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Photosynthesis of Arid and Subtropical Succulent Plants

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PHOTOSYNTHESIS OF ARID AND SUBTROPICAL SUCCULENT PLANTS[1]

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ABSTRACT

The hypothesis of Crassulacean acid metabolism (CAM) is that it is a physiological adaptation to arid or otherwise dry habitats. Stomata are closed during the day and open at night when the evaporative demand is low. Thus exogenous CO_2 is fixed at night with relatively little water loss. CAM is typically found in succulents occurring in desert and dry Mediterranean regions, but not in the cold deserts of Asia. Recently, it has become known that many arid tropical succulent plants are CAM as well, particularly those growing epiphytically. The vegetation of St. John, U.S. Virgin Islands, ranges from desertlike cacti at the windward, dry eastern side of the island to near tropical rainforest at the higher elevations. Native CAM plants are found in families Agavaceae, Bromeliaceae, Cactaceae, Clusiaceae, Orchidaceae, Piperaceae and Vitaceae. Exotic CAM species are in the families Aizoaceae, Crassulaceae, and Liliaceae. The distribution of these plants is entirely consistent with the hypothesis of CAM being an adaptation to arid habitats. All species in the Agavaceae and Cactaceae are CAM. All of the Bromeliaceae with the exception of the terrestrial *Pitcairnia* and the epiphytic *Catopsis* are CAM. The epiphytic and dry habitat orchids occurring in the genera *Epidendrum, Oncidium, Vanilla,* and *Tetramicra* are CAM. Of three species of *Cissus,* only the species occurring in the most arid zones, *C. trifoliata,* is CAM. *Clusia rosea* is enigmatic in that it is epiphytic when young and a rooted tree when mature. It is the only known genus of true dicotyledonous trees to have CAM. Two of the most serious exotic weeds naturalized in arid scrub areas are CAM, *Sansevieria trifasciata* and *Bryophyllum pinnatum.*

Key words: Crassulacean acid metabolism, photosynthesis, subtropical, succulent plants, epiphyte, orchid, bromeliad, cactus.

INTRODUCTION

One of the unique ecophysiological adaptations to arid and otherwise water-stressed environments is Crassulacean acid metabolism (CAM). CAM is the only physiological and biochemical process studied in depth that is specifically related to water balance (Kluge and Ting 1978), C_4-photosynthesis notwithstanding which is more related to high-light, high-temperature environments and reduced photorespiration (Edwards and Walker 1983). In CAM-photosynthesis, stomata are open at night and closed during the day. Hence all exogenous CO_2 taken up and all water loss is at night. As a consequence, CAM plants lose much less water than most plants because stomata are open at night when the evaporative demand is lower, lower than it would be during the day.

The criteria for CAM are as follows: (1) Succulence, but not necessarily in the horticultural sense. There appears to be a requirement for large succulent chlorenchyma cells with large central storage vacuoles accompanied by reduced intercellular air space. The vacuoles and succulence are related to organic acid storage and not necessarily water storage *per se*. (2) Stomata are open at night and closed

during the day, and thus most CO_2 uptake and water loss are at night. (3) A massive diurnal fluctuation of titratable acidity attributable to malic acid with a reciprocal fluctuation of storage glucan. The latter may be starch, smaller glucose polymers, or soluble sugars. (4) An enriched deuterium and carbon-13 content relative to other plants. The enriched deuterium content is related to the carbohydrate metabolism of the CAM plant and the enriched carbon-13 is a function of CO_2 fixation. (5) High activities of the carboxylating enzyme P-enolpyruvate carboxylase and of decarboxylating enzymes such as malate enzyme and P-enolpyruvate carboxykinase. The details of CAM-photosynthesis have been reviewed extensively (Kluge and Ting 1978; Osmond 1978; Osmond and Holtum 1981; Ting and Gibbs 1982; Edwards and Walker 1983; Ting 1985).

There are now many flowering plant families known to have CAM species (see Kluge and Ting 1978; Szarek and Ting 1977; and Table 1). In some families, CAM appears to be almost exclusive such as in the Cactaceae, Agavaceae, and Crassulaceae (Kluge and Ting 1978). As far as is known, all of the succulent south African lilies and euphorbias are CAM (Nuernbergk 1961; McWilliams 1970). Many of the orchids and bromeliads are CAM (Nuernbergk 1961; Coutinho 1969; McWilliams 1970). In some families, CAM is restricted to one or only a few genera. For example, many succulent species in the genus *Senecio* (or *Kleinia*) of the Asteraceae are CAM (Schutte, Steyn, and Van der Westhuizan 1967). In the Vitaceae, some *Cissus* species are CAM (Schutte et al. 1967). In the Geraniaceae, some *Pelargonium* species are CAM (Kluge and Ting 1978). There are a few succulent *Oxalis* species with CAM and two known CAM genera in the Cucurbitaceae (Kluge and Ting 1978). Many of the Portulacaceae and Aizoaceae are CAM (Nuernbergk 1961; Schutte et al. 1967; Kluge and Ting 1978). A few succulent species in the Asclepiadaceae are known to be CAM (Nuernbergk 1961; Milburn, Pearson, and Ndegwe 1968) including the epiphytic Hoya species (Kluge and Ting 1978). The succulent species of *Plectranthus* in the Labiatae are CAM (Kluge and Ting 1978). The little-known family endemic to Madagascar, the Didiereaceae, appears to be CAM (Kluge and Ting 1978). The hemiepiphytic genus *Clusia* in the Clusiaceae (Guttiferae) is the only known true dicotyledonous tree with CAM (Ting, Lord et al. 1985). Among the nonflowering plants, *Welwitschia* has aspects of CAM (Ting and Burk 1983) as does *Isoetes* (Keeley 1983) and two genera of ferns, *Drymoglossum* and *Pyrrosia* (Wong and Hew 1976). Undoubtedly, a few more families of flowering plants with CAM will be discovered, but in all probability most are now known.

Most CAM species occur in desert and arid regions along or adjacent to the tropics (Kluge and Ting 1978). They are very common in the southern African deserts, the Mediterranean region, and the North and South American deserts. None occurs in the cold deserts of Asia. Recently, it has become generally known that many of the succulent epiphytic plants of the tropics are CAM as well (Winter et al. 1983; Sternberg, DeNiro, and Ting 1984; Guralnick, Ting, and Lord 1986; Ting et al. 1987). Epiphytes tend to grow in water deficient environments and thus CAM is not unexpected (Sinclair 1984).

The site chosen for this project was the St. John National Park, U.S. Virgin Islands (Woodbury and Weaver 1987). Geographically, St. John is 18 degrees north of the equator. Thus it is a tropical island, but because of its small size and relatively low altitude, its eastern end is desertlike exposed to the prevailing winds.

St. John is approximately 11 km long and 5 km wide with an area of 5180 hectares. The topography is steep with many slopes 30 degrees or more. Its altitude ranges from 389 m to just under sea level at salt ponds on the desertlike east end.

