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Photosynthesis in hemiepiphytic species of *Clusia* and *Ficus*

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Summary. Hemiepiphytic species in the genera *Clusia* and *Ficus* were investigated to study their mode of photosynthetic metabolism when growing under natural conditions. Despite growing sympatrically in many areas and having the same growth habit, some *Clusia* species show Crassulacean acid metabolism (CAM) whereas all species of *Ficus* investigated are C_3. This conclusion is based on diurnal CO_2 fixation patterns, diurnal stomatal conductances, diurnal titratable acidity fluctuations, and $\delta^{13}C$ isotope ratios. *Clusia minor*, growing in the savannas adjacent to Barinas, Venezuela, shows all aspects of Crassulacean acid metabolism (CAM) on the basis of nocturnal gas exchange, stomatal conductance, total titratable acidity, and carbon isotope composition when measured during the dry season (February 1986). During the wet season (June 1986), the plants shifted to C_3-type gas exchange with all CO_2 uptake occurring during the daylight hours. The carbon isotope composition of new growth was -28 to $-29‰$ typical of C_3 plants.

Key words: *Clusia* – *Ficus* – Strangler – CAM – Photosynthesis – Hemiepiphyte

The "strangler" *Clusia rosea* shows aspects of Crassulacean acid metabolism (CAM) on the basis of ^{13}C isotope composition, diurnal titratable acid fluctuations, malic acid fluctuations, and leaf succulence (Ting et al. 1985). *Clusia rosea* is a hemiepiphyte, a growth form in which the seedling generally begins as an epiphyte growing on a tree and eventually becomes a dominant, soil rooted, free-standing tree that completely replaces its host tree. The roots growing down from the epiphyte anastomoze around the host tree giving the appearance of strangulation. The observation of CAM in *Clusia* is important because it represents the first report of a true dicotyledonous tree with this adaptative photosynthetic metabolism (Kluge and Ting 1978). CAM was not completely unexpected in this genus because a high proportion of the tropical epiphytic angiosperms have CAM (Winter et al. 1983; Benzing 1984; Sinclair 1984; Guralnick et al. 1986). *Ficus* (Moraceae) is another genus having "stranglers." Since *Ficus* frequently grows sympatrically with *Clusia*, we wanted to compare photosynthesis in *Clusia* and hemiepiphytes in the Moraceae, especially *Ficus* under natural field conditions using gas exchange parameters, titratable diurnal acidity fluctuations, and carbon-13 isotope compositions as indicators of CAM- or C_3-photosynthesis.

Clusia is a tropical genus in the family Clusiaceae (= Guttiferae) with perhaps over 200 species (Lawrence 1951). The species range in growth form from hemiepiphytes, like *C. rosea*, through true epiphytes and species that grow as ordinary trees. The genus *Ficus* is larger than *Clusia* with an estimated 600 species (Lawrence 1951; Condit 1969), but also has species that show a complete range of growth habits including epiphytes, hemiepiphytes, and trees. The existence of hemiepiphytic species in the two unrelated genera raises the question of whether they have similar drought-tolerating or avoiding mechanisms (Putz and Holbrook 1986).

Materials and methods

Plant material and study sites

Four study sites were used in this investigation. The Virgin Islands National Park on St. John, U.S. Virgin Islands, was the site for the investigation of *Clusia rosea* and *Ficus trigonata*. Studies were conducted during a very dry period in July 1985, and during the beginning of the rainy season in August 1986. The Marie Selby Botanical Garden in Sarasota, Florida was the site for the investigation of exotic *Ficus* species and the native *F. aurea*. These studies were conducted in January 1986. Five species of *Clusia* were investigated in their native habitat at Finca La Selva, the Organization for Tropical Studies (OTS) site in Costa Rica in March 1986. Plants were considered to be epiphytic only if no root to soil connections existed.

Finally, studies were conducted in the pastures and adjacent grassland savannas of the Caballeria Santa Rosa, located at 400 m elevation on the north slope of the Andes near the town of Quebrada Seca, Estado Barinas, Venezuela. The site is characterized by grass fields created by burning and clearing of the savannas that ordinarily would have woody or forest vegetation. Palms of the species *Attalea maracaibensis* remained and acted as the host species for the hemiepiphytes. The climate is characterized by a very dry, 4-month rainless season and a wet, rainy season that extends from April to November. Epiphytic and tree individuals of *Clusia minor*, and *Ficus nymphaeifolia*, *F. obtusifolia*, and *Coussapoa villosa* (all Moraceae), were stud-

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ied. Plants in the epiphytic phase lacked terrestrial root connections. Tree individuals gave evidence of their epiphytic origins, in that they were situated on the host palm, but were rooted in the soil and, thus, functioning physiologically as trees. Only healthy, well-illuminated plants of each species and life-form were included in the study.

