

SHORT COMMUNICATION

Do Melastomataceae perform CAM photosynthesis? A survey of neotropical species using carbon isotope ratios

Gilberto Ocampo¹ and Frank Almeda

California Academy of Sciences, Department of Botany, 55 Music Concourse Drive, Golden Gate Park, San Francisco, California 94118, USA

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Abstract: Leaf anatomical and carbon isotope ratio ($\delta^{13}\text{C}$) data from previous studies suggest that the species of the Melastomataceae perform C_3 photosynthesis and that leaf anatomical features of some epiphytic taxa resemble the characteristics found in CAM plants. The $\delta^{13}\text{C}$ values of 67 species of neotropical Melastomataceae (including epiphytes) were obtained from herbarium material deposited at the California Academy of Sciences for assessing the presence of the CAM pathway. The $\delta^{13}\text{C}$ values obtained from leaves (-23.4‰ to -34.5‰) were congruent with C_3 photosynthesis ($< -20\text{‰}$), and the $\delta^{13}\text{C}$ data from terrestrial (56 samples) and epiphytic species (11 samples) were not statistically different. Our results suggest that CAM photosynthesis is not found in neotropical Melastomataceae. The leaf anatomical features found in some species of Melastomataceae represent adaptations to cope with water stress and are not necessarily correlated with CAM photosynthesis. Photosynthetic pathways can be assessed with the use of leaf anatomical and $\delta^{13}\text{C}$ data, but further biochemical assays are warranted to corroborate the absence of the CAM pathway in the Melastomataceae.

Key Words: C_3 photosynthesis, carbon isotope ratios, crassulacean acid metabolism, leaf anatomy, Melastomataceae, photosynthesis

The Melastomataceae are a family of flowering plants distributed in the tropics and subtropics of the world. With over 5000 species, about two-thirds of which are distributed in the New World, it is one of the most diverse families (Renner 1993). Members of the Melastomataceae can be found from sea level to high altitudes above 3500 m asl where they prefer humid and sub-humid habitats. The species of the family can be annual to perennial herbs, shrubs and trees, and many are epiphytic (Renner 1986). It is well known that many epiphytes utilize the crassulacean acid metabolism (CAM) pathway of photosynthesis, which is found in more than 20 angiosperm families (Sayed 2001). The Bromeliaceae and Orchidaceae, among others, have an important number of epiphytic species that use CAM (Sayed 2001). Plants that use the CAM pathway open their stomata at night, and with the aid of phosphoenolpyruvate carboxylase (PEPC) they fix CO_2 , which is stored as malic acid inside the

cell vacuoles. During daylight hours, the stomata close and the malic acid is decarboxylated, entering the Calvin cycle in the mesophyll (Nelson & Sage 2008). Closure of the stomata during the day helps to decrease water loss while maintaining a high intracellular CO_2 concentration (Ehleringer & Monson 1993). Plants with this water-efficient strategy are found from semi-arid environments to tropical and subtropical forests, particularly in areas with intermittent or seasonal rain (Cushman 2001).

Anatomical data and carbon isotope ratios ($\delta^{13}\text{C}$) from leaves can be used to assess photosynthetic pathways. The presence of a palisade parenchyma and intercellular spaces between the cells of the spongy mesophyll (Cutler *et al.* 2008), as well as $\delta^{13}\text{C}$ values $< -20\text{‰}$ (Winter & Holtum 2002), suggest that the species of Melastomataceae studied to date perform C_3 photosynthesis (e.g. Brito-Ramos *et al.* 2010, Lüttge *et al.* 1998, Mentik & Baas 1992, Somavilla & Graciano-Ribeiro 2011, Souza & Marquete 2000). However, Reginato *et al.* (2009) reported the potential presence of the CAM pathway in four species of the epiphytic genus

¹ Corresponding author. Email: gocampo@calacademy.org.

Pleiochiton. Those species have succulent leaves, mesophyll with reduced intercellular spaces, and cells with large vacuoles, features that are correlated with CAM photosynthesis (Cushman 2001, Nelson *et al.* 2005).

