PHOTOSYNTHETICA 47 (1): 33-40, 2009

Carbon isotope composition and mode of photosynthesis in *Clusia* species from Mexico

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Abstract

The neotropical genus *Clusia* comprises arborescent species exhibiting Crassulacean Acid Metabolism (CAM) as was first reported for a Mexican species, *Clusia lundellii*. Here, the occurrence of CAM photosynthesis was studied in 20 species of *Clusia*, 18 from Mexico, and 2 from Guatemala, using leaf carbon isotopic composition. In most species, samples from individuals collected in different locations were analyzed. CAM was present in at least 11 species, eight of which contained specimens with $\delta^{13}C$ values less negative than –20.0 ‰, indicating strong CAM (*C. chanekiana*, *C. flava*, *C. lundellii*, *C. mexicana*, *C. quadrangula*, *C. rosea*, *C. suborbicularis*, and *C. tetra-trianthera*). $\delta^{13}C$ was highly variable in some species, but CAM expression was not correlated to life form (epiphytic, hemiepiphytic, terrestrial) or habitat. CAM specimens were not collected at altitudes above 1 700 m a.s.l.

Additional key words: Crassulacean acid metabolism; photosynthetic pathway; species differences; stable carbon isotopes.

Introduction

The neotropical genus *Clusia*, which comprises about 300 woody species, exhibits great diversity of life forms including epiphytes, hemi-epiphytes (some stranglers), lianas, shrubs, and trees (Hammel 1986, Lüttge 2006). Moreover, the genus shows great plasticity in expression of photosynthetic pathways. Many *Clusia* species are C_3 plants, numerous species exhibit pronounced Crassulacean Acid Metabolism (CAM), and some species exhibit varying proportions of daytime *versus* night time net CO_2 uptake depending on environment (C_3-CAM intermediates and facultative CAM species) (Tinoco-Ojanguren and Vázquez-Yanes 1983, Holtum *et al.* 2004, Lüttge 2006, Winter *et al*. 2008).

Clusia species from Central America can be divided into three major clades, which correspond to three morphological species groups, the *C. flava* group, the *C. minor* group, and the *C. multiflora* group (Hammel 1986). This grouping has recently been corroborated by molecular phylogenies suggesting that CAM is present in mainly two of the three clades, the *C. flava* and the *C. minor* groups (Gustafsson *et al*. 2002, Vaasen *et al.* 2002, Gehrig *et al.* 2003). However, probably less than 25 % of *Clusia* species have been investigated regarding the presence of CAM photosynthesis, a task that is complicated by variation in CAM expression due to environment. Furthermore, only a few species have been studied in contrasting environments (Holtum *et al*. 2004, Lüttge 2006).

Surveys to determine the presence of CAM activity can be based on carbon isotope composition ($\delta^{13}C$) of plants because of the differential enzyme-mediated discrimination against $^{13}CO_2$ between C_3 ($\delta^{13}C$ values can range from –35 to –20 ‰) and CAM ($\delta^{13}C$ values ranging typically from –22 to –10 ‰) photosynthetic carbon assimilation (Ehleringer and Osmond 1989, Santiago *et al.* 2005). However, $\delta^{13}C$ values alone cannot detect CAM when dark CO_2 fixation makes a small but significant contribution to total carbon gain. Combining information on $\delta^{13}C$ values and net CO_2 exchange or diel variations in leaf titratable acidity has shown that weak CAM may occur in many species of Bromeliaceae, Clusiaceae, and Orchidaceae with $\delta^{13}C$ values typical of C_3 photosynthesis (Pierce *et al.* 2002, Winter and Holtum 2002, Crayn *et al.* 2004, Holtum *et al.* 2004, Silvera *et al.* 2005).

Received 21 March 2008, *accepted* 11 September 2008.

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Acknowledgments: We thank Luis Simá for field assistance, Gerardo A. Salazar for advice in the herbarium MEXU, Jerzy Rzedowski for providing information on some herbarium samples, and Casandra Reyes-García, M. Fernanda Ricalde, Claudia González-Salvatierra, Louis Santiago, and two anonymous reviewers for comments on the manuscript. This research was partially supported by the grant Fondo Sectorial SEP-CONACYT 48344/24588 (to JLA) and by the Andrew W. Mellon Foundation (to KW). G. Vargas-Soto was recipient of a fellowship by Consejo Nacional de Ciencia y Tecnología, Mexico.

Although the very first report of CAM in *Clusia* was made for *C. lundellii* in Mexico (Tinoco-Ojanguren and Vázquez-Yanes 1983), no further CAM studies on Mexican *Clusia* species have been carried out since then. In order to extend the knowledge on photosynthetic modes in *Clusia* species, we have measured $\delta^{13}C$ values for 20 species from sites in Mexico, Belize, and Guatemala.

