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How prevalent is crassulacean acid metabolism among vascular epiphytes?

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Abstract The occurrence of crassulacean acid metabolism (CAM) in the epiphyte community of a lowland forest of the Atlantic slope of Panama was investigated. I hypothesized that CAM is mostly found in orchids, of which many species are relatively small and/or rare. Thus, the relative proportion of species with CAM should not be a good indicator for the prevalence of this photosynthetic pathway in a community when expressed on an individual or a biomass basis. In 0.4 ha of forest, 103 species of vascular epiphytes with 13,099 individuals were found. As judged from the C isotope ratios and the absence of Kranz anatomy, CAM was detected in 20 species (19.4% of the total), which were members of the families Orchidaceae, Bromeliaceae, and Cactaceae. As predicted, the contribution of CAM epiphytes to the total number of individuals and to total biomass (69.6 kg ha⁻¹) was considerably lower (3.6% or 466 individuals and, respectively, 3.0% or 2.1 kg ha⁻¹).

Keywords Biomass · Bromeliaceae · Cactaceae · Crassulacean acid metabolism · Orchidaceae

Introduction

For decades, the occurrence of crassulacean acid metabolism (CAM) was associated primarily with succulent and shrub-like plants from arid habitats (Osmond et al. 1982). Particularly the work of Nuernbergk (1960), Coutinho (1969) and Winter (1985) initiated a change in our perception of a “typical” CAM plant. We now know that

the majority of plant species using this water-preserving photosynthetic pathway live in trees as epiphytes. In a recent review on the taxonomic occurrence of CAM, Winter and Smith (1996) pointed out that Orchidaceae present the greatest uncertainty concerning the number of CAM plants. This family with >800 genera and at least 20,000 species (Dressler 1981) is estimated to have 7,000, mostly epiphytic, CAM species (Winter and Smith 1996), which alone would account for almost 50% of all CAM plants. A number of studies, mostly using stable isotope techniques, documented a steady increase in the proportion of CAM plants among local epiphyte floras from wet tropical rainforest and moist tropical forests to dry forests. For example, while about 25% of the epiphytic orchid species in New Guinean and Australian rain forests showed CAM (Winter et al. 1983; Earnshaw et al. 1987), this proportion increased to 40% in a moist forest in Panama (Zotz and Ziegler 1997) and reached 100% in a Mexican dry forest (Mooney et al. 1989).

While it seems unlikely that future studies will challenge this general picture, the relative importance of CAM in epiphyte communities of moist or wet tropical forests may be exaggerated by these numbers, because they are merely based on the number of *species* with CAM. Although the proportion of CAM species is sometimes treated, implicitly or even explicitly, as evidence for a similar degree of importance of CAM for the entire epiphyte community and associated functions within the ecosystem (Pierce et al. 2002b), this may be misleading for two reasons. First, abundances in a given community vary strongly between epiphyte species (Zotz et al. 1999; Nieder et al. 2000). While CAM is particularly common among epiphytic orchids, local rarity is also a frequent feature of many members of this family (e.g. Tremblay et al. 1998; Flores-Palacios and Garcia 2001). Secondly, plant biomass may also differ by many orders of magnitude—take, e.g., tiny twig orchids versus massive aroids or large tank bromeliads (Hietz and Hietz-Seifert 1995). Thus, if CAM were particularly common in small and/or rare epiphyte species, the importance of CAM

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within an epiphyte community will be quite different from what could be concluded from species numbers alone.

Consequently, this paper asks the question whether we are using the right currency when studying CAM in epiphytes in the traditional way by screening species. To address this problem, I took advantage of a comprehensive census of an epiphyte community in a tropical lowland forest on the Caribbean slope of Panama (G. Zotz, unpublished data; Zotz and Vollrath 2003). There, all species in a 0.4-ha plot were identified and the size of all individuals determined. Subsequently, the occurrence of CAM was derived from literature data or determined for hitherto unstudied species by stable isotope techniques. The biomass of each individual was estimated by establishing regressions of maximum leaf or stem length and plant dry weight. As expected, the relative importance of CAM differed substantially when expressed on a species, individual or biomass basis.

Materials and methods

Field site and census work

This study was conducted at the Fort Sherman Canopy Crane site, which is located within the former Fort Sherman area near the Atlantic coast of the Republic of Panama. The average annual rainfall is estimated to be ca. 3,500 mm (Lerdau and Throop 1999). Canopy height of this primary rain forest is quite variable and reaches a maximum of ca. 40 m. The use of a small gondola allowed access to all strata of the forest.

