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Crassulacean acid metabolism in australian vascular epiphytes and some related species

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Summary. The occurrence of crassulacean acid metabolism (CAM) among epiphytes and related plant species from tropical and subtropical rainforests in Eastern Australia was investigated. As judged from $\delta^{13}C$ value and the absence of Kranz anatomy, indications of CAM were found in 66 species belonging to the families, Polypodiaceae (3), Orchidaceae (55), Asclepiadaceae (6) and Rubiaceae (2).

Two thirds of orchidaceous plants examined appeared to use CAM. Those species with thicker leaves generally had less negative $\delta^{13}C$ values, as did those species growing on more exposed sites; leaves thicker than about 1 mm in most species yielded $\delta^{13}C$ values indicative of pronounced CAM. Two leafless species, *Chiloschista phyllorhiza* and *Taeniophyllum malianum*, which depend on chloroplast-containing, stomata-less roots for photosynthesis also showed $\delta^{13}C$ values typical of CAM. Pseudobulbs and swollen stems, a characteristic of many orchids, were usually somewhat enriched in ^{13}C compared to corresponding leaves.

In Polypodiaceae CAM was found in the genus *Pyrrosia*. While $\delta^{13}C$ values were generally less negative with increasing frond thickness, the leaf morphology was extremely variable within species. *Pyrrosia confluens* plants from shaded habitats had long, relatively thin and dark-green fronds whereas specimens from sun-exposed sites were characterized by short, thick, bleached fronds. Both types showed the capacity for nocturnal accumulation of titratable acidity and exhibited continuous net CO_2 fixation during 12 h light/12 h dark cycles under laboratory conditions. Shade-fronds showed this capacity even when irradiance was lower than 2% of full sunlight during the 12 h light period.

In Asclepiadaceae CAM was found in species of two genera which usually have fleshy leaves, *Hoya* and *Dischidia*. In Rubiaceae CAM was recorded in two genera of epiphytic ant plants, *Hydnophytum* and *Myrmecodia*.

It is concluded that CAM is widespread in Australian epiphytes. It is most prevalent in species found in exposed microhabitats where the growing conditions are characterised by relatively high light intensities and short but frequent periods of water stress.

Introduction

Climatic and edaphic conditions of large semi-arid areas of Eastern Australia are capable of supporting high biomass of CAM plants. This is indicated by the success of several species of *Opuntia* which were introduced to Australia and, temporarily, even became a serious pest in Queensland and Northern New South Wales (Osmond et al. 1979). Nevertheless, native stem- or leaf-succulent species are rare and families known to contain many CAM plants such as Cactaceae, Euphorbiaceae, Crassulaceae etc. are absent from, or contribute insignificantly to the indigenous Australian flora. It was only recently that a survey in Western Australia revealed the occurrence of CAM in a few native species, i.e. in *Sarcostemma australe* (Asclepiadaceae) and in some species of *Calandrinia* (Portulacaceae) (Winter et al. 1981). However, periodic water stress is also characteristic of many epiphytic environments (e.g., Richards 1952) and although most vascular epiphytes are found in warm mesic forests, unlike their phorophytes, they have no direct access to water in the soil. CAM has been reported from several Neotropical and Asiatic epiphytes – mainly in the families Orchidaceae and Bromeliaceae (Coutinho 1969; McWilliams 1970; Medina and Troughton 1974; Medina 1975; Neales and Hew 1975; Goh et al. 1977). This paper is the first to examine the occurrence of CAM in representatives of the approximate 380 species (Wallace 1982) of vascular epiphytes in the Australian flora.

Materials and methods

The plant material used in this study was either collected from natural habitats in Eastern Australia or taken from plants cultivated outdoors or in glasshouses. Some details of collection localities and their environments are recorded in Table 1 and Figs. 1 and 2. Since many of these sites are remote from meteorological stations with long term records, the temperature and rainfall data shown are, of necessity, the best available estimates.

Leaf or frond thickness was determined in the middle between tip and base of blade and between midrib and edge. Anatomical examination to detect evidence of Kranz anatomy was by light microscopy of cross-sectioned fresh leaf or frond material. The $\delta^{13}C$ determinations were made by drying the samples at 100° C and combusting them in an oxygen atmosphere. $\delta^{13}C$ values of CO_2 were determined by ratio mass spectrometry as described elsewhere (Osmond et al. 1979). The $\delta^{13}C$ value is a measure of the relative abundance of ^{13}C in a given material and is calculated by the formula

$$\delta^{13}C\ (‰) = \left[\frac{^{13}C/^{12}C_{sample}}{^{13}C/^{12}C_{standard}} - 1 \right] \times 1{,}000.$$

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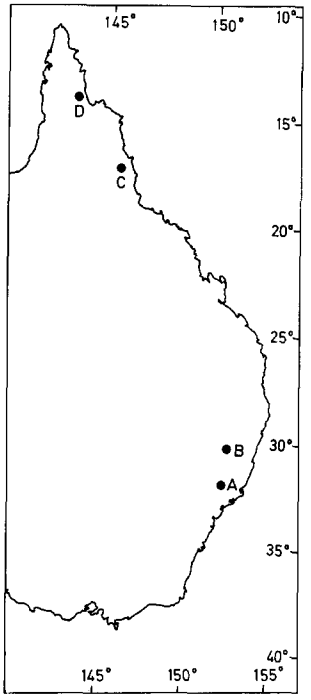


Fig. 1. Map of Eastern Australia showing the location of study sites. A Barrington Tops and Allyn-River area; B Armidale; C Atherton Tableland and surroundings (Gordonvale, Babinda, Mount Haig, Kaban etc.; see Table 1); D Cape York, McIlwraith Range

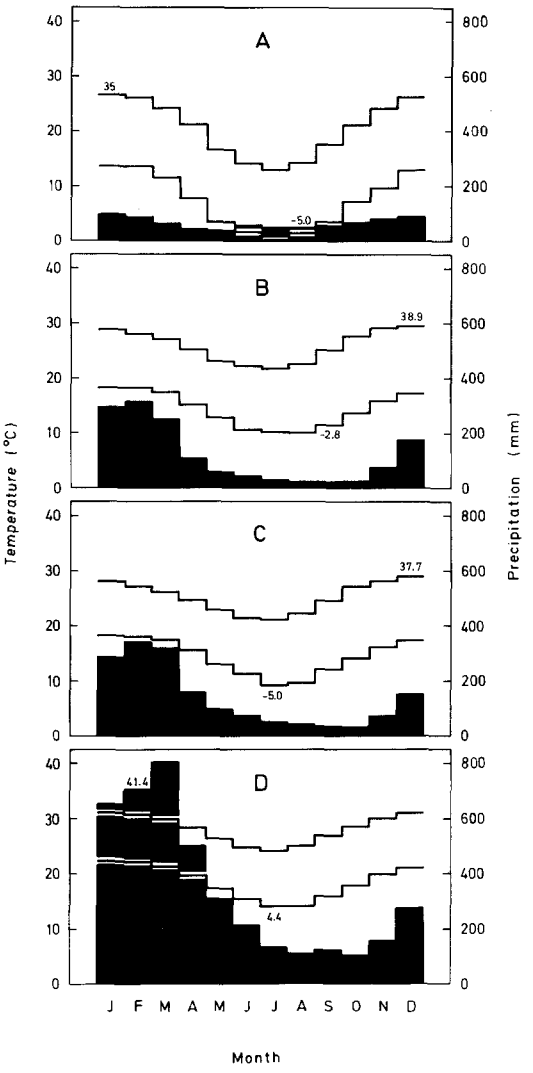


Fig. 2A–D. Climatic conditions at some study sites. Upper closed line = average maximum temperature per month; lower closed line = average minimum temperature per month; filled area = precipitation per month; J–D = January–December. Individual temperature values represent extremes. **A** Armidale, **B** Atherton, **C** Mount Haig, **D** Babinda. Regarding Mount Haig, temperature data refer to Herberton and rainfall data to Malanda. Temperature conditions given for Babinda refer to Innisfall. Data for sites **B–D** were obtained from "Resources and Industry of Far North Queensland, Australian Government Publishing Service, Canberra 1971"

Plants are depleted in ^{13}C compared to atmospheric CO_2 which has a $\delta^{13}C$ value of approximately $-8^0/_{00}$ relative to the Pee Dee belemnite limestone standard. The degree of depletion varies depending on the mode of carbon assimilation operating in the plants. Discrimination against ^{13}C is most pronounced in conventional C_3 plants which utilize ribulose bisphosphate carboxylase as the initial carboxylase and have $\delta^{13}C$ values of about $-27^0/_{00}$. In contrast, plants with predominant initial CO_2 fixation via phosphoenolpyruvate carboxylase (C_4 species, CAM plants exhibiting pronounced nocturnal CO_2 fixation) show less discrimination against ^{13}C during uptake of atmospheric CO_2. Their $\delta^{13}C$ values are typically around $-15^0/_{00}$.

