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Updating the occurrence of crassulacean acid metabolism (CAM) in the genus *Clusia* through carbon isotope analysis of species from Colombia

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Abstract

Clusia is a widely distributed neotropical genus with 321 currently described species. This remarkable genus is the only one known to contain trees *sensu stricto* with CAM photosynthesis. To survey the occurrence of CAM in *Clusia* species from Colombia, we determined the leaf stable carbon isotope composition ($\delta^{13}C$) of 568 specimens from 114 species deposited in 12 Colombian herbaria. In the vast majority of specimens, $\delta^{13}C$ values indicated that C_3 photosynthesis was the principal contributor to carbon gain. $\delta^{13}C$ values typical of strong CAM (less negative than –20‰) were observed in only five species, in four of them for the first time. All samples with CAM-type isotopic signatures were collected below 1,000 m a.s.l., whereas species with predominantly C_3 occurred from sea level to 3,500 m a.s.l. Together with information already available in the literature, we conclude that CAM is present in 22% (35/156) of the species of *Clusia* investigated thus far.

Keywords: C_3 photosynthesis; CAM photosynthesis; carbon isotope discrimination; epiphytes; hemiepiphytes; $\delta^{13}C$.

Introduction

Clusia is a widely distributed neotropical genus with currently 321 accepted species (POWO 2021). The northern limit of its natural distribution is the Bahamas (*e.g.*, *Clusia rosea* Jacq.), and the southern boundary reaches the state of Rio Grande do Sul, Brazil (*Clusia criuva* Cambess.; Lüttge 2007). Species can be found in various habitats, including tropical lowland humid forests, montane forests, swamp forests, dry semi-deciduous forests, páramo, dry scrub in the inter-Andean valleys, coastal plains, and sandstone and granite rocks in inselbergs (Araujo 1997, Gustafsson *et al.* 2002, Gustafsson 2010). The elevational range of distribution goes from near sea level to at least

Highlights

- CAM occurrence was assessed in 568 specimens of 114 species of *Clusia*
- C_3 photosynthesis was the principal pathway of carbon acquisition in most specimens
- CAM-type $\delta^{13}C$ values were detected in four species of *Clusia* for the first time

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Abbreviations: m a.s.l. – meter above sea level; $\delta^{13}C$ – $^{13}C/^{12}C$ isotope ratio.

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Conflict of interest: The authors declare that they have no conflict of interest.

3,500 m elevation in the Andes. The wide distribution of *Clusia* has been ascribed in part to its great photosynthetic plasticity. *Clusia* is the only genus that contains tree species with the water-conserving crassulacean acid metabolism (CAM) photosynthetic pathway. Arborescent growth forms also occur in CAM species of other families (*e.g.*, Cactaceae, Didiereaceae, Euphorbiaceae), but these species lack secondary growth based on a circumferential stem cambium, a feature that can be found in *Clusia* and that is characteristic of dicotyledonous trees (Lüttge 2008). *Clusia* species may show different photosynthetic physiotypes, such as obligate C_3, C_3–CAM intermediacy (including facultative CAM), and strong obligate CAM (Holtum *et al.* 2004, Andrade *et al.* 2007, Lüttge 2007, Winter *et al.* 2008). Recently, Leverett *et al.* (2021) investigated the relative roles of CAM, turgor loss point, and water-storage hydrenchyma tissue in the adaptation of *Clusia* species to drought and explored how these traits contributed to the distribution of species. The authors concluded that CAM was more important than the other two traits in determining the species' climatic niche distributions, highlighting the prominent role of CAM in coping with drought. Moreover, it was shown that *Clusia* species with constitutive, obligate CAM are more frequently found in habitats with sustained year-round precipitation deficits, while species with facultative CAM occur predominantly at sites with short-term drought events (Leverett *et al.* 2021). What is clear from the most recent reviews of the major CAM families is that there is a wide range of photosynthetic phenotypes between C_3 and full CAM not only in *Clusia* but also in many other CAM lineages (Winter *et al.* 2015, Winter 2019, Luján *et al.* 2021, Messerschmid *et al.* 2021).

The genus *Clusia* also varies greatly in life forms. Species can germinate on the ground and develop into shrubs and trees, or germinate on trees where they either remain as epiphytes (Holbrook and Putz 1996) or send roots to the ground and become hemiepiphytes (Lüttge 2007). In all stages, where there is a lack of connection with the ground and higher susceptibility to water-deficit stress, engaging in CAM is considered a critical physiological adaptation (Holtum *et al.* 2004, Silvera *et al.* 2009, Crayn *et al.* 2015). For example, in epiphytic orchids, strong CAM is frequent: from 9% in Colombian to 64% in Australian epiphytic species surveyed (Winter *et al.* 1983, Zotz and Ziegler 1997, Torres-Morales *et al*. 2020). In *Clusia*, CAM has been reported in all growth forms, *i.e*., in epiphytes, hemiepiphytes, and terrestrial plants (Ting *et al*. 1987, Zotz and Winter 1994a,b; Lüttge 2007).

Further exploration of the different metabolic pathways in this genus is needed to understand the adaptive value of CAM and its role in determining species distribution and its relationship to growth form. CAM in *Clusia* has previously been studied through carbon isotope analysis, measurements of diurnal and nocturnal net CO_2 exchange, and/or measurements of titratable acid (or malate) levels at dawn and dusk (*e.g*., Tinoco-Ojanguren and Vázquez-Yanes 1983, Ting *et al*. 1987, Winter *et al.* 1992, 2009; Holtum *et al.* 2004, Cernusak *et al.* 2008, Vargas-Soto *et al.* 2009, Lüttge *et al.* 2015). Although physiological measurements allow for the detection of weakly expressed CAM, these methods are time-consuming and require the use of living plants. By contrast, the carbon isotope technique is an efficient way to screen a large number of species (including herbarium specimens) for the presence or absence of strong CAM.

We still have only limited knowledge on photosynthetic pathway distribution in the genus *Clusia*. Most of the South American, and in particular Andean, *Clusia* species remain unexplored. Photosynthetic pathway information, coupled with a robust phylogeny of the group, is critical to the understanding of the evolution of CAM in this genus and the role of CAM in the observed geographic distribution patterns. Colombia hosts almost half of the *Clusia* species globally, with 153 accepted species reported in the Global Biodiversity Information Facility (GBIF.org 2021). Here, by using carbon isotopic signatures, we explore the photosynthetic pathways of 114 *Clusia* species deposited in Colombian herbaria, in order (*1*) to update the incidence of CAM in the genus, and (*2*) to consolidate previous information on CAM occurrence in *Clusia* in the context of terrestrial, epiphytic, and hemiepiphytic life forms.

Materials and methods

Site description and sample collection: At least two dispersal centers are recognized in *Clusia*: the Andean region (Gentry 1995) and the Guyana shield (Pipoly and Cogollo 1998). Colombia includes ecosystems in the Andean region and the Guiana shield and is one of the world's most megadiverse countries (Arbeláez-Cortés 2013). Due to its high topographic variability and the presence of three Andean ranges, the country is divided into five different hydroclimatic regions (Andean, Caribbean, Pacific, Amazon, and the Orinoco), presenting a broad mosaic of climates and microclimates, ranging from annual mean maximum temperatures of 35°C in the coasts and plains to temperatures below 0°C in the mountain summits of Los Andes and the Sierra Nevada of Santa Marta. We studied representative samples from many of these regions through the survey of 568 herbarium specimens from 114 species from 12 Colombian herbaria (Fig. 1, Table 1). Most species (106) were collected in Colombia. In four of these species, replicates were also obtained from Ecuador, Peru, and Mexico. Eight species in Table 1 are represented by specimens collected outside Colombia only (Costa Rica, Brazil, Dominican Republic, Ecuador, and Panama), although four of these species (*C. criuva*, *C. pseudomangle*, *C. rotundata*, and *C. schultesii*) have also been reported for Colombia. The sampling covered 30 of the 32 departments in Colombia (Fig. 1).

The herbaria were as follows: University of Los Andes (ANDES-collection LEBTYP), Valle University (CUVC), Botanical Garden Guillermo Piñeres (JBGP), Technological University of Chocó Diego Luis Córdoba (CHOCO), Alexander von Humboldt Biological Resources Research Institute (FMB), Javeriana University (HPUJ), University of Antioquia (HUA), Botanical Garden Joaquin

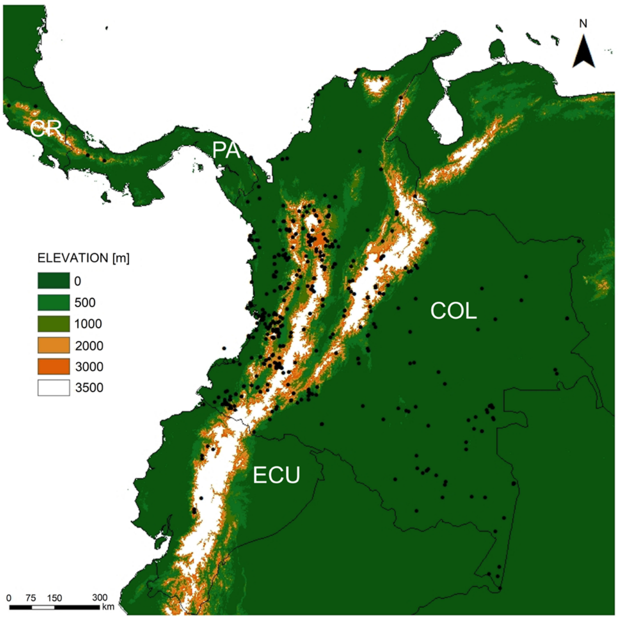

Fig. 1. Geographical location of collection sites of *Clusia* specimens in Colombia (COL), including two sites in Costa Rica (CR), two in Panama (PA), and eleven in Ecuador (ECU).

Antonio Uribe (JAUM), National University of Colombia, Palmira (VALLE), Cauca University (CAUP), Amazon Institute of Scientific Research SINCHI (COAH), and Tolima University (TOLI). We collected 3–5 mg of leaf dry mass from each herbarium specimen. The information present on the herbarium sheet was recorded, such as voucher number, collection site coordinates and elevation, and growth form (terrestrial, epiphytic, hemiepiphytic). Only mature leaves were considered.

δ¹³C: The $^{13}C/^{12}C$ ratio of leaf samples was determined by isotope ratio mass spectrometry at the Smithsonian Tropical Research Institute (Republic of Panama) using a *Flash HT* elemental analyzer coupled to a *Delta V* isotope ratio spectrometer through a *ConFlo III* interface (*Thermo Scientific*, Bremen, Germany). The isotopic signature was calculated as $\delta^{13}C$ relative to the internationally accepted standard Vienna Pee Dee Belemnite (VPDB) from *Belemnitella americana* (Crayn *et al*. 2015) using the formula:

$$\delta^{13}C\ [‰] = [(^{13}C/^{12}C \text{ in sample})/(^{13}C/^{12}C \text{ in standard}) - 1] \times 1{,}000$$

Plants were classified as exhibiting predominantly C_3 if their isotopic values were more negative than –20‰, and as exhibiting strong CAM if values were less negative than –20‰ (Crayn *et al.* 2015, Winter *et al.* 2015).

Updating the list of *Clusia* species with CAM: We first downloaded the complete list of all accepted *Clusia* species according to the 'Plants of the World Online' website (POWO 2021) which currently comprises 321 species (*see* Table 1S, *supplement*). As stated above, a species was classified as being capable of CAM when a $\delta^{13}C$ value of less negative than –20‰ had been reported, and/or nocturnal net CO_2 uptake and/or nocturnal increases in titratable acidity (including enzymatically determined malate) had been observed. In addition to our results, information was included from the surveys from Mexico (Vargas-Soto *et al.* 2009) and Panama (Holtum *et al.* 2004); the meta-analysis conducted by Leverett *et al.* (2021), who reviewed all publications in '*Web of Science*' on *Clusia* documenting CAM from 1983 (year of the first report of CAM in *Clusia*) to 2020; from Messerschmid *et al.* (2021), Luján *et al.* (2021), and other publications. All these data were incorporated into Table 1S.

