Review article

The Occurrence of Plants with Crassulacean Acid Metabolism (CAM) Photosynthesis in Tropical and Subtropical Rain Forests with Very High Rainfall[1)]

Craig E. Martin[2,3)]

【Summary】

Crassulacean acid metabolism (CAM) is a photosynthetic pathway that conserves water by restricting stomatal opening, hence water loss, to the night. Thus, it is not surprising to find that floras of arid regions include a large number of CAM plants. In addition, CAM is common among epiphytes in tropical and subtropical environments, where water is plentiful. Despite the latter, evidence exists that comparatively short periods of drought, coupled with the unusual morphology and/or microhabitat of such epiphytes, comprise stress substantial enough that the CAM pathway proves highly adaptive.

It is more difficult to explain the adaptive significance of CAM in tropical and subtropical rain forests with exceedingly high annual rainfall, i.e., in excess of 4 meters per year. This review explores a variety of hypotheses proffered as explanations for this apparent conundrum. Such hypotheses include:

1. CAM allows an epiphytic CAM plant to capitalize on the high concentrations of atmospheric CO_2 at night in the canopies of its host trees;
2. even in such rain forests, rainless periods are long enough and/or frequent enough that CAM proves advantageous as a water conservation adaptation.
3. The ability of many CAM plants to assimilate CO_2 during *both* the day and night is advantageous in such environments.
4. The increase in daytime CO_2 levels in CAM photosynthetic tissue prevents photoinhibition and minimizes CO_2 losses during the day.
5. The high acid content of CAM photosynthetic tissue, at least early in the day, deters herbivory.
6. The stimulation of CO_2 uptake following wetting of the leaves reported for at least one epiphytic CAM plant is advantageous in such high-rainfall environments.

[1)] Much of the inspiration for, and many of the ideas presented in, this review are the result of 2 decades of collaborative research with Professor Teng-Chiu Lin, much of which was funded by grants from the Taiwan Forestry Research Institute and from the National Science Council of Taiwan to Prof. T.-C. Lin.

[2)] Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045 U.S.A.; e-mail:ecophys@ku.edu.

[3)] Address for past and future work related to this review: Taiwan Forestry Research Institute, 53 Nanhai Rd., Taipei 10066, Taiwan.

Received November 2009, Accepted February 2010. 2009年11月送審 2010年2月通過。

7. The low demand for essential elements observed in at least one CAM plant increases the nutrient efficiency of such plants, which is adaptive in rain forests with excessive rainfall and, hence, high levels of nutrient leaching from the leaf tissues.
8. Guttation resulting from osmotically-driven high tissue water contents benefits CAM plants several ways.
9. Epiphytic CAM plants are well-adapted to shady microhabitats, comprising a valuable adaptation to the cloudy environment of high-rainfall rain forests.
10. CAM is not beneficial for such plants in these environments for at least 3 possible reasons.

All of the hypotheses have only rarely been examined in past studies. Thus, all are in need of further investigation.

Key words: adaptations, CO_2 concentration, CO_2 uptake, CAM (Crassulacean acid metabolism), drought.

Martin CE. 2010. The occurrence of plants with Crassulacean Acid Metabolism (CAM) photosynthesis in tropical and subtropical rain forests with very high rainfall. Taiwan J For Sci 25(1):3-16.

學術論述

景天酸代謝(CAM)植物竟出現在高雨量熱帶及亞熱帶雨林[1)]

Craig E. Martin[2,3)]

摘　要

景天酸代謝(Crassulacean acid metabolism, CAM)是一種將氣孔開啟限制在夜間以減少水份散失的光合作用途徑，因此在乾燥氣候區有眾多的CAM植物。除了乾燥地區，熱帶和亞熱帶水份充足的地區也有許多附生的CAM植物。雖然雨量充足，但有證據顯示相對乾燥的時期以及附生植物特殊的型態與微棲地足以造成逆壓而使CAM成為相當有利的適應方式。

然而要解釋在年雨量極高(超過4000毫米)的熱帶亞熱帶雨林，CAM在適應上的意義是有相當難度的。本文回顧檢視多個用以解釋此一看似難解現象的假說，這些假說包括：

1. 景天酸代謝使附生的CAM植物能利用夜間宿主林木冠層內空氣中高濃度的CO_2。
2. 即使在雨林無雨的時期仍夠長或者夠頻繁讓景天酸代謝成為有利的保水適應。
3. 許多CAM植物能在白天和夜晚均能固定CO_2在這種環境是有利的。
4. CAM代謝組織內白天CO_2濃度升高可以避免光抑制而減少CO_2的損失。
5. 至少在白晝的初期CAM代謝組織內高的酸含量可以減少植食。
6. 至少在一種附生CAM植物曾有研究指出葉面潮濕可刺激CO_2利用在多雨的環境中是有利的。
7. 至少在一種CAM植物發現其對必需元素的需求低可提高其營養利用效率，這在多雨因而葉組織淋溶旺盛的的雨林中是有利的適應。
8. 滲透引起的高組織水含量所造成的泌液作用對CAM植物有多重好處。
9. 附生CAM植物對遮蔽的適應良好，這在高雨量且多雨的森林而言是極具價值的適應能力。
10. CAM在此環境中並非有利的適應，而是因為其它原因而在此環境出現，其可能原因至少有3個。

