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REVIEW

Crassulacean Acid Metabolism 1975-2000, a check list*

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Abstract

A list of plant species documented over the past 25 years to exhibit Crassulacean Acid Metabolism (CAM) is presented. The list compiles all available information on these species including their growth habits, succulent parts, carbon isotope discrimination values, CAM types, CAM inducers, and CAM modifications.

Additional key words: angiosperms; CAM inducers; CAM modifications; CAM types; carbon discrimination; ferns; gymnosperms; habitat; phosphoenolpyruvate carboxylase.

Introduction

Although nocturnal CO_2 uptake and cell sap acidification have early been recognised as features of some succulent plants (Bonner and Bonner 1948, Bruinsma 1958), details of these phenomena in relation to CAM have only been documented four decades ago (Ranson and Thomas 1960). As active research revealed more details, a huge body of information on CAM has accumulated in the literature over the past 25 years. These details have extensively been reviewed (Kluge and Ting 1978, Osmond 1978, 1984, Osmond and Holtum 1981, Osmond *et al.* 1982, Ting and Gibbs 1982, Edwards and Walker 1983, Ting 1985, Winter 1985, Kluge 1987, Smith 1987, Griffiths 1988, Leegood and Osmond 1990, Smith and Bryce 1992, Leegood 1993, Winter and Smith 1996a,b). However, except for a few published lists of CAM plants related to a particular family (Keeley 1982, Griffiths and Smith 1983, Griffiths *et al.* 1986, Lüttge *et al.* 1986, Nobel 1988, Raven *et al.* 1988, Keeley 1996, Lüttge 1996, Smith and Winter 1996, Holtum and Winter 1999), or a region of the world (Osmond *et al.* 1975, Winter and Troughton 1978, 1985, Willert *et al.* 1979, 1983, Winter 1979, Earnshaw *et al.* 1987b, Griffiths 1988), information on CAM plants stayed scattered over the enormous CAM literature. The present paper aims at providing a detailed list of plant species documented to exhibit CAM. This list gives all available information related to the species such as growth habits, succulent parts, carbon isotope discrimination values, CAM types, CAM inducers, and CAM modifications.

Physiology and biochemistry of CAM

Plants assimilate atmospheric CO_2 *via* three metabolic pathways, namely C_3, C_4, and CAM. Contrary to the C_3 and C_4 pathways, CAM involves nocturnal CO_2 uptake and fixation by cytosolic phosphoenolpyruvate carboxylase (PEPC) into malic acid that is stored in the vacuole causing nocturnal cell sap acidification (Barkla and Pantoja 1996, Osmond *et al.* 1996, Lüttge 2000). During the subsequent light period, malic acid is released from the vacuole in the form of malate that is then decarboxylated leading to deacidification of cell sap, formation of pyruvate and/or phosphoenolpyruvate, and liberation of CO_2. Repeated acidification-deacidification cycles represent a characteristic physiological feature of CAM plants. The liberated CO_2 is then assimilated by ribulose-1,5-bisphosphate carboxylase oxygenase (RuBPCO) *via* the C_3 pathway under closed stomata (Black *et al.* 1996). The circadian pattern of CAM is probably regulated by irradiation (Carter *et al.* 1996), and transport across the vacuolar membrane may be influenced by temperature (Kluge *et al.* 1996, Smith *et al.* 1996). However, many CAM plants are able to take up CO_2 for a certain length of time during the onset and/or the end of the light period. These plants also fix this CO_2 directly *via* the C_3 pathway. Hence, the diurnal time course for CO_2 uptake in these plants includes four phases (Osmond *et al.* 1996, Winter and Smith 1996a,b,c). A variety of malate decarboxylating enzymes have been recognised in different CAM plants (Black *et al.* 1996). Recent research was directed to investigating gene expression (Dietz and

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Arbinger 1996, Krisch *et al.* 2000) and enzyme regulation (Kluge and Schomburg 1996, Nimmo 2000).

Carbon isotope discrimination of CAM

Discrimination against the carbon isotope ^{13}C during photosynthetic incorporation of the stable carbon isotopes ^{12}C and ^{13}C is a characteristic of the carboxylating enzyme (Bender *et al.* 1973, Osmond *et al.* 1973, Lerman 1975, Troughton 1979, Griffiths 1993). Some differences are related to diffusional fractionation (Griffiths 1993, Ehleringer and Osmond 1994). Due to small differences in ^{13}C abundance, very small amounts are measured, and discrimination results assessed by mass spectroscopy techniques are expressed as the carbon isotope ratio ($\delta^{13}C$) with values in parts per thousand (‰). The carboxylase of the C_3 pathway, RuBPCO, strongly discriminates against ^{13}C, whereas the carboxylase of the C_4 pathway, PEPC, discriminates less (Ehleringer and Osmond 1994). Hence, the $\delta^{13}C$ of plants falls in the range of –7 to –35 ‰, with C_4 plants having values of –7 to –15 ‰, CAM plants –10 to –22 ‰, and C_3 plants –20 to –35 ‰ (Ehleringer and Osmond 1994). Moreover, the $\delta^{13}C$ value is very useful for CAM research in determining the relative contribution of dark and light CO_2 fixation to the total carbon gain of the CAM plant (Ziegler 1996).