Statistical analysis: To evaluate whether CAM is more abundant in epiphytic and hemiepiphytic than in terrestrial plants of *Clusia*, we first only considered data from the present survey which included 476 terrestrial plants, 56 epiphytic plants, and 37 hemiepiphytic plants. We then combined our data with those from Mexico (Vargas-Soto *et al.* 2009) and Panama (Holtum *et al.* 2004), which resulted in a total of 706 terrestrial plants, 125 epiphytic plants, and 78 hemiepiphytic plants. We ran a *Chi-squared* test comparing the observed distribution of CAM and C_3 specimens against the expected distribution under the null hypothesis that CAM was equally distributed in all growth forms. We ran this analysis for our database and the combined database. Additionally, we used a nonparametric test (*Wilcoxon/Kruskal-Wallis*) to determine whether the $\delta^{13}C$ value varied between the terrestrial, hemiepiphytic, and epiphytic samples depending upon elevation and explored if there was an interaction between elevation and growth habit on isotope data using a nonparametric factorial analysis of variance (*ANOVA*) based upon *ARTool* in *R* (Wobbrock *et al.* 2011, Kay *et al.* 2021). These analyses were performed to control for the effect of elevation on the isotopic signal (Cernusak *et al.* 2013, Crayn *et al.* 2015) and were run only with the combined dataset. We worked at the plant (specimen) level for these tests and not at the species level because individuals of a given species can differ in C_3 *vs*. CAM engagement and growth form. Changes of C_3-type $\delta^{13}C$ values with elevation were evaluated by linear least square regression.

Results

Across the 114 *Clusia* species under investigation, specimens of only five species showed isotopic signatures less negative of –20‰ typical of strong CAM (Table 1; Fig. 1S, *supplement*): *C. cochliformis* (one specimen studied), *C. eugenioides* (one of four specimens), *C. nigrolineata* (two of three specimens), *C. uvitana* (all two specimens), and *C. veneralensis* (two of three specimens). Except for *C. uvitana*, these results were indicative of the presence of CAM in four 'new' species of *Clusia*. Given the low number of specimens with $\delta^{13}C$ values less negative than –20‰, the frequency histogram of Fig. 2 does not show the bimodal distribution typically reported for plant families containing large numbers of C_3 and CAM species.

Table 1. $\delta^{13}C$ values of 568 herbarium specimens from 114 species of *Clusia*. Specimens of 106 species were from Colombia, of three species from Ecuador, of two species from Panama, and of one each from Brazil, Costa Rica, and the Dominican Republic. Country is indicated next to the herbarium acronyms only for samples collected outside Colombia. Elevation (Elev) and growth habit (Habit) are provided from information extracted from the herbarium sheet label. E – epiphytic; T – terrestrial; H – hemiepiphytic. If the species name on the herbarium sheet was different to the current accepted name according to the Plants of the World Online (POWO 2021) we included it in parenthesis after the accepted name. The $\delta^{13}C$ value of one additional species, *Arawakia oblanceolata* (Clusiaceae), which was collected as *Clusia oblanceolata*, is listed at the end of the table. '?' denotes tentative identification by B.E. Hammel. For those specimens, we show in parenthesis the species name on the herbarium sheet.

Accepted name	Collector(s), voucher number, herbarium, and country	Habit	Date	$\delta^{13}C$ [‰]	Elev [m]
C. abbottii Urb.	Thomas B. *et al.* 32203 CUVC (Dominican Republic)	T	1997	–28.8	999
C. alata Planch. & Triana	Prieto C. *et al.* 1236 FMB	T	2002	–27.4	2,200
C. alata Planch. & Triana	Velez J. *et al.* 67540 FMB	T	2004	–27.6	1,690
C. alata Planch. & Triana	Velez J. *et al.* 66934 FMB	T	2003	–32.2	1,800
C. alata Planch. & Triana	Velez J. *et al.* 67095 FMB	T	2003	–25.0	2,000
C. alata Planch. & Triana	Mendoza H. *et al.* 16232 FMB	H	1997	–24.6	1,500
C. alata Planch. & Triana	Stevenson P. *et al.* 638 GUAC	T	2006	–26.9	1,900
C. alata Planch. & Triana	Barbosa C. *et al.* 5769 ANDES	T	2003	–25.9	1,788
C. alata Planch. & Triana	Casas A. *et al.* 21829 HPUJ	T	2004	–28.0	2,850
C. alata Planch. & Triana	Jaramillo J. *et al.* 2934 TOLI	T	1946	–21.8	1,900
C. alata Planch. & Triana	Chagualo N. *et al.* 7705 TOLI	T	1996	–23.9	2,500
C. alata Planch. & Triana	Chagualo N. *et al.* 77051 TOLI	T	1996	–23.6	2,500
C. alata Planch. & Triana	Alvarez L. *et al.* 2686 CAUP	T	1991	–30.2	2,000
C. alata Planch. & Triana	Espinal S. *et al.* 22286 CUVC	T	1969	–22.5	3,200
C. alata Planch. & Triana	Arias J. *et al.* 328 HUA	T	1995	–25.9	360
C. alata Planch. & Triana	Saldarriaga D. *et al.* 28432 JAUM	T	1996	–24.5	1,794
C. amazonica Planch. & Triana	Cordoba M. *et al.* 21035 FMB	T	1996	–31.1	231
C. amazonica Planch. & Triana	Cano A. *et al.* C184 GUAC	T	2008	–33.9	200
C. amazonica Planch. & Triana	Cardenas D. *et al.* 83095 COAH	T	2013	–34.2	320
C. amazonica Planch. & Triana	Cardenas D. *et al.* 20650 COAH	T	1994	–30.3	126
C. amazonica Planch. & Triana	Jaramillo R. *et al.* 2121 COAH (Brazil)	T	1984	–30.8	160
C. amazonica Planch. & Triana	Castro F. *et al.* 78460 COAH	H	2010	–29.5	130
C. amazonica Planch. & Triana	Cogollo A. *et al.* 13070 JAUM	E	1982	–29.6	790
C. amazonica Planch. & Triana	Cogollo A. *et al.* 302 JAUM	E	1982	–29.7	790
C. androphora Cuatrec.	Betancur J. *et al.* 10663 HUA	H	2004	–27.1	1,700
C. androphora Cuatrec.	Betancur J. *et al.* 169663 HUA	T	2004	–26.2	1,710
C. androphora Cuatrec.	Lopez J. *et al.* 1058 HUA	T	2001	–28.5	200
C. androphora Cuatrec.	Betancur J. *et al.* 10965 HUA	T	2004	–27.1	1,710
C. androphora Cuatrec.	Cogollo A. *et al.* 32748 JAUM	T	1993	–27.7	1,450
C. articulata Vesque	Mendoza H. *et al.* 17301 FMB	T	1997	–28.0	2,000
C. articulata Vesque	Henao *et al.* 37822 HUA	T	1981	–25.9	1,000
C. articulata Vesque	Shepherd J. *et al.* 661 HUA	T	1976	–28.9	400
C. articulata Vesque	Shepherd J. *et al.* 197 HUA	T	1976	–31.5	400
C. articulata Vesque	Cruz C. *et al.* 12971 JAUM	T	1983	–25.3	860
C. bernardoi Pipoly & Cogollo	Serna R. *et al.* 1193 CAUP	T	1999	–27.6	1,600
C. brachycarpa Cuatrec.	Jaramillo M. *et al.* 519 TOLI	T	1962	–27.1	1,000
C. brachycarpa Cuatrec.	Cuatrecasas J. *et al.* 15397 VALLE	T	1943	–26.5	1,250
C. brachycarpa Cuatrec.	Cuatrecasas J. *et al.* 15454 VALLE	T	1943	–24.8	1,400
C. brachycarpa Cuatrec.	Castrillon L. *et al.* 18443 JAUM	T	1989	–25.4	1,700
C. bracteosa Cuatrec.	Casas C. *et al.* 39754 CAUP	T	2005	–27.6	1,450
C. bracteosa Cuatrec.	Hurtado D. *et al.* 29482 CAUP	T	2006	–29.2	1,654
C. bracteosa Cuatrec.	Serna R. *et al.* 1359 CAUP	T	1999	–31.7	1,620
C. bracteosa Cuatrec.	Mahecha G. *et al.* 766 VALLE	T	1971	–23.7	365
C. bracteosa Cuatrec.	Escobar E. *et al.* 279 VALLE	T	1998	–28.6	956

Accepted name	Collector(s), voucher number, herbarium, and country	Habit	Date	δ13C [‰]	Elev [m]
C. bracteosa Cuatrec.	Cogollo A. *et al.* 41215 JAUM	E	1997	–31.3	1,450
C. cajambrensis Cuatrec.	Hammel B. *et al.* 23093 CUVC	E	1987	–30.7	50
C. cajambrensis Cuatrec.	Cuatrecasas J. *et al.* 17283 VALLE	T	1997	–31.7	567
C. caudata (Planch. & Triana) Pipoly	Taylor C. *et al.* 2184 CHOCO	E	2014	–32.3	300
C. caudata (Planch. & Triana) Pipoly	Jaramillo F. *et al.* 1362 CHOCO	E	1979	–32.3	200
C. caudata (Planch. & Triana) Pipoly	Espina H. *et al.* 119 CHOCO	T	1983	–32.7	65
C. caudata (Planch. & Triana) Pipoly	Betancur J. *et al.* 8039 CHOCO	H	1999	–32.6	50
C. caudata (Planch. & Triana) Pipoly	Castaño A. *et al.* 33241 CAUP	T	2010	–31.3	1,000
C. caudata (Planch. & Triana) Pipoly	Lozano G. *et al.* 10769 CAUP	T	1995	–27.3	1,150
C. caudata (Planch. & Triana) Pipoly	Betancur J. *et al.* 392663 CUVC	H	1999	–31.4	230
C. caudata (Planch. & Triana) Pipoly	Pipoly J.J. *et al.* 26521 JAUM	E	1992	–31.7	1,340
C. cerroana Steyerm.	Etter A. *et al.* 262 FMB	T	1995	–29.2	203
C. cerroana Steyerm.	Renjifo L. *et al.* 833 HPUJ	T	2009	–24.9	3,080
C. cerroana Steyerm.	Petter M. *et al.* 9043 HPUJ	T	1995	–28.9	2,969
C. cerroana Steyerm.	Callejas R. *et al.* 6482 HUA	T	1998	–26.9	410
C. cerroana Steyerm.	Arbelaez V. *et al.* 96298 HUA	T	1993	–29.4	350
C. chiribiquetensis Maguire	Barbosa C. *et al.* 30778 FMB	T	1991	–27.7	175
C. chiribiquetensis Maguire	Petter M. *et al.* 8670 HPUJ	T	1995	–28.9	92
C. chiribiquetensis Maguire	Arbelaez V. *et al.* 146 HUA	T	1992	–27.8	350
C. chiribiquetensis Maguire	Arbelaez V. *et al.* 420 HUA	T	1991	–28.8	350
C. chiribiquetensis Maguire	Arbelaez V. *et al.* 966269 HUA	T	1992	–26.9	100
C. chusqueae Ewan	Correa M. *et al.* 117138 HUA	T	1996	–25.5	2,350
C. chusqueae Ewan	Correa M. *et al.* 1166718 HUA	T	1990	–24.9	2,400
C. chusqueae Ewan	Correa M. *et al.* 116225 HUA	T	1996	–21.6	2,630
C. chusqueae Ewan	Roldan F. *et al.* 164378 HUA	E	2006	–27.8	2,300
C. chusqueae Ewan	Ramirez F. *et al.* 81271 HUA	E	1992	–24.3	3,100
C. chusqueae Ewan	Pherson G. *et al.* 59045 HUA	T	1988	–24.7	2,700
C. chusqueae Ewan	Cogollo A. *et al.* 30678 JAUM	T	1996	–22.3	2,650
C. chusqueae Ewan	Correa M. *et al.* 2400 JAUM	T	1996	–26.6	2,400
C. cochliformis Maguire	Vargas W. *et al.* 120945 HUA	T	1998	–19.8	730
C. colombiana Pipoly	Gomez B. *et al.* 38756 CAUP	T	2004	–24.7	2,200
C. colombiana Pipoly	Rosero R. *et al.* 38766 CAUP	T	2014	–28.7	1,850
C. colombiana Pipoly	Ramirez B. *et al.* 26470 CAUP	T	2012	–29.6	1,850
C. colombiana Pipoly	Ramirez B. *et al.* 23603 CAUP	T	2007	–26.4	1,820
C. colombiana Pipoly	Ramirez B. *et al.* 27395 CAUP	T	2007	–28.6	1,950
C. colombiana Pipoly	Ferreire F. *et al.* 3328 CAUP	T	2000	–26.7	1,750
C. colombiana Pipoly	Ramirez B. *et al.* 21285 CAUP	T	2000	–25.6	1,830
C. colombiana Pipoly	Ramirez B. *et al.* 431 CAUP	T	1995	–28.1	1,850
C. colombiana Pipoly	Ramirez B. *et al.* 47460 CUVC	T	2007	–29.4	1,850
C. colombiana Pipoly	Gentry A. *et al.* 4768 JAUM	E	1983	–31.4	100
C. columnaris Engl.	Betancur B. *et al.* 93977 FMB	T	2000	–27.8	800
C. columnaris Engl.	Etter A. *et al.* 344 FMB	T	1995	–29.5	153
C. columnaris Engl.	Duque A. *et al.* 67355 ANDES	T	1997	–33.9	1,600
C. columnaris Engl.	Galeano M. *et al.* 100 HPUJ	T	1993	–30.8	570
C. columnaris Engl.	Mejia A. *et al.* 8501 HPUJ	T	1993	–29.3	570
C. columnaris Engl.	Mejia A. *et al.* 101 HPUJ	T	1993	–31.7	570
C. columnaris Engl.	Betancur J. *et al.* 70687 COAH	T	2009	–30.7	250
C. columnaris Engl.	Cardenas D. *et al.* 70916 COAH	T	2009	–30.5	183
C. columnaris Engl.	Zarucchi J. *et al.* 24601 COAH	T	1985	–30.4	110
C. columnaris Engl.	Cardenas D. *et al.* 83385 COAH	T	2012	–31.5	200
C. columnaris Engl.	Cardenas D. *et al.* 83378 COAH	T	2012	–30.6	200
C. columnaris Engl.	Castaño N. *et al.* 67441 COAH	T	2008	–29.4	97