For determination of titratable acidity, tissue samples were harvested at dawn and dusk in the field and preserved in 80% (v/v) ethanol. Samples were made to 20% (v/v) ethanol, boiled for 15 min, and extracts were titrated with 5 or 10 mM NaOH to pH 6.5. Extracts were also used for determination of L-malate after Hohorst (1970). CO_2 exchange was studied in attached fronds of *Pyrrosia confluens* immediately after plants had been brought from the field to the laboratory. The equipment used for gas exchange studies has been described by Powles and Osmond (1978) and Powles et al. (1979).

Results and discussion

A list of the species examined with a key to collection sites, their habitats, the thicknesses and type of the plant parts sampled and the $\delta^{13}C$ values is shown in Table 2. None of the plants collected showed Kranz anatomy. Therefore, the possibility that some may use the C_4 photosynthetic pathway can be ignored and $\delta^{13}C$ value is a valid criterion for classification of species into C_3 type and CAM type plants.

(1) Fern allies

The *Psilotum* and *Lycopodium* species examined had $\delta^{13}C$ values in the range -24.3 to $-30.9^0/_{00}$ and were thus classed as C_3 plants. These genera are only found in moist, well protected rainforest environments and even then they are often observed to grow from water-retaining humus accumulations suspended below mid canopy level.

Table 1. Collecting localities (see also Fig. 1)

Locality code	Place, Name	Lat. S	Long. E	Elevation (m)	Habitat
A	Barrington Tops	32°05′	151°25′	1,000	Temperate rainforest
B1	Long Point	30°25′	151°55′	850	Dry subtropical rainforest
B2	Chandler Gorge	30°25′	151°55′	950	Shrubby eucalypt woodland
B3	Armidale	30°30′	151°35′	1,000	Glasshouse – limited ventilation
B4	Armidale	30°30′	151°35′	1,000	Glasshouse – good ventilation
C1	Malanda	17°24′	145°35′	760	Open rainforest remnants
C2	Mulgrave River	17°08′	145°43′	5	Lowland rainforest
C3	Gordonvale	17°08′	145°49′	5	Open eucalypt forest
C4	Babinda	17°31′	145°47′	100	Wet lowland rainforest
C5	Mt Haig	17°06′	145°35′	1,200	Submontane rainforest
C6	Kaban	17°32′	145°25′	960	Tall open eucalypt forest
C7	Malanda	17°24′	145°35′	760	Outdoor cultivation
C8	Malanda	17°24′	145°35′	760	Glasshouse – limited ventilation
C9	Malanda	17°24′	145°35′	760	Glasshouse – good ventilation
D	McIlwraith Range	13°45′	143°18′	300	Lowland rainforest

Table 2. $\delta^{13}C$ values and some characteristics of the plant species surveyed. The code for the collection sites is explained in Table 1. Life forms: *Ep* Epiphyte, *Cl* Climber, *Li* Lithophyte, *Te* Terrestrial

Taxon	Site	Life form	Plant part	Thickness (mm)	$\delta^{13}C$ (‰)
a) Div. Psilophyta					
Psilotaceae					
Psilotum complanatum Sw.	B3	Ep	Aerial stem	0.77	−30.7
b) Div. Lycopodophyta					
Lycopodiaceae					
Lycopodium phlegmaria L.	C4	Ep	Microphyll	0.35	−30.9
Lycopodium phlegmaria L.	C7	Ep	Microphyll	0.46	−27.7
Lycopodium proliferum Bl.	B4	Ep	Microphyll	0.33	−24.3
c) Div. Pterophyta					
Aspleniaceae					
Asplenium australasicum (Sm.) Hook.	C1	Ep	Frond	0.34	−28.0
Asplenium obtusatum Forst. f.	B4	Li	Frond	0.30	−30.1
Asplenium simplicifrons F. Muell.	C5	Ep	Frond	0.33	−30.3
Lomariopsidaceae					
Elaphoglossum queenslandicum S.B. Andrews	C5	Ep	Frond	0.52	−32.0
Ophioglossaceae					
Ophioglossum pendulum L.	C4	Ep	Frond	0.55	−31.8
Polypodiaceae					
species 1	C4	Ep	Frond	0.19	−33.3
species 2	C4	Ep	Frond	0.22	−34.4
Belvisia mucronata (Fée) Copeland	C1	Ep	Frond	0.95	−25.1
Belvisia mucronata (Fée) Copeland	C4	Ep	Frond	0.70	−29.5
Drynaria rigidula (Sw.) Bedd.	C1	Ep	Frond	0.22	−27.6
Dictymia brownii (Wikstr.) Copeland	A	Ep	Frond	0.45	−29.9
Microsorium punctatum (L.) Copeland	C7	Te	Frond	0.83	−25.2
Platycerium bifurcatum (Cav.) C. Chr.	B4	Ep	Frond	0.90	−24.9
Platycerium bifurcatum (Cav.) C. Chr.	C1	Ep	Frond (fertile)	0.73	−25.2
Platycerium bifurcatum (Cav.) C. Chr.	C1	Ep	Frond (sterile)	0.40	−25.2
Platycerium hillii T. Moore	C1	Ep	Frond	0.70	−24.6
Platycerium superbum G. Jonch. & E. Hennip.	C5	Ep	Frond	0.45	−22.8
Platycerium veitchii (Underw.) C. Chr.	C7	Ep	Frond	1.15	−26.4
Platycerium veitchii (Underw.) C. Chr.	B4	Li	Frond	1.25	−24.5
Pyrrosia confluens (R. Br.) Ching	A	Ep	Frond	0.80	−19.2
Pyrrosia dielsii (C. Chr.) Tindale	C1	Ep	Frond	to 2.25[a] 3.10 2.93	to −25.3[b] −19.1 −17.3

Table 2 (continued)