過去的研究對以上所有假說的探討都非常少，因此極需進一步的研究加以深入探討檢測。
關鍵詞：適應、CO_2濃度、CO_2吸取、CAM(景天酸代謝)、乾旱。
Martin CE。2010。景天酸代謝(CAM)植物竟出現在高雨量熱帶及亞熱帶雨林。台灣林業科學25(1): 3-16。

INTRODUCTION

Most higher plants can be categorized according to different suites of photosynthetic and, in some cases, leaf anatomical criteria as C_3, C_4, or CAM (Crassulacean Acid Metabolism) plants (Black 1973, Edwards and Walker 1983, Salisbury and Ross 1992). Not surprisingly, numerous exceptions exist, typically plants that exhibit features intermediate between 2 of these categories (Griffiths 1988, Martin 1996, Guralnick et al. 2008, Voznesenskaya et al. 2008, Winter et al. 2008, Herrera 2009). It is widely accepted that plants with CAM are especially well-adapted, with one glaring exception, to arid environments or microenvironments (Kluge and Ting 1978, Osmond 1978, Winter 1985, Lüttge 1987). The primary feature of CAM plants that proves so important in arid surroundings is a reversal in diel stomatal activity, i.e., unlike in C_3 and C_4 plants, the stomata of CAM plants are closed throughout the warm, lower-humidity day and are open during much of the cooler, more humid night, resulting in very low amounts of diel water loss from the photosynthetic tissue. Of course, conserving water in this manner creates a different problem in that the high-energy compounds resulting from the activity of the light reactions during the day are not available for carbon reduction once CO_2 is assimilated by the photosynthetic tissue at night. As a result, CAM plants form the 4-carbon malic acid from CO_2 uptake at night, and this acid is stored in a vacuole until its release and decarboxylation during the subsequent daytime. The internally-released CO_2 is then reduced to carbohydrate using the high-energy compounds provided by the light reactions in the light of the day. Despite the added biochemical complexity associated with nighttime CO_2 uptake, CAM plants are very abundant, and their phylogenetic diversity can be remarkably high in arid regions and dry microenvironments such as that typical of epiphytes in tropical and subtropical environments (Kluge and Ting 1978, Griffiths 1989, Winter and Smith 1996, Zotz and Ziegler 1997).

Although the great majority of CAM plants clearly appear to be well-adapted to dry habitats, there is at least one notable exception – that of CAM plants that are submerged aquatics and presumably never experience dry periods (Griffiths 1988, Boston et al. 1989, Keeley 1996). In these plants, CAM appears to constitute an adaptation to CO_2 availability in the water and not to water conservation. CAM allows CO_2 assimilation from the water at night when aqueous CO_2 concentrations are higher as a result of greater gas solubility in the cooler water at night, as well as the release of respiratory CO_2 into the water from surrounding non-CAM aquatic plants. During the day, CO_2 availability in the water is substantially reduced as a result of higher water temperatures and the use of CO_2 in photosynthesis by non-CAM aquatic neighbors, yet CAM provides a source of CO_2 internally in the photosynthetic tissues of these aquatic CAM plants (Lüttge 1987, Griffiths 1988, Boston et al. 1989, Keeley 1996).

Until the above aqueous CO_2 availability scenario was fully understood, the presence

of CAM in submerged aquatic plants was puzzling to many investigators. Nearly as puzzling is the geographically widespread occurrence of CAM plants in tropical and subtropical rain forests that receive exceptionally high amounts of rain (e.g., over several meters annually; Pierce et al. 2002, Martin et al. 2005). Clearly, the term "drought", even if short-term, seems inappropriate for such environments. Given the 2 disparate adaptive benefits conferred by CAM to plants growing in arid habitats or submerged in water, several hypotheses have been offered to explain the presence of CAM in high-rainfall tropical and subtropical rain forests. First, as was suggested previously by Knauft and Arditti (1969), Martin et al. (2005), and Hsu et al. (2006), CAM may have evolved in such plants, particularly epiphytic CAM plants, in response to diel changes in CO_2 concentrations in the air surrounding such plants. For example, atmospheric CO_2 concentrations in the canopies of tropical and subtropical forest trees are higher at night (see below) as a result of respiratory release by the tree leaves, whereas during the day, these leaves photosynthesize, reducing the CO_2 concentrations of the tree canopy air. An epiphyte with CAM should then be able to capitalize on the higher nighttime CO_2 concentrations.

A second possible benefit of CAM in tropical and subtropical rain forests with high rainfall reflects the more traditional role of CAM in plants growing in arid lands, that of water conservation. Although "drought", as traditionally defined, is a rare event in these forests, periods without rain occur frequently, and such periods vary greatly in length from a day to more than a week (see below). Furthermore, most CAM epiphytes are not rooted in much soil, or even lack absorptive roots, and often lack tissue succulence, and those with morphological adaptations that impound water usually lack CAM (Benzing 1990, Martin 1994). These factors may have comprised a strong selective pressure during the evolution of such plants, resulting in CAM as a water-conservation feature.

Distilling the above, coupled with other considerations, including those offered by Pierce et al. (2002), a number of hypotheses are forwarded here in an attempt to explain the adaptive significance of the widespread occurrence of CAM plants, especially among epiphytic taxa, in tropical and subtropical rain forests with unusually high annual rainfall where one would least expect to find such plants. A focus on epiphytes is appropriate, as many of the CAM plants found in subtropical and tropical rain forests are, with some notable exceptions, epiphytic (Winter et al. 1986, Earnshaw et al. 1987, Zotz and Ziegler 1997, Zotz 2004; also compare Kress 1986, 1989 with Smith and Winter 1996 and Sayed 2001).