Accepted name	Collector(s), voucher number, herbarium, and country	Habit	Date	δ13C [‰]	Elev [m]
C. columnaris Engl.	Betancur J. *et al.* 51148 COAH	T	2003	–29.4	258
C. columnaris Engl.	Rangel O. *et al.* 27652 COAH	T	1992	–27.5	580
C. columnaris Engl.	Palacios P. *et al.* 3088 COAH	T	1980	–28.6	200
C. columnaris Engl.	Soejarto D. *et al.* 4192 TOLI	E	1971	–26.9	500
C. columnaris Engl.	Echeverry R. *et al.* 4877 TOLI	T	1990	–26.2	2,700
C. columnaris Engl.	Echeverry R. *et al.* 5697 TOLI	T	2001	–28.1	120
C. columnaris Engl.	Pino N. *et al.* 3252 CHOCO	T	1985	–29.9	100
C. columnaris Engl.	Callejas R. *et al.* 5508 CHOCO	T	1986	–29.4	325
C. columnaris Engl.	Pino N. *et al.* 3252 CHOCO	T	1985	–29.7	100
C. columnaris Engl.	Aguilar C. *et al.* 4642 CHOCO	T	1987	–29.1	43
C. columnaris Engl.	Castillo A. *et al.* 4906 CHOCO	T	1987	–30.4	100
C. columnaris Engl.	Betancur B. *et al.* 12094 CAUP	T	2000	–28.7	800
C. congestiflora Cuatrec.	Esquivel H. *et al.* 2576 TOLI	T	1998	–30.3	2,100
C. congestiflora Cuatrec.	Puerta J. *et al.* 10758 TOLI	T	2001	–26.8	940
C. congestiflora Cuatrec.	Puerta J. *et al.* 107581 TOLI	T	2001	–27.3	940
C. congestiflora Cuatrec.	Ramirez B. *et al.* 8197 CAUP	T	1996	–27.5	1,156
C. congestiflora Cuatrec.	Espinal S. *et al.* 22277 CUVC	T	1968	–25.4	1,700
C. congestiflora Cuatrec.	Ramos J. *et al.* 22460 CUVC	T	1988	–27.9	1,900
C. congestiflora Cuatrec.	Ramos J. *et al.* 20415 CUVC	T	1988	–29.8	1,900
C. congestiflora Cuatrec.	Silverstone P. *et al.* 16841 CUVC	T	1984	–29.3	1,910
C. crenata Cuatrec.	Zarucchi J. *et al.* 5854 CHOCO	T	1987	–30.0	1,870
C. crenata Cuatrec.	Gentry A. *et al.* 55761 CUVC	T	1986	–26.3	1,960
C. crenata Cuatrec.	Lozano G. *et al.* 29989 CUVC	T	1995	–31.4	1,450
C. crenata Cuatrec.	Gentry A. *et al.* 23016 CUVC	T	1986	–27.4	1,960
C. crenata Cuatrec.	Zak V. *et al.* 8170 JBGP	T	1987	–25.1	2,200
C. crenata Cuatrec.	Zak V. *et al.* 8166 JBGP (Ecuador)	T	1987	–29.6	1,800
C. crenata Cuatrec.	Zak V. *et al.* 8165 JBGP (Ecuador)	T	1987	–23.9	1,900
C. criuva Cambess.	Kummrow R. *et al.* 30182 CUVC (Brazil)	T	1988	–30.3	2,960
C. criuva Cambess.	Silva J. *et al.* 27103 CUVC (Brazil)	T	1993	–30.2	1,292
C. croatii D'Arcy	Pherson G. *et al.* 6845 JBGP (Panama)	T	1986	–27.9	1,250
C. cruciata Cuatrec.	Aldana A. *et al.* 031–6 GUAC	T	2005	–27.2	362
C. cruciata Cuatrec.	Aldana A. *et al.* 60285 ANDES	T	2005	–31.5	362
C. cruciata Cuatrec.	Puentes P. *et al.* 1071 ANDES	T	2004	–31.5	450
C. cruciata Cuatrec.	Puentes H. *et al.* 60566 COAH	T	2009	–29.2	450
C. cruciata Cuatrec.	Mendoza H. *et al*. 45487 COAH	T	1998	–31.9	1,300
C. cruciata Cuatrec.	Mendoza H. *et al*. 45501 COAH	H	1998	–30.1	1,400
C. cruciata Cuatrec.	Forero E. *et al.* 1350 CHOCO	T	1979	–32.1	100
C. cruciata Cuatrec.	Jaramillo R. *et al*. 5040 CHOCO	T	1979	–30.6	90
C. cuneata Benth.	Ramirez B. *et al.* 15010 CAUP	T	1996	–30.5	350
C. cuneifolia Cuatrec.	Hammel B. *et al.* 16072 CUVC	T	1968	–29.9	2,200
C. cuneifolia Cuatrec.	Espinal S. *et al.* 15124 CUVC	T	1994	–26.7	2,200
C. cuneifolia Cuatrec.	Giraldo J. *et al.* 50237 CUVC	T	1968	–29.3	1,900
C. cuneifolia Cuatrec.	Sigifredo E. *et al.* 16071 CUVC	T	1987	–29.1	2,200
C. cuneifolia Cuatrec.	Correa M. *et al.* 41734 JAUM	T	1996	–24.9	2,350
C. cuneifolia Cuatrec.	Correa M. *et al.* 58931 JAUM	T	1996	–24.4	2,350
C. cuneifolia Cuatrec.	Correa M. *et al.* 49346 JAUM	T	1996	–25.7	2,470
C. cuneifolia Cuatrec.	Zarucchi J. *et al.* 6667 CHOCO	T	1987	–27.6	2,320
C. cuneifolia Cuatrec.	Zarucchi J. *et al.* 6834 CHOCO	T	1987	–29.6	2,160
C. cuneifolia Cuatrec.	Hammel B. *et al.* 16073 CUVC	T	1988	–30.2	2,200
C. cuneifolia Cuatrec.	Espinal S. *et al.* 15123 CUVC	T	1968	–27.0	2,200
C. cylindrica Hammel	Ariza W. *et al.* 86369 FMB	T	2005	–29.9	1,750
C. cylindrica Hammel	Alcazar C. *et al.* 7955 CAUP	T	2001	–29.9	1,740

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C. cylindrica Hammel	Giraldo L. *et al.* 23693 JAUM	T	1999	–27.3	560
C. decussata Ruiz & Pav. ex Planch. & Triana	Aldana A. *et al.* P4–685 GUAC	T	ND	–32.8	1,900
C. decussata Ruiz & Pav. ex Planch. & Triana	Juncosa A. *et al.* 2724 CHOCO	T	1989	–30.9	600
C. decussata Ruiz & Pav. ex Planch. & Triana	Escobar L. *et al.* 33408 CAUP	T	1984	–28.8	2,440
C. decussata Ruiz & Pav. ex Planch. & Triana	Escobar L. *et al.* 60600 CUVC	T	1984	–27.8	2,440
C. decussata Ruiz & Pav. ex Planch. & Triana	Escobar L. *et al.* 51790 CUVC	T	1984	–30.1	2,440
C. decussata Ruiz & Pav. ex Planch. & Triana	Gentry A. *et al.* 23871 CUVC	E	1985	–30.6	527
C. decussata Ruiz & Pav. ex Planch. & Triana	Gentry A. *et al.* 22879 CUVC	H	1986	–26.7	2,370
C. decussata Ruiz & Pav. ex Planch. & Triana	Gentry A. *et al.* 23872 CUVC	E	1986	–29.6	473
C. decussata Ruiz & Pav. ex Planch. & Triana	Ramirez J. *et al.* 19333 JAUM	E	1987	–27.5	550
C. decussata Ruiz & Pav. ex Planch. & Triana	Correa M. *et al.* 31123 JAUM	T	1996	–28.0	2,640
C. deminuta Pipoly	Callejas R. *et al.* 36656 HUA	T	1986	–30.3	1,160
C. dixonii Little	Herrera G. *et al.* 49360 FMB	T	1997	–29.1	1,600
C. dixonii Little	Andes H. *et al.* 61262 ANDES	T	2009	–31.8	1,800
C. dixonii Little	Gomez M. *et al.* 6119 ANDES	T	2009	–28.3	1,800
C. dixonii Little	Mondragon M. *et al.* 18398 CUVC	E	1987	–26.2	1,800
C. dixonii Little	Urrea L. *et al.* 188185 HUA	T	2009	–30.4	2,056
C. dixonii Little	MacDougal J. *et al.* 64229 HUA	T	1989	–27.9	1,770
C. ducu Benth.	Molina J. *et al.* 59918 FMB	T	1969	–27.4	1,900
C. ducu Benth.	Velazques P. *et al.* 31949 HUA	T	1986	–24.4	2,440
C. ducu Benth.	Callejas R. *et al.* 83617 HUA	T	1990	–25.2	2,140
C. ducu Benth.	Callejas R. *et al.* 1109 JAUM	T	1978	–26.3	2,700
C. ducu Benth.	Luteyn J. *et al.* 6476 JAUM	E	1984	–32.1	2,100
C. ducu Benth.	Cardenas D. *et al.* 14083 JAUM	T	1987	–29.6	200
C. ducuoides Engl.	Ramírez P. *et al.* 66672 FMB	T	2001	–27.5	1,850
C. ducuoides Engl.	Silverstone P. *et al.* 3381 CHOCO	T	1984	–25.3	2,730
C. ducuoides Engl.	Giraldo J. *et al.* 50317 CUVC	T	1995	–28.7	1,900
C. ducuoides Engl.	Giraldo J. *et al.* 50323 CUVC	T	1996	–31.1	1,900
C. ducuoides Engl.	Escobar L. *et al.* 51593 CUVC	T	1984	–28.3	1,950
C. ducuoides Engl.	Giraldo P. *et al.* 42126 CUVC	T	2002	–28.7	1,900
C. ducuoides Engl.	Silverstone P. *et al.* 17193 CUVC	T	1984	–29.3	2,500
C. ducuoides Engl.	Silverstone P. *et al.* 17195 CUVC	T	1984	–23.3	2,770
C. ducuoides Engl.	Harling A. *et al.* 61776 CUVC	T	1985	–27.9	1,180
C. ducuoides Engl.	Correa M. *et al.* 58432 JAUM	T	1996	–29.7	2,100
C. ducuoides Engl.	Correa M. *et al.* 49285 JAUM	T	1996	–26.1	2,350
C. dukei Maguire	Ortiz C. *et al.* 836 HPUJ	T	1949	–24.3	1,400
C. elliptica Kunth	Benitez D. *et al.* 29556 JAUM	T	1995	–29.1	2,600
C. elliptica Kunth	Van der Werff H. *et al.* 8999 JBGP (Peru)	T	1986	–25.8	2,700
C. elliptica Kunth	Robles A. *et al.* 65969 FMB	T	2008	–29.1	3,220
C. elliptica Kunth	Mendoza H. *et al.* 89574 FMB	T	2007	–26.1	2,980
C. elliptica Kunth (syn *C. peruviana*)	Muñoz E. *et al.* 18498 CAUP	T	2003	–32.0	2,700
C. ellipticifolia Cuatrec.	Gonzales D. *et al.* 99206 FMB	T	2009	–27.5	1,980
C. ellipticifolia Cuatrec.	Pavayeau L. *et al.* 827 HPUJ	T	1993	–26.1	2,700
C. ellipticifolia Cuatrec.	Pavayeau L. *et al.* 826 HPUJ	T	1989	–24.8	2,700
C. ellipticifolia Cuatrec.	Pavayeau L. *et al.* 825 HPUJ	T	1989	–26.5	2,700
C. ellipticifolia Cuatrec.	Esquivel H. *et al.* 7831 TOLI	T	1997	–29.5	2,100
C. ellipticifolia Cuatrec.	Vivas S. *et al.* 37349 CAUP	T	2013	–30.1	1,800
C. ellipticifolia Cuatrec.	Chito E. *et al.* 7524 CAUP	T	2001	–24.8	1,920
C. ellipticifolia Cuatrec.	Ramirez C. *et al.* 7810 CAUP	T	2002	–26.2	1,870
C. ellipticifolia Cuatrec.	Agredo O. *et al.* 2016 CAUP	T	2008	–27.6	1,780
C. ellipticifolia Cuatrec.	Aguilar M. *et al.* 30092 CAUP	T	2010	–30.3	193
C. ellipticifolia Cuatrec.	Macias D. *et al.* 9512 CAUP	T	2001	–26.6	1,900