Taxon	Site	Life form	Plant part	Thickness (mm)	$\delta^{13}C$ (‰)
Pyrrosia dielsii (C. Chr.) Tindale	C6	Ep	Frond	1.80	−18.7
				2.20	−20.1
Pyrrosia longifolia (Burm. f.) Morton	C2	Ep	Frond	0.82	−14.2
Pyrrosia longifolia (Burm. f.) Morton	C5	Ep	Frond	1.80	−13.6
Pyrrosia rupestris (R. Br.) Ching	A	Ep	Frond	0.77	−29.1
Pyrrosia rupestris (R. Br.) Ching	C2	Ep	Frond	0.90	−23.9
Vittariaceae					
Antrophyum reticulatum (Forst.) Kaulf.	C4	Ep	Frond	0.78	−30.0
Vittaria elongata Sm.	C4	Ep	Frond	0.84	−30.1
d) Div. Cycadophyta					
Cycadaceae					
Bowenia spectabilis Hook.	C4	Te	Leaf	0.19	−30.5
e) Div. Anthophyta					
i) Class Magnoliatae					
Apocynaceae					
Parsonsia straminea (R. Br.) F. Muell.	B1	Cl	Leaf	0.30	−29.5
Araliaceae					
Schefflera actinophylla Harms	C4	Ep	Leaf	0.28	−33.4
Asclepiadaceae					
Dischidia major (Vahl.) Merr.	B3	Ep	Leaf (hollow ant leaf)	1.70	−17.8
Dischidia nummularia R. Br.	B3	Ep	Leaf	5.20	−17.6
Dischidia nummularia R. Br.	B4	Ep	Leaf	4.50	−17.1
Dischidia nummularia R. Br.	C3	Ep	Leaf	3.20	−15.7
Dischidia ovata Benth.	C9	Ep	Leaf	5.80	−14.8
Hoya australis R. Br.	B4	Ep	Leaf	1.00	−18.4
Hoya australis R. Br.	C4	Ep	Leaf	1.72	−19.2
Hoya australis R. Br.	C9	Ep	Leaf	3.00	−15.8
Hoya keysii F.M. Bail.	B4	Ep	Leaf	2.00	−18.6
Hoya keysii F.M. Bail.	C2	Ep	Leaf	1.57	−16.9
Hoya keysii F.M. Bail.	C9	Ep	Leaf	5.45	−15.9
Hoya nicholsoniae F. Muell.	C4	Ep	Leaf (shade)	1.70	−18.3
			Leaf (sun)	1.81	−17.2
Marsdenia suberosa S.T. Blake	B1	Cl	Leaf	0.22	−29.3
Ericaceae					
Dimorphanthera sp. F. Muell. (from New Guinea)	C7	Ep	Leaf	1.65	−25.9
Gesneriaceae					
Boea hygroscopica F. Muell.	C5	Li	Leaf	0.65	−30.4
Boea hygroscopica F. Muell.	C2	Li	Leaf	0.33	−34.0
Lamiaceae					
Plectranthus graveolens R. Br.	B1	Te	Leaf	0.65	−32.4
Plectranthus sp.	C2	Li	Leaf	0.55	−31.4
Loranthaceae					
Amyema quandang (Lindl.) Tiegh.	B2	Ep[c]	Leaf	0.57	−29.2
Amyema queenslandicum (Blakely) Dans.	C1	Ep[c]	Leaf	1.00	−28.0
Notothixus subaureus Oliv.	C1	Ep[c]	Leaf	0.60	−30.9
Moraceae					
Ficus crassipes F.M. Bail.	C1	Ep	Leaf	0.70	−28.4
Piperaceae					
Peperomia johnsonii C. DC.	B3	Ep	Leaf	3.20	−27.7
Peperomia johnsonii C. DC.	C5	Ep	Leaf	2.93	−30.0
Peperomia leptostachya Hook. & Arn.	C2	Li	Leaf	1.43	−30.2
Peperomia leptostachya Hook. & Arn.	C6	Li	Leaf (old, thin, large)	0.52	−30.0
			Leaf (young, thick, small)	1.75	−26.8
Peperomia tetraphylla (Forst. f.) Hook. & Arn.	B3	Ep	Leaf	2.10	−29.0
Peperomia sp.	C4	Ep	Leaf	1.50	−29.9
Potaliaceae					
Fragraea berteriana A. Gray ex Benth.	C7	Ep	Leaf	0.69	−26.3

Table 2 (continued)

Taxon	Site	Life form	Plant part	Thickness (mm)	$\delta^{13}C$ (‰)
Rubiaceae					
Hydnophytum formicarium Jack	D	Ep	Leaf		−21.8
Hydnophytum sp.	D	Ep	Leaf	1.10	−28.4
Myrmecodia antonii Becc.	D	Ep	Leaf	0.40	−25.7
Myrmecodia beccarii Hook.	B3	Ep	Leaf	1.00	23.3
Myrmecodia beccarii Hook.	B4	Ep	Leaf	1.20	−22.2
Myrmecodia beccarii Hook.	C3	Ep	Leaf	1.15	−20.7
Myrmecodia muelleri Becc.	D	Ep	Leaf	0.50	−22.4
Timonius singularis (F. Muell.) L.S. Smith	C4	Ep	Leaf	0.53	−28.7
Timonius singularis (F. Muell.) L.S. Smith	C7	Ep	Leaf	0.60	−26.4
Urticaceae					
Elatostemma reticulatum Wedd.	C5	Li	Leaf	0.24	−33.8
Procris cepalida Comm. ex Poir.	C4	Ep	Leaf	0.82	−33.8
Vacciniaceae					
Agapetes meiniana F. Muell.	C7	Ep	Leaf		−27.8
ii) Class Liliatae					
Araceae					
Pothos longipes Schott	C4	Cl	Leaf	0.22	−33.6
Rhaphidophora pachyphylla K. Krause	C4	Cl	Leaf	0.53	−30.1
Commelinaceae					
Pollia crispata (R. Br.) Benth.	A	Te	Leaf	0.28	−27.5
Liliaceae					
Geitonoplesium cymosum (R. Br.) A. Cunn. ex Hook.	B1	Cl	Leaf	0.18	−29.2
			Stem (green)	2.20	−26.1
Orchidaceae					
Acianthus exsertus R. Br.	B2	Te	Leaf	0.24	−28.2
Bulbophyllum aurantiacum F. Muell.	C1	Ep	Leaf	2.30	−12.4
Bulbophyllum baileyi F. Muell.	C4	Li(Ep)	Leaf	1.87	−16.8
			Pseudobulb		−14.9
Bulbophyllum crassulifolium (A. Cunn.) Rupp	A	Ep	Leaf (sun)	4.00	−13.9
			Leaf (shade)	2.00	−12.1
Bulbophyllum elisae (F. Muell.) Benth.	B2	Li(Ep)	Leaf	0.55	−25.1
			Pseudobulb		−22.1
Bulbophyllum evasum T.E. Hunt	C5	Ep	Leaf	2.30	−27.4
Bulbophyllum exiguum F. Muell.	A	Ep	Leaf	0.27	−26.2
Bulbophyllum johnsonii T.E. Hunt & Rupp	C5	Ep	Leaf	0.98	−22.6
Bulbophyllum lilianae Rendle	C5	Ep	Leaf	0.50	−27.9
			Pseudobulb		−25.3
Bulbophyllum macphersonii Rupp	C1	Ep	Leaf	1.95	−12.2
			Pseudobulb		−12.0
Bulbophyllum minutissimum (F. Muell.) F. Muell.	Port Macquarie	Ep	Whole plant		−17.0
Bulbophyllum nematopodum F. Muell.	C5	Ep	Leaf	1.05	−24.0
Cadetia maideniana (Schltr.) Schltr.	C4	Ep	Leaf	1.60	−13.1
Cadetia taylori (F. Muell.) Schltr.	B4	Ep	Leaf	0.70	−27.9
Cadetia taylori (F. Muell.) Schltr.	C5	Ep	Leaf	0.97	−23.7
Cadetia wariana Schltr.	B4	Ep	Leaf	1.65	−16.1
Calanthe triplicata (Willem.) Ames	C5	Te, Li	Leaf	0.30	−27.1
Chiloschista phyllorhiza (F. Muell.) Schltr.	C9	Ep	Root	1.55	a) −14.5
					b) −17.5
Cymbidium canaliculatum R. Br.	C6	Ep	Leaf	1.61	−18.7
			Pseudobulb		−16.8
Cymbidium madidum Lindl.	C1	Ep	Leaf	0.65	−27.0
Cymbidium suave R. Br.	C6	Ep	Leaf	0.59	−27.0
Dendrobium adae F.M. Bail.	C5	Ep	Leaf	0.40	−26.3
			Swollen stem		−23.6
Dendrobium agrostophyllum F. Muell.	C5	Ep	Leaf	0.27	−27.7
			Swollen stem		−24.9
Dendrobium antennatum Lindl.	C9	Ep	Leaf	1.67	−14.1
Dendrobium baileyi F. Muell.	C1	Ep	Leaf	0.27	a) −26.7
					b) −27.6
Dendrobium baileyi F. Muell.	C4	Ep	Leaf	0.27	a) −32.0

Table 2 (continued)