Gas exchange parameters

Gas exchange parameters were measured with a Li-Cor Inc., model 6000 portable gas exchange system (Li-Cor Inc., PO Box 4425, Lincoln, NB 68504). The instrument measures CO_2 with a single path, nondispersive-type analyzer in a closed system, atmospheric water vapor with a Vaisala humidity sensor, light with a Li-Cor LI-1905-1 quantum sensor sensitive over a waveband of 400 to 700 nm (PAR), and leaf and chamber temperatures with chromel-constantan thermocouples. A computer console performs appropriate calculations of transpiration rates, CO_2 fixation rates, internal leaf CO_2, and stomatal conductances. Raw data are retrievable from the console. A 1 liter polycarbonate teflon-coated leaf chamber equipped with two fans for air circulation was used. Each datum point is the average of at least three radings taken from different leaves of the same plant. Data were recorded every 6 s for 1 min in order to obtain each point. The CO_2 drawdown was less than optimum, but was minimized in order to prevent leaf changes while in the chamber.

Acid titrations

Leaf disks were collected from mature leaves using a 1 cm diameter cork borer and the acid rapidly extracted either by grinding in distilled water with a hand-held, glass-glass tissue grinder or by boiling in 80% alcohol (ethanol or propanol depending upon availability at the field sites) for several minutes. Acidity was titrated to a pH 7 endpoint with 0.01 N KOH. Each point represents the average of 3 titrations from different leaves. Data are expressed as μeq acid per cm^2 of leaf surface.

Isotope analyses

Samples of plant material for ^{13}C analysis were collected following the field observations, air dried, and returned to the laboratory for determination. In the laboratory, samples were dried at 50° C, further desiccated in a freeze-drier, and ground to a fine powder in a Wiley mill. Carbon isotope ratios were determined as previously described (Northfelt et al. 1981) and expressed as $\delta^{13}C$ values in units of ‰ relative to a PDB standard.

PEP carboxylase and malate enzyme assay

Phosphoenolpyruvate (PEP) carboxylase activity was assayed in *Clusia rosea* and selected *Ficus* species all growing in a greenhouse at Riverside. Protein was extracted from approximately 1 g of leaf tissue by grinding in a tissue grinder in 10 ml of extraction buffer at 4° C containing 100 M Hepes-NaOH, 10 mM $MgCl_2$, 10 mM DTT, and 1% PVP 360 adjusted to pH 7.8. The extract was centrifuged at 4000 rpm at 4° C for 10 min, and desalted by passage through a small sephadex G-25 column pre-equilibrated in the Hepes-NaOH buffer. The PEP carboxylase activity was assayed spectrophotometrically at 340 nm in a buffer containing 50 mM Hepes-NaOH, pH 7.8, 10 mM $MgCl_2$, 1 mM $NaHCO_3$, 0.2 mM NADH, 2 M PEP, and about 100 μl enzyme preparation. Malate enzyme was determined in the same preparation by following the reduction of NADP to NADPH at 340 nm. The assay preparation contained 25 mM Hepes-NaOH, 25 mM Bicine, 3 mM $MgCl_2$, 1 mM $MnCl_2$, 0.25 mM NADP, and 3 mM malate, all adjusted to pH 7.2.

Results

Clusia species

Gas exchange parameters. Measurements taken in July, 1985 on the island of St. John, indicated that the epiphytic, lithophytic (growing on rock outcrops), and free-standing trees of *Clusia rosea* had high stomatal conductance during the night with a maximum just after sunrise (Fig. 1). There was little stomatal conductance during the day. Significant CO_2 uptake occurred only during the dark period and the early morning just after sunrise (Fig. 1a). The gas exchange data obtained are typical of plants with CAM.