Each tree in a roughly square area of ca. 0.4 ha was inspected for the occurrence of vascular epiphytes. Not included were woody hemi-epiphytes of the genera *Ficus*, *Coussapoa*, *Clusia* and *Havetiopsis* and abundant climbing aroids such as *Philodendron schottianum*. There are a number of species in the Araceae, which may grow either as an epiphyte or as secondary hemiepiphyte (Croat 1978). At my study site, both life forms were observed in individuals of *Philodendron radiatum* and *P. sagittifolium*. In these two species, I included only truly epiphytic individuals.

The following data were collected for each individual: height of attachment (minimum and maximum in creeping species), leaf/frond number, leaf length, stem length, or number of shoots (depending on species). The delimitation of individual plants was sometimes difficult, and we use "individual" sensu Sanford (1968), i.e. as a group of rhizomes and leaves belonging to one species, which forms a clearly delimited stand. With the exception of small seedlings, which could normally not be identified to species, all plant sizes were included in the census.

Species names of flowering plants follow the Flora of Panama Checklist and Index (D'Arcy 1987), authorities for ferns are according to Lellinger (1989) and Croat (1978), for filmy ferns compare also Zotz and Büche (2000). *Encyclia aemula* was treated as a separate species following Dressler (1993). Voucher specimens are deposited in the herbarium of the Smithsonian Tropical Research Institute, Panama (Tupper Center).

Occurrence of CAM, biomass estimates

For a large number of species the photosynthetic pathway was already known. In all other cases, leaf/frond samples were collected over the course of several months in 2001 and 2002 from mature plants (compare Zotz and Ziegler 1999) in their natural habitat. After transfer to the laboratory, fresh cross-sections were examined by light microscopy to detect Kranz anatomy. Samples were then dried

at 60°C for 7–10 days. The natural abundance of ^{13}C was determined by isotope ratio mass spectrometry (IRMS) at the Institute of Ecology and Conservation Biology, University of Vienna, Vienna, as described by Wanek et al. (2002). Briefly, a continuous flow IRMS system was used, consisting of an elemental analyser (EA 1110; CE instruments, Milan) connected to a gas isotope ratio mass-spectrometer (Finnigan MAT, Bremen, Germany). The SD of repeated determinations was 0.1‰ external precision. The $\delta^{13}\text{C}$ value as a measure of the relative abundance of ^{13}C in a given sample was calculated as:

$$\delta^{13}\text{C}(\text{‰}) = \left(\frac{^{13}\text{C}/^{12}\text{C in sample}}{^{13}\text{C}/^{12}\text{C in standard}} - 1 \right) \times 1000 \quad (1)$$

Plant tissues are depleted in ^{13}C compared to atmospheric CO_2 which has a $\delta^{13}\text{C}$ value of approximately -8‰ relative to a standard, a belemnite from the Pee Dee formation in South Carolina, USA (PDB). Plants with the C_4 photosynthetic pathway typically have $\delta^{13}\text{C}$ values between -9 and -19‰ , similar to obligate CAM plants. C_3 plants typically have C isotope ratios in the range of -22 to -32‰ (Troughton 1979). While $\delta^{13}\text{C}$ values at the lower and upper extremes provide clear evidence for the photosynthetic pathway of a sample, intermediate levels cannot be interpreted unequivocally. CO_2 near the forest floor may be depleted in ^{13}C because of root respiration and respiratory composition of organic material. As a consequence, $\delta^{13}\text{C}$ values of C_3 plants in the understorey can be several ‰ more negative than those of canopy leaves. Moreover, $\delta^{13}\text{C}$ values in the range of -21 to -27‰ can still be indicative of some nocturnal CO_2 uptake or diel acidity rhythms (Winter et al. 1983; Winter and Holtum 2002). In this paper we follow other studies (e.g. Winter et al. 1983) and consider only $\delta^{13}\text{C}$ values higher (i.e. less negative) than -20‰ as an unambiguous indication of CAM.

With few exceptions (see below) we collected at least five specimens (median=7) per species, which covered the entire size range. All collections were made in the vicinity of our study area. Plant were carefully removed from the substrate with their roots and dried for at least 1 week at 60°C to determine total dry mass (subsamples were used in the case of larger plants). Subsequently, best-fit regressions between the variables measured in the field (length of the longest leaf, stem length, number of shoots, respectively) and plant biomass were established using TableCurve (Jandel Scientific, San Rafael, Calif.). Depending on species, power functions, exponential functions or linear regressions were used. Regression coefficients ranged from 0.6 to 0.99. In the case of rare species we only collected one or two individuals of similar size to those found inside our study plot, or data of species with similar morphology were used. Applying these regressions I obtained a biomass estimate for each individual in the sample plot.