Materials and methods

Plant material was obtained from the National Herbarium of Mexico (MEXU) and from the herbarium of Centro de Investigación Científica de Yucatán, A. C. (CICY). Species names, collector, voucher number, location, altitude and life form were obtained from the specimen vouchers. Carbon isotope ratios ($^{13}C/^{12}C$) were determined from about 3 mg of dried material (Pierce *et al.* 2002, Winter and Holtum 2002, Holtum *et al.* 2004). Samples were analyzed at the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, Athens, GE, USA by isotope ratio mass spectrometry. The abundance of ^{13}C in each sample was calculated relative to the abundance of ^{13}C in standard CO_2 that had been calibrated against Pee Dee belemnite (*Belemnitella americana*) and the stable carbon isotope composition was expressed in conventional delta (δ) notation as the $^{13}C/^{12}C$ ratio relative to the standard: $\delta^{13}C = [(^{13}C/^{12}C \text{ of sample})/(^{13}C/^{12}C \text{ of standard}) - 1] \times 1\,000$.

Results

The $\delta^{13}C$ values of leaves of 140 specimens of 20 species of *Clusia* ranged from a minimum of –33.6 to a maximum of –13.5 ‰ (Table 1). In eight species, at least one specimen had a $\delta^{13}C$ less negative than –20 ‰ characteristic of pronounced CAM (*C. chanekiana*, *C. flava*, *C. lundellii*, *C. mexicana*, *C. quadrangula*, *C. rosea*, *C. suborbicularis*, and *C. tetra-trianthera*). CAM was most prominent in *C. flava*, which was sampled 39 times. All specimens of *C. flava* except one exhibited $\delta^{13}C$ values less negative than –20 ‰ and $\delta^{13}C$ values of 31 specimens were in the very narrow range between –16.5 and –13.5 ‰. *C. rosea* ranked second in terms of the importance of CAM to carbon gain, with 5 of 7 specimens showing $\delta^{13}C$ values less negative than –20 ‰ (–18.5 to –14.5 ‰). *C. lundellii* (13 specimens), *C. quadrangula* (12 specimens), and *C. mexicana* (5 specimens) had one specimen each with a $\delta^{13}C$ value less negative than –20 ‰, and 2 (*C. quadrangula*) to 4 specimens (*C. lundellii*, *C. mexicana*) in the –24 to –20 ‰ range, indicative of a potential contribution of net dark CO_2 fixation to carbon gain. Further species containing specimens with $\delta^{13}C$ values in the –24 to –20 ‰ range were *C. minor*, a known CAM species, *C. guatemalensis*, and *C. salvinii*. Specimens of the remaining 9 species (*C. belizensis*, *C. gentlei*, *C. pringlei*, *C. stenophylla*, *C. torresii*, *C. uniflora*, and *C. uvitana*) had $\delta^{13}C$ values more negative than –24.8 ‰. One of these species (*C. uvitana*) is known to exhibited CAM.

The mean $\delta^{13}C$ values showed a bimodal distribution with a large mode at –26.0 ‰ and a small mode at –14.0 ‰ (Fig. 1). Several species showed a very broad range of leaf $\delta^{13}C$ values. Fig. 2 depicts the frequency distribution of leaf $\delta^{13}C$ values for the six species for which 7 or more specimens were analyzed. *C. quadrangula* covered the largest range of $\delta^{13}C$ values (–33.6 to –19.9 ‰; Fig. 2*C*).

The ecological amplitude for most species of Mexican *Clusia* is large. Species were distributed over a mean-annual-precipitation range of 300–4 500 mm and occurred at altitudes from 0–2 300 m a.s.l. (Tables 1 and 2). Many species were present in dry, wet, and cloud forests (Table 2). Specimens of *C. flava* and *C. quadrangula* were also collected in coastal dune and desert scrub habitats (Table 2).

Specimens with C_3-type leaf $\delta^{13}C$ values were collected across the entire altitudinal sampling range. The upper limit for the occurrence of strong CAM was 1 700 m (*C. tetra-trianthera*, –13.5 ‰). Eighty two percent of all specimens with $\delta^{13}C$ values less negative than –20.0 ‰ were collected at altitudes ≤500 m a.s.l. (Fig. 3). *C. salvinii*, which was sampled multiple times at mainly high altitudes (1 562±103 m a.s.l., $n = 24$; $\delta^{13}C = -26.8 \pm 0.8$ ‰, $n = 26$) showed a particularly wide range of $\delta^{13}C$ values from –31.4 ‰ for a plant at 350 m a.s.l. to –20.9 ‰ for a plant at 2 100 m a.s.l.

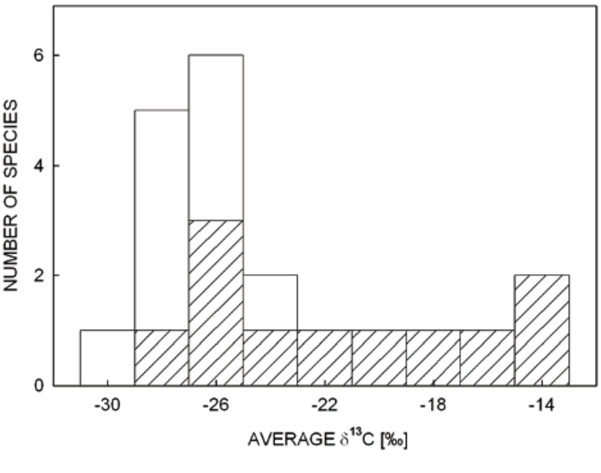

Fig. 1. Frequency of leaf $\delta^{13}C$ for Mexican species of *Clusia* with presence (*diagonal*) or absence (*open*) of CAM. The presence of CAM was based on carbon stable isotopes values and on previously published data. Each bar represents a 2 ‰ range of $\delta^{13}C$.