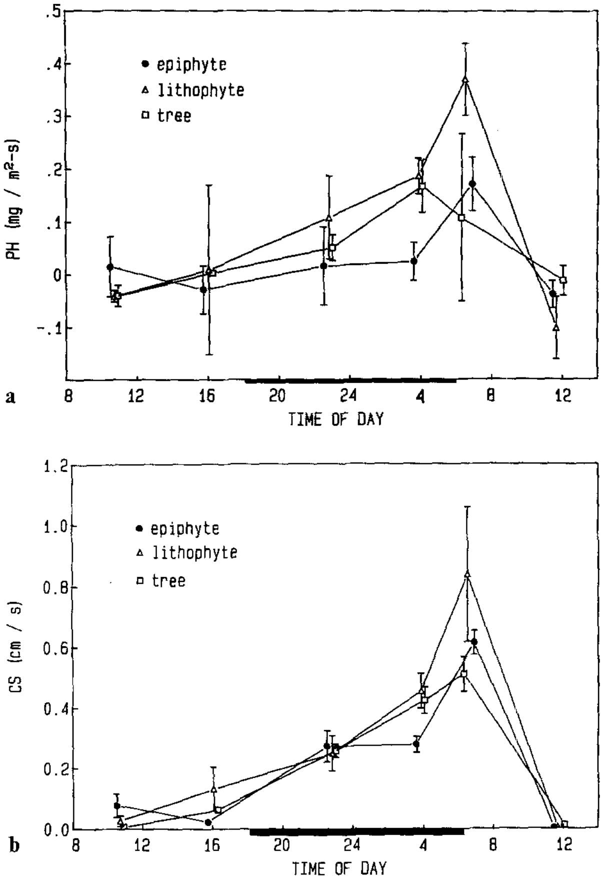

Fig. 1a, b. CO_2 uptake (PH) **a** and stomatal conductance (CS) **b** data for a rooted tree of *Clusia rosea*, an epiphytic form growing on a rock outcrop, and an unrooted epiphytic form growing on a host tree. The data indicate CAM photosynthesis with most CO_2 uptake toward the end of the dark period and some during the early morning hours. Data were obtained in July, 1985, on St. John, US Virgin Islands. Each point is the mean of 3 readings. The error bars are the SE of the means. The black bar in the abscissa is the dark period

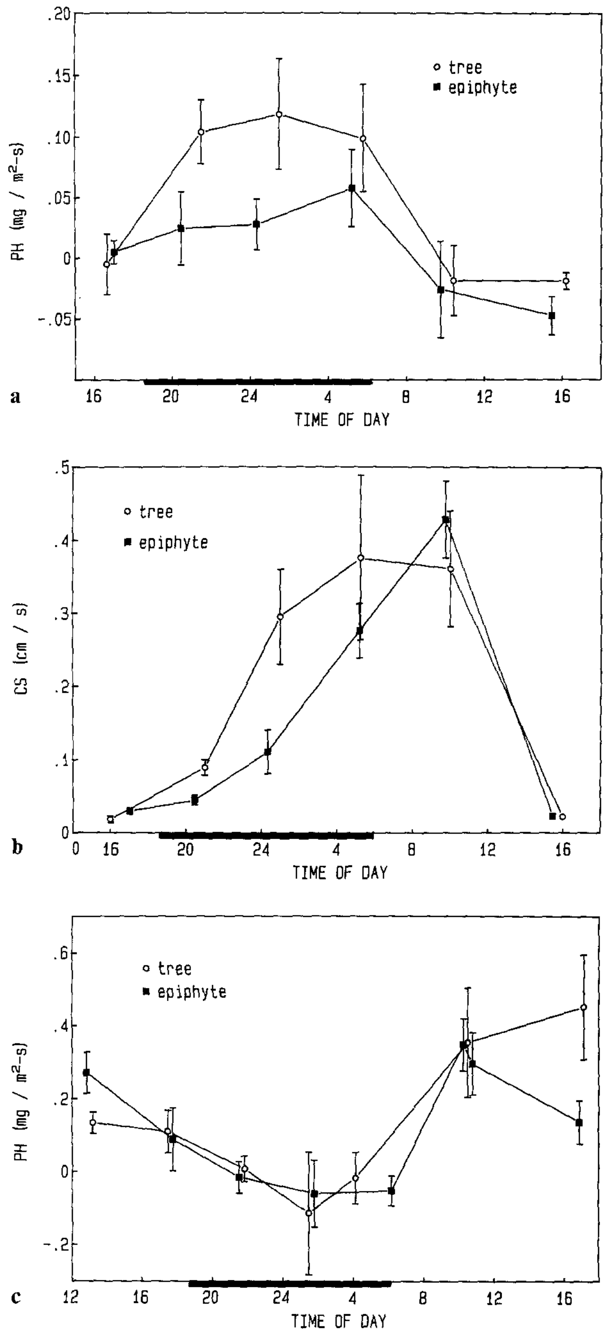

Fig. 2a–c. Gas exchange parameters for *Clusia minor*. **a** CO_2 exchange for epiphytic and tree forms during dry season = CO_2. **b** Stomatal conductance for the two forms during dry season (Cs = stomatal conductance). **c** Diurnal course of CO_2 uptake for *Clusia minor* measured during the wet season. The error bars are the SE of the mean

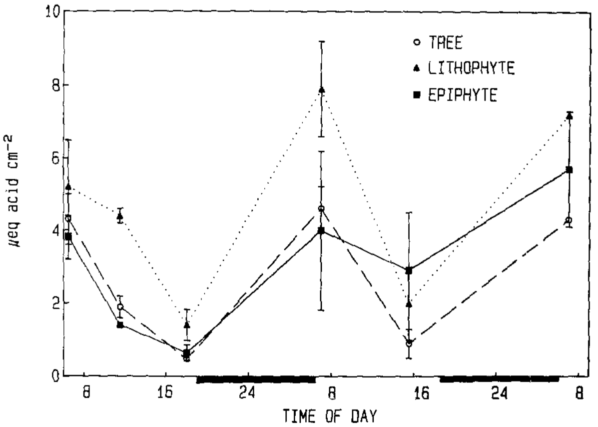

Fig. 3. Diurnal acidity patterns for *Clusia rosea*. The data were obtained from the plants used in Fig. 1. Each point is the mean of 3 readings. The error bars are the SE of the means

Gas exchange data for *Clusia minor* growing in the savannas of Venezuela during the dry season indicated typical CAM (Fig. 2). CO_2 uptake occurred during the night hours with no evidence of any daytime assimilation (Fig. 2a). CO_2 uptake rates by the epiphytes were lower than by the trees, which we interpret to mean better water balance by the trees than the epiphytes (Fig. 2a). This is also evident in the stomatal conductance data shown in Fig. 2b. Although the peak stomatal opening that occurred just after sunrise was comparable in the epiphytes and trees; the trees generally had greater conductance throughout the night than did the epiphytes (Fig. 2b). Except for the early morning stomatal conductance, we obtained no evidence for daytime stomatal opening.