Results

In the 0.4 ha of lowland forest, I encountered 13,099 individuals belonging to 103 species (Fig. 1, Table 1). The most species-rich family were the Orchidaceae with 45 species. Taken together, ferns and fern-allies accounted for another 28% of all vascular epiphyte species. The remaining 29 species belonged to five families (Araceae, Bromeliaceae, Cactaceae, Gesneriaceae, Piperaceae). The orchids represented more individuals than all other taxa together, but were less important than aroids and ferns in terms of their contribution to epiphyte biomass.

The $\delta^{13}\text{C}$ values of plant material collected in Fort Sherman ranged from -12.3 to -34.5‰ (Table 1). None of these samples showed Kranz anatomy. The possibility that some species may use the C_4 photosynthetic pathway can

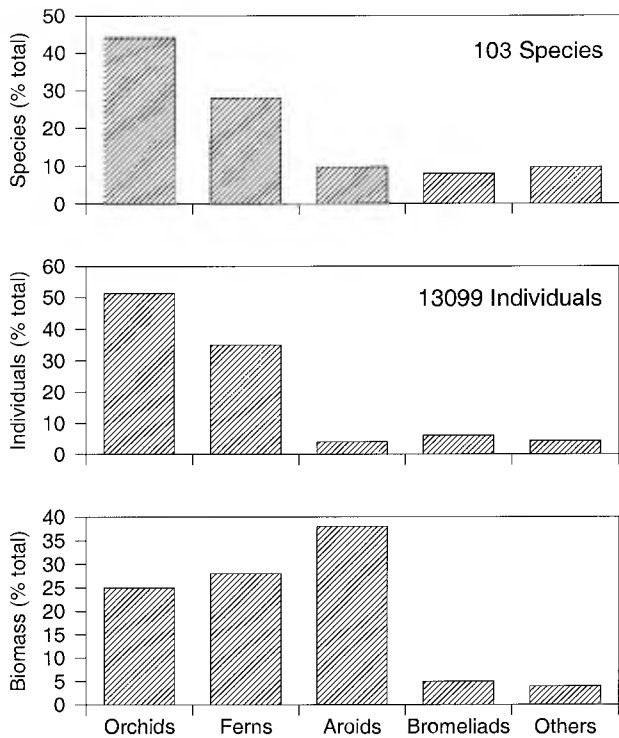


Fig. 1 Relative contribution of different taxa to the total species count, the total individual count and the total biomass of vascular epiphytes in a lowland forest in Panama. The total number of species and individuals in the 0.4-ha study plot are also given

therefore be ruled out. A total of 20 species (19.4%) showed unequivocal evidence of CAM (Table 1, Fig. 2). Most of these species were orchids (16 species, 80%), while Bromeliaceae and Cactaceae each contributed two CAM species. Two genera in the Orchidaceae (*Jacqui-niella* Schltr. and *Trichocentrum* Poepp. & Endl.) were not previously known to engage in CAM (Smith and Winter 1996). Many CAM species were very rare (Table 1). For example, the orchids *Caularthron bilamellatum*, *Jacqui-niella pedunculata*, *Jacqui-niella* sp., *Lockhartia pittieri*, and *Maxillaria crassifolium* were all found only once or twice. The most common CAM species, *Tillandsia bulbosa*, was found just 187 times in the study plot, whereas the most common C₃ species (*Scaphyglottis longicaulis*) contributed almost 9 times this number (1,568 individuals). Consequently, the number of individuals with CAM was much lower than the relative proportion of CAM species would suggest: only 3.6% of all epiphyte individuals showed clear evidence of CAM. The contribution of these plants to the total epiphyte biomass (i.e. 69.6 kg ha⁻¹) was even lower at 2.1 kg ha⁻¹ (3.0% of the total).

While total epiphyte biomass was largest at intermediate heights within the forest (Fig. 3), the relative contribution of CAM species reached a maximum in the upper canopy. Similarly, the proportion of CAM biomass increased almost threefold from epiphytes growing on stems (2.6%) to those growing on larger branches (3.1%) to those attached to small branches and twigs (7.2%) (Fig. 4).