Table 1. $\delta^{13}C$ values of leaves from herbarium samples of *Clusia* spp. Samples were obtained from the National Herbarium of Mexico (MEXU) and from the herbarium of the Centro de Investigación Científica de Yucatán (CICY). Life forms: shrub (S), tree (T), hemi-epiphyte (H) or epiphyte (E). ND not determined.

Taxon	Collector, voucher number, herbarium	Altitude [m]	Life-form	$\delta^{13}C$ [‰]
C. belizensis Standl.	Lundell 20218 MEXU	540	T	–28.4
	E. Martínez 15621 MEXU	180	S	–27.8
C. chanekiana Lundell	E. Martínez 28126 CICY	129	E	–17.1
C. flava Jacq.	B. Croat 39480 MEXU	1260	T	–22.4
	E. Ucan 948 CICY	100	T	–19.9
	Ramamoorthy 3298 MEXU	200	S	–18.9
	D. Vásquez 229 MEXU	300	H	–18.3
	Levy and Durán 451 MEXU	400	T	–17.7
	E. Rojas 21 MEXU	0	T	–17.5
	E. Martínez 28126 MEXU	129	E	–17.4
	P. Simá 786 CICY	20	T	–16.7
	Laurence 3920 MEXU	150	E	–16.5
	E. Ucan 3881 CICY	22	T	–16.4
	P. Vera Caletti 218 MEXU	430	H	–16.3
	Reyes García 182 MEXU	500	T	–16.3
	O. Téllez 3425 MEXU	10	T	–16.2
	Durán y Marmolejo 1075 MEXU	10	T	–16.2
	C. Cowan 4662 CICY	200	T	–16.1
	Lundell 6366 MEXU	126	H	–16.0
	Schatz *et al*. MEXU	200	E	–16.0
	S. Koch 8419 MEXU	0	S	–16.0
	R. M. López MEXU	20	T	–15.7
	P. Simá 766 CICY	20	E	–15.6
	S. Sinaca 867 MEXU	300	E	–15.4
	E. Cabrera 6392 MEXU	10	T	–15.4
	R. Durán 1541 CICY	20	T	–15.4
	E. Rojas 021 CICY	20	T	–15.3
	A. Gómez-Pompa 4847 MEXU	10	E	–15.2
	Magaña 331 MEXU	60	T	–15.2
	Reyes García 1050 MEXU	1150	T	–15.2
	C. Chan 5095 CICY	25	T	–15.1
	E. Ucan y C. Chan 3836 CICY	21	E	–15.1
	E. Ucan 3310 CICY	20	H	–15.0
	O. Téllez 1282 CICY	5	T	–15.0
	O. Téllez 3193 MEXU	10	T	–14.8
	E. Cabrera 3467 MEXU	10	T	–14.7
	C. Chan 2360 CICY	5	T	–14.6
	Reyes García 1286 MEXU	1050	T	–14.3
	G. Ibarra 806 MEXU	200	S	–14.2
	Steere MEXU	29	T	–14.2
	E. Martínez 30799 MEXU	300	T	–13.6
	F. Menendez 120 MEXU	10	S	–13.5
C. gentlei Lundell	Espejo 1123 MEXU	900	T	–24.9
C. guatemalensis Hemsl.	T. Wendt 3866 MEXU	350	H	–30.4
	Hawkins 1453 MEXU	665	E	–29.5
	F. Ventura 7662 MEXU	1400	S	–28.7
	Lundell 20109 MEXU	ND	E	–28.7
	A. Durán and S. Levy 118 MEXU	950	E	–28.1
	Heath and Long 817 MEXU	1400	T	–27.7
	Alonso Méndez 9593 MEXU	ND	T	–26.4
	F. Ventura 4576 MEXU	760	S	–26.3
	R. Torres 5922 MEXU	1170	ND	–26.0
	Sousa MEXU	1500	E	–25.3
	E. Martínez 8782 MEXU	1600	T	–24.8
	Campos 4272 MEXU	ND	T	–24.8
	J. Rzedowski 19097 MEXU	650	ND	–24.2
	R. del Castillo 873 MEXU	1985	S	–23.2

Table 1 (continued)