St. John is arid-tropical rather than wet tropical (Bowden et al. 1970). Precipitation may come in the form of tropical or Atlantic storms, but frequently it is from summer convectional storms as moisture laden air arrives from the northeast pushed by the prevailing trade winds. Much of this precipitation is quickly lost by evapotranspiration. Thus the eastern end of the island tends to be very dry and desertlike. Contributing to the arid conditions are shallow clay and clay-loamy soils with good drainage and high solar radiation (Rivera et al. 1970).

The annual mean temperature is about 26.5 degrees C with only a few degrees variation diurnally. Although cooler in the winter than the summer, the seasonal temperature variation is not much different than the diurnal variation. The relative humidity averages about 75% (Woodbury and Weaver 1987).

The island has had a long history of use and abuse (Jadan 1985). Human occupation eliminated most virgin forests. In the early 1700s, European colonization to cultivate cotton and sugarcane displaced the native Carib Indians, who had previously displaced the more peaceful Arawak Indians. Land was cleared and under extensive cultivation until the late nineteenth century when agriculture was abandoned. Subsequently, regrowth was cut again to encourage forage for cattle. A third growth, at least for modern times, is now present.

The vegetation of the island, for purposes of this paper, can loosely be categorized into six types (see Beard 1955; Britton 1918; Ewel and Whitmore 1973; Eggers 1879; and Woodbury and Weaver 1987 for more extensive classifications). These types are the wet forests, the dry forests, dry scrub forests, the arid-cactus scrub, mangrove swamps, and disturbed secondary habitats. Succulent plants with CAM tend to occur in all of the habitat types except the mangrove swamps. Although some of the mangrove species have succulent leaves, no evidence of CAM was found during this study or other studies by my group. Succulent aizoids and purslanes may be adjacent to the swamps.

The purpose of this study was to assess the succulent plants of this arid-tropical island, determine their distribution within arid or moist habitat types, and to ascertain their photosynthetic mode. The latter was done with the hypothesis that the CAM succulents would be more predominant in arid regions or occupy otherwise dry niches within moist habitats. Because epiphytic plants typically occur in water-stressed habitats, I hypothesized that many would be CAM. The study was restricted to flowering plants.

MATERIALS AND METHODS

Assessment of Succulent Plants

A list was prepared of the succulent and epiphytic plants of St. John using the checklist prepared by Woodbury and Weaver (1987). Subsequently, five expeditions of two weeks each were conducted to St. John for purposes of locating species with a probability for CAM and then, using various tests listed below, each was assessed for CAM. In some cases, where CAM was generally known to occur in the species, no tests were conducted. Efforts were made to locate and characterize species not included in Woodbury and Weaver.

Table 1. Families of flowering plants with CAM species.

Agavaceae,*+	Geraniaceae
Aizoaceae,*+	Gesneriaceae
Asclepiadaceae*	Lamiaceae*
Asteraceae*	Liliaceae*
Bromeliaceae,*+	Orchidaceae,*+
Cactaceae,*+	Oxalidaceae*
Clusiaceae,*+	Passifloraceae*
Crassulaceae,*+	Piperaceae,*+
Cucurbitaceae*	Portulacaceae*
Didiereaceae	Rubiaceae*
Euphorbiaceae,*+	Vitaceae,*+

* = family occurs on St. John.
+ = family is represented by CAM-species on St. John.

Gas Exchange Parameters

Gas exchange parameters were measured with a Li-Cor Inc., Model 6000 portable gas exchange system (Li-Cor Inc., PO Box 4425, Lincoln, Neb. 68504). The instrument measures CO_2 with a single path, nondispersive-type analyzer in a closed system. Water vapor is measured with a Vaisala humidity sensor and light with a Li-Cor LI-1905-1 quantum sensor from 400 to 700 nm (PAR). Tissue and air temperature are measured with chromel-constantan thermocouples enclosed in a 1 liter polycarbonate teflon-coated analyzing chamber. A computer console performs appropriate calculations of CO_2 fixation, stomatal conductances, and water loss. Datum points, obtained from ten 6 s readings for 1 min, are the average of at least three readings.

Acid Titrations

Leaf discs were collected from mature leaves using a 1-cm cork borer morning and evening and rapidly extracted either by boiling in 80% ethanol or methanol, or by grinding in distilled water using a glass-glass tissue grinder. Samples were titrated to a pH 7 endpoint using 0.01 N KOH. Data are the average of at least three determinations from different leaves and are expressed as μeq acid per cm^2 of leaf surface.

Other Measurements

For some selected plants, carbon-13 compositions were determined using the method of Northfelt, DeNiro, and Epstein (1981). For plants that were returned and grown in the greenhouse, assays for P-enolpyruvate carboxylase and malate enzyme were performed by standard methods (Ting et al. 1987).

RESULTS AND DISCUSSION

There are about 22 flowering plant families that have succulent species known to have CAM metabolism (Table 1). Of these families, 19 occur on St. John. Of these 19 families, 10 have one or more species that are succulent and show CAM-photosynthesis.

Table 2 lists the succulent and epiphytic flowering plants that are either native

Table 2.   The succulent plants of St. John.

Family	Species	Habit	CAM
Agavaceae	*Agave missionum* Trel.	T	Yes
	A. americana L.	T	Yes
	A. sisalana Perrine	T	Yes
	Yucca guatemalensus Baker	T	Yes
Aizoaceae	*Cypselea humifusa* Turp.	T	ns
	Mollugo nudicaulis Lam.	T	ns
	Sesuvium portulacastrum L.	T	Yes
	Trianthema portulacastra L.	T	ns
Batidaceae	*Batis maritima* L.	T	No
Bromeliaceae	*Aechmea lingulata* (L.) Baker	E, T	Yes
	Bromelia pinquin L.	T	Yes
	Catopsis floribunda (Sw.) Griseb.	E	No
	Pitcairnia angustifolia (Sw.) Rodoute	T	No
	Tillandsia fasciculata Sw.	E	Yes
	T. lineatispica Mez	E	Yes
	T. recurvata L.	E	Yes
	T. usneoides (L.) L.	E	Yes
	T. utriculata L.	E	Yes
Cactaceae	*Consolea rubescens* (Salm. Dyck.) Lem.	T	Yes
	Hylocereus trigonatus (Haw.) Safford	E	Yes
	H. undatus (Haw.) Brit.	E	Yes
	Lemaireocereus hystrix (Haworth) Brit. & Rose	T	Yes
	Mammillaria nivosa Link	T	Yes
	Melocactus intortus (Mill.) Urb.	T	Yes
	Nopalea cochenillifera (L.) Salm. Dyck.	T	Yes
	Opuntia antillana Brit. & Rose	T	Yes
	O. dillenii (Ker-Gawl.) Haw.	T	Yes
	O. repens Bello	T	Yes
	O. ficus-indica (L.) Mill.	T	Yes
	Pilosocereus royenii (L.) Byles & Rowl.	T	Yes
	Selenicereus grandiflorus (L.) Brit. & Rose	E	Yes
Clusiaceae	*Clusia rosea* Jacq.	H	Yes
Commelinaceae	*Callisia repens* (Jacq.) L.	T	No
	Commelina diffusa Brum. F.	T	No
	C. elegans HBK.	T	No
	Rhoeo spothacea (Sw.) Stearn	E, T	No
	Spironema fragrans Lindl.	T	No
Crassulaceae	*Bryophyllum pinnatum* (Lam.) Kurz.	T	Yes
	B. tubiflorum Harvey	T	Yes
	B. daigremontianum (Hamet et Perr.) Bgr.	T	Yes
Cruciferae	*Cakile lanceolata* (Willd.) Schulz.	T	No
Euphorbiaceae	*Pedilanthus angustifolius* Poit.	T	Yes
Liliaceae	*Aloe barbedensis* Mill.	T	Yes
	Sansevieria trifasciata Prain	T	Yes
Nyctaginaceae	*Boerhaavia diffusa* L.	T	No
	B. erecta L.	T	No
	B. scandens L.	T	No
	Pisonia aculeata L.	V	No
Orchidaceae	*Epidendrum bifidum* Sw.	E	Yes
	E. cilarae L.	E	Yes
	Oncidium prionochilum Kranz.	E	Yes
	O. variegatum Sw.	E	Yes
	Ponthieva racemosa (Walt.) Mohr.	T	No
	Prescottia oligantha (Sw.) Lindl.	T	No