The gas exchange measurements taken from epiphytic and tree forms of *Clusia minor* during the wet season did not reveal any indication of nocturnal CO_2 uptake (Fig. 2c). Thus the plants had evidently shifted from CAM-like gas exchange in the dry season to C_3-like gas exchange during the wet season. Because of extensive rains and very high humidity during the night (in excess of 95%), our stomatal conductance data were probably not reliable and are not reported.

Titratable acidity. Figure 3 shows the alternating acid fluxes for the three *Clusia rosea* types studied on St. John. All three show the typical acid fluctuation of CAM plants. Young, but fully expanded leaves had greater acid, but less diurnal fluctuation than older leaves (data not shown). These data are consistent with previous values reported for CAM plants (Kluge and Ting 1978). Much of the acid flux in *C. rosea* can be accounted for by malic acid, a pattern consistent with observations on other CAM plants (Ting et al. 1985).

Of the five species of *Clusia* investigated at La Selva, Costa Rica, two, *C. flava* and *C. uvitana*, showed a marked diurnal fluctuation of titratable acidity (Fig. 4). The other three species investigated, *C. gracilis*, *C. cylindrica* and *C. valerii*, had titratable acidity levels greater than what would be expected in a usual C_3 plant, but there was little evidence of any diurnal fluctuation. The general morphology of *C. flava* and *C. uvitana* was similar to *C. rosea* in that they are hemiepiphytes that eventually become large trees. These two species were growing in pastures. The leaves of the three species that did not show typical CAM are less succulent than the species with CAM. *Clusia cylindrica* was growing epiphytically and did not have the appearance of a succulent plant. *Clusia gracilis* was epiphytic on a fallen tree in heavy forest and *C. valerii* was growing as a free-standing tree in a clearing.

Total acidity measurements made in the middle of the dry season (February 1986) indicated that both the epiphytic and tree forms of *Clusia minor* were CAM (Fig. 5). The epiphytic forms had less acid synthesis and less diurnal fluctuation. Measurements of total titratable acidity of *Clusia minor* during the wet season indicated that levels were

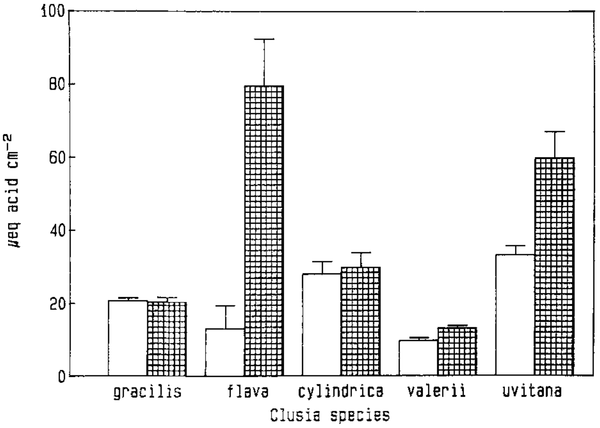

Fig. 4. Diurnal acidity data for 5 species of *Clusia* collected at Finca La Selva, Costa Rica in January, 1986. The unshaded bar is the evening measurement about 1600 h and the dark bar is the morning measurement from samples collected about 0600 h. The error bars are the SE of the means

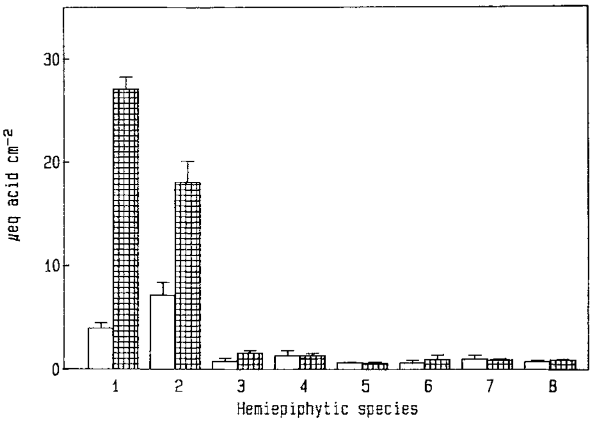

Fig. 5. Determination of total titratable acidity during the dry season (February 1986) for epiphytic and rooted forms of four different species of hemiepiphytes. Only *Clusia* shows evidence of CAM on the basis of diurnal acid fluctuation. The first bar in each pair represents measurements at the end of the day period, whereas the second bar is the end of the night period. The error bars are the SE of the mean; *1 Clusia minor* tree; *2 Clusia minor* epiphyte; *3 Ficus nymphaeifolia* tree; *4 Ficus nymphaeifolia* epiphyte; *5 Ficus obtusifolia* tree; *6 Ficus obtusifolia* epiphyte; *7 Coussapoa villosa* tree; *8 Coussapoa villosa* epiphyte

