

FUNCTIONAL CORRELATES OF DECIDUOUSNESS IN
CATASETUM INTEGERRIMUM (ORCHIDACEAE)

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INTRODUCTION

Most epiphytic orchids bear long-lived leaves of at least moderate xeromorphic character. Their canopies remain full the year round, maintained by a balance between annual additions of new organs and abscissions of old ones. Individual leaves persist for several seasons. Members of a few genera (e.g. *Catasetum*, *Cyrtopodium*, *Dendrobium* sect., *Eugenanthe*) generate crops of more mesomorphic organs at the beginning of each growing season and then abruptly shed their entire foliar display well before year's end. While the functional correlates of these two growth patterns are not known, many deciduous orchid taxa are decidedly more vigorous than persistent-leaf relatives. For example, *Catasetum integerrimum* Hook., a very robust species with short-lived leaves, can flower and achieve adult size in about two years under optimal conditions -- considerably less than half the time required for most well-grown nondeciduous taxa to reach maturity (C. H. Dodson, personal communication).

Pronounced precocity is unusual among perennials adapted to resource-limited habitats, as are most forest canopies. This inconsistency could be interpreted as evidence that vigorous, epiphytic, deciduous orchids, like some of their terrestrial relatives, remain mycotrophic well beyond seedling stages. Several authors have in fact ascribed this potential to Orchidaceae as a whole or specifically to one or more of its canopy-dwelling members (e.g. Sanford, 1974; Johansson, 1977; Jonsson and Nylund, 1979). The predilection of *Catasetum* for rotting knotholes and dead or dying hosts heightens suspicion that this genus, more than most, might supplement its autotrophic efforts via saprophytic or parasitic mycorrhizal associates. We report here on the photosynthetic behavior and water use patterns of deciduous *C. integerrimum* and *Encyclia tampensis* (Lindl.) Small, a slower-growing evergreen species, and offer an alternative to biotrophy to explain why the deciduous member of this pair might outperform the other in activities influenced by rates of carbon gain and patterns of water use.

THE EXPERIMENTAL SUBJECTS

Encyclia tampensis is a small to medium-sized sympodial epiphyte whose adult stages consist of numerous, closely-packed, determinate shoots, the youngest of which bear one or two coriaceous, slender elongate one- to four-year-old leaves (Fig. 1C). Old pseudobulbs remain green for several more years after leaf fall. Single terminal inflorescences emerge from year-old shoots. One or more new shoots begin to develop concurrently from an equal number of basal axillary buds. Fruits dehisce within 8-10 months, requiring about the same interval to ripen their contents as young shoots need to achieve mature size. Roots with a life span of two or more years arise from one- and two-year-old shoots. Specimens used in this study were originally collected in southwestern Florida where they were growing on pond cypress.

Catasetum integerrimum is also sympodial (Fig. 1A, B). Each elongate, fleshy shoot supports 6-12 thin plicate leaves through the first 6-8 months of