Table 2.   Continued.

Family	Species	Habit	CAM
	P. stachyoides (Sw.) Lindl.	T	No
	Spiranthes elata (Sw.) L C Rich.	T	No
	Tetramicra canaliculata (Aubl.) Urb.	T	Yes
	Vanilla barbellata Rchb. F.	E	Yes
	V. planifolia G. Jackson	E	Yes
Piperaceae	*Peperomia glabella* (Sw.) Dietr.	E, T	Yes
	P. humilis (Vahl) Dietr.	T	Yes
	P. magnoliaefolia (Jacq.) Dietr.	E	Yes
	P. myrtifolia (Vahl) Dietr.	T	Yes
	P. pellucida (L.) HBK.	E, T	Yes
Portulacaceae	*Portulaca halimoides* L.	T	No
	P. oleracea L.	T	No
	P. pilosa L.	T	No
	P. teretifolia HBK.	T	No
	P. quadrifida L.	T	No
	Talinum paniculatum (Jacq.) Gaertn.	T	Yes
	T. triangulare (Jacq.) Willd.	T	Yes
Vitaceae	*Cissus trifoliata* L.	V	Yes

E, epiphytic; H, hemiepiphytic; P, parasitic; T, terrestrial; V, vine. The plant nomenclature with few exceptions is according to the check list of Woodbury and Weaver (1987).

or naturalized on St. John. The table lists the family and species, whether terrestrial or epiphytic in habit, and if CAM-photosynthesis occurs in the species. Figure 1 shows representive acid titration data for several CAM species representing all the major taxonomic groups. Table 3 lists carbon-13 isotope compositions for several species also representing all the major taxonomic groups. The isotope data are consistent with the titration data making the assignment of CAM to a taxon relatively unequivocal. As an example, *Catopsis floribunda* and *Pitcairnia angustifolia* show no acid flux and low carbon-13 compositions consistent with C_3-photosynthesis and not with CAM-photosynthesis. The remainder of the bromeliads have measurable acid flux and enriched carbon-13 compositions indicative of CAM-photosynthesis. Similarly, the orchids with acid flux also have enriched carbon-13 compositions consistent with CAM. In the case of *Clusia rosea,* the carbon-13 composition is intermediate between C_3 and CAM, yet all other parameters are similar to CAM. The relatively low carbon-13 composition is explainable noting that *Clusia rosea* takes up substantial CO_2 during the early morning hours (see Fig. 4 and Ting et al. 1987). *Peperomia* species consistently show C_3 carbon-13 isotope compositions despite having some aspects of CAM. Even more so than *Clusia, Peperomia* spp. assimilate much CO_2 during the light diluting the expected CAM carbon-13 value to the usual C_3 value (Ting, Lord et al. 1985).