In this survey we assessed the photosynthetic pathway of selected species of neotropical Melastomataceae based on $\delta^{13}\text{C}$ values. Sampling included neotropical species that are herbs, shrubs and trees, some of which are epiphytes. For the purposes of this study, we adopted the broad definition of epiphytism in the Melastomataceae proposed by Renner (1986). We considered as epiphytes those plants that are true epiphytes (plants that spend most of their life cycle on another plant and are not rooted in the ground), those that behave as secondary hemiepiphytes (climbing plants that germinate terrestrially, ascend nearby trees by adventitious roots and later become epiphytic by losing root contact with the ground), and climbers (plants that ascend nearby trees but never lose root contact with the ground) (Putz & Holbrook 1986, Renner 1986). Leaf material (*c.* 1 mg) from each taxon was taken from herbarium specimens deposited at the California Academy of Sciences (CAS). The samples were analysed with a GV Instruments IsoPrime continuous flow IRMS (IsoPrime, Cheadle, UK) interfaced to a Costech elemental analyser (Costech, Valencia, USA) at the Washington State University at Pullman Stable Isotope Core facility. Because the photosynthetic pathways discriminate in different proportion the stable isotope ^{13}C (isotope fractionation; O'Leary 1988), we used the following scale reference to infer photosynthetic pathways: C_3 , $< -20\text{‰}$ (Sage *et al.* 2007, Winter & Holtum 2002), and CAM, -9‰ to -20‰ (O'Leary 1988, Winter & Holtum 2002).

We surveyed 67 species distributed in 40 genera (Appendix 1). The epiphytic habit was represented by 11 species (16.4%), including *Pleiochiton blepharodes*, a species described as a putative CAM taxon by Reginato *et al.* (2009; considered as *Clidemia blepharodes* DC. in that study).

All species under study showed $\delta^{13}\text{C} < -20\text{‰}$, including samples that were collected in the seasonally dry savannas of South America (e.g. *Chaetostoma*, *Lavoisiera*, *Microlicia*). The range of $\delta^{13}\text{C}$ values was from -23.4‰ to -34.5‰ , with an average of $-27.9\text{‰} \pm 2.1\text{‰}$, which is well within the range of C_3 photosynthesis. The average $\delta^{13}\text{C}$ value was of $-27.9\text{‰} \pm 2.1\text{‰}$ for terrestrial species, and of $-28.3\text{‰} \pm 2.0\text{‰}$ for epiphytic taxa. The Shapiro–Wilk test reported probabilities of 0.40 and 0.31 for normal distribution of the $\delta^{13}\text{C}$ data for terrestrial and epiphytic species, respectively, so normality was assumed. The samples also had equal variances ($F = 1.05$, $P = 0.99$); therefore, the Student's *t*-test for equality of means was used. The result for the test was $t = 0.63$ and $P = 0.52$, so there was no

statistically significant difference in the mean $\delta^{13}\text{C}$ values of the two habits.

The $\delta^{13}\text{C}$ data reported here agree with the values documented for C_3 plants, thus confirming the absence of the CAM photosynthesis in neotropical Melastomataceae. In addition, the $\delta^{13}\text{C}$ values retrieved from terrestrial and epiphytic plants were not significantly different, providing additional evidence that the two habits in the family use the same photosynthetic pathway. Although the reported anatomical characteristics of the samples studied by Reginato *et al.* (2009) resemble the CAM anatomy, our data indicate that one of the species studied by those authors, *P. blepharodes*, is a C_3 plant ($\delta^{13}\text{C} = -28.9\text{‰}$). Closer examination of cross-sections of the leaves presented by Reginato *et al.* (2009, figs 9–12) reveal the existence of an incipient adaxial layer of elongated cells that resembles the palisade parenchyma of C_3 species (Cutler *et al.* 2008). Prediction of CAM photosynthesis based solely on leaf anatomy is challenging (Nelson *et al.* 2005) and additional evidence for confirming its presence may be required (e.g. $\delta^{13}\text{C}$ data and biochemical essays).