Hypotheses

Hypotheses That CAM Plants Are Better Adapted to Any Epiphytic Habitat (Not Just in High-Rainfall Rain Forests) Than Are C_3 Plants.

Hypothesis I: CAM comprises an adaptation that allows such plants, particularly CAM epiphytes, to capitalize on higher CO_2 concentrations found in tree canopies at night, relative to those during the day. {Note: this hypothesis is based on theoretical considerations, not experimental data}.

I.1. Diel changes in CO_2 concentrations in subtropical and tropical rain forest tree canopy atmospheres

As stated earlier, atmospheric CO_2 concentrations in the canopies of tropical and subtropical rain forests are substantially higher at night than during the day (Table 1). This diel fluctuation in canopy CO_2 concentrations

Table 1. Day and night CO_2 concentrations (in ppm) and night-day change in the canopy of tropical and subtropical rain forests. All values were estimated from figures (occasionally the text) in the references cited

Study	Location	Day [CO_2]	Night [CO_2]	Diel Change
Lemon et al. 1970	Costa Rica	285	330	45
Odum et al. 1970	Puerto Rico*	325	345	20
Aoki et al. 1975, 1978	Malaysia	310	430	120
Fan et al. 1990	Brazil†	340	380	40
Delmas et al. 1992	Congo	285	335	50
Grace et al. 1995, 1996	Brazil†	485	360	125
Lloyd et al. 1996	Brazil†	345	430	85
Culf et al. 1997	Brazil	360	486	126
Hsu et al. 2006	Taiwan*	370	405~415	35~45
De Araújo et al. 2008	Brazil	365~375	410~430	45~55
Fisch et al. 2000	Brazil	380	430	50
Overall range	Global	310~380	330~486	20~126
Average‡	Global	350 (53)	394 (49)	67§ (37)
Pierce et al. 2002	Panama*	[unknown]	[unknown]	6~20

* rain forest known to have very high (over several m) annual rainfall.

† different studies of the same forest.

‡ mid-point used for ranges given (standard deviations in parentheses; N = 12).

§ Day and night averages different at $P < 0.05$ (result of paired *t*-test).

is attributable to daytime photosynthetic CO_2 uptake, followed by nighttime respiratory CO_2 release, by the leaves of the canopy trees, all of which are C_3 plants.

I.2. Diel changes in atmospheric CO_2 concentrations as a strong selection pressure in the evolution of CAM in subtropical and tropical rain forests

The rationale of Hsu et al. (2006) is followed here. If day/night fluctuations in atmospheric CO_2 concentrations in the tree canopies of epiphytes were indeed the primary selective agent that resulted in the evolution of CAM in epiphytes, then it seems reasonable to expect that epiphytes should still be capable of utilizing the CO_2 added by the host tree to the canopy atmosphere at night. This possibility can be (and has been) investigated through the use of stable carbon isotopes. CO_2 respired by the host tree will be enriched in ^{13}C, relative to CO_2 in air unaffected by tree respiration (Griffiths 1992, 1993). Thus, if a CAM epiphyte uses canopy CO_2 at night, its tissue $\delta^{13}C/^{12}C$ value should reflect a greater enrichment in ^{13}C than another individual of that species growing where the atmospheric CO_2 is not influenced by tree respiration at night.

Although Hsu et al. (2006) used this approach and found no evidence for the uptake of host-respired CO_2 by *Hoya carnosa*, an epiphytic CAM vine in a high-rainfall subtropical rain forest, more such work with additional species is needed before firm conclusions can be drawn.

Hypothesis II: CAM constitutes an adaptation that conserves water, allowing survival and avoidance of drought stress injury during episodic rainless periods in these forests. {Note: this hypothesis is based on a great deal

of experimental data with both terrestrial and epiphytic plants}.

II.1. Rainless periods in subtropical and tropical rain forests with high rainfall

CAM, by definition, entails stomatal closure during the day, followed by opening at night, resulting in greater water conservation, relative to non-CAM plants. Furthermore, the biochemical events of CAM should minimize the potential for photoinhibition during the day, during which most or all of the photochemical energy harvested by the photosynthetic pigments is dissipated by the utilization of high concentrations of CO_2 produced by the decarboxylation of malic acid during the day. Evidence that CAM minimizes photoinhibition during the day has been reported in a number of studies (Lüttge 1987, Griffiths 1989, Pierce et al. 2002, Osmond et al. 2008, Herrera 2009).

If CAM benefits plants in high-rainfall forests as a result of its drought tolerance features, the question arises about how frequent and severe are droughts in high-rainfall rain forests. Ignoring some exceptions, rainless periods occur in the majority of tropical and subtropical rain forests with high yearly precipitation totals. These rainless periods vary in length, depending on the geographic location, topography, time of year, and particular year. Table 2 presents the frequency of rainless periods of varying lengths for the Fushan Experimental Forest, a high-rainfall (annual amount over several m) subtropical rain forest in northeastern Taiwan. In Table 3 the same drought frequency data are presented for a high-rainfall tropical rain forest at El Verde, Puerto Rico.