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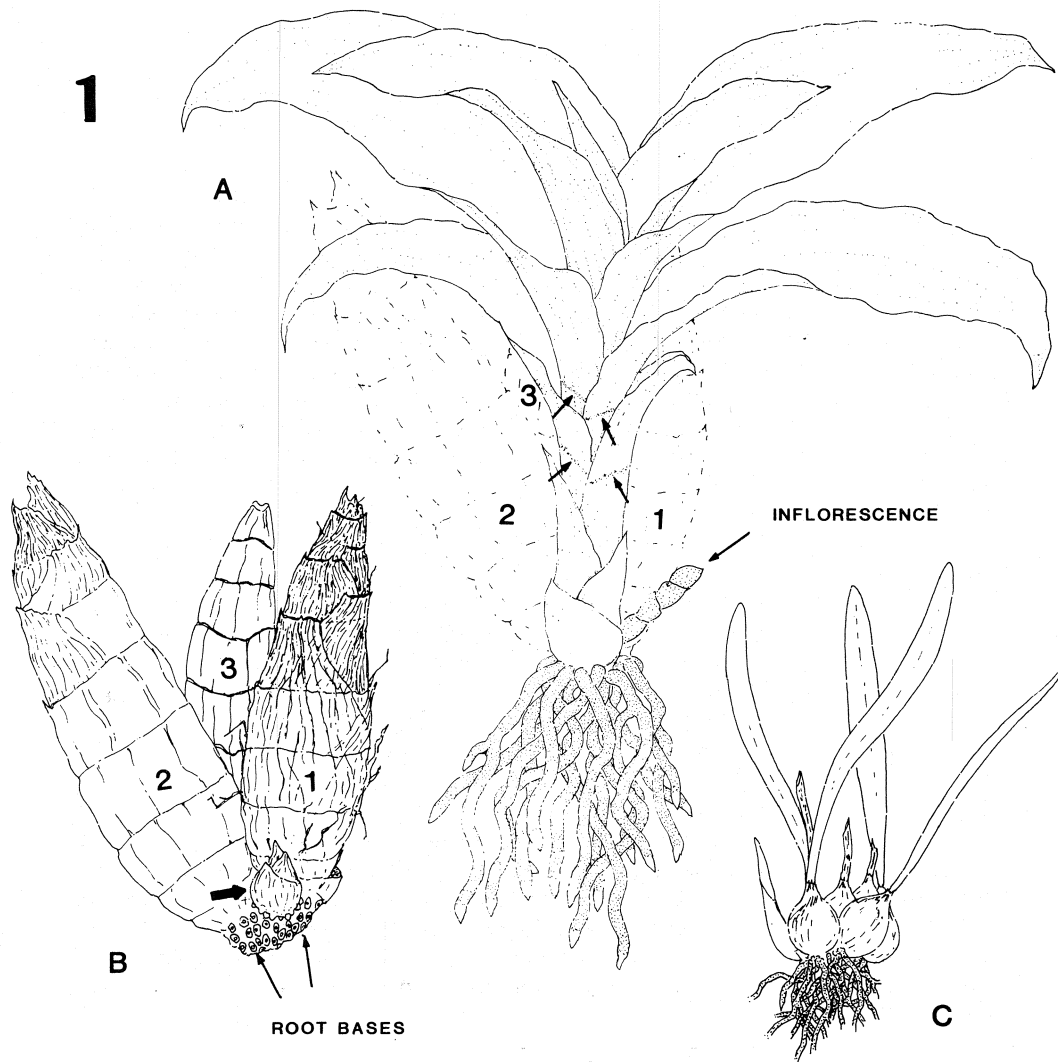


Fig. 1A-C. Growth habits of *Catasetum integerrimum* and *Encyclia tampensis* ($\times 0.2$). 1A. *Catasetum integerrimum* approaching the fully leafed condition. Numbered 1-, 2- and 3-year-old leafless pseudobulbs are present. Arrows on the immature leafy shoot indicate future abscission points. 1B. *Catasetum integerrimum* with dead roots removed. A new shoot is beginning to expand at the base of the 1-year-old leafless pseudobulb. 1C. *Encyclia tampensis* initiating a new shoot. Only part of its extensive system of living roots is included.

life. During this leafy phase, subtending stems mature to full thickness and generate from basal axils inflorescences bearing staminate or pistillate flowers. An extensive velamentous root system matures over the same interval. Later, leaves senesce quickly and disarticulate at preformed abscission zones located at the summits of sheathing bases (Fig. 1A). All the roots die at about the same time, but they remain in place after death. Leafless pseudobulbs generate new shoots the following spring and stay green for 3-4 more years while gradually shrinking as successive generations of offshoots mature. Experimental subjects were obtained from broadleaf shade trees growing in a coffee plantation in East Central Mexico.