Taxon	Site	Life form	Plant part	Thickness (mm)	$\delta^{13}C$ (‰)
					b) −32.5
Dendrobium beckleri F. Muell.	B1	Ep	Leaf	4.40	−14.7
Dendrobium bifalce Lindl.	C9	Ep	Leaf	1.02	−18.1
Dendrobium bigibbum Lindl.	C9	Ep	Leaf	0.79	−11.9
Dendrobium canaliculatum R. Br.	C3	Ep	Leaf	2.40	−13.1
			Swollen stem		−10.5
Dendrobium cancroides T.E. Hunt	C4	Ep	Leaf	0.53	−28.8
Dendrobium cucumerium Macleay ex Lindl.	B4	Ep	Leaf	2.80	−13.5
Dendrobium dicuphum F. Muell.	C9	Ep	Leaf	0.90	−14.1
Dendrobium discolor Lindl.	C9	Ep	Leaf	1.19	−13.8
Dendrobium fleckeri Rupp & C.T. White	C9	Ep	Leaf	0.44	−25.0
Dendrobium gracilicaule F. Muell.	A	Ep	Leaf (young)	0.39	−18.3
			Leaf (old)	0.59	−25.2
Dendrobium gracilicaule F. Muell.	C1	Ep	Leaf	0.55	−21.1
Dendrobium johannis Rchb. f.	C9	Ep	Leaf	1.10	−13.9
Dendrobium lichenastrum (F. Muell.) Krnzl.	C1	Ep	Leaf	4.15	−13.4
Dendrobium lichenastrum (F. Muell.) Krnzl.	C4	Ep	Leaf	4.07	−14.4
Dendrobium lichenastrum (F. Muell.) Krnzl. var. *prenticei* (F. Muell.) Dockrill	C5	Ep	Leaf	4.45	−12.6
Dendrobium linguiforme Sw.	B1	Ep	Leaf	6.60	−11.9
Dendrobium linguiforme Sw. var. *nugentae* F.M. Bail.	C1	Ep	Leaf	7.40	−14.5
Dendrobium luteocilium Rupp	C9	Ep	Leaf	1.52	−18.7
Dendrobium malbrownii Dockrill	C9	Ep	Leaf	0.30	−25.8
Dendrobium monophyllum F. Muell.	C7	Ep	Leaf	0.58	−25.2
Dendrobium nindii W. Hill	C8	Ep	Leaf	1.70	−13.5
Dendrobium nobile Lindl. (naturalized from India)	C1	Ep	Leaf	0.55	−25.1
Dendrobium pugioniforme A. Cunn.	B1	Ep	Leaf (sun)	3.00	−15.4
			Leaf (shade)	2.00	−13.9
Dendrobium racemosum (Nicholls) Clemesha & Dockrill	C1	Ep	Leaf	5.15	−14.5
Dendrobium rigidum R. Br.	C9	Ep	Leaf	4.70	−15.0
Dendrobium ruppianum A.D. Hawkes	C1	Ep	Leaf	0.60	−26.8
			Swollen stem		−24.2
Dendrobium ruppianum A.D. Hawkes	C5	Ep	Leaf	0.63	−28.5
			Swollen stem		−27.9
Dendrobium speciosum Sm.	A	Ep	Leaf	1.40	−14.5
Dendrobium speciosum Sm.	B1	Ep	Leaf (shade)	1.20	−14.8
Dendrobium speciosum Sm.	B1	Li	Leaf (sun)	2.90	−15.3
Dendrobium speciosum Sm.	C1	Ep	Leaf	1.55	−15.9
Dendrobium smilliae F. Muell.	C7	Ep	Leaf	0.34	−25.9
Dendrobium teretifolium R. Br.	B1	Ep	Leaf	3.10	−15.9
Dendrobium teretifolium R. Br.	C1	Ep	Leaf	3.95	−15.8
Dendrobium tetragonum A. Cunn.	C4	Ep	Leaf	0.47	−18.2
			Swollen stem		−15.7
Dendrobium toressae (F.M. Bail.) Dockrill	C4	Ep	Leaf	1.93	−17.6
Dendrobium tozerensis Lavarack	C9	Ep	Leaf	0.30	−25.4
Dendrobium wassellii S.T. Blake	C7	Ep	Leaf	8.90	−13.1
Diplocaulobium glabrum (J. J. Sm.) Krnzl.	D	Ep	Leaf		−27.7
Dipodium ensifolium F. Muell.	C9	Te	Leaf	0.43	−26.3
Dipodium pandanum F.M. Bail.	C8	Ep	Leaf	0.60	−23.5
Eria eraeoides (F.M. Bail.) Rolfe	C4	Ep	Leaf	0.48	−28.9
			Swollen stem		−28.7
Eria fitzalani F. Muell.	C4	Ep	Leaf	0.70	−28.4
			Swollen stem		−28.4
Eria irukandjiana St. Cloud	D	Ep	Leaf	2.60	−19.8
Flickingeria comata (Bl.) A.D. Hawkes	C9	Ep	Leaf	0.64	−23.5
Flickingeria convexa (Bl.) A.D. Hawkes	D	Ep	Leaf		−13.0
Goodyera viridiflora (Bl.) Bl.	C5	Li, Te	Leaf	thin	−33.6
Liparis bracteata T.E. Hunt	C5	Li	Leaf	0.44	−30.2
			Pseudobulb		−27.5
Liparis coelogynoides (F. Muell.) Benth.	B2	Li, Ep	Leaf	0.45	−26.3
			Pseudobulb		−27.3
Liparis nugentae F.M. Bail.	C1	Ep	Leaf	0.68	−24.7
Liparis persimilis Schltr.	C9	Ep	Leaf	0.52	−24.1
Liparis reflexa (R. Br.) Lindl.	B2	Li	Leaf	1.00	−26.0
			Pseudobulb		−24.1
Luisia teretifolia Gaud.	B4	Ep	Leaf	1.77	−14.7

Table 2 (continued)

Taxon	Site	Life form	Plant part	Thickness (mm)	$\delta^{13}C$ (‰)
Micropera fasciculata (Lindl.) Garay	C1	Ep	Leaf	2.10	−12.7
Micropera fasciculata (Lindl.) Garay	C4	Ep	Leaf	1.75	−14.4
Mobilabium hamatum Rupp	C1	Ep	Leaf	0.80	−16.1
Oberonia muellerana Schltr.	B4	Ep	Leaf	1.75	−18.2
Oberonia muellerana Schltr.	D	Ep	Leaf		−17.8
Phalaenopsis amabilis Bl.	C8	Ep	Leaf	1.73	−14.1
Pholidota pallida Lindl.	C4	Ep	Leaf	0.87	−15.5
			Pseudobulb		−15.1
Pholidota pallida Lindl.	C9	Ep	Leaf	1.20	−11.8
Phreatia baileyana Schltr.	C5	Ep	Leaf	2.70	−30.6
Plectorrhiza tridentata (Lindl.) Dockrill	B1	Ep	Leaf	0.80	−15.4
Podochilus australiensis (F.M. Bail.) Schltr.	C4	Ep	Leaf	0.39	−31.1
Potamocalpa macphersonii (F. Muell.) T.E. Hunt	D	Ep	Leaf		−16.3
Pterostylis obtusa R. Br.	B2	Te	Leaf	0.22	−29.1
Rhinerrhiza divitiflora (F. Muell. ex Benth.) Rupp	B4	Ep	Leaf	0.68	−15.5
Rhinerrhiza divitiflora (F. Muell. ex Benth.) Rupp	C9	Ep	Leaf	1.10	−14.2
Rhynchophreatia micrantha (A. Rich.) N. Hallé	C4	Ep	Leaf	0.28	−28.2
Robiquetia wassellii Dockrill	B4	Ep	Leaf	1.10	−13.9
Robiquetia wassellii Dockrill	C9	Ep	Leaf	1.15	−14.5
Robiquetia tierneyana (Rupp) Dockrill	C4	Ep	Leaf	2.40	−15.2
Robiquetia tierneyana (Rupp) Dockrill	D	Ep	Leaf		−13.5
Saccolabiopsis armitii (F. Muell.) Dockrill	D	Ep	Leaf		−15.2
Sarcochilus ceciliae F. Muell.	C6	Li	Leaf	1.40	−13.4
Sarcochilus ceciliae F. Muell.	B2	Li	Leaf	1.05	−15.3
Sarcochilus falcatus R. Br.	C6	Ep	Leaf	1.37	−15.0
Sarcochilus falcatus R. Br.	B1	Ep	Leaf	1.30	−14.9
Sarcochilus hillii (F. Muell.) F. Muell.	B1	Ep	Leaf	1.50	−13.8
Sarcochilus moorei (Rchb. f.) Schltr.	C8	Ep	Leaf	1.00	−15.3
Schoenorchis densiflora Schltr.	B4	Ep	Leaf	1.50	−14.6
Schoenorchis densiflora Schltr.	C4	Ep	Leaf	1.65	−14.8
Taeniophyllum malianum Schltr.	D	Ep	Root		−15.8
Thelasis carinata Bl.	D	Ep	Leaf		−34.0
Thelymitra ixioides Sw.	B4	Te	Leaf	0.65	−27.1
Thrixspermum congestum (F.M. Bail.) Dockrill	B4	Ep	Leaf	0.70	−16.7
Thrixspermum congestum (F.M. Bail.) Dockrill	D	Ep	Leaf		−14.9
Trachoma rhopalorrachis (Rchb. f.) Garay	D	Ep	Leaf		−13.6
Trachoma subluteum (Rupp) Garay	B4	Ep	Leaf	0.85	−15.2
Trichoglottis australiensis Dockrill	D	Ep	Leaf		−14.1
Vanda whiteana Herbert & S.T. Blake	C9	Ep	Leaf	1.17	−14.8
Xanthorrhoeaceae					
Xanthorrhoea sp.	C6	Te	Leaf	1.00	−28.7