The leaf anatomical features in *Pleiochiton* (Reginato *et al.* 2009) that may resemble CAM anatomy can also be found in other members of the Melastomataceae; however, these species are reported to have a well-defined palisade parenchyma. For instance, a number of shrubs and trees from different genera are known to develop a multiseriate hypoderm (Gröger & Renner 1997, Mentik & Baas 1992), which may serve as an additional water-storage tissue (Carlquist 1994). Also, the leaves of some species of *Miconia* that grow in places with seasonal drought (e.g. dry savanna and Andean alpine vegetation) have been reported to have a well-developed hypoderm and a spongy mesophyll with reduced intercellular spaces (Brito-Ramos *et al.* 2010, Ely *et al.* 2005). The latter feature is known to increase efficiency of gas exchange and water transport (Fahn & Cutler 1992, Mauseth 1988). However, it is noteworthy that the intercellular space of the spongy mesophyll of *Miconia ibaguensis* and *M. stenostachya* varies with the amount of incident light on the leaves (e.g. leaves of plants that grow in the shade tend to have reduced intercellular spaces), suggesting this is a plastic trait (Marques *et al.* 2000).

This study found no evidence for the presence of CAM photosynthesis in neotropical species of Melastomataceae, and it is inferred that they perform the C_3 pathway, including the epiphytic taxa sampled. The leaf anatomical features reported in other studies suggest that some species of Melastomataceae have developed strategies for increasing water storage and water-use efficiency, and are not necessarily related to the CAM photosynthetic pathway. However, leaf anatomy and $\delta^{13}\text{C}$ data only provide an estimation of the photosynthesis pathway in plants, and additional studies of gas exchange and changes in titratable acidity are warranted to rule

out the presence of the CAM pathway or its variants (e.g. facultative CAM and CAM-cycling). Some lineages are apparently more predisposed to evolve C₄ and/or CAM photosynthesis (Edwards & Ogburn 2012), thus the absence of these photosynthetic strategies within Myrtales (Sage *et al.* 2011, Sayed 2001) may support the hypothesis that the Melastomataceae lack the CAM pathway.

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Appendix 1. Taxon name, carbon isotope ratio ($\delta^{13}\text{C}$) values, habit, and voucher information of sample material. NA = Not available. All specimens are deposited at the herbarium of the California Academy of Sciences (CAS).