Types and modifications of CAM

Plants that predominantly exhibit the CAM pathway are commonly known as obligate CAM plants, and are said to have a constitutive type of CAM (Ting 1985, Winter 1985). In addition, C_3 and C_4 plants with an ability to switch their carbon metabolism to the CAM pathway are commonly known as C_3- and C_4-intermediates, and are said to exhibit an inducible type of CAM (Ting 1985, Winter 1985; cf. also Fernández *et al.* 1999). Inducers of CAM in such species may include developmental stage of the plant itself and/or stressful environmental conditions such as drought, salinity, temperature, and photoperiod (Olesen and Bailey 1995, Cushman and Bohnert 1996, Edwards *et al.* 1996, Guralnick and Strand 1996, Eastmond and Ross 1999, Malda *et al.* 1999). Furthermore, two modifications of CAM have been reported (Ting and Sipes 1985). One modification termed CAM-idling occurs when CAM plants become severely water stressed so that stomata close both day and night, and a low rate of cycling of organic acids through the CAM pathway occurs. With this low level of metabolism, biochemical activities of the plant are maintained until water becomes available and the plant recovers again (Rayder and Ting 1983a). In the second modification termed CAM-cycling, gas exchange occurs largely during the day as in C_3 plants, yet a diurnal cycling of organic acids similar to that of CAM is observed (Ting and Sipes 1985).

Ecophysiology of CAM

Plants exhibiting the CAM pathway are mostly succulents with high water storage capacity that helps survival in habitats with low water availability. This succulence also provides high capacity for the storage of malic acid formed during nocturnal CO_2 fixation (Edwards and Walker 1983, Osmond *et al.* 1996).

In arid regions with low erratic rainfall, CAM represents an important ecological advantage. In such habitats, stomata opening during the night for nocturnal CO_2 uptake and stomata closure during the day imply avoidance of gas exchange when environmental conditions strongly favour water loss by transpiration. Exhibiting CAM leads, therefore, to reduction of the amount of water transpired per unit CO_2 fixed, and hence improved water use efficiency (Ting 1985, Winter 1985). Moreover, nocturnal cytosolic CO_2 fixation by PEPC occurs in presence of low mesophyll CO_2 contents, a feature that results in high rates of CO_2 influx per unit stomatal conductance, that is per unit CO_2 fixed (Leegood 1993, Nobel 1996, Winter and Smith 1996a).

In tropical regions, seasonal rainfall and high photon flux density make drought and photoinhibition a combined periodical hazard. In CAM, daytime fixation of CO_2 released from malate decarboxylation by RuBPCO proceeds under closed stomata. Such conditions generate high CO_2 concentrations that favour carboxylation activity of RuBPCO over its photorespiratory oxygenase activity (Leegood 1993), and may prevent damage to photosystems (Osmond *et al.* 1994). The CAM pathway is a feature of many tropical epiphytes (Griffiths and Smith 1983, Winter *et al.* 1983, Sinclair 1984, Griffiths *et al.* 1986, Lüttge *et al.* 1986, Earnshaw *et al.* 1987b). In addition to terrestrial and epiphytic CAM mentioned above, CAM is an advantage for some aquatic plants due to depletion during day of dissolved CO_2 as a result of increased activities of photosynthetic planktonic and benthic organisms (Raven *et al.* 1988, Keeley 1996).

The list

The list (Table 1) is a compilation of available information documented on 407 CAM plants over the past 25 years. Of these species 17 belong to two fern families, one is a gymnosperm, and 389 species belong to 24 angiosperm families. The list summarises information on these species including growth habits, succulent parts, carbon isotope discrimination, CAM types, CAM inducers, and CAM modifications. A blank space in the list denotes absence of a particular parameter, whereas a space filled with '–' implies that this parameter does not apply for this particular species. Moreover, plant species listed as having inducible CAM are C_3-intermediates except *Portulaca oleraceae* L. (*Portulacaceae*) which is

Table 1. Plant species reported to exhibit CAM with their habitat (H; a = aquatic, e = epiphytic, t = terrestrial), succulent part (P; f = frond, l = leaf, s = stem), carbon discrimination value (CD) CAM type (T; c = constitutive, i = inducible), inducer (I; d = drought, g = age, Na = salinity, ph = photoperiod, t = temperature), and CAM modification (M; cyc = cycling, idl = idling).