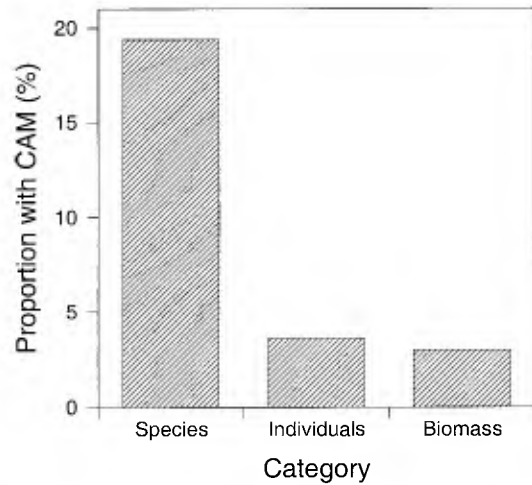


Fig. 2 Relative importance of crassulacean acid metabolism (CAM) in a community of vascular epiphytes as indicated by the proportion of CAM species, the proportion of CAM individuals, and the relative contribution of these individuals to the total biomass of the community. Evidence for the occurrence of CAM is presented in Table 1

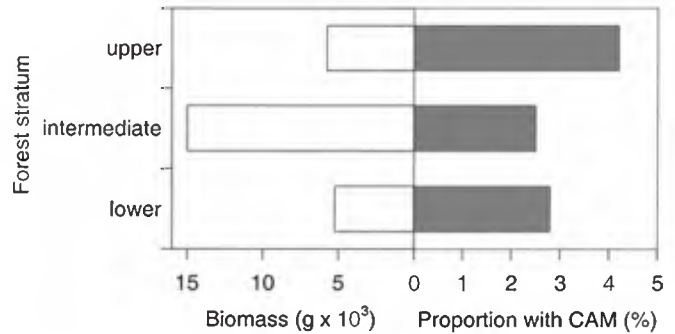


Fig. 3 Vertical stratification of total epiphyte biomass and the relative proportion of CAM biomass (in percent of total biomass) within the forest. Strata are defined as *lower* (<10 m above the ground), *intermediate* (10–20 m) and *upper* canopy (>20 m)

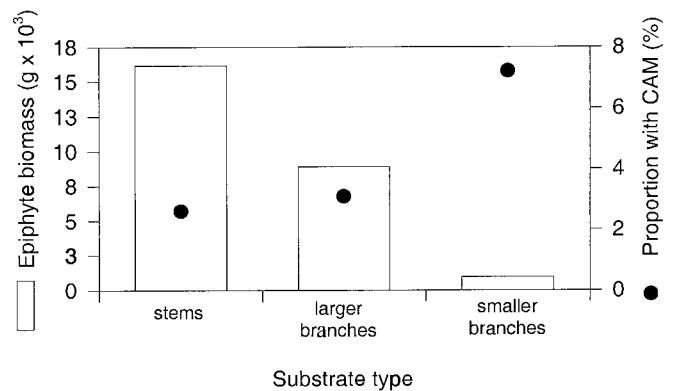


Fig. 4 Distribution of epiphyte biomass and the relative proportion of CAM biomass in relation to the site of attachment. Categories are main tree *stem*, *larger branches* (≥5 cm diameter), and *smaller branches* (<5 cm diameter)

Table 1 Photosynthetic pathway^a, number of individuals and total biomass (g dry mass) of epiphyte species in 0.4 ha of forest at the Fort Sherman Crane Site, Panama. $\delta^{13}\text{C}$ values (‰) were

determined from plants collected in their natural habitat or taken from the literature (Source). *ND* Not determined

