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Physiological Ecology of the Bromeliaceae

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Hence also it is that some plants flourish best in one climate, and others in another; that much moisture is kindly to some, and hurtful to others; that some require a strong, rich, and others a poor, sandy soil; some do best in the shade, and others in the sun, &c. And could our eyes attain to a sight of the admirable texture of the parts on which the specifick differences in plants depend, what an amazing and beautiful scene of inimitable embroidery should we behold?—Stephen Hales, 1727

Abstract

The physiological ecology of members of the Bromeliaceae is reviewed with an emphasis on photosynthesis and water relations. Terrestrial and epiphytic species are, for the most part, treated separately. Water relations, photosynthetic pathways, and photosynthetic responses to light, temperature, drought, atmospheric moisture, elemental nutrients, and pollutants are considered from an ecological perspective. In addition, appendices provide values of numerous ecophysiological parameters for all species studied thus far. Results of this review include the following: (1) the ecophysiology of terrestrial and epiphytic species is surprisingly similar; (2) approximately two-thirds of bromeliads are CAM plants and occupy arid sites or are epiphytic; (3) many species are adapted to full or partial shade, yet can grow in full sunlight; (4) photosynthesis is optimal when day temperatures are warm and night temperatures are cool; (5) species with heavy trichome indumenta on their leaf surfaces are capable of absorbing atmospheric water vapor, yet improvement of tissue water relations is unlikely; (6) heavy trichome covers also suppress CO_2 exchange when leaf surfaces are wetted; (7) high levels of recycling of respiratory CO_2 via CAM occur in many species, especially under stress; and (8) tissue osmotic and water potentials of nearly all bromeliads investigated are seldom more negative than -1.0 MPa. A potential explanation of the mechanisms underlying maintenance of high tissue water potentials despite large water losses during droughts is discussed. In summary, the diversity of physiological adaptations to the environment in the few bromeliads studied thus far is impressive, but likely will be surpassed with investigation of more species in the Bromeliaceae.

I. Introduction

A. PHYSIOLOGICAL ECOLOGY OF THE BROMELIACEAE

After exploring the enormous anatomical, morphological, and ecological variability among the approximately 2500 species in the Bromeliaceae (Benzing, 1980, 1990; Downs, 1974; Isley, 1987; Kress, 1989; Mez, 1896; Padilla, 1973; Rauh, 1979; Smith & Downs, 1974, 1977, 1979), it is easier to appreciate the bewildering array of physiological adaptations possible in this family. Differences in life form, e.g., terrestrial versus epiphytic, or tank versus atmospheric (see Benzing, 1980), entail radically different modes of water and nutrient acquisition. Likewise, differences in photosynthetic pathway, e.g., C_3 or CAM (see Kluge & Ting, 1978), necessitate numerous alterations at the biochemical level. Furthermore, successful colonization of different habitats, e.g., exposed versus shaded, rain forest versus cloud forest, coastal versus inland, requires the integration of suites of adaptive characters at all levels, i.e., biochemical, anatomical, physiological, and organismal.

The purpose of this review is to elucidate the physiological adaptations of various bromeliads to their environment, with an emphasis on carbon and water relations. Such an approach is hardly comprehensive; however, it is justified for two reasons. First, this approach reflects past and current emphases in research in physiological plant ecology; few ecophysiological studies include aspects other than carbon and water relations. Second, although not perfect, the causal links between carbon relations and survival, growth, and reproduction are indisputable. Thus, measurements of photosynthetic activity can often be extrapolated to plant performance in the field. Further-

more, because the water relations of a plant are so directly tied to activity at both a cellular and organismal level, determinations of the water status of a plant can provide considerable insight into the success or demise of a plant in a particular habitat. Of course, there are always exceptions to these generalizations, and some of these exceptions may prove crucial in understanding the biology of a species. Nonetheless, detailed information on the carbon and water relations of a species provides a first approximation in understanding whether a plant is flourishing or fading in a particular environment.

The title of this review, "Physiological Ecology of the Bromeliaceae," is admittedly overzealous. Only several per cent of the species in the Bromeliaceae have been examined from an ecophysiological perspective. Because of this, the few generalizations made throughout this review, even when caveats are included, must be applied with caution to other species. Many of the ecophysiological investigations of bromeliads have focused exclusively on one of two species, the highly derived (Tomlinson, 1969) epiphyte *Tillandsia usneoides* (Spanish moss) or the agronomically important terrestrial species *Ananas comosus* (pineapple). Extrapolation of results obtained with either of these species to the entire family, or even to a subset of species within the family, is potentially problematic.

Excluding introductory material, conclusions, and appendices, this review comprises four sections. The first deals with terrestrial bromeliads only. Given the limited number of studies of the ecophysiology of terrestrial bromeliads, as well as the disproportionate number dealing exclusively with *A. comosus,* this section divides the material according to individual species. By comparison, the next two sections on epiphytic bromeliads divide the material into water relations and physiological responses to environmental factors for all species of epiphytic bromeliads viewed collectively. A fourth section is devoted to the special topic of the recycling of respiratory CO_2 via the CAM photosynthetic pathway. This phenomenon has received the attention of several intensive studies and is not limited solely to terrestrial or epiphytic bromeliads.

Research limited to the biochemistry, physiology, or elemental nutrition of bromeliads was considered beyond the scope of this review. In addition, speculative evolutionary scenarios, e.g., the long-standing debate whether the progenitors of modern-day epiphytes were shade- or sun-adapted (Benzing & Burt, 1970; Medina, 1974; Pittendrigh, 1948; Schimper, 1888; Smith, 1989; Tietze, 1906), are not included in this review.

The usage of several terms throughout the review requires clarification. A plant growing on the ground is considered a "terrestrial bromeliad," although it may be found in the trees as well and qualify as an "epiphytic bromeliad." If so, discussion of this species would appear in both the appropriate sections. A "tank epiphyte" relies on water and nutrients trapped in the overlapping bases of numerous leaves arranged in a rosette (Benzing, 1980). An "atmospheric epiphyte" obtains its water and elements by surface absorption via numerous, multicellular trichomes covering the leaf and stem surfaces of the plant.

The appendices found at the end of the review comprise compendia of quantitative data on the ecophysiology of bromeliads for all species investigated thus far. Appendix I lists photosynthetic pathways, criteria for their determination, and stable carbon isotope ratios. Appendix II lists water and osmotic potentials. Appendix III presents rankings of degrees of sun or shade adaptation of photosynthesis in 21 species studied

by Benzing and Renfrow (1971a). Appendix IV lists data pertinent to adaptation of the photosynthetic apparatus to high and low light. Appendix V lists representative photosynthetic (CO_2 uptake) rates, transpiration (H_2O loss) rates, stomatal conductances, and water-use efficiencies. Stomatal sizes and densities are listed in Appendix VI. Appendix VII lists acid accumulation data for all CAM species, and Appendix VIII presents rates of photosynthetic O_2 evolution and respiratory O_2 uptake (or CO_2 release).

B. PHOTOSYNTHETIC PATHWAYS IN THE BROMELIACEAE

In spite of an intriguing description of suberized bundle sheath cells in some members of the Bromeliaceae (Tomlinson, 1969), an anatomical feature characteristic of C_4 plants, there are no confirmed reports of C_4 species in this family. Of the species investigated as of this review, 76 (31% of the total) are C_3 plants and 173 (69%) exhibit CAM or C_3-CAM intermediacy (Appendix I). Fifty-four (70%) of the 77 species of terrestrial bromeliads are CAM (or C_3-CAM), whereas 120 (69%) of the 173 species of epiphytic bromeliads exhibit evidence of CAM (or C_3-CAM).

Nearly all atmospheric epiphytes are CAM plants. On the other hand, tank epiphytes exhibit both the C_3 and CAM modes of carbon metabolism. Those tank species with narrow, stiff leaves covered with trichomes exhibit CAM, while those with broader, thinner leaves lacking dense trichomes are typically C_3 plants. As discussed by Smith (1989), although C_3 bromeliads tend to occupy shaded, less stressful habitats, e.g., the forest understory, while CAM species occur at higher frequencies in more arid habitats, numerous exceptions exist in both sets of plants. It is probably safe to conclude that the water-conservative CAM mode of photosynthesis is often beneficial to terrestrial bromeliads that frequently occupy arid sites, and to epiphytic species, especially those lacking the tank habit, in the potentially arid microclimate of the host tree canopy (Sinclair, 1983).

There is only one species known to clearly exhibit C_3-CAM intermediacy. Under well-watered conditions, *Guzmania monostachia* exhibits a C_3 gas exchange pattern; however, under drought stress, this epiphyte switches to CAM (Lüttge et al., 1986c; Medina, 1987; Medina et al., 1977). Thus, if CAM occurs frequently enough, the $\delta^{13}C$ value of this plant can be less negative than a typical C_3 value. On the other hand, the $\delta^{13}C$ values of most individuals are in the range of values typical of C_3 plants (Appendix I). The latter individuals have apparently experienced little stress during the lifetime of the tissue measured. Other genera of interest regarding the possibility of photosynthetic pathway intermediacy include *Greigia, Puya, Billbergia, Catopsis, Nidularium, Vriesea*, and *Wittrockia.* Various species in these genera exhibit characteristics of CAM, i.e., intermediate $\delta^{13}C$ values or nocturnal increases in acid content, often without concomitant CO_2 uptake, while others do not (Appendix I). A most intriguing genus in this regard is *Puya*; stable carbon isotope ratios of several species indicate C_3-CAM intermediacy. Unfortunately, field work on these unusual and often inaccessible plants presents a formidable challenge.

II. Photosynthesis and Water Relations of Terrestrial Bromeliads

A. PHOTOSYNTHESIS AND WATER RELATIONS OF *ANANAS COMOSUS*

More physiological research has focussed on *Ananas comosus* (pineapple) than on any other terrestrial bromeliad. Reasons for this are obvious given the commercial

value of this agricultural species. Not surprisingly, only a few studies have examined "wild" plants in their natural habitat; most results have been obtained in the field, greenhouse, or growth chamber using cultivars which have been selected for agriculturally important traits. Thus, the results of research using these plants should be extrapolated with caution to other species in the family. Although a considerable amount of work has been done on the biochemistry, physiology, and elemental nutrition of *A. comosus* (e.g., Carnal & Black, 1979; Cote et al., 1989; Crews et al., 1975; Dodson, 1968; Everson et al., 1983; Kenyon & Black, 1986; Moradshahi et al., 1977; Sideris et al., 1938), this section will focus on photosynthesis and water relations only as they relate to the ecophysiology of this species.

Leaves of *A. comosus* are thick, tough, and covered by a thick cuticle. Thus, when leaf sections were desiccated over $CaCl_2$ for 120 hours, they lost relatively small amounts of water (Benzing & Burt, 1970). Similarly, months of desiccation were required to reduce the water content of detached shoots by over 50% (Sideris & Krauss, 1928, 1955). Detached leaf tissue that had been desiccated also regained water very slowly (Benzing & Burt, 1970). Desiccation of the leaves results in preferential water loss from the water-storage parenchyma (Ekern, 1965), as has been found for stem tissues of desert cacti (Barcikowski & Nobel, 1984). As a result of the above morphological features, *A. comosus* exhibits very low rates of transpiration during either day or night (Ekern, 1965; Joshi et al., 1965; Neales et al., 1968). As expected for a xerophytic CAM plant, its water-use efficiency (CO_2 uptake/water lost; mass basis) can be quite high, up to 0.050 (Joshi et al., 1965; Nose et al., 1981).

Studies of the water relations and photosynthetic responses to drought in *A. comosus* are surprisingly rare given its importance as a crop species. Nose et al. (1981) grew plants in a greenhouse in Okinawa at four levels of soil moisture, ranging from "excessive moisture" to "the permanent wilting point" (presumably the wilting point of a typical C_3 crop species). Rates of nocturnal CO_2 uptake were optimal under the two intermediate moisture treatments, although differences among treatments were often small. Bartholomew (1982) reported decreases in CAM activity and growth when plants were watered monthly as opposed to weekly. Unfortunately, tissue water potentials were not measured in either study, making the results difficult to interpret.

There are only two studies that report leaf water potential in *A. comosus*. Wambiji and El-Swaify (1974) and Kadzimin (1975) monitored water potentials after addition of salt to the soil or during drought. Water potentials decreased to between –2.0 and –3.0 MPa under these treatments. Maximum growth occurred at –0.1 and –0.5 MPa and declined at –1.0 MPa (Kadzimin, 1975).

Photosynthetic responses to light in *A. comosus* have been investigated in two studies using well-watered plants grown in a greenhouse. Nose et al. (1977) measured the response of nocturnal CO_2 exchange to light levels ranging from approximately 200 to 1500 $\mu mol\ m^{-2}s^{-1}$ (all light levels given as photosynthetic photon flux density). Higher light levels consistently elicited greater amounts of nocturnal CO_2 uptake, suggesting that the saturation level of CO_2 uptake is at or above 1500 $\mu mol\ m^{-2}s^{-1}$. Likewise, Sale and Neales (1980) found increasing amounts of nocturnal CO_2 uptake under increasingly sunny days. Nocturnal accumulations of acidity in the leaves also increased with increasing light levels (Aubert, 1971; Bartholomew & Kadzimin, 1977) and, furthermore, exceeded the amounts of CO_2 absorbed by nearly two times, indicative of recycling of respiratory CO_2 (Sale & Neales, 1980). It is quite likely that much of this CO_2 recycling results in the production of citrate instead of malate

(Borland & Griffiths, 1989; Sideris et al., 1948; see Lüttge, 1988 for discussion of citrate accumulation). Sale and Neales (1980) reported similar responses to light in field-grown plants. Furthermore, growth rates correlated well with patterns of CO_2 exchange for plants grown at different light levels.

Growth of *A. comosus* at light levels of 60 and 600 μmol $m^{-2}s^{-1}$ resulted in the development of classic sun/shade features (Borland & Griffiths, 1989). Plants grown at low light exhibited lower maximum CO_2 uptake rates, lower light levels at which photosynthesis saturated, lower light compensation points, and higher apparent quantum yields, relative to plants grown at higher light. These differences were more apparent in plants grown with supplemental nitrogen, relative to those that were nitrogen-deficient.

Results of the above studies indicate that *A. comosus* performs maximally at high light levels, i.e., near full sunlight. On the other hand, although numerous methodological differences make comparisons difficult, other studies indicate otherwise. Exposure of *A. comosus* in a growth chamber to the same light level but for different photoperiods, i.e., different diurnal amounts of light, resulted in only small differences in plant biomass or degree of CAM, as measured by diurnal changes in tissue acidity (Friend & Lydon, 1979). Also, 24-hour CO_2 uptake totals of plants grown at three different photoperiods, manipulated by artificial shading or supplemental lighting, were similar at the two longer photoperiods regardless of instantaneous daytime light levels ranging from approximately 150 to 1000 μmol $m^{-2}s^{-1}$ (Nose et al., 1986). Although rates of nocturnal CO_2 uptake were higher under the shorter photoperiods, plants grown under the longer photoperiods exhibited greater amounts of CO_2 uptake in the late afternoon (Phase IV).

Further work by Nose and coworkers also suggests that *A. comosus* may be incapable of utilizing high light levels. Using potted plants, Nose et al. (1981) found only slight increases in nocturnal CO_2 uptake with increasing daytime light level from approximately 600 to 1200 μmol $m^{-2}s^{-1}$. Similarly, plants grown hydroponically exhibited increased rates of nocturnal CO_2 uptake from 200 to 500 μmol $m^{-2}s^{-1}$ but not from 500 to 1100 μmol $m^{-2}s^{-1}$ (Nose et al., 1985).

The differences in experimental approaches in the studies described above make generalizations about the light requirements of *A. comosus* difficult. There is evidence for both a relatively low and a high light requirement for maximal photosynthetic activity in this CAM bromeliad. It is interesting to note in light of these conflicting findings that the putative progenitors of *A. comosus* are found in the shade of forest understories (Medina et al., 1991a), while cultivars are usually grown in full sunlight. Furthermore, investigations of these progenitors in the field and laboratory emphasize the complexity of the physiological responses to light in this cultivated species. Medina et al. (1991b) collected two cultivars from Venezuela and grew them under high and low light levels in the laboratory. The cultivar collected from partially shaded swamps exhibited the highest CO_2 uptake rates, regardless of growth light level, although nocturnal accumulations of malate were comparable in the two cultivars. In the field in Venezuela, on the other hand, nocturnal increases in acidity were greater in cultivars growing fully exposed relative to cultivars and a related species growing in forest understories (Medina et al., 1993).

The optimum temperatures for nocturnal CO_2 uptake in *A. comosus* have been investigated in several studies. Daytime temperatures of approximately 30°C followed by night temperatures of 15-25°C stimulated nocturnal CO_2 uptake (Neales et al.,

1980). Constant day/night temperatures, as well as inverted temperature regimes, i.e., higher night than day temperatures, typically reduced rates of CO_2 uptake during the night, and occasionally during the day as well. Similar results were obtained by Aubert (1971), Connelly (1972), and Neales (1973). In general, rates of nighttime CO_2 uptake (Phase I) were inversely correlated with rates of daytime CO_2 uptake (Phases II and IV; Connelly, 1972; Neales, 1973; Neales et al., 1980). Bartholomew (1982) reported fairly broad temperature optima (day and night) for CO_2 uptake. Nocturnal CO_2 uptake was inhibited when daytime temperatures exceeded 35°C, nighttime temperatures exceeded 26°C, or, as noted above, day/night temperatures were held constant.

Thus, maximal photosynthetic activity in *A. comosus* apparently occurs at a day/night temperature regime centered around 30/15°C. One potential problem in interpreting the results of the above studies, however, lies in the relatively low light levels (between approximately 400 and 800 $\mu mol\ m^{-2}s^{-1}$) used during most experiments (Bartholomew, 1982; Neales, 1973; Neales et al., 1980). It is quite possible that different results might have been obtained had plants been exposed to higher light levels.

The influence of different amounts of nitrogen in the rooting medium on photosynthesis in *A. comosus* has been examined in two studies. Nose et al. (1985) reported a nitrogen-use efficiency (rate of CO_2 uptake as a function of tissue nitrogen content) in this species of only 1–2% of that in most other plants! Reasons for this unusual finding are unclear. They also found a direct correlation between leaf nitrogen content and nocturnal CO_2 uptake rates in hydroponically grown plants. Likewise, rates of nocturnal CO_2 uptake were higher in plants grown with supplemental nitrogen, relative to those grown without added nitrogen (Borland & Griffiths, 1989). Furthermore, nitrogen deficiency, when combined with relatively high light, resulted in greater contributions of respiratory CO_2 to nocturnal increases in tissue acidity, as well as slight increases in the contribution of citrate to the total acid pool in plants grown at high and low light.

Medina et al. (1991a) found higher tissue nitrogen contents in four species of *Ananas,* including *A. comosus,* in plants growing in the shade relative to those in the sun. They postulated that shade plants may have greater access to nitrogen in the forest understory and/or that the higher nitrogen concentration in leaves of shade plants may simply reflect the lower specific leaf weight characteristic of shade versus sun leaves. In a subsequent field study in Venezuela, however, leaf nitrogen contents of cultivars growing in full sunlight were greater than those of cultivars and a related species growing in forest understories (Medina et al., 1993). It is clear that information on the physiological responses of *A. comosus* to nitrogen availability, not to mention other essential elements, is too scarce to warrant generalization at this time.

In summary, in spite of the importance of *A. comosus* as an agricultural species, there are surprisingly few studies on photosynthesis and water relations, especially in an ecophysiological context, of this CAM bromeliad. Until more work is done, both in the field and in the laboratory, little can be said with confidence about the ecophysiology of this species.

B. PHOTOSYNTHESIS AND WATER RELATIONS OF *BROMELIA HUMILIS*

The ecophysiology of *Bromelia humilis,* a terrestrial CAM bromeliad, has been

studied in the field in northern Venezuela, as well as in the laboratory using greenhouse-grown specimens. In the field, three forms can be identified: dark green plants in partial shade, light green plants in the sun, and yellow plants also growing fully exposed. Shade plants were larger and had thinner leaves that contained more chlorophyll and nitrogen than those of the exposed plants (Lee et al., 1989; Medina et al., 1986a). In all forms, leaf osmotic and water potentials were seldom more negative than –1.2 MPa. Furthermore, only small differences in water relations were observed between the wet and dry seasons in northern Venezuela, although irrigation during the dry season resulted in less negative leaf osmotic and water potentials (Lee et al., 1989). Maximum *in situ* rates of nocturnal CO_2 uptake measured during the wet season were highest in the green, exposed plants, intermediate in the shaded plants, and lowest in the yellow, exposed form (Lee et al., 1989). Nighttime increases in tissue acid content reflected these differences in CO_2 uptake, although to a lesser degree. In addition, citrate comprised approximately 50% of the total amount of acid accumulated at night in the shaded and yellow forms during the dry season, and up to 20% in the shaded plants in the wet season as well.

Overall, the results of field work with *B. humilis* in northern Venezuela indicate that this species may be better adapted to partial shade than full sunlight. Although *in situ* photosynthetic rates were higher in the green, exposed plants, relative to those in the shade, the exposed forms were often photoinhibited in the field and grew more slowly than the plants in the shade (Lee et al., 1989; Medina et al., 1986a).

Laboratory work with *B. humilis* collected from Venezuela supports the above conclusions. Plants were grown at two light levels (20–30 μmol $m^{-2}s^{-1}$ and 700–800 μmol $m^{-2}s^{-1}$) and two levels of nitrogen nutrition (Fetene et al., 1990). Plants grown under low light exhibited classic acclimation responses to shade, e.g., large granal thylakoid stacks, high chlorophyll concentrations, and lower light compensation points. On the other hand, dark CO_2 uptake rates (on a leaf area basis), nocturnal increases in malate, quantum yields, and saturation levels of daytime photosynthesis were similar in both sets of plants, although differences were noted between plants grown at the two levels of nitrogen. Enhanced nocturnal acid accumulations in plants grown at high light and high nitrogen were attributable to accumulations of citrate. Only plants grown under high light contained substantial amounts of zeaxanthin, a pigment most likely involved in the prevention of photodamage to the photosynthetic apparatus (Demmig-Adams, 1990). Individuals grown at low light exhibited a slightly higher nitrogen content and lower nitrogen-use efficiency relative to plants grown at the higher light level (Fetene et al., 1990). Regardless of growth light level, nitrogen-use efficiencies in plants lacking nitrogen were substantially lower than plants supplied with nitrogen. Also, growth under nitrogen deficiency decreased nocturnal CO_2 uptake rates and increased the amount of respiratory CO_2 recycled during CAM at all growth light levels. Carbon dioxide recycling in this species was also stimulated by high night temperatures, high vapor pressure deficits at night, and drought stress (Fetene & Lüttge, 1991).