Taxon	Collector, voucher number, herbarium	Altitude [m]	Life-form	δ^{13}C [‰]
C. aff. *guatemalensis* Hemsl.	X. Munn 60 MEXU	1835	T	–26.9
C. lundellii Standl.	Davidse 31924 MEXU	150	T	–28.1
	P. Zamora 2427 MEXU	ND	T	–27.5
	S. Avendaño y Durán 3114 MEXU	ND	T	–27.4
	Castillo and Vasquez 1382 MEXU	1300	T	–26.6
	E. Martínez 15621 MEXU	180	S	–26.4
	H. Navare 396 MEXU	1650	T	–25.9
	M. Cházaro 1066 MEXU	ND	S	–25.6
	Calzado *et al*. 8895 MEXU	1550	T	–25.4
	M. Rosas 173 MEXU	1400	T	–23.4
	Merino Rosas 173 MEXU	1400	ND	–23.3
	Nevling and Gómez-P. 2280 MEXU	1300	E	–22.8
	R. Cedillo 86 MEXU	ND	E	–21.4
	G. Ibarra 1094 MEXU	160	S	–19.0
C. massoniana Lundell	Davidse and Brandt 31960 MEXU	300-620	T	–29.5
	G. Ibarra 4015 MEXU	400	T	–29.4
	E. Martínez 7648 MEXU	540	T	–27.4
	J. Meave and A. Howe 1109 MEXU	510	T	–27.3
C. mexicana Vesque	Valdivia 2430 MEXU	650	E	–23.3
	F. Ventura MEXU	1500	S	–22.9
	F. Ventura 4210 MEXU	1030	S	–22.1
	Avendaño and Durán 3051 MEXU	ND	T	–21.7
	G. Ibarra 2937 MEXU	520	E	–15.8
C. minor L.	E. Martínez 8952 MEXU	80	T	–28.6
	Estrada 792 MEXU	1120	T	–28.5
	B. Vásquez 187 MEXU	152	T	–27.1
	P. Basurto and Ramam. 2395 MEXU	100	T	–27.1
	G. Ibarra 1986 MEXU	200	E	–26.1
	Gilly and Hernández X 214 MEXU	10	H	–26.0
	T. Wendt *et al*. 3181 MEXU	130	E	–23.5
C. multiflora Kunth	Croat and Hammel 63664 MEXU	1800	T	–26.2
C. pringlei Lundell	J. L. Panero 3923 MEXU	1900	S	–27.5
C. quadrangula Bartlett	Davidse and Prantt 32054 MEXU	80-420	E	–33.6
	E. Contreras 6773 MEXU	300	T	–33.0
	R. Cedillo 1915 MEXU	1500	T	–31.8
	F. Martínez *et al*. 25068 MEXU	150	E	–31.3
	B. Ortiz 100 MEXU	150	E	–30.2
	D. Lorente 2975 MEXU	750	E	–29.4
	E. Martínez *et al*. 21058 MEXU	200	T	–29.0
	G. Ibarra 3753 MEXU	550	H	–27.9
	Castillo *et al*. 17075 MEXU	690	S	–26.0
	R. Ortega 445 MEXU	600	S	–21.5
	Dorantes 1234 MEXU	650	S	–21.0
	Medina 133 MEXU	600	T	–19.9
C. rosea Jacq.	A. Espejo 1971 MEXU	1400	T	–25.8
	Nuñez 983bis MEXU	1680	T	–24.2
	E. Martínez 30274 MEXU	250	T	–18.5
	H. Uitzil 34 CICY	0	T	–18.4
	E. Martínez 30274 CICY	250	T	–16.2
	Lundell 16233 MEXU	600	E	–15.4
	C. Beutelspachel MEXU	800	T	–14.5
C. salvinii Donn. Sm.	R. Cedillo 2976 MEXU	350	S	–31.4
	Campos A. 3322 MEXU	1900	T	–29.7
	Flores Franco 4470 MEXU	1515	T	–29.2
	S. Salas 1223 MEXU	1760	S	–28.8
	J. Soto 12380 MEXU	950	T	–28.7
	Machoca and Chazado 7514 MEXU	1550	T	–28.5
	J. Soto 7895 MEXU	1150	S	–27.8

Table 1 (continued)

Taxon	Collector, voucher number, herbarium	Altitude [m]	Life-form	δ^{13}C [‰]
C. salvinii Donn. Sm.	O. Téllez 12924 MEXU	ND	T	–27.8
	Cedillo 3326 MEXU	950	T	–27.7
	García A. 1304 MEXU	1870	T	–27.5
	E. Martinez MEXU	1800	E	–27.2
	M. Ishinki 726 MEXU	1880	T	–27.1
	MEXU	2000	ND	–27.0
	S. Moreno 157 MEXU	1900	T	–26.9
	G. Medrano 5161 MEXU	1500	T	–26.9
	Breedlove 28158 MEXU	800	T	–26.8
	E. Guizar y Niembro 381 MEXU	1850	T	–26.4
	C. Soto and R. Moreno MEXU	1300	T	–26.0
	Vasquez and Phillips 275 MEXU	1350	T	–25.6
	O. Téllez 9735 MEXU	ND	T	–25.0
	Zamudio and Pérez 8287 MEXU	1820	T	–24.8
	R. Mallorga 1541 MEXU	2300	T	–24.5
	M. Osorio 2619 MEXU	2300	T	–24.0
	J.Clónico (12153) MEXU	1210	S	–22.5
	Cházaro *et al*. (7763) MEXU	2100	S	–20.9
C. stenophylla Standl.	G. Ibarra 2358 MEXU	1000	T	–29.6
C. suborbicularis Lundell	E. Contreras 8276 MEXU	600	T	–14.5
C. tetra-trianthera Maguire	Breedlove 28177 MEXU	1350	T	–13.7
	Breedlove 37928 MEXU	1700	T	–13.5
C. torresii Standl.	A. Méndez 6664 MEXU	150	T	–27.8
C. uniflora Lundell	Hamshire *et al*. 620 MEXU	1400	T	–25.1
C. uvitana Pittier	González Espinosa *et al*. 1384 MEXU	900	E	–25.9