METHODS

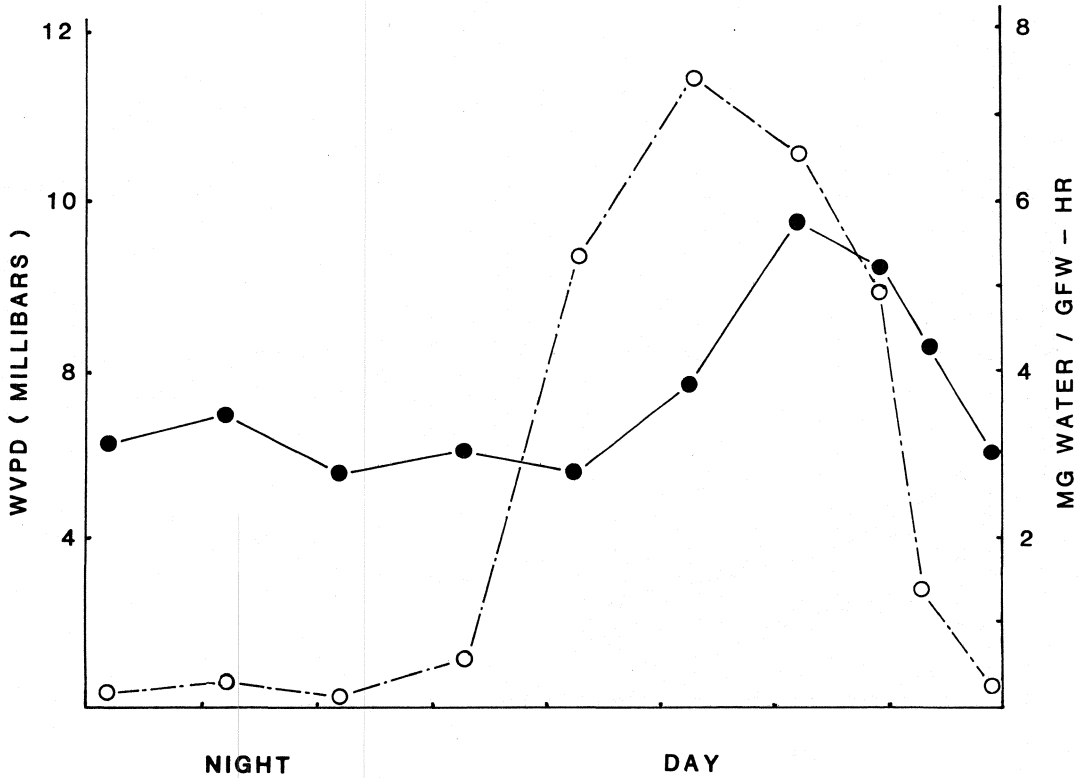
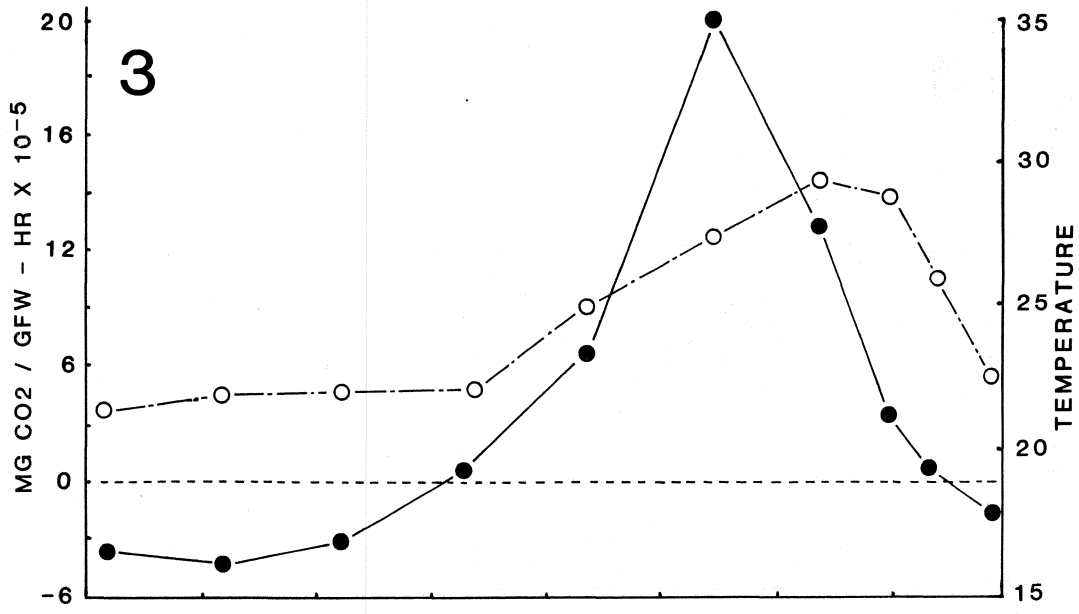
Both subjects were grown in the Oberlin College greenhouse for several years prior to this study. *Encyclia tampensis* was affixed to lathe strips where its roots were fully exposed as they would be on a host. *Catasetum integerrimum* was planted in pots of fir bark chips. They received ambient light, irrigation every 1-3 days, and dilute fertilizer sprays at 4-6 week intervals. In the late spring, leafless *Catasetum* specimens were shorn of roots, assayed, and placed in clay pots filled with washed pea gravel. They were returned to this medium after each test run to deny the growing roots access to any organic substrates. During midsummer runs, root systems of the now leafy plants were incased in plastic bags. Roots of *E. tampensis* were left exposed during its runs, which were carried out in May and again in late June-early July.