Table 1. Carbon isotope compositions for *Clusia* and *Ficus* species

Species	Fla	St. John	Costa Rica	Life form
Ficus aurea	−28.5			epiphyte
F. aurea	−28.3			tree
F. trigonata		−30.3		epiphyte
F. trigonata		−29.0		tree
F. altissima	−31.6			tree
F. benjamina	−32.1			tree
F. carica	−29.1			tree
F. macrophylla	−28.1			tree
F. microcarpa	−30.2			epiphyte
F. microcarpa	−29.9			tree
F. religiosa	−30.7			tree
F. virens	−29.0			tree
F. vogelli	−29.4			tree
Clusia cylindrica			−25.0	epiphyte
C. flava			−14.8	tree
C. gracilis			−28.1	epiphyte
C. rosea	−19.2			tree
C. rosea			−24.0	epiphyte
C. rosea			−24.0	tree
C. rosea			−17.7	epiphyte[a]
C. uvitana			−21.2	tree
C. valerii			−30.2	tree
Hylocereus undatus	−12.4			epiphyte[b]
H. trigonatus		−13.3		epiphyte[b]

[a] previously reported (Ting et al. 1985)
[b] known epiphytic CAM species

Table 2. Carbon isotope ratios of hemiepiphytic species growing in a savanna (Quebrada Seca, Barinas, Venezuela)

Species	Life form	$\delta^{13}C$ (‰)	
		DS*	WS[a]
Clusia minor	epiphyte	−24.1	−29.4
	tree	−23.4	−28.3
Ficus nymphaeifolia	epiphyte	−23.8	−27.4
	tree	−29.1	−29.1
Ficus obtusifolia	epiphyte	−29.6	
	tree	−29.3	
Coussapoa villosa	epiphyte	−28.4	
	tree	−28.8	
Attalea maracaibensis	host palm	−26.1	
Rhipsalis sp.	epiphytic CAM	−13.3	
Panicum maximum	terrestrial C_4	−12.8	

[a] DS = dry, WS = wet season

high, suggesting CAM activity, but variable (data not shown). While acid fluctuation was measured in some plants, other individuals were basically constant in acidity. Furthermore, individual plants varied from day to day in the extent of acid fluctuation, and the overall proportion of individuals showing marked fluctuations appeared to be uncorrelated with either the previous day's rainfall or degree of insolation.

^{13}C isotope composition. All of our available data for *Clusia rosea* indicate that the ^{13}C isotope composition is consistent with a CAM plant that assimilates some atmospheric CO_2 during the daylight period by carboxylation catalyzed by ribulose-bisphosphate carboxylase (Table 1). Data collected in 1984 from St. John are somewhat more positive than those collected in 1985 (Ting et al. 1985). We suspect that CAM metabolism in *Clusia* is variable and responds to precipitation as previously shown for many other CAM species in other genera (Szarek and Ting 1974; Hanscom and Ting 1978; Winter et al. 1978; Koch and Kennedy 1980).

Samples taken from both epiphytic and tree forms of *Clusia minor* indicated a grater $\delta^{13}C$ value than what would be expected for a typical C_3 plant which would usually by lower than −26‰ (Table 2). These values of −24.18‰ for the epiphyte and −23.4‰ for the tree form are consistent results for *Clusia rosea.*

Samples of *Clusia* taken from new growth during the wet season showed $\delta^{13}C$ values in the range of −28 to −29‰ typical of C_3-plants.

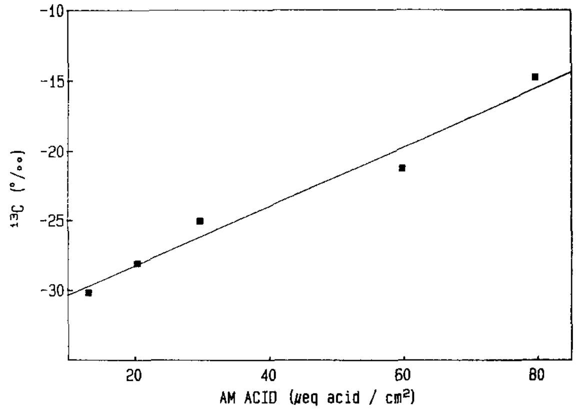

Fig. 6. Correlation between carbon isotope composition and total morning titratable acidity from the 5 species of *Clusia* collected at La Selva. ($r = 0.99$)

Table 3. Phosphoenolpyruvate carboxylase (PEPC) and malate enzyme (ME) activities in *Clusia* and *Ficus*

Species	PEPC[a]	ME
Clusia rosea	19.5 ± 0.31	3.4 ± 0.32
Ficus elastica	1.8 ± 0.03	0.6 ± 0.02
Ficus benjamina	1.1 ± 0.11	1.3 ± 0.16

[a] μmol/mg Chl/min

A graph of $\delta^{13}C$ versus maximum morning titratable acidity for the five species studied at La Selva is linear with high acidity correlating with a less negative (more CAM-like) isotope ratio (Fig. 6). Because of limited data, we do not know if the graph is fortuitous; however, based on previous information about ^{13}C isotope compositions in CAM plants, (O'Leary 1981), and their malic acid storage capacity (Teeri et al. 1981), this pattern is expected.