II.2. Effects of drought on epiphytic CAM plants growing in tropical/subtropical forest with high rainfall

Although a number of studies have examined the effects of drought stress on epiphytic CAM plants in or collected from tropical environments with moderate amounts of rainfall (Fu and Hew 1982, Sinclair 1983, Zheng et al. 1992, Sekizuka et al. 1995, Zotz and Tyree 1996), few studies have investigated the effects of drought stress on CAM epiphytes growing in high-rainfall tropical

Table 2. Frequency of rainless periods at the Fushan Experimental Forest, a high-rainfall (annual amount over several m) subtropical rain forest in northeastern Taiwan (unpublished data provided by Y-J Hsia)

Length of rainless period, d	Number of rainless periods in 3 yr	Number of rainless periods per yr	Resultant days without rain in 3 yr	Days without rain per yr
1	67	22.3	67	22.3
2	27	8.3	54	18.0
3	21	7.0	63	21.0
4	9	3.0	36	12.0
5	9	3.0	45	15.0
6	5	1.7	30	10.0
7	4	1.3	28	9.3
8	1	0.3	8	2.7
9	3	1.0	27	9.0
11	1	0.3	11	3.7
16	1	0.3	16	5.3
1~16	148	49.2	385	128.3

Table 3. Frequency of rainless periods at a high-rainfall (annual amount over several m) tropical rain forest at El Verde, Puerto Rico (data estimated from figures in Odum et al. 1970)

Length of rainless period, d	Number of rainless periods in 2 yr*	Number per yr*	Resultant days without rain in 2 yr*	Days without rain per yr*
< 8	28	14.0	224	112
ca. 8	9	4.5	72	36
ca. 10	6	3.0	60	30
≥ 15	4	2.0	≥ 60	≥ 30
< 8~ ≥ 15	47	23.5	≥ 416	≥ 138

* data presented are maxima based on data in first column.

and subtropical rain forests, perhaps because droughts seem highly unlikely in such high-rainfall forests (yet see above section). Photosynthetic CO_2 exchange in 2 CAM ferns collected from tropical rain forests in Singapore and measured under controlled conditions in Germany was very sensitive to short drought periods; rates fell to zero within 5~6 d without water (Ong et al. 1986). In contrast, the CAM species *Aechmea dactylina* maintained higher photosynthetic electron transport capability and daily carbon gain than did the C_3 epiphyte *Werauhia capitata* during a month-long dry season in a high-rainfall tropical rain forest in Panama (Pierce et al. 2002). The results of these 2 studies appear contradictory, and serve to emphasize the need for more work of this nature.

Other potential benefits of CAM in tropical and subtropical forests with high rainfall

Pierce et al. (2002) compared the ecophysiology of CAM and C_3 epiphytic bromeliads in an extremely wet tropical cloud forest in Panama and reported evidence for the following benefits of CAM over C_3 photosynthesis in these plants.

Hypothesis III.1.: CAM allows higher diel carbon gain as a result of CO_2 uptake during both the night and day. {Note: this hypothesis is based on limited experimental data, i.e., Pierce et al. 2002}.

Although most CAM plants assimilate the majority of their atmospheric carbon at night ("Phase I" gas exchange; Osmond 1978), they also can absorb substantial amounts of CO_2 during the daytime, either early in the morning ("Phase II" gas exchange) and/or late in the afternoon ("Phase IV" gas exchange). The combination of daytime and nighttime CO_2 uptake may allow for the assimilation of more CO_2 during a 24-h period than is possible in C_3 plants, in which CO_2 uptake is restricted to the daytime. Although this was true in the *Aechmea-Werauhia* CAM-C_3 comparison made by Pierce et al. (2002) in Panama, this is not always the case, however, as different rates of CO_2 uptake (e.g., lower CO_2 uptake rates in CAM, relative to C_3 plants, as is often observed) may counterbalance these differences in periods of uptake. Thus, this hypothesis requires further investigation, requiring more comparative studies of CAM and C_3 species in high-rainfall tropical and subtropical forests.

Hypothesis III.2.: CAM allows higher diel carbon gain as a result of respiratory CO_2 recycling during periods when atmospheric CO_2 uptake does not occur. {Note: this hypothesis is based on limited experimental data, i.e., Pierce et al. 2002}.

In the *Aechmea-Werauhia* CAM-C_3 comparison made by Pierce et al. (2002) in Panama, both species exhibited stomatal closure during the day, the CAM response being typical of CAM gas exchange ("Phase III"), and the C_3 response being typical of C_3 plants under stress ("mid-day depression" of gas exchange as a result of excessive water loss, high air vapor pressure deficits, or both). Both species intercepted high irradiances at this time, resulting in evidence of photoinhibition in the C_3 plant, but not in the CAM plant, presumably a result of its high internal CO_2 concentration characteristic of CAM at mid-day (see above). Because the CAM plant remained photosynthetically active at mid-day, albeit without assimilating atmospheric CO_2, only the CAM plant was capable of minimizing respiratory CO_2 losses at mid-day (see also Martin 1996 and Maxwell 2002). As a result, the diel carbon budget of the C_3 plant suffered losses, while that of the CAM plant did not. Of course, if this hypothesis is to apply to C_3-CAM comparisons in other tropical and subtropical rain forests with high amounts of rainfall, periods of drought must be long enough to effect stress-caused mid-day stomatal closure in the C_3 taxa.

Hypothesis III.3.: The accumulation of malic acid and its resultant low pH in CAM leaf tissue might deter herbivory during the early part of each day by insects and other herbivores. {Note: this hypothesis is based solely on theoretical considerations.}.