	Family/Species	H	P	CD	T	I	M	Reference
A. Ferns								
Isoetaceae	*Isoetes andicola* (Amstutz) H.P. Fuchs	a			c			Keeley 1996
	I. andina Spurce	a			c			Keeley 1996
	I. bolenderi Engelm.	a			c			Keeley *et al.* 1983
	I. howelii Engelm.	a			c			Keeley 1983
	I. lacustris L.	a			c			Keeley 1996
	I. macrospora Dur.	a			c			Keeley 1996
	I. malinveriana Cesati & De Not	a			c			Keeley 1996
	I. orcutii Eaton	a			c			Keeley 1996
	I. strokii Palmer	a			c			Keeley *et al.* 1981
	I. triquerta R. Br.	a			c			Keeley 1996
Polypodiaceae	*Drymoglossum piloselloides* (L.) Presl.	e	f		c		cyc	Griffiths *et al.* 1989
	Pyrrosia adnascent (Forst.) Ching	e	f		c		cyc	Sinclair 1984
	P. angustata (Sw.) Ching	e	f		c		cyc	Sinclair 1984
	P. confluens (R. Br.) Ching	e	f	–19.2	c		cyc	Adams 1988
	P. dielsii (C. Chr.) Tindal.	e	f	–17.3	c		cyc	Winter *et al.* 1983
	P. longifolia (Burm.) Morton	e	f	–14.5	c		cyc	Winter *et al.* 1986b
	P. rupestris (R. Br.) Ching	e	f	–22.3	c		cyc	Keeley 1996
B. Gymnosperms								
Welwitschiaceae	*Welwitschia mirabilis* Hooker fil.	t	l	–14.4	c		cyc	Ting and Burk 1983
C. Angiosperms								
Agavaceae	*Agave americana* L.	t	l		c			Neales 1973
	A. deserti Engelm.	t	l		c			Wang and Nobel 1998
	A. fourcryodes Lem.	t	l		c			Nobel 1976
	A. heteracantha Zucc.	t	l		c			Kluge and Ting 1978
	A. lechuguilla Torr.	t	l		c			Nobel *et al.* 1989
	A. mapisaga Trelease	t	l		c			Nobel *et al.* 1989
	A. tequilana Web.	t	l		c			Nobel and North 1996
	A. salmiana Otto	t	l		c			Nobel *et al.* 1989
	A. vilmoriniana Berger	t	l		c			Szarek *et al.* 1987
	Yucca alata L.	t	l		c			Griffiths 1988
	Y. baccata Torr. in Emory	t	l	–14.5	c			Griffiths 1988
	Y. gloriosa (Salsb.) Engelm.	t	l	–22.0	c			Winter and Smith 1996b
Aizoaceae	*Aptenia cordifolia* (L. f.) Schwantes	t	l		i	Na		Treichel 1975
	Brownanthus schlichtianus Ehlenfel. & Bitt.	t	l		c			Winter and Smith 1996b
	Carpobrotus acinaciformis (L.) L. Bolus	t	l		i	d		Ziegler 1996
	C. edulis (L.) L. Bolus	t	l	–25.2	i	d		Earnshaw *et al.* 1987a
	Cheiridopsis robusta L. Bolus	t	l		i	d		Winter and Smith 1996b
	Conophytum aequatum L. Bolus	t	l		c			Schütte *et al.* 1967
	C. flavum (N.E. Br.) S.A. Hammer	t	l		c			Schütte *et al.* 1967
	Delosperma pergamentaceum Lavis	t	l		c			Willert *et al.* 1992
	Lithops karasmontana (N.E. Br.) D.T. Cole	t	l		c			Willert *et al.* 1992
	L. lesliei D.T. Cole	t	l		c			Willert *et al.* 1992
	L. salicola D.T. Cole	t	l		c			Cockburn 1974
	L. turbiniformis (L. Bolus) D.T. Cole	t	l		c			Willert *et al.* 1992
	M. crystallinum L.	t	l	–16.0	i	d		Winter *et al.* 1978
	M. nodiflorum L.	t	l		i	d		Sayed and Hegazy 1991
	M. pellitum Freidrich	t	l		i	d		Willert *et al.* 1992
	Mitrophyllum clivorum (L. Bolus) Rowley	t	l		c			Willert *et al.* 1992
	Prenia sladeniana (L. Bolus) M. Gerbaulet	t	l		i	d		Herppich and Peckmann 2000
	Psilocaulon subnodosum L. Bolus	t	l		c			Willert *et al.* 1992
	Ruschia schneideriana L. Bolus	t	l		c			Winter and Smith 1996b
	R. subaphylla Freidrich	t	l		c			Winter and Smith 1996b
	Tetragonia fruticosa L.	t	l		C			Schütte *et al.* 1967
	Trichodiaderma barbatum L. Bolus	t	l		C			Schütte *et al.* 1967

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Alloaceae	*Aloe arborescence* Mill.	t	l		C			Denius and Homann 1972
	A. aristata Haw.	t	l		C			Nurenbergk 1961
	A. dichotoma L. f.	t	l		c			Ziegler 1996
	A. ferox Mill.	t	l		c			Lüttge and Ball 1987
	A. pearsoni Schonland	t	l		c			Willert *et al.* 1992
	A. pillansii A. Berg.	t	l		c			Willert *et al.* 1992
	A. ramosissima Pillans	t	l		c			Willert *et al.* 1992
	A. vera (L.) Burm. f.	t	l		c			Ting and Gibbs 1982
	Gasteria excelsa Baker	t	l		c			Schütte *et al.* 1967
Asclepiadaceae	*Caralluma indica* N.E. Br.	t	s		c			Lange and Zuber 1977
	C. negevensis D. Zohary	t	s		c			Lange *et al.* 1975
	Dischia major (Vahl.) Merr.	e	l	−17.8	c			Winter *et al.* 1983
	D. nummularia R. Br.	e	l	−17.6	c			Winter *et al.* 1983
	D. orata Berth.	e	l	−14.8	c			Winter *et al.* 1983
	Hoya australis R. Br.	e	l	−18.4	c			Winter *et al.* 1983
	H. carnosa (L.f.) B. Br.	t	l	−15.4	c			Griffiths 1988
	H. keysii F.M. Bail.	e	l	−18.6	c			Winter *et al.* 1983
	H. nicolsaniae F. Muell.	t	l	−14.3	c			Griffiths 1988
	Stapelia nobilis N.E. Br. *ex* Hook. f.	t	s		c			Milburn *et al.* 1968
Asteraceae	*Aster tripolium* L.	t	l		i	d		Kluge and Ting 1978
	Kleinia articulata Haw.	t	l		i	d		Schütte *et al.* 1967
	K. tomentosa Haw.	t	l		i	d		Schütte *et al.* 1967
	Notonia grandiflora DC.	t	l		i	d		Chellappan *et al.* 1980
	Senecio cephalophorus (Compton) Jacobs.	t	l		i	d		Schütte *et al.* 1967
	S. corymbeferus DC.	t	l		i	d		Willert *et al.* 1992
	S. longiflorus Sch. Bip.	t	l		i	d		Willert *et al.* 1992
	S. mandraliscae (Ten.) Jacobs.	t	l	−25.8	i	d		Earnshaw *et al.* 1987a
	S. medley-woodii	t	l	−13.9	i	d		Griffiths 1988
Bromeliaceae	*Ananas ananassoides* (Baker) L.B. Sm.	t	l		c			Kluge and Ting 1978
	A. comosus (L.) Merr.	t	l	−12.4	c			Borland and Griffiths 1989
	A. lucidus L.	t	l		c			Kluge and Ting 1978
	A. sativus L.	t	l		c			Milburn *et al.* 1968
	Aechmea aquilega (Salisbury) Griseback	e	l	−15.0	c		cyc	Griffiths 1988
	A. bromeliifolia (Rudge) Baker	e	l	−12.9	c			Griffiths 1988
	A. dichlamydea (Baker) L.B. Smith	e	l	−15.3	c			Griffiths 1988
	A. fasciata (Lindl.) Bak.	e	l		c			Lüttge and Ball 1987
	A. fendleri Andre *ex* Mez.	e	l	−12.3	c		cyc	Griffiths 1988
	A. mertensii (Meyer) Schulter fil.	e	l	−18.5	c			Ting and Gibbs 1982
	A. nudicaulis (L.) Griseback	e	l	−14.1	c		cyc	Griffiths 1988
	Araeococcus micranthus Brongniart	e	l	−18.5	c			Ting and Gibbs 1982
	Bilbergia amoena Lindl.	t	l		c			Black *et al.* 1996
	B. pyramidalis (Sims) Lindl.	t	l	−15.9	c			Kluge and Ting 1978
	B. rosea Hortus *ex* Beer	t	l	−13.7	c			Kluge and Ting 1978
	Bromelia chrysantha Jacq.	e	l	−10.2	c			Kluge and Ting 1978
	B. humilis Jacq.	t	l	−16.2	c		cyc	Fetene *et al.* 1990
	B. plumieri (E. Morren) L.B. Smith	e	l		c			Kluge and Ting 1978
	Dychia brevifolia Hortus *ex* Baker	t	l	−16.3	c		cyc	Griffiths 1988
	Guzmania monostachia (L.) Rusby *ex* Mez.	e	l	−26.5	i	d	cyc	Kluge and Ting 1978
	Hechtia glomerata Zucc.	e	l	−13.4	i	d		Lüttge and Ball 1987
	Hohenbergia stellata Schulter fil.	e,t	l	−14.5	i	d		Winter *et al.* 1983
	Nidularium innocenti E. Pereira	e	l	−24.0	i	d		Kluge and Ting 1978
	Tillandsia balbisiana Schulter fil.	e			c		cyc	Martin 1996
	T. balbosa Hooker	e		−18.5	c		cyc	Ting and Gibbs 1982
	T. eleganta Homboldt	e			c		cyc	Ting and Gibbs 1982
	T. fasiculata Swart	e		−14.1	c		cyc	Ting and Gibbs 1982
	T. flexosa Swart	e		−13.1	c		cyc	Griffiths 1988
	T. gardneri Lindl.	e		−14.7	c		cyc	Ting and Gibbs 1982
	T. ionantha Hooker	e			c		cyc	Martin 1996
	T. juncea (Ruiz & Pavon) Poiret	e		−13.4	c		cyc	Ting and Gibbs 1982