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C. ellipticifolia Cuatrec.	Ramirez B. *et al.* 27401 CAUP	T	2007	–29.8	1,950
C. ellipticifolia Cuatrec.	Escobar E. *et al.* 129 VALLE	T	1997	–26.8	1,200
C. ellipticifolia Cuatrec.	Cuatrecasas J. *et al.* 19469 VALLE	T	1944	–25.8	1,103
C. eugenioides Planch. & Linden	Mesa A. *et al.* 4849 CHOCO	T	1987	–28.6	43
C. eugenioides Planch. & Linden	Espina J. *et al.* 2094 CHOCO	T	1986	–15.0	8
C. eugenioides Planch. & Linden	Mosquera M. *et al.* 4988 CHOCO	T	1987	–29.7	43
C. firmifolia Cuatrec. (syn *C. sclerophylla*)	Monzalve M. *et al.* 18223 CUVC	T	1987	–30.3	50
C. fistulosa Cuatrec.	Cuatrecasas J. *et al.* 19888 VALLE	T	1946	–27.1	10
C. flavida (Benth.) Pipoly	Aldana A. *et al.* P4–930 GUAC	T	ND	–29.9	1,900
C. flavida (Benth.) Pipoly	Juncosa A. *et al.* 2187 CHOCO	T	1983	–30.5	506
C. flavida (Benth.) Pipoly	Mendoza H. *et al.* 11521 CAUP	T	1997	–27.3	253
C. flavida (Benth.) Pipoly	MacDougal J. *et al.* 62840 HUA	T	1988	–31.7	1,480
C. flavida (Benth.) Pipoly	Gomez A. *et al.* 65804 JAUM	T	2014	–27.9	2,393
C. flavida (Benth.) Pipoly	Toro F. *et al.* 48779 JAUM	H	1905	–28.7	150
C. flavida (Benth.) Pipoly	Correa M. *et al.* 58928 JAUM	T	1906	–26.7	2,470
C. fructiangusta Cuatrec.	Sarmiento F. *et al.* 3003 TOLI	T	1979	–28.8	338
C. fructiangusta Cuatrec.	Ramirez B. *et al.* 24304 CAUP	T	2007	–29.9	300
C. fructiangusta Cuatrec.	Gentry A. *et al.* 58709 CUVC	E	1986	–28.2	500
C. fructiangusta Cuatrec.	Reina G. *et al.* 54645 CUVC	T	2013	–23.9	1,420
C. fructiangusta Cuatrec.	Reina G. *et al.* 52363 CUVC	T	2012	–25.7	1,300
C. fructiangusta Cuatrec.	Monzalve M. *et al.* 21888 CUVC	T	1988	–28.0	100
C. fructiangusta Cuatrec.	Monzalve M. *et al.* 55161 CUVC	T	1987	–27.5	100
C. fructiangusta Cuatrec.	Meneses O. *et al.* 54483 CUVC	T	2013	–23.8	1,230
C. fructiangusta Cuatrec.	Cuatrecasas J. *et al.* 21138 VALLE	T	1946	–28.8	53
C. fructiangusta Cuatrec.	Cuatrecasas J. *et al.* 15845 VALLE	T	1944	–27.9	50
C. fructiangusta Cuatrec.	Cuatrecasas J. *et al.* 17023 VALLE	T	1944	–26.5	1,122
C. fructiangusta Cuatrec.	Cuatrecasas J. *et al.* 172667 VALLE	T	1944	–27.0	80
C. garcibarrigae Cuatrec.	Ramirez B. *et al.* 10642 CAUP	T	1998	–26.8	1,200
C. garcibarrigae Cuatrec.	Lozano G. *et al.* 8090 CAUP	T	1995	–28.9	1,100
C. garcibarrigae Cuatrec.	Gonzales M. *et al.* 11193 CAUP	T	1995	–25.5	550
C. garcibarrigae Cuatrec.	Gonzales M. *et al.* 10414 CAUP	T	1995	–29.3	580
C. garcibarrigae Cuatrec.	Betancur J. *et al.* 111696 HUA	T	1997	–28.4	1,180
C. gaudichaudii Cambess.	Quiñones M. *et al.* 4959 ANDES	T	1990	–27.9	350
C. gaudichaudii Cambess.	Vincelli P. *et al.* 119167 HUA	T	1979	–30.4	160
C. gaudichaudii Cambess.	Restrepo D. *et al.* 85295 HUA	E	1991	–29.4	150
C. glomerata Cuatrec.	Espina J. *et al.* 224 CHOCO	T	1983	–24.0	110
C. glomerata Cuatrec.	Moreno R. *et al.* 3486 CHOCO	T	1985	–31.7	43
C. glomerata Cuatrec.	Moreno R. *et al.* 971 CHOCO	T	1979	–31.1	96
C. glomerata Cuatrec.	Serna A. *et al.* 2381 CAUP	T	1999	–29.9	1,000
C. glomerata Cuatrec.	Castañas O. *et al.* 6619 CAUP	E	2000	–32.2	1,550
C. gracilis Standl.	Hammel B. *et al.* 9440 JBGP (Costa Rica)	T	1987	–31.8	360
C. gracilis Standl.	Herrera G. *et al.* 9448 JBGP (Costa Rica)	E	1987	–29.0	800
C. grammadenioides Pipoly	Parrado A. *et al.* 1122923 HUA	H	1998	–31.8	160
C. grandiflora Splitg.	Stevenson P. *et al.* 4501 ANDES	H	1994	–28.8	350
C. grandiflora Splitg.	Villanueva B. *et al.* 122321 TOLI	T	2012	–30.9	539
C. grandiflora Splitg.	Villanueva B. *et al.* 923 TOLI	T	2012	–30.9	486
C. grandiflora Splitg.	Reina G. *et al.* 60576 CUVC	T	2012	–29.8	635
C. grandiflora Splitg.	Reina G. *et al.* 54525 CUVC	T	2012	–30.6	635
C. hachensis Cuatrec.	Calderon E. *et al.* 57540 FMB	T	1991	–26.4	3,400
C. hachensis Cuatrec.	Vargas W. *et al.* 121456 HUA	T	1998	–25.6	3,300
C. hammeliana Pipoly	Torres J. *et al.* ACS70 GUAC	T	2008	–34.4	200
C. hammeliana Pipoly	Parrado A. *et al.* 39669 COAH	T	1998	–31.5	160

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C. hammeliana Pipoly	Parrado A. *et al.* 51956 COAH	T	2002	–32.4	200
C. hammeliana Pipoly	Mohr O. *et al.* 4267 COAH	E	1987	–32.6	242
C. hammeliana Pipoly	Duivenvoorden J. *et al.* 19115 COAH	E	1991	–31.5	228
C. hammeliana Pipoly	Duivenvoorden J. *et al.* 18459 COAH	E	1991	–34.2	228
C. hammeliana Pipoly	Cardenas D. *et al.* 76041 COAH	H	2011	–32.7	403
C. hammeliana Pipoly	Cardenas D. *et al.* 76181 COAH	H	2011	–31.3	588
C. hammeliana Pipoly	Gentry A. *et al.* 22710 JAUM	H	1988	–30.5	130
C. hammeliana Pipoly	Zapata D. *et al.* 62104 JAUM	T	2013	–31.6	225
C. hammeliana Pipoly	Alvares D. *et al.* 62901 JAUM	T	2006	–35.9	150
C. haughtii Cuatrec.	Stevenson P. *et al.* GUAC – 939 GUAC	H	2013	–27.3	1,900
C. haughtii Cuatrec.	Stevenson P. *et al.* GUAC–939 ANDES	H	2013	–27.5	1,900
C. haughtii Cuatrec.	Castro S. *et al.* 58367 COAH	T	2004	–31.2	242
C. haughtii Cuatrec.	Betancur J. *et al.* 9417 COAH	T	1990	–28.9	640
C. haughtii Cuatrec.	Cardenas D. *et al.* 76201 COAH	H	2010	–29.7	500
C. haughtii Cuatrec.	Cardenas D. *et al.* 76315 COAH	T	2010	–32.2	332
C. haughtii Cuatrec.	Ramirez J. *et al.* 39926 COAH	T	2000	–30.8	275
C. haughtii Cuatrec.	Blanco C. *et al.* 58909 COAH	T	2007	–32.2	580
C. haughtii Cuatrec.	Aguilar M. *et al.* 82484 COAH	H	ND	–31.6	670
C. haughtii Cuatrec.	Martinez Y. *et al.* 29622 COAH	T	1998	–27.2	1,295
C. haughtii Cuatrec.	Cardenas D. *et al.* 74879 COAH	T	2010	–32.0	800
C. haughtii Cuatrec.	Martinez Y. *et al.* 29621 COAH	T	1998	–28.8	1,295
C. haughtii Cuatrec.	Zarucchi J. *et al.* 6167 CHOCO	E	1985	–27.1	1,500
C. huberi Pipoly	Petter M. *et al.* 8671 HPUJ	T	1995	–30.5	92
C. hydrogera Cuatrec.	Acevedo C. *et al.* 36088 FMB	T	1993	–27.5	2,600
C. hydrogera Cuatrec.	Luteyn J. *et al.* 5783 CHOCO	E	1988	–26.6	2,000
C. hydrogera Cuatrec.	Silverstone P. *et al.* 3390 CHOCO	T	1984	–28.9	1,920
C. hydrogera Cuatrec.	Silverstone P. *et al.* 3412 CHOCO	T	1984	–28.9	1,870
C. hydrogera Cuatrec.	Rico N. *et al.* 2996 CAUP	T	1993	–25.4	2,600
C. hydrogera Cuatrec.	Silverstone P. *et al.* 17191 CUVC	T	1984	–29.5	1,920
C. hydrogera Cuatrec.	Silverstone P. *et al.* 16533 CUVC	T	1984	–26.9	1,870
C. hydrogera Cuatrec.	Silverstone P. *et al.* 20104 CUVC	T	1988	–30.6	1,900
C. hydrogera Cuatrec.	Ramos J. *et al.* 21133 CUVC	T	1988	–27.7	1,800
C. hydrogera Cuatrec.	Fomegra R. *et al.* 84055 HUA	T	1992	–29.9	1,990
C. hydrogera Cuatrec.	Ramirez J. *et al.* 35241 JAUM	T	1987	–28.3	1,900
C. inesiana Cuatrec.	Barbosa C. *et al.* 8178 FMB	T	1986	–28.1	1,384
C. inesiana Cuatrec.	Callejas R. *et al.* 82434 HUA	T	1992	–21.7	2,900
C. inesiana Cuatrec.	Londoño L. *et al.* 188167 HUA	T	2009	–25.9	2,670
C. insignis Mart.	Galeano M. *et al.* 104 HPUJ	T	1993	–32.0	570
C. insignis Mart.	Mejia A. *et al.* 103 HPUJ	T	1993	–31.1	570
C. insignis Mart.	Cardenas D. *et al.* 83371 COAH	T	2012	–30.8	290
C. insignis Mart.	Barrero J. *et al.* 19790 COAH	T	2013	–29.5	163
C. insignis Mart.	Cardenas D. *et al.* 83369 COAH	T	2012	–32.3	290
C. insignis Mart.	Restrepo D. *et al.* 19512 COAH	T	1993	–27.4	1,400
C. insignis Mart.	Galeano M. *et al.* 25319 COAH	T	1993	–28.9	183
C. insignis Mart.	Galeano G. *et al.* 7225 COAH	T	1986	–31.9	200
C. insignis Mart.	Lopez R. *et al.* 47269 COAH	T	2001	–32.2	183
C. insignis Mart.	Cardenas D. *et al.* 71467 COAH	T	2005	–31.5	183
C. insignis Mart.	Cardenas D. *et al.* 71657 COAH	T	2009	–30.5	183
C. insignis Mart.	Martinez X. *et al.* 116741 HUA	T	1993	–30.9	500
C. insignis Mart.	Marulanda O. *et al.* 90816 HUA	T	1989	–27.6	350
C. latipes Planch. & Triana	Silverstone P. *et al.* 13787 CUVC	T	1981	–29.7	1,550
C. latipes Planch. & Triana	Killip E. *et al.* 38984 VALLE	T	1944	–29.1	30