Although little or no empirical evidence exists for this hypothesis, it is, nonetheless, an attractive one. The tissue of CAM plants is highly acidic (e.g., with pH values as low as 3~4) for hours before and after sunrise. Such acidic tissue may prove too bitter for consumption by herbivores, thus preventing tissue losses in CAM plants as a result.

Hypotheses that CAM plants are better adapted to the epiphytic habitat than are C_3 plants solely in high-rainfall rain forests.

Hypothesis III.4.: CAM minimizes inhibition of gas exchange resulting from wet leaf surfaces. {Note: this hypothesis is based on limited experimental data, i.e., Pierce et al. 2002}.

Pierce et al. (2002) found that gas exchange in both the CAM plant *Aechmea dactylina* and the C_3 *Werauhia capitata* in Panama was similarly inhibited by wetting of the leaf surfaces, a frequent event in high-rainfall tropical and subtropical rain forests, yet only in the CAM plant was CO_2 uptake stimulated once the leaves dried. The mechanism of this stimulation has not been investigated. Nonetheless, this could prove to be an important benefit of the CAM pathway in tropical and subtropical rainforests characterized by very high amounts of annual precipitation, yet this phenomenon has rarely been investigated.

Hypothesis III.5.: CAM results in higher nutrient-use efficiencies than does C_3 photosynthesis. {Note: this hypothesis is based on limited experimental data, i.e., Pierce et al. 2002}.

For the reasons described in Hypotheses III.1 through III.3 above, the CAM plant in the C_3-CAM comparison made by Pierce et al. (2002) in Panama exhibited greater diel net carbon uptake, relative to the C_3 plant. As a result of this and the greater mineral nutrient concentrations in leaves of the latter species, the CAM plant had greater nutrient-use efficiencies than did the C_3 plant. Given the general paucity of available nutrients in tropical and subtropical rainforests, which is exacerbated by leaching due to excessive rainfall in high-rainfall rain forests, this difference may be an important benefit of CAM in these environments. Of course, this suggestion is predicated on the simultaneous occurrence of

all the C_3-CAM differences described above applying to other C_3-CAM comparisons in other high-rainfall tropical and subtropical forests.

Hypothesis III.6.: The accumulation of malic acid in CAM leaf tissue will decrease tissue osmotic potential with beneficial effects. {Note: this hypothesis is based solely on theoretical considerations}.

The decreased osmotic potential (hence, water potential) should effect potentially excessive water uptake, at least for the early half of each day during which tissue malic acid levels are high. The resultant high leaf turgor might result in high levels of guttation by the CAM leaves, possibly avoiding flooding of the leaf tissue (Feild et al. 2005), removing leaf toxins (Chen and Chen 2007), inhibiting leaf surface pathogens (Fukui et al. 1999, Grunwald et al. 2003), and/or enhancing the uptake and movement of essential elements (Singh et al. 2008) in these CAM epiphytes.

Hypothesis III.7.: CAM epiphytes are particularly well-adapted to the low-light conditions characteristic of rain forests with exceptionally high rainfall. {Note: this hypothesis is based on experimental data in many studies}.

Cloud cover in the sky above high-rainfall rain forests is frequently heavy and constant; thus, epiphytes are shaded by clouds, as well as by their host canopy. Many CAM epiphytes are well-adapted to such low-light conditions (Martin et al. 1985, 1986, Winter et al. 1986, Adams et al. 1987, 1988, Adams 1988, Griffiths et al. 1989, Martin et al. 1989, Adams et al. 1992, 1996, Skillman and Winter 1997, Martin et al. 1999). There are too few comparative studies, however, to know whether CAM epiphytes are better adapted to shade than are C_3 epiphytes.

Hypothesis IV: CAM may offer no special benefits to an epiphyte in high-rainfall rain forests for one or more of the following reasons: {Note: these hypotheses are based solely on theoretical considerations and lack specific experimental support. They are presented here as potential jumping-points for further consideration and research}.

IV.1. CAM epiphytes invaded rain forests with exceptionally high rainfall from surrounding habitats with lower annual amounts of rainfall. {This possibility has not been investigated}.

IV.2. CAM epiphytes are currently present in rain forests with exceptionally high rainfall as a result of their presence in the area when annual amounts of rainfall were much lower. {This possibility has also not been investigated}. Although examples of such instances are not known to this author, this possibility was included because current plant distributions do occasionally reflect past climates that differ from modern conditions in that geographic area, e.g., the flora of arid regions of Australia (Cox and Moore 2005).

IV.3. CAM epiphytes in high-rainfall forests might be on the verge of losing CAM and reverting to C_3 photosynthesis or C_3-CAM intermediacy. {This possibility has also not been investigated}.

Because CAM may provide little to no adaptive value (but see above), such CAM taxa in tropical and subtropical rain forests with exceedingly high rainfall may, over time, "revert" to C_3 photosynthesis, which should allow higher growth rates, especially with such an abundant supply of water. Several phylogenetic surveys of families in which numerous CAM taxa are found provide evidence of putative CAM-to-C_3 "reversions" (Crayn et al. 2004, Mort et al. 2007). Thus, in the distant future, it is possible that high-rainfall rain forests will be devoid of CAM taxa. Further

phylogenetic analyses may allow identification of taxa particularly susceptible to such a dramatic evolutionary change.