	Family/Species	H	P	CD	T	I	M	Reference
(cont.)	*T. recurvata* (L.) L.	e			c		cyc	Martin 1996
	T. schiedeana Zucc.	e		−13.4	c		cyc	Martin 1996
	T. setacea Hooker	e			c		cyc	Martin 1996
	T. stricta Solander	e		−14.9	c		cyc	Ting and Gibbs 1982
	T. tenuifolia L.	e		−11.4	c		cyc	Ting and Gibbs 1982
	T. usneoides L.	e		−13.4	c		cyc	Griffiths 1988
	T. utriculata L.	e		−11.2	c		cyc	Martin 1996
Cactaceae	*Carnegia gigantea* (Engelm.) Britt. & Rose	t	s		c			Barcikovski and Nobel 1986
	Cereus validus Haw.	t	s		c			Nobel *et al.* 1994
	Cephalocereus hoppenstedii K. Schum.	t	s		c			Willert *et al.* 1992
	Echinocereus engelmanii Rümpl.	t	s		c			Dinger and Patten 1974
	E. fendleri Engelm.	t	s		c			Dinger and Patten 1974
	E. ledingii Peeples	t	s		c			Dinger and Patten 1974
	Echinomastus intertextus Britt. & Rose	t	s	−19.8	c			Ting and Gibbs 1982
	Echinopsis chilensis Friedrich & Rowley	t	s		c			Ziegler 1996
	E. triglochidiatus Engelm.	t	s		c			Dinger and Patten 1974
	E. eyriesii Pfeiff. & Otto	t	s		c			Nurenbergk 1961
	E. skottsbergii (Backb.) Friedrich & Rowley	t	s		c			Ziegler 1996
	Epiphyllum phyllanthus (L.) Haw.	e	s		c			Nobel and North 1996
	Ferrocactus acanthodes Britt & Rose	t	s		c			Nobel 1977
	Mammillaria rhodontha Link & Otto	t	s		c			Nurenbergk 1961
	M. tetrancistra Engelm.	t	s		c			Ting and Dugger 1968
	M. woodsii Graig.	t	s		c			Nurenbergk 1961
	Nopalea dejecta Salm. Dyck	t	s		c			Mukerji 1968
	N. cochenellifera (L.) A. Lyons	t	s		c			Moster 1959
	Opuntia acanthocarpa Engelm. & Bigel.	t	s		c			Nobel and North 1996
	O. acanthodes Engelm.	t	s		c			Patten and Dinger 1969
	O. amyclaea Tenore	t	s		c			Nobel *et al.* 1992
	O. aurantiaca Lindl.	t	s		c			Whiting *et al.* 1979
	O. basilaris Engelm. & Bigel.	t	s	−12.4	c			Szarek and Ting 1979
	O. begilovii Engelm.	t	s		c			Didden-Zopfy and Nobel 1982
	O. chlorotica Engelm. & Bigel.	t	s		c			Nobel 1980
	O. echinocarpa Engelm & Bigel.	t	s		c			Kluge and Ting 1978
	O. ficus-indica (L.) Mill.	t	s	−10.7	c			Acevedo *et al.* 1983
	O. humifusa Raf.	t	s		c			Koch and Kennedy 1980
	O. inermis (DC.) DC.	t	s	−13.5	c			Osmond *et al.* 1979
	O. monocantha	t	s		c			Kluge and Ting 1978
	O. phaeacantha Engelm.	t	s	−12.5	c			Kluge and Ting 1978
	O. polycantha Haw.	t	s		c			Gerwick and Williams 1978
	O. puberlua Hort. Vindob. *ex* Pfeiff.	t	s		c			Kausch 1965
	O. ramosissima Engelm.	t	s		c			Kluge and Ting 1978
	O. stricta Haw.	t	s		c			Adams 1988
	O. versicolor Engel. *ex* J.M. Coult.	t	s		c			Kluge and Ting 1978
	O. vulgaris Mill.	t	s		c			Kluge and Ting 1978
	Pereskia aculeata Mill.	t	s		c			Rayder and Ting 1981
	P. grandiflora Hortus *ex* Pfeiff.	t	s		c			Rayder and Ting 1981
	P. guamacho Webber	t	s		c			Griffiths 1988
	Phyllocactus pfersdorfii Link.	t	s		c			Kluge and Ting 1978
	Tricocereus pachanoi Britt. & Rose	t	s		c			Lüttge and Ball 1987
	Zygocactus tuncatus Haw.	t	s		c			Kluge and Ting 1978
Clusiaceae	*Clusia alata* Planch. & Triana	t	l		i	d		Lüttge 1996
	C. aripoensis Britton	t	l		i	d		Lüttge 1996
	C. articulata Vesque	t	l		i	d		Lüttge 1996
	C. intertexta Britton	t	l		i	d		Lüttge 1996
	C. lanceolata Cambess.	t	l		i	d		Lüttge 1996
	C. lundelii Standley	t	l		i	d		Lüttge 1996
	C. minor L.	t	l		i	d		Haag-Kerver *et al.* 1992
	C. multiflora H.B. & K.	t	l		i	d		Lüttge 1996
	C. rosea Cambess.	t	l		I	d		Popp *et al.* 1987
	C. tocuchensis Britton	t	l		I	d		Lüttge 1996