CAM may seem unlikely in the arid-tropics where humidity is usually high, but the decrease in vapor pressure deficit during the night when temperatures are slightly less and humidity is higher can be substantial. Figure 2 shows typical data for vapor pressure deficit during a 24-h period in July. There is a 2.5-fold decrease in vapor pressure deficit during the night. All other factors being equal, this would translate into a reduction in water loss of 2.5 times.
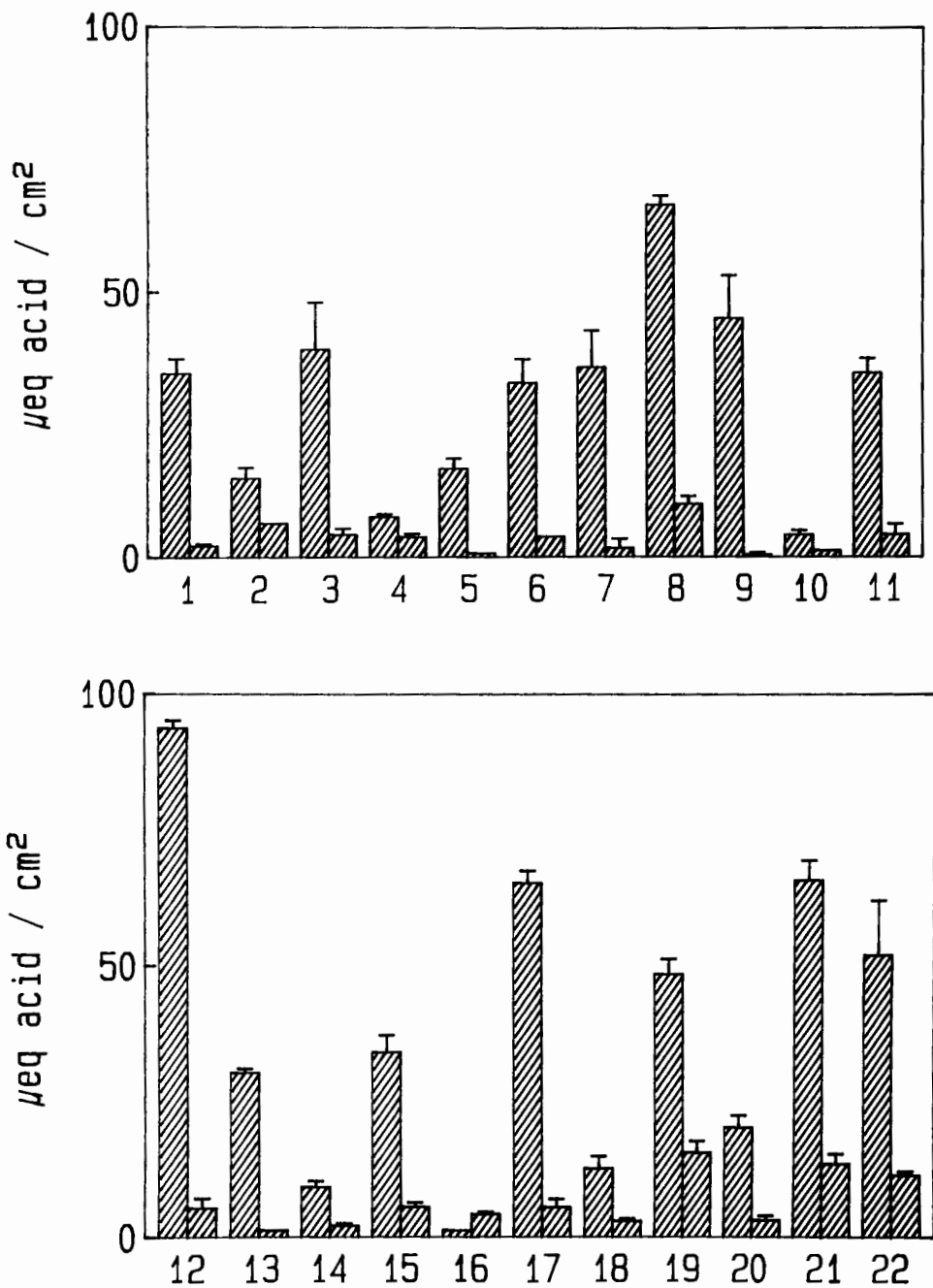
Fig. 1.   Representative acid titrations for succulent plants of St. John. The first bar represents samples taken in the morning and the second bar, samples in the afternoon. 1 = *Yucca guatamalensus*; 2 = *Clusia rosea*; 3 = *Aechmea lingulata*; 4 = *Aloe barbedensis*; 5 = *Talinum triangulare*; 6 = *Consolea rubescens*; 7 = *Hylocereus trigonatus*; 8 = *Lemaireocereus hystrix*; 9 = *Opuntia dillenii*; 10 = *Opuntia repens*; 11 = *Pilocereus royenii*; 12 = *Epidendrum bifidum*; 13 = *Oncidium pronochilum*; 14 = *Tetramicra caniculata*; 15 = *Vanilla barbellata*; 16 = *Tillandsia fasciculata*; 17 = *Bromilia pinquin*; 18 = *Cissus trifoliata*; 19 = *Bryophyllum tubiflorum*; 20 = *Agave missionum*; 21 = *Sesuvium portulacastrum*; 22 = *Sansevieria fasciculata*.

Table 3. Carbon isotope compositions for selected succulent and epiphytic plants of St. John.*

Family/species	$\delta^{13}C$‰
Araceae	
Anthurium acaule	−26.0
A. cordatum	−28.1
A. selloum	−25.1
Bromeliaceae	
Aechmea lingulata	−12.6
Bromelia pinquin	−12.4
Catopsis nutans	−24.5
Pitcairnia angustifolia	−27.2
Tillandsia fasciculata	−12.9
T. recurvata	−13.2
T. usneoides	−14.7
Cactaceae	
Hylocereus trigonatus	−13.2
Clusiaceae	
Clusia rosea	−18.3
Orchidaceae	
Epidendrum cilarae	−13.8
E. bifidum	−11.3
Oncidium prionochilum	−12.8
Piperaceae	
Peperomia glabella	−26.6
P. humilis	−31.7
P. magnoliaefolia	−27.6
P. pellucida	−23.9

* Data analysis by L. Sternberg, Univ. of Miami, Miami, Florida.

Cactaceae

The largest family with succulent plants found on St. John is the Cactaceae. The data available indicate that all 13 species are CAM and hence highly adapted to arid conditions. Indeed, most of these species are found in the arid-cactus scrub habitat. The most prominent species of this habitat are *Consolea rubescens, Melocactus intortus,* and *Pilosocereus royenii.* Less conspicuous but still important are *Opuntia dillenii, O. repens, O. antillana,* and *Mammillaria nivosa. Nopalea cochenillifera* and *Opuntia ficus-indica* are less prominent escapes that can be found in the arid regions. The prominent epiphytic cactus *Hylocereus trigonatus* occurs in most mesic regions, but in dry microhabitats since it is epiphytic. The acid flux and carbon-13 isotope composition of *Hylocereus* are consistent with CAM (Fig. 1 and Table 3). Thus the Cactaceae are an excellent group illustrating the adaptive nature of Crassulacean acid metabolism.

Orchidaceae

Second to the Cactaceae, are the Orchidaceae with 11 species represented on St. John. Seven of the 11 species are CAM, and all of these occur in dry habitats. The most conspicuous xerophytic orchids are the two species in the genus *Epi-*
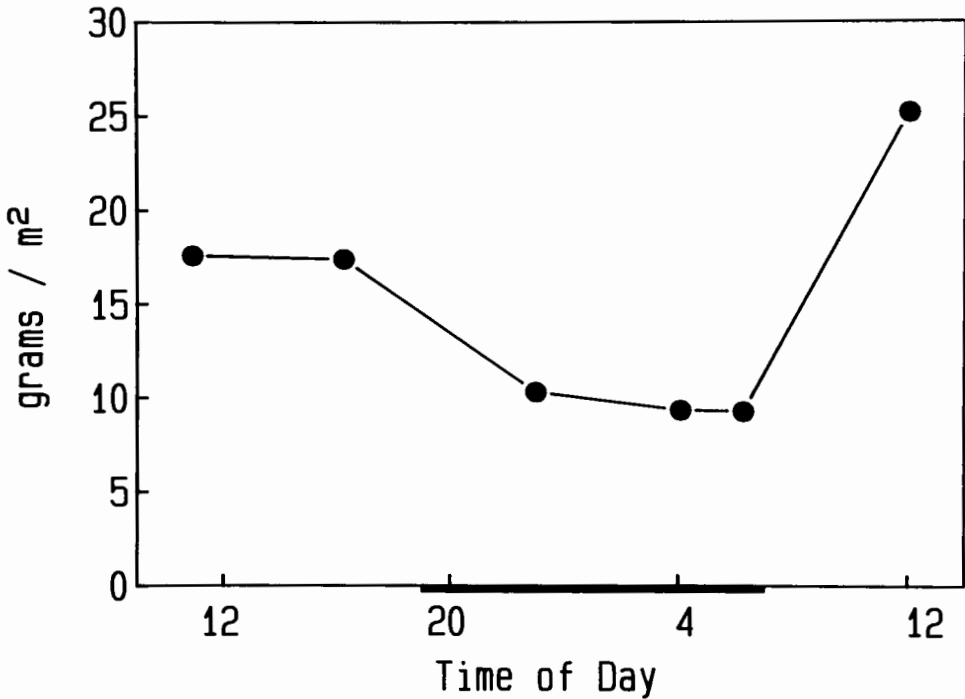
Fig. 2. Vapor pressure deficit, an indication of the potential for evaporation, during a typical summer day.