PEP carboxylase and malate enzyme. Assay of PEP carboxylase activity extracted from *Clusia rosea* seedlings grown from seed in the greenhouse at Riverside indicated high activity (Table 3) and comparable to CAM plants (Ting and Osmond 1973). Malate enzyme was also high, consistent with a plant that decarboxylates with this enzyme (Ting 1985).

Ficus species

Gas exchange parameters. Gas exchange parameters for *Ficus aurea* measured at the Marie Selby Garden in September are quite unlike those of *Clusia* inasmuch as *F. aurea* shows typical C_3-type gas exchange with all CO_2 uptake during the day (Fig. 7). The data for the epiphyte and free standing tree are similar except that the tree showed greater stomatal conductance and CO_2 assimilation than the epiphyte. There was some stomatal conductance toward the beginning of the night period, but this was not accompanied by CO_2 uptake. We were unable to obtain any gas exchange measurements of *Ficus* on St. John because the leaves were not accessible.

Measurements of *Ficus nymphaeifolia* at Barinas, Venezuela, revealed typical C_3-type gas exchange with all CO_2 uptake during the day (Fig. 8). Similarly to *Clusia minor*, the trees were more active than the epiphytes (Fig. 8a). Although neither form exhibited much CO_2 uptake in the early morning, this represented the peak value for the epiphytic forms. The stomatal conductance data were consistent with the CO_2 uptake data, although for both life-forms, the early morning peak of conductance did not correspond with the maximum CO_2 uptake rates (Fig. 8b).

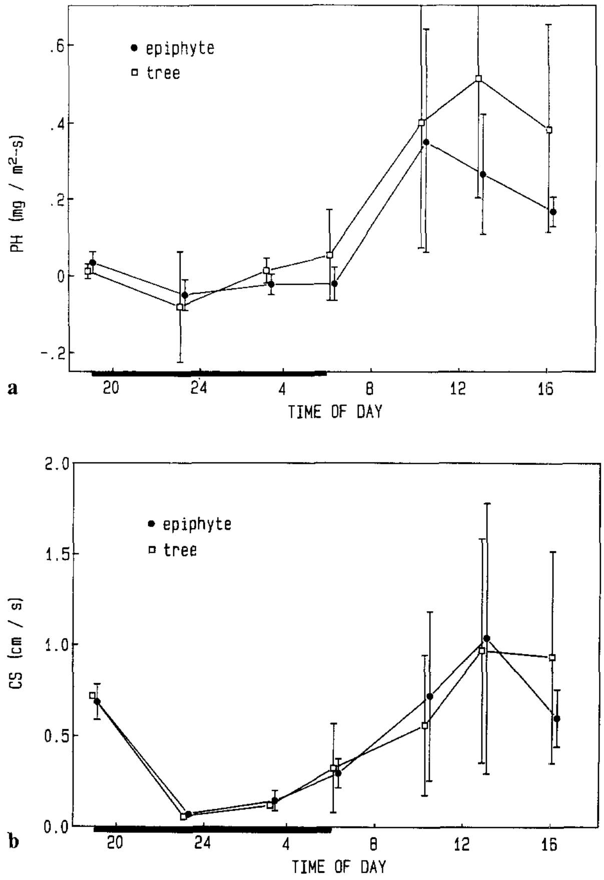

Fig. 7a, b. CO_2 uptake (PH) **a** and stomatal conductance (CS) **b** for epiphytic and rooted *Ficus aurea* growing at the Marie Selby Botanical Garden, Sarasota, Florida. Data obtained in September, 1985. Each part is the means of 3 measurements. The error bars are the SE of the means

The gas exchange data obtained during the wet season for *Ficus nymphaeifolia* were consistent with the data taken during the dry season except the CO_2 uptake rates were generally greater (Fig. 8c). Similarly to the dry season measurements, the tree forms had greater rates of CO_2 uptake. Wet season rates of the tree forms were approximately 1.5 times higher than in the dry season and 4 to 5 times greater for epiphytic forms.

Titratable acidity. No evidence for a diurnal fluctuation of titratable acidity was obtained for *Ficus* species either in the field at Selby Gardens or Barinas, or in the laboratory with *F. elastica, F. benjamina,* and *F. lyrata.* Leaf extracts from the native *Ficus aurea* studied at the Selby Gardens were alkaline and could not be titrated for acids. *Coussapoa* showed no acid flux.