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(cont.)	*C. uvitana* Pittier	t	l		i	d		Zotz and Winter 1996
	C. venosa Jacq.	t	l		i	d		Lüttge 1996
Commelinaceae	*Tradescantia acaulis* Mart. & Gal.	t	l		c			Schmitt *et al.* 1988
Crassulaceae	*Aeonium haworthii* Webb. & Berth.	t	l		i	d		Neales *et al.* 1968
	A. orbicum Rowley	t	l		i	d		Pilon-Smits *et al.* 1996
	Cotyledon ladysmithiensis Poelln.	t	l		i	d		Schütte *et al.* 1967
	C. orbiculata L.	t	l		i	d		Willert *et al.* 1992
	C. peacockii Baker	t	l		i	d		Nishida 1963
	Crassula aqautica (L.) Schonl.	a	l		i	d		Winter 1985
	C. arborescence Willd.	t	l		i	d		Kluge and Ting 1978
	C. argentea L. f.	t	l		i	d		Rustin *et al.* 1988
	C. brevifolia Harv.	t	l		i	d		Willert *et al.* 1992
	C. cinerea Friedrich	t	l		i	d		Willert *et al.* 1992
	C. clavata N.E. Br.	t	l		i	d		Willert *et al.* 1992
	C. deceptor Schoenl. & Baker f.	t	l		i	d		Willert *et al.* 1992
	C. elegans Schoenl. & Baker f.	t	l		i	d		Willert *et al.* 1992
	C. erolusa N.E. Br.	t	l		i	d		Willert *et al.* 1992
	C. eracta A. Berger	t	l		i	d		Pilon-Smits *et al.* 1996
	C. fusca Herre	t	l		i	d		Willert *et al.* 1992
	C. helmsii A. Berger	t	l		i	d		Keeley 1996
	C. lycopodioides Lam.	t	l		i	d		Herppich and Peckmann 2000
	C. macowaniana Schoenl. & Baker f.	t	l		i	d		Willert *et al.* 1992
	C. multicava Lem.	t	l		i	d		Kluge and Ting 1978
	C. natans Thunb.	t	l		i	d		Keeley 1996
	C. ovata E. Mey. *ex* Harv. & Sond.	t	l		i	d		Ziegler 1996
	C. paludosa P. Duzen	t	l		i	d		Keeley 1996
	C. portulacea Lam.	t	l		i	d		Ziegler 1996
	C. rupestris L. f.	t	l		i	d		Black *et al.* 1996
	C. sieberiana Domin	t	l		i	d		Brulfert *et al.* 1991
	Diamorpha cymosa (Nutt.) Britt. & Rose	t	l	–26.6	i	d		Teeri 1982a
	Dudleya attenuata (S. Watson) Moran	t	l	–12.0	i	d		Mooney *et al.* 1974
	D. blochmaniae (East.) Moran	t	l	–16.0	i	d		Teeri 1982b
	D. caespitosa (Haw.) Britt. & Rose	t	l	–15.5	I	d		Troughton *et al.* 1977
	D. cultrata Rose	t	l	–12.5	i	d		Mooney *et al.* 1974
	D. cymosa (Lemaire) Britt. & Rose	t	l	–18.7	i	d		Troughton *et al.* 1977
	D. farinosa (Lindl.) Britt. & Rose	t	l	–16.1	i	d		Bartholomew 1973
	D. ingens Rose	t	l	–14.5	i	d		Mooney *et al.* 1974
	D. lanceolata (Nutt.) Britt. & Rose	t	l	–16.1	i	d		Mooney *et al.* 1974
	D. palmeri (S. Watson) Britt. & Rose	t	l	–18.9	i	d		Troughton *et al.* 1977
	D. parva Rose & Davidson	t	l	–17.0	i	d		Troughton *et al.* 1977
	D. pulverulenta (Nutt.) Britt. & Rose	t	l	–14.0	i	d		Troughton *et al.* 1977
	D. saxosa (M.E. Jones) Britt. & Rose	t	l	–16.0	I	d		Troughton *et al.* 1977
	Echeveria columbiana Poelln.	t	l	–12.0	i	d	cyc	Medina and Delgado 1976
	E. gibbiflora DC.	t	l	–13.2	i	d		Griffiths 1988
	E. kircheriana DC.	t	l	–13.7	i	d		Griffiths 1988
	E. pumila Schutdl.	t	l		i	d		Meinzer and Rundel 1973
	Kalanchoë beharensis Drake	t	l		i	d		Kluge and Brulfert 1996
	K. campanulata Baill.	t	l		i	d		Kluge and Brulfert 1996
	K. crenata Haw.	t	l		i	d		Lyndon 1962
	K. daigremontiana Hamet & Perr.	t	l	–17,3	i	d	cyc	Balsamo and Uribe 1975
	K. fedtschkoi Hemet & Perr.	t	l	–17.0	i	d,g		Jones 1975
	K. marmorata Baker	t	l		i	d		Nishida 1963
	K. miniata Hilsenb. & Boj *ex* Tul.	t	l		i	d		Kluge and Brulfert 1996
	K. pinnata (Lam.) Pers.	t	l	–16.0	i	d	cyc	Lüttge *et al.* 1991
	K. porphyrocalyx Baill.	t	l		i	d		Kluge and Brulfert 1996
	K. tubiflora (Harv.) Hamet	t	l		i	d		Ritz and Kluge 1987
	K. uniflora (Stapf.) Hamet	t	l		c			Schäfer and Lüttge 1988
	K. velutina Pers.	e	l		i	ph,g		Kluge and Brulfert 1996
	K. welwitschii Britton	t	l		i	d		Kluge and Brulfert 1996
	Sedum acre L.	t	l	–26.5	i	d	cyc	Kluge 1977