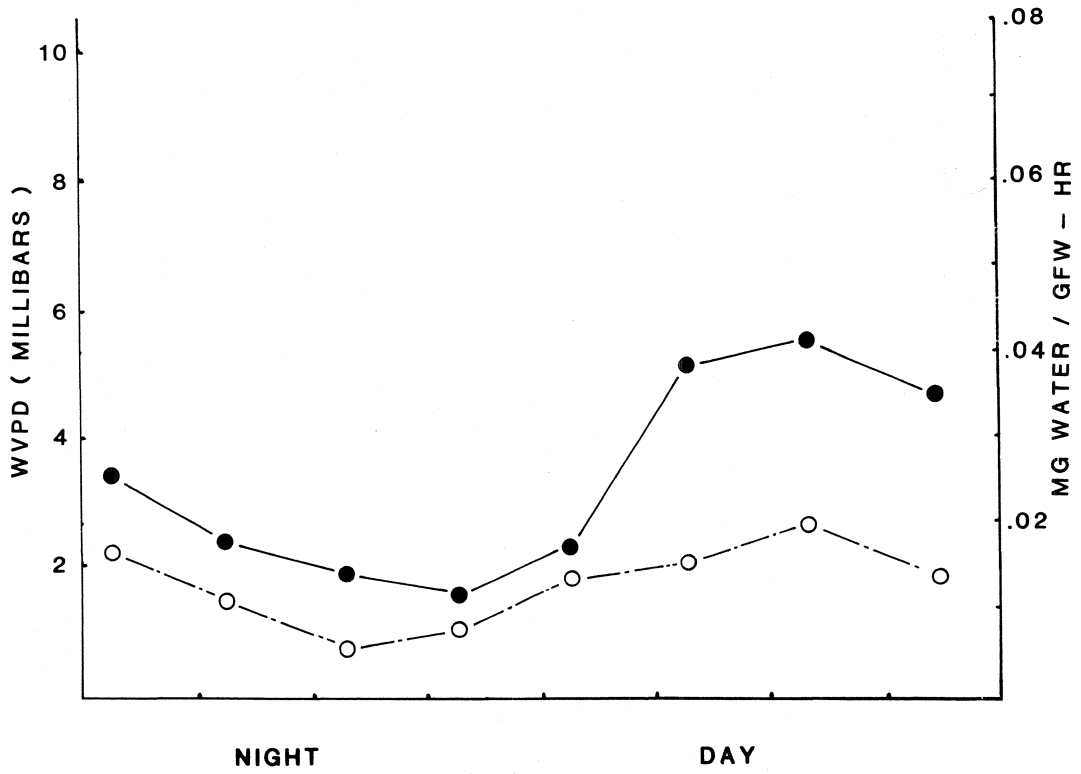
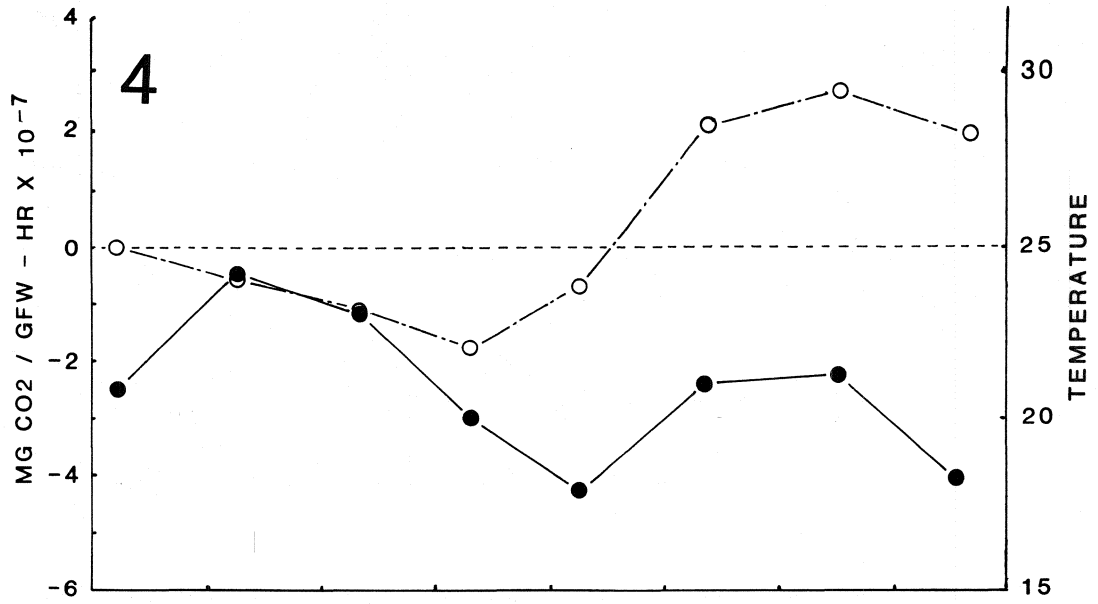
Each run was conducted in the laboratory on 1-3 plants enclosed in a confined air stream circulated through a Beckman 215A infrared CO₂ analyzer and the sample chamber of an EG & G Model 880 dew point hygrometer. A recirculating rather than an open flowthrough system was chosen to maximize sensitivity since CO₂ exchanges and water losses were often very small. Readings were taken periodically during continuous 24-hour runs. An on-line tube of Drierite and a humidifier were used to adjust treatment atmospheres to desired water vapor pressures. Because of possible effects on stomatal apertures, abrupt or large changes in dew point were always avoided. Time intervals required for a rise in dew point of approximately 2.5 C were recorded as indices of transpiration. Over the normal photoperiod, plants were illuminated with natural light passing first through a southern-exposure window and then a water bath filter. At times, this source was supplemented with emissions from a single GE tungsten 150-W bulb. Intensities determined with a Lambda LI-170 photometer varied with time of day and atmospheric conditions, approaching a maximum of 1500 $\mu\text{E m}^{-2} \text{sec}^{-1}$ during cloudless intervals. Experimental parameters varied among 24-hour runs, but were maintained within the following ranges: temperatures from 16-32 C; light exposures from dark to 1500 $\mu\text{E m}^{-2} \text{sec}^{-1}$; humidities from 55-75 per cent. Greenhouse conditions fluctuated over similar intervals during the months these orchids were monitored. Four replications using separate plants were recorded for each species.