In conclusion, *B. humilis* grows in fully exposed and partly shaded locations, yet appears to be better adapted to the partly shaded habitats. Although this species grows in seasonally arid environments, reductions in photosynthetic gas exchange as a result of drought stress were observed at leaf water potentials near -1.0 MPa (Lee et al., 1989). In addition, drought, as well as other stresses, stimulated CO_2 recycling during CAM (Fetene & Lüttge, 1991).

C. PHOTOSYNTHESIS AND WATER RELATIONS OF *PITCAIRNIA INTEGRIFOLIA*

The ecophysiology of *Pitcairnia integrifolia* was investigated in plants cultivated on rock terraces in Trinidad, as well as in the laboratory using greenhouse-grown plants (Lüttge et al., 1986b). In the field, daytime CO_2 uptake in this C_3 species declined at mid-day when leaf temperatures exceeded 35°C. Rates of transpiration were high throughout the day, resulting from either high stomatal conductances or high vapor pressure deficits. Because of this, water-use efficiencies tended to be fairly low. Leaf osmotic potential of *P. integrifolia* in the field was less negative than –1.0 MPa. Net CO_2 exchange of *in situ* and greenhouse grown individuals saturated between 200 and 400 μmol $m^{-2}s^{-1}$, light compensation points were 10–15 μmol $m^{-2}s^{-1}$, and apparent quantum yields were 0.02-0.03 (Lüttge et al., 1986a). Although this species can grow in apparently harsh, exposed locations, the results of the above studies suggest that the physiology of this species may be better adapted to less severe conditions.

D. PHOTOSYNTHESIS AND WATER RELATIONS OF TERRESTRIAL *AECHMEA* SPECIES

Aechmea aquilega grows as an epiphyte throughout most of Trinidad, yet this CAM bromeliad is found on the ground in the more arid portions of the island (Griffiths et al., 1986). Nocturnal CO_2 uptake and acid fluctuations in terrestrial plants were very low, relative to epiphytic individuals growing at moister sites. Furthermore, respiratory CO_2 accounted for up to 89% of the malate synthesized at night. Leaf osmotic and water potentials were always less negative than –0.9 MPa (Smith et al., 1986b). Although included as a terrestrial species here, it is probable that these plants did not rely on soil water as leaf water potentials of nearby shrubs were more negative than –3.0 MPa.

Aechmea magdalenae typically grows as a terrestrial species in the shady understory of tropical moist forests. This is quite surprising because this species exhibits CAM which is considered more characteristic of plants growing in exposed habitats (Kluge & Ting, 1978). Photosynthesis and growth were examined using plants removed from a forest in Panama and grown in a greenhouse at 5% and 35% of full sunlight (Pfitsch & Smith, 1988), approximating light levels in the forest understory and in tree-fall gaps, respectively. Nocturnal CO_2 uptake was highly variable and differed little among plants grown and measured at any of the light regimes, with one exception; rates of nocturnal CO_2 exchange of plants grown at high light and measured at low light were near zero. Differences in 24-hour CO_2 uptake were negligible in all but the latter. The results of this study indicate that *Aechmea magdalenae* is a shade-adapted CAM plant.

E. PHOTOSYNTHESIS AND WATER RELATIONS OF OTHER TERRESTRIAL BROMELIADS

The ecophysiology of few other species of terrestrial bromeliads has been investigated. Benzing and Burt (1970) compared water losses of leaves desiccated for 120 hours in eight species of terrestrial bromeliads. Water deficits, expressed as a percent of initial water content, ranged from 18% in *Ananas comosus* to 61% in a species of *Puya*. Degrees of rehydration after soaking 12 hours correlated with the degree of water deficit in the eight species. Rates of water loss and gain correlated inversely with tissue succulence and epidermal/cuticle thickness.

Medina et al. (1991a) examined nitrogen concentrations, stable carbon isotope ratios, and stable hydrogen isotope ratios in several terrestrial species throughout northern Venezuela, including four species of *Ananas*, three species of *Bromelia*,

Pitcairnia bulbosa, and *Brocchinia micrantha*. Carbon isotope ratios clearly differentiated the CAM species (all but the latter two; Appendix I) from the C_3 species, while hydrogen isotope ratios were less conclusive. Higher nitrogen concentrations were characteristic of the shade plants, relative to the sun plants, possibly a result of greater nitrogen availability and/or lower specific leaf weights of the shade plants. Stable carbon isotope ratios were lower in the shade plants, possibly resulting from increased amounts of daytime CO_2 uptake (Phases II and IV) in the CAM species and/or an altered carbon isotope composition of the air in the understory.

III. Water Relations of Epiphytic Bromeliads

A. GENERAL WATER RELATIONS

Early investigators focussed their efforts on the manner in which water is absorbed by these unusual plants (Haberlandt, 1914; Mez, 1904; Picado, 1913; Schimper, 1884, 1888; Tietze, 1906). Tank epiphytes retain their own supplies of water for absorption by epidermal trichomes at the leaf bases; atmospheric epiphytes also absorb water via trichomes on the leaf surfaces, although these trichomes tend to be larger and more elaborate than those characteristic of tank epiphytes. Dissolved nutrients are similarly absorbed, as has been shown more recently using radioactive tracers (Benzing, 1970, 1973, 1980, 1989, and references therein).

Many investigations of epiphyte water relations have relied on tissue water content as an indicator of the hydration status of the plant. Penfound and Deiler (1947) measured extraordinary changes in tissue water content (given as [fresh weight–dry weight]/dry weight × 100 throughout) of *Tillandsia usneoides* from nearly 700% after a rain to almost 300% after a "severe" drought in southern Louisiana. They also recorded substantial diurnal changes in tissue water content. In a more extensive study of epiphytes in Puerto Rico, Biebl (1964) also found dramatic changes in plant water content of *T. recurvata* and *T. usneoides* associated with the frequency of rains. At several locations on Puerto Rico and neighboring islands, the water content of *T. recurvata* varied from less than 200% before hydration by rains to nearly 700% after rain. In addition, Biebl (1964) determined that the length of time necessary for recovering full tissue hydration was approximately four to five hours. Martin and coworkers also monitored the water content of *T. usneoides* before and after hydration by rain. Tissue water contents of individuals in North Carolina were lower than in the above studies, and ranged from approximately 130% to 250% over the course of a year (Martin et al., 1981; Martin & Schmitt, 1989). Furthermore, in a gas exchange chamber in the laboratory, the water content of *T. usneoides* decreased from 362% to 247% after nine days without water (Martin & Schmitt, 1989).

Benzing and coworkers investigated the ability of numerous species of epiphytic bromeliads, representing several morphological types, to resist desiccation under extremely dry conditions. Excised leaves from numerous terrestrial and epiphytic species were sealed in desiccators containing $CaCl_2$ for up to 120 hours (Benzing & Burt, 1970; Benzing & Renfrow, 1971b). After this time, those species with thick, succulent leaves and thick cuticles lost the least amount of water, while species with more mesomorphic leaves lost up to 50% of their initial water content. After 12–16 hours of rehydration, only several atmospheric species of *Tillandsia* recovered their initial water content.

After a 120-day desiccation treatment, the tissue water content of *T. ionantha* declined by approximately two-thirds (Benzing & Dahle, 1971). Although this ex-

treme desiccation was not lethal, one plant which had desiccated to a greater degree died after rehydration. Seedlings and detached roots of *T. ionantha* lost water at much higher rates than those observed in mature plants.

Results of the studies described above emphasize the extreme fluctuations of tissue water content exhibited by at least some epiphytic bromeliads. Although comparable data are scarce, it is highly improbable that leaf tissue of all but poikilohydric species can withstand these extreme changes in tissue hydration. Therefore, it is tempting to classify epiphytic bromeliads as extreme xerophytes, if not tending toward poikilohydric in nature (e.g., see Benzing & Dahle, 1971). On the other hand, further consideration of the water relations of these plants indicates that this generalization may be inappropriate (see below).

Harris (1918) measured osmotic potentials of 13 species of epiphytic bromeliads in Jamaica and southern Florida. These values averaged approximately –0.4 to –0.5 MPa; none were more negative than –0.9 MPa. Likewise, Biebl (1964) reported osmotic potentials between –0.6 and –0.9 MPa for *T. recurvata* in Puerto Rico. Very similar values of leaf osmotic and water potentials were found for numerous species, including tank and atmospheric types, as well as C_3 and CAM species, during extensive field investigations in Trinidad (Griffiths et al., 1986; Lüttge et al., 1986b; Smith et al., 1985, 1986b). Diurnal changes in tissue water potential ranged from approximately 0.1 to 0.4 MPa, with minimum (most negative) values at the end of the night in CAM species and at the end of the day in C_3 species. In spite of extensive sampling during wet and dry seasons at various sites on the island using epiphytes in shade or full sun and of any morphological type or photosynthetic pathway, osmotic and water potentials were never much more negative than –1.0 MPa.

In spite of the enormous range of tissue water contents experienced by at least some bromeliads in the field, their tissue water potential varies only slightly. Furthermore, the water potential characteristic of epiphytic bromeliads is very high (between 0 and –1.0 MPa) relative to non-bromeliad species (Appendix II). Consideration of these findings indicates that the categorization of epiphytic bromeliads as poikilohydric may be inaccurate. On the other hand, the extremely labile water content of some epiphytic bromeliads, coupled with their ability to tolerate occasionally extensive droughts certainly classify these taxa as xerophytes. It is remarkable that these plants can experience apparently severe tissue dehydration during droughts yet maintain high tissue water potentials. The maintenance of high water potentials during extended drought, however, is not unique to epiphytic bromeliads. The majority of succulent, terrestrial CAM plants, many of which inhabit the most arid regions on earth, likewise appear incapable of tolerating tissue water potentials much below –1.0 MPa (Nobel, 1988; Smith, 1984). At these water potentials, the relative water content of succulent tissues is apparently low enough to impair physiological activity.

B. WATER VAPOR ABSORPTION

Only poikilohydric taxa are known to benefit from the absorption of atmospheric water vapor (Lange et al., 1975, 1986; Rundel, 1982). Thus, scattered reports of water vapor uptake by epiphytic bromeliads in the literature are intriguing. Picado (1913) first indicated that water vapor uptake was possible in several atmospheric species of *Tillandsia*. Subsequently, Penfound and Deiler (1947) demonstrated that the water content of *T. usneoides* tracked changes in atmospheric humidity over 24-hour cycles. This surprising finding was subsequently confirmed by Virzo De Santo et al. (1976)

in this and other species of epiphytic *Tillandsia*. Although Walter (1971) reported that Alvim and Uzeda found slight increases in the weight of *T. straminea* leaves after exposure for one day to 80–100% relative humidity, he attributed this to condensation of water on the leaves. It is unclear why Biebl (1964) and Benzing and Dahle (1971) found no increases in tissue water content of three species of *Tillandsia* after incubation in saturated or nearly saturated atmospheres.

The most extensive work quantifying water vapor absorption at different relative humidities was done by Martin and Schmitt (1989) using *T. usneoides*. Numerous field and laboratory measurements confirmed the absorption of atmospheric water vapor whenever the relative humidity of the air increased. Thus, in the field, plants gain water throughout the night as relative humidity increases and lose water throughout the day as relative humidity decreases. Research in the laboratory showed that an increase in relative humidity of the air surrounding the plants, regardless of the level of humidity, resulted in water vapor absorption by the plants, and any decrease in relative humidity likewise resulted in water loss. The absorption and release of water vapor following changes in air relative humidity occurred in dead plants of *T. usneoides* as well (Martin & Schmitt, 1989; Penfound & Deiler, 1947). Thus, the extensive surface indumentum of trichomes is apparently responsible for this phenomenon (Martin & Schmitt, 1989). The outer shields of the trichomes comprise numerous dead cells, each with relatively thick walls and considerable amounts of pectic materials, both of which are hygroscopic in nature (Billings, 1904; Mez, 1904; Tomlinson, 1969).

Thus, it appears as if most atmospheric epiphytes are capable of absorbing water vapor from the atmosphere whenever the relative humidity of the air increases. Given the humid nature of the typical epiphytic habitat, this phenomenon should be quite common. Therefore, epiphytic bromeliads appear to be unique among non-poikilohydric plants. A crucial question is whether or not these plants benefit from this absorption of water vapor. The answer appears to be no. Martin and Schmitt (1989) compared the probable water potentials of the living tissue and the non-living trichomes of *T. usneoides* and the atmosphere. They concluded that during the absorption of water vapor at all but the highest humidities, i.e., >99%, the living tissue of the plant must lose water to the trichomes (from the stomata underneath) simultaneously with the absorption of water from the atmosphere by the trichomes. Once equilibrium is reached, i.e., if the humidity level is constant after an increase, as in a laboratory setting, the trichomes no longer absorb water vapor, and transpiration from the living tissue can be observed. Given that the water potential of the living tissue (excluding the dead trichomes) in epiphytic bromeliads is always higher than −1.0 MPa (Appendix II), it is thus impossible for the trichomes, if absorbing water vapor from the atmosphere at any humidities less than 99% (water potential of atmosphere = approx. −1.4 MPa), to supply the living tissue of these plants with water. In conclusion, the absorption of atmospheric water vapor is most likely a common occurrence among atmospheric bromeliads. An improvement in plant water relations, however, is improbable.

IV. Carbon Relations of Epiphytic Bromeliads

A. PHOTOSYNTHETIC RESPONSES TO LIGHT

In a classic study of the environmental factors associated with the local distributions of epiphytic bromeliads in Trinidad, Pittendrigh (1948) categorized species into three

groups related to light requirements: exposure, sun, and shade-tolerant. Based on numerous field observations, most epiphytic bromeliads were found in the upper layers of the forest canopy. According to Pittendrigh (1948), even those species in the shade-tolerant group did not require shade, but rather required the high humidity of the subcanopy or forest understory. This emphasis on high light as the preferred environment of epiphytic bromeliads is commonly found throughout the literature on the biology of these plants (Billings, 1904; Birge, 1911; Garth, 1964; Medina, 1974, 1987).

Benzing and Renfrow (1971b) undertook an ambitious study to test the generalizations of Pittendrigh (1948) with detailed analyses of photosynthetic responses to light in 21 species of epiphytic bromeliads, including C_3, CAM, and C_3-CAM epiphytes, as well as tank and atmospheric species. In general, their findings supported Pittendrigh (1948) to the extent that gas exchange in the exposure species usually saturated at high light, and that light compensation points in these species were high (Appendix III). There were, however, exceptions. For example, the two species of *Catopsis* listed in the exposure group by Pittendrigh (1948) ranked intermediate (*C. floribunda*) or low (*C. berteroniana*) when all 21 species were ranked according to three indicators of photosynthetic adaptation to high light (Appendix III). In addition, *Tillandsia usneoides*, also included in the exposure group by Pittendrigh (1948), was characterized by an intermediate ranking. Furthermore, *T. monadelpha* and *T. anceps* were categorized as shade-tolerant by Pittendrigh (1948), yet received an intermediate ranking based on the results of Benzing and Renfrow (1971b; Appendix III). An important finding of Benzing and Renfrow (1971b) that contradicts Pittendrigh (1948) is that many species growing in the shade appeared adapted to low light and were not simply avoiding more exposed locations. Caution is appropriate in interpreting the results of Benzing and Renfrow (1971b), however, because their plants were grown at very low PPFD (approximately 130 μmol $m^{-2}s^{-1}$), tissue pieces were slit to facilitate gas exchange, and CO_2 concentrations during measurements were approximately 40 times ambient.

In agreement with the results of Benzing and Renfrow (1971b), responses of CO_2 exchange to light in the C_3 epiphytes *C. nutans* and *Guzmania lingulata* were characteristic of shade plants (Benzing & Renfrow, 1971a). Light compensation points of both species were low, as were the saturation light levels. Similar results were obtained with the C_3 epiphytes *T. spiculosa* (Medina et al., 1977) and *T. deppeana* (Adams & Martin, 1986b). On the other hand, photosynthesis in the C_3 species *G. lingulata, T. fendleri*, and *Vriesea jonghei* was often limited by low light at several sites in Trinidad, indicative of high light requirements in these species (Griffiths et al., 1986). The response of photosynthesis to a range of light levels was analyzed in further detail for *G. lingulata*, and the results suggest a relatively low light saturation level as found by Benzing and Renfrow (1971b). In addition, photosynthetic responses to light were measured in plants grown at 45 and 250 μmol $m^{-2}s^{-1}$ (Smith, 1989). Although shade-grown plants exhibited slightly lower light compensation points and saturation levels, all values were quite low, indicative of adaptation to shade in both sets of plants.

In a study of the influence of unusual patterns of leaf pigmentation on photosynthesis in leaves of selected tank epiphytes, Benzing and Friedman (1981) measured photosynthetic responses to light in eight C_3 species. The results indicate that these species, with one exception, are shade-adapted. Surprisingly, the exception was *C. nutans*, which exhibited a substantially higher level of photosynthetic light saturation than the

other species and relative to results obtained previously by Benzing and Renfrow (1971a). Reasons for this discrepancy are unknown.

Photosynthetic responses to light were measured in two C_3 bromeliads, *Guzmania minor* and *Vriesea splendens*, and compared with other species by Bierhuizen et al. (1984). Relative to the other species, maximum photosynthetic rates were low, light compensation points were intermediate to high, and quantum yields were low in the two bromeliads. Bierhuizen et al. (1984) suggested that the comparatively low rates of CO_2 uptake in *V. splendens* might be attributable to very low stomatal densities. This is particularly interesting in light of the discussion later in this review of drought tolerance in the Bromeliaceae (see below).

Aechmea nudicaulis and *A. fendleri* were collected in Trinidad and grown at 120 and 300 μmol $m^{-2}s^{-1}$ for six weeks prior to experimentation (Griffiths, 1988a). Nocturnal CO_2 uptake and, to a lesser degree, accumulation of tissue acidity typically increased with increasing light at most temperatures investigated implying that saturation of CAM should occur above 300 μmole $m^{-2}s^{-1}$ in both species.

Maxwell et al. (1992) examined photosynthetic characteristics of the C_3-CAM species *Guzmania monostachia* under natural conditions during the dry season in Trinidad. Plants were growing in full sunlight, at approximately 60% of full sunlight, or were transferred to shade at 3% of full sunlight. Full-shade individuals had thinner, less succulent leaves with more chlorophyll than the plants growing at higher light levels. Although leaf water potentials were most negative in the exposed plants, water potentials of all plants were never more negative than –0.8 MPa. Greater nocturnal increases in tissue acidity were measured in the exposed and partially shaded individuals. Photosynthetic rates and apparent quantum yields of these plants decreased throughout the day. The degree of non-photochemical quenching of photosynthesis also decreased in the morning but then increased during the afternoon. These results indicate that *Guzmania monostachia* may tolerate both deep shade and full sun. This broad tolerance of widely differing light levels should allow survival and perhaps growth of the epiphyte during wet and dry seasons in this tropical deciduous forest (Maxwell et al. 1992).

Photosynthetic responses to light have been most closely examined in *T. usneoides*. Using plants that were grown in a partially shaded greenhouse and pretreated six days at approximately 200 μmol $m^{-2}s^{-1}$, Kluge et al. (1973) measured substantial increases in CO_2 uptake with increasing light level from 200 to 1000 μmol $m^{-2}s^{-1}$. This response included increases in CO_2 uptake during both the day (Phases II and IV) and night (Phase I), as well as decreases in daytime CO_2 release (Phase III). Martin and coworkers expanded on the work of Kluge et al. (1973) such that a fairly complete characterization of the light requirements of *T. usneoides* now exists. For plants growing *in situ* in southern South Carolina at three different exposure levels (approximately 50, 80, and 1000 μmol $m^{-2}s^{-1}$ at mid-day in mid-summer), tissue chlorophyll content increased with decreasing exposure, while diurnal changes in tissue titratable acidity did not change across this light gradient (Martin et al., 1985). These results indicate that CAM saturated at less than 100 μmol $m^{-2}s^{-1}$, and that less exposed plants were at least partly acclimated to the shade (Boardman, 1977). On the other hand, plants grown two months in a greenhouse at maximum light levels of approximately 150 and 1550 μmol $m^{-2}s^{-1}$ exhibited increased levels of CAM in response to higher light (Martin et al., 1985). Differences in daily integrated light levels received by the plants in these two studies may explain the inconsistencies in the results.

Rates of nocturnal CO_2 uptake in *T. usneoides* collected from the field immediately before analysis in the laboratory were identical in spite of a 75% reduction in light levels from approximately 450–2000 μmol $m^{-2}s^{-1}$ (the range across the gas exchange cuvette) to 100–400 μmol $m^{-2}s^{-1}$ (Martin & Siedow, 1981). Thus, photosynthesis apparently saturated at light levels at or below 400 μmol $m^{-2}s^{-1}$. These results were supported by subsequent work using individuals grown three weeks at five light levels from 65 to 2000 μmol $m^{-2}s^{-1}$ (Martin et al., 1986). The greatest amounts of CO_2 uptake were observed in plants exposed to 250 μmol $m^{-2}s^{-1}$ during growth. In addition, regardless of growth light level, a measurement light level of 160-260 μmol $m^{-2}s^{-1}$ elicited the highest amount of nocturnal CO_2 uptake. Furthermore, nocturnal increases in tissue acidity were highest in plants grown at 125 μmol $m^{-2}s^{-1}$. Rates of photosynthetic O_2 evolution of leaf sections of *T. usneoides* after an eight-week exposure to approximately 33, 275, and 775 μmol $m^{-2}s^{-1}$ saturated at approximately 500 μmol $m^{-2}s^{-1}$ (Martin et al., 1989), regardless of exposure light level. This was also true of leaves taken from the lower portions (light level of approximately 140 μmol $m^{-2}s^{-1}$) versus those from the upper portions (approximately 800 μmol $m^{-2}s^{-1}$) of a clump of *T. usneoides* that had been growing in a greenhouse for ten years. The higher saturation light levels of O_2 evolution, relative to results obtained for CO_2 exchange, are presently unclear. Regardless, the results of these investigations indicate that this CAM epiphyte is, at least to some degree, shade-adapted. In support of this, decreases in nocturnal CO_2 uptake were occasionally observed when light exceeded optimal levels (Martin et al., 1986).

To summarize, the majority of epiphytic bromeliads that have been examined to date exhibit photosynthetic responses to light more characteristic of shade, not sun, plants, or are intermediate in this regard (Appendix IV). This conclusion contrasts with that which might be expected based on the field observations of Pittendrigh (1948). On the other hand, given that full or partial shading of all epiphytic bromeliads by the canopy of the host tree must be far more common than not, perhaps this conclusion comes as no surprise. This is not to say that these epiphytes cannot tolerate high light levels. Indeed, many epiphytic bromeliads survive and grow in fully exposed locations, e.g., species of *Tillandsia* are often found growing on dead trees or telephone lines without suffering apparent damage. Furthermore, many epiphytic bromeliads grow in tropical deciduous or semidecidous forests in which individuals are exposed to higher light levels during the dry season when host trees are leafless (Maxwell et al., 1992).