	Family/Species	H	P	CD	T	I	M	Reference
(cont.)	*Sedum aetense* L.	t	l		i	d		Pilon–Smits *et al.* 1996
	S. album L.	t	l	–24.4	i	d		Sayed *et al.* 1994
	S. buritto Moran	t	l		i	d		Pilon-Smits *et al.* 1996
	S. coeruleum Vahl	t	l	–23.7	i	d		Pilon-Smits *et al.* 1996
	S. comprassum Rose	t	l	–18.7	i	d		Kluge and Ting 1978
	S. dendroideum DC.	t	l		i	d		Pilon-Smits *et al.* 1996
	S. fusiforme Lowe	t	l		i	d		Pilon-Smits *et al.* 1996
	S. gattefossei Battand. & Jahandiez	t	l		i	d		Pilon-Smits *et al.* 1996
	S. grisebachii Boiss. & Heldr.	t	l		i	d		Pilon-Smits *et al.* 1996
	S. mite Gil.	t	l	–25.9	i	d		Schuber and Kluge 1981
	S. montanum E.H.L. Krause.	t	l		i	d		Pilon-Smits *et al.* 1996
	S. morganianum E. Walther	t	l	–14.6	i	d		Pilon-Smits *et al.* 1996
	S. nussbaunerianum Bitter	t	l		i	d		Pilon-Smits *et al.* 1996
	S. praealtum DC.	t	l		i	d		Kluge and Osmond 1972
	S. pulchellum Michx.	t	l		i	d		Martin *et al.* 1988
	S. reflexum L.	t	l		i	d		Pilon-Smits *et al.* 1996
	S. rosea (L.) Scop.	t	l		i	d		Woodward 1975
	S. rubrotinctum R.T. Clausen	t	l		i	d		Teeri *et al.* 1986
	S. rupestre All. *ex* Reut.	t	l		i	d		Pilon-Smits *et al.* 1990
	S. sieboldii Hort. *ex* G. Don	t	l		i	d		Smirnoff 1996
	S. spectabile Bor.	t	l	–25.5	i	d		Brulfert *et al.* 1988b
	S. telephium L.	t	l	–19.0	i	d,ph	cyc	Lee and Griffiths 1987
	S. ternatum Michx.	t	l		i	d		Pilon-Smitts *et al.* 1996
	S. tymphaeum Quezel & Contandr.	t	l		i	d		Pilon-Smitts *et al.* 1996
	S. wrightii A. Gray	t	l		i	d		Gurevitch *et al.* 1986
	Sempervivum montanum L.	t	l	–18.2	i	d	cyc	Earnshaw *et al.* 1985
	Tylecodon paniculatus (L. f.) H. Tolken	t	l		i	d		Woodward 1975
	Umbilicus rupestris (Salisb.) Danaly	t	l		i	d		Daniel *et al.* 1984
Cucurbitaceae	*Xerosicyos danguyi* Humbert	t	l	–14.6	c			Rayder and Ting 1983b
	X. perrieri Humbert	t	l		c			De Luca *et al.* 1977
Didieriacea	*Alluadia ascendens* Drake	t	l		i	d		Kluge and Ting 1978
	A. comosa Drake	t	l		i	d		Ziegler 1996
	A. dumosa A & Drake	t	l		i	d		Ziegler 1996
	A. humberti Choux	t	l		i	d		Kluge and Ting 1978
	A. montagnacii Rauh	t	l		i	d		Ziegler 1996
	A. procera Drake	t	l		i	d		Ziegler 1996
	Didieria trolli Capuron & Rauh	t	l		i	d		Ziegler 1996
Dracaenaceae	*Sansevieria liberica* Thunb.	t	l		i	d		Milburn *et al.* 1968
	S. trifasciata Thunb.	t	l		i	d		Kowalczyk *et al.* 1984
	S. zeylamica Thunb.	t	l		i	d		Kluge and Ting 1978
Euphorbiaceae	*Euphorbia caducifolia* Haines	t	l		c			Sen 1970
	E. dregeana E. Mey	t	l		c			Winter and Smith 1996a,b,c
	E. grandidens Haw.	t	l		c			Nurenbergk 1961
	E. submamillaris Berger *ex* Pax	t	l		c			McWilliams 1970
	E. xylophylloides Brongn. *ex* Lem.	t	l		c			McWilliams 1970
	Monadenium lugardae N.E. Br.	t	l		c			McWilliams 1970
	Synadenium grantii Hooker f.	t	l		c			McWilliams 1970
	S. cupulare Wheeler	t	l		c			McWilliams 1970
Gesneriaceae	*Codonanthe crassifolia* (Focke) Morton	t	l	–24.0	i	d		Smith and Winter 1996
Lamiaceae	*Plectranthus marrubioides* Hochst.	t	l		i	d,g		Herppich *et al.* 1998
	P. parviflorus Henckel.	t	l		i	d,g		Nobel *et al.* 1975
	P. prostratus Guerke	t	l		i	d,g		Willert *et al.* 1992
Orchidaceae	*Arachnis hookeriana* Reichb. f.	e	l	–15.1	c		cyc	Fu and Hew 1982
	Ascocentrum ampullaceum Schlechter	e	l		c			McWilliams 1970
	Brassaolaeliocattleya plexa Hiroe	e	l		c			McWilliams 1970
	Bulbophyllum aurantiacum F. Muell.	e	l	–12.4	c			Winter *et al.* 1983
	B. baileyi F. Muell.	e	l	–16.8	c			Winter *et al.* 1983
	B. crassulifolium (A. Cunn.) Rupp	e	l	–12.1	c			Winter *et al.* 1983