RESULTS

Each of the three types of material (*E. tampensis* and both leafy and leafless *Catasetum integerrimum*) exhibited internally consistent patterns of water loss and CO₂ exchange during each set of experimental conditions tested. *Encyclia tampensis* showed CAM characteristics; Fig. 2 illustrates the profile of a representative run. Specifically, a modest carbon gain occurred at night, a smaller loss by day. Water losses were always low and differentials between day and night transpiration relatively small.

Uptake of CO₂ by leafy *Catasetum integerrimum* (Fig. 3.) commenced in the morning at light intensities as low as 20-30 $\mu\text{E m}^{-2} \text{sec}^{-1}$. Leafy specimens exposed to light at approximately 800-900 $\mu\text{E m}^{-2} \text{sec}^{-1}$ attained a maximum CO₂ uptake about seven-fold greater than the nighttime value for *E. tampensis*. (Leafy *Catasetum* photosaturates at less than 1000 $\mu\text{E m}^{-2} \text{sec}^{-1}$). In contrast to the performance of its leafy stage, dormant (leafless) *Catasetum* respired and transpired at very depressed rates throughout the diurnal cycle (Fig. 4). Its succulent, leafless, green stems therefore exhibited no outward evidence of either C₃ or CAM activity. Free-hand sections of





Catasetum roots removed from the pea gravel were free of endocellular fungal pelotons, yet by mid-January, as leaves were beginning to yellow, new stems had achieved normal adult size.

A note of qualification seems appropriate at this point. At least a few succulents are facultative CAM types. Relieved of moisture stress, they assume C₃ photosynthesis and continue to operate in this mode until tissue water potentials drop again at some later date (Hartsock and Nobel, 1976). However, we believe that *E. tampensis* is an obligate CAM plant. Our experiments were conducted with well-watered materials. Also, CO₂ exchange by this species previously measured during winter months (personal observation) has shown no evidence of C₃ activity (i.e., midday CO₂ consumption). Even though CO₂ fixation pathways may remain unchanged, however, precise comparisons of plant carbon and water economies are, of course, only possible when subjects are monitored *in situ* over an entire year.

DISCUSSION

Soil-dwelling xerophytes with aboveground perennial parts employ one of several strategies to cope with drought. Among homiohydrous taxa studied in Mediterranean climates by Mooney and Dunn (1970), for example, one group utilizes persistent, relatively costly but durable, sclerophyllous C₃ leaves of moderate photosynthetic capacity. So equipped, these plants maintain a positive carbon balance at sustainable transpiration rates through the driest months of the year. Other arid-land terrestrials display canopies of less expensive, more productive, more ephemeral, mesomorphic C₃ leaves produced for exploitation of abundant moisture during periodic wet seasons. These leaves are incapable of operating at high water use efficiencies; they atrophy with the approach of dry weather, as may much of the plant's peripheral root system (Kummerow, 1980). Photosynthetic organs of deciduous species must be much more productive than those of evergreen types if they are to match or exceed yields of leaves which persist the entire year.

While sclerophylly and deciduousness both provide substantial drought adaptiveness, representatives of a third assemblage, the succulent evergreen (CAM) types, outperform all others in water economy (Kluge and Ting, 1978). Given the inherent constraints associated with CAM, however, their rates of carbon gain are modest at best -- well below those of most sclerophyllous and deciduous types. Along moisture gradients examined by Mooney and Dunn (1970), C₃ evergreens, C₃ drought-deciduous types, and CAM succulents replace each other as aridity increases. Slow-growing succulents are probably relegated to very dry microsites because their competitive ability is poor; unshaded and better watered, these plants grow quite well.