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C. latipes Planch. & Triana	Killip E. *et al.* 38632 VALLE	T	1944	–27.8	373
C. latipes Planch. & Triana	Cuatrecasas J. *et al*. 21304 VALLE	T	1946	–27.0	53
C. latipes Planch. & Triana	Killip E. *et al.* 38897 VALLE	E	1946	–27.8	106
C. laurifolia Planch. & Triana	Reira G. *et al.* 8702 CAUP	T	2000	–31.0	35
C. laurifolia Planch. & Triana	Ramirez B. *et al.* 7459 CAUP	T	1995	–30.9	250
C. laurifolia Planch. & Triana	Gonzales M. *et al.* 11196 CAUP	T	1995	–30.5	600
C. laurifolia Planch. & Triana	Baca A. *et al.* 18997 CAUP	T	2002	–30.3	50
C. laurifolia Planch. & Triana	Gonzales M. *et al.* 1197 CAUP	T	1995	–31.6	600
C. laurifolia Planch. & Triana	Killip E. *et al.* 39139 VALLE	T	1944	–31.9	6
C. laurifolia Planch. & Triana	Juncosa A. *et al.* 16330 JAUM	T	1983	–31.4	475
C. laurifolia Planch. & Triana (syn *C. formosa*)	Luteyn J. *et al.* 5812 CHOCO	T	1988	–33.9	1,000
C. laurifolia Planch. & Triana (syn *C. formosa*)	Juncosa A. *et al.* 2490 CHOCO	T	1983	–29.2	475
C. laurifolia Planch. & Triana (syn *C. formosa*)	Reina G. *et al.* 34969 CAUP	H	2000	–30.9	30
C. laurifolia Planch. & Triana (syn *C. formosa*)	Lozano G. *et al.* 10771 CAUP	T	1995	–34.2	680
C. laurifolia Planch. & Triana (syn *C. formosa*)	Ramos J. *et al.* 162499 CUVC	T	1987	–27.7	1,800
C. laurifolia Planch. & Triana (syn *C. formosa*)	Silverstone P. *et al.* 22358 CUVC	T	1985	–26.0	1,900
C. laurifolia Planch. & Triana (syn *C. formosa*)	Ramos J. *et al.* 16248 CUVC	T	1987	–26.9	1,700
C. laurifolia Planch. & Triana (syn *C. formosa*)	Gentry A. *et al.* 19213 CUVC	T	1986	–29.3	1,960
C. laurifolia Planch. & Triana (syn *C. formosa*)	Juncosa. A et al. 17778 CUVC	T	1984	–30.1	600
C. laurifolia Planch. & Triana (syn *C. formosa*)	Cuatrecasas J. *et al.* 15997 VALLE	T	1994	–29.6	20
C. laxiflora (Poepp.) Planch. & Triana	Ayala F. *et al.* 47656 JAUM	T	1987	–33.6	92
C. lechleri Rusby	Hurtado R. *et al*. 45949 CUVC	T	2006	–25.9	1,890
C. leptanthera Cuatrec.	Monzalve M. *et al.* 56867 CUVC	E	1987	–29.1	100
C. leptanthera Cuatrec.	Monzalve M. *et al.* 55604 CUVC	E	1987	–29.9	100
C. leptanthera Cuatrec.	Gentry A. *et al.* 23027 CUVC	H	1987	–30.2	50
C. leptanthera Cuatrec.	Gentry A. *et al.* 22545 CUVC	E	1987	–28.9	100
C. leptanthera Cuatrec.	Gentry A. *et al.* 19040 CUVC	H	1984	–32.2	50
C. leptanthera Cuatrec.	Gentry A. *et al.* 23025 CUVC	E	1987	–30.1	50
C. leptanthera Cuatrec.	Gentry A. *et al.* 19178 CUVC	E	1984	–32.6	50
C. leptanthera Cuatrec.	Monzalve M. *et al.* 19777 CUVC	E	1987	–33.1	100
C. leptanthera Cuatrec.	Monzalve M. *et al.* 19778 CUVC	E	1987	–33.2	100
C. lineata (Benth.) Planch. & Triana	Mendoza H. *et al*. 18122515 FMB	T	1997	–28.1	1,500
C. lineata (Benth.) Planch. & Triana	Alvear N. *et al.* 25901 HPUJ	T	2006	–30.7	2,150
C. lineata (Benth.) Planch. & Triana	Alvear N. *et al.* 25902 HPUJ	T	2006	–30.4	2,150
C. lineata (Benth.) Planch. & Triana	Malage W. *et al.* 9226 TOLI	T	2005	–28.5	1,500
C. lineata (Benth.) Planch. & Triana	Espina J. *et al*. 8993 CHOCO	T	1989	–30.1	43
C. lineata (Benth.) Planch. & Triana	Renteria E. *et al.* 17380 CHOCO	T	2008	–32.1	80
C. lineata (Benth.) Planch. & Triana	Ramos *et al.* 9537 CHOCO	E	1988	–29.2	1,900
C. lineata (Benth.) Planch. & Triana	Renteria E. *et al.* 17385 CHOCO	T	2008	–29.7	80
C. lineata (Benth.) Planch. & Triana	Benavidez O. *et al.* 2977 CAUP	T	1987	–27.2	1,800
C. lineata (Benth.) Planch. & Triana	Londoño L. *et al.* 189091 HUA	T	2009	–30.8	2,670
C. lineata (Benth.) Planch. & Triana	Espina J. *et al*. 72533 HUA	T	1989	–31.5	152
C. lineata (Benth.) Planch. & Triana	Luteyn J. *et al.* 6492 JAUM	E	1984	–29.2	671
C. longistyla Cuatrec.	Forero E. *et al.* 5088 CHOCO	T	1976	–28.6	2,100
C. longistyla Cuatrec.	Paz N. *et al.* 24877 CUVC	T	1992	–27.5	1,800
C. loranthacea Planch. & Triana	Cano A. *et al.* C513 GUAC	T	2008	–33.1	200
C. loranthacea Planch. & Triana	Umaña N. *et al.* 444–2C GUAC	T	2009	–29.9	200
C. loranthacea Planch. & Triana	Cardenas D. *et al.* 37158 COAH	T	1995	–32.6	400
C. loranthacea Planch. & Triana	Cardenas D. *et al.* 10946 COAH	T	1995	–31.3	140
C. loranthacea Planch. & Triana	Eusse A. *et al.* 6858 COAH	T	2001	–32.4	2,400
C. loranthacea Planch. & Triana	Cano A. *et al.* 68956 COAH	T	2008	–34.6	100
C. loranthacea Planch. & Triana	Eusse A. *et al.* 41659 COAH	T	1999	–31.9	204

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C. loranthacea Planch. & Triana	Zarucchi J. *et al.* 6417 CHOCO	E	1987	–29.7	140
C. loranthacea Planch. & Triana	Gonzales M. *et al.* 11199 CAUP	T	1995	–32.7	580
C. loranthacea Planch. & Triana	Jarvis A. *et al.* 12107 CAUP	T	2000	–31.1	1,856
C. loranthacea Planch. & Triana	Escobar L. *et al*. 53809 CUVC	T	1981	–27.6	2,300
C. loranthacea Planch. & Triana	Cuatrecasas J. *et al*. 15184 VALLE	T	1943	–26.9	1,180
C. loranthacea Planch. & Triana	Cuatrecasas J. *et al*. 39008 VALLE	T	1944	–30.9	8
C. loranthacea Planch. & Triana	Cuatrecasas J. *et al*. 39157 VALLE	T	1944	–30.6	25
C. magnifolia Cuatrec.	Stevenson P. *et al*. GUAC – 178 GUAC	T	2005	–25.3	1,900
C. magnifolia Cuatrec.	Silverstone P. *et al.* 20105 CUVC	T	1988	–28.6	1,800
C. magnifolia Cuatrec.	Silverstone P. *et al.* 22997 CUVC	T	1988	–27.2	1,800
C. magnifolia Cuatrec.	Silverstone P. *et al.* 22380 CUVC	T	1988	–26.7	2,430
C. magnifolia Cuatrec.	Gentry A. *et al.* 18357 CUVC	T	1985	–29.2	1,970
C. mamillata Cuatrec.	Panesso N. *et al.* 14429 CHOCO	T	2004	–33.1	50
C. mamillata Cuatrec.	Panesso N. *et al.* 14360 CHOCO	T	2004	–32.9	50
C. mamillata Cuatrec.	Espina J. *et al*. 8996 CHOCO	T	1989	–27.8	43
C. mamillata Cuatrec.	Monzalve M. *et al.* 23303 CUVC	E	1987	–29.5	100
C. mamillata Cuatrec.	Gentry A. *et al.* 33696 JAUM	H	1981	–29.7	43
C. martiana Engl.	Echeverry R. *et al.* 467 TOLI	T	1962	–28.4	949
C. martiana Engl.	Echeverry R. *et al.* 4671 TOLI	T	1962	–27.7	949
C. martiana Engl.	Daly D. *et al.* 48965 HUA	H	1987	–27.4	1,500
C. martiana Engl.	Roldan A. *et al.* 113601 HUA	T	1992	–30.7	100
C. martiana Engl.	Ramirez J. *et al.* 19394 JAUM	E	1986	–27.3	770
C. microstemon Planch. & Triana	Botero L. *et al.* 2602 TOLI	T	1988	–32.8	2,000
C. microstemon Planch. & Triana	Gomez *et al.* 8623 TOLI	T	2006	–32.1	1,400
C. minor L.	Lozano G. *et al*. 70627 FMB	T	1995	–28.5	1,000
C. minor L.	Mora *et al.* 26981 HPUJ	T	2000	–28.7	1,370
C. minor L.	Villanueva B. *et al.* 12210 TOLI	T	2012	–25.4	539
C. minor L.	Villanueva B. *et al.* 12218 TOLI	T	2015	–26.3	539
C. minor L.	Villanueva B. *et al.* 12232 TOLI	T	2012	–24.9	539
C. minor L.	Zarucchi J. *et al.* 6890 CHOCO	T	1988	–24.6	875
C. minor L.	Cediel J. *et al.* 10468 CHOCO	T	1992	–31.5	80
C. minor L.	Ramirez B. *et al.* 36285 CAUP	T	2012	–30.9	1,200
C. minor L.	Macias D. *et al.* 25888 CAUP	T	2007	–27.2	1,130
C. minor L.	Macias D. *et al.* 29076 CAUP	T	2007	–20.6	1,170
C. minor L.	Figueroa V. *et al.* 55703 CUVC	T	2010	–25.9	970
C. minor L.	Cuatrecasas J. *et al*. 22949 VALLE	T	1946	–24.5	1,000
C. minor L.	Escobar P. *et al*. 391571 VALLE	T	1993	–27.8	1,100
C. minor L.	Cuadros H. *et al.* 2385 JBGP	T	1983	–27.9	1,300
C. minor L.	Cuadros H. *et al.* 4886 JBGP	T	1986	–21.2	900
C. minor L.	McPherson G. *et al.* 6849 JBGP	E	1986	–28.7	1,100
C. aff *minor* L. (*C. macropoda*) ?	Sanchez D. *et al.* 9987 HUA	T	1988	–26.8	1,550
C. aff *minor* L. (*C. macropoda*) ?	Sanchez D. *et al.* 10699 HUA	T	1980	–14.2	160
C. aff *minor* L. (*C. eugenioides*) ?	Mendoza H. *et al.* 17283 FMB	T	1997	–27.7	1,200
C. mocoensis Cuatrec.	Acevedo C. *et al.* 38972 FMB	T	1993	–27.1	1,950
C. mocoensis Cuatrec.	Pino N. *et al.* 12579 CHOCO	T	2000	–30.9	100
C. mocoensis Cuatrec.	Pino N. *et al.* 12593 CHOCO	T	2004	–32.6	100
C. mocoensis Cuatrec.	Juncosa A. *et al.* 2225 CHOCO	T	1984	–29.7	50
C. mocoensis Cuatrec.	Forero E. *et al.* 1590 CHOCO	T	1979	–32.7	79
C. mocoensis Cuatrec.	Pino N. *et al.* 12525 CHOCO	T	2004	–31.9	100
C. mocoensis Cuatrec.	Ramirez B. *et al.* 1917 CAUP	T	1991	–27.3	2,200
C. mocoensis Cuatrec.	Ramirez B. *et al.* 22245 CAUP	T	2012	–32.4	1,150
C. mocoensis Cuatrec.	Zak V. *et al.* 8498 JBGP	E	1987	–30.8	1,800