^{13}C isotope composition. Carbon isotope ratios from several species of *Ficus* collected in the Selby Gardens fell within the range typical of C_3 plants (Table 1). Both epiphytic

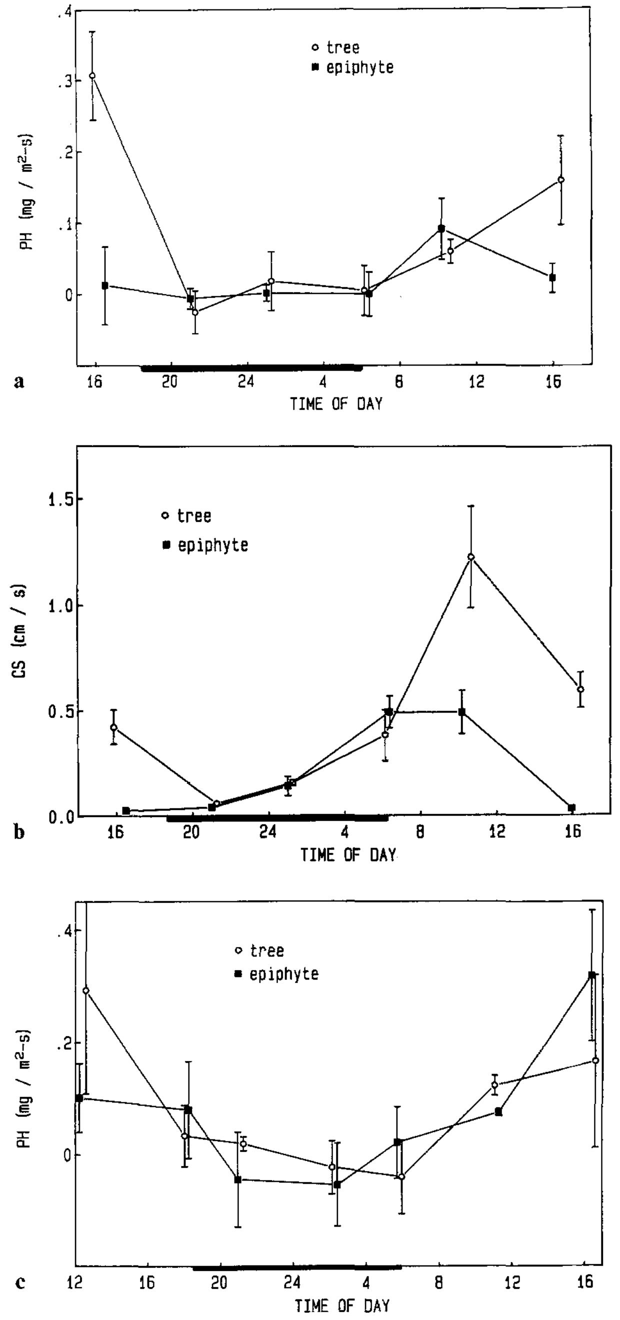

Fig. 8a–c. Gas exchange parameters for *Ficus nyphaeifolia*. **a** CO_2 exchange for epiphytic and tree forms (PH = CO_2). **b** Stomatal conductance for the two forms collected during the dry season. (Cs = stomatal conductance). **c** The error bars are the SE of the mean

and free-standing trees of *Ficus trigonata* growing on St. John had C_3-like $\delta^{13}C$ values. With the exception of the epiphytic form of *Ficus nymphaeifolia* which had an isotope composition of $-23‰$ during the dry season in Barinas, the *Ficus* species and *Coussapoa villosa* had typical C_3-like carbon isotope compositions (Table 2). The host *Attalea* had a composition of $-26.08‰$. *Rhipsalis*, a known CAM plant, growing epiphytically on *Attalea* had an isotope composition of $-13.3‰$.

PEP carboxylase and malate enzyme assay. The *Ficus* species tested for PEP carboxylase and malate enzyme activity showed levels comparable to C_3 plants (Ting and Osmond 1973) supporting the conclusion that *Ficus* shows only C_3 photosynthesis.

Discussion

All of the data that we have available indicate that certain species of *Clusia* show CAM. However, since the genus is large with 200 or more species, we can not make a broad generalization at this time regarding the extent of CAM in *Clusia*. Of the seven species that we have investigated, *C. rosea*, *C. minor*, *C. flava*, and *C. uvitana* have shown definite CAM characteristics. *C. cylindrica* shows aspects of CAM, while there was little suggestion of CAM in *C. gracilis* and *C. valerii* except that titratable acids were higher than what would be expected in typical C_3 plants. High acidity may be an indication of potential or latent CAM as is the case with *Portulacaria afra* (Ting and Hanscom 1977). An additional study by Tinoco and Vazquez-Yanes (1983) showed that *C. lundelli* has several physiological aspects of CAM.