	Family/Species	H	P	CD	T	I	M	Reference
(cont.)	*B. gibbosum* Lindl.	e	l		c			McWilliams 1970
	B. macphersonii Rupp	e	l	−12.2	c			Winter *et al.* 1983
	B. minutissimum Rupp	e	l	−17.0	c			Winter *et al.* 1983
	Cadetia maideniana (Schtlr.) Schtlr.	e	l	−13.1	c			Winter *et al.* 1983
	C. wariana Schultr.	e	l	−16.1	c			Winter *et al.* 1983
	Campylocentrum tyridion Garay & Dunsterr	e	l		c			Winter *et al.* 1986b
	C. pachyrrhizum Rolfe	e	l		c			Nobel and North 1996
	Cattleya labiata Lindl.	e	l		c			Knauff and Arditti 1969
	Chiloschista phylorhiza (F. Muel.) Schultr.	e	l	−14.5	c			Winter *et al.* 1983
	C. usneoides (Don) L.D.L.	e	l		c			Kockburn *et al.* 1985
	Cymbidium canaliculatum R. Br.	e	l	−18.7	c			Winter *et al.* 1983
	Dendrobium attenuatum Lindl.	e	l	−14.1	c			Winter *et al.* 1983
	D. beckleri F. Muell.	e	l	−14.7	c			Winter *et al.* 1983
	D. bifalce Lindl.	e	l	−18.1	c			Winter *et al.* 1983
	D. bigibbum Lindl.	e	l	−11.9	c			Winter *et al.* 1983
	D. canaliculum R. Br.	e	l	−13.1	c			Winter *et al.* 1983
	D. crumenatum Swart	e	l		c			Kockburn *et al.* 1985
	D. cucumerium Macley *ex* Lindl.	e	l	−13.2	c			Winter *et al.* 1983
	D. dicyphum F. Muell.	e	l	−14.1	c			Winter *et al.* 1983
	D. discolor Lindl.	e	l	−13.8	c			Winter *et al.* 1983
	D. gracilicaule F. Muell.	e	l	−18.3	c			Winter *et al.* 1983
	D. johannis Rchb. F.	e	l	−13.9	c			Winter *et al.* 1983
	D. lichenastrum (F. Muell.) Krunzl.	e	l	−13.4	c			Winter *et al.* 1983
	D. linguliforme Swart	e	l	−11.9	c			Winter *et al.* 1983
	D. luteocilium Rupp	e	l	−18.7	c			Winter *et al.* 1983
	D. nidii W. Hill	e	l	−13.5	c			Winter *et al.* 1983
	D. pugioniforme A. Cunn.	e	l	−13.9	c			Winter *et al.* 1983
	D. racemosum Clemesha & Dockrill	e	l	−14.5	c			Winter *et al.* 1983
	D. rigidum R. Br.	e	l	−15.0	c			Winter *et al.* 1983
	D. speciosum Smith	e	l	−15.4	c		cyc	Winter *et al.* 1983
	D. taurinum R. Br.	e	l		c			Fu and Hew 1982
	D. terretifolium R. Br.	e	l	−15.9	c			Winter *et al.* 1983
	D. tetragonum A. Cunn.	e	l	−18.2	c			Winter *et al.* 1983
	D. toressae (F. M. Bail.) Dockrill	e	l	−17.6	c			Winter *et al.* 1983
	D. tortile Lindl.	e	l	−15.4	c			Winter *et al.* 1983
	D. wessellii S.T. Blake	e	l	−13.1	c			Winter *et al.* 1983
	Encyclia atropurpurea Schlechter	e	l		c			Nuernbergk 1961
	Eria irucandijiana S.T. Cloud	e	l	−19.8	c			Winter *et al.* 1983
	E. velutina Lindl.	e	l		c			Winter *et al.* 1983
	Epidendrum alatum Lindl.	e	l		c			McWilliams 1970
	E. radicans Lindl.	e	l		c			Milburn *et al.* 1968
	E. schomburgkii Lindl.	e	l		c			Nuernbergk 1961
	Flickingeria convexa (Bl.) A.D. Hawkes	e	l	−13.0	c			Winter *et al.* 1983
	Micropera fasciculata (Lindl.) Garay	e	l	−12.7	c			Winter *et al.* 1983
	Oberonia muelerana Schultr.	e	l	−18.2	c			Winter *et al.* 1983
	Phalaenopsis amabilis Bl.	e	l	−14.1	c			Winter *et al.* 1983
	P. schilleriana Reichb. f.	e	l		c			Winter *et al.* 1983
	Pholidota pallida Lindl.	e	l	−15.5	c			Winter *et al.* 1983
	Plectorhiza tridentata (Lindl.) Dockrill	e	l	−15.4	c			Winter *et al.* 1983
	Potamocalpa macphersonii (Muell.) Hunt	e	l	−16.3	c			Winter *et al.* 1983
	Rhinerrhiza divitiflora (F. Muell.) Rupp	e	l	−15.5	c			Winter *et al.* 1983
	Robiquetia wassellii Dockrill	e	l	−13.9	c			Winter *et al.* 1983
	Saccolabiopsis armitii (F. Muell.) Dockrill	e	l	−15.2	c			Winter *et al.* 1983
	Sarcochilus ceiliae F. Muell.	e	l	−15.3	c			Winter *et al.* 1983
	S. falcatus R. Br.	e	l	−14.9	c			Winter *et al.* 1983
	S. hilii (F. Muell.) F. Muell.	e	l	−13.8	c			Winter *et al.* 1983
	S. moorei (Rchb. f.) Schultr.	e	l	−15.3	c			Winter *et al.* 1983
	Schoenorchis densiflora Schultr.	e	l	−14.8	c			Winter *et al.* 1983
	Schomburgkia crispa Lindl.	e	l		c		cyc	McWilliams 1970
	S. humboldtii Ruchb. f.	e	l	−13.4	c			Griffiths 1988
	Taeniophyllum malianum Schultr.	e	l	−15.8	c			Winter *et al.* 1983