B. PHOTOSYNTHETIC RESPONSES TO TEMPERATURE

Benzing and Renfrow (1971a) noted that both the pattern and rates of CO_2 exchange in the CAM species *Tillandsia paucifolia* (= *circinnata*) and *T. ionantha* were identical when measured at nighttime air temperatures of either 15°C or 25°C. Griffiths et al. (1989) reported high *in situ* rates of nocturnal CO_2 uptake at 27°C in *T. flexuosa* in Venezuela. In addition, field work in Trinidad with *Aechmea nudicaulis* yielded similar results (Smith et al., 1986b). The latter results were supported by subsequent laboratory studies with the same species and with *A. fendleri* (Griffiths, 1988a). At a light level of 250 μmol $m^{-2}s^{-1}$, nocturnal CO_2 uptake rates increased with increasing night temperature from 12 to 25°C in both species. On the other hand, at a lower light level (100 μmol $m^{-2}s^{-1}$), both species exhibited an optimum of 18°C for CO_2 uptake.

Griffiths (1988a) also examined CO_2 recycling during CAM (see below) in these two species. The percentage of acid resulting from nighttime refixation of respiratory CO_2 was not directly related to temperature. This contrasted with results of field work with *A. nudicaulis, A. aquilega,* and two other *Aechmea* species in Trinidad; Griffiths et al. (1986) found a significant correlation between the degree of CO_2 recycling and nighttime air temperature. In contrast to the report by Smith et al. (1986b) of high levels of CAM in *A. nudicaulis* during a warm night in Trinidad, Griffiths et al. (1986) observed reductions in stomatal conductance and nighttime CO_2 uptake in the same species and in *A. aquilega* during a warm (26°C) wind at night. Cessation of this wind resulted in resumption of high nocturnal stomatal conductances and net CO_2 uptake rates.

One problem in interpreting the effects of temperature on gas exchange in the above field studies, as well as in many laboratory studies, is that of changing vapor pressure deficit at different temperatures. Thus, it is possible that decreases in stomatal conductance and CO_2 uptake rates might be attributable to the increases in vapor pressure deficit that typically accompany increases in air temperature, and not solely the latter.

Few studies have included C_3 epiphytes in investigations of temperature effects on photosynthesis. Daytime CO_2 uptake in *Vriesea amazonica* decreased once air temperatures exceeded 35°C in Trinidad (Griffiths et al., 1986). In addition, similar declines in photosynthesis were observed at air temperatures above 31°C in *Guzmania monostachia* while in the C_3 mode (Lüttge et al., 1986c). Adams and Martin (1986b) compared the responses of net CO_2 exchange to temperature in juvenile and adult forms of *T. deppeana*. Both growth forms exhibited broad, overlapping photosynthetic temperature optima of approximately 13–17°C for the juveniles and approximately 15–19°C for the adults. These relatively low values may reflect the cool cloud forest habitat from which the plants were collected.

The effects of temperature on CO_2 exchange have been examined in detail in only several species of epiphytic CAM bromeliads as well. Net CO_2 uptake rates of *T. recurvata* were highest at 15–17°C, while temperatures above 26°C or near 7°C inhibited CO_2 uptake (Medina, 1984, 1987; Medina et al., 1977). Also, whenever nighttime CO_2 uptake was reduced, rates of daytime CO_2 uptake (mostly Phase IV) increased. Similar results were obtained with the CAM epiphyte *T. utriculata* (Medina, 1987; Medina et al., 1977). The responses of net CO_2 exchange to temperature in *T. usneoides* were investigated by Kluge et al. (1973) and Martin and Siedow (1981). Kluge et al. (1973) exposed plants to isothermal day/night conditions at each temperature investigated and found that nocturnal CO_2 uptake was maximal at 15°C and 20°C and declined dramatically above and below these temperatures. Nighttime CO_2 uptake rates were reduced by approximately 50% at 10°C, then changed to mostly CO_2 release at 3°C and 25°C. Above 25°C, CO_2 was lost continuously for the 24 hours of measurement. One unusual finding of Kluge et al. (1973) was a stimulation of daytime CO_2 uptake (Phase III) by 3°C. Martin and Siedow (1981) obtained different results; high rates of nocturnal CO_2 uptake occurred at a broad range of day/night temperatures: 25/10, 25/15, 25/20, 30/20, and 35/20°C. Day temperatures exceeding 40°C or night temperatures less than 5°C drastically inhibited nighttime CO_2 uptake. No stimulation of daytime CO_2 uptake was observed at any temperature. In general, the results of Martin and Siedow (1981) were substantiated by *in situ* measurements of CO_2 uptake in this species in North Carolina (Martin et al., 1981). Furthermore, in

both studies, day/night isothermal conditions inhibited nocturnal CO_2 uptake. Reasons for the discrepancies between the results of Kluge and coworkers and those of Martin and coworkers are unclear.

Given the above results, the photosynthetic temperature optima of C_3 epiphytic bromeliads appear surprisingly low considering the tropical environments in which these species are found. Similarly low temperature optima were reported for the epiphytic CAM bromeliads *T. recurvata* and *T. utriculata*. Unlike the results obtained with these species, extensive work with *T. usneoides* indicates that nocturnal CO_2 uptake in this CAM epiphyte can occur at high rates across a fairly broad range of nighttime temperatures.

C. PHOTOSYNTHETIC RESPONSES TO DROUGHT STRESS

In the first detailed study of metabolic responses of an epiphytic bromeliad to drought stress, Benzing and Dahle (1971) subjected intact plants of *Tillandsia ionantha* to increasing levels of desiccation by enclosing them in desiccators containing $CaCl_2$. Plants survived this treatment, even after four months, despite having lost approximately two-thirds of their initial water content. At intervals during desiccation, Benzing and Dahle (1971) measured respiration and photosynthetic rates of leaves with a Warburg manometer. Rates of photosynthetic O_2 evolution remained high until tissue water content dropped to nearly 50% of initial values. When plants had lost more than two-thirds of their initial water content, photosynthetic rates declined to zero, or nearly so. Respiration rates, after an initial decline, remained relatively constant as plants desiccated until they lost over two-thirds of their initial water content whereupon respiration ceased. Initial rehydration (soaking 15 hours in distilled water) of the desiccated plants resulted in respiration rates similar to non-desiccated plants, whereas photosynthetic rates were lower. Daily watering of the previously desiccated plants for nearly a month resulted in high rates of both metabolic processes, often exceeding those of non-desiccated tissues. The above results suggest that *T. ionantha* is highly resistant to drought stress. Lack of data on tissue water potentials, however, precludes comparisons with other species.

Medina and coworkers (Medina, 1987; Medina et al., 1977) examined photosynthetic responses to drought in the tank epiphyte *Guzmania monostachia*, a C_3-CAM intermediate. When well-watered, atmospheric CO_2 was taken up only during the day, and small malate fluctuations were observed, whereas nighttime CO_2 uptake and larger acid fluctuations, as well as severely curtailed daytime CO_2 uptake, were observed after approximately one week without water. Re-watering desiccated plants resulted in a rapid (within one day) reversion to C_3 photosynthesis (Medina et al., 1977). Medina (1978) also investigated the photosynthetic responses to drought in the CAM bromeliad *T. utriculata*. Nocturnal acidification remained constant, and rates of nocturnal CO_2 uptake were variable during a week without water, possibly indicative of considerable drought resistance.

Adams and Martin (1986b) monitored 24-hour CO_2 exchange of intact juvenile plants and of leaves of mature individuals of *T. deppeana*, a C_3 tank epiphyte collected in northeastern Mexico, for nearly ten days without water. Water was removed from the leaf impoundments of the adult plants prior to the gas exchange measurements. Unlike the tank habit of the adults, the juvenile plants of this species have a morphology characteristic of atmospheric epiphytes (Adams & Martin, 1986a). Whereas

juvenile plants maintained positive net CO_2 uptake, on a 24-hour basis, through the last day of the drought treatment, mature plants exhibited net daily CO_2 losses on the second day. The results of this study suggest that epiphytic bromeliads having the atmospheric morphology are more tolerant of drought than are those with the tank morphology.

Martin and Adams (1987) measured CO_2 exchange in individuals of the CAM species *T. schiedeana* that were well-watered or without water for varying lengths of time up to 34 days. Nocturnal rates of CO_2 uptake declined but remained relatively high during the imposed desiccation treatment such that after 34 days without water, 24-hour CO_2 exchange was still positive. During this treatment, tissue water content (as a per cent of fresh weight) declined from approximately 78% to 75%. Unfortunately, leaf water potentials were not measured. The amount of respiratory CO_2 recycled via CAM was surprisingly high in well-hydrated plants (accounting for nearly 60% of acid accumulated overnight) and increased throughout the desiccation treatment. It is probable that under more severe drought stress, this recycling of respiratory CO_2 will eventually lead to CAM-idling (see below).

Smith et al. (1986b) measured rates of CO_2 exchange and transpiration, tissue acid fluctuations (in CAM species), and leaf water potentials (using the Scholander pressure chamber) in several C_3 and CAM species of epiphytes *in situ* at arid and mesic sites during both dry and rainy seasons in Trinidad. Epiphytes with CAM included species of *Aechmea* and *Tillandsia*; C_3 species were in the genus *Vriesea*. Although different populations and different species were compared, plants at the more arid sites on the island typically exhibited lower CO_2 uptake rates and nocturnal acid accumulations during the dry season, relative to plants at the more mesic sites. Shortly after a rain, rates of nocturnal CO_2 uptake and tissue acid fluctuations in *A. nudicaulis* at the arid site were comparable to plants at the mesic sites (Smith et al., 1986b). In all cases, nocturnal acid accumulation in the CAM plants reflected contributions of large amounts of internally recycled CO_2 (see below). As expected, water-use efficiencies (WUE) of the CAM species exceeded those of the C_3 species in most comparisons (Griffiths et al., 1986). Griffiths (1988a) also measured high WUE in two species of *Aechmea* under laboratory conditions, especially at high light levels and vapor pressure deficits.

In situ leaf water potentials of both C_3 and CAM species in Trinidad were relatively high, regardless of the aridity of the site or the season (Smith et al., 1986b). In fact, out of numerous measurements under various conditions, the most negative leaf water potential reported by Smith et al. (1986b) was only –1.0 MPa. Leaf water potentials were not substantially different among C_3 and CAM epiphytic bromeliads (Appendix II). Also, diurnal fluctuations in leaf water potential were similar between these plants, ranging from 0.1 to 0.4 MPa, with the minimum (most negative) value occurring late in the day for C_3 species and late in the night for CAM species. In spite of the relatively small variations (diurnally, seasonally, and geographically) in tissue water potentials observed in Trinidad, lower photosynthetic rates correlated with more negative water potentials.

In a field investigation of the ecophysiology of two CAM species in Venezuela, Griffiths et al. (1989) measured CO_2 exchange, transpiration, tissue acid fluctuation, and leaf water potential in the CAM epiphyte *T. flexuosa* during both the wet and dry seasons. All photosynthetic parameters were substantially reduced in the dry season, although tissue water potentials declined from –0.2/–0.4 MPa (day/night values) in

the wet season to only –0.3/–0.6 MPa in the dry season. Water-use efficiencies were relatively high and decreased slightly in the dry season.

Transpiration rates of all epiphytic bromeliads investigated in Trinidad and Venezuela, regardless of photosynthetic pathway, were low relative to most other plants (Griffiths et al., 1989; Lüttge et al., 1986c; Smith et al., 1986b). Surprisingly, transpiration rates of CAM species were not always lower than those of C_3 species. In a survey of gas exchange characteristics of ten CAM species of *Tillandsia*, Virzo De Santo et al. (1977) found that all species exhibited very low rates of transpiration (Appendix V) and that rates were lowest in those species collected from more arid habitats.

A considerable amount of work has focussed on the ability of the epiphytic CAM bromeliad *T. usneoides* to withstand drought stress. Earlier investigations of photosynthetic responses to drought yielded puzzling results. Kluge et al. (1973) reported similarly high rates of nocturnal CO_2 uptake in "dry" and "desiccated" individuals, although tissue water contents were not markedly different. Surprisingly, CO_2 uptake rates were substantially reduced in well-hydrated plants. These results suggest that CAM is enhanced by drought. It is unclear, however, whether or not the well-hydrated plants used by Kluge et al. (1973) were completely surface-dry. If not, the retention of some surface water might be responsible for these unusual results (see below).

The findings of a possible drought enhancement of CAM in *T. usneoides* by Kluge et al. (1973) was supported by earlier results of both field and laboratory studies of photosynthesis by Martin and coworkers. Nocturnal CO_2 uptake rates were higher in plants measured after several days of drought, relative to rates of the same plants after wetting and drying one day (Martin & Siedow, 1981). Again, it was unclear whether or not the plants were completely surface-dry by the nighttime. In spite of a range in tissue water content of 130 to 200% (dry weight basis) in plants at different times during the growing season in North Carolina, nocturnal CO_2 uptake rates did not correlate with plant water content (Martin et al., 1981). These findings are not conclusive, however, because other environmental factors varied between the sampling dates that might explain any differences, or lack of differences, in CAM at these times.

In an effort to conclusively determine whether or not drought stress enhances CAM in *T. usneoides,* Martin and Schmitt (1989) monitored CO_2 exchange of the same individuals continuously for nine days without water after initially hydrating the plants. Tissue water content (dry weight basis) decreased from 362 to 247% during the desiccation treatment. Although nocturnal CO_2 uptake rates did not decline noticeably on the second day, and did not decline significantly until later in the experiment, nocturnal CO_2 uptake rates were never stimulated by the drought treatment.

Taylor and Martin (unpublished data) equilibrated leaf tissue of *T. usneoides* and *T. setacea,* as well as three non-bromeliad species, in solutions of different water potentials, then measured, using a polarographic O_2 electrode, respiratory O_2 uptake and photosynthetic O_2 evolution at each water potential. Although photosynthetic rates in the two epiphytes declined with decreasing water potential, substantial rates of photosynthesis were maintained down to –4.0 MPa. These responses to declining water potential were similar to those of the xerophytic species included in the study and were unlike those of the mesophytic species. Respiration rates did not vary significantly with decreasing water potential. The results of this study are difficult to

reconcile with data on the water relations of epiphytic bromeliads. As presented earlier, tissue osmotic potentials of epiphytic bromeliads are typically no more negative than –1.0 MPa (Appendix II). Furthermore, Taylor and Martin (unpublished data) measured osmotic potentials of approximately –1.0 MPa in well-watered individuals of *T. usneoides*. After severe desiccation, this value decreased to –1.8 MPa. Assuming this represents an absolute minimum value of leaf water potential in this species (although it was not known whether or not the plants survived at this water potential), it is unclear how photosynthesis can occur in tissue having a water potential of –4.0 MPa when its osmotic potential is no lower than –1.8 MPa; the cells in these plants should be plasmolyzed. These paradoxical findings are not unique to bromeliads; Kaiser (1982) reported similar findings with other species. It is possible that photosynthetic O_2 evolution, as opposed to net CO_2 exchange, can occur under conditions in which the plant cell is plasmolyzed.

Briefly summarizing, it appears as if metabolic activity in epiphytic bromeliads, at least those with the atmospheric morphology, is relatively resistant to drought. One possible explanation for this drought resistance may be the consistently high tissue water potential characteristic of epiphytic bromeliads (including C_3 and CAM, and atmospheric and tank species; Appendix II). Thus, even well into a drought, tissue water potentials may remain high enough to sustain high levels of metabolic activity. Maintenance of a consistently high plant water potential may be explained, at least in part, by consideration of the extremely low transpiration rates characteristic of bromeliads (Appendix V). These low rates of transpiration probably reflect the low vapor pressure deficits characteristic of most epiphytic habitats and the low stomatal densities typical of most epiphytic bromeliads examined to date (Appendix VI). One potential problem with the above scenario, at least for atmospheric taxa, is the discrepancy between the low rates of transpiration reported for these epiphytes and the reportedly labile nature of their tissue water content. On the other hand, it is possible that short-term changes in tissue water content are mediated by trichome hydration status, while long-term changes reflect loss of water from living cells. Further research is necessary before a complete picture of the water relations of epiphytic bromeliads will materialize. If the above scenario is accurate, for example, one would predict much higher rates of transpiration (and possibly CO_2 uptake) in terrestrial species of *Cottendorfia* and *Navia*, given their high stomatal densities (Appendix VI). Furthermore, one might also predict that these species can tolerate more negative leaf water potentials than most other bromeliads. To date, however, the ecophysiology of species in these genera has not been investigated.

D. PHOTOSYNTHETIC RESPONSES TO ATMOSPHERIC MOISTURE

Increases in atmospheric vapor pressure deficit resulted in decreased rates of nocturnal CO_2 uptake in *Tillandsia recurvata* (Lange & Medina, 1979) and in *T. usneoides* (Martin & Siedow, 1981) and in decreased rates of daytime CO_2 uptake in both juvenile (atmospheric) and adult (tank) forms of *T. deppeana* (Adams & Martin, 1986b). Conversely, decreases in vapor pressure deficits effected increases in CO_2 uptake rates. Similar correlations between gas exchange parameters and atmospheric vapor pressure deficits were observed in several species of C_3 and CAM bromeliads studied *in situ* in Trinidad (Griffiths et al., 1986; Lüttge et al., 1986b). As mentioned previously, however, it is especially difficult in the field to separate the effects of

simultaneously changing environmental parameters from each other.

The effects of different night-long vapor pressure deficits have scarcely been considered in ecophysiological investigations of CAM bromeliads. Nocturnal CO_2 uptake rates of *T. recurvata* were depressed throughout the night when the air vapor pressure deficit was increased relative to a control night (Lange & Medina, 1979). On the other hand, Schmitt et al. (1989) reported no consistent correlation between nocturnal CO_2 uptake and nighttime vapor pressure deficit in *T. usneoides*. Reasons for these contradictory results are presently unknown.

Surface wetting of leaves reduced nighttime CO_2 uptake rates substantially, or even stimulated CO_2 release, in the following species: *T. paucifolia* (=*T. circinnata*) and *T. ionantha* (Benzing & Renfrow, 1971a; Benzing et al., 1978), *T. tectorum* (Benzing et al., 1978), and *T. usneoides* (Martin et al., 1981; Martin & Siedow, 1981). On the other hand, Benzing and Renfrow (1971a) and Benzing et al. (1978) reported little or no effect of surface wetting on gas exchange in *Aechmea bracteata, Catopsis nutans, Guzmania monostachia, T. bulbosa*, and to a lesser degree, in *T. butzii*. A major difference between these two sets of species is the density and nature of trichomes on the leaf surfaces. Those species susceptible to inhibition of CO_2 uptake as a result of surface wetting are characterized by a dense indumentum of epidermal trichomes with large, flexible shields. These trichomes trap water on the surface of the leaf after wetting and spread the water by capillary action (Benzing et al., 1978, and references therein). This layer of water undoubtedly slows the rate of CO_2 diffusion such that net CO_2 exchange of the wet leaves approaches zero. Those species unaffected by surface wetting lack a dense covering of flexible trichomes on their exposed leaf surfaces (Benzing et al., 1978). Both flexible and inflexible trichomes are found on the leaves of *T. butzii*, resulting in a partial inhibition of CO_2 exchange upon wetting of this species.

It is possible that surface wetting via dew deposition might improve the water relations of CAM epiphytes beyond that expected. Lüttge (1986, 1987) and Smith and Lüttge (1985) have postulated that the decrease in tissue osmotic potential that results from the overnight accumulation of malate (formed from polysaccharides) should effect a decrease in tissue water potential, thus allowing greater amounts of liquid water absorption than otherwise expected. Because dew deposition is common in the early morning in habitats of many epiphytic bromeliads and this timing coincides with maximal tissue acid concentrations, this hypothesis may represent a potentially new benefit of CAM (Smith & Lüttge, 1985). Smith et al. (1986b) reported excellent correlations between nighttime acid accumulations and decreases in cell-sap osmotic potential in *A. aquilega* and *A. nudicaulis* in Trinidad. Similar results were obtained with *T. flexuosa* in Venezuela (Griffiths et al., 1989). In neither study, however, was this decrease in tissue osmotic potential unequivocally linked with enhanced rates of water absorption in the morning. Schmitt and Bonk (as shown in Lüttge, 1987) monitored tissue water relations, malate concentrations, and the ability to absorb liquid water throughout a day-night cycle in *T. recurvata*. Although the results are suggestive of enhanced water uptake when tissue acidity is maximal, only two plants were examined (A. Schmitt, pers. comm.), and the correlation between water uptake and tissue malate content was not strong.

Recent unpublished work with the CAM epiphyte *T. ionantha* has also shown a correlation between tissue malate content and absorption of liquid water (E. Swanson & C. E. Martin, unpubl.). The amount of water absorbed was, however, more highly correlated with the degree of tissue desiccation resulting from nighttime transpiration

than with tissue malate concentrations. Further work with other species is necessary to differentiate the relative influences of nocturnal desiccation versus tissue acid content as the primary factors effecting water absorption from deposited dew in the early morning by epiphytic CAM bromeliads.

E. PHOTOSYNTHETIC RESPONSES TO NUTRIENTS AND POLLUTANTS

Medina et al. (1977) measured nocturnal increases in malate content as well as tissue nitrogen content of leaves of numerous bromeliads collected at different elevations in Brazil. The two parameters were positively correlated, suggesting that leaf nitrogen content may be an important factor influencing the level of CAM.

Given the complex and effective adaptations characteristic of many epiphytic bromeliads for the acquisition of essential elements from rainwater and host tree leachates (Benzing, 1980, 1981, 1989), it is not surprising that these plants concentrate not only essential elements, but potentially harmful compounds as well. Although several studies have reported substantial accumulations of pollution-derived elements in epiphytic bromeliads growing adjacent to sources of air pollution (Arndt & Strehl, 1989; Schrimpff, 1984; Shacklette & Connor, 1973), only two published studies include information on physiological responses of epiphytes to pollutants. Applications of copper or cadmium solutions to *Tillandsia usneoides* substantially reduced nocturnal CO_2 uptake rates, with cadmium having a more severe effect (Flores, 1980). Concentrations of these heavy metals in the tissue of the treated plants were apparently very high (see Shacklette & Connor, 1973).

Benzing et al. (1992) exposed four species of *Tillandsia* to acute doses of SO_2 and O_3 at relatively high concentrations. No significant effects on nocturnal increases in tissue acidity were observed in these CAM plants in response to the exposures. Furthermore, samples of *T. usneoides* collected alongside a major highway in central Florida and exposed to greater levels of pollution exhibited rates of nighttime CO_2 uptake and malate accumulations not significantly different from those of control specimens that were collected approximately 10 km from the highway (C. E. Martin, unpubl.). Unfortunately, tissue concentrations of heavy metals or other pollutants were not measured in this study.