Our data indicate that *Clusia*, as evidenced here by measurements with *C. minor*, is yet another group with the capacity of shifting from C_3-type photosynthesis to CAM-photosynthesis. During the wet season when ample water is available, *C. minor* functions as a C_3 plant with more efficient CO_2 uptake during the daylight hours. Maximum CO_2 uptake rates by the trees during the C_3, wet-season phase of the life cycle of *C. minor* are over twice that measured for the nocturnal CO_2 uptake during the CAM phase in the dry season. For the epiphytes, the rates are nearly 4 times as high.

In some respects, CAM was expected in *Clusia* since it grows as a tropical epiphyte and CAM is common in tropical epiphytes (Medina 1974; Winter et al. 1983; McWilliams 1970; Sinclair 1984; Ting et al. 1985; Guralnick et al. 1986). The species of *Clusia* with CAM tend to have more succulent leaves. Paradoxically, however, as likely as CAM is in the epiphytic forms of *Clusia*, it is equally unlikely in the free-standing tree forms since CAM has not previously been reported to occur in true dicotyledonous trees (Szarek and Ting 1977; Szarek 1979; Ting et al. 1985). Thus, the finding of CAM in *Clusia* trees is unique among the dicotyledons (Klug and Ting 1978).

The carbon-13 isotope composition of *Clusia* is variable even within a single species and among the various species. Interspecific variability could be accounted for by assuming that not all species in the genus are CAM and thus species would be expected to have $\delta^{13}C$ values ranging from values typical of C_3 species to those typical of full CAM plants depending on their photosynthetic mode (O'Leary 1981). An alternate hypothesis is that all species in the genus are potentially CAM, but only express CAM metabolism during certain developmental stages or environmental conditions as shown here for *C. minor*. The variable isotope compositions may thus be the integrative result of C_3 and CAM produced biomass. The gas exchange data clearly indicate a substantial amount of CO_2 uptake during the early morning, which would dilute the contribution of CAM to the isotope composition rendering the actual value as an intermediate number.

Our gas exchange, titration, and carbon-13 isotope composition, and PEP carboxylase data all support the contention that *Ficus* has C_3 photosynthesis. All of the *Ficus* species listed in Tables 1 and 2, except possibly for the common commercial fig, *F. carica*, evidently are stranglers in their native habitat. However, *F. carica* is occasionally found growing epiphytically where it is cultivated and, in humid environments, produces aerial roots typical of stranglers that develop into banyans (Condit 1969). Thus two unrelated genera which both have hemiepiphytic species with the strangler habit and frequently grow sympatrically, have different modes of photosynthesis. *Clusia* has species that are CAM and all species of *Ficus* so far tested are C_3.

Since it appears likely that CAM in *Clusia* is an adaptation to water stress and/or drought (Kluge and Ting 1978; Sinclair 1984), the question arises as to the nature of drought adaptation in the strangler *Ficus* species. *Ficus*, like *Clusia*, appears to be adapted to severe water stress, yet *Ficus* has typical C_3 gas exchange with all CO_2 uptake during the daylight hours. We do not know the answer to the question of drought adaptation in *Ficus* except to note that the more water-stressed epiphytic stage has a lower stomatal conductance and, hence, less water loss. The more positive $\delta^{13}C$ value measured for *F. nymphaeifolia* during the dry season could be the result of lower stomatal conductances in the laboratory with other hemiepiphytic species of *Ficus* suggest that the stomata are extremely sensitive to water deprivation.

Hemiepiphytes growing in seasonally dry climates, such as savannas, may experience drought in two ways, annually during the dry season (November–April) and developmentally during the epiphytic phase of their life cycle, when frequent and severe periods of low water availability occur (Benzing 1984; Sinclair 1984). While both the epiphytic and tree phases of the life cycle of *Clusia minor* can exhibit CAM, it would appear that the consequences of CAM would be more relevant to the epiphytic phase (Winter et al. 1983; Benzing 1984). The epiphytic phase of the life cycle of hemiepiphytes is among the few woody, tropical savanna plants that actually experience seasonal drought. Most woody savanna species, particularly trees, have physiological and/or ecological mechanisms that circumvent seasonal shortages in soil water availability. Some savanna trees are drought-deciduous, dropping their leaves before the onset of the dry season. Evergreen savanna trees, on the other hand, renew leaves during the middle of the dry season, a period that would seem least likely for leaf expansion. Several studies in the Brasilian and Venezuelan savannas indicate that evergreen species access the deeper, abundant soil water during the entire year (Sarmiento et al. 1985; Goldstein et al. 1986). Meinzer et al. (1983) have shown that despite the scleromorphic appearance of their leaves, several evergreen woody species growing in seasonal savannas located close to the present study site, were adapted only to short-term diurnal water deficits. Evergreen and deciduous savanna trees have typical C_3 photosynthetic metabolism.

Evidently CAM is not common among the genera showing the strangler habit. *Blakea grandifolia* (Melastomataceae) growing at La Selva did not show aspects of CAM, nor did *Coussapoa villosa* growing in the savannas of the Andes. The hemiephytic life history is found in over 300 species (10 families) of flowering plants (Putz and Holbrook 1986), but to date we have evidence for CAM only in the genus *Clusia*.

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