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C. monantha Cuatrec.	Tuberquía D. *et al.* 65527 HUA	T	1983	–25.8	1,600
C. monantha Cuatrec.	Betancur J. *et al.* 55869 HUA	T	1988	–27.9	2,410
C. monantha Cuatrec.	Betancur J. *et al.* 55868 HUA	T	1988	–28.3	2,350
C. monantha Cuatrec.	Zapata D. *et al.* 62265 JAUM	T	2014	–26.2	2,722
C. multiflora Kunth	Prieto C. *et al.* 66014 FMB	T	2002	–27.7	3,250
C. multiflora Kunth	Stevenson P. *et al*. GUAC – 197 GUAC	H	1976	–25.8	1,900
C. multiflora Kunth	Stevenson P. *et al*. GUAC – 382 GUAC	T	2006	–29.2	1,900
C. multiflora Kunth	Stevenson P. *et al*. GUAC – 507 GUAC	T	2006	–29.9	1,900
C. multiflora Kunth	Stevenson P. *et al*. GUAC – 120 GUAC	H	2005	–30.0	1,900
C. multiflora Kunth	Stevenson P. *et al*. GUAC – 668 GUAC	T	2007	–25.0	1,900
C. multiflora Kunth	Stevenson P. *et al*. GUAC – 468 GUAC	T	2006	–29.1	1,900
C. multiflora Kunth	Vargas O. *et al.* 3164 ANDES	T	2005	–21.7	3,000
C. multiflora Kunth	Silva H. *et al.* 831 HPUJ	T	1948	–25.9	1,600
C. multiflora Kunth	Renjifo L. *et al.* 830 HPUJ	T	1989	–26.5	2,700
C. multiflora Kunth	Pavayeau L. *et al.* 828 HPUJ	T	1993	–25.1	2,620
C. multiflora Kunth	Bernal Y. *et al.* 829 HPUJ	T	2011	–25.7	1,908
C. multiflora Kunth	Casas A. *et al.* 21140 HPUJ	T	2004	–30.5	2,850
C. multiflora Kunth	Vidal A. *et al.* 12882 HPUJ	T	2014	–26.2	2,350
C. multiflora Kunth	Espina H. *et al*. 3894 CHOCO	T	1985	–29.6	12
C. multiflora Kunth	Hartman D. *et al.* 22617 CUVC	T	ND	–26.9	3,200
C. multiflora Kunth	Stevenson P. *et al*. GUAC – 139 GUAC	T	2005	–28.3	1,800
C. multiflora Kunth	Zarucchi J. *et al.* 6623 CHOCO	T	1987	–23.9	2,370
C. multiflora Kunth	Zarucchi J. *et al.* 6786 CHOCO	T	1987	–23.6	2,380
C. multiflora Kunth	Costa A. *et al.* 10433 CAUP	T	2006	–29.5	3,264
C. nemorosa G.Mey. (syn *C. bicolor*)	Daly D. *et al.* 18611 CUVC	E	1989	–33.2	30
C. niambiensis Pipoly, Cogollo & M.S. González	Ramirez B. *et al.* 8130 CAUP	T	1995	–29.0	560
C. niambiensis Pipoly, Cogollo & M.S. González	Ramirez B. *et al.* 10503 CAUP	T	1995	–33.3	560
C. nigrolineata P.F.Stevens, confirmed by B.E. Hammel	Pipoly J.J. *et al.* 15445 FMB	E	1991	–15.9	120
C. nigrolineata P.F.Stevens	Stevenson P. *et al.* 1272 ANDES	H	1994	–31.6	350
C. nigrolineata P.F.Stevens, confirmed by B.E. Hammel	Gentry A. *et al.* 18420 JAUM	E	1977	–16.9	120
C. nutans Planch. & Triana	Cuatrecasas J. *et al.* 19970 VALLE	T	1946	–28.2	10
C. obovata (Spruce ex Planch. & Triana) Pipoly	Petter M. *et al.* 8667 HPUJ	T	1995	–26.4	51
C. octandra (Poepp.) Pipoly	Lopez R. *et al.* 46357 COAH	T	1999	–31.6	200
C. octandra (Poepp.) Pipoly	Cuatrecasas J. *et al.* 16265 VALLE	T	1944	–29.6	500
C. octandra (Poepp.) Pipoly	Cuatrecasas J. *et al*. 21231 VALLE	T	1946	–28.7	600
C. octandra (Poepp.) Pipoly	Monsalve M. *et al.* 7256 JAUM	T	1989	–33.8	100
C. octandra (Poepp.) Pipoly	Monsalve M. *et al.* 7282 JAUM	T	1989	–29.9	100
C. octopetala Cuatrec.	Medina T. *et al.* 7917 TOLI	T	2002	–28.3	1,200
C. octopetala Cuatrec.	Medina T. *et al.* 79171 TOLI	T	2002	–25.6	1,200
C. octopetala Cuatrec.	Gentry A. *et al.* 22857 CUVC	T	1985	–29.4	2,020
C. octopetala Cuatrec.	Gentry A. *et al.* 22736 CUVC	T	1985	–29.1	1,960
C. octopetala Cuatrec.	Gentry A. *et al.* 22736 CUVC	T	1985	–30.8	1,960
C. octopetala Cuatrec.	Pipoly J.J. *et al.* 41151 JAUM	H	1997	–28.7	1,350
C. orthoneura Standl.	Arthur S. *et al.* 1408 FMB	T	1972	–26.6	1,800
C. orthoneura Standl.	Silva H. *et al.* 832 HPUJ	T	1948	–24.8	1,600
C. orthoneura Standl.	Esquivel H. *et al.* 9664 TOLI	T	2010	–26.8	1,100
C. orthoneura Standl.	Esquivel H. *et al.* 5629 TOLI	T	2000	–26.3	1,170
C. orthoneura Standl.	Esquivel H. *et al.* 7728 TOLI	T	2000	–27.2	1,600
C. orthoneura Standl.	Esquivel H. *et al.* 2849 TOLI	T	1998	–27.2	2,100
C. orthoneura Standl.	Ortegon N. *et al.* 374406 CAUP	T	2013	–31.2	1,800
C. ovalis Cuatrec.	Ramirez J. *et al.* 55084 FMB	T	1991	–31.9	1,350
C. paisarum Pipoly	Luteyn J. *et al.* 42065 HUA	E	1987	–30.5	861

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C. pallida Engl.	Gaviria J. *et al.* 165371 HUA	T	2004	–28.7	1,550
C. pallida Engl. (syn *C. vaginata*)	Mendoza H. *et al*. 23285 FMB	H	1998	–30.5	1,400
C. pallida Engl. (syn *C. vaginata*)	Silverstone P. *et al.* 22369 CUVC	H	1991	–29.9	1,025
C. palmana Standl.	Gentry A. *et al.* 19672 CUVC	T	1984	–29.0	1,180
C. palmana Standl.	Rosalba D. *et al.* 25085 JAUM	T	1997	–26.9	1,950
C. palmicida Rich. ex Planch. & Triana	Cardenas D. *et al.* 21659 FMB	H	1990	–26.9	800
C. palmicida Rich. ex Planch. & Triana	Sanchez M. *et al.* 6837 ANDES	T	1997	–32.3	200
C. palmicida Rich. ex Planch. & Triana	Stevenson P. *et al*. 3316 ANDES	H	1988	–29.1	350
C. palmicida Rich. ex Planch. & Triana	Juncosa A. *et al.* 2667 CHOCO	T	1984	–30.0	910
C. palmicida Rich. ex Planch. & Triana	Cabrera I. *et al.* 22485 CUVC	T	1975	–27.9	1,050
C. palmicida Rich. ex Planch. & Triana	Cabrera I. *et al.* 22449 CUVC	T	1975	–30.1	1,050
C. palmicida Rich. ex Planch. & Triana	Cardona F. *et al.* 171786 HUA	T	2009	–27.2	550
C. panapanari (Aubl.) Choisy	Pipoly J.J. *et al*. 34133 FMB	E	1990	–30.0	300
C. panapanari (Aubl.) Choisy	Sanchez M. *et al.* 6602 ANDES	T	1997	–30.9	122
C. penduliflora Engl.	Aldana A. *et al.* P–11084 GUAC	T	ND	–28.6	1,900
C. penduliflora Engl.	Escobar L. *et al*. 52103 CUVC	T	1982	–26.5	2,400
C. penduliflora Engl.	Giraldo D. *et al.* 77005 HUA	T	1991	–26.7	1,300
C. penduliflora Engl.	Mendoza H. *et al*. 51644 JAUM	H	2001	–31.3	350
C. pentandra Cuatrec.	Gonzales C. *et al.* 11909 CAUP	T	1999	–31.2	1,500
C. pentandra Cuatrec.	Ramirez *et al.* 21914 CAUP	T	1995	–25.2	2,150
C. pentandra Cuatrec.	Bedoya M. *et al.* 420 CAUP	T	1991	–27.7	2,300
C. pentandra Cuatrec.	Oliver M. *et al.* 30825 CAUP	T	1999	–31.0	1,320
C. pentandra Cuatrec.	Ramirez B. *et al.* 2191 CAUP	T	1995	–28.4	1,850
C. pentandra Cuatrec.	Escobar L. *et al*. 51595 CUVC	T	1984	–27.6	1,730
C. pentarhyncha Planch. & Triana	Killip E. *et al.* 39165 VALLE	T	1944	–29.9	17
C. pentarhyncha Planch. & Triana	Dryander *et al.* 2708 VALLE	T	1943	–26.1	1,800
C. petiolaris Planch. & Triana	Vasquez R. *et al.* 8430 JBGP	H	1986	–29.9	150
C. polyantha Cuatrec.	Zarucchi J. *et al.* 792 CHOCO	T	ND	–29.5	792
C. polyantha Cuatrec.	Brant A. *et al.* 5873 CHOCO	T	1979	–26.6	45
C. pseudohavetia Planch. & Triana	Zarucchi J. *et al.* 44015 JAUM	T	1988	–26.7	1,930
C. pseudomangle Planch. & Triana	Zak V. *et al.* 8636 JBGP (Ecuador)	T	1987	–27.2	2,450
C. pseudomangle Planch. & Triana	Zak V. *et al.* 8175 JBGP (Ecuador)	T	1987	–26.9	2,300
C. pseudomangle Planch. & Triana	Zak V. *et al.* 8486 JBGP (Ecuador)	T	1987	–26.0	2,100
C. pseudomangle Planch. & Triana	Zak V. *et al.* 8180 JBGP (Ecuador)	T	1987	–26.1	2,200
C. pseudomangle Planch. & Triana	Zak V. *et al.* 8650 JBGP (Ecuador)	T	1987	–26.3	2,100
C. renggerioides Planch. & Triana	Acevedo C. *et al.* 55426 FMB	T	1993	–27.7	1,950
C. renggerioides Planch. & Triana	Aldana A. *et al.* P3–1212 GUAC	T	ND	–28.2	1,900
C. renggerioides Planch. & Triana	Stevenson P. *et al*. 3631 ANDES	H	1995	–30.8	350
C. rosea Jacq.	Gonzalez R. *et al.* 102989 FMB	T	2013	–26.6	910
C. rosea Jacq.	Campo D. *et al.* 42 VALLE	T	1995	–24.8	950
C. rosea Jacq.	Escobar E. *et al*. 42.1 VALLE	T	1995	–22.2	950
C. rosea Jacq.	Escobar E. *et al*. 183 VALLE	T	1995	–26.5	950
C. rotundata Standl.	Zak V. *et al.* 8419 JBGP (Ecuador)	T	1987	–24.7	1,800
C. salvinii Donn. Sm.	Cuadros H. *et al.* 3909 JBGP	T	1985	–23.9	2,300
C. salvinii Donn. Sm.	Miller J. *et al.* 8017 JBGP (Mexico)	E	1987	–26.9	2,100
C. schomburgkiana (Planch. & Triana) Benth. ex Engl.	Mendoza H. *et al.* 16212 FMB	H	1997	–27.5	1,500
C. schomburgkiana (Planch. & Triana) Benth. ex Engl.	Parrado A. *et al.* 39666 COAH	T	1998	–31.0	160
C. schomburgkiana (Planch. & Triana) Benth. ex Engl.	Echeverry R. *et al.* 55699 COAH	T	2001	–30.3	120
C. schomburgkiana (Planch. & Triana) Benth. ex Engl.	Londoño A. *et al.* 31732 COAH	H	2006	–29.4	150
C. schomburgkiana (Planch. & Triana) Benth. ex Engl.	Cordero Z. *et al.* 13534 COAH	E	2006	–31.2	280
C. schomburgkiana (Planch. & Triana) Benth. ex Engl.	Cortes R. *et al.* 16662 COAH	T	1995	–26.4	800
C. schomburgkiana (Planch. & Triana) Benth. ex Engl.	Cardenas D. *et al.* 31434 COAH	E	1997	–34.5	200