A worldwide pollutant of increasing concern is CO_2. Although the responses of numerous C_3 and C_4 species to elevated CO_2 concentrations have been extensively studied (Kimball et al., 1993; Rogers & Dahlman, 1993), very few CAM plants have been included in such investigations. Furthermore, the results of the few studies on CAM responses to high CO_2 concentrations (Nobel & Hartsock, 1986; Szarek et al., 1987) may apply only to terrestrial desert succulents. Photosynthetic responses of bromeliads to elevated CO_2 concentrations have not been investigated with one exception. Nowak and Martin (unpubl.) exposed individuals of *T. ionantha* to nighttime CO_2 concentrations ranging from 360 to 920 $\mu l\ l^{-1}$. Nocturnal accumulations of malate nearly doubled when CO_2 concentrations increased from 360 to 430 $\mu l\ l^{-1}$, then saturated thereafter. These findings indicate that responses of at least some CAM epiphytes to global increases in atmospheric CO_2 via increased CAM and possibly increased productivity are probable. In addition, the results of this study may lend support to speculations on the potential importance of diurnal fluctuations in host canopy CO_2 concentrations as a selective factor in the evolution of CAM in epiphytes (Knauft & Arditti, 1969).

V. Recycling of CO_2 and Crassulacean Acid Metabolism in the Bromeliaceae

The photosynthetic variations referred to as CAM-cycling and CAM-idling (Ting, 1985) are similar in that both involve nighttime assimilation of respiratory CO_2 while stomata are closed, and the resultant malate is decarboxylated during the subsequent day. On the other hand, CAM-idling occurs in drought-stressed plants while CAM-cycling occurs in well-watered plants. Also, stomata remain closed throughout the day (and night) in plants exhibiting CAM-idling, while the stomata are open and atmospheric CO_2 is taken up during the day in CAM-cycling (Martin & Zee, 1983; Sipes & Ting, 1985; Ting & Sipes, 1985). Thus, plants exhibiting the latter absorb CO_2 internally as well as from the external atmosphere simultaneously during the day. It is currently thought that the benefit of CAM-idling lies in its maintenance of metabolic activity during severe droughts, such that a plant undergoing CAM-idling can rapidly respond to brief rain showers, which are characteristic of many arid regions, without re-assembling its photosynthetic apparatus (Ting, 1985). Although never tested, this hypothetical scenario is widely accepted as a plausible explanation for the significance of CAM-idling (Monson, 1989; Osmond, 1982; Ting, 1985). The potential benefit accrued by a plant undergoing CAM-cycling is less clear. Ting and coworkers claim that this phenomenon is simply a precursor to CAM-idling and may not be directly beneficial (Rayder & Ting, 1981; Sipes & Ting, 1985; Ting & Burk, 1983), while Martin and coworkers (Harris & Martin, 1991a,b; Martin et al., 1988; but see Martin, 1994) support the contention that CAM-cycling conserves water by reducing daytime (at least morning) stomatal conductance as a result of the high internal CO_2 concentration generated by malate decarboxylation. Furthermore, elevated tissue CO_2 concentrations during the daytime may minimize damage resulting from photoinhibition (Adams & Osmond, 1988; Osmond, 1982; Osmond et al., 1980).

Apparently because few bromeliads have been investigated while under severe drought stress, there are no reported instances of CAM-idling, *sensu stricto*, in the Bromeliaceae. On the other hand, extremely low rates of nocturnal CO_2 uptake accompanied by large accumulations of malate have been found in both terrestrial and epiphytic bromeliads (Appendix VII). In fact, nocturnal uptake of atmospheric CO_2, as opposed to respiratory CO_2, accounted for only 1% of the amount of malate accumulated overnight in the terrestrial bromeliad *Bromelia plumieri* in Trinidad (Griffiths et al., 1986). This value was 11% for terrestrial individuals of *Aechmea aquilega*, also in Trinidad, and as low as 13% for exposed individuals of the terrestrial species *B. humilis* in northern Venezuela (Lee et al., 1989). Similar values have been reported for epiphytic species as well (Appendix VII; Griffiths et al., 1986, 1989; Martin & Adams, 1987). This phenomenon of CO_2 recycling during CAM, as opposed to CAM-idling, is discussed below; however, it appears highly likely that many or all of the above species would undergo CAM-idling if stressed further, i.e., stomata would close throughout the night (and day) yet tissue acid fluctuations would continue. This prediction is based, in part, on the observation that most CAM plants exhibit CAM-idling when severely droughted (Ting, 1985). In contrast, however, a large group of CAM plants in southern Africa do not exhibit CAM-idling under severe drought stress (von Willert et al., 1983, 1985). Therefore, more research is necessary before generalizations about CAM-idling in the Bromeliaceae can be made.

The photosynthetic variation CAM-cycling has been described in several species in

the Bromeliaceae, including one with an unusually flexible metabolism. Well-watered individuals of the epiphyte *Guzmania monostachia* exhibited CO_2 uptake during the day only, with stomatal closure at night, while tissue acidity fluctuated diurnally as in CAM (Medina, 1987; possibly also Lüttge et al., 1986c and Smith et al., 1986b). Also, McWilliams (1970) found a small nocturnal accumulation of acid without CO_2 uptake in the epiphytic species *Vriesea fenestralis*. Furthermore, Medina (1974) reported small accumulations of malate overnight in the following terrestrial and epiphytic bromeliads, all of which lacked nighttime CO_2 fixation: *Puya floccosa, Catopsis nutans, G. mucronata, Tillandsia adpressiflora*, and *V. platynema*.

Although there is no question that respiratory CO_2 released at night is re-fixed in all CAM plants, apparently the amounts of malate thus formed are undetectable against the background of the normally massive accumulation of malate characteristic of CAM (Eickmeier, 1979; Martin et al., 1981; Medina & Delgado, 1976; Nobel & Hartsock, 1978, 1983; Nobel et al., 1984; Virzo De Santo et al., 1987; Winter et al., 1986). On the other hand, if the amount of acid formed as a result of CO_2 fixation from the atmosphere is reduced, e.g., by high temperature or drought stress (the latter, if severe enough, leading to CAM-idling), it is possible to measure the contribution of respiratory CO_2 to overnight malate formation (Griffiths et al., 1986, 1989; Lee et al. 1989; Martin et al., 1981; Winter et al., 1986).

Recently, high levels of CO_2 recycling during CAM have been reported in several species of terrestrial and epiphytic bromeliads (Appendix VII). During field work in Trinidad, *in situ* measurements of nocturnal CO_2 uptake and malate accumulation revealed high levels of CO_2 recycling during CAM in two terrestrial and seven epiphytic species (Griffiths et al., 1986). In fact, in several cases, the fixation of atmospheric CO_2, as opposed to internally generated respiratory CO_2, contributed so little to overnight acid accumulation that it is tempting to classify these photosynthetic traits as CAM-idling instead. Excessive accumulations of malate, relative to nocturnal CO_2 fixation have also been reported in the terrestrial bromeliads *Ananas comosus* (Borland & Griffiths, 1989; Sale & Neales, 1980) and *B. humilis* (Fetene et al., 1990; Fetene & Lüttge, 1991;Lee et al., 1989). In both species, the amount of CO_2 recycled, as a proportion of the nocturnal increase in tissue acidity, was stimulated by nitrogen deficiency (Borland & Griffiths, 1989; Fetene et al., 1990). Further work with *B. humilis* indicated that increases in nighttime temperature, vapor pressure deficit, and drought stress increased the amount of CO_2 recycled during CAM (Fetene & Lüttge, 1991). As in their terrestrial counterparts, CO_2 recycling during CAM was also stimulated by non-optimal temperatures and light levels, surface wetting of the shoots, and drought in the epiphytes *T. usneoides* (Martin et al., 1981), two species of *Aechmea* (Griffiths, 1988a; Griffiths et al., 1986), and *T. schiedeana* (Martin & Adams, 1987).

In a laboratory study of photosynthesis in *T. schiedeana*, nocturnal CO_2 uptake accounted for only 43% of the acid accumulated at night, even under apparently optimal environmental conditions (Martin & Adams, 1987). Not surprisingly, this value declined dramatically with increasing desiccation of the plants. Given these findings, it seems likely that the "apparently optimal" environmental conditions may have been stressful to these plants, resulting in CO_2 recycling during CAM (see, for example, Fetene et al., 1990; Griffiths, 1988b, 1989). Further manipulations of these conditions, including reduced light levels, reduced temperatures, and increased humidities, however, altered these results only slightly (Martin, 1994).

It is puzzling why plants would expend the considerable amounts of energy

necessary to reduce carbon that was previously reduced, then oxidized (Benzing, 1990). Ignoring for the moment the possibility that CO_2 recycling during CAM is an artifact resulting from non-optimal (i.e., stressful) conditions, i.e., that it is simply a variant of CAM-idling instead, there are two major hypotheses that offer an explanation of this phenomenon. First, it has been suggested that respiration rates in these species are unusually high as a result of their warm tropical or subtropical habitat (Griffiths et al., 1986; Lüttge & Ball, 1987). On the other hand, several temperate CAM plants exhibit CO_2 recycling during CAM, including *T. usneoides* in North Carolina (Martin et al., 1981) and *Sedum telephium* in England (Borland & Griffiths, 1990). Furthermore, two species of *Kalanchoe* did not exhibit this phenomenon as day and night temperatures were increased (Medina 1982; Medina & Osmond, 1981). Differences in respiration rates between two species of *Aechmea*, one exhibiting higher levels of CO_2 recycling during CAM than the other, were small or non-existent (Appendix VIII; Griffiths, 1988a). Furthermore, respiration rates of *T. schiedeana*, which exhibits substantial levels of CO_2 recycling during CAM (Martin & Adams, 1987), were similar to those of five other species of *Tillandsia* (Appendix VIII; Martin, 1994) that do not exhibit CO_2 recycling (Loeschen et al., 1993).

The second hypothesis regarding the mechanism underlying CO_2 recycling during CAM relates to leaf anatomy. During field research in Trinidad (Griffiths et al., 1986), as well as laboratory work with two species of *Aechmea* (Griffiths, 1988a), the degree of CO_2 recycling during CAM correlated with the amount of water-storage parenchyma (= hydrenchyma) in the leaves of several species. The living hydrenchyma tissue actively respires but lacks any photosynthetic apparatus, thus, should contribute "extra" respiratory CO_2 to the nearby photosynthetic tissue. Plants with large amounts of hydrenchyma exhibited greater degrees of CO_2 recycling during CAM. Lüttge and Ball (1987) measured respiration rates in leaf sections and, in one case, excised hydrenchyma and chlorenchyma (green, photosynthetic tissue), of several species of CAM bromeliads, including the terrestrial species *Ananas comosus* and *Hechtia glomerata* and the epiphytic *Aechmea fasciata*. Respiratory contributions from hydrenchyma tissue were inadequate to explain high levels of CO_2 recycling during CAM.

Another test of the anatomical hypothesis is offered by a study of twelve epiphytic species of *Tillandsia*, only one of which—*T. schiedeana*—exhibited CO_2 recycling during CAM (Loeschen et al., 1993). In this study, proportions of leaf cross-sectional areas occupied by hydrenchyma were compared with the degree of CO_2 recycling during CAM, estimated from measurements of nocturnal CO_2 uptake and increases in tissue malate concentrations. The proportion of leaf cross-sectional area occupied by hydrenchyma ranged from zero to 53% in the twelve species, yet only *T. schiedeana*, with a hydrenchyma value of 30%, exhibited CO_2 recycling during CAM. Thus, it appears highly unlikely that CO_2 recycling during CAM results from a contribution of respiratory CO_2 from non-photosynthetic hydrenchyma tissue.

In summary, CO_2 recycling during CAM most likely represents a transitional state between CAM and CAM-idling (Martin, 1994). Direct evidence for this conclusion stems from the fact that, in most cases, CO_2 recycling during CAM decreased or disappeared under some (presumably optimal) environmental conditions, while it increased in magnitude with changes in these conditions (Borland & Griffiths, 1989; Fetene et al., 1990; Fetene & Lüttge, 1991; Griffiths, 1988a, 1988b, 1989; Lee et al., 1989).

VI. Conclusions

The Bromeliaceae is rich in physiological diversity. The great variety of ecophysiological adaptations uncovered in the small number of species examined thus far, relative to the total number of species in the Bromeliaceae, is impressive. One can only guess at the new ecophysiological variations and adaptations awaiting discovery in the remaining, unexplored species.

From an ecophysiological perspective, there are surprisingly few consistent differences between terrestrial and epiphytic species. Approximately two-thirds of the bromeliads investigated thus far are CAM plants (Appendix I). Although these species tend to occur more frequently, relative to the C_3 species, in more arid sites or in the upper, more exposed portions of the canopy, bromeliads with CAM, both terrestrial and epiphytic species, are also found in the shaded forest understory.

Generalizations based on detailed studies of only a few terrestrial species should be applied to other terrestrial bromeliads only tentatively. Most species maintain tissue water potentials less negative than –1.0 MPa (Appendix II). The terrestrial species are either shade-adapted, e.g., *Aechmea magdalenae*, or possibly sun-adapted, e.g., *Ananas comosus* (Appendix IV). Whether or not the latter species is truly heliophilic is complicated by evidence to the contrary and by the fact that more primitive cultivars of *A. comosus* are typically grown in the shade. Photosynthesis is optimal when daytime temperatures are warm but not hot and nighttime temperatures are cool. In several species, CO_2 recycling during CAM may result in nocturnal accumulations of citrate (Appendix VII).

In contrast with terrestrial bromeliads, epiphytic members of the family have been more extensively investigated. Although exceptions exist, many species are shade-adapted yet can tolerate and grow in full sunlight (Appendix IV). Rates of net CO_2 exchange during the day (C_3 species) or night (CAM species) are maximal across a broad range of temperatures with optima occurring during warm days and cool to warm nights. Net CO_2 exchange is sensitive to abrupt changes in air vapor pressure deficit in both C_3 and CAM species. This response is apparently unrelated to the absorption of water vapor by trichomes of atmospheric epiphytes. Hydration of epidermal trichomes has little or no apparent influence on the water balance of the living tissue. Gas exchange in most atmospheric species is inhibited by surface wetting. Photosynthetic responses to tissue elemental content have been examined in only a few studies of terrestrial and epiphytic bromeliads. In most cases, photosynthetic rates increased as tissue nitrogen increased. Ecophysiological responses to foliar concentrations of elemental nutrients and pollutants are in need of further investigation.

The contribution of recycled CO_2 to overnight acid accumulation can exceed that from the fixation of atmospheric CO_2 in many species of terrestrial and epiphytic bromeliads (Appendix VII). Furthermore, in some species there appears to be a correlation between CO_2 recycling during CAM and citrate accumulation. In the majority of cases, high degrees of CO_2 recycling during CAM are correlated with stress.

Investigations of the water relations of bromeliads, especially atmospheric epiphytes, have yielded three important findings. First, photosynthesis is little affected by drought. Second, tissue water potentials typically remain less negative than –1.0 MPa (Appendix II), even well into a drought. Third, the water content of some taxa

can change dramatically throughout a drought or even on a daily basis. The first two findings may be causally related, i.e., photosynthetic rates may remain high under drought conditions because tissue water potentials remain high. Thus, metabolically active cells maintain their turgor under seemingly severe drought stress. One mechanism for maintaining high tissue water potentials during droughts suggested in this review is the restriction of rates of water loss, perhaps a result of very low stomatal densities (Appendix VI), such that little water is lost in spite of a long-term drought. Although this scenario is appealing, it is difficult to reconcile with the extremely labile nature of tissue water content in some atmospheric species. Perhaps some of the large fluctuations in water content reported in these taxa are the result of hydration and dehydration of the dense layer of foliar trichomes. It is also possible that some of these species store large amounts of water (in water-storage parenchyma) that is preferentially lost during droughts, maintaining high water potentials in the actively metabolizing tissue. Clearly, a complete understanding of bromeliad water relations must await further research.

Many of the most interesting and unusual life forms in the Bromeliaceae have not been investigated. There is no doubt that much more remains to be discovered than is currently known about the carbon and water relations of members of the Bromeliaceae.

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Appendix I

Photosynthetic pathways and stable carbon isotope ratios ($\delta^{13}C = \{[(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard}] - 1\} \times 1{,}000$) of terrestrial and epiphytic species in the Bromeliaceae. Carbon isotope ratios are typically single values or ranges for plants grown under a variety of conditions in the field or laboratory. Criteria for determination of photosynthetic pathway include: presence or absence of nocturnal CO_2 uptake ("CO_2"), presence or absence of nighttime accumulation of organic acid ("acid"), high or low carbon isotope ratio ("δ"). Only selected references are provided for well-studied species. Some epiphytic species may occur as occasional terrestrials or saxicoles.

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
TERRESTRIAL SPECIES				
Abromeitiella brevifolia	CAM	δ	-15.6	Griffiths 1984
Abromeitiella chlorantha	CAM	δ	-12.7	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Abromeitiella lattese	CAM	δ	-13.8	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Aechmea magdalenae	CAM	δ	-15.5	Griffiths & Smith 1983
Aechmea magdalenae	CAM	acid, CO_2	-	Pfitsch & Smith 1988
Ananas ananassoides	CAM	CO_2	-	Coutinho 1969
Ananas ananassoides	CAM	δ	-	Medina et al. 1991a
Ananas ananassoides	CAM	acid		Medina et al. 1993
Ananas comosus	CAM	acid	-	Sideris et al. 1948
Ananas comosus	CAM	(enzymes)	-	Dittrich et al. 1973
Ananas comosus	CAM	δ	-14.6	Bender et al. 1973
Ananas comosus	CAM	acid, δ	-12.4	Griffiths & Smith 1983
Ananas comosus	CAM	acid, δ	-14.7	Medina et al. 1986b
Ananas comosus	CAM	acid, CO_2	-	Borland & Griffiths 1989
Ananas comosus	CAM	δ	-13.5 to -16.5	Medina et al. 1991a
Ananas lucidus	CAM	CO_2	-	Medina 1974
Ananas lucidus	CAM	δ	-17.1	Medina et al 1986b
Ananas lucidus	CAM	δ	-16.5	Medina et al. 1991a
Ananas parguazensis	CAM	acid, δ	-12.2 to -15.0	Medina et al. 1986b
Ananas sativus	CAM	acid	-	Warburg 1886

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Ananas sativus	CAM	CO_2	-	Seshagiri & Suryanarayana-Murthy 1951
Ananas sativus	CAM	acid	-	Milburn et al. 1968
Brocchinia acuminata	C_3	CO_2	-	Medina 1974
Brocchinia micrantha	C_3	CO_2	-	Medina 1974
Brocchinia micrantha	C_3	δ	-26.0	Medina et al. 1991a
Brocchinia reducta	C_3	δ	-	Medina et al. 1991a
Brocchinia tatei	C_3	CO_2, δ	-27.3	Medina & Troughton 1974
Bromelia arenaria	CAM	CO_2	-	Nuernbergk 1961
Bromelia chrysantha	CAM	CO_2	-	Medina 1974
Bromelia chrysantha	CAM	δ	-10.2	Griffiths & Smith 1983
Bromelia goeldiana	CAM	δ	-14.1	Medina et al. 1991a
Bromelia humilis	CAM	acid, CO_2	-	Medina 1974
Bromelia humilis	CAM	acid, CO_2, δ	-14.1	Medina & Troughton 1974
Bromelia humilis	CAM	δ	-12.1	Griffiths & Smith 1983
Bromelia humilis	CAM	acid, CO_2, δ	-16.2 to -17.7	Lee et al. 1989
Bromelia palmeri	CAM	δ	-12.7 to -13.2	Mooney et al. 1989
Bromelia pinguin	CAM	CO_2	-	Medina 1974
Bromelia pinguin	CAM	acid, δ	-12.4	Ting 1989
Bromelia plumieri	C_3-CAM?	acid, δ	-20.4	Griffiths & Smith 1983
Bromelia plumieri	CAM	acid, CO_2	-	Griffiths et al. 1986
Bromelia plumieri	CAM	δ	-18.6	Smith et al. 1986a
Bromelia plumieri	CAM	δ	-12.9 to -15.1	Mooney et al. 1989
Canistrum cyathiforme	CAM	CO_2	-	Coutinho 1963
Cottendorfia guianensis	C_3	CO_2	-	Medina 1974

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Cryptanthus sp.	CAM	δ	-17.8	Medina et al. 1977
Cryptanthus acaulis	CAM	acid	-	Bendrat 1929
Cryptanthus bivittatus	CAM	(enzymes)	-	Dittrich et al. 1973
Cryptanthus bromelioides	CAM	δ	-16.2	Medina et al. 1977
Cryptanthus diversifolius	CAM	(enzymes)	-	Dittrich et al. 1973
Deuterocohnia longipetala	CAM	δ	-14.3	Griffiths 1984
Dyckia brevifolia	CAM	acid, CO_2	-	McWilliams 1970
Dyckia brevifolia	CAM	δ	-16.3	Griffiths 1984
Dyckia encholirioides	CAM	CO_2	-	Coutinho 1969
Dyckia fosteriana	CAM	acid, CO_2	-	McWilliams 1970
Dyckia remotiflora	CAM	acid	-	Warburg 1886
Dyckia selloa	C_3	δ	-26.8	Griffiths 1984
Dyckia tuberosa	CAM	CO_2	-	Coutinho 1969
Dyckia tuberosa	CAM	acid, CO_2	-	Medina 1974
Dyckia tuberosa	CAM	CO_2, δ	-12.3	Medina & Troughton 1974
Dyckia velascana	CAM	δ	-16.7	Griffiths 1984
Encholirium hoehneanum	CAM	δ	-12.4	Medina et al. 1977
Fosterella penduliflora	C_3	acid, CO_2	-	McWilliams 1970
Greigia columbiana	C_3	δ	-24.7	Medina et al. 1986b
Greigia nudfordii	C_3	δ	-30.3	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Greigia ocellata	C_3	δ	-26.2	Medina et al. 1986b
Hechtia sp.	CAM	δ	-13.8 to -14.4	Mooney et al. 1989
Hechtia glomerata	CAM	acid, CO_2	-	Lüttge & Ball 1987