Taxon	$\delta^{13}\text{C}$	Source	Individuals	Biomass
Araceae				
<i>Anthurium acutangulum</i> Engl.	-29.6	Zotz and Ziegler (1997)	98	1,010
<i>Anthurium bakeri</i> Hook.f.	-32.7	this study	1	18
<i>Anthurium brownii</i> Mast.	-26.6	Zotz and Ziegler (1997)	32	349
<i>Anthurium clavigerum</i> Poepp.	-26.0		44	1,680
<i>Anthurium durandii</i> Engl.	-24.2		40	334
<i>Anthurium friedrichsthali</i> Schott	-28.2		159	761
<i>Anthurium hacumense</i> Engl.	-33.0	This study	75	1,111
<i>Anthurium scandens</i> (Aubl.) Engl.	-28.6	Zotz and Ziegler (1997)	34	216
<i>Philodendron radiatum</i> Schott	-25.4		13	3,003
<i>Philodendron sagittifolium</i> Liebm.	-30.4		31	1,932
<i>Stenospermation angustifolium</i> Hemsl.	-28.2		22	92
Aspleniaceae				
<i>Asplenium juglandifolium</i> Lam.	-34.5	This study	156	53
<i>Asplenium serratum</i> L.	-23.8	Zotz and Ziegler (1997)	142	802
Bromeliaceae				
<i>Aechmea tillandsioides</i> (Mart.) Baker var. <i>kienastii</i>	-17.2 ^a	Zotz and Ziegler (1997)	19	101
<i>Catopsis sessiliflora</i> (R. & P.) Mez	-24.2		92	32
<i>Guzmania musaica</i> (Linden & Andre) Mez in DC.	-28.7	This study	3	88
<i>Guzmania subcorymbosa</i> L.B. Sm.	-22.6		70	391
<i>Tillandsia anceps</i> Lodd.	-28.1		248	255
<i>Tillandsia bulbosa</i> Hook.	-17.5	Zotz and Ziegler (1997)	187	176
<i>Vriesea gladioliflora</i> (Wendl.) Ant.	-28.6	This study	106	354
<i>Vriesea sanguinolenta</i> Cogn. & Marchal	-32.0	Zotz and Ziegler (1997)	1	9.0
Cactaceae				
<i>Epiphyllum phyllanthus</i> L.	-16.1 ^a	Zotz and Ziegler (1997)	13	222
<i>Hylocereus monacanthus</i> (Lem.) Britt. & Rose.	-10.0 ^a	Winter and Holtum (2002)	19	158
Gesneriaceae				
<i>Codonanthe macradenia</i> J.D. Sm.	-22.9	This study	239	574
<i>Columnnea billbergiana</i> Beurl.	-32.6	Zotz and Ziegler (1997)	12	11
<i>Drymonia serrulata</i> (Jacq.) Mart.	-30.1		1	13
Hymenophyllaceae				
<i>Hymenophyllum brevifrons</i> Kunze	<i>ND</i>	This study	1	0.4
<i>Trichomanes godmanii</i> Hook	<i>ND</i>		3	1.6
<i>Trichomanes nummularium</i> C.Chr.	<i>ND</i>		205	210
<i>Trichomanes ovale</i> W.Boer	-33.4 ^c		120	87
<i>Trichomanes punctatum</i> W.Boer	<i>ND</i>		3	2.0
<i>Trichomanes anadromum</i> Rosenstr.	<i>ND</i>		2	6.0
<i>Trichomanes ekmannii</i> W.Boer	-33.4 ^c		43	26
<i>Trichomanes angustifrons</i> W.Boer	-33.4 ^c		17	21
Lomariopsidaceae				
<i>Elaphoglossum</i> sp.	-31.1	This study	103	213
<i>Elaphoglossum herminieri</i> (Bory & Fee) Moore	-29.1	Zotz and Ziegler (1997)	197	555
<i>Elaphoglossum sporadolepis</i> (Kunze) Moore	-29.3		1,187	1,462

Table 1 (continued)