Discussion

Of the 20 species studied, five can be considered strong CAM species based on carbon isotope ratios: *C. chanekiana*, *C. flava*, *C. rosea*, *C. suborbicularis*, and *C. tetra-trianthera*. While CAM in *C. rosea* has been documented previously (Ting *et al*. 1985, Holtum *et al.* 2004), our broad survey amongst 39 specimens of *C. flava* now provides unequivocal evidence for the presence of strong CAM in this species as suggested by Holtum *et al.* (2004). CAM in *C. chanekiana*, *C. suborbicularis*, and *C. tetra-trianthera* has not been reported before. For *C. suborbicularis* only one specimen collected in Guatemala was analyzed and further studies of this species are warranted.

In three additional CAM species, *C. quadrangula*, *C. lundellii*, and *C. mexicana*, mean δ^{13}C values were –25.1, –24.8, and –21.1 ‰, respectively, with some specimens showing δ^{13}C values typical of strong CAM. δ^{13}C values in the C_3 range do not exclude the presence of CAM. According to the calibration regression by Winter and Holtum (2002), which applies to non-stressed plants at or close to sea-level, the above-mentioned mean δ^{13}C values may reflect a 10, 12, and 32 % contribution, respectively, of dark CO_2 fixation to total carbon gain. *C. lundellii* was the first *Clusia* species ever reported to possess CAM based on measurements of diel changes in leaf acidity (Tinoco-Ojanguren and Vázquez-Yanes 1983). *C. mexicana* was reported to lack daytime CO_2 assimilation in 1937 by Willy Hartenburg (Lüttge 2006) consistent with the operation of the CAM pathway, and *C. quadrangula* has been shown to exhibit weak CAM (Holtum *et al*. 2004).

C. minor is an extremely well characterized C_3-CAM species (Franco *et al*. 1991, Borland *et al*. 1996, Roberts *et al*. 1998, de Mattos and Lüttge 2001). In our study, δ^{13}C values of seven specimens ranged from –23.5 to –28.6 ‰, indicating that plants gained carbon mainly *via* the C_3 pathway. The same is true for a single specimen of *C. uvitana* (–25.9 ‰), a species having the capacity for CAM (Winter *et al*. 1992).

Leaf acidity and CO_2 exchange measurements are required to examine whether any of the other *Clusia* species in our study can exhibit CAM. In *C. guatemalensis* δ^{13}C values of 15 specimens ranged from –30.4 to –23.2 ‰ (mean –26.7 ‰), and preliminary measurements of day/night changes in leaf titratable acidity suggested the presence of CAM in this species from the Yucatan peninsula (Gustavo Vargas-Soto and Jose Luis Andrade, unpublished). Thus, at least 10 of 18 *Clusia* species from Mexico seem to be able to perform CAM, and some of these are strong CAM species. It also appears that the Mexican flora contains fewer *Clusia* species than the Panamanian flora (Holtum *et al*. 2004), but that the proportion of strong CAM species is larger in Mexico than in Panama, where only *C. rosea* can be

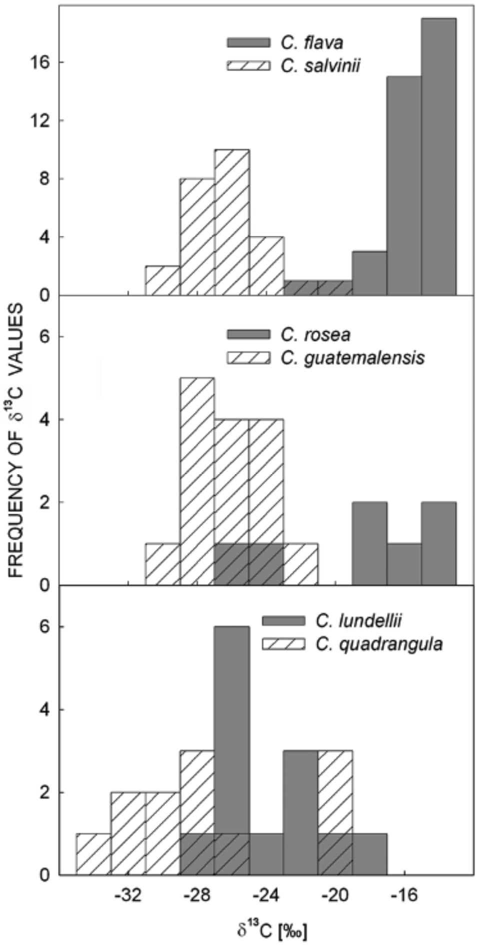

Fig. 2. Frequency of leaf δ^{13}C values of the six *Clusia* species with ≥7 specimens analyzed. (*A*) *C. salvinii* (*diagonal bars*) and *C. flava* (*gray bars*). (*B*) *C. guatemalensis* (*diagonal bars*) and *C. rosea* (*gray bars*). (*C*) *C. lundellii* (*diagonal bars*) and *C. quadrangula* (*gray bars*). Each bar represents a 2 ‰ range of δ^{13}C.