[a] Extremes of 50 fronds
[b] Extremes of 20 fronds
[c] Parasitic species

(2) True ferns

Most epiphytic fern species appear to require environmental conditions similar to the fern allies and of the 21 species examined only 3 species of the genus *Pyrrosia* – *P. longifolia, P. dielsii* and *P. confluens* yielded $\delta^{13}C$ values less negative than −20‰, indicative of CAM. One of these species (*P. longifolia*) had previously been reported to open its stomata at night and to exhibit nocturnal acidification (Wong and Hew 1976). The three CAM species are characterized by relatively succulent fronds (Fig. 3) and occupy the most exposed microhabitats of any epiphytic fern. A fourth species of *Pyrrosia* examined (*P. rupestris*) flourishes best in cooler, moister conditions. It yielded $\delta^{13}C$ values of −23.9 and −29.1‰. *Platycerium* and *Drynaria* spp. are found in relatively exposed microhabitats but unlike the three *Pyrrosia* spp. exhibiting CAM, form nests of litter and dead fronds which assist in retaining moisture around the roots.

Pyrrosia confluens was found in both shaded and exposed sites and showed a great variability in the shape of fronds which were dwarfed, bleached and succulent or thickly leathery in sunny habitats, while in shaded situations they were long, thin and dark green (Fig. 4, Tables 3 and 4). We expected plants growing in sunny habitats to rely more on CAM for CO_2 fixation than plants from shaded environments. Consistent with this expectation, there were higher dark acidification values in plants from exposed habitats (Fig. 4, Table 3). Yet, $\delta^{13}C$ values did not clearly follow this trend; they ranged from −19.2 to −25.3‰ for 20 specimens from different sites and there was no apparent correlation with habitat exposure and type of frond (Fig. 4, Tables 3 and 4).

When examined under laboratory conditions, sun- and

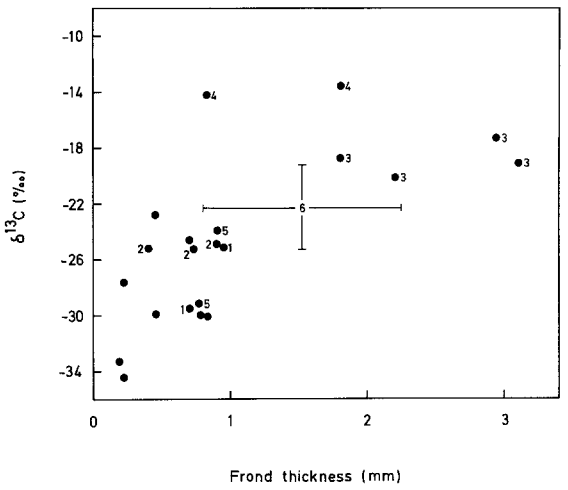


Fig. 3. Relation between frond thickness and $\delta^{13}C$ value in specimens of epiphytic ferns listed in Table 1. Numbered values refer to different specimens of a given species. *1 = Belvisia mucronata*; *2 = Platycerium bifurcatum*; *3 = Pyrrosia dielsii*; *4 = Pyrrosia longifolia*; *5 = Pyrrosia rupestris*. For *Pyrrosia confluens* (6) extremes are given for frond thickness ($n = 50$) and for $\delta^{13}C$ value ($n = 20$)

shade-fronds of *P. confluens* showed net CO_2 fixation almost continuously during 12 h light/12 h dark cycles with 2–4 times higher rates in the light than in the dark (Figs. 5 and 6). Fronds of shade-specimens even showed net CO_2 dark fixation when the level of irradiance was as low as 25 μE m^{-2} s^{-1} during the preceding light period (Fig. 5B). Sun- and shade-fronds also exhibited dark and light CO_2 fixation under low temperature conditions (12° C light/5° C dark; data not shown) which often occur during winter in the natural habitats of *P. confluens* (see Fig. 2A). Stomata of *P. confluens* were deeply sunken (Fig. 7), a typical xeromorphic characteristic, and transpiration rates of fronds were so low that we were unable to detect any transpirational water loss with our gas exchange system.

Table 3. Nocturnal acidification and $\delta^{13}C$ value in *Pyrrosia confluens* from 3 sun-exposed and 3 shaded sites in the area of Barrington Tops and of Allyn River (New South Wales). Date of measurements: May 1979; $T_{max} = 19.5$–21.5° C, $T_{min} = 9.7$–11.4° C

Habitat	Nocturnal increase in titratable acidity (μeq g^{-1} FW)	Frond thickness (mm)	$\delta^{13}C$ (‰)
exposed	15	1.25	−24.2
exposed	24	1.25	−20.5
exposed	21	2.00	−22.5
shaded	0	1.15	−25.3
shaded	9	0.92	−24.3
shaded	4	0.92	−22.9

(3) Asclepiadaceae

Three species each of *Dischidia* and *Hoya* had $\delta^{13}C$ values of between −15.7 and −19.2‰ indicating substantial