DISCUSSION

It is clear from this review that an answer to the question about why CAM plants are often found in tropical and subtropical rain forests characterized by excessive annual rainfall remains elusive, primarily as a result of inadequate data addressing the hypotheses presented above. Although all such hypotheses generate intrigue, and some support exists for several of these hypotheses, more comparative studies of CAM and C_3 plants are required before one or more of these hypotheses can be accepted as an explanation for the occurrence of CAM plants in high-rainfall rain forests.

Dr. Craig E. Martin is a senior professor of the Department of Ecology and Evolutionary Biology at the University of Kansas. Dr. Martin is a plant ecophysiologist and has been working on CAM plants for more than 30 years. Ever since his first visit to Taiwan in 1994 he loves Taiwan and enjoys the friendship that he has built over the last two decades with many scientists. By February 2010 he has visited Taiwan approximately 10 times and each time he visited Taiwan he spent time at Fushan Experimental Forest studying plant ecophysiology especially epiphytic CAM plants, with most of them ferns. Fushan is now one of his major research sites and likely his favorite one. He has already published with local scientists approximately 10 papers that involved research projects at Fushan but he still thinks that there is a lot more ecophysiological mysteries waiting for discovery and solving. He would be more than happy to explore these mysteries and others in Taiwan in general and specifically at Fushan with friends in Taiwan and from all over the world. Over the last decade he helped and enjoyed working with many students in Taiwan developing and conducting their research projects. Anyone interested in plant ecophysiology is encouraged to contact Dr. Craig Martin for future collaboration. I believe that anyone working with Dr. Craig Martin would find him intelligent, interesting, inspiring and, equally important, fun to work with. (by Teng-Chiu Lin, Professor, National Taiwan Normal University, Department of Life Science).

LITERATURE CITED

Adams WW III. 1988. Photosynthetic acclimation and photoinhibition of terrestrial and epiphytic CAM tissues growing in full sunlight and deep shade. Aust J Plant Physiol 15:123-34.

Adams WW III, Demmig-Adams B, Barker DH, Kiley S. 1996. Carotenoids and photosystem II characteristics of upper and lower halves of leaves acclimated to high light. Aust J Plant Physiol 23:669-77.

Adams WW III, Osmond CB, Sharkey TD. 1987. Responses of two CAM species to different irradiances during growth and susceptibility to photoinhibition by high light. Plant Physiol 83:213-8.

Adams WW III, Terashima I, Brugnoli E, Demmig B. 1988. Comparisons of photosynthesis and photoinhibition in the CAM vine *Hoya australis* and several C_3 vines growing on the coast of eastern Australia. Plant Cell Environ 11:173-81.

Adams WW III, Volk M, Hoehn A, Demmig-Adams B. 1992. Leaf orientation and the response of the xanthophyll cycle to incident light. Oecologia 90:404-10.

Aoki M, Yabuki K, Koyama H. 1975. Micrometeorology and assessment of primary production of a tropical rain forest in west Malaysia. J Agric Meteorol 31:115-24.

Aoki M, Yabuki K, Koyama H. 1978. Micro-

meteorology of Pasoh forest. Malaysian Nature J 30:149-59.

Benzing DH. 1990. Vascular epiphytes. General biology and related biota. Cambridge, NY: Cambridge University Press. 354 p.

Black CC Jr. 1973. Photosynthetic carbon fixation in relation to net CO_2 uptake. Annu Rev Plant Physiol 24:253-86.

Boston HL, Adams MS, Madsen JD. 1989. Photosynthetic strategies and productivity in aquatic systems. Aq Bot 34:27-57.

Chen CC, Chen YR. 2007. Study on laminar hydathodes of *Ficus formosana* (Moraceae) III. Salt injury of guttation on hydathodes. Bot Studies 48:215-26.

Cox BC, Moore PD. 2005. Biogeography. An ecological and evolutionary approach. 7th ed. Malden, MA: Blackwell Publish. 428 p.

Crayn DM, Winter K, Smith JAC, Medina E. 2004. Multiple origins of Crassulacean acid metabolism and the epiphytic habit in the Neotropical family Bromeliaceae. Proc Nat Acad Sci USA 101:3703-8.

Culf AD, Fisch D, Malhi Y, Nobre CA. 1997. The influence of the atmospheric boundary layer on carbon dioxide concentrations over a tropical forest. Agric Forest Meteorol 85:149-58.

De Araújo A, et al. 2008. Nocturnal accumulation of CO_2 along a topographical gradient. Ecol Applic 18:1406-19.

Delmas RA, Servant J, Tathy JP, Cros B, Labat M. 1992. Sources and sinks of methane and carbon dioxide exchanges in mountain forest in equatorial Africa. J Geophys Res Atmos 97:6169-79.

Earnshaw MJ, et al. 1987. Altitudinal changes in the incidence of Crassulacean acid metabolism in vascular epiphytes and selected life forms in Papua New Guinea. Oecologia 73: 566-72.

Edwards G, Walker DA. 1983. C_3, C_4: mechanisms, and cellular and environmental regulation, of photosynthesis. Oxford, UK: Blackwell Scient Publish. 542 p.

Fan SM, Wofsy SC, Bakwin PS, Jacob DJ. 1990. Atmosphere-biosphere exchange of CO_2 and O_3 in the central Amazon forest. J Geophys Res 95:16851-64.