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Hechtia marmaria	CAM	δ	-13.5	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Navia reflexa	C_3	CO_2	-	Medina 1974
Navia reflexa	C_3	acid, δ	-27.7	Medina et al. 1986b
Neoglaziovia variegata	CAM	δ	-13.4	Medina et al. 1977
Neoregelia ampullacea	CAM	CO_2	-	Nuernbergk 1961
Neoregelia carolinae	CAM	(enzymes)	-	Dittrich et al. 1973
Neoregelia concentrica	CAM	CO_2	-	Coutinho 1963
Neoregelia concentrica	CAM	δ	-15.9	Medina et al. 1977
Neoregelia coriacea	CAM	δ	-15.8	Medina et al. 1977
Neoregelia cruenta	CAM	acid, CO_2	-	McWilliams 1970
Neoregelia cruenta	CAM	δ	-14.0	Medina et al. 1977
Orthophytum sp.	CAM	CO_2	-	Coutinho 1969
Orthophytum foliosum	CAM	δ	-17.2	Medina et al. 1977
Orthophytum saxicola	CAM	δ	-16.4	Medina et al. 1977
Pitcairnia andreana	C_3	δ	-30.8	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Pitcairnia angustifolia	C_3	acid, δ	-27.2	Ting 1989
Pitcairnia armata	C_3	CO_2	-	Medina 1974
Pitcairnia bulbosa	C_3	CO_2	-	Medina 1974
Pitcairnia bulbosa	C_3	δ	-27.2	Medina et al. 1991a
Pitcairnia flammea	C_3	δ	-27.9	Medina et al. 1977
Pitcairnia integrifolia	C_3	acid, δ	-32.9	Griffiths & Smith 1983
Pitcairnia integrifolia	C_3	CO_2	-	Lüttge et al. 1986b
Pitcairnia juncoides	C_3	CO_2	-	Medina 1974
Pitcairnia pruinosa	C_3	acid, CO_2	-	Medina 1974

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Pitcairnia pruinosa	C_3	CO_2, δ	-26.0	Medina & Troughton 1974
Pitcairnia recurvata	C_3	acid, CO_2	-	McWilliams 1970
Portea kermesina	C_3	acid	-	Bendrat 1929
Portea petropolitana	CAM	δ	-13.5	Medina et al. 1977
Puya sp.	C_3	acid, CO_2	-	McWilliams 1970
Puya alpestris	C_3?	δ	-25.4	Troughton et al. 1974
Puya alpestris	C_3	δ	-24.4	Medina et al. 1977
Puya berteroniana	C_3-CAM?	δ	-20.9	Medina et al. 1977
Puya chilensis	CAM?	δ	-17.9	Medina et al. 1977
Puya chilensis	C_3?	δ	-24.4	Griffiths 1984
Puya copiapina	CAM	δ	-15.4	Medina et al. 1977
Puya densiflora	C_3-CAM?	δ	-20.4	Medina et al. 1977
Puya dyckioides	C_3-CAM?	δ	-22.7	Medina et al. 1977
Puya ferruginea	C_3	δ	-24.8	Medina et al. 1977
Puya floccosa	C_3-CAM	acid, CO_2	-	Medina 1974
Puya floccosa	C_3-CAM?	CO_2, δ	-22.5	Medina & Troughton 1974
Puya laxa	CAM	δ	-16.7	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Puya laxa	CAM?	δ	-18.2	Griffiths 1984
Puya mirabilis	C_3	δ	-25.7	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Puya ponderosa	C_3-CAM?	δ	-23.8	Medina et al. 1977
Puya raimondii	C_3-CAM?	δ	-22.7	Medina et al. 1977
Puya vallo-greigensis	C_3-CAM?	δ	-23.5	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Puya venusta	C_3-CAM?	δ	-23.2	Medina et al. 1977
Puya werdermannii	CAM	δ	-15.0	Griffiths 1984
Quesnelia arvensis	CAM	CO_2	-	Coutinho 1969
Quesnelia humilis	CAM	CO_2	-	Coutinho 1969
Quesnelia marmorata	CAM	δ	-14.2	Medina et al. 1977

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Quesnelia quesneliana	CAM	δ	-13.7	Medina et al. 1977
Quesnelia testudo	CAM	CO_2	-	Coutinho 1963
EPIPHYTIC SPECIES				
Acanthostachys strobilacea	CAM	acid	-	Warburg 1886
Acanthostachys strobilacea	CAM	CO_2	-	Coutinho 1969
Acanthostachys strobilacea	CAM	δ	-14.9	Medina et al. 1977
Aechmea (commercial varieties)	CAM	(enzymes)	-	Dittrich et al. 1973
Aechmea sp.	C_3?	CO_2	-	Nuernbergk 1961
Aechmea aquilega	CAM	acid, CO_2	-	Medina 1974
Aechmea aquilega	CAM	acid, δ	-14.5	Griffiths & Smith 1983
Aechmea aquilega	CAM	acid, CO_2	-	Griffiths et al. 1986
Aechmea aquilega	CAM	δ	-13.8 to -15.0	Smith et al. 1986a
Aechmea aquilega	CAM	δ	-16.5 to -17.3	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Aechmea aripensis	CAM	δ	-12.0	Griffiths & Smith 1983
Aechmea blanchetiana	CAM	δ	-13.9	Medina et al. 1977
Aechmea bracteata	CAM	CO_2	-	Medina 1974
Aechmea bracteata	CAM	δ	-15.4	Mooney et al. 1989
Aechmea brevicollis	CAM	CO_2	-	Medina 1974
Aechmea brevicollis	CAM	acid, δ	-14.4	Medina et al. 1986b
Aechmea brevicollis	CAM	acid	-	Medina 1987
Aechmea bromeliifolia	CAM	CO_2	-	Coutinho 1969
Aechmea bromeliifolia	CAM	CO_2, δ	-13.6	Medina & Troughton 1974
Aechmea bromeliifolia	CAM	acid	-	Medina 1974
Aechmea bromeliifolia	CAM	δ	-12.9	Griffiths & Smith 1983

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Aechmea chantinii	CAM	CO_2	-	Medina 1974
Aechmea chantinii	CAM	acid, δ	-14.0	Medina et al. 1986b
Aechmea dichlamydea	CAM	acid, δ	-15.3	Griffiths & Smith 1983
Aechmea distichantha	CAM	CO_2	-	Coutinho 1969
Aechmea downsiana	CAM	δ	-9.7	Griffiths & Smith 1983
Aechmea fasciata	CAM	acid	-	Lüttge & Ball 1987
Aechmea fendleri	CAM	acid, CO_2	-	Medina 1974
Aechmea fendleri	CAM	δ	-13.3	Griffiths & Smith 1983
Aechmea fendleri	CAM	δ	-12.3 to -14.1	Smith et al. 1986a
Aechmea fendleri	CAM	acid, CO_2	-	Griffiths 1988a
Aechmea fendleri	CAM	δ	-17.3	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Aechmea gamosepala	CAM	δ	-15.4	Medina et al. 1977
Aechmea gigantea	CAM	(enzymes)	-	Dittrich et al. 1973
Aechmea lasseri	CAM	acid	-	Medina 1987
Aechmea lasseri	CAM?	δ	-19.5	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Aechmea lingulata	CAM	δ	-16.7	Medina et al. 1977
Aechmea lingulata	CAM	δ	-12.2	Griffiths & Smith 1983
Aechmea lingulata	CAM	acid, CO_2	-	Griffiths et al. 1986
Aechmea lingulata	CAM	δ	-15.4	Smith et al. 1986a
Aechmea lingulata	CAM	acid, δ	-12.6	Ting 1989
Aechmea marmorata	CAM	CO_2	-	Coutinho 1969
Aechmea mertensii	CAM	acid, δ	-18.5	Griffiths & Smith 1983
Aechmea mexicana (= *Hoplophytum grande*)	CAM	acid	-	Warburg 1886

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Aechmea nudicaulis	CAM	CO_2	-	Coutinho 1969
Aechmea nudicaulis	CAM	acid, δ	-14.7	Griffiths & Smith 1983
Aechmea nudicaulis	CAM	δ	-13.4 to -16.1	Griffiths 1984
Aechmea nudicaulis	CAM	acid, CO_2, δ	-13.7 to -14.5	Smith et al. 1986a
Aechmea nudicaulis	CAM	δ	-13.4 to -15.6	Medina 1987
Aechmea nudicaulis	CAM	acid, CO_2	-	Griffiths 1988a
Aechmea nudicaulis	CAM	δ	-15.4 to -17.3	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Aechmea pectinata	CAM	CO_2	-	Coutinho 1963
Aechmea pectinata	CAM	δ	-15.7	Medina et al. 1977
Aechmea penduliflora	CAM	CO_2	-	Medina 1974
Aechmea rubiginosa	CAM	δ	-	Medina et al. 1991a
Aechmea setigera	CAM	CO_2	-	Medina 1974
Aechmea tillandsioides	CAM	CO_2	-	Medina 1974
Aechmea tillandsioides	CAM	CO_2, δ	-15.2	Medina & Troughton 1974
Aechmea tillandsioides	CAM	acid, δ	-13.0 to -13.7	Medina et al. 1986b
Aechmea weilbachii	CAM	acid	-	Warburg 1886
Araeococcus flagellifolius	CAM	acid, CO_2	-	McWilliams 1970
Araeococcus micranthus	CAM	δ	-16.7	Medina et al. 1977
Araeococcus micranthus	CAM	δ	-18.5	Griffiths & Smith 1983
Billbergia amoena	CAM	CO_2	-	Coutinho 1963
Billbergia amoena	CAM	δ	-15.9	Medina et al. 1977
Billbergia mexicana	CAM	δ	-14.1 to -15.3	Mooney et al. 1989
Billbergia nutans	CAM	CO_2	-	Nuernbergk 1961
Billbergia nutans	CAM	acid, CO_2	-	McWilliams 1970
Billbergia porteana	CAM	δ	-12.0	Medina et al. 1977

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Billbergia pyramidalis	CAM	δ	-15.6	Medina et al. 1977
Billbergia pyramidalis	CAM	δ	-15.9	Griffiths & Smith 1983
Billbergia rosea	CAM	δ	-13.7	Griffiths & Smith 1983
Billbergia sanderiana	C_3?	CO_2	-	Benzing & Friedman 1981
Billbergia saundersii	CAM	(enzymes)	-	Dittrich et al. 1973
Billbergia thyrsoidea	CAM	acid	-	Bendrat 1929
Billbergia venezuelana	CAM	CO_2	-	Medina 1974
Billbergia zebrina	CAM	acid	-	Warburg 1886
Canistrum lindenii	CAM	δ	-18.3	Medina et al. 1977
Canistrum triangulare	CAM	δ	-16.3	Medina et al. 1977
Catopsis berteroniana	C_3	CO_2	-	Medina 1974
Catopsis berteroniana	C_3	acid, δ	-32.2	Griffiths & Smith 1983
Catopsis floribunda	C_3	acid, CO_2	-	McWilliams 1970
Catopsis floribunda	C_3	δ	-24.6	Griffiths & Smith 1983
Catopsis floribunda	C_3	acid, δ	-	Ting 1989
Catopsis morreniana	C_3	acid, CO_2	-	McWilliams 1970
Catopsis nutans	C_3	CO_2	-	Benzing & Renfrow 1971a
Catopsis nutans	C_3-CAM?	acid, CO_2	-	Medina 1974
Catopsis nutans	C_3-CAM?	CO_2, δ	-23.7	Medina & Troughton 1974
Catopsis nutans	C_3	acid, δ	-24.5	Ting 1989
Catopsis sessiliflora	C_3	δ	-25.7	Medina et al. 1977
Catopsis sessiliflora	C_3	δ	-24.2	Griffiths & Smith 1983
Glomeropitcairnia erectiflora	C_3	acid, δ	-33.7	Griffiths & Smith 1983
Glomeropitcairnia erectiflora	C_3	acid	-	Smith et al. 1985
Guzmania acorifolia	C_3	CO_2	-	Medina 1974
Guzmania lingulata	C_3	CO_2	-	Benzing & Renfrow 1971a

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Guzmania lingulata	C_3-CAM?	(enzymes)	-	Dittrich et al. 1973
Guzmania lingulata	C_3	acid, δ	-29.5	Griffiths & Smith 1983
Guzmania lingulata	C_3	acid	-	Smith et al. 1985
Guzmania lingulata	C_3	acid, CO_2	-	Griffiths et al. 1986
Guzmania lingulata	C_3	δ	-24.8 to -28.3	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Guzmania megastachya	C_3	δ	-28.3	Griffiths & Smith 1983
Guzmania minor	C_3	CO_2	-	Bierhuizen et al. 1984
Guzmania mitis	C_3	CO_2	-	Medina 1974
Guzmania monostachia	C_3-CAM	acid, CO_2	-	McWilliams 1970
Guzmania monostachia	C_3-CAM	acid, CO_2	-	Medina 1974
Guzmania monostachia	C_3-CAM	acid, CO_2, δ	-23.7	Medina & Troughton 1974
Guzmania monostachia	C_3-CAM	CO_2	-	Benzing & Friedman 1981
Guzmania monostachia	C_3-CAM	acid, δ	-26.5 to -31.5	Griffiths & Smith 1983
Guzmania monostachia	C_3-CAM	acid	-	Smith et al. 1985
Guzmania monostachia	C_3-CAM	acid, CO_2	-	Griffiths et al. 1986
Guzmania monostachia	C_3-CAM	δ	-26.7	Smith et al. 1986a
Guzmania monostachia	C_3-CAM	δ	-26.5 to -31.5	Medina 1987
Guzmania monostachia	C_3-CAM	δ	-24.9 to -26.5	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Guzmania monostachia	C_3-CAM	acid, CO_2, δ	-23.2 to -25.6	C. E. Martin & A. Schmitt, unpubl.
Guzmania mucronata	C_3	acid, CO_2	-	Medina 1974
Guzmania mucronata	C_3	CO_2, δ	-24.7	Medina & Troughton 1974
Guzmania musaica	C_3	CO_2	-	Benzing & Friedman 1981
Guzmania patula	C_3	CO_2	-	Medina 1974

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Guzmania sanguinea	C_3	δ	-26.8	Griffiths & Smith 1983
Guzmania virescens	C_3	CO_2	-	Medina 1974
Hohenbergia brachycephala	CAM	δ	-15.6	Medina et al. 1977
Hohenbergia disjuncta	CAM	δ	-17.1	Medina et al. 1977
Hohenbergia littoralis	CAM	δ	-12.1	Medina et al. 1977
Hohenbergia salzmannii	CAM	δ	-15.7	Medina et al. 1977
Hohenbergia stellata	CAM	acid, δ	-14.5	Griffiths & Smith 1983
Hohenbergia stellata	CAM	acid	-	Smith et al. 1985
Hohenbergia utriculosa	CAM	δ	-12.4	Medina et al. 1977
Neoregelia princeps (= Nidularium meyendorffii)	CAM	acid	-	Warburg 1886
Neoregelia princeps (= Nidularium meyendorffii)	CAM	CO_2	-	Nuernbergk 1961
Nidularium sp.	C_3	CO_2	-	Coutinho 1969
Nidularium burchellii	C_3	CO_2	-	Benzing & Friedman 1981
Nidularium fulgens	CAM	acid	-	Bendrat 1929
Nidularium innocentii	CAM?	acid, CO_2	-	McWilliams 1970
Nidularium innocentii	C_3	δ	-24.0	Medina et al. 1977
Nidularium scheremetiewii	CAM	δ	-16.3	Medina et al. 1977
Streptocalyx floribundus	CAM	δ	-14.5	Medina et al. 1977
Streptocalyx poeppigii	CAM	δ	-14.0	Medina et al. 1977
Tillandsia adpressa	C_3	CO_2	-	Medina 1974
Tillandsia adpressa	C_3	CO_2, δ	-25.3	Medina & Troughton 1974
Tillandsia adpressiflora	C_3-CAM?	acid, CO_2	-	Medina 1974
Tillandsia adpressiflora	C_3-CAM?	acid, CO_2, δ	-25.3	Medina & Troughton 1974

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Tillandsia adpressiflora	C_3	acid, δ	-28.0	Medina et al. 1986b
Tillandsia aëranthos	CAM	CO_2	-	Kluge et al. 1973
Tillandsia aëranthos	CAM	acid, CO_2	-	Virzo De Santo et al. 1977
Tillandsia albida	CAM	CO_2	-	Kluge et al. 1973
Tillandsia anceps	C_3	CO_2	-	Medina 1974
Tillandsia anceps	C_3	CO_2, δ	-28.3	Medina & Troughton 1974
Tillandsia anceps	C_3	acid, δ	-28.6	Griffiths & Smith 1983
Tillandsia andreana	CAM	CO_2	-	Medina 1974
Tillandsia andreana	CAM	CO_2, δ	-13.3	Medina & Troughton 1974
Tillandsia araujei	CAM	δ	-14.3	Medina et al. 1977
Tillandsia atroviridipetala	CAM	CO_2	-	Kluge et al. 1973
Tillandsia baileyi	CAM	CO_2	-	Kluge et al. 1973
Tillandsia baileyi	CAM	CO_2, acid	-	C. E. Martin, unpubl.
Tillandsia balbisiana	CAM	CO_2	-	Kluge et al. 1973
Tillandsia balbisiana	CAM	CO_2, δ	-12.2	Medina & Troughton 1974
Tillandsia balbisiana	CAM	acid, CO_2	-	Loeschen et al. 1993
Tillandsia bergeri	CAM	acid, CO_2	-	Loeschen et al. 1993
Tillandsia biflora	CAM	acid	-	Warburg 1886
Tillandsia boyoides	CAM	δ	-13.7	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Tillandsia brachycaulos	CAM	acid, CO_2	-	Virzo De Santo et al. 1977
Tillandsia bulbosa	CAM	CO_2	-	Medina 1974
Tillandsia bulbosa	CAM	δ	-16.5	Medina et al. 1977
Tillandsia bulbosa	CAM	acid, δ	-18.5	Griffiths & Smith 1983

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Tillandsia bulbosa	CAM	acid	-	Smith et al. 1986b
Tillandsia buseri	C_3-CAM?	δ	-22.4	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Tillandsia canescens	C_3	acid, δ	-32.4	Griffiths & Smith 1983
Tillandsia canescens	C_3	acid	-	Smith et al. 1985
Tillandsia caput-medusae	CAM	acid, CO_2	-	Virzo De Santo et al. 1977
Tillandsia compacta	C_3	acid, CO_2	-	Medina 1974
Tillandsia compacta	C_3	CO_2, δ	-25.6	Medina & Troughton 1974
Tillandsia complanata	C_3	CO_2	-	Medina 1974
Tillandsia complanata	C_3-CAM?	CO_2, δ	-23.6	Medina & Troughton 1974
Tillandsia complanata	C_3	δ	-30.7	Griffiths & Smith 1983
Tillandsia deppeana	C_3	acid, CO_2, δ	-24.1 to -24.7	Adams & Martin 1986b
Tillandsia didistichoides	CAM	acid	-	Medina 1974
Tillandsia diguetii	CAM	δ	-14.2	Mooney et al. 1989
Tillandsia disticha	CAM	CO_2	-	Kluge et al. 1973
Tillandsia duidae	C_3	CO_2	-	Medina 1974
Tillandsia elongata	CAM	acid, CO_2	-	Medina 1974
Tillandsia elongata	C_3?	δ	-26.4	Griffiths & Smith 1983
Tillandsia elongata	CAM	δ	-16.2	Smith et al. 1986a
Tillandsia elongata	CAM	acid, CO_2	-	Griffiths et al. 1986
Tillandsia fasciculata	CAM	acid, CO_2	-	Medina 1974
Tillandsia fasciculata	CAM	acid, δ	-14.1	Griffiths & Smith 1983
Tillandsia fasciculata	CAM	acid	-	Smith et al. 1985
Tillandsia fasciculata	CAM	δ	-12.0 to -14.2	Mooney et al. 1989

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Tillandsia fasciculata	CAM	acid, δ	-12.9	Ting 1989
Tillandsia fasciculata	CAM	acid, CO_2	-	Loeschen et al. 1993
Tillandsia fendleri	C_3	CO_2	-	Medina 1974
Tillandsia fendleri	C_3	CO_2, δ	-24.8	Medina & Troughton 1974
Tillandsia fendleri	C_3	δ	-31.8	Griffiths & Smith 1983
Tillandsia fendleri	C_3	δ	-27.8	Smith et al. 1986a
Tillandsia fendleri	C_3	acid, CO_2	-	Griffiths et al. 1986
Tillandsia fenebris	CAM	CO_2	-	Kluge et al. 1973
Tillandsia festucoides	CAM	CO_2	-	Kluge et al. 1973
Tillandsia filifolia	C_3	CO_2	-	Kluge et al. 1973
Tillandsia flabellata	CAM	acid, CO_2	-	Virzo De Santo et al. 1977
Tillandsia flexuosa	CAM	acid, CO_2	-	Medina 1974
Tillandsia flexuosa	CAM	acid, δ	-19.2	Griffiths & Smith 1983
Tillandsia flexuosa	CAM	δ	-15.5	Medina et al. 1986b
Tillandsia flexuosa	CAM	acid, CO_2, δ	-13.1	Griffiths et al. 1989
Tillandsia flexuosa	CAM	δ	-13.6	Medina et al. 1991a
Tillandsia flexuosa	CAM	δ	-14.2 to -16.0	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Tillandsia funebris	CAM	CO_2	-	Kluge et al. 1973
Tillandsia gardneri	CAM	CO_2	-	Medina 1974
Tillandsia gardneri	CAM	CO_2, δ	-13.9	Medina & Troughton 1974
Tillandsia gardneri	CAM	δ	-14.7	Griffiths & Smith 1983
Tillandsia incarnata	CAM	CO_2	-	Medina 1974
Tillandsia incarnata	CAM	CO_2, δ	-16.0	Medina & Troughton 1974
Tillandsia incurva	C_3	CO_2	-	Medina 1974
Tillandsia ionantha	CAM	CO_2	-	Benzing & Renfrow 1971a
Tillandsia ionantha	CAM	δ	-11.5 to -14.7	Mooney et al. 1989

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Tillandsia ionantha	CAM	acid, CO_2	-	Loeschen et al. 1993
Tillandsia ixioides	CAM	acid, CO_2	-	Virzo De Santo et al. 1977
Tillandsia jenmanii	C_3	CO_2	-	Medina 1974
Tillandsia juncea	CAM	acid, CO_2	-	McWilliams 1970
Tillandsia juncea	CAM	CO_2	-	Kluge et al. 1973
Tillandsia juncea	CAM	(enzymes)	-	Dittrich et al. 1973
Tillandsia juncea	CAM	δ	-13.4	Griffiths & Smith 1983
Tillandsia latifolia	CAM	acid, CO_2	-	Virzo De Santo et al. 1977
Tillandsia lindenii	CAM	acid	-	Bendrat 1929
Tillandsia lineatispica	CAM	acid, δ	-	Ting 1989
Tillandsia loliacea	CAM	δ	-15.2	Medina et al. 1977
Tillandsia longifolia	C_3	CO_2	-	Medina 1974
Tillandsia makoyana	CAM	δ	-10.4 to -15.3	Mooney et al. 1989
Tillandsia monadelpha	C_3	δ	-26.7	Griffiths & Smith 1983
Tillandsia myriantha	CAM	CO_2	-	Medina 1974
Tillandsia paleacea	CAM	CO_2	-	Kluge et al. 1973
Tillandsia paleacea	CAM	acid, CO_2	-	Virzo De Santo et al. 1977
Tillandsia paleacea	CAM	acid, CO_2	-	Loeschen et al. 1993
Tillandsia paraënsis	CAM	CO_2	-	Medina 1974
Tillandsia paraënsis	CAM	acid, δ	-15.6	Medina et al. 1986b
Tillandsia paucifolia[a]	CAM	CO_2	-	Benzing & Renfrow 1971a
Tillandsia paucifolia[a]	CAM	CO_2, δ	-12.7	Medina & Troughton 1974
Tillandsia paucifolia[a]	CAM	δ	-11.6 to -13.0	Mooney et al. 1989
Tillandsia paucifolia[a]	CAM	acid, CO_2	-	Loeschen et al. 1993