dendrum. Epidendrum bifidum is very common in the arid-cactus scrub at the east end, but very difficult to see unless in flower. Along with *E. cilare,* these two epiphytes make up the most common CAM orchids of the island. Secondly, are the two epiphytic CAM species of *Oncidium, O. prionochilum* and *O. variegatum.* The terrestrial species, *Tetramicra canaliculata* occurring in dry habitats, is also CAM. Of the two species of *Vanilla, V. barbellata,* occurs as an epiphytic, leafless vine in dry scrub regions and is CAM. The other species, *Vanilla planifolia,* occurs in forest regions, but is also CAM. It is a large leafed species with commercial value. In all probability, the specimens on St. John are cultivated or recently abandoned. The remaining four, nonsucculent species of orchids found on the island, *Ponthieva racemosa, Prescottia oligantha, P. stachyoides,* and *Spiranthes elata,* occur in wet forests and are not CAM-like. Thus the orchids like the cacti are an excellent example of the adaptive nature of CAM-photosynthesis. Those occurring in arid regions and those that are epiphytes are CAM, while the non-succulent mesic forms of the wet forests are not.

Bromeliaceae

Interpretation within the Bromeliaceae is more difficult than for the Cactaceae and the Orchidaceae. Many of the terrestrial bromeliads of the Pitcairnioidae are not CAM (Medina 1974; Medina and Troughton 1974; Griffiths and Smith 1983). This is true of the terrestrial *Pitcairnia angustifolia* of St. John which is frequently growing among the rocks in dry coastal regions. The terrestrial *Bromelia pinquin,*

in the Bromelioidae, however, is an excellent CAM plant with typical characteristics of this adaptive metabolism. Of the remaining bromeliads, all are epiphytic and CAM with the exception of the epiphytic *Catopsis floribunda. Aechmea lingulata,* which grows epiphytically or in shallow soils is a good example of a succulent CAM plant. The six species of *Tillandsia* are all CAM. Thus 7 of the 9 species of bromeliads on St. John are CAM.

Vitaceae

An excellent example of the adaptive nature of CAM is in the genus *Cissus* of the Vitaceae. There are three species of vinelike epiphytes in the genus *Cissus* on St. John. The most succulent, *C. trifoliata,* occurs commonly in the arid-cactus scrub and in the dry-scrub forest. It is a typical CAM plant. *Cissus sicyoides* L., which has somewhat succulent leaves, occurs in dry-scrub but is not CAM. The nonsucculent *C. caustica* Tussac. occurring in even more mesic habitats is not CAM. Thus the most xerophytic *Cissus* species of St. John is CAM, whereas the others are not. This find is consistent with previous observations of the genus *Cissus.* The south African species with succulent leaves and stems, such as *C. juttae* Dtr. et Gilg tend to be CAM, whereas the nonsucculent species are not (Schutte et al. 1967; Milburn et al. 1968; Kluge and Ting 1978).

Agavaceae

There are four species in the Agavaceae found commonly on St. John. All occur in arid habitats including the arid-cactus scrub and the arid-scrub forest. *Agave missionum,* the native species, is very common. Evidently, *A. americanum* occurs sympatrically with *A. missionum. Agave sisalana* is a cultivated form as is *Yucca guatamalensus.* As far as we know, all species of *Agave* are CAM (Woodhouse, Williams, and Nobel 1980) and many species of *Yucca* are (LaPre 1979). All on St. John are CAM.

Euphorbiaceae

The succulent euphorbias of southern Africa and the Mediterranean region are CAM whereas the nonsucculent species within the family are not (Kluge and Ting 1978). Native CAM euphorbias in the New World are extremely rare, and indeed thought to be nonexistent until just recently. The nearly leafless, stem succulent, *Pedilanthus angustifolia,* shows acid fluctuation and thus is most likely a CAM species. *Pedilanthus* is of possible commercial interest inasmuch as it synthesizes a small molecular weight polymer comparable to rubber (Wiggins 1980). It occurs rarely in the arid-scrub forest.

This observation, like that of *Cissus trifoliata,* represents a new find for the New World. There are several species of succulent, south African euphorbias grown as ornamentals in the drier parts of St. John which are undoubtedly CAM (Kluge and Ting 1978).

Piperaceae

The Piperaceae are a large American family with two main genera, *Piper* and *Peperomia.* Pipers are nonsucculent and show no evidence of CAM. They are terrestrial and represented on St. John by *Piper amalgo* L., the Black Waddle.

The succulent species are found in the genus *Peperomia*. Many to most are epiphytic and they range from strong CAM species through species with little indication of CAM (Sternberg et al. 1984; Ting, Bates et al. 1985). Five species of *Peperomia* occur on St. John. All of these are succulent and show some aspects of CAM including a variable acid flux and succulence, but do not have a CAM-like carbon-13 isotope composition (Table 3). *Peperomia magnoliaefolia, P. glabella,* and *P. pellucida* are epiphytic and also occur on shallow soils and rock outcrops. *P. magnoliaefolia* occurs as an epiphyte in the wet forests whereas *P. glabella* and *P. pellucida* occur less commonly in drier regions. *P. humilis* occurs commonly in the dry-scrub on shallow soils and rock outcrops whereas *P. myrtifolia* is rare on shallow soils.

These *Peperomia* species are of interest because they frequently shift from C_3-photosynthesis (Black 1973) to CAM or a modification of CAM called CAM-cycling in response to drought (Sipes and Ting 1985). In CAM-cycling, there is the usual CAM diurnal fluctuation of organic acids, but only daytime uptake of CO_2. Thus they show a combination of C_3 and CAM photosynthesis. Most interestingly, there appears to be a division of labor among the complicated tissues of the leaf with respect to photosynthesis. The upper multiple epidermis shows little metabolic activity, but seems to act as a water storage tissue. The median densely packed palisade parenchyma is C_3-like in photosynthesis and the lower spongy parenchyma is more similar to CAM tissue than the spongy parenchyma found in the typical plant. It is this tissue that has most of the CAM-photosynthesis (Nishio and Ting 1987). The stomata occur within the lower, single layered epidermis.

In the case of the *Peperomia* species occurring on St. John, the CAM activity seems to be related to their epiphytic habit, thus supporting the hypothesis that CAM is an adaptation to dry habitats.