Accepted name	Collector(s), voucher number, herbarium, and country	Habit	Date	$\delta^{13}C$ [‰]	Elev [m]
C. schomburgkiana (Planch. & Triana) Benth. ex Engl.	Torobo J. *et al.* 28302 COAH	E	1951	–26.9	1,300
C. schomburgkiana (Planch. & Triana) Benth. ex Engl.	Echeverry R. *et al.* 2374 TOLI	T	1976	–24.1	1,200
C. schomburgkiana (Planch. & Triana) Benth. ex Engl.	Camacho J. *et al.* 58855 CUVC	T	1992	–25.5	544
C. schultesii Maguire	Zak V. *et al.* 8169 JBGP (Ecuador)	T	1987	–29.5	1,720
C. spathulifolia Engl.	Matapi A. *et al.* 0 FMB	T	1989	–28.6	929
C. spathulifolia Engl.	Galeano M. *et al.* 102 HPUJ	T	1993	–26.0	570
C. spathulifolia Engl.	Echeverry R. *et al.* 518 TOLI	T	1962	–26.9	280
C. sphaerocarpa Planch. & Triana	Smith D. *et al.* 8975 JBGP	H	1984	–26.1	2,700
C. stenophylla Standl.	Stevenson P. *et al*. GUAC – 756 GUAC	T	2007	–26.4	1,900
C. stenophylla Standl.	Cogollo A. *et al.* 26529 JAUM (Ecuador)	E	1992	–33.0	1,340
C. tequendamae Cuatrec.	Prieto A. *et al.* 75942 FMB	T	2004	–29.7	2,250
C. tetragona Pipoly & Cogollo	Ramirez B. *et al.* 10335 CAUP	T	1995	–26.9	1,500
C. tetragona Pipoly & Cogollo	Ramirez B. *et al.* 7454 CAUP	T	1995	–27.4	1,800
C. thurifera Planch. & Triana	Cogollo A. *et al.* 26784 JAUM	T	1993	–28.6	1,450
C. thurifera Planch. & Triana	Zak V. *et al.* 8500 JBGP (Ecuador)	T	1987	–25.5	1,600
C. torresii Standl.	McPherson G. *et al.* 6836 JBGP (Panama)	E	1986	–28.3	1,100
C. triflora Cuatrec.	Barbosa C. *et al.* 6406 FMB	T	1983	–29.9	730
C. triflora Cuatrec.	Forero R. *et al.* 1478 CHOCO	T	1979	–30.5	45
C. triflora Cuatrec.	Espina J. *et al*. 3955 CHOCO	T	1985	–31.8	12
C. triflora Cuatrec.	Uribe A. *et al.* 25597 HUA	T	1985	–27.7	1,850
C. triflora Cuatrec.	Martinez G. *et al.* 60550 HUA	E	1987	–29.6	1,750
C. triflora Cuatrec. (syn *C. discolor*)	Ruiz N. *et al.* 70416 FMB	T	1995	–28.7	1,800
C. triflora Cuatrec. (syn *C. discolor*)	Ruiz N. *et al.* 10778 CAUP	T	1995	–27.6	1,700
C. triflora Cuatrec. (syn *C. discolor*)	Ramirez B. *et al.* 405 CAUP	T	1993	–26.2	2,640
C. triflora Cuatrec. (syn *C. discolor*)	Ruiz N. *et al.* 144246 HUA	T	1995	–29.2	200
C. triflora Cuatrec. (syn *C. discolor*)	Murillo I. *et al.* 109856 HUA	T	1996	–29.4	2,400
C. trochiformis Vesqne	Stevenson P. *et al*. GUAC – 653 GUAC	T	2007	–28.5	1,900
C. trochiformis Vesqne	Cardona F. *et al.* 60103 HUA	E	1988	–29.7	2,000
C. trochiformis Vesqne	Urrea L. *et al.* 188156 HUA	T	2009	–31.8	2,056
C. trochiformis Vesqne	Correa M. *et al.* 41738 JAUM	T	1996	–25.9	2,350
C. uvitana Pittier	Hoyos S. *et al.* 15461 CHOCO	T	2005	–17.7	43
C. uvitana Pittier	Hoyos S. *et al.* 15460 CHOCO	T	2005	–16.4	43
C. veneralensis Cuatrec. ?	Cuatrecasas J. *et al*. 14039 VALLE	E	1943	–28.8	20
C. veneralensis Cuatrec.	Roldan R. *et al.* 3263 HUA	T	2000	–14.9	500
C. veneralensis Cuatrec.	Fonnegra R. *et al.* 7314 HUA	T	2000	–14.8	500
C. venulosa Cuatrec.	Acevedo C. *et al.* 55410 FMB	T	1993	–25.3	1,555
C. venulosa Cuatrec.	Cordoba A. *et al.* 10075 CHOCO	T	1984	–30.2	43
C. venulosa Cuatrec.	Cordoba A. *et al.* 4635 CHOCO	T	1986	–29.9	1,220
C. venulosa Cuatrec.	Casas C. *et al*. 39757 CAUP	T	2010	–32.9	1,450
C. venulosa Cuatrec.	Hurtado *et al*. 29422 CAUP	T	2005	–30.7	2,200
C. venulosa Cuatrec.	Cuatrecasas J. *et al.* 15639 VALLE	T	1943	–31.7	1,400
C. venusta Little	Ramirez B. *et al.* 28211 CAUP	T	2002	–30.6	65
C. venusta Little	Cabrera I. *et al.* 22625 CUVC	T	1975	–28.4	1,900
C. venusta Little	Fernandez J. *et al.* 12495 HUA	T	1995	–33.8	680
C. venusta Little	Fernandez J. *et al.* 124951 HUA	T	1995	–34.3	680
C. venusta Little	Pipoly J.J. *et al.* 41198 JAUM	E	1997	–30.1	1,350
C. viscida Engl.	Zarucchi J. *et al.* 6202 CHOCO	E	1988	–26.3	800
C. viscida Engl.	Shepherd J. *et al.* 6362 HUA	H	1977	–30.9	400
C. viscida Engl.	Castaño N. *et al.* 157178 HUA	T	2001	–27.0	150
C. volubilis Kunth	Hartman D. *et al.* 22618 CUVC	T	1997	–28.1	2,500
C. volubilis Kunth	Cuatrecasas J. *et al*. 19250 VALLE	T	1944	–27.3	1,122
C. volubilis Kunth	Cuatrecasas J. *et al*. 23347 VALLE	T	1946	–28.1	1,824

Accepted name	Collector(s), voucher number, herbarium, and country	Habit	Date	$\delta^{13}C$ [‰]	Elev [m]
C. volubilis Kunth	Giraldo D. *et al.* 83279 HUA	T	1992	–22.7	2,000
C. weberbaueri Engl.	Tupac J. *et al.* 47873 CUVC	T	1994	–27.6	1,850
C. weberbaueri Engl.	Tupac J. *et al.* 27594 CUVC	T	1994	–24.9	1,850
C. weberbaueri Engl.	Giraldo D. *et al.* 84971 HUA	T	1992	–29.0	1,800
Arawakia oblanceolata (Rusby) L. Marinho (syn *C. oblanceolata*)	Zuluaga S. *et al.* 3040 FMB	T	ND	–34.4	600

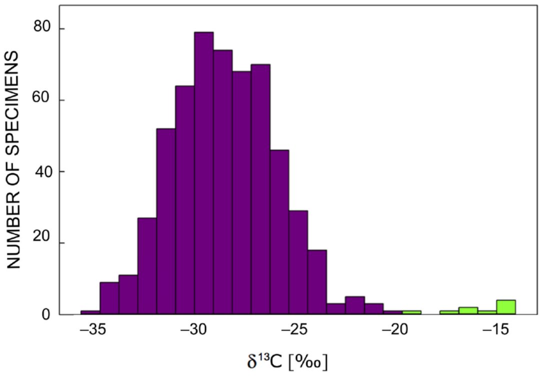

Fig. 2. Frequency histogram of $\delta^{13}C$ values of 568 specimens of 114 largely Colombian species of *Clusia*. *Green bars* denote specimens with $\delta^{13}C$ values less negative than –20‰, indicating CO_2 fixation predominantly by CAM. *Purple bars* denote specimens with $\delta^{13}C$ values more negative than –20‰, indicating CO_2 fixation predominantly or exclusively by the C_3 pathway.

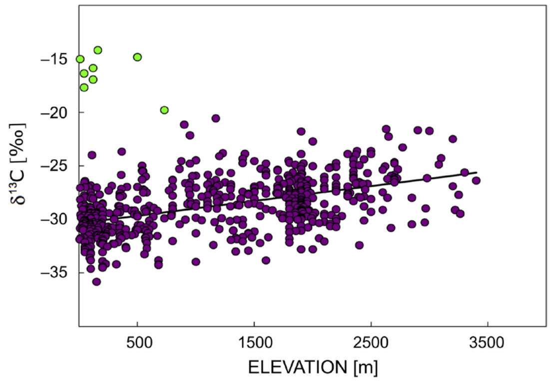

Fig. 3. Elevation versus $\delta^{13}C$ values for 568 samples of largely Colombian species of *Clusia* (including multiple specimens for most species). For the $\delta^{13}C$ values more negative than –20‰ (*purple symbols*), $\delta^{13}C$ significantly increased with increasing elevation (r^2 = 0.23; P<0.0001). Equation: $\delta^{13}C$ = 0.0014 × × elevation – 30.42.

Samples were collected from 0 to 3,500 m a.s.l. (Fig. 3). A large group of samples were from 0 to 500 m and included those from the wet forests of the Pacific region of the Chocó/Darien biodiversity hotspot. Samples with isotopic signatures indicative of strong CAM were only collected at low elevations. $\delta^{13}C$ values within the predominantly C_3 isotopic cluster (values more negative than –20‰) significantly increased with increasing elevation (R^2 = 0.23; P<0.0001; Fig. 3)

Largely due to the scarcity of isotope values less negative than –20‰ in our study on the Colombian *Clusia* flora, we did not find evidence that strong CAM was more frequent in epiphytic than in terrestrial plants (*Chi-squared* test: χ^2 = 6.25, P=0.18; Fig. 4*A*). Furthermore, there was no record of CAM-type isotopic signatures in hemiepiphytic plants. Adding the data from the *Clusia* $\delta^{13}C$ surveys in Panama (Holtum *et al.* 2004) and Mexico (Vargas-Soto *et al.* 2009), we ended up with 49 terrestrial CAM plants, 15 epiphytic CAM plants, and 8 hemiepiphytic CAM plants (CAM meaning strong CAM), *vs*. 666 terrestrial C_3 plants, 114 epiphytic C_3 plants, and 70 hemiepiphytic C_3 plants (C_3 meaning 100% C_3 or predominantly C_3) (Fig. 4*B*). Again, despite this larger data set, there was no evidence that strong CAM was favored in epiphytic *vs*. hemiepiphytic and terrestrial plants (χ^2 = 4.47, P=0.107; Fig. 4*B*). Most specimens with $\delta^{13}C$ values typical of CAM were found at low elevations regardless of their growth habit (Fig. 4*C*,*D*). Consistent with the *Chi-squared* test, $\delta^{13}C$ values from this survey together with those in Holtum *et al.* (2004) and Vargas-Soto *et al.* (2009) did not differ between terrestrial, epiphytic, and hemiepiphytic *Clusia* specimens from each of four elevational ranges between 0 and 2,000 m.a.s.l. (Table 2). Furthermore, there was no significant interaction between elevation and growth habit (F = 0.92, DF = 6, P=0.48; Table 2).

Overall, we document a total of 156 species with photosynthetic pathway information based on carbon isotopes, and/or gas exchange, and/or tissue acidity (Table 1S), representing 48% of all *Clusia* species (POWO 2021). For 35 of the 156 species, there is evidence of CAM, *i.e.*, 22% of the *Clusia* species studied thus far are capable of some degree of CAM. Of the 153 species of *Clusia* known to occur in Colombia, photosynthetic pathway information is available for 109 species, 15 of which (about 14%) show evidence of CAM (Table 1S).