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Tillandsia polystachia	CAM	acid, CO_2	-	Medina 1974
Tillandsia polystachia	CAM	acid, CO_2	-	Medina & Troughton 1974
Tillandsia rauhii	C_3-CAM?	δ	-20.5	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Tillandsia recurvata	CAM	acid, CO_2	-	Medina 1974
Tillandsia recurvata	CAM	CO_2, δ	-15.3	Medina & Troughton 1974
Tillandsia recurvata	CAM	CO_2	-	Lange & Medina 1979
Tillandsia recurvata	CAM	acid, δ	-13.2	Ting 1989
Tillandsia recurvata	CAM	acid, CO_2	-	Loeschen et al. 1993
Tillandsia schiedeana	CAM	CO_2	-	Medina 1974
Tillandsia schiedeana	CAM	acid, CO_2	-	Virzo De Santo et al. 1977
Tillandsia schiedeana	CAM	acid, CO_2	-	Martin & Adams 1987
Tillandsia schiedeana	CAM	acid, CO_2	-	Loeschen et al. 1993
Tillandsia setacea	CAM	δ	-10.9 to -11.4	Mooney et al. 1989
Tillandsia setacea	CAM	acid, CO_2	-	Loeschen et al. 1993
Tillandsia setacea	CAM	δ	-14.4	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Tillandsia spiculosa	C_3	CO_2	-	Medina 1974
Tillandsia spiculosa	C_3	CO_2, δ	-25.0	Medina & Troughton 1974
Tillandsia spiculosa	C_3	acid, δ	-29.4	Griffiths & Smith 1983
Tillandsia spiculosa	C_3	acid	-	Smith et al. 1985
Tillandsia stenoglossa	C_3	CO_2	-	Medina 1974
Tillandsia straminea	CAM	CO_2	-	Kluge et al. 1973
Tillandsia streptocarpa	CAM	CO_2	-	Coutinho 1969

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Tillandsia streptocarpa	CAM	CO_2	-	Kluge et al. 1973
Tillandsia streptocarpa	CAM	δ	-12.7	Medina et al. 1977
Tillandsia stricta	CAM	δ	-17.3	Medina et al. 1977
Tillandsia stricta	CAM	δ	-14.9	Griffiths & Smith 1983
Tillandsia stricta	CAM	acid	-	Smith et al. 1986b
Tillandsia tenuifolia	CAM	CO_2	-	Kluge et al. 1973
Tillandsia tenuifolia	CAM	acid	-	Medina 1974
Tillandsia tenuifolia	CAM	CO_2, δ	-15.2	Medina & Troughton 1974
Tillandsia tenuifolia	CAM	δ	-11.4	Griffiths & Smith 1983
Tillandsia tenuispica	C_3	CO_2	-	Medina 1974
Tillandsia tetrantha	C_3	CO_2	-	Medina 1974
Tillandsia tricholepsis	CAM	δ	-16.5	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Tillandsia tricolor	CAM	acid, CO_2	-	McWilliams 1970
Tillandsia usneoides	CAM	CO_2	-	Coutinho 1969
Tillandsia usneoides	CAM	δ	-18.6	Smith & Epstein 1971
Tillandsia usneoides	CAM	acid, CO_2	-	Kluge et al. 1973
Tillandsia usneoides	CAM	(enzymes)	-	Dittrich et al. 1973
Tillandsia usneoides	CAM	CO_2, δ	-13.7	Medina & Troughton 1974
Tillandsia usneoides	CAM	acid, CO_2	-	Martin et al. 1981
Tillandsia usneoides	CAM	acid, CO_2, δ	-15.0	Martin et al. 1982
Tillandsia usneoides	CAM	acid, δ	-19.8	Griffiths & Smith 1983
Tillandsia usneoides	CAM	δ	-13.9	Mooney et al. 1989
Tillandsia usneoides	CAM	acid, δ	-14.7	Ting 1989

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Tillandsia utriculata	CAM	acid, CO_2	-	Medina 1974
Tillandsia utriculata	CAM	CO_2, δ	-13.7	Medina & Troughton 1974
Tillandsia utriculata	CAM	acid, δ	-11.2	Griffiths & Smith 1983
Tillandsia utriculata	CAM	δ	-15.3	Smith et al. 1986a
Tillandsia utriculata	CAM	acid, CO_2	-	Griffiths et al. 1986
Tillandsia utriculata	CAM	acid, CO_2, δ	-17.4	Griffiths et al. 1990
Tillandsia utriculata	CAM	δ	-15.8 to -17.8	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Tillandsia valenzuelana	CAM	acid, CO_2	-	Loeschen et al. 1993
Tillandsia violacea	CAM	acid, CO_2	-	Virzo De Santo et al. 1977
Vriesea altodaserrae	C_3	(daytime transpiration)	-	Coutinho 1962
Vriesea altodaserrae	C_3	CO_2	-	Coutinho 1969
Vriesea amazonica	C_3	δ	-28.0	Griffiths & Smith 1983
Vriesea amazonica	C_3	δ	-27.8	Smith et al. 1986a
Vriesea amazonica	C_3	acid, CO_2	-	Griffiths et al. 1986
Vriesea appenii	C_3-CAM?	δ	-21.2	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Vriesea barclayana	C_3-CAM?	δ	-21.8	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Vriesea broadwayi	C_3	δ	-24.8	Griffiths & Smith 1983
Vriesea capituligera	C_3	CO_2	-	Medina 1974
Vriesea capituligera	C_3-CAM?	δ	-23.1	Griffiths & Smith 1983
Vriesea cereicola	CAM	δ	-13.4 to -17.1	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Vriesea chrysostachys	C_3	δ	-25.1	Griffiths & Smith 1983
Vriesea cylindrica	C_3-CAM?	δ	-22.9	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Vriesea didistichoides	C_3	CO_2	-	Medina 1974
Vriesea didistichoides	C_3-CAM?	δ	-23.9	Griffiths & Smith 1983
Vriesea espinosae	C_3-CAM?	δ	-15.5 to -19.4	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Vriesea fenestralis	C_3-CAM?	acid, CO_2	-	McWilliams 1970
Vriesea fenestralis	C_3	CO_2	-	Benzing & Friedman 1981
Vriesea fosteriana	C_3	CO_2	-	Benzing & Friedman 1981
Vriesea fragrans	C_3	δ	-26.9	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Vriesea geniculata	C_3	δ	-24.2 to -27.2	F. Reinert & H. Griffiths, unpubl.
Vriesea glutinosa	C_3	δ	-27.3	Griffiths & Smith 1983
Vriesea hitchcockiana	CAM?	δ	-18.2	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Vriesea inflata	C_3	CO_2	-	Coutinho 1963
Vriesea johnstonii	C_3	δ	-31.4	Griffiths & Smith 1983
Vriesea jonghei	C_3	δ	-29.0	Smith et al. 1986a
Vriesea jonghei	C_3	acid, CO_2	-	Griffiths et al. 1986
Vriesea olmosana	C_3-CAM?	δ	-21.9	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Vriesea platynema	C_3-CAM?	acid, CO_2	-	Medina 1974
Vriesea platynema	C_3	acid, CO_2, δ	-28.6	Medina & Troughton 1974
Vriesea platynema	C_3	δ	-24.6	Griffiths & Smith 1983

Appendix I (continued)

Species	Photosynthetic pathway	Criteria for determination	$\delta^{13}C$ ‰	Reference
Vriesea procera	C_3	δ	-27.9	Medina et al. 1977
Vriesea procera	C_3	δ	-26.0	Griffiths & Smith 1983
Vriesea rauhii	C_3-CAM?	δ	-21.2 to -22.0	H. Griffiths, H. S. J. Lee & J. A. C. Smith, unpubl.
Vriesea regina	C_3	δ	-25.9	Medina et al. 1977
Vriesea ringens	C_3	δ	-24.0	Griffiths & Smith 1983
Vriesea rubra	C_3	CO_2	-	Medina 1974
Vriesea rubra	C_3	δ	-25.6	Griffiths & Smith 1983
Vriesea scalaris	C_3	CO_2	-	Benzing & Friedman 1981
Vriesea simplex	C_3	CO_2	-	Medina 1974
Vriesea simplex	C_3	δ	-24.4	Griffiths & Smith 1983
Vriesea splendens	C_3	CO_2	-	Medina 1974
Vriesea splendens	C_3	acid, δ	-34.8	Griffiths & Smith 1983
Vriesea splendens	C_3	acid	-	Smith et al. 1985
Vriesea splitgerberi	C_3	δ	-32.4	Griffiths & Smith 1983
Vriesea splitgerberi	C_3	δ	-28.8	Smith et al. 1986a
Vriesea splitgerberi	C_3	acid, CO_2	-	Griffiths et al. 1986
Wittrockia campos-portoi	C_3-CAM?	δ	-23.1	Medina et al. 1977
Wittrockia superba	CAM	δ	-15.4	Medina et al. 1977

[a]Same as *T. circinnata*

Appendix II

Maximum and minimum values of tissue water potential (Ψ) and osmotic potential (Ψ_π) for terrestrial and epiphytic species in the Bromeliaceae. Measurements were made under a variety of conditions in the field or laboratory. Values are typically averages for plants under one or more conditions. All data are in MPa (1 MPa = 10 bars). Some epiphytic species may occur as occasional terrestrials or saxicoles.

Species	Maximum Ψ	Minimum Ψ	Maximum Ψ_π	Minimum Ψ_π	Reference
TERRESTRIAL SPECIES					
Ananas comosus	-	-3.0	-	-	Kadzimin 1975
Bromelia humilis	-0.2	-0.6	-0.8	-1.2	Lee et al. 1989
Pitcairnia integrifolia	-	-	-0.9[a]	-	Lüttge et al. 1986b
EPIPHYTIC SPECIES					
Aechmea aquilega	-0.2	-0.6	-0.5	-0.9	Smith et al. 1985
Aechmea aquilega	-	-	-0.5	-0.9	Lüttge et al. 1986c
Aechmea aquilega	-0.3	-0.9	-0.5	-0.3	Smith et al. 1986b
Aechmea nudicaulis	-0.2	-0.5	-0.5	-1.1	Smith et al. 1985
Aechmea nudicaulis	-0.3	-1.0	-0.6	-1.2	Smith et al. 1986b
Catopsis berteroniana	-	-	-0.6[a]	-	Harris 1918
Glomeropitcairnia erectiflora	-0.2	-0.4	-0.7[a]	-	Smith et al. 1985
Guzmania capituligera	-	-	-0.5[a]	-	Harris 1918
Guzmania lingulata	-0.2	-0.5	-0.3	-0.5	Smith et al. 1985
Guzmania monostachia	-	-	-0.6[a]	-	Harris 1918
Guzmania monostachia	-0.2	-0.5	-0.5	-0.6	Smith et al. 1985
Guzmania monostachia	-0.2	-0.5	-0.5	-0.7	Smith et al. 1986b
Guzmania monostachia	-0.5	-0.7	-	-	Maxwell et al. 1992
Guzmania sintenisii	-	-	-0.4[a]	-	Harris 1918
Hohenbergia stellata	-0.2	-0.4	-0.4	-0.7	Smith et al. 1985
Tillandsia aloifolia	-	-	-0.5[a]	-	Harris 1918
Tillandsia balbisiana	-	-	-0.6[a]	-	Harris 1918
Tillandsia balbisiana	-	-	-0.6	-1.0	C. E. Martin, unpubl.

Appendix II (continued)

Species	Maximum Ψ	Minimum Ψ	Maximum Ψ_n	Minimum Ψ_n	Reference
Tillandsia canescens	-0.2	-0.5	-0.3[a]	-	Smith et al. 1985
Tillandsia fasciculata	-	-	-0.5[a]	-	Harris 1918
Tillandsia fasciculata	-	-	-0.6	-1.3	Smith et al. 1985
Tillandsia fasciculata	-	-	-0.5	-1.0	C. E. Martin, unpubl.
Tillandsia flexuosa	-0.2	-0.6	-0.4	-1.2	Griffiths et al. 1989
Tillandsia incurva	-	-	-0.3[a]	-	Harris 1918
Tillandsia ionantha	-	-	-0.4	-0.6	C. E. Martin, unpubl.
Tillandsia recurvata	-	-	-0.6[a]	-	Harris 1918
Tillandsia recurvata	-	-	-0.6	-0.8	Biebl 1964
Tillandsia recurvata	-	-	-0.9	-1.5	Lüttge 1987
Tillandsia schiedeana	-	-	-0.6	-0.8	C. E. Martin, unpubl.
Tillandsia spiculosa	-0.2	-0.3	-0.5[a]	-	Smith et al. 1985
Tillandsia straminea	-	-	-0.8[a]	-	Walter 1971
Tillandsia tenuifolia	-	-	-0.5[a]	-	Harris 1918
Tillandsia usneoides	-	-	-0.9[a]	-	Harris 1918
Tillandsia usneoides	-	-	-0.6	-0.8	C. E. Martin, unpubl.
Tillandsia utriculata	-	-	-0.5[a]	-	Harris 1918
Tillandsia utriculata	-0.2	-0.5	-0.5	-1.2	Smith et al. 1985
Tillandsia valenzuelana	-	-	-0.4[a]	-	Harris 1918
Vriesea amazonica	-0.2	-0.6	-0.6	-0.7	Smith et al. 1986b
Vriesea splendens	-	-	-0.6[a]	-	Smith et al. 1985

[a]Only one value given (not necessarily a maximum value).

Appendix III

Photosynthetic responses to light in 21 species of epiphytic bromeliads. Data were derived from manometric determinations of O_2 evolution. Light levels were converted from foot-candles to μmol m^{-2} s^{-1} photosynthetic photon flux density. Numbers in parentheses are the rankings of each datum on a sun (#1) to shade (#21) adaptation gradient, given commonly accepted physiological adaptations to sun and shade. Tie rankings were given average ranks of all tied values. The mean ranking is an average of rankings for the three data sets (data from Benzing & Renfrow, 1971b).

Species	Slope of light response curve	Light compensation point μmol m^{-2} s^{-1}	Light level of saturation of photosynthesis μmol m^{-2} s^{-1}	Mean ranking
Catopsis berteroniana	7.5 (18.5)	7 (18)	360 (17)	18
Catopsis floribunda	8.6 (20)	9 (14)	850 (9)	14
Catopsis nutans	3.2 (11)	10 (12)	720 (11)	11
Guzmania lingulata	5.5 (17)	3 (20.5)	320 (19)	19
Guzmania monostachia	7.5 (18.5)	8 (16)	290 (20)	18
Tillandsia anceps	1.6 (7)	9 (14)	1000 (5)	9
Tillandsia baileyi	1.1 (4.5)	15 (8.5)	770 (10)	8
Tillandsia bulbosa	0.8 (2)	18 (5.5)	1150 (1)	3
Tillandsia capitata	2.7 (10)	25 (2)	625 (14)	9
Tillandsia concolor	2.3 (9)	18 (5.5)	1035 (4)	6
Tillandsia fasciculata	1.3 (6)	18 (5.5)	925 (6)	6
Tillandsia imperialis	4.9 (15)	3 (20.5)	330 (18)	18
Tillandsia ionantha	3.3 (12)	15 (8.5)	645 (13)	11
Tillandsia juncea	0.9 (3)	23 (3)	1095 (3)	3
Tillandsia lindenii	3.7 (13)	11 (11)	895 (8)	11
Tillandsia monadelpha	5.1 (16)	9 (14)	710 (12)	14
Tillandsia pueblensis	0.7 (1)	31 (1)	1140 (2)	1
Tillandsia tricolor	1.7 (8)	12 (10)	915 (7)	8
Tillandsia usneoides	1.1 (4.5)	18 (5.5)	475 (15)	8
Vriesea carinata	9.1 (21)	7 (18)	370 (16)	18
Vriesea simplex	3.9 (14)	7 (18)	235 (21)	18

Appendix IV

Representative values of photosynthetic parameters related to adaptation to low or high light for terrestrial and epiphytic species in the Bromeliaceae (comparative values for non-bromeliads can be found at the end of the table). Some studies provide data for plants grown under low (LL) and high (HL) light. Data may reflect measurement of CO_2 exchange or O_2 exchange. Values for some of the CAM species represent CO_2 uptake integrated throughout nights following different daytime light levels (units provided in these cases). Measurements were made under a variety of conditions in the field or laboratory. Values are typically averages for plants under one or more conditions. Whenever possible, unit conversions were estimated based on information provided in the appropriate reference. Units are given in the table only if different from those in the heading. Some epiphytic species may occur as occasional terrestrials or saxicoles.

Species	Light compensation point $\mu mol\ m^{-2}\ s^{-1}$	Apparent quantum yield	Light level at which photosynthesis saturated $\mu mol\ m^{-2}\ s^{-1}$	Chlorophyll concentration $mg\ g^{-1}$ DW	Chloro-phyll a/b ratio	Reference
TERRESTRIAL SPECIES						
Ananas comosus	-	-	-	1.2 $mg\ g^{-1}$ FW	-	Sideris 1947
Ananas comosus	-	-	-	1.0 $mg\ g^{-1}$ FW	-	Sideris & Young 1947
Ananas comosus	-	-	-	0.7 $mg\ g^{-1}$ FW	-	Sideris et al. 1948
Ananas comosus	-	-	-	0.9 $mg\ g^{-1}$ FW	-	Sideris & Young 1956
Ananas comosus	200	-	800	-	-	Nose et al. 1977
Ananas comosus	-	-	-	-	-	Sale & Neales 1980
Ananas comosus	-	-	600	0.4 $mg\ g^{-1}$ FW	-	Nose et al. 1985
Ananas comosus	5 $mol\ m^{-2}\ d^{-1}$	-	20 $mol\ m^{-2}\ d^{-1}$	-	-	Nose et al. 1986
Ananas comosus	-	-	-	0.2 $mg\ g^{-1}$ FW	-	Aromose 1989
Ananas comosus LL	26	0.07	300	-	-	Borland & Griffiths 1989
Ananas comosus HL	50	0.03	700	-	-	Borland & Griffiths 1989
Ananas comosus LL	-	-	-	504 $\mu mol\ m^{-2}$	-	Medina et al. 1991b
Ananas comosus HL	-	-	-	323 $\mu mol\ m^{-2}$	-	Medina et al. 1991b
Brocchinia micrantha	-	-	-	0.5	-	Medina et al. 1977
Bromelia humilis LL	-	-	-	600 $mg\ m^{-2}$	-	Medina et al. 1986a
Bromelia humilis HL	-	-	-	40 $mg\ m^{-2}$	-	Medina et al. 1986a
Bromelia humilis LL	-	-	-	0.2 $mg\ g^{-1}$ FW	1.9	Lee et al. 1989
Bromelia humilis HL	-	-	-	0.1 $mg\ g^{-1}$ FW	1.3	Lee et al. 1989

Appendix IV (continued)

Species	Light compensation point $\mu mol\ m^{-2}\ s^{-1}$	Apparent quantum yield	Light level at which photosynthesis saturated $\mu mol\ m^{-2}\ s^{-1}$	Chlorophyll concentration $mg\ g^{-1}$ DW	Chloro-phyll a/b ratio	Reference
Bromelia humilis LL	10	0.09	1000	0.7 $mg\ g^{-1}$ FW	2.3	Fetene et al. 1990
Bromelia humilis HL	33	0.08	1000	0.1 $mg\ g^{-1}$ FW	2.8	Fetene et al. 1990
Cottendorfia guianensis	-	-	-	0.4	-	Medina et al. 1977
Pitcairnia integrifolia	13	0.03	300	-	-	Lüttge et al. 1986b
Pitcairnia juncoides	-	-	-	0.3	-	Medina et al. 1977
Pitcairnia pruinosa	-	-	-	0.5	-	Medina et al. 1977
EPIPHYTIC SPECIES						
Aechmea chantinii	-	-	-	0.7	-	Medina et al. 1977
Aechmea penduliflora	-	-	-	0.3	-	Medina et al. 1977
Aechmea setigera	-	-	-	0.2	-	Medina et al. 1977
Aechmea tillandsioides	-	-	-	0.2	-	Medina et al. 1977
Billbergia saundersiana	-	-	-	0.2 $g\ m^{-2}$	-	Benzing & Friedman 1981
Catopsis berteroniana	7	-	360	8.4	-	Benzing & Renfrow 1971b
Catopsis berteroniana	-	-	-	1.2	-	Medina et al. 1977
Catopsis floribunda	9	-	850	7.4	-	Benzing & Renfrow 1971b
Catopsis nutans	10	-	720	12.2	-	Benzing & Renfrow 1971b
Catopsis nutans	55	-	430	-	-	Benzing & Renfrow 1971a
Catopsis nutans	50	-	1000	0.4 $g\ m^{-2}$	-	Benzing & Friedman 1981

Appendix IV (continued)

Species	Light compensation point µmol $m^{-2} s^{-1}$	Apparent quantum yield	Light level at which photosynthesis saturated µmol $m^{-2} s^{-1}$	Chlorophyll concentration mg g^{-1} DW	Chloro-phyll a/b ratio	Reference
Guzmania acorifolia	-	-	-	1.1	-	Medina et al. 1977
Guzmania lingulata	3	-	320	11.8	-	Benzing & Renfrow 1971b
Guzmania lingulata	43	-	430	-	-	Benzing & Renfrow 1971a
Guzmania lingulata	15	-	400	0.3 g m^{-2}	-	Benzing & Friedman 1981
Guzmania lingulata	20	0.01	600	-	-	Griffiths et al. 1986
Guzmania lingulata LL	7	0.02	140	5.9		Smith 1989
Guzmania lingulata HL	18	0.02	230	4.0		Smith 1989
Guzmania minor	23	-	-	-	-	Bierhuizen et al. 1984
Guzmania mitis	-	-	-	0.5	-	Medina et al. 1977
Guzmania monostachia	8	-	290	6.6	-	Benzing & Renfrow 1971b
Guzmania monostachia	60	-	400	0.2 g m^{-2}	-	Benzing & Friedman 1981
Guzmania monostachia LL	80	0.05	200	1.0 mg g^{-1} FW	1.0	Maxwell et al. 1992
Guzmania monostachia HL	90	0.04	200	0.2 mg g^{-1} FW	1.2	Maxwell et al. 1992
Guzmania musaica	35	-	250	0.4 g m^{-2}	-	Benzing & Friedman 1981
Guzmania patula	-	-	-	0.6	-	Medina et al. 1977
Guzmania virescens	-	-	-	3.0	-	Medina et al. 1977
Nidularium burchellii	-	-	-	0.9 g m^{-2}	-	Benzing & Friedman 1981
Tillandsia adpressiflora	-	-	-	1.0	-	Medina et al. 1977
Tillandsia anceps	9	-	1000	9.0	-	Benzing & Renfrow 1971b
Tillandsia andreana	-	-	-	1.0	-	Medina et al. 1977