Taxon	$\delta^{13}\text{C}$	Source	Individuals	Biomass
Orchidaceae				
<i>Aspasia principissa</i> Reichb.f.	-38.2	Zotz and Ziegler (1997)	53	48
<i>Campylocentrum micranthum</i> (Lindl.) Maury	-14.2 ^a		30	33
<i>Catasetum viridiflavum</i> Hook.	-29.3		70	526
<i>Caularthron bilamellatum</i> (Reichb.f.) Schult.	-16.6 ^a		1	3.4
<i>Cochleanthes lipscombiae</i> (Rolfe) Garay	-33.5		3	5.9
<i>Dichaea panamensis</i> Lindl.	-29.5		279	36
<i>Dimerandra emarginata</i> (G. Meyer) Hoehne	-28.7		16	21
<i>Elleanthus longibracteatus</i> (Lindl. ex Griseb.) Fawc.	-30.1		4	13
<i>Encyclia chacaoensis</i> (Reichb.f.) Dressl.	-29.7		16	128
<i>Encyclia aemula</i> (Lindl.) Carn. & Ram.	-28.6	This study	- ^d	- ^d
<i>Encyclia chimborazoensis</i> (Schlechter) Dressl.	-27.8	Zotz and Ziegler (1997)	- ^d	- ^d
<i>Epidendrum difforme</i> Jacq.	-15.1 ^a		36	35
<i>Epidendrum inatophyllum</i> Lindl.	-14.6 ^a		4	11
<i>Epidendrum nocturnum</i> Jacq.	-25.6		38	98
<i>Epidendrum schlechterianum</i> Ames	-17.6 ^a		5	0.6
<i>Gongora quinquenervis</i> R. & P.	-30.5		10	41
<i>Jacqiniella pedunculata</i> Dressler ^b	-14.9 ^a	This study	2	0.1
<i>Jacquinella</i> sp.	-14.9 ^a		1	0.2
<i>Kefersteinia</i> sp	-32.8		1	1.1
<i>Lockhartia acuta</i> (Lindl.) Reichb.f.	-20.1 ^a	Zotz and Ziegler (1997)	58	35
<i>Lockhartia pittieri</i> Schltr. ^b	-18.2 ^a	This study	2	0.6
<i>Masdevallia livinstoneana</i> Rchb. f.	-32.6		45	37
<i>Maxillaria crassifolia</i> (Lindl.) Rchb.	-13.4 ^a	Zotz and Ziegler (1997)	2	7.9
<i>Maxillaria discolor</i> Rchb. f.	-30.8	This study	55	401
<i>Maxillaria uncatata</i> Lindl.	-30.3	Zotz and Ziegler (1997)	857	368
<i>Maxillaria variabilis</i> Batem. ex Lindl.	-32.2		1	1.1
<i>Mormodes powellii</i> Schltr.	-25.1	This study	14	55
<i>Notylia albida</i> Klotsch ^b	-12.9 ^a		18	6.7
<i>Oncidium ampliatum</i> Lindl.	-15.3 ^a	Zotz and Ziegler (1997)	14	36
<i>Ornithocephalus bicornis</i> Lindl. in Benth.	-13.3 ^a		17	2.7
<i>Ornithocephalus powellii</i> Schlechter	-13.9 ^a	This study	- ^d	- ^d
<i>Pleurothallis brighamii</i> S. Wats.	-28.3	Zotz and Ziegler (1997)	800	231
<i>Pleurothallis grobyi</i> Lindl.	-30.0	This study	2	0.3
<i>Pleurothallis verecunda</i> Schlechter	-14.0 ^a	Zotz and Ziegler (1997)	7	13
<i>Polystachya foliosa</i> (Lindl.) Reichb.f.	-27.6		62	80
<i>Scaphyglottis behrii</i> Hemsl.	-29.4		1,514	1,765
<i>Scaphyglottis longicaulis</i> S. Wats.	-27.9		1,568	2,037
<i>Scaphyglottis prolifera</i> Cogn.	-29.3	This study	284	108
<i>Sobralia feniziana</i> Rchb.f.	-24.3	Zotz and Ziegler (1997)	9	28
<i>Sobralia fragans</i> Lindl.	-28.5		169	221
<i>Stelis crescentiicola</i> Schlechter	-29.8		119	19
<i>Trichocentrum capistratum</i> Rchb.f. ^b	-14.2 ^a	This study	31	3.3
<i>Trichopilia maculata</i> Reichb.f.	-30.2	Zotz and Ziegler (1997)	390	103
<i>Trichosalpinx orbicularis</i> (Lindl.) Luer.	-30.3	This study	12	9.1
<i>Trigonidium egertonianum</i> Batem. ex. Lindl.	-30.8	Zotz and Ziegler (1997)	60	435
Piperaceae				
<i>Peperomia cordulata</i> C. DC.	-24.9	Zotz and Ziegler (1997)	5	14
<i>Peperomia ebingeri</i> Yunck.	-34.8		2	5
<i>Peperomia macrostachya</i> (Vahl) A. Dietr. in L.	-27.3		100	114
<i>Peperomia obtusifolia</i> (L.) A.Dietr.	-32.3	This study	39	23
<i>Peperomia rotundifolia</i> (L.) H.B.K.	-35.0	Zotz and Ziegler (1997)	157	75

Table 1 (continued)

Taxon	$\delta^{13}\text{C}$	Source	Individuals	Biomass
Polypodiaceae				
<i>Campyloneurum occultum</i> Gomez	-27.7	This study	137	51
<i>Campyloneurum phylliditis</i> (L.) K.Presl.	-26.0	Zotz and Ziegler (1997)	120	771
<i>Dicranoglossum panamense</i> (Christensen) Gómez	-32.7		559	210
<i>Microgramma lycopodioides</i> (L.) Copel.	-23.1	This study	96	93
<i>Microgramma reptans</i> (Cav.) A.R. Sm.	-26.1	Zotz and Ziegler (1997)	44	43
<i>Niphidium crassifolium</i> (L.) Lellinger	-23.5		478	2,175
<i>Pechuma pectinata</i> (L.) MG Price	-27.3		29	71
<i>Polypodium costaricense</i> H.Christ	-23.7		5	40
<i>Polypodium percussum</i> Cav.	-25.8		170	302
<i>Polypodium triseriale</i> Sw.	-27.7		11	141
Selaginellaceae				
<i>Huperzia dichotoma</i> (Jacq.) Trevis	-29.5	This study	6	0.8
Vittariaceae				
<i>Ananthacorus angustifolius</i> (Sw.) Und. & Max.	-31.2	Zotz and Ziegler (1997)	591	181
<i>Anetium citrifolium</i> (L.) Splitg.	-33.4		8	3.5
<i>Anthrophyum lanceolatum</i> (L.) Kaulf.	-32.3	This study	61	14
<i>Hecistopteris pumila</i> (Spreng) J.Smith	-31.9		10	0.2
<i>Vittaria lineata</i> (L.) J. Sm.	-29.4	Zotz and Ziegler (1997)	54	182