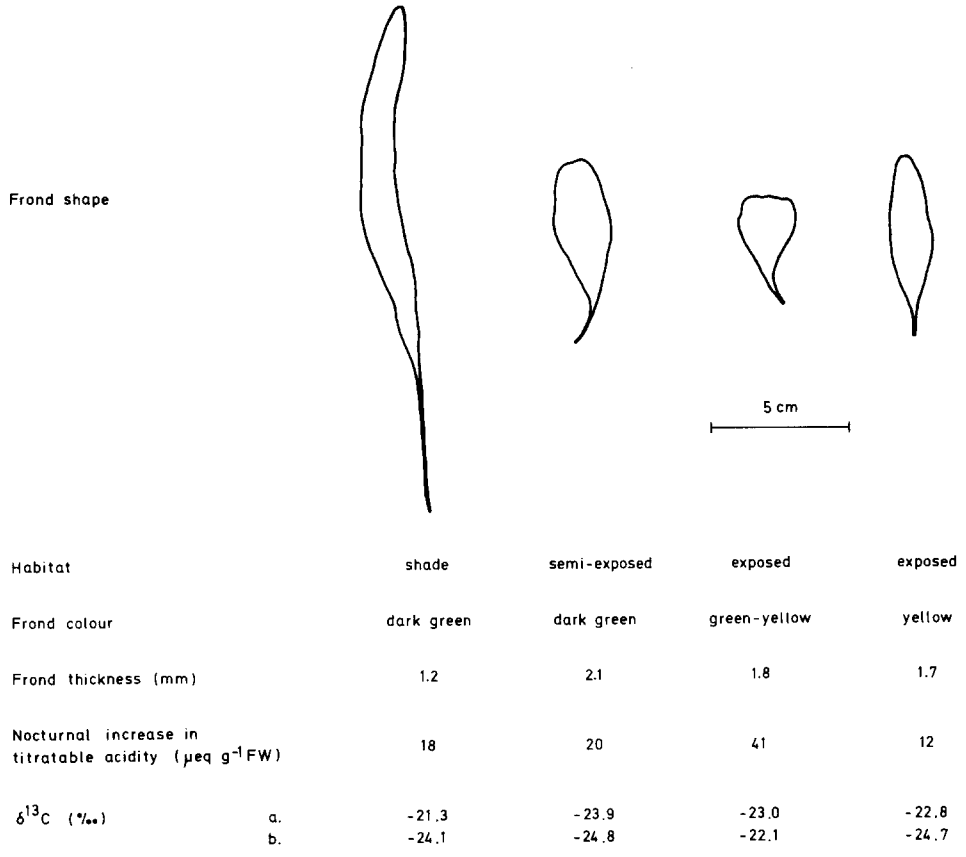


Fig. 4. Different types of fronds of a population of *Pyrrosia confluens* growing on the base of a trunk in the Allyn-River area, N.S.W. Nocturnal increase in acidity was measured in March 1979 (maximum and minimum temperatures of the particular day were 21.5 and 9.7° C, respectively). $\delta^{13}C$ values were determined for specimens collected in July 1978 (series a) and for specimens collected in March 1979 (series b)

Table 4. $\delta^{13}C$ values of different populations of *Pyrrosia confluens* on a tree in the Allyn-River area, New South Wales. Date of collection: July 1978

Frond shape and colour	$\delta^{13}C$ (‰)
long-linear, dark green	−20.6
long-linear, yellow	−20.2
short-oblong, dark green	−19.3
short-oblong, yellow	−19.8
short-round, dark green	−23.3
short-round, yellow	−22.3

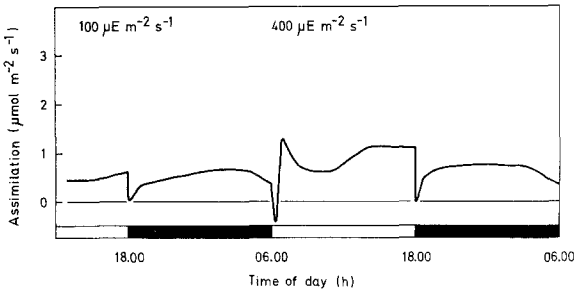
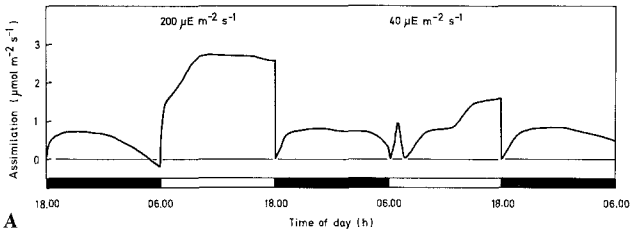
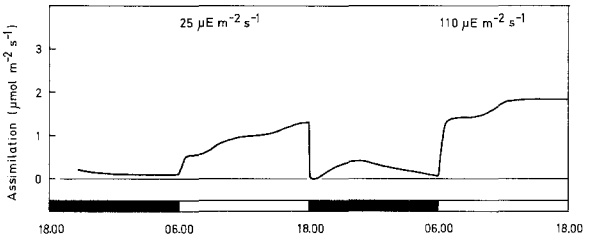


Fig. 6. Net CO_2 exchange of sun-type fronds of *Pyrrosia confluens* during 12 h light/12 h dark cycles at 2 levels of irradiance. Frond temperature during the light period was 25° C, and during the dark period 15° C. Relative air humidity was between 60 and 70%



A



B

Fig. 5A, B. Net CO_2 exchange of shade-type fronds of *Pyrrosia confluens* during 12 h light/12 h dark cycles at varying levels of irradiance. Experiments **A** and **B** were performed with different fronds. Frond temperature during the light period was 25° C, and during the dark period 15° C. Relative air humidity was between 65 and 80%

dark CO_2 fixation. The species examined had succulent leaves 1–5.5 mm thick. They are climbers on trees or over rocks (often terrestrial in *Hoya*). One thin leaved climber belonging to this family (*Marsdenia suberosa*) had a $\delta^{13}C$ value typical of C_3 plants.

(4) Rubiaceae

Although the $\delta^{13}C$ values of *Myrmecodia beccarii* ranged from −20.7 (field sample) to −23.3‰ (glasshouse sample) a significant nocturnal acidification from 6 µeq g^{-1} FW at 5 p.m. to 26 µeq g^{-1} FW at 9 a.m. was observed in plants kept in a glass-house in Armidale. *Hydnophytum formicarium* had similar $\delta^{13}C$ values. Both these species are epiphytic ant plants. This is the first occasion on which CAM has been reported from the Rubiaceae.

(5) Orchidaceae

Of the 82 epiphytic species examined 53 exhibited $\delta^{13}C$ values ranging from about −12 to −20‰ and were evidently characterised by varying degrees of CO_2 dark fixation involving CAM. The remaining species had $\delta^{13}C$ values ranging from −23 to −34‰ and were thus classi-

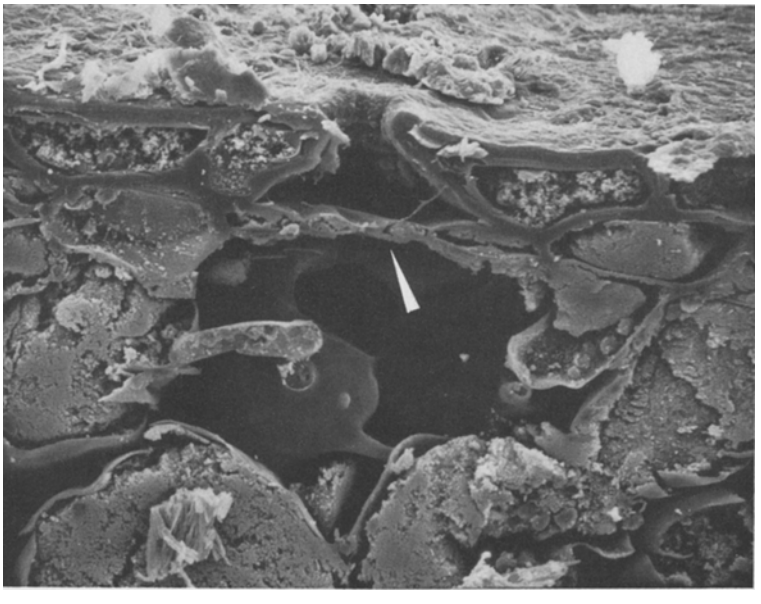


Fig. 7. Scanning electron micrograph of a cross-sectioned shadetype frond of *Pyrrosia confluens*. The photo depicts a sunken stoma. The arrow designates the location of guard cells. ×450

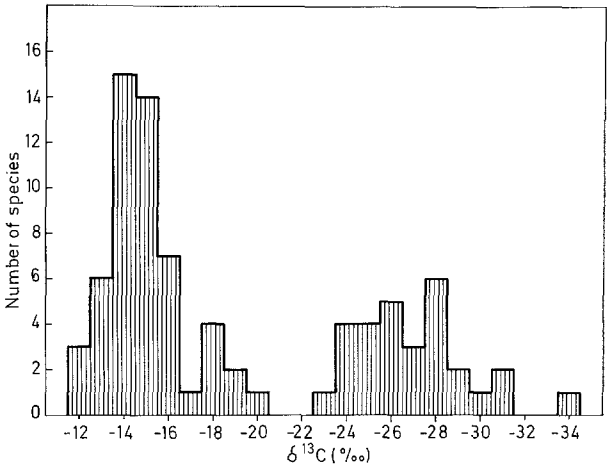


Fig. 8. Histogram showing the distribution of $\delta^{13}C$ values of epiphytic orchids native to Australia. Data are taken from Table 2. When $\delta^{13}C$ values for more than one specimen of a species were obtained, mean values are given. *Dendrobium gracilicaule* was not considered in the histogram because of the large range of $\delta^{13}C$ values for 3 different specimens

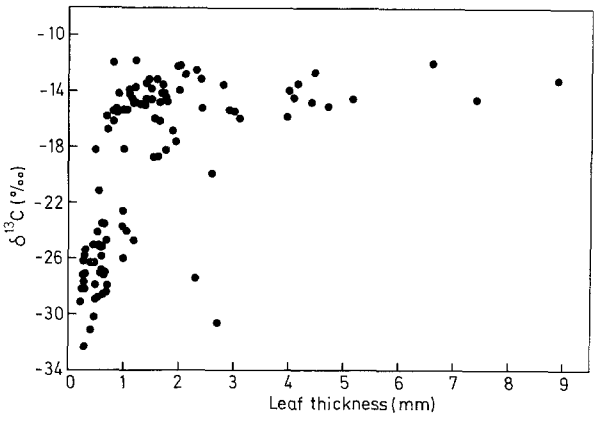


Fig. 9. Relation between leaf thickness and $\delta^{13}C$ value for samples of orchids listed in Table 2

fied as C_3 type plants. The frequency distribution of $\delta^{13}C$ values in Fig. 8 clearly defines these two groups.