Appendix IV (continued)

Species	Light compensation point $\mu mol\ m^{-2}\ s^{-1}$	Apparent quantum yield	Light level at which photosynthesis saturated $\mu mol\ m^{-2}\ s^{-1}$	Chlorophyll concentration $mg\ g^{-1}$ DW	Chloro-phyll a/b ratio	Reference
Tillandsia baileyi	15	-	770	3.1	-	Benzing & Renfrow 1971b
Tillandsia balbisiana	-	-	-	0.8	-	Medina et al. 1977
Tillandsia bulbosa	18	-	1150	5.9	-	Benzing & Renfrow 1971b
Tillandsia bulbosa	-	-	-	2.5	-	Medina et al. 1977
Tillandsia capitata	25	-	625	3.6	-	Benzing & Renfrow 1971b
Tillandsia compacta	-	-	-	1.4	-	Medina et al. 1977
Tillandsia complanata	-	-	-	0.7	-	Medina et al. 1977
Tillandsia concolor	18	-	1035	2.8	-	Benzing & Renfrow 1971b
Tillandsia deppeana sdlg	-	-	200	1.0	2.8	Adams & Martin 1986b
Tillandsia deppeana adult	-	-	200	5.0	2.8	Adams & Martin 1986b
Tillandsia elongata	-	-	-	0.4	-	Medina et al. 1977
Tillandsia fasciculata	18	-	925	3.8	-	Benzing & Renfrow 1971b
Tillandsia fasciculata	-	-	-	0.5	-	Medina et al. 1977
Tillandsia flexuosa	-	-	-	1.0	-	Medina et al. 1977
Tillandsia gardneri	-	-	-	1.4	-	Medina et al. 1977
Tillandsia imperialis	3	-	330	10.2	-	Benzing & Renfrow 1971b
Tillandsia incarnata	-	-	-	2.0	-	Medina et al. 1977

Appendix IV (continued)

Species	Light compensation point $\mu mol\ m^{-2}\ s^{-1}$	Apparent quantum yield	Light level at which photosynthesis saturated $\mu mol\ m^{-2}\ s^{-1}$	Chlorophyll concentration $mg\ g^{-1}$ DW	Chloro-phyll a/b ratio	Reference
Tillandsia ionantha	15	-	645	4.0	-	Benzing & Renfrow 1971b
Tillandsia juncea	23	-	1095	3.5	-	Benzing & Renfrow 1971b
Tillandsia juncea	-	-	-	1.0	-	Medina et al. 1977
Tillandsia lindenii	11	-	895	9.0	-	Benzing & Renfrow 1971b
Tillandsia monadelpha	9	-	710	7.5	-	Benzing & Renfrow 1971b
Tillandsia paraënsis	-	-	-	1.5	-	Medina et al. 1977
Tillandsia paucifolia[a]	-	-	-	1.1	-	Medina et al. 1977
Tillandsia polystachia	-	-	-	0.4	-	Medina et al. 1977
Tillandsia pueblensis	31	-	1140	2.1	-	Benzing & Renfrow 1971b
Tillandsia recurvata	-	-	-	2.5	-	Medina et al. 1977
Tillandsia schiedeana	-	-	-	4.1	-	Medina et al. 1977
Tillandsia spiculosa	60	-	500	3.7	-	Medina et al. 1977
Tillandsia tenuifolia	-	-	-	5.1	-	Medina et al. 1977
Tillandsia tetrantha	-	-	-	1.3	-	Medina et al. 1977
Tillandsia tricolor	12	-	915	5.6	-	Benzing & Renfrow 1971b
Tillandsia usneoides	18	-	475	3.8	-	Benzing & Renfrow 1971b
Tillandsia usneoides	-	-	>1000	-	-	Kluge et al. 1973
Tillandsia usneoides LL	-	-	-	4.1	2.8	Martin et al. 1985

Appendix IV (continued)

Species	Light compensation point $\mu mol\ m^{-2}\ s^{-1}$	Apparent quantum yield	Light level at which photosynthesis saturated $\mu mol\ m^{-2}\ s^{-1}$	Chlorophyll concentration $mg\ g^{-1}$ DW	Chloro-phyll a/b ratio	Reference
Tillandsia usneoides HL	-	-	-	1.5	2.7	Martin et al. 1985
Tillandsia usneoides LL	50	-	250	2.2	3.1	Martin et al. 1986
Tillandsia usneoides HL	80	-	250	1.3	2.4	Martin et al. 1986
Tillandsia usneoides LL	50	-	500	-	-	Martin et al. 1989
Tillandsia usneoides HL	50	-	500	-	-	Martin et al. 1989
Vriesea capituligera	-	-	-	0.5	-	Medina et al. 1977
Vriesea carinata	7	-	370	8.8	-	Benzing & Renfrow 1971b
Vriesea fenestralis	25	-	400	$0.7\ g\ m^{-2}$	-	Benzing & Friedman 1981
Vriesea fosteriana	50	-	700	-	-	Benzing & Friedman 1981
Vriesea scalaris	65	-	250	$0.4\ g\ m^{-2}$	-	Benzing & Friedman 1981
Vriesea simplex	7	-	235	9.0	-	Benzing & Renfrow 1971b
Vriesea splendens	-	-	-	3.1	-	Medina et al. 1977
Vriesea splendens	56	-	-	-	-	Bierhuizen et al. 1984
NON-BROMELIAD C_3 SPECIES						
Herbaceous shade plants	4-10	0.05-0.10[b]	100-200	14-27[c]	2.3-3.1[c]	Larcher 1983
Herbaceous sun plants	20-40	0.06-0.09[b]	1000-1600	4-8[c]	2.9-4.2[c]	Larcher 1983

[a]Same as *T. circinnata*.

[b]Values dependent on leaf characteristics, conditions of growth, and method of measurement; range from Ehleringer and Pearcy (1983) and Björkman and Demmig (1987).

[c]Shade values for forest understory C_3 herbs (Masarovičová & Eliáš, 1980), sun values for outer canopy leaves of forest trees (Eliáš & Masarovičová, 1980).

Appendix V

Representative values of photosynthetic CO_2 uptake (A), transpiration (E), conductance (g), and water-use efficiency (WUE) for terrestrial and epiphytic species in the Bromeliaceae (comparative values for non-bromeliads can be found at the end of the table). Measurements were made under a variety of conditions in the field or laboratory. Values may be averages or maxima for daytime gas exchange (C_3 species) or nighttime gas exchange (CAM species) for plants under various conditions. Whenever possible, unit conversions were estimated based on information provided in the appropriate reference. Units are given in the table only if different from those in the heading. WUE values were calculated, based on instantaneous gas exchange rates or integrated rates, as mmol CO_2 mol^{-1} H_2O.

Species	A $\mu mol\ m^{-2}\ s^{-1}$	E $mmol\ m^{-2}\ s^{-1}$	g $mmol\ m^{-2}\ s^{-1}$	WUE	Reference
TERRESTRIAL SPECIES					
Aechmea magdalenae	0.3	-	-	-	Pfitsch & Smith 1988
Ananas comosus	0.5	0.15	2.0	3	Neales et al. 1968
Ananas comosus	-	0.09	5.7	-	Aubert 1971
Ananas comosus	2.8	-	-	-	Moradshahi et al. 1977
Ananas comosus	3.6	0.28	12.0	13	Neales et al. 1980
Ananas comosus	3.9	-	-	-	Sale & Neales 1980
Ananas comosus	1.4	0.9	-	50	Nose et al. 1981
Ananas comosus	2.0	0.04	1.0	-	Nose et al. 1985
Ananas comosus	2.3	-	0.8	-	Nose et al. 1986
Ananas comosus	2.2	-	-	-	Borland & Griffiths 1989
Ananas comosus	5.0	-	60.0	-	Medina et al. 1991b
Bromelia humilis	2.0	-	-	-	Lee et al. 1989
Bromelia humilis	-	-	10.8	190	Fetene & Lüttge 1991
Bromelia plumieri	-	-	-	1	Griffiths et al. 1986
Dyckia brevifolia	15.2 $nmol\ g^{-1}\ DW\ s^{-1}$	-	-	-	McWilliams 1970
Dyckia fosteriana	9.3 $nmol\ g^{-1}\ DW\ s^{-1}$	-	-	-	McWilliams 1970
Neoregelia cruenta	6.6 $nmol\ g^{-1}\ DW\ s^{-1}$	-	-	-	McWilliams 1970
Pitcairnia integrifolia	5.0	0.39	43	13	Lüttge et al. 1986a
Pitcairnia integrifolia	6.2	2.00	100	3	Lüttge et al. 1986b

Appendix V (continued)

Species	A μmol $m^{-2} s^{-1}$	E mmol $m^{-2} s^{-1}$	g mmol $m^{-2} s^{-1}$	WUE	Reference
EPIPHYTIC SPECIES					
Aechmea aquilega	1.5	-	-	40	Griffiths et al. 1986
Aechmea aquilega	3.0	0.20	50	15	Lüttge et al. 1986c
Aechmea chantinii	-	-	80	-	Medina et al. 1986b
Aechmea fendleri	1.5	-	-	11	Griffiths et al. 1986
Aechmea fendleri	2.0	0.30	50	6	Griffiths 1988a
Aechmea lingulata	-	-	-	8	Griffiths et al. 1986
Aechmea lingulata	1.5	0.15	120	10	Lüttge et al. 1986c
Aechmea nudicaulis	-	-	-	8	Griffiths et al. 1986
Aechmea nudicaulis	2.0	0.08	30	25	Smith et al. 1986b
Aechmea nudicaulis	2.3	0.30	50	8	Griffiths 1988a
Araeococcus flagellifolius	4.2 nmol g^{-1} DW s^{-1}	-	-	-	McWilliams 1970
Billbergia amoena	-	0.05	-	-	Coutinho 1962
Billbergia nutans	3.3 nmol g^{-1} DW s^{-1}	-	-	-	McWilliams 1970
Catopsis nutans	1.1 nmol g^{-1} FW s^{-1}	-	-	-	Benzing & Renfrow 1971a
Catopsis nutans	1.7	-	-	-	Benzing & Friedman 1981
Guzmania lingulata	1.7 nmol g^{-1} FW s^{-1}	-	-	-	Benzing & Renfrow 1971a
Guzmania lingulata	1.9	-	-	-	Benzing & Friedman 1981
Guzmania lingulata	1.6	-	-	-	Griffiths et al. 1986
Guzmania minor	1.8	-	-	-	Bierhuizen et al. 1984

Appendix V (continued)

Species	A $\mu mol\ m^{-2}\ s^{-1}$	E $mmol\ m^{-2}\ s^{-1}$	g $mmol\ m^{-2}\ s^{-1}$	WUE	Reference
Guzmania monostachia	3.2 nmol g^{-1} DW s^{-1}	-	-	-	McWilliams 1970
Guzmania monostachia	1.3	-	-	-	Benzing & Friedman 1981
Guzmania monostachia	-	-	-	1	Griffiths et al. 1986
Guzmania monostachia	1.0	0.10	15	10	Lüttge et al. 1986c
Guzmania monostachia	5.0 nmol g^{-1} DW s^{-1}	-	-	-	C. E. Martin, unpubl.
Guzmania musaica	1.9	-	-	-	Benzing & Friedman 1981
Nidularium innocentii	2.2 nmol g^{-1} DW s^{-1}	-	-	-	McWilliams 1970
Tillandsia aëranthos	-	8.02 nmol g^{-1} FW s^{-1}	-	-	Virzo De Santo et al. 1977
Tillandsia balbisiana	4.1 nmol g^{-1} DW s^{-1}	0.22 µmol g^{-1} DW s^{-1}	22.3 µmol g^{-1} DW s^{-1}	19	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia bergeri	6.0 nmol g^{-1} DW s^{-1}	0.32 µmol g^{-1} DW s^{-1}	32.3 µmol g^{-1} DW s^{-1}	19	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia brachycaulos	-	16.67 nmol g^{-1} FW s^{-1}	-	-	Virzo De Santo et al. 1977
Tillandsia caput-medusae	-	10.65 nmol g^{-1} FW s^{-1}	-	-	Virzo De Santo et al. 1977
Tillandsia deppeana sdlg	4.2 nmol g^{-1} DW s^{-1}	0.77 µmol g^{-1} DW s^{-1}	0.1 mmol g^{-1} DW s^{-1}	9	Adams & Martin 1986b
Tillandsia deppeana adult	25.0 nmol g^{-1} DW s^{-1}	4.63 µmol g^{-1} DW s^{-1}	0.4 mmol g^{-1} DW s^{-1}	9	Adams & Martin 1986b
Tillandsia elongata	-	-	-	6	Griffiths et al. 1986
Tillandsia fasciculata	4.2 nmol g^{-1} DW s^{-1}	0.19 µmol g^{-1} DW s^{-1}	18.2 µmol g^{-1} DW s^{-1}	22	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia fendleri	1.5	-	-	9	Griffiths et al. 1986
Tillandsia flabellata	-	24.54 nmol g^{-1} FW s^{-1}	-	-	Virzo De Santo et al. 1977
Tillandsia flexuosa	1.2	0.20	30	5	Griffiths et al. 1989
Tillandsia ionantha	0.2 nmol g^{-1} FW s^{-1}	-	-	-	Benzing & Renfrow 1971a

Appendix V (continued)

Species	A μmol $m^{-2} s^{-1}$	E mmol $m^{-2} s^{-1}$	g mmol $m^{-2} s^{-1}$	WUE	Reference
Tillandsia ionantha	11.8 nmol g^{-1} DW s^{-1}	0.71 μmol g^{-1} DW s^{-1}	58.8 μmol g^{-1} DW s^{-1}	17	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia ixioides	-	8.49 nmol g^{-1} FW s^{-1}	-	-	Virzo De Santo et al. 1977
Tillandsia juncea	7.6 nmol g^{-1} DW s^{-1}	-	-	-	McWilliams 1970
Tillandsia latifolia	-	6.33 nmol g^{-1} FW s^{-1}	-	-	Virzo De Santo et al. 1977
Tillandsia paleacea	-	2.62 nmol g^{-1} FW s^{-1}	-	-	Virzo De Santo et al. 1977
Tillandsia paleacea	6.7 nmol g^{-1} DW s^{-1}	0.36 μmol g^{-1} DW s^{-1}	34.1 μmol g^{-1} DW s^{-1}	19	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia paucifolia[a]	0.7 nmol g^{-1} FW s^{-1}	-	-	-	Benzing & Renfrow 1971a
Tillandsia paucifolia[a]	5.1 nmol g^{-1} DW s^{-1}	0.28 μmol g^{-1} DW s^{-1}	27.6 μmol g^{-1} DW s^{-1}	18	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia recurvata	3.9 nmol g^{-1} FW s^{-1}	-	-	-	Medina et al. 1977
Tillandsia recurvata	3.2 nmol g^{-1} DW s^{-1}	0.46 μmol g^{-1} DW s^{-1}	-	7	Lange & Medina 1979
Tillandsia recurvata	4.7 nmol g^{-1} DW s^{-1}	-	-	-	Medina 1984
Tillandsia recurvata	0.6 nmol g^{-1} FW s^{-1}	50 nmol g^{-1} FW s^{-1}	3.4 μmol g^{-1} FW s^{-1}	12	Schmitt et al. 1989
Tillandsia recurvata	6.8 nmol g^{-1} DW s^{-1}	0.29 μmol g^{-1} DW s^{-1}	33.8 μmol g^{-1} DW s^{-1}	23	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia schiedeana	-	13.58 nmol g^{-1} FW s^{-1}	-	-	Virzo De Santo et al. 1977
Tillandsia schiedeana	2.5 nmol g^{-1} DW s^{-1}	-	-	-	Martin & Adams 1987
Tillandsia schiedeana	3.8 nmol g^{-1} DW s^{-1}	0.22 μmol g^{-1} DW s^{-1}	18.1 μmol g^{-1} DW s^{-1}	17	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia setacea	3.7 nmol g^{-1} DW s^{-1}	0.21 μmol g^{-1} DW s^{-1}	19.4 μmol g^{-1} DW s^{-1}	18	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia spiculosa	0.8 nmol g^{-1} FW s^{-1}	-	-	-	Medina et al. 1977
Tillandsia tricolor	4.1 nmol g^{-1} DW s^{-1}	-	-	-	McWilliams 1970

Appendix V (continued)

Species	A $\mu mol\ m^{-2}\ s^{-1}$	E $mmol\ m^{-2}\ s^{-1}$	g $mmol\ m^{-2}\ s^{-1}$	WUE	Reference
Tillandsia usneoides	3.2 nmol g^{-1} DW s^{-1}	-	-	-	Kluge et al. 1973
Tillandsia usneoides	-	14.35 nmol g^{-1} FW s^{-1}	-	-	Virzo De Santo et al. 1977
Tillandsia usneoides	3.8 nmol g^{-1} DW s^{-1}	-	-	-	Flores 1980
Tillandsia usneoides	7.6 nmol mg^{-1} Chl s^{-1}	-	-	-	Martin et al. 1981
Tillandsia usneoides	3.8 nmol mg^{-1} Chl s^{-1}	-	-	-	Martin & Siedow 1981
Tillandsia usneoides	3.1 nmol mg^{-1} Chl s^{-1}	-	-	-	Martin & Peters 1984
Tillandsia usneoides	6.9 nmol mg^{-1} Chl s^{-1}	-	-	-	Martin et al. 1986
Tillandsia usneoides	5.7 nmol g^{-1} DW s^{-1}	10 nmol g^{-1} FW s^{-1}	-	100	Martin & Schmitt 1989
Tillandsia usneoides	4.8 nmol g^{-1} DW s^{-1}	0.34 µmol g^{-1} DW s^{-1}	37.0 µmol g^{-1} DW s^{-1}	14	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia utriculata	-	-	-	2	Griffiths et al. 1986
Tillandsia utriculata	4.4 nmol g^{-1} DW s^{-1}	-	-	-	Medina 1987
Tillandsia utriculata	0.6	-	-	-	Griffiths et al. 1990
Tillandsia utriculata	-	-	8	-	Benzing et al. 1992
Tillandsia utriculata	4.1 nmol g^{-1} DW s^{-1}	0.36 µmol g^{-1} DW s^{-1}	37.0 µmol g^{-1} DW s^{-1}	11	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia valenzuelana	3.5 nmol g^{-1} DW s^{-1}	0.34 µmol g^{-1} DW s^{-1}	30.7 µmol g^{-1} DW s^{-1}	10	C. E. Martin, V. S. Loeschen & F. Mohtashemipour, unpubl.
Tillandsia violacea	-	3.24 nmol g^{-1} FW s^{-1}	-	-	Virzo De Santo et al. 1977
Vriesea altodaserrae	-	0.11	-	-	Coutinho 1962
Vriesea amazonica	1.2	-	-	13	Griffiths et al. 1986
Vriesea amazonica	1.0	0.15	140	7	Smith et al. 1986b
Vriesea fenestralis	1.6	-	-	-	Benzing & Friedman 1981

Appendix V (continued)

Species	A $\mu mol\ m^{-2}\ s^{-1}$	E $mmol\ m^{-2}\ s^{-1}$	g $mmol\ m^{-2}\ s^{-1}$	WUE	Reference
Vriesea fosteriana	2.7	-	-	-	Benzing & Friedman 1981
Vriesea inflata	-	0.05	-	-	Coutinho 1962
Vriesea jonghei	1.8	-	-	3	Griffiths et al. 1986
Vriesea scalaris	0.4	-	-	-	Benzing & Friedman 1981
Vriesea splendens	0.6	-	-	-	Bierhuizen et al. 1984
Vriesea splitgerberi	1.0	-	-	2	Griffiths et al. 1986
NON-BROMELIAD C_3 SPECIES					
Herbaceous shade plants	2-13	1-2	20-400[b]	0.5-3.0[b]	Larcher 1983; Nobel 1991
Herbaceous sun plants	13-30	1-5	20-400[b]	0.5-3.0[b]	Larcher 1983; Nobel 1991

[a]Same as *T. circinnata*.

[b]Values include both sun and shade plants.

Appendix VI

Representative values of stomatal densities and dimensions in terrestrial and epiphytic species in the Bromeliaceae (comparative values for non-bromeliads can be found at the end of the table). Values are typically averages for abaxial leaf surfaces of plants grown under a variety of conditions in the field or laboratory. Some epiphytic species may occur as occasional terrestrials or saxicoles.