Feild TS, Sage TL, Czerniak C, Iles WJD. 2005. Hydathodal leaf teeth of *Chloranthus japonicus* (Chloranthaceae) prevent guttation-induced flooding of the mesophyll. Plant Cell Environ 28:1179-90.

Fisch G, Culf AD, Malhi Y, Nobre CA, Nobre AD. 2000. Carbon dioxide measurements in the nocturnal boundary layer over Amazonian tropical forest. In: Lai, R, Kimble JM, Stewart BA, editors. Global climate change and tropical ecosystems. Boca Raton, FL: CRC Press. p 391-404.

Fu CF, Hew CS. 1982. Crassulacean acid metabolism in orchids under water stress. Bot Gaz 143:294-7.

Fukui R, Fukui H, Alvarez AM. 1999. Suppression of bacterial blight by a bacterial community isolated from the guttation fluids of anthuriums. Appl Environ Microbiol 65:1020-8.

Grace J, et al. 1995. Fluxes of carbon dioxide and water vapour over undisturbed tropical forest in south-west Amazonia. Global Change Biol 1:1-12.

Grace J, et al. 1996. The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. Global Change Biol 2:209-17.

Griffiths H. 1988. Crassulacean acid metabolism: a re-appraisal of physiological plasticity in form and function. Adv Bot Res 15:43-92.

Griffiths H. 1989. Carbon dioxide concentrating mechanisms and the evolution of CAM in vascular epiphytes. In: Lüttge U, editor. Vascular plants as epiphytes. Evolution and ecophysiology. Berlin, Germany: Springer-Verlag. p 42-86.

Griffiths H. 1992. Carbon isotope discrimination

and the integration of carbon assimilation pathways in terrestrial CAM plants. Plant Cell Environ 15:1051-62.

Griffiths H. 1993. Carbon isotope discrimination. In: Hall DO, Scurlock JMO, Bolhàr-Nordenkampf HR, Leegood RC, Long SP, editors. Photosynthesis and production in a changing environment: a field and laboratory manual. London, UK: Chapman & Hall. p 181-92.

Griffiths H, Ong BL, Avadhani PN, Goh CJ. 1989. Recycling of respiratory CO_2 during Crassulacean acid metabolism: alleviation of photoinhibition in *Pyrrosia piloselloides*. Planta 179:115-22.

Grunwald I, Rupprecht I, Schuster G, Klopstech K. 2003. Identification of guttation fluid proteins: the presence of pathogenesis-related proteins in non-infected barley plants. Physiol Plant 119:192-202.

Guralnick LJ, Cline A, Smith M, Sage RF. 2008. Evolutionary physiology: the extent of C_4 and CAM photosynthesis in the genera *Anacampseros* and *Grahamia* of the Portulacaceae. J Exp Bot 59:1735-42.

Herrera A. 2009. Crassulacean acid metabolism and fitness under water deficit stress: if not for carbon gain, what is facultative CAM good for? Ann Bot 103:645-53.

Hsu CC, Lin TC, Chiou WL, Lin SH, Lin KC, Martin CE. 2006. Canopy CO_2 concentrations and Crassulacean acid metabolism in *Hoya carnosa* in a subtropical rain forest in Taiwan: consideration of CO_2 availability and the evolution of CAM in epiphytes. Photosynthetica 44:130-5.

Keeley JE. 1996. Aquatic CAM photosynthesis. In: Winter K, Smith JAC, editors. Crassulacean acid metabolism. biochemistry, ecophysiology and evolution. Berlin, Germany: Springer. p 281-95.

Kluge M, Ting IP. 1978. Crassulacean acid metabolism. Analysis of an ecological adaptation. Berlin, Germany: Springer-Verlag. 210 p.

Knauft RL, Arditti J. 1969. Partial identification of dark $^{14}CO_2$ fixation products in leaves of *Cattleya* (Orchidaceae). New Phytol 68:657-61.

Kress WJ. 1986. The systematic distribution of vascular epiphytes: an update. Selbyana 9:2-22.

Kress WJ. 1989. The systematic distribution of vascular epiphytes. In: Lüttge U, editor. Vascular plants as epiphytes. Evolution and ecophysiology. Berlin, Germany: Springer-Verlag. p 234-61.

Lemon E, Allen LH Jr, Müller L. 1970. Carbon dioxide exchange of a tropical rain forest. Part II. BioScience 20:1054-9.

Lloyd J, et al. 1996. Vegetation effects on the isotopic composition of atmospheric CO_2 at local and regional scales: theoretical aspects and a comparison between rain forest in Amazonia and a boreal forest in Siberia. Aust J Plant Physiol 232:371-99.

Lüttge U. 1987. Carbon dioxide and water demand: Crassulacean acid metabolism (CAM), a versatile ecological adaptation exemplifying the need for integration in ecophysiological work. New Phytol 106:593-629.

Martin CE. 1994. Physiological ecology of the Bromeliaceae. Bot Rev 60:1-82.

Martin CE. 1996. Putative causes and consequences of recycling CO_2 via Crassulacean acid metabolism. In: Winter K, Smith JAC, editors. Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution. Berlin, Germany: Springer-Verlag. p 192-203.

Martin CE, Eades CA, Pitner RA. 1986. Effects of irradiance on Crassulacean acid metabolism in the epiphyte *Tillandsia usneoides* L. (Bromeliaceae). Plant Physiol 80:32-26.

Martin CE, McKee JM, Schmitt AK. 1989. Responses of photosynthetic O_2 evolution to PPFD in the CAM epiphyte *Tillandsia usneoides* L. (Bromeliaceae). Photosyn Res 21:145-50.