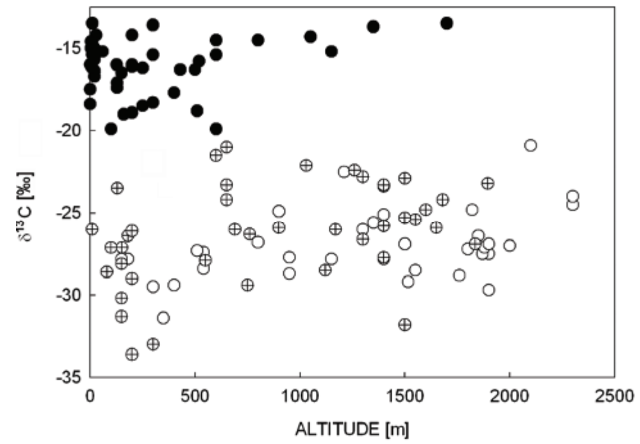

Fig. 3. Relationship between leaf δ^{13}C values and altitude for Mexican species of *Clusia* that exhibited strong CAM (*closed circles*), those known to perform CAM (*crossed circles*), and those in which CAM has not been detected (*open circles*).

considered strong CAM. The mean annual precipitation range within the Mexican habitats of the present study is much larger (300−4 500 mm) than that for Panamanian habitats (1 800−4 000 mm; Condit 1998), and the greater aridity of many Mexican sites is expected to favour CAM. Consistent with previous studies in Venezuela and Panama (Diaz *et al*. 1996, Holtum *et al*. 2004), no Mexican *Clusia* species known to exhibit CAM was collected above 1 700 m a.s.l. The δ^{13}C values of C$_3$ plants become less negative with increasing altitude (Körner *et al*. 1991). We did not find a clear altitudinal trend in δ^{13}C for Mexican *Clusia*, not even for the species currently considered C$_3$ plants. High altitude effects on δ^{13}C (Körner *et al*. 1988, Cordell *et al*. 1999, Hultine and Marshall 2000, Crayn *et al*. 2001), independent of CAM, may be largely responsible for δ^{13}C values up to –20.9 ‰ at 2 100 m a.s.l. in *C. salvinii*, although we cannot

Table 2. Ecological range for *Clusia* species from Mexico. Dry forest category includes seasonally dry, dry deciduous, and seasonally flooded tropical forests. Other include disturbed vegetation and cultivated lands. Each symbol signifies 1 herbarium specimen. [1]Moreno-Casasola and Espejel (1986); [2]Rzedowski (1978); [3]Trejo and Dirzo (2002); [4]García (1987); [5]Webster (1995).

Species	Habitat						
	Coastal dune	Desert scrub	Dry forest	Rain forest	Riparian	Cloud forest	Other
C. flava	●●	●	●●●●●●●●●●●● ●●●●●●●●●●●●	●●●●●●●●● ●●		●	
C. guatemalensis			●	●●●●●		●●●●●●●●	●
C. lundellii			●●●	●●●	●	●●●●●●	
C. massoniana			●	●●		●	
C. mexicana			●	●●	●		●
*C. mino*r				●●●●●		●●●	
C. quadrangula		●●	●●	●●●●●	●	●	●
C. rosea			●●●●	●		●●	
C. salvinii		●	●●	●●●		●●●●●●●●●●●● ●●●●●●	●●
Annual precip. [mm]	450[1]	300−400[2]	600−1800[3]	2200−4000[4]	80−1030	1500−4500[5]	1350−1500

exclude a capacity for CAM in this species in the absence of titratable acidity measurements.

Our survey provides a foundation for future rigorous field and laboratory studies on Mexican *Clusia* species, especially on those exhibiting CAM and covering a wide range of habitats, involving titratable acidity measurements to determine weak CAM. It has been predicted that as temperature increases and precipitation decreases in Mexico in the context of climate change, drier ecosystems such as dry tropical forests and thorn desert scrub communities will be favoured (Villers-Ruiz and Trejo-Vázquez 1997). Under this scenario, *Clusia* species with water-conserving CAM photosynthesis could become more important ecologically, and should also be considered for reforestation purposes.

References

Borland, A.M., Griffiths, H., Maxwell, C., Fordham, M.C., Broadmeadow, M.S.J.: CAM induction in *Clusia minor* L. during the transition from wet to dry season in Trinidad: The role of organic acid speciation and decarboxylation. – Plant Cell Environ. **19**: 655-664, 1996.