^aCrassulacean acid metabolism (CAM) present

^bCAM detected in these species for the first time

^cMaterial from three individuals was pooled for analysis

^dNon-flowering individuals could not be distinguished from congeners in the field

Discussion

Nineteen percent of all epiphyte species or, respectively, 36% of all epiphytic orchid species showed CAM in this lowland moist forest (Fig. 2, Table 1). The latter figure lies between the 25% CAM orchids in New Guinean and Australian rain forests (Winter et al. 1983; Earnshaw et al. 1987) and the proportion of 40% in a moist forest in Panama with a much more pronounced dry season (Zotz and Ziegler 1997). Consistent with the original hypothesis, most CAM species of the Fort Sherman epiphyte community were orchids and were relatively small and rare. While in the present study the proportion of CAM species exceeded by far the proportion of individuals with CAM and their relative contribution to the biomass of the epiphyte community (Fig. 2), the reverse may also be true. Zotz et al. (1999) studied the epiphyte community of a particular host tree, *Annona glabra*, a small tree species with a very open crown in the lowlands of central Panama. In this epiphyte community, which is largely deprived of large aroids and the typical, hygrophytic understory epiphytes such as filmy ferns (Zotz and Büche 2000), the relative number of individuals with CAM (46%) was much higher than the proportion of CAM species (29%) suggested. Clearly, knowledge of the proportion of species with CAM alone does not allow one to draw unambiguous conclusions on the prevalence of CAM in a given community. The traditional "species approach" may still be valid in large-scale comparisons between vastly

differing forest types (Hietz and Hietz-Seifert 1995; Hietz et al. 1999). In extreme cases, e.g. in upper montane forests with a complete absence of CAM species (e.g. Earnshaw et al. 1987) or in tropical dry forests with the opposite situation (Mooney et al. 1989), there is little ambiguity as to the prevalence or the adaptive significance of CAM in an epiphyte community. This clarity strongly diminishes when comparing forests at similar altitude or with rather similar precipitation regimes. Then, the determination of the proportion of CAM species can only be a first step in a study of the importance of CO₂ fixation via phosphoenolpyruvate-carboxylase in vascular epiphytes at the community level. Unfortunately, even when counts of individuals and estimates of relative biomass are included (Fig. 2), we still face the problem that some species may possess a certain capacity for nocturnal CO₂ fixation that cannot be detected with stable isotope analysis. Consequently, additional measurements of oscillations in titratable acidity and/or diel patterns of CO₂ gas exchange are needed (Winter and Holtum 2002). A recent study by Pierce et al. (2002a) suggests, however, that adding these species to C₃ plants will introduce a rather small error in our considerations. In their survey of 50 bromeliads, only 13% of the species with C₃-like $\delta^{13}\text{C}$ values showed a rather low degree of nocturnal acidification.

Following the results of earlier studies (Griffiths and Smith 1983; Zotz and Ziegler 1997) I expected a pronounced vertical stratification of C₃ and CAM species.

Although the relative proportion of CAM biomass was indeed highest in the upper forest canopy, the differences between lower and upper strata were rather small (Fig. 3). This limited vertical stratification may be due to the rugged surface of the forest canopy: absolute height above the ground is probably only crudely related to moisture availability. Much more marked differences in the proportion of CAM biomass were observed in respect to the nature of the substrate (Fig. 4). Smaller branches, which presumably constitute drier microhabitats even at intermediate heights within the forest, had a much higher proportion of epiphytic CAM biomass than larger branches and stems.