Aizoaceae

There are at least four species of aizoids naturalized on St. John. All of these occur in dry habitats including the arid-cactus scrub and the arid-scrub forest. The most common is *Sesuvium portulacastrum* occurring along the beach areas among rocks on dry, saline areas and around the salt ponds. *Cypselia humifusa, Mollugo nudicaulis,* and *Trianthema portulacastra* are rather rare occurring in dry areas around the salt ponds. Many of the aizoids shift from C_3-photosynthesis to CAM in response to salt and/or water stress (Winter 1973). In the case of *Sesuvium portulacastrum,* CAM was present whenever sampled. *Mollugo* was not CAM, but is a genus known to have C_4-species (Edwards and Walker 1983). *Cypselia* and *Trianthema* were not sampled.

Although none is native to the New World, they are of extreme interest in dry habitats because of their facultative photosynthetic behavior shifting from C_3 to CAM under water stress (Winter 1973). They thus have some features in common with *Peperomia*.

Crassulaceae

There are three species in the Crassulaceae commonly grown as ornamentals on St. John that have become naturalized. The most common is *Bryophyllum pinnatum,* which is becoming a serious, weedy pest in the dry-scrub. In some
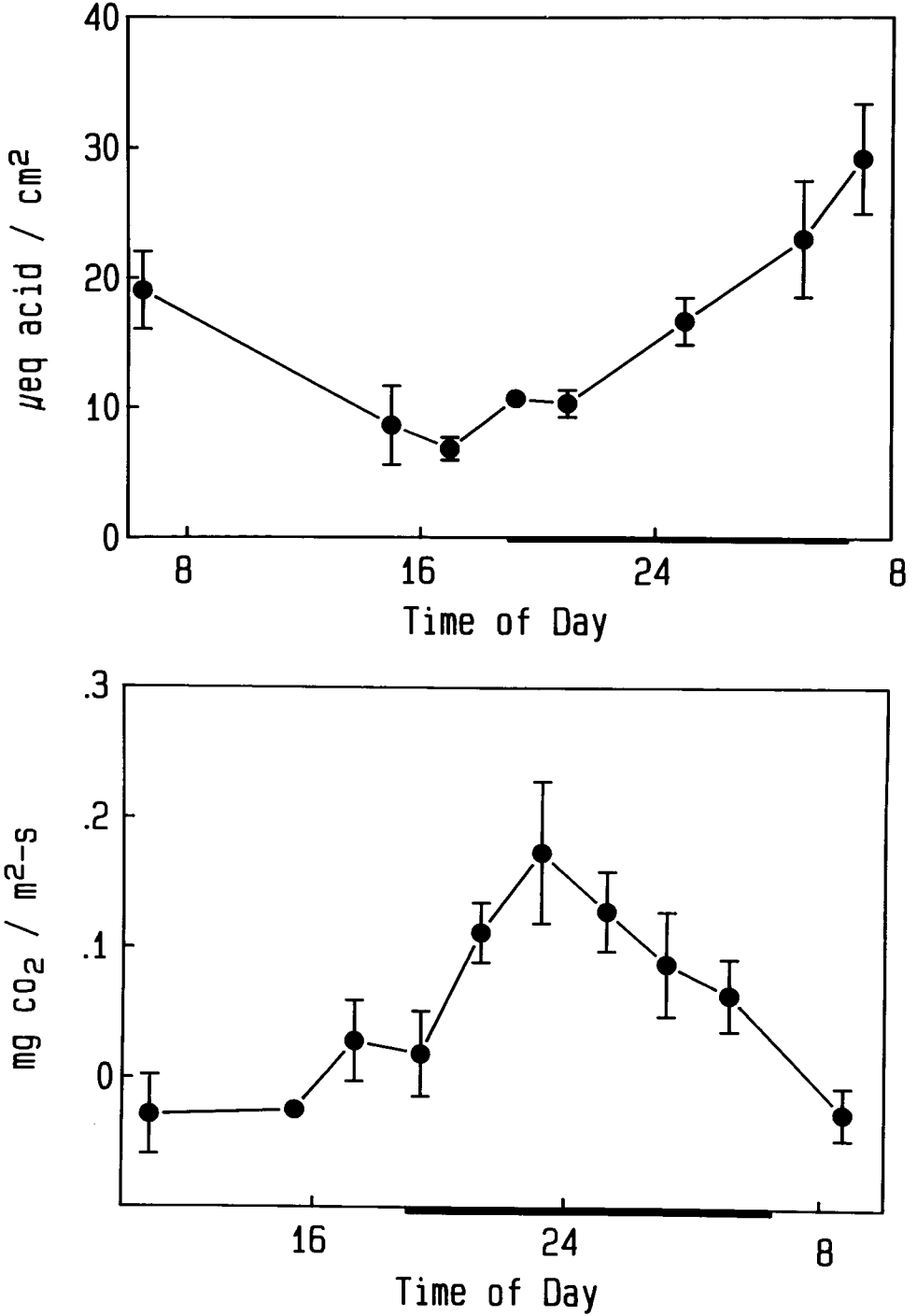
Fig. 3.   Diurnal acid fluctuation in *Sansevieria fasciculata* during a 24-h period in the summer (upper panel). Diurnal CO_2 fixation pattern for *Sansevieria fasciculata* during a 24-h period in the summer (lower panel).

areas, this *Bryophyllum* forms dense stands crowding out native herbaceous vege-
tation. *Bryophyllum tubiflorum* and *B. daigremontianum* are seen less commonly
and do not at this time appear to be a problem. All are CAM and have been
extensively studied. In fact, these three species are probably the most frequently
studied examples of CAM plants (Kluge and Ting 1978).

Liliaceae

The succulent CAM species of Liliaceae are native to southern Africa and the
Mediterranean region (Kluge and Ting 1978). There are two common exotic
species of CAM, succulent lilies growing on St. John in arid regions. *Aloe bar-
bedensis* (commonly called Aloe vera), cultivated for the presumed medicinal
value of its mucilage is relatively common. *Sansevieria trifasciata* which was
commonly grown around sugar mill plantations has escaped and is thoroughly
naturalized in arid regions of the arid-scrub. It is a serious weedy pest occupying
vast disturbed regions within the arid-scrub. Both are strong CAM plants (Kluge
and Ting 1978) and highly adapted to the drier regions of the island. The success
of *Sansevieria* is attributable to CAM-photosynthesis (Fig. 3) resulting in survival
in the dry arid-scrub and its vigorous vegetative reproduction by rhizomes.

Clusiaceae

There are two tree species in the Clusiaceae that occur on St. John, *Mammea
americana* L. and *Clusia rosea*. Both occur in forests, but *Clusia rosea* can be
found occasionally in dry habitats such as the arid-scrub. *Clusia* is of particular
interest because it is the only known genus of true dicotyledonous tree known to
possess CAM-photosynthesis (Ting, Lord et al. 1985).