Martin CE, McLeod KW, Eades CA, Pitzer

AF. 1985. Morphological and physiological responses to irradiance in the CAM epiphyte *Tillandsia usneoides* L. (Bromeliaceae). Bot Gaz 146:489-94.

Martin CE, Tüffers A, Herppich WB, Von Willert DJ. 1999. Utilization and dissipation of absorbed light energy in the epiphytic CAM bromeliad *Tillandsia ionantha*. Int J Plant Sci 160:307-13.

Martin S, Davis R, Protti P, Lin TC, Lin SH, Martin CE. 2005. The occurrence of Crassulacean acid metabolism in epiphytic ferns, with an emphasis on the Vittariaceae. Int J Plant Sci 166:623-30.

Maxwell K. 2002. Resistance is useful: diurnal patterns of photosynthesis in C_3 and crassulacean acid metabolism epiphytic bromeliads. Funct Plant Biol 29:679-87.

Mort ME, Soltis DE, Soltis PS, Santos-Guerra A, Javier FO. 2007. Physiological evolution and association between physiology and growth form in *Aeonium* (Crassulaceae). Taxon 56: 453-64.

Odum HT, Drewry G, Kline JL. 1970. Climate at El Verde, 1963-1966. In: Odum HT, Pigeon RF, editors. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico: Vol 1. Oak Ridge, TN: US Atomic Energy Commission, Division Technical Information. p B347-418.

Ong BL, Kluge M, Friemert V. 1986. Crassulacean acid metabolism in the epiphytic ferns *Drymoglossum piloselloides* and *Pyrrosia longifolia*: studies on responses to environmental signals. Plant Cell Environ 9:547-57.

Osmond CB. 1978. Crassulacean acid metabolism: a curiosity in context. Annu Rev Plant Physiol 29:379-414.

Osmond B, Neales T, Stange G. 2008. Curiosity and context revisited: Crassulacean acid metabolism in the Anthropocene. J Exp Bot 59:1489-502.

Pierce S, Winter K, Griffiths H. 2002. The role of CAM in high rainfall cloud forests: an *in situ* comparison of photosynthetic pathways in Bromeliaceae. Plant Cell Environ 25:1181-9.

Salisbury FB, Ross CW. 1992. Plant physiology. 4th ed. Belmont, CA: Wadsworth Publish Co. 673 p.

Sayed OH. 2001. Crassulacean acid metabolism 1975-2000, a check list. Photosynthetica 39:339-52.

Sekizuka F, Kawamitsu Y, Nose A, Murayama S, Shinjo CY. 1995. Effects of water stress on gas exchange characteristics in Crassulacean acid metabolism plant, *Dendrobium ekapol* cv. Panda. Jpn J Crop Sci 64:235-42.

Sinclair R. 1983. Water relations of tropical epiphytes. II. Performance during droughting. J Exp Bot 34:1664-75.

Singh S, Chauhan JS, Singh TN. 2008. Guttation: a potential yield enhancing trait in rice. Curr Sci 95:455-6.

Skillman JB, Winter K. 1997. High photosynthetic capacity in a shade-tolerant Crassulacean acid metabolism plant. Implications for sunfleck use, nonphotochemical energy dissipation, and susceptibility to photoinhibition. Plant Physiol 113:441-50.

Smith JAC, Winter K. 1996. Taxonomic distribution of Crassulacean acid metabolism. In: Winter K, Smith JAC, editors. Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution. Berlin, Germany: Springer-Verlag. p 427-36.

Voznesenskaya EV, et al. 2008. Structural, biochemical, and physiological characterization of photosynthesis in two C_4 subspecies of *Tecticornia indica* and the C_3 species *Tecticornia pergranulata* (Chenopodiaceae). J Exp Bot 59:1715-34.

Winter K. 1985. Crassulacean acid metabolism. In: Barber J, Baker NR, editors. Photosynthetic mechanisms and the environment. Amsterdam, Netherlands: Elsevier Science Publish BV. p 329-87.

Winter K, Garcia M, Holtum JAM. 2008. On the nature of facultative and constitutive CAM: environmental and developmental control of CAM expression during early growth of *Clusia*, *Kalanchoë*, and *Opuntia*. J Exp Bot 59: 1829-40.

Winter K, Osmond CB, Hubick KT. 1986. Crassulacean acid metabolism in the shade. Studies on an epiphytic fern, *Pyrrosia longifolia*, and other rainforest species from Australia. Oecologia 68:224-30.

Winter K, Smith JAC. 1996. Crassulacean acid metabolism: current status and perspectives. In: Winter K, Smith JAC, editors. Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution. Berlin, Germany: Springer-Verlag. p 389-426.

Zheng XN, Wen ZQ, Pan RC, Hew CS. 1992. Response of *Cymbidium sinense* to drought stress. J Hort Sci 67:295-9.

Zotz G. 2004. How prevalent is Crassulacean acid metabolism among vascular epiphytes? Oecologia 138:184-92.

Zotz G, Tyree MT. 1996. Water stress in the epiphytic orchid, *Dimerandra emarginata* (G. Meyer) Hoehne. Oecologia 107:151-9.

Zotz G, Ziegler H. 1997. The occurrence of Crassulacean acid metabolism among vascular epiphytes from central Panama. New Phytol 137:223-9.