There was a general tendency for $\delta^{13}C$ values to be less negative with increasing leaf thickness (Fig. 9). Most species with leaves over 1 mm thick had $\delta^{13}C$ values less negative than $-18^0/_{00}$ indicative of pronounced CAM. Exceptions were *Bulbophyllum evasum* and *Phreatia baileyana* both of which had leaves over 2 mm thick but $\delta^{13}C$ values of -27.4 and $-30.6^0/_{00}$ respectively. Anatomical examinations of leaf cross-sections indicated that leaf succulence in these species is mainly due to water storage tissues which either lack or contain very few chloroplasts. Both species are found in moist well protected microhabitats. A strong relationship between leaf thickness and leaf δ^{13} C values has also been reported for species of the Crassulaceae (Teeri et al. 1981).

The observation that the swollen stems or pseudobulbs of 14 of the 17 species examined were enriched in ^{13}C by up to $3^0/_{00}$ compared to the corresponding leaves cannot currently be explained. These swollen stems and pseudobulbs generally have few chloroplasts and are thought to be storage organs for water and carbohydrate but virtually nothing is known of their CO_2 exchange characteristics, photosynthetic abilities or chemical compositions. *Bulbophyllum minutissimum* is one of the few leafless, pseudobulbous orchids. Its pseudobulbs possess a well developed succulent chlorenchyma. Stomata are located in a sunken, almost closed-over crypt in the top of the pseudobulb. The $\delta^{13}C$ value of $-17^0/_{00}$ suggests the operation of CAM in this species.

It is interesting to record that the chloroplast-containing roots of the two leafless, monopodial orchid species, *Chiloschista phyllorhiza* and *Taeniophyllum malianum* had $\delta^{13}C$ values of -14.5 and $-15.8^0/_{00}$ respectively since both these species lack other photosynthesizing organs and an examination of their roots did not reveal the presence of stomata. Although it is possible that the $\delta^{13}C$ values could partly be a consequence of diffusional limitations of CO_2 uptake (O'Leary 1981) through velamen and exodermis, roots of *C. phyllorhiza* showed a nocturnal increase in malate content by 12 to 40 μeq g^{-1} FW when kept for 2 days in a growth cabinet under a 12 h light (600 μE m^{-2} s^{-1}, 25° C)/12 h dark (15° C) regime. Further, dark net CO_2 fixation was recently reported for roots of 3 related "shootless" species of orchids (Benzing and Ott 1981).

The results of Table 2 also show the relationship between habitat and CAM. For instance, while $\delta^{13}C$ values of none of the terrestrial orchids were less negative than $-26^0/_{00}$, 2 species collected from exposed rocks, *Bulbophyllum baileyi* and *Sarcochilus ceciliae* had $\delta^{13}C$ values typical of CAM. The remaining lithophytes were all found in well shaded localities. Of the epiphytes, 62% of those from the three relatively open forest types in north Queensland (Malanda, Gordonvale, Kaban) had $\delta^{13}C$ values less negative than $-20^0/_{00}$ while only 24% from wet lowland and montane rainforests (Babinda, Mount Haig) exhibited $\delta^{13}C$ values less negative than $-20^0/_{00}$. For the four species obtained from both types of sites (*Dendrobium baileyi, Dendrobium lichenastrum, Dendrobium ruppianum, Micropera fasciculata*), $\delta^{13}C$ values of samples from the rainforests were more negative than those from the open forests. The least negative $\delta^{13}C$ values were recorded for orchid species which are often found in dry open forest or woodland habitats (*Dendrobium bigibbum*, $-11.9^0/_{00}$; *D. dicuphum*, $-14.1^0/_{00}$; *D. linguiforme*, $-11.9^0/_{00}$; *D. canaliculatum*, $-13.1^0/_{00}$). *Cymbidium canaliculatum* is also widespread in this type of habitat and although this species is an epiphyte it establishes a root system in decaying wood in the centre of its host, sometimes reaching down below ground level. Perhaps the more negative $\delta^{13}C$ value observed in its leaves ($-18.7^0/_{00}$) reflects the relatively large volume of moisture holding material within its root zone.

The distribution of CAM and C_3 epiphytes in relation to the environment can also be observed on a micro-scale on the branches and bole of a single tree. The positions of the epiphytes on a large emergent tree are shown in Fig. 10; species known to utilize CAM occupy the more exposed microhabitats.

The Orchidaceae account for about 150 of the 380 species of vascular epiphytes found in Australia and many of those orchids not included in this survey could, on the basis of their morphology, anatomy and ecology,

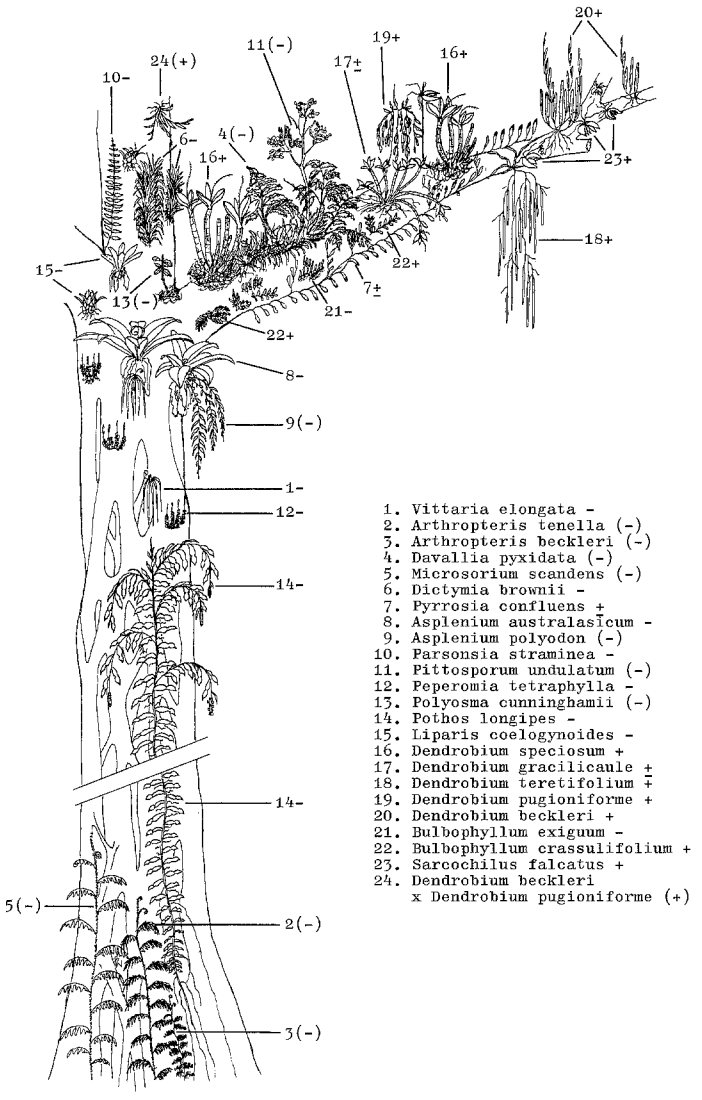


Fig. 10. Semischematic summary of distribution of epiphytes on a 40 m, emergent *Ficus watkinsiana* in Subtropical Rainforest, Dorrigo National Park, N.S.W. with respect to microhabitat zone and photosynthetic pathway. The +sign indicates pronounced CAM, the ±sign indicates weak CAM and the −sign indicates C_3 photosynthetic CO_2 fixation. Evaluation of photosynthetic pathways was based on the data of Table 2. Signs in parenthesis indicate suspected conditions on the basis of leaf succulence