Many of the species of *Clusia* found in the New World tropics including *Clusia
rosea* are hemiepiphytes or "stranglers." The hemiepiphytes start their life cycle
as true epiphytes sending roots around host trees and eventually to the soil. After
a period of growth depending upon the species, the hemiepiphytes will become
rooted and in the case of *C. rosea* become a dominant forest tree shading out and
to some extent restricting the growth of the host (Putz and Holbrook 1986). Carbon
isotope analyses, acid titration data, and diurnal gas exchange patterns for *Clusia
rosea* are shown in Table 3 and Figure 4. Although apparently CAM at all times,
epiphytic stages appear to be more CAM-like than tree forms (Sternberg et al.
1987). The latter could be the result of greater water stress when epiphytic (Sinclair
1984; Putz and Holbrook 1986). Before precipitation when the plants are drought-
ed, all CO_2 uptake is at night; however, after precipitation, stomata remain open
during the early morning hours resulting in photosynthetic CO_2 fixation (Fig. 4).
During most of the day, there is no gas exchange typical of CAM plants.

To some extent, the finding of CAM in *Clusia* was unexpected because it grows
as a tree in wet and dry forests. However, since it is epiphytic for part of its life
cycle, CAM could have been predicted. And indeed as mentioned above, it is
more CAM-like when an epiphyte than when a free standing, rooted tree (Sternberg
et al. 1987).

Although genera with hemiepiphytes are common in the tropics, only *Clusia*
and *Ficus* in the Moraceae occur on St. John. The two species of hemiepiphytic
Ficus on St. John, *F. trigonita* L. and *F. citrifolia* Mill., are not CAM, nor are any
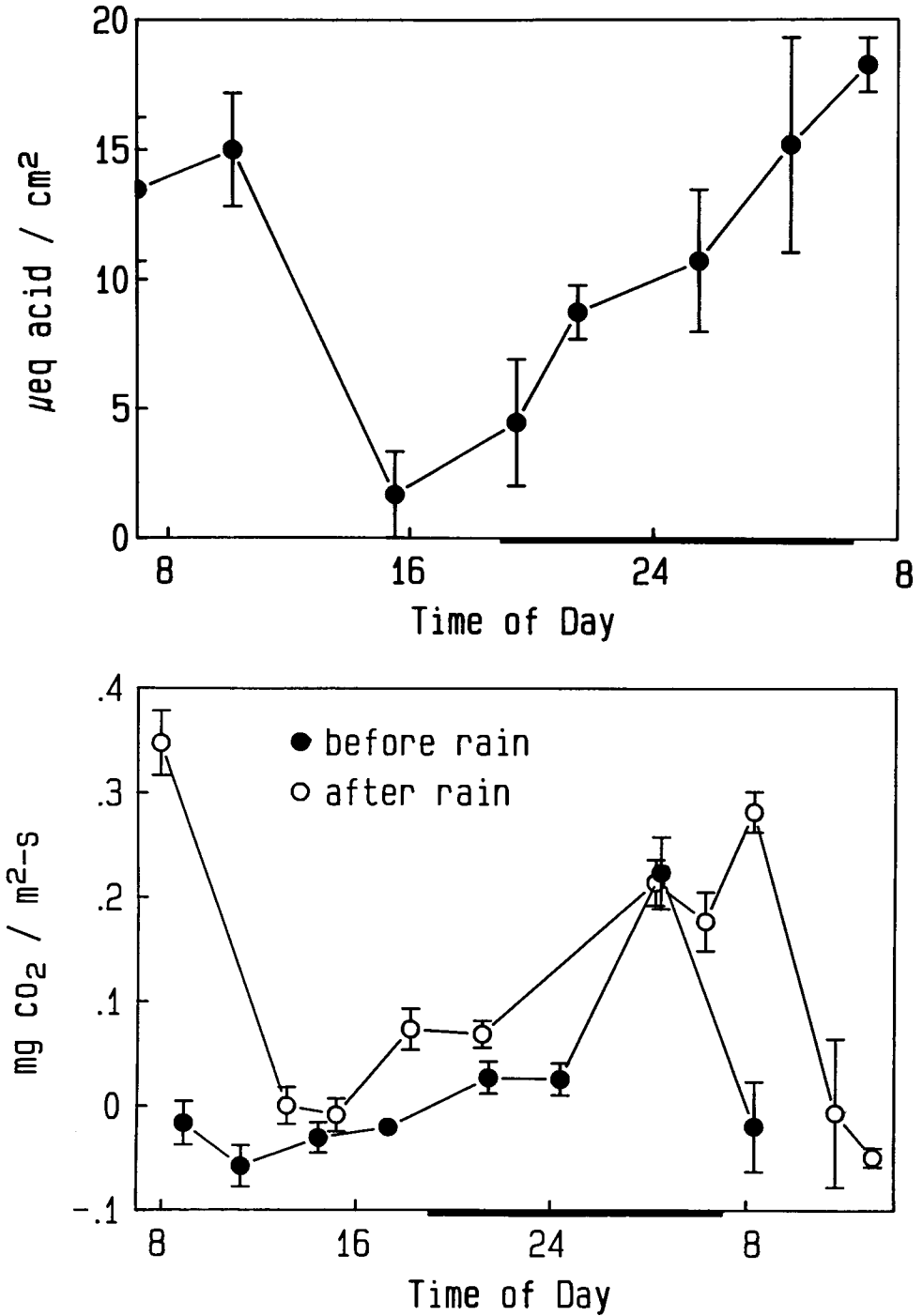
Fig. 4. Diurnal acid fluctuation in *Clusia rosea* during a 24-h period in the summer (upper panel). Diurnal CO_2 fixation before rain and after a rain episode by *Clusia rosea*. The effect of rain is to enhance stomatal opening and hence CO_2 fixation and to extend CO_2 fixation into the early morning hours (lower panel).

of the other *Ficus* species studied (Ting et al. 1987). To date, only *Clusia* among the many hemiepiphytes of the tropics is CAM. This could account for its occurrence occasionally in the arid-scrub regions. As well, it is common to find *Clusia rosea* seedlings growing in shallow soils or on rock outcrops in full sun under severe water stress.

Araceae

There are three species of epiphytic, nonsucculent aroids found on St. John in the dry and rain forests. None is CAM. *Anthurium crenatum* (L.) Kunth., *A. cordatum* (Willd.) Don., and *A. selloum* C. Koch are common in forest regions. All will grow terrestrially in exposed areas in shallow soils or on rock outcrops or as true epiphytes.

Commelinaceae, Nyctaginaceae, Portulacaceae

Three families with semisucculent to succulent species occurring in the arid-cactus scrub and arid-scrub habitats are the Commelinaceae, Nyctaginaceae, and the Portulacaceae. The five common species of the Commelinaceae do not appear to be CAM. They occur as ground covers in the drier parts of the island and at least the ornamental *Rhoeo spothacea* is seen as a rock epiphyte particularly around habitation.

