid metabolism among vascular epiphytes? *Oecologia* **138**: 184–192. doi:10.1007/s00442-003-1418-x.
- Zotz G. 2016. *Plants on plants. The biology of vascular epiphytes*. Cham: Springer International Publishing Switzerland.
- Zotz G, Bogusch W, Hietz P, Ketteler N. 2010. Growth of epiphytic bromeliads in a changing world: the effect of elevated CO₂ and varying water and nutrient supply. *Acta Oecologica* **36**: 659–665. doi:10.1016/j.actao.2010.10.003.
- Zotz G, Hietz P, Einzmann HJR. 2021a. Functional ecology of vascular epiphytes. *Annual Plant Reviews Online* **4**: 869–905.
- Zotz G, Leja M, Aguilar-Cruz Y, Einzmann HJR. 2020. How much water is in the tank? An allometric analysis with 205 bromeliad species. *Flora – Morphology, Distribution, Functional Ecology of Plants* **264**: 151557. doi:10.1016/j.flora.2020.151557.
- Zotz G, Hietz P. 2001. The physiological ecology of vascular epiphytes: current knowledge, open questions. *Journal of Experimental Botany* **52**: 2067–2078. doi:10.1093/jexbot/52.364.2067.
- Zotz G, Thomas V. 1999. How much water is in the tank? Model calculations for two epiphytic bromeliads. *Annals of Botany* **83**: 183–192.
- Zotz G, Tyree MT. 1996. Water stress in the epiphytic orchid, *Dimerandra emarginata* (G. Meyer) Hoehne. *Oecologia* **107**: 151–159. doi:10.1007/bf00327898.
- Zotz G, Winkler U. 2013. Aerial roots of epiphytic orchids: the *velamen radicum* and its role in water and nutrient uptake. *Oecologia* **171**: 733–741. doi:10.1007/s00442-012-2575-6.
- Zotz G, Winter K. 1994. Annual carbon balance and nitrogen use efficiency in tropical C₃ and CAM epiphytes. *New Phytologist* **126**: 481–492. doi:10.1111/j.1469-8137.1994.tb04245.x.
- Zotz G, Vollrath B, Schmidt G. 2003. Carbon relations of fruits of epiphytic orchids. *Flora* **198**: 98–105.
- Zotz G, Weigelt P, Kessler M, Kreft H, Taylor A. 2021b. EpiList 1.0: a global checklist of vascular epiphytes. *Ecology* **102**: e03326.
- Zotz G, Ziegler H. 1997. The occurrence of crassulacean acid metabolism among vascular epiphytes from Central Panama. *New Phytologist* **137**: 223–229. doi:10.1046/j.1469-8137.1997.00800.x.