Condit, R.: Ecological implications of changes in drought patterns: shifts in forest composition in Panama. – Climate Change **39**: 413-427, 1998.

Cordell, S., Goldstein, G., Meinzer, F.C., Handley, L.L.: Allocation of nitrogen and carbon in leaves of *Metrosideros polymorpha* regulates carboxylation capacity and δ^{13}C along an altitudinal gradient. – Funct. Ecol. **13**: 811-818, 1999.

Crayn, D.M., Smith, J.A.C., Winter, K.: Carbon-isotope ratios and photosynthetic pathways in the neotropical family Rapateaceae. – Plant Biol. **3**: 569-576, 2001.

Crayn, D.M., Winter, K., Smith, J.A.C.: Multiple origins of crassulacean acid metabolism and the epiphytic habit in the Neotropical family Bromeliaceae. – Proc. nat. Acad. Sci. USA **101**: 3703-3708, 2004.

de Mattos, E.A., Lüttge, U.: Chlorophyll fluorescence and organic acid oscillations during transition from CAM to C_3-photosynthesis in *Clusia minor* L. (Clusiaceae). – Ann. Bot. **88**: 457-463, 2001.

Diaz, M., Haag-Kerwer, A., Wingfield, R., Ball, E., Olivares, E., Grams, T.E.E., Ziegler, H., Lüttge, U.: Relationships between carbon and hydrogen isotope ratios and nitrogen levels in leaves of *Clusia* species and two other Clusiaceae genera at various sites and different altitudes in Venezuela. – Trees **10**: 351-358, 1996.

Ehleringer, J.R., Osmond, C.B.: Stable isotopes. – In: Pearcy, R.W., Ehleringer, J.R., Rundel, P.W. (ed.): Plant Physiological Ecology, Field Methods and Instrumentation. Pp. 281-300. Chapman and Hall, London 1989.

Franco, A.C., Ball, E., Lüttge, U.: The influence of nitrogen, light and water stress on CO_2 exchange and organic acid accumulation in the tropical C_3-CAM tree, *Clusia minor*. – J. exp. Bot. **42**: 597-603, 1991.

García, E.: [Modificaciones al sistema de clasificación climática de Koeppen.] – Instituto de Geografía, Universidad Nacional Autónoma de México, Mexico City 1987. [In Span.]

Gehrig, H.H., Aranda, J., Cushman, M.A., Virgo, A., Cushman, J.C., Hammel, B.E., Winter, K.: Cladogram of Panamanian *Clusia* based on nuclear DNA: implications for the origin of crassulacean acid metabolism. – Plant Biol. **5**: 59-70, 2003.

Gustafsson, M.H.G., Bittrich, B., Stevens, P. F.: Phylogeny of Clusiaceae based on *RBCL* sequences. – Int. J. Plant Sci. **163**: 1045-1054, 2002.

Hammel, B.E.: New species of Clusiaceae from Central America with notes on *Clusia* and synonymy in the tribe Clusieae. – Selbyana **9**: 112-120, 1986.

Holtum, J.A.M., Aranda, J., Virgo, A., Gehrig, H.H., Winter, K.: δ^{13}C values and crassulacean acid metabolism in *Clusia* species from Panama. – Trees **18**: 658-668, 2004.

Hultine, K.R., Marshall, J.D.: Altitude trends in conifer leaf morphology and stable carbon isotope composition. – Oecologia **123**: 32-40, 2000.

Körner, C., Farquhar, G.D., Roksandic, Z.: A global survey of carbon isotope discrimination in plants from high-altitude. – Oecologia **74**: 623-632, 1988.

Körner, C., Farquhar, G.D., Wong, S.C.: Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. – Oecologia **88**: 30-40, 1991.

Lüttge, U.: Photosynthetic flexibility and ecophysiological plasticity: questions and lessons from *Clusia,* the only CAM tree, in the neotropics. – New Phytol. **171**: 7-25, 2006.

Moreno-Casasola, P., Espejel, I.: Classification and ordination of coastal sand dune vegetation along the Gulf and Caribbean Sea of Mexico. – Vegetatio **66**: 147-182, 1986.

Pierce, S., Winter, K., Griffiths, H.: Carbon isotope ratio and the extent of daily CAM use by Bromeliaceae. – New Phytol. **156**: 75-83, 2002.

Roberts, A., Borland, A.M., Maxwell, C., Griffiths, H.: Ecophysiology of the C_3-CAM intermediate *Clusia minor* L. in Trinidad: seasonal and short-term photosynthetic characteristics of sun and shade leaves. – J. exp. Bot. **49**: 1563-1573, 1998.

Rzedowsky, J.: [Vegetación de México.] – Limusa, Mexico City 1978. [In Span.]

Santiago, L.S., Silvera, K., Andrade, J.L., Dawson, T.E.: [The use of stable isotopes in tropical biology.] – Interciencia **30**: 536-542, 2005. [In Span.]