| Taxon | $\delta^{13}\text{C}$ (‰) | Habit | Collection number | Provenance |
|--|---------------------------|-------------|--|-------------|
| <i>Aciotis indecora</i> (Bonpl.) Triana | -28.1 | Terrestrial | R.L. Wilbur & G. Moore 70062 | Costa Rica |
| <i>Acisanthera quadrata</i> Pers. | -27.9 | Terrestrial | W.D. Stevens & E. Duarte 28371 | Nicaragua |
| <i>Adelobotrys ascendens</i> (Sw.) Triana | -27.0 | Epiphyte | D.L. Holland 58 | Belize |
| <i>Arthrostemma ciliatum</i> Pav. ex D.Don | -25.2 | Terrestrial | F. Almeda <i>et al.</i> 2868 | Costa Rica |
| <i>Axinaea costaricensis</i> Cogn. | -25.2 | Terrestrial | G. Umaña & R. Chacón 493 | Costa Rica |
| <i>Bellucia pentamera</i> Naudin | -24.9 | Terrestrial | F. Almeda <i>et al.</i> 3309 | Costa Rica |
| <i>Blakea chlorantha</i> Almeda | -25.6 | Terrestrial | F. Almeda <i>et al.</i> 5013 | Costa Rica |
| <i>Blakea elliptica</i> (Gleason) Almeda | -26.7 | Epiphyte | F. Almeda <i>et al.</i> 7563 | Panama |
| <i>Blakea fuchsoides</i> Almeda | -29.1 | Epiphyte | D.S. Penneys & M.A. Blanco 1744 | Panama |
| <i>Blakea storkii</i> (Standl.) Almeda | -26.1 | Epiphyte | D.S. Penneys 1825 | Costa Rica |
| <i>Cambessedesia cambessedesoides</i> (Wurdack) A.B.Martins | -28.9 | Terrestrial | K.F. Rodrigues <i>et al.</i> 280 | Brazil |
| <i>Cambessedesia espora</i> (A.St.Hil. ex Bonpl.) DC. | -25.3 | Terrestrial | G. Hatschbach & H. Haas 13965 | Brazil |
| <i>Cambessedesia membranacea</i> Gardner ssp. <i>bahiana</i> A.B. Martins | -26.2 | Terrestrial | K.F. Rodrigues <i>et al.</i> 245 | Brazil |
| <i>Centradenia inaequilateralis</i> (Schltdl. & Cham.) G.Don | -28.3 | Terrestrial | T.B. Croat 35844 | Costa Rica |
| <i>Chaetolepis cufodontisii</i> Standl. | -24.2 | Terrestrial | W.D. Stevens 14298 | Costa Rica |
| <i>Chaetostoma pungens</i> DC. | -24.6 | Terrestrial | R.M. King & F. Almeda 8368 | Brazil |
| <i>Clidemia clandestina</i> Almeda | -28.2 | Terrestrial | S. Knapp <i>et al.</i> 6008 | Panama |
| <i>Clidemia fulva</i> Gleason | -26.7 | Terrestrial | T.B. Croat 41593 | Guatemala |
| <i>Clidemia lanuginosa</i> Almeda | -27.7 | Terrestrial | G. McPherson 6770 | Panama |
| <i>Clidemia sericea</i> D.Don | -29.5 | Terrestrial | I. Montoya 139 | Honduras |
| <i>Clidemia spectabilis</i> Gleason | -26.6 | Terrestrial | G. Herrera 3345 | Costa Rica |
| <i>Conostegia macrantha</i> O.Berg ex Triana | -28.4 | Terrestrial | F. Almeda <i>et al.</i> 2873 | Costa Rica |
| <i>Conostegia xalapensis</i> (Bonpl.) D.Don ex DC. | -28.8 | Terrestrial | S.D. Koch <i>et al.</i> 78222 | Mexico |
| <i>Graffenrieda cucullata</i> (Triana) L.O.Williams | -27.5 | Terrestrial | M. Lewis 37931 | Bolivia |
| <i>Heterocentron elegans</i> (Schltdl.) Kuntze | -26.1 | Terrestrial | R. Evans 1384 | Honduras |
| <i>Heterocentron subtriplinervium</i> (Link & Otto) A.Braun & C.D.Bouché | -29.3 | Terrestrial | J. González 369 | El Salvador |
| <i>Lavoisiera glandulifera</i> Naudin | -25.5 | Terrestrial | F. Almeda <i>et al.</i> 9199 | Brazil |
| <i>Lavoisiera tetragona</i> DC. | -27.1 | Terrestrial | F. Almeda <i>et al.</i> 5371 | Brazil |
| <i>Leandra chaetodon</i> (DC.) Cogn. | -31.6 | Terrestrial | J. Schunke-V. 13766 | Peru |
| <i>Leandra mexicana</i> (Naudin) Cogn. | -30.4 | Terrestrial | M. Nee <i>et al.</i> 46915 | Belize |
| <i>Leandra subulata</i> Gleason | -26.3 | Epiphyte | F. Almeda <i>et al.</i> 6457 | Panama |
| <i>Maieta poeppigii</i> Mart. ex Cogn. | -34.5 | Terrestrial | T.W. Henkel <i>et al.</i> 4148 | Guyana |
| <i>Marcetia macrophylla</i> Wurdack | -26.7 | Terrestrial | R.M. Harley 22459 | Brazil |
| <i>Marcetia taxifolia</i> (A.St.-Hil.) DC. | -27.3 | Terrestrial | R.M. Harley <i>et al.</i> 25352 | Brazil |
| <i>Meriania macrophylla</i> (Benth.) Triana | -23.4 | Terrestrial | J.P. Folsom 2207 | Panama |
| <i>Miconia argentea</i> (Sw.) DC. | -28.6 | Terrestrial | A. Grijalva & F.J. Grijalva 3522 | Nicaragua |
| <i>Miconia benthamiana</i> Triana | -28.0 | Terrestrial | F. Almeda <i>et al.</i> 2932 | Costa Rica |
| <i>Miconia confertiflora</i> Almeda | -28.4 | Epiphyte | F. Almeda & K. Nakai 4599 | Costa Rica |
| <i>Miconia grandidentata</i> Almeda | -25.8 | Epiphyte | F. Almeda & B. Anderson 5251 | Costa Rica |
| <i>Miconia prasina</i> (Sw.) DC. | -27.7 | Terrestrial | H. van der Werff & C. van Hardeveld 6915 | Panama |
| <i>Miconia urticoides</i> Triana | -30.6 | Epiphyte | G. McPherson 14071 | Panama |
| <i>Microlicia balsamifera</i> (DC.) Mart. | -25.4 | Terrestrial | R.M. Harley <i>et al.</i> 50531 | Brazil |
| <i>Microlicia euphorbioides</i> Mart. | -28.0 | Terrestrial | B.A.S. Pereira 477 | Brazil |
| <i>Microlicia isophylla</i> DC. | -26.6 | Terrestrial | R. Romero <i>et al.</i> 1902 | Brazil |
| <i>Microlicia viminalis</i> Triana | -27.6 | Terrestrial | R.C. Mendoca <i>et al.</i> 2338 | Brazil |
| <i>Monochaetum floribundum</i> (Schltdl.) Naudin | -28.0 | Terrestrial | F. Almeda & R.L. Wilbur 1036 | Costa Rica |
| <i>Monochaetum neglectum</i> Almeda | -27.6 | Terrestrial | F. Almeda & B. Anderson 5241 | Costa Rica |
| <i>Monolena primuliflora</i> Hook. f. | -31.9 | Epiphyte | A. Rojas <i>et al.</i> 437 | Peru |
| <i>Mouriri myrtilloides</i> (Sw.) Poir. ssp. <i>parvifolia</i> (Benth.) Morley | -30.4 | Terrestrial | C.L. Lundell & E. Contreras 20064 | Guatemala |