Species	Stomatal density mm^{-2}	Stomatal length[a,b] µm	Stomatal width[a] µm	Reference
TERRESTRIAL SPECIES				
Ananas comosus	78	25	27	Bartholomew & Kadzimin 1977
Ananas comosus	70	-	-	Aromose 1989
Bromelia sp.	10	-	-	Kluge & Ting 1978
Connellia guelchii	214	37	26	Robinson 1969[c]
Cottendorfia dyckioides	267	30	24	Robinson 1969[c]
Cottendorfia maguirei	285	26	26	Robinson 1969[c]
Cottendorfia phelpsiae	306	26	26	Robinson 1969[c]
Cottendorfia serrulata	238	19	22	Robinson 1969[c]
Cottendorfia wurdackii	356	30	26	Robinson 1969[c]
Navia garcia-barrigae	297	30	28	Robinson 1969[c]
Navia hohenbergioides	285	32	24	Robinson 1969[c]
Navia intermedia	110	37	30	Robinson 1969[c]
Navia lasiantha	407	22	22	Robinson 1969[c]
Navia lepidota	446	26	26	Robinson 1969[c]
EPIPHYTIC SPECIES				
Guzmania lingulata	24	-	-	Smith et al. 1985
Guzmania monostachia	26	-	-	Smith et al. 1985
Tillandsia baileyi	12	-	-	Gómez & Winkler 1991
Tillandsia baileyi	14	22	22	C. E. Martin, unpubl.
Tillandsia balbisiana	23	52	39	C. E. Martin, unpubl.
Tillandsia bergeri	14	30	30	C. E. Martin, unpubl.
Tillandsia caput-medusae	15	-	-	Gómez & Winkler 1991
Tillandsia dasyliriifolia	40	-	-	Gómez & Winkler 1991
Tillandsia deppeana sdlg	24	-	-	Adams & Martin 1986a
Tillandsia deppeana adult	41	-	-	Adams & Martin 1986a

Appendix VI (continued)

Species	Stomatal density mm^{-2}	Stomatal length[a,b] µm	Stomatal width[a] µm	Reference
Tillandsia fasciculata	12	37	37	C. E. Martin, unpubl.
Tillandsia ionantha	6	37	41	C. E. Martin, unpubl.
Tillandsia paleacea	10	34	34	C. E. Martin, unpubl.
Tillandsia paucifolia[e]	16	41	37	C. E. Martin, unpubl.
Tillandsia recurvata	12	33	33	C. E. Martin, unpubl.
Tillandsia rupestris	4	-	-	Chodat & Vischer 1916
Tillandsia schiedeana	11	-	-	Gómez & Winkler 1991
Tillandsia schiedeana	12	43	43	C. E. Martin, unpubl.
Tillandsia setacea	17	39	33	C. E. Martin, unpubl.
Tillandsia usneoides	7	-	-	Billings 1904
Tillandsia usneoides	-	44	50	Martin & Peters 1984
Tillandsia usneoides	20	30	30	Martin et al. 1985
Tillandsia utriculata	29	-	-	Smith et al. 1985
Tillandsia utriculata	14	41	39	C. E. Martin, unpubl.
Tillandsia valenzuelana	13	33	33	C. E. Martin, unpubl.
Vriesea splendens	17	76	41	Bierhuizen et al. 1984
NON-BROMELIAD C_3 SPECIES				
Herbaceous shade plants	40-150	24-70[d]	11-53[d]	Larcher 1983, Willmer 1983
Herbaceous sun plants	100-300	24-70[d]	11-53[d]	Larcher 1983, Willmer 1983

[a]Length is parallel with the long axis of the pore; width is perpendicular to the long axis of the pore.

[b]Solereder and Meyer (1929) list stomatal lengths from 24 to 45 µm for species in the following genera: *Ananas, Cryptanthus, Dyckia, Neoregelia, Nidularium, Pitcairnia,* and *Puya* (terrestrials); *Acanthostachys, Aechmea, Billbergia, Guzmania, Tillandsia,* and *Vriesia* (epiphytes).

[c]All data from this reference are estimated based on drawings of epidermal surfaces showing at least three stomata. In addition to the species listed here, Robinson provides drawings for 18 species of *Cottendorfia* and 70 species of *Navia*.

[d]Values include both sun and shade plants.

[e]Same as *T. circinnata*.

Appendix VII

Representative values of nocturnal acid accumulation and per cent of total acid accumulation attributable to recycling respiratory CO_2 (% recycling) for terrestrial and epiphytic species in the Bromeliaceae that exhibit CAM (or a variation of CAM). Measurements of nocturnal increases in malate, citrate, and/or total acidity, as well as of CO_2 recycling, were made under a variety of conditions in the field or laboratory. Values may be averages or maxima (rarely minima) for plants under one or more conditions. Whenever possible, unit conversions were estimated based on information provided in the appropriate reference. Some epiphytic species may occur as occasional terrestrials or saxicoles.

Species	% Recycling	ΔMalate	ΔCitrate	ΔTotal acidity	Reference
TERRESTRIAL SPECIES					
Aechmea magdalenae	-	-	-	40 μmol g^{-1} FW	Pfitsch & Smith 1988
Ananas ananassoides	-	85 mmol m^{-2}	9 mmol m^{-2}	198 mmol m^{-2}	Medina et al. 1993
Ananas comosus	-	44 μmol g^{-1} FW	13 μmol g^{-1} FW	-	Sideris et al. 1948
Ananas comosus	-	-	-	40 μmol g^{-1} FW	Moradshahi et al. 1977
Ananas comosus	-	-	-	110 μmol g^{-1} FW	Bartholomew & Kadzimin 1977
Ananas comosus	-	-	-	70 μmol g^{-1} FW	Friend & Lydon 1979
Ananas comosus	-	-	-	200 μmol g^{-1} FW	Sale & Neales 1980
Ananas comosus	-	1100 μmol g^{-1} DW	-	-	Kenyon et al. 1985
Ananas comosus	-	-	-	220 mmol m^{-2}	Medina et al. 1986b
Ananas comosus	-	120 μmol g^{-1} FW	-	130 μmol g^{-1} FW	Carnal & Black 1989
Ananas comosus	34	90 mol m^{-3}	18 mol m^{-3}	200 mol m^{-3}	Borland & Griffiths 1989
Ananas comosus	50	126 mmol m^{-2}	18 mmol m^{-2}	276 mmol m^{-2}	Medina et al. 1991b
Ananas comosus	-	156 mmol m^{-2}	18 mmol m^{-2}	330 mmol m^{-2}	Medina et al. 1993
Ananas parguazensis	-	-	-	120 mmol m^{-2}	Medina et al. 1986b
Ananas sativus	-	-	-	10%	Warburg 1886
Ananas sativus	-	144 μmol g^{-1} FW	-	315 μmol g^{-1} FW	Milburn et al. 1968
Bromelia humilis	-	245 μmol g^{-1} DW	-	-	Medina 1974
Bromelia humilis	-	39 μmol g^{-1} FW	-	-	Medina and Troughton 1974
Bromelia humilis	-	-	-	70 μmol g^{-1} FW	Medina et al. 1986a
Bromelia humilis	-	-	-	191 mmol m^{-2}	Medina 1987

Appendix VII (continued)

Species	% Recycling	ΔMalate	ΔCitrate	ΔTotal acidity	Reference
Bromelia humilis	40	50 mol m^{-3}	27 mol m^{-3}	200 mol m^{-3}	Lee et al. 1989
Bromelia humilis	80	100 mol m^{-3}	30 mol m^{-3}	330 mol m^{-3}	Fetene et al. 1990
Bromelia humilis	55	33 mol m^{-3}	10 mol m^{-3}	-	Fetene & Lüttge 1991
Bromelia pinguin	-	-	-	650 mmol m^{-2}	Ting 1989
Bromelia plumieri	99	-	-	72 mol m^{-3}	Griffiths et al. 1986
Bromelia plumieri	-	-	-	82 mol m^{-3}	Smith et al. 1986b
Cryptanthus acaulis	-	-	-	18 mol m^{-3}	Bendrat 1929
Dyckia brevifolia	-	-	-	320 µmol g^{-1} FW	McWilliams 1970
Dyckia fosteriana	-	-	-	260 µmol g^{-1} FW	McWilliams 1970
Dyckia remotiflora	-	-	-	32%	Warburg 1886
Dyckia tuberosa	-	154 µmol g^{-1} FW	-	198 µmol g^{-1} FW	Medina 1974
Hechtia glomerata	-	60 µmol g^{-1} FW	-	-	Lüttge & Ball 1987
Neoregelia cruenta	-	-	-	141 µmol g^{-1} FW	McWilliams 1970
Puya floccosa	-	18 µmol g^{-1} DW	-	-	Medina 1974
EPIPHYTIC SPECIES					
Acanthostachys strobilacea	-	-	-	118%	Warburg 1886
Aechmea aquilega	-	240 µmol g^{-1} DW	-	-	Medina 1974
Aechmea aquilega	-	-	-	203 mol m^{-3}	Smith et al. 1985
Aechmea aquilega	-	-	-	250 mol m^{-3}	Lüttge et al. 1986c
Aechmea aquilega	78	-	-	248 mol m^{-3}	Griffiths et al. 1986
Aechmea aquilega	-	-	-	393 mol m^{-3}	Smith et al. 1986b
Aechmea brevicollis	-	-	-	100 mmol m^{-2}	Medina et al. 1986b
Aechmea bromeliifolia	-	247 µmol g^{-1} FW	-	275 µmol g^{-1} FW	Medina 1974
Aechmea chantinii	-	-	-	122 mmol m^{-2}	Medina 1987
Aechmea fasciata	-	260 µmol g^{-1} FW	-	-	Lüttge & Ball 1987
Aechmea fendleri	-	128 µmol g^{-1} DW	-	-	Medina 1974

Appendix VII (continued)

Species	% Recycling	ΔMalate	ΔCitrate	ΔTotal acidity	Reference
Aechmea fendleri	51	-	-	281 mol m^3	Griffiths et al. 1986
Aechmea fendleri	-	-	-	336 mol m^3	Smith et al. 1986b
Aechmea fendleri	49	-	-	250 mol m^3	Griffiths 1988a
Aechmea lasseri	-	-	-	109 µmol g^{-1} FW	Medina 1987
Aechmea lingulata	65	-	-	309 mol m^3	Griffiths et al. 1986
Aechmea lingulata	-	-	-	350 mmol m^{-2}	Ting 1989
Aechmea mexicana (= *Hoplophytum grande*)	-	-	-	208%	Warburg 1886
Aechmea nudicaulis	-	-	-	303 mol m^3	Smith et al. 1985
Aechmea nudicaulis	73	-	-	313 mol m^3	Griffiths et al. 1986
Aechmea nudicaulis	-	-	-	474 mol m^3	Smith et al. 1986b
Aechmea nudicaulis	52	-	-	250 mol m^3	Griffiths 1988a
Aechmea tillandsioides	-	-	-	91 mmol m^2	Medina et al. 1986b
Aechmea weilbachii	-	-	-	79%	Warburg 1886
Araeococcus flagellifolius	-	-	-	70 µmol g^{-1} FW	McWilliams 1970
Billbergia nutans	-	-	-	150 µmol g^{-1} FW	McWilliams 1970
Billbergia thyrsoidea	-	-	-	17 mol m^3	Bendrat 1929
Billbergia zebrina	-	-	-	86%	Warburg 1886
Catopsis nutans	-	32 µmol g^{-1} DW	-	-	Medina 1974
Guzmania monostachia	-	-	-	200 µmol g^{-1} FW	McWilliams 1970
Guzmania monostachia	-	28 µmol g^{-1} FW	-	-	Medina & Troughton 1974
Guzmania monostachia	-	133 µmol g^{-1} DW	-	-	Medina 1974
Guzmania monostachia	-	-	-	88 mol m^3	Smith et al. 1985
Guzmania monostachia	94	-	-	70 mol m^3	Griffiths et al. 1986
Guzmania monostachia	-	-	-	88 mol m^3	Smith et al. 1986b
Guzmania monostachia	-	45 µmol g^{-1} FW	-	83 mol m^3	Medina 1987

Appendix VII (continued)

Species	% Recycling	ΔMalate	ΔCitrate	ΔTotal acidity	Reference
Guzmania monostachia	-	-	-	65 mol m^{-3}	Maxwell et al. 1992
Guzmania monostachia	70	28 μmol g^{-1} DW	-	-	C. E. Martin, unpubl.
Guzmania mucronata	-	2 μmol g^{-1} DW	-	-	Medina 1974
Hohenbergia stellata	-	-	-	57 mol m^{-3}	Smith et al. 1985
Neoregelia princeps (= Nidularium meyendorffii)	-	-	-	103%	Warburg 1886
Nidularium fulgens	-	-	-	30 mol m^{-3}	Bendrat 1929
Nidularium innocentii	-	-	-	17 μmol g^{-1} FW	McWilliams 1970
Tillandsia adpressiflora	-	43 μmol g^{-1} DW	-	-	Medina 1974
Tillandsia adpressiflora	-	4 μmol g^{-1} FW	-	-	Medina & Troughton 1974
Tillandsia aëranthos	-	22 μmol g^{-1} FW	-	-	Virzo De Santo et al. 1977
Tillandsia baileyi	-	230 μmol g^{-1} DW	-	-	C. E. Martin, unpubl.
Tillandsia balbisiana	-	119 μmol g^{-1} DW	-	-	Medina 1974
Tillandsia balbisiana	-	-	-	25 μmol g^{-1} FW	Benzing et al. 1992
Tillandsia balbisiana	0	100 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Tillandsia bergeri	0	130 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Tillandsia biflora	-	-	-	75%	Warburg 1886
Tillandsia brachycaulos	-	89 μmol g^{-1} FW	-	-	Virzo De Santo et al. 1977
Tillandsia bulbosa	-	-	-	147 mol m^{-3}	Smith et al. 1986b
Tillandsia caput-medusae	-	49 μmol g^{-1} FW	-	-	Virzo De Santo et al. 1977
Tillandsia didistichoides	-	181 μmol g^{-1} DW	-	-	Medina 1974
Tillandsia elongata	-	104 μmol g^{-1} DW	-	-	Medina 1974
Tillandsia elongata	82	-	-	271 mol m^{-3}	Griffiths et al. 1986

Appendix VII (continued)

Species	% Recycling	ΔMalate	ΔCitrate	ΔTotal acidity	Reference
Tillandsia elongata	-	-	-	191 mol m^{-3}	Smith et al. 1986b
Tillandsia fasciculata	-	138 μmol g^{-1} DW	-	-	Medina 1974
Tillandsia fasciculata	-	-	-	365 mol m^{-3}	Smith et al. 1985
Tillandsia fasciculata	-	-	-	210 mol m^{-3}	Smith et al. 1986b
Tillandsia fasciculata	-	-	-	50 mmol m^{-2}	Ting 1989
Tillandsia fasciculata	0	130 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Tillandsia flabellata	-	45 μmol g^{-1} FW	-	-	Virzo De Santo et al. 1977
Tillandsia flexuosa	-	163 μmol g^{-1} DW	-	-	Medina 1974
Tillandsia flexuosa	-	-	-	201 mol m^{-3}	Smith et al. 1986b
Tillandsia flexuosa	76	45 mol m^{-3}	7 mol m^{-3}	270 mol m^{-3}	Griffiths et al. 1989
Tillandsia ionantha	0	420 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Tillandsia juncea	-	-	-	220 μmol g^{-1} FW	McWilliams 1970
Tillandsia juncea	-	53 μmol g^{-1} DW	-	-	Medina 1974
Tillandsia latifolia	-	15 μmol g^{-1} FW	-	-	Virzo De Santo et al. 1977
Tillandsia paleacea	-	15 μmol g^{-1} FW	-	-	Virzo De Santo et al. 1977
Tillandsia paleacea	0	260 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Tillandsia paraënsis	-	-	-	120 mmol m^{-2}	Medina et al. 1986b
Tillandsia paucifolia[a]	-	-	-	35 μmol g^{-1} FW	Benzing et al. 1992
Tillandsia paucifolia[a]	0	140 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Tillandsia polystachia	-	104 μmol g^{-1} DW	-	-	Medina 1974
Tillandsia polystachia	-	32 μmol g^{-1} FW	-	-	Medina & Troughton 1974

Appendix VII (continued)

Species	% Recycling	ΔMalate	ΔCitrate	ΔTotal acidity	Reference
Tillandsia recurvata	-	136 μmol g^{-1} DW	-	-	Medina 1974
Tillandsia recurvata	-	-	-	26 μmol g^{-1} FW	Benzing et al. 1992
Tillandsia recurvata	0	210 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Tillandsia schiedeana	-	45 μmol g^{-1} FW	-	-	Virzo De Santo et al. 1977
Tillandsia schiedeana	43	-	-	400 μmol g^{-1} DW	Martin & Adams 1987
Tillandsia schiedeana	48	220 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Tillandsia setacea	0	110 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Tillandsia stricta	-	-	-	173 mol m^{-3}	Smith et al. 1986b
Tillandsia tenuifolia	-	167 μmol g^{-1} DW	-	-	Medina 1974
Tillandsia tricolor	-	-	-	250 μmol g^{-1} FW	McWilliams 1970
Tillandsia usneoides	-	26 μmol g^{-1} FW	-	-	Kluge et al. 1973
Tillandsia usneoides	-	45 μmol g^{-1} FW	-	-	Virzo De Santo et al. 1977
Tillandsia usneoides	0	-	-	500 μmol g^{-1} DW	Martin et al. 1981
Tillandsia usneoides	-	-	-	499 μmol g^{-1} DW	Martin et al. 1985
Tillandsia usneoides	-	-	-	500 μmol g^{-1} DW	Martin et al. 1986
Tillandsia usneoides	-	-	-	961 μmol g^{-1} DW	Martin et al. 1989
Tillandsia usneoides	0	160 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Tillandsia utriculata	-	236 μmol g^{-1} DW	-	181 μmol g^{-1} FW	Medina 1974
Tillandsia utriculata	-	-	-	286 mol m^{-3}	Smith et al. 1985
Tillandsia utriculata	95	-	-	251 mol m^{-3}	Griffiths et al. 1986
Tillandsia utriculata	-	-	-	267 mol m^{-3}	Smith et al. 1986b
Tillandsia utriculata	-	55 μmol g^{-1} FW	-	-	Medina 1987

Appendix VII (continued)

Species	% Recycling	ΔMalate	ΔCitrate	ΔTotal acidity	Reference
Tillandsia utriculata	-	85 mol m^{-3}	-	174 mol m^{-3}	Griffiths et al. 1990
Tillandsia utriculata	-	-	-	32 μmol g^{-1} FW	Benzing et al. 1992
Tillandsia utriculata	0	130 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Tillandsia valenzuelana	0	70 μmol g^{-1} DW	-	-	Loeschen et al. 1993
Vriesea fenestralis	-	-	-	7 μmol g^{-1} FW	McWilliams 1970
Vriesea platynema	-	21 μmol g^{-1} DW	-	-	Medina 1974

[a]Same as *T. circinnata*.

Appendix VIII

Representative values of photosynthetic O_2 evolution and respiratory O_2 uptake for terrestrial and epiphytic species in the Bromeliaceae (comparative values for non-bromeliads can be found at the end of the table). Measurements were made under a variety of conditions in the laboratory. Values are typically averages for plants under one or more conditions. Whenever possible, unit conversions were estimated based on information provided in the appropriate reference. Units are given in the table only if different from those in the heading. Some respiration rates are expressed as CO_2 evolved. Some epiphytic species may occur as occasional terrestrials or saxicoles.

Species	Photosynthetic O_2 evolution nmol g^{-1} DW s^{-1}	Respiratory O_2 uptake nmol g^{-1} DW s^{-1}	Reference
TERRESTRIAL SPECIES			
Ananas comosus	-	0.3 nmol g^{-1} FW s^{-1}	Lüttge & Ball 1987
Ananas comosus	8 µmol $m^{-2}s^{-1}$	2.0 µmol $m^{-2}s^{-1}$	Borland & Griffiths 1989
Bromelia humilis	18 µmol $m^{-2}s^{-1}$	1.3 µmol $m^{-2}s^{-1}$	Fetene et al. 1990
Bromelia humilis	-	0.8 nmol g^{-1} FW s^{-1}	Fetene & Lüttge 1991
Fosterella penduliflora	-	1.8	McWilliams 1970
Hechtia glomerata	-	3.5	Lüttge & Ball 1987
Pitcairnia integrifolia	-	0.4 nmol CO_2 g^{-1} FW s^{-1}	Lüttge et al. 1986a
Pitcairnia recurvata	-	0.4	McWilliams 1970
EPIPHYTIC SPECIES			
Aechmea fasciata	-	0.8 nmol g^{-1} FW s^{-1}	Lüttge & Ball 1987
Aechmea fendleri	-	4.2 nmol g^{-1} FW s^{-1}	Griffiths 1988a
Aechmea nudicaulis	-	6.1 nmol g FW s^{-1}	Griffiths 1988a
Catopsis berteroniana	134	16	Benzing & Renfrow 1971b
Catopsis floribunda	-	0.2	McWilliams 1970
Catopsis floribunda	73	13	Benzing & Renfrow 1971b
Catopsis morreniana	-	0.9	McWilliams 1970
Catopsis nutans	76	15	Benzing & Renfrow 1971b

Appendix VIII (continued)

Species	Photosynthetic O_2 evolution nmol g^{-1} DW s^{-1}	Respiratory O_2 uptake nmol g^{-1} DW s^{-1}	Reference
Guzmania lingulata	96	12	Benzing & Renfrow 1971b
Guzmania lingulata	-	0.2 µmol CO_2 m^{-2} s^{-1}	Griffiths et al. 1986
Guzmania lingulata	-	0.3 µmol CO_2 m^{-2} s^{-1}	Smith 1989
Guzmania monostachia	141	18	Benzing & Renfrow 1971b
Guzmania monostachia	3 µmol m^{-2} s^{-1}	2 µmol m^{-2} s^{-1}	Maxwell et al. 1992
Tillandsia anceps	35	9	Benzing & Renfrow 1971b
Tillandsia baileyi	49	9	Benzing & Renfrow 1971b
Tillandsia balbisiana	-	3	Martin 1994
Tillandsia bulbosa	51	8	Benzing & Renfrow 1971b
Tillandsia capitata	68	20	Benzing & Renfrow 1971b
Tillandsia concolor	30	8	Benzing & Renfrow 1971b
Tillandsia fasciculata	54	10	Benzing & Renfrow 1971b
Tillandsia imperialis	104	10	Benzing & Renfrow 1971b
Tillandsia ionantha	102	22	Benzing & Renfrow 1971b
Tillandsia ionantha	50	14	Benzing & Dahle 1971
Tillandsia ionantha	-	4	Martin 1994
Tillandsia juncea	38	9	Benzing & Renfrow 1971b
Tillandsia lindenii	55	12	Benzing & Renfrow 1971b
Tillandsia monadelpha	81	12	Benzing & Renfrow 1971b
Tillandsia pueblensis	28	8	Benzing & Renfrow 1971b
Tillandsia recurvata	-	2	Martin 1994
Tillandsia schiedeana	-	2	Martin 1994

Appendix VIII (continued)

Species	Photosynthetic O_2 evolution nmol g^{-1} DW s^{-1}	Respiratory O_2 uptake nmol g^{-1} DW s^{-1}	Reference
Tillandsia setacea	4	2	C. E. Martin, unpubl.
Tillandsia tricolor	33	11	Benzing & Renfrow 1971b
Tillandsia usneoides	26	9	Benzing & Renfrow 1971b
Tillandsia usneoides	30	2	Martin et al. 1989
Tillandsia usneoides	8	3	C. E. Martin, unpubl.
Tillandsia usneoides	-	2	Martin 1994
Vriesea carinata	161	17	Benzing & Renfrow 1971b
Vriesea fenestralis	-	0.1	McWilliams 1970
Vriesea simplex	55	6	Benzing & Renfrow 1971b
NON-BROMELIAD C_3 SPECIES			
Herbaceous shade plants	-[a]	13-32[b]	Larcher 1983
Herbaceous sun plants	-[a]	32-50[b]	Larcher 1983

[a]See Appendix V for rates of photosynthetic CO_2 uptake (similar to O_2 evolution rates) for non-bromeliads.

[b]Values for CO_2 release.