Canopy-dwelling orchids have already been segregated into ecological categories based on substratum preferences (Sanford, 1974), and these must in part be dictated by drought tolerance. *Catasetum integerrimum* is a humus epiphyte, a designation which helps explain the efficacy of its deciduous habit. Naked green shoots--organs which, one might suspect, would fix significant quantities of carbon as do the cladodes of many CAM succulents-- apparently do not provide much nutritional input. Their primary function seems to be that of harboring reserves needed to produce new shoots and roots at the beginning of each rainy season. Most of the carbon gained by the plant is fixed by cheap throwaway leaves which abscise after a relatively brief term of service and thus offer no further benefit to the bearer. Thick velamentous roots, on the contrary, retain considerable utility long after death. Successive spent root systems, accumulating at the base of the plant,

provide an ever-increasing volume of absorbent humus for exploitation by future shoots whose drought-sensitive foliage will be expending moisture at high rates. In addition, the dormant organism probably conserves water so effectively that its perennial parts need little or no replenishment through an entire dry season. *Catasetum* is thus a drought avoider. Its unusual vigor among epiphytic Orchidaceae is consistent with the widespread strategy of drought avoidance via deciduousness and, in this specific case, with the exploitation of periodically equable patches of space in what are, more broadly, very stressful habitats. Functionally, *C. integerrimum* resembles numerous deciduous, soil-rooted taxa endemic to seasonally arid terrestrial habitats in many parts of the world. Less conventional is this orchid's ability to increase its resource base through substrate modification and thereby help assure that a drought-deciduous strategy is sustainable in habitats characterized by pronounced but predictable droughts.

Encyclia tampensis and most succulent evergreen orchids qualify as bark or twig epiphytes. By definition, roots of these plants are either suspended above, or mostly exposed on, bark surfaces. Access to moisture is very limited; the outer layers of bark which these plants tap for water and minerals dry out within a few hours despite the most thorough soaking. Hence transpiration ratios must be low the year round, a requirement best accommodated by obligate CAM. Considering the large number of twig- and bark-dwelling members in Orchidaceae, drought endurance of the kind exemplified by *E. tampensis* is likely to be common there.

Co-occurrences of deciduous and evergreen orchids on the same phorophyte (e.g., *Cyrtopodium punctatum* (L.) Lindl. and *E. tampensis* on Florida cypress) also suggest to us that significant moisture gradients can exist across short distances even in a single tree crown, just as they do in many terrestrial habitats. Since at least some canopy-dwelling species exhibit C₃ photosynthesis (Arditti, 1979), even greater diversity in water use than that revealed by this study may occur in epiphytic Orchidaceae. Orchid floras on a variety of sites should be examined to determine whether moisture gradients can indeed be steep enough in forest canopies to support a broad range of homiohydrous water use strategies in close proximity. Should C₃-evergreen, C₃-deciduous and CAM evergreen species be found in mixed populations and their moisture requirements quantified, those plants may then be used to map supporting tree crowns into zones of water availability; this will permit clearer identification of the factors which create these zones, such as exposure, bark thickness, and the kinds and densities of investing thallophytes. Once categorized, plants representing each functional type can be scrutinized further for additional within-group consistencies in root and shoot structure that may underlie their ability to partition tree crowns into separate water use zones. These kinds of data will help the orchid anatomist place the myriad structural variations exhibited by orchid leaves and roots into a more coherent functional context. Many foliar and root characters such as velamen thickness, and presence of tracheoidal ideoblasts and exodermal aeration cells (Benzing et al., in press) are undoubtedly convergent. One can best assess the functional significance of these and other structural details by comparing subjects that share common selective pressures and have evolved the same mechanisms to acquire and use basic resources.

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