Appendix 1. Continued

| Taxon | $\delta^{13}\text{C}$ (‰) | Habit | Collection number | Provenance |
|--|---------------------------|-------------|---------------------------------------|------------|
| <i>Nepsera aquatica</i> (Aubl.) Naudin | -28.2 | Terrestrial | R.L. Wilbur & G. Moore 70136 | Costa Rica |
| <i>Ossaea brenesii</i> Standl. | -26.0 | Terrestrial | F. Almeda <i>et al.</i> 4313 | Costa Rica |
| <i>Ossaea quadrisulca</i> (Naudin) Wurdack | -31.3 | Terrestrial | C.E. Cerón <i>et al.</i> 9395 | Ecuador |
| <i>Pachyanthus lundellianus</i> (L.O. Williams) Judd & Skee | -28.8 | Terrestrial | W.D. Stevens <i>et al.</i> 19581 | Nicaragua |
| <i>Pilocosta nana</i> (Standl.) Almeda & Whiffin | -27.7 | Terrestrial | F. Almeda <i>et al.</i> 6425 | Panama |
| <i>Pleiochiton blepharodes</i> (DC.) Reginato <i>et al.</i> | -28.9 | Epiphyte | R. Kummrow <i>et al.</i> 2575 | Brazil |
| <i>Pterolepis trichotoma</i> (Rottb.) Cogn. | -29.0 | Terrestrial | W.D. Stevens & O.M. Montiel 26774 | Nicaragua |
| <i>Rhexia mariana</i> L. | -29.6 | Terrestrial | S. Renner 2151 | USA |
| <i>Rhynchanthera paludicola</i> (Donn. Sm.) Gleason | -29.6 | Terrestrial | F. Ortiz 1734 | Nicaragua |
| <i>Stammarkia spectabilis</i> Almeda | -25.9 | Terrestrial | D.E. Breedlove & F. Almeda 64802 | Guatemala |
| <i>Tessmannianthus gordonii</i> Almeda | -27.2 | Terrestrial | G. McPherson 9877 | Panama |
| <i>Tibouchina inopinata</i> Wurdack | -26.5 | Terrestrial | F. Almeda <i>et al.</i> 3365 | Costa Rica |
| <i>Tibouchina longifolia</i> (Vahl) Baill. | -28.0 | Terrestrial | T.B. Croat & D.P. Hannon 63228 | Mexico |
| <i>Tococa guianensis</i> Aubl. | -30.6 | Terrestrial | R. Rueda <i>et al.</i> 4443 | Nicaragua |
| <i>Topobea arboricola</i> Almeda | -30.5 | Epiphyte | J. Aranda <i>et al.</i> 2676 | Panama |
| <i>Triolena hirsuta</i> (Benth.) Triana | -31.5 | Terrestrial | R. Robles 2120 | Costa Rica |
| <i>Triolena scorpioides</i> Naudin | -31.2 | Terrestrial | E. Torres 504 | Mexico |
| <i>Votomita guianensis</i> Aubl. | -31.3 | Terrestrial | M.J. Jansen-Jacobs <i>et al.</i> 2900 | Guyana |