be expected to perform CAM. The largest genus is *Dendrobium* with 46 species, of which 23 use CAM and a further 6 are suspected of exhibiting this metabolic pathway. The second largest genus, *Bulbophyllum* (25 spp.) has relatively few CAM species. In Australia, *Bulbophyllum* sp. tend to occur in more mesic microhabitats and have much thinner roots (with a uniseriate velamen) than the *Dendrobium* species (multiseriate velamen). The subtribe Sarcanthinae has 22 genera represented in Australia but can be regarded as a supergenus like *Dendrobium* for the purpose of comparison here. Of the 46 species, 22 were tested and all exhibited pronounced CAM (yielding $\delta^{13}C$ values less negative than $-16.8^0/_{00}$) and a further 10 at least, are suspect. Most of these species occupy relatively exposed epiphyte microhabitats.

(6) Other families

There is no evidence for the operation of CAM in other families of seed plants examined in Table 2 even though they included representatives of two other genera, i.e. *Peperomia* (Piperaceae) and *Plectranthus* (Lamiaceae), from which CAM had previously been recorded (Kluge and Ting 1978). *Xanthorrhoea* sp., a terrestrial arborescent monocot which is closely related to the Liliaceae and which exhibits extreme xeromorphy and sclerophylly, showed a C_3 type $\delta^{13}C$ value.

General discussion

In interpreting the results of the $\delta^{13}C$ analysis it should be noted that although the $\delta^{13}C$ value of CO_2 in the earth's atmosphere is about $-8^0/_{00}$ it may be more negative near the floor of rainforests where CO_2 enriched in ^{12}C is produced by root respiration and the respiratory decay of plant materials. While there does not appear to be any record of $\delta^{13}C$ values for atmospheric CO_2 in a rainforest understorey, Medina and Minchin (1980) found that tree leaf samples from the lower levels of a rainforest were on average, $5^0/_{00}$ more negative than tree leaf samples from the upper canopy. Differences in the intercellular CO_2 partial pressure during C_3 photosynthesis at low, compared to high levels of irradiance may also influence the $\delta^{13}C$ value (Farquhar et al. 1982). We observed a tendency for $\delta^{13}C$ values to be more negative in samples of a given epiphytic species from shade compared to sun habitats. It is thus important to note that a $\delta^{13}C$ value of e.g. $-23^0/_{00}$ may indicate some degree of CAM in a rainforest species, although the same $\delta^{13}C$ value would be viewed as clearly indicating a C_3 type plant when obtained for a species from an open desert environment. For example, *Pyrrosia confluens* showed dark CO_2 fixation and nocturnal acidification although $\delta^{13}C$ values were mainly around -21 to $-24^0/_{00}$. Some other species listed in Table 2 with $\delta^{13}C$ values ranging from -23 to $-25^0/_{00}$ may thus possess the capacity for CAM but have not been classified as CAM type plants in the absence of additional information on CO_2 exchange characteristics and nocturnal levels of malic acid.

The exposed epiphytic microhabitat is characterized by moderate to high light intensities and despite frequent water inputs most epiphytes may be subject to periodic water stress for the water holding capacity of the most common substrate, tree bark, is usually relatively limited. Our results show that CAM is an important mechanism to enable epiphytic plants to exist under these extreme conditions, allowing for net carbon gain at relatively low water cost. It has long been known (e.g. Walter 1951) that water loss by succulent orchids is slow when they are subjected to drought, and that waterstressed orchids are able to increase their fresh weight to near the original value within 1 h of supplying water to the aerial roots. Slow water loss combined with rapid intake of water when available seem to be major characteristics of many succulents and in this respect, there are parallels between epiphytic CAM plants (Gessner 1956) and terrestrial stem succulents exhibiting CAM (Kausch 1965; Szarek and Ting 1974).

In spite of the obvious preference of CAM epiphytes for exposed sites, some such as *Pyrrosia confluens* occur under conditions of rather heavy shade. We found a specimen of *Dendrobium speciosum* exhibiting $\delta^{13}C$ values less

Table 5. Nocturnal acidification of some epiphytes in their natural habitats at Barrington Tops and Long Point near Armidale (New South Wales)

Species	Nocturnal increase in titratable acidity (μeq g^{-1} FW)
A. Barrington Tops (March 1979, $T_{max}=19.5°$ C, $T_{min}=11.4°$ C)	
Dendrobium beckleri F. Muell.	25
Bulbophyllum crassulifolium (A. Cunn.) Rupp	13
Bulbophyllum exiguum F. Muell., leaf	0
pseudobulb	0
Pyrrosia rupestris (R. Br.) Ching	0
B. Armidale (Long Point) (May 1979, $T_{max}=12.5°$ C, $T_{min}=4°$ C)	
Dendrobium beckleri F. Muell.	35
Dendrobium linguiforme Sw.	4
Dendrobium pugioniforme A. Cunn., sun-leaf	18
shade-leaf	11
Dendrobium speciosum Sm.	3
Dendrobium teretifolium R. Br.	21
Plectorrhiza tridentata (Lindl.) Dockrill	35
Sarcochilus falcatus R. Br.	34
Plectranthus graveolens R. Br.	0

negative than $-16‰$ at sites where irradiance rarely exceeded 3% of full sunlight on bright days. It is further noteworthy that the epiphytes of temperate and subtropical rainforests in New South Wales and of montane rainforests in Queensland experience low temperatures during the dry winter months. Minimum temperatures may be as low as $-5°$ C and maximum temperatures not above 10° C (Fig. 2). A detailed study on seasonal changes in dark CO_2 fixation capacity of epiphytes should show to what extent winter conditions modify the expression of CAM in these forest habitats. Even so, our data show that some epiphytes are capable of nocturnal CO_2 fixation and nocturnal acidification under low temperature conditions (Table 5 and unpublished data) (seee also Medina and Delgado 1976).

Conclusions

Given the absence of native cactus-like stem succulents in Australia and the apparent dearth of other forms of terrestrial CAM plants as shown by a recent survey in Western Australia (Winter et al. 1981), the study presented here shows that Australian CAM plants are mainly represented by epiphytic species, the majority in rainforests. This survey also supports the view that CAM has developed independently in widely divergent phylogenetic groups. Most of the earth's terrestrial CAM species are found in the families Cactaceae (total species number of 2,000, 150 of which are epiphytic), Euphorbiaceae (5,000 species), Aizoaceae (1,200 species), Crassulaceae (1,500 species) and Asclepiadaceae (2,500 species) (Willis and Airy Shaw 1973). All Cactaceae studied thus far are capable of exhibiting CAM and we assume that this is also true for the majority of Aizoaceae and Crassulaceae. In the Euphorbiaceae, CAM occurs mainly in the stem-succulent members of the genus *Euphorbia* (about 450 species; Rowley 1978). In the Asclepiadaceae approximately 500 species are succulent (Rowley 1978) and probably show CAM. These numbers compare with a total of about 20,000 or more known species of Orchidaceae, two thirds of which are epiphytic and many of these succulent. Further, CAM occurs in a great number of epiphytic Bromeliaceae (Medina et al. 1977), a family with more than 1,000 epiphytic species of a total of 2,000 plus (Benzing 1980). Thus, from the standpoint of species numbers it may be that more CAM plants exist as epiphytes in tropical and subtropical rainforests than exist in arid terrestrial habitats. If this is so, we should perhaps reconsider the validity of the commonly accepted notion of a "typical CAM plant", characterized as a cactus-like stem succulent growing in a desert environment.

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