	Family/Species	H	P	CD	T	I	M	Reference
(cont.)	*Trachoma rhopalorrachis* (Rchb. f.) Garay	e	l	–13.6	c			Winter *et al.* 1983
	T. subluteum (Rupp) Garay	e	l	–14.1	c			Winter *et al.* 1983
	Trispermum congestum Dockrill	e	l	–16.7	c			Winter *et al.* 1983
	Vanda whiteana Herbert & S.T. Blake	e	l	–14.8	c			Winter *et al.* 1983
	Vanilla fragrans Ames	e	l	–20.0	c			Kluge and Ting 1978
	V. planifolia Andrews	e	l		c			Nobel and North 1996
Oxalidaceae	*Oxalis carnosa* var. *hirta* R. Knuth	t	l		i	d		Kluge and Ting 1978
Plantaginaceae	*Littorella americana* Fernald	a			c			Keeley 1996
	L. uniflora Rusby	a			c			Robe and Griffiths 2000
Piperaceae	*Peperomia alata* Ruiz. & Pavon	t	l	–29.4	c		cyc	Ting and Bates 1985
	P. camptotricha Mig.	e	l	–27.7	c		cyc	Sipes and Ting 1985
	P. glabella Griseb.	t	l	–31.0	c		cyc	Ting *et al.* 1985
	P. magnoliaefolia Jacq.	t	l		c		cyc	Schmidt and Kaiser 1987
	P. macrostachya	t	l	–28.5	c		cyc	Ting *et al.* 1996
	P. obtusifolia A. Dietr.	t	l	–24.9	c		cyc	Ziegler 1996
	P. orba Bunting	t	l	–29.5	c		cyc	Ting *et al.* 1985
	P. orstedii C. DC.	t	l	–28.4	c		cyc	Ting *et al.* 1985
	P. panamensis C. DC.	t	l	–31.6	c		cyc	Ting *et al.* 1985
	P. peltifolia C. DC.	t	l	–25.5	c		cyc	Ting *et al.* 1985
	P. rotundifolia (L.) Knuth	t	l	–27.6	c		cyc	Ting *et al.* 1985
	P. scandens Ruiz. & Pavon	t	l	–22.3	c		cyc	Ting *et al.* 1996
	P. serpens C. DC.	t	l	–33.8	c		cyc	Ting *et al.* 1985
Portulacaceae	*Anacampseros ablissiema* Marloth	t	l		i	d		Kluge and Ting 1978
	Ceraria fruticulosa Pearson & Stephens	t	l		i	d		Winter and Smith 1996c
	C. namaquensis Pearson & Stephens	t	l		i	d		Winter and Smith 1996c
	C. pygmaea (Pillans) G.D. Rowley	t	l		i	d		Winter and Smith 1996c
	Portulaca oleraceae L.	t	l		i	d		Koch and Kennedy 1982
	Portulacaria afra (L.) Jacq.	t	l		i	d,Na	idl	Guralnick and Ting 1987
	Talinum calycinum Engelm.	t	l		i	d	cyc	Martin and Zee 1983
	T. guadalupense Dudley	t	l		i	d	cyc	Martin and Zee 1983
	Hydrophyllum formicarium Jacq.	e	l	–21.8	c			Winter *et al.* 1983
	Myrmecodia beccarii Hook.	e	l	–20.7	i	d		Winter *et al.* 1983
Salvadoraceae	*Salvadora persica* L.	t	l		i	d		Gaur 1968
	Prosopis juliflora DC.	t	l		i	d		Gaur 1968
Vitaceae	*C. gongyloides* Planch. in A. DC. & C. DC.	t	l		i	d		De Santo and Bartoli 1996
	C. hypoglauca A. Gray	t	l		i	d		De Santo and Bartoli 1996
	C. quadrangularis L.	t	l		i	d		De Santo and Bartoli 1996
	C. quinquangularis Chior.	t	l		i	d		De Santo and Bartoli 1996
	C. rotundifolia B. Verdcourt	t	l		i	d		De Santo and Bartoli 1996
	C. trifoliata var. *caustica* (Tussac) Griseb.	t	l		i	d		De Santo and Bartoli 1996

a C_4-intermediate (but see Mazen 2000). The reference given opposite to each species may not be the only work published on this species. Choosing a reference included criteria such as being first work to report CAM in the species, being a key work on the species, being the work that presented the $\delta^{13}C$ value, or being the most recent work that enables the reader to pursue more information on the species by cross referencing its reference list.

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