The Nyctaginaceae are represented by three species of *Boerhaavia* and one *Pisonia*. These are common in dry disturbed areas, but none is CAM. They do possess C_4-photosynthesis as judged from their Kranz anatomy (Edwards and Walker 1983), a highly adaptive photosynthetic metabolism common to herbaceous tropical grasses and dicotyledonous herbs of desert regions (Black 1973).

The Portulacaceae are represented by five species of *Portulaca* that also have C_4-photosynthesis and perhaps CAM (Koch and Kennedy 1982) and two species of *Talinum* with CAM (Kluge and Ting 1978; Martin and Zee 1983). The herbaceous *T. paniculatum* occurs commonly as a ground cover in exposed regions of the arid-scrub. The less common, woody *T. triangulare* occurs in similar habitats. The family is interesting because it has species with C_3-photosynthesis, C_4-photosynthesis, and CAM-photosynthesis (Martin and Zee 1983).

Batidaceae and Cruciferae

Two families are represented by single succulent species that are not CAM. *Batis maritima* in the Batidaceae and *Cakile lanceolata* in the Cruciferae have succulent leaves related to their growth in saline regions of the arid-cactus scrub and arid-scrub forests particularly around salt pond regions. The succulence here is undoubtedly related to the accumulation of salt, and not to organic acid accumulation as in CAM (Ting 1985).

Cassythaceae, Cuscutaceae, Loranthaceae

There are three families with epiphytic, vine-like parasitic flowering plants on St. John. The very common *Cassytha filiformis* L. in the Cassythaceae and the two species of *Cuscuta* in the Cuscutaceae are somewhat succulent, but largely nonphotosynthetic and thus not potentially CAM plants. The mistletoe, *Dendro-*

pemon caribaeus K. & Urb., in the Loranthaceae, has green succulent leaves with some photosynthesis (unpublished data). There is no evidence of CAM-metabolism. All of these parasites can be found in arid regions particularly in the arid-scrub forests.

<div align="center">CONCLUSIONS</div>

On St. John, there are approximately 22 families of flowering plants that contain either succulent or epiphytic species. Of these, there are about 70 species within 18 families that are succulent. Over 45 are known to be CAM. For the most part, these are found primarily in the families Cactaceae, Bromeliaceae, Orchidaceae, Piperaceae, and Agavaceae. The non-CAM succulent species are in the Nyctaginaceae and Portulacaceae, although *Talinum* of the latter family is CAM. The Aizoaceae has succulent species that shift from C_3-photosynthesis to CAM under salt and/or water stress (Winter 1973).

Ten families of flowering plants have epiphytic species. Of the approximately 28 species of epiphytic flowering plants, about 21 show CAM.

The distribution of CAM succulents on St. John clearly supports the hypothesis that CAM is functionally related to drought resistance. For the most part, all of the CAM succulents occupy arid and dry niches. The vast majority including the cacti, bromeliads, agaves, peperomias, and orchids are found in the arid-cactus scrub and arid-scrub forests. The bromeliads, cacti, and peperomias of the dry and wet forests are epiphytic or occur as rock epiphytes and on very shallow rocky soils, and thus also occupy dry niches. A most interesting succulent with CAM is *Clusia rosea* found as a hemiepiphyte in the wet and dry forests. Being epiphytic when young, it is not inconsistent with the drought adaptive hypothesis of CAM.

Another excellent illustration of the adaptive nature of CAM is within the genus *Cissus*. The arid-region *Cissus* species of southern Africa such as *C. juttae* have succulent leaves and water storage stems. These are excellent examples of CAM plants. The mesic *Cissus* species are not succulent and not CAM. Of the three species of *Cissus* on St. John, the species common in the arid-cactus scrub and in the drier parts of the arid-scrub, *C. trifoliata,* is CAM. The other two species occurring in less arid regions are not CAM.

Since water is the single most important factor the world over limiting plant growth, one might wonder why CAM is not more common. In part, the answer might be that CAM results in slow growth that is energetically expensive. CO_2 accumulation at night is less efficient that during the day when it is accompanied directly by CO_2 assimilation through photosynthesis (Edwards, Foster, and Winter 1982). Not only is the CO_2 fixed metabolically into malic acid, but the acid is transported and accumulated in storage vacuoles, a process requiring much ATP (Lüttge, Smith, and Winter 1982). During the subsequent day period, the malic acid is further metabolized to CO_2 before photosynthesis occurs. Thus it appears that slow growth is a consequence of drought adaptation by Crassulacean acid metabolism.

Some groups of plants have partially overcome the problem of slow growth by initially functioning as C_3 plants and then shifting to CAM at later stages of development or in response to water stress (Winter 1973; Winter et al. 1978; Guralnick, Rorabaugh, and Hanscom 1984; Holthe, Sternberg, and Ting 1987). On St. John, CAM species in the Aizoaceae and Piperaceae have the capacity to shift from C_3-photosynthesis to CAM.

A comparison between St. John, an arid tropical island, and the deserts of North America is superfically possible. The most prominent desert, CAM succulents of North America are found in the Cactaceae, Agavaceae, and the genus *Dudleya* of the Crassulaceae (see Gentry 1982; Shreve and Wiggins 1964; Wiggins 1980; Britton and Rose 1919–1923; Ting and Jennings 1976). On St. John, the predominant terrestrial CAM succulents of the arid scrub region are in the Cactaceae and Agavaceae.

There are virtually no epiphytic succulent plants of the North American deserts, the Bromeliaceae, Piperaceae, and Orchidaceae only becoming common towards southern Mexico as the tropics are approached (Rzedowski 1983). On St. John, epiphytic CAM species of the Orchidaceae and the Bromeliaceae are common. Evidently, epiphytism even though frequent in dry environments, requires higher humidity than found in typical deserts.

The other major families with CAM such as Euphorbiaceae, Liliaceae, and Asclepiadaceae are represented in both the Caribbean and the North American deserts, but not by CAM succulent species, with the single possible exception of *Pedilanthus* in the Euphorbiaceae.

The Aizoaceae, although present in arid regions of St. John and occasionally adjacent to North American deserts, are not native (Jacobsen 1960).

The southern African deserts and arid regions, which are only rivaled by the North and South American deserts for CAM, have the Aizoaceae, Liliaceae, Euphorbiaceae, Portulacaceae, Asclepiadaceae, and Crassulaceae as the predominant families with CAM succulents (Kluge and Ting 1978; Court 1981). Thus with the exception of the Crassulaceae represented primarily by *Dudleya* and a few other species, the affinities between the CAM succulents of southern Africa and the northern hemisphere are not apparent.

A comparison with the South American deserts is not possible. However, the predominant terrestrial CAM succulents are in the Cactaceae and thus affinities with the Caribbean and the North American deserts are evident.

In conclusion, CAM-photosynthesis is a metabolic adaptation to arid and otherwise dry habitats. The distribution of CAM succulent species on the arid tropical St. John of the Caribbean clearly illustrates and supports this hypothesis.

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