Silvera, K., Santiago, L.S., Winter, K.: Distribution of crassulacean acid metabolism in orchids of Panama: evidence of selection for weak and strong modes. – Funct. Plant Biol. **32**: 397-407, 2005.

Ting, I.P., Lord, E.M., Sternberg, L.D.L., DeNiro, M.J.: Crassulacean acid metabolism in the strangler *Clusia rosea* Jacq. – Science **229**: 969-971, 1985.

Tinoco-Ojanguren, C., Vázquez-Yanes, C.: [CAM species in the tropical rain forest of Los Tuxtlas, Veracruz.] – Bol. Soc. Bot. Mex. **45**: 150-153, 1983. [In Span.]

Trejo, I., Dirzo, R.: Floristic diversity of Mexican seasonally dry tropical forests. – Biodivers. Conserv. **11**: 2063-2084, 2002.

Vaasen, A., Begerow, D., Lüttge, U., Hampp, R.: The genus *Clusia* L.: molecular evidence for independent evolution of photosynthetic flexibility. – Plant Biol. **4**: 86-93, 2002.

Villers-Ruiz, L., Trejo-Vázquez, I.: Assessment to the vulnerability of forest ecosystems to climate change in Mexico. – Climate Res. **9**: 87-93, 1997.

Webster, G.L.: Panorama of neotropical cloud forests. – In: Biodiversity and Conservation of Neotropical Montane

Forests: Proceedings. Pp. 53-77. New York Botanical Garden, Bronx 1995.

Winter, K., García, M., Holtum, J.A.M.: On the nature of facultative and constitutive CAM: environmental and developmental control of CAM expression during early growth of *Clusia, Kalanchoe* and *Opuntia*. – J. exp. Bot. **59**: 1829-1840, 2008.

Winter, K., Holtum, J.A.M.: How closely do the $\delta^{13}C$ values of crassulacean acid metabolism plants reflect the proportion of CO_2 fixed during day and night? – Plant Physiol. **129**: 1843-1851, 2002.

Winter, K., Zotz, G., Baur, B., Dietz, K.J.: Light and dark CO_2 fixation in *Clusia uvitana* and the effects of plant water status and CO_2 availability. – Oecologia **91**: 47-51, 1992.

Fromme, P. (ed.): **Photosynthetic Protein Complexes**. WILEY-VCH Verlag, Weinheim 2008. ISBN 978-3-527-31730. € 159.00.

The book provides a comprehensive overview of current knowledge on membrane protein complexes involved in the photochemical energy conversion performed by photosynthetic bacteria, algae and plants. The subtitle of the book, “A structural approach”, clearly expresses the main emphasis of the book, which is given to the high resolution structures of these complexes recently obtained using X ray analysis of protein crystals. Fifteen chapters of the book written by leading scientists in the field from around the world cover architectures of oxygenic and anoxygenic reaction centers, their external light harvesting antennae, connecting electron and proton transferring protein complexes and also chloroplast ATP-synthase. The book is illustrated by a large number of color figures mostly documenting the beauty of the above mentioned molecular machines. It is only unfortunate that despite the advertisement on the back cover, these pictures are not freely available *via* the web site of the book at www.wiley-vch.de/publish/en/books/ ISBN978-3-527-31730-1.

The first chapter by the editor giving a short but very compact and informative survey on photosynthetic “light” reactions is followed by two chapters dedicated to the cyanobacterial and plant Photosystem I complex. The structural data on protein subunits, pigments, secondary electron acceptors and other cofactors document high similarity between complexes from these different organisms. The following chapter deals with overall structure of another cyanobacterial complex, Photosystem II (PSII). One chapter obviously cannot provide such exhaustive information like the recent book “Photosystem II” of the series “Advances in Photosynthesis and Respiration” (volume 22, 2006), nevertheless it provides sufficient, compact and up-to date knowledge for everybody interested in structure and function of this fascinating complex. PSII is the only photosynthetic complex which is able to use water as the source of electrons and therefore a special chapter is focused on the mechanism of water splitting and oxygen evolution. Chapter 6 together with chapters 10 and 11 illustrate differences in the light harvesting strategies between oxygenic prokaryots and eukaryots. Chapters 7, 8 and 15 describe the structural and functional properties of proteins and complexes that catalyze electron transport to and from both photosystems (cytochrome b6-f complex, plastocyanin, cytochrome c6, ferredoxin and flavodoxin). The chapter 9 targets the current structural concept of the chloroplast ATP-synthase which together with plant Photosystem II represents the only photosynthetic membrane complex with limited structural information due to the lack of high resolution models. The remaining chapters12, 13 and 14 are devoted to structure of anoxygenic reaction centres and their antennae. This part of the book also includes discussion on a putative evolution of both anoxygenic and oxygenic reaction centers indicating an existence of the common ancestor for all these energy transducing enzymes.

The book Photosynthetic Protein Complexes is very useful guide through the structural aspects of all photosynthetic membrane complexes for everybody interested in structural biology of membrane proteins and should not be missing in bookshelves of any laboratory working in the field of photosynthesis research.

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