Discussion

Our study represents the largest $\delta^{13}C$ survey of South American *Clusia* species to date. The vast majority of samples had $\delta^{13}C$ values below (more negative than) the –20‰ threshold, indicating that leaf carbon was mainly or exclusively derived from C_3 photosynthetic CO_2

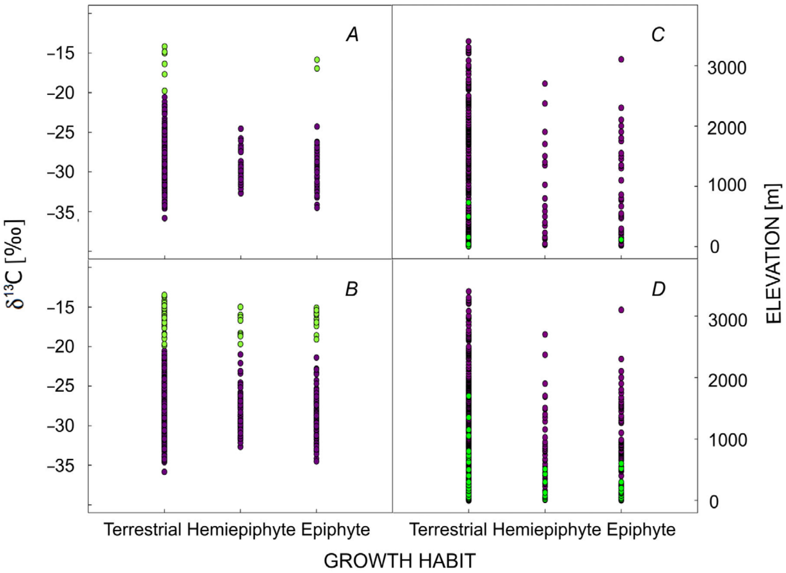

Fig. 4. Relationship between $\delta^{13}C$ value and growth habit (*A*,*B*) and elevational distribution of specimens with different growth habit (*C*,*D*). Panels at the top (*A*,*C*) show the Colombian dataset (this study), including 476 terrestrial, 56 epiphytic, and 37 hemiepiphytic plants. Panels at the bottom (*B*,*D*) show the Colombian dataset plus data from Panama (Holtum *et al.* 2004) and Mexico (Vargas-Soto *et al.* 2009), including 706 terrestrial, 125 epiphytic, and 78 hemiepiphytic plants. *Green symbols* indicate $\delta^{13}C$ values less negative than –20‰, indicating CO_2 fixation predominantly by CAM, and *purple symbols* indicate $\delta^{13}C$ values more negative than –20‰, indicating CO_2 fixation predominantly or exclusively by the C_3 pathway.

Table 2. Values of $\delta^{13}C$ [‰] by growth habit and elevation. Data come from this study, Holtum *et al.* (2004), and Vargas-Soto *et al.* (2009). Data are means ± standard error. Numbers in parenthesis indicate the number of specimens analyzed for each growth habit and elevation category. Results from the nonparametric analysis comparing $\delta^{13}C$ [‰] values between growth habits at different elevations are presented in the last column. Result from a two-way *ANOVA* of aligned ranks exploring the interaction effect of elevation and growth habit are shown at the bottom of the table.

Elevation [m.a.s.l.]	Epiphytic	Hemiepiphytic	Terrestrial	*Wilcoxon*/*Kruskal-Wallis* test values
0–500	–26.8 ± 0.8 (57)	–27.2 ± 0.9 (39)	–27.2 ± 0.4 (210)	χ^2 = 0.07; *DF* = 2; *P*=0.96
500–1,000	–27.2 ± 0.6 (34)	–26.5 ± 0.8 (19)	–27.5 ± 0.3 (133)	χ^2 = 1.25; *DF* = 2; *P*=0.53
1,000–1,500	–28.4 ± 0.8 (15)	–28.3 ± 0.9 (11)	–27.1 ± 0.3 (104)	χ^2 = 3.78; *DF* = 2; *P*=0.15
1,500–2,000	–28.2 ± 0.6 (15)	–27.7 ± 0.9 (7)	–27.6 ± 0.2 (155)	χ^2 = 0.50; *DF* = 2; *P*=0.78.
All elevations	–27.3 ± 0.4 (121)	–27.2 ± 0.5 (76)	–27.3 ± 0.2 (602)	χ^2 = 0.73; *DF* = 2; *P*=0.69
Growth habit effect (*F* = 0.12; *DF* = 2; *P*=0.89)				
Elevation effect (*F* = 3.41; *DF* = 3; *P*=0.017)				
Growth habit × elevation effect (*F* = 0.92; *DF* = 6; *P*=0.48)				

uptake during the daytime. Only five of 114 species in our survey had specimens with $\delta^{13}C$ values above (less negative than) the –20‰ threshold typical of strong CAM. *C. uvitana* was among them, for which the presence of CAM, especially facultative CAM, is well established (Winter *et al.* 1992, Zotz and Winter 1993, 1994a,b). In the other four species, *i.e.*, *C. cochliformis* (–19.8‰), *C. eugenioides* (–15.0, –27.7, and –28.6‰), *C. nigrolineata* (–15.9, –17.0, and –31.6‰), and *C. veneralensis* (–14.8, –14.9, and –28.8‰), features of CAM have not been demonstrated before and we have tentatively included all four species into the CAM category in Table 1S. However, in three of the species, we also noted specimens with C_3-type isotopic signatures. There are two possible explanations for these contrasting isotopic signatures: (*1*) some specimens may have been identified incorrectly (Goodwin *et al.* 2015), and (*2*) provided species identity is correct, plants exhibit facultative CAM, *i.e.*, plants can operate in both the C_3 mode when conditions are favorable (in terms of water supply), or in the CAM-mode when experiencing water-deficit stress. We were able to have the species identity independently verified for two vouchers of *C. nigrolineata* with CAM-type isotopic signatures and for one voucher of *C. veneralensis* which exhibited a C_3-type carbon isotopic signature (Barry Hammel, personal communication). For logistic reasons, independent evaluation of the other specimens of *C. veneralensis* and *C. eugenoides* has not yet been possible. Conclusions about the presence of facultative CAM, the proof of which would require physiological measurements on living plants, are therefore premature. Nonetheless, for the time being, it seems safe to consider at least *C. nigrolineata* as 'new' *Clusia* species with CAM.

Remarkably, several well-studied species for which there is ample previous evidence of CAM activity had $\delta^{13}C$ values below the –20‰ threshold indicating that despite their capacity to exhibit CAM, C_3 photosynthetic CO_2 fixation in the light was the major contributor to carbon gain. For example, the iconic *C. rosea* has long been considered a species with strong obligate CAM based on high rates of nocturnal net CO_2 uptake and high levels of nocturnal acid increase, both *in situ* and in the laboratory (Ball *et al.* 1991, Franco *et al.* 1994, Haag-Kerwer *et al.* 1996, Borland *et al.* 1998). Furthermore, $\delta^{13}C$ values as high as –14.5‰ have been consistently reported for this species, although $\delta^{13}C$ values in the C_3 range were also noted. In this study, the mean $\delta^{13}C$ of four specimens was –25.0‰ (–22.2 to –26.5‰) and thus entirely within the C_3 range. By contrast, leaves collected from different locations in Mexico had a mean $\delta^{13}C$ of –19.0‰ (–14.5 to –25.8‰, *n* = 7), with the two lowest values from plants at relatively high elevations (Vargas-Soto *et al.* 2009), and in a Panamanian study, $\delta^{13}C$ ranged from –16.7 to –27.5‰, with a mean of –21.2‰ (*n* = 6) (Holtum *et al.* 2004). $\delta^{13}C$ values of northern Venezuelan *C. rosea* were between about –15.0 and –19.2‰ (Popp *et al*. 1987), and a study in southern Florida revealed $\delta^{13}C$ values mostly around –16.5‰ (Sternberg *et al.* 1987).

C. alata is another species previously considered to exhibit obligatory CAM, with high rates of dark CO_2 fixation, substantial nocturnal increases in acid content (Franco *et al*. 1990, Kornas *et al*. 2009), and CAM-type $\delta^{13}C$ values as high as –15.7‰ (Popp *et al.* 1987, Franco *et al*. 1994), although in one particular study, *C. alata* was referred to as 'supposedly obligate CAM species' (Walter *et al.* 2008) because the authors could not detect high CAM activity. With 15 specimens, *C. alata* was extremely well presented in our study. To our surprise, all specimens had $\delta^{13}C$ values below the –20‰ threshold with a mean of –26.0‰ and a range from –21.8 to –32.2‰ (Fig. 1S). It seems that the sites in Colombia where the samples of *C. rosea* and *C. alata* were collected were considerably less stressful in terms of water supply and light exposure than the collection sites in Mexico, Panama, Venezuela, and elsewhere.

Another well-sampled species (*n* = 16) in our survey is *C. minor*, probably the most-studied of all *Clusia* species. It is known for its highly flexible photosynthetic pathway physiology and capacity to exhibit facultative CAM (Borland *et al*. 1993, 1998; Lüttge 2006). In our study, the mean $\delta^{13}C$ was –26.6‰ with a range from –21.2 to –31.5‰. This result is consistent with previously published isotope data for *C. minor* from Mexico (mean –26.7‰, range –23.5 to –28.6‰, *n* = 7) (Vargas-Soto *et al*. 2009), and Panama (mean –26.7‰, range –24.0 to –29.1‰, *n* = 3). Thus, although CAM does contribute to carbon gain in the natural habitats of *C. minor* during the dry season (Borland *et al*. 1992), during the annual cycle of leaf growth most carbon is derived *via* C_3 photosynthesis. A year-round study of *C. minor* in Panama revealed nocturnal acid accumulation during the four-month dry season only. For the remainder of the year, no nocturnal acid accumulation was observed (K. Winter, unpublished).

Our research highlights, as other studies have done before (*e.g.*, Winter *et al.* 2015), the limitations of the carbon isotope technique in species surveys about the presence/absence of CAM. While many species can be rapidly screened and those with strong CAM fairly conclusively identified, it is not possible to distinguish between C_3–CAM species and regular C_3 species. In *Clusia*, where many species express CAM only weakly, and if strongly often only periodically, this is a serious issue that can only be overcome by studying CO_2 gas exchange and diel acid levels in live plants as well. For example, when using acid titrations and gas exchange, Holtum *et al.* (2004), Winter *et al.* (2009), and Winter and Holtum (2014) established weakly/periodically expressed CAM in *C. croatii*, *C. cylindrica*, *C. fructiangusta*, *C. lineata*, *C. odorata*, *C. pratensis*, *C. quadrangula*, and *C. valeroi*, although in all these species $\delta^{13}C$ values were C_3-like, *i.e.*, more negative than –20‰.

Because of the paucity of $\delta^{13}C$ values less negative than –20‰, the frequency histogram of Fig. 2 does not show the bimodal distribution of $\delta^{13}C$ values that has been observed previously in at least seven plant families containing large numbers of C_3 and CAM species such as the Bromeliaceae (Crayn *et al.* 2015). In Fig. 2, frequency refers to 'the number of samples' and not 'the number of species' as in previously published frequency histograms for other taxa. This 'number-of-sample approach', also employed in the recent analyses of Messerschmid *et al.* (2021), can lead to strongly biased results when the number of samples per species is not standardized, and when, in the case of facultative CAM species, the conditions under which sample leaves developed, are not defined. On the other hand, in lineages containing species with high C_3–CAM plasticity such as *Clusia*, using species means of $\delta^{13}C$ values in frequency histograms is not a good option either, because this would not capture the full amplitude of $\delta^{13}C$ values in species exhibiting facultative CAM.

It may be tempting to suggest that some additional species in our survey have the capacity for CAM, *e.g.*, *C. chusqueae* (–21.6‰), *C. crenata* (–23.9‰), *C. ducuoides* (–23.3‰), and *C. inesiana* (–21.7‰), because of their $\delta^{13}C$ values on the right-hand side of the C_3 cluster (Fig. 2) close to the –20‰ threshold. However, these specimens were all collected at very high elevations (Table 1), and the relatively high $\delta^{13}C$ values probably result from the well-known effect elevation has on $\delta^{13}C$ values in C_3 plants independent of CAM (*see* Cernusak *et al.* 2013, Crayn *et al.* 2015). This trend towards less negative $\delta^{13}C$ values with increasing elevation can be seen in our data set for values more negative than –20‰ (Fig. 3). It is also worth noting that most *C. alata* samples in our survey were collected at very high elevations up to 3,200 m a.s.l. (Table 1, Fig. 1S). Such high elevations are, with few exceptions, generally not conducive to CAM functioning.

Conclusions: Colombia is a center of *Clusia* diversity but strongly expressed CAM does not seem to be common amongst its species. Our current estimate suggests that albeit about 14% of the Colombian *Clusia* species can perform CAM, even species with potentially high CAM capacity seem to depend mainly on C_3 photosynthesis for carbon gain in their natural Colombian habitats. This contrasts with the performance of CAM-exhibiting *Clusia* species in other parts of the neotropics where greater CAM engagement has been reported. Future studies on CAM presence/absence need to cover the remaining 52% of *Clusia* species in the neotropics that have not been examined yet and need to include physiological measurements of gas exchange and titratable acidity to detect weakly expressed and facultative CAM. To better understand the relationship between habitat conditions and CAM engagement, detailed studies of carbon isotope signatures of species such as *C. rosea* growing in a large range of habitats are warranted. These studies should be based on the broad sampling of multiple plants at each study site throughout the annual cycle and should be combined with observations of leaf phenology.

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