The biomass of the entire epiphyte community in the studied lowland forest, 66.8 kg ha^{-1} , is within the range of other reports from lowland forests (Table 2). Remarkably, the highest epiphyte biomass in the tropical lowlands has been reported from a dry forest in Puerto Rico (Murphy and Lugo 1986) and is built up almost completely by CAM plants such as *Tillandsia utriculata*. In contrast, the generally observed rise in epiphyte biomass with altitude is explained by an *increase* in annual precipitation (Gentry and Dodson 1987). Even in montane forest, however, vascular epiphytes contribute <1% to the total forest biomass (Edwards and Grubb 1977; Tanner 1980). Although the proportion of CAM species decreases with altitude (e.g. Griffiths et al. 1986; Hietz et al. 1999), the much better development of epiphytes in montane forests should still lead to a substantial increase in CAM biomass. The only data set available to test this notion is that of Hietz and Hietz-Seifert (1995; and P. Hietz, unpublished data). The CAM biomass of six epiphyte communities, studied along an altitudinal gradient (720–2,370 m a.s.l.) in Mexico, averaged $363 \pm 186 \text{ kg ha}^{-1}$ (average \pm SE). This figure exceeds that of the lowland forest of the present study by >2 orders of magnitude. The highest CAM biomass (998 kg ha^{-1}) was detected at intermediate elevations (1,450 m a.s.l.), in spite of a reduction in the proportion of CAM species from 48% to 26% from 720 m a.s.l. to 1,450 m a.s.l. The lowest CAM biomass was found at altitudes above ca. 2,000 m a.s.l., i.e. $<2 \text{ kg ha}^{-1}$.

Although tropical forest canopies are the global hot spot of CAM in terms of species diversity (Winter and Smith 1996), it is doubtful whether this is also true in terms of biomass (Winter 1985), even when acknowledging the contribution of hemiepiphytes with CAM (Lüttge 1997). However, it is still difficult to address this question quantitatively. On the one hand, the available information on epiphyte biomass has a strong Neotropical bias (Table 2), on the other hand, the data-base for arid non-forest biomes inside and outside the tropics is hardly better than that for tropical forests. It is known that CAM plants are rarely found in deserts, while being frequently abundant in semi-arid areas (Evenari 1985). With few exceptions, quantitative information beyond this general statement is missing. For example, there are no published estimates for CAM biomass in north American deserts (P. S. Nobel, personal communication). Most of the published reports on CAM biomass from other places around the

Table 2 Vascular epiphyte biomass in tropical and subtropical forests. Only sources that allow the distinction between vascular and non-vascular plant biomass were considered

Forest type	Country	Altitude	Biomass (kg ha^{-1})	Source	Comments
Moist forest	Panama	Lowland	2	Golley et al. (1969)	
Gallery forest	Panama	Lowland	30		
Moist forest	Brasil	Lowland	c. 50	Klinge et al. (1975)	
Mangrove	Panama	Lowland	21	Golley et al. (1969)	
Subtropical dry forest	Puerto Rico	Lowland	140	Murphy and Lugo (1986)	
Premontane	Panama	250–600 m NN	1,440	Golley et al. (1969)	
Subtropical wet forest	Taiwan	400–1,400 m NN	325	Hsu et al. (2002)	Only holocpiphytes, calculated from original figures
Montane forests	Mexico	720–2,370 m NN	62–2,300	Hietz and Hietz-Seifert (1995)	Only holocpiphytes, range of six plots
Premontane floodplain forest	Puerto Rico	750 m NN	1,400	Frangi and Lugo (1992)	Primarily <i>Guzmania berteriana</i>
Montane rainforest	Jamaica	1,600 m NN	260–1,500	Tanner (1980)	Only bromeliads, range of two plots
Montane rainforest	Costa Rica	1,600 m NN	710	Nadkarni (1984)	Only holocpiphytes, calculated from original figures
Montane rainforest	New Guinea	2,500 m NN	1,060	Edwards and Grubb (1977)	Average of six plots

world refer to localized patches of discontinuous vegetation in arid environments (e.g. Liang et al. 1989; Rundel et al. 1997). With such local estimates of CAM standing crop, scaling to a landscape level is virtually impossible, because most of these terrestrial CAM succulents show rather localized, patchy distribution patterns (Smith et al. 1997).

In summary, when studying the prevalence of vascular epiphytes with CAM at the community level, relative species numbers are not a reliable indicator for the number of individuals with CAM or their relative contribution to community biomass. A large percentage of CAM plants are small and rare orchids, hence species numbers may frequently exaggerate the importance of CAM plants in an epiphyte community. Although tropical tree crowns are the global centre of diversity of CAM species, the current data base remains too sketchy as to decide whether most CAM biomass is found in tropical moist and wet forests or rather in semiarid tropical-subtropical vegetation.

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