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Leaf Gas-exchange Characteristics of Sixteen Cycad Species

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ABSTRACT. **Leaf gas exchange characteristics for 16 species of cycad were determined under field conditions in Miami, Fla. Net CO_2 assimilation (A_{CO2}) ranged from 4.9 μmol·m^{-2}·s^{-1} for *Lepidozamia peroffskyana* Regel to 10.1 μmol·m^{-2}·s^{-1} for *Zamia furfuracea* L. fil. in Aiton. Stomatal conductance to H_2O (g_s) was more variable, ranging from 85 mmol·m^{-2}·s^{-1} for *Cycas seemannii* A. Br. to 335 mmol·m^{-2}·s^{-1} for *Encephalartos hildebrandtii* A. Br. & Bouche. Transpiration (E) ranged from 1.7 mmol·m^{-2}·s^{-1} for *Cycas chamberlainii* W.H. Brown & Keinholz to 4.8 mmol·m^{-2}·s^{-1} for *Encephalartos hildebrandtii*. Highly variable E was more controlling of water-use efficiency than the less-variable A_{CO2}. The difference between air and pinnae temperature ranged from 0.3 to 1.6 °C and was inversely related to mean g_s among the species. The values within geographic regions representative of the native habitats of the species were highly variable. For example, two of the African species exhibited the highest and lowest values of water-use efficiency in the survey. Leaf gas exchange for the four largest species with arborescent growth form was less than that for the three small species with subterranean or short bulbous growth form. The diurnal variation in leaf gas exchange for *Zamia furfuracea* exhibited a two-peaked pattern with a distinct midday depression in A_{CO2} and g_s. The ratio of dark respiration to maximum A_{CO2} for *Zamia furfuracea* was 0.04. As a group, the values for A_{CO2} and g_s for these cycads ranked at the lower end of the range for all plants species.**

Leaves respond to a myriad of stimuli while balancing water loss, carbon gain, maintenance of adequate leaf temperature, and other factors. Simultaneously measuring net CO_2 assimilation (A_{CO2}), stomatal conductance (g_s), transpiration (E), and other components of gas exchange is beneficial in many areas of plant science, including determining the short-term potential productivity of plants and studying the response of plants to the environment (e.g., Long and Hällgren, 1985; Schaffer and Andersen, 1994). The importance of studying leaf gas exchange is obvious, since photosynthesis is the initial step in the series of processes that produce a plant and photosynthetic capacity is highly variable among species (Kozlowski et al., 1991). Maximum photosynthesis under saturating light provides a relative measure of investment in photosynthetic machinery (Kozlowski et al., 1991; von Caemmerer and Farquhar, 1981).

Körner et al. (1979) assembled an extensive review of leaf conductance and A_{CO2} for 246 species and grouped the species according to 13 morphological and/or ecological traits. Leaf conductance and A_{CO2} were highly correlated and were lowest in succulent species (mean A_{CO2} about 6 μmol·m^{-2}·s^{-1}) and highest in species from aquatic habitats (mean A_{CO2} about 22 μmol·m^{-2}·s^{-1}). No cycad representative was included in the study by Körner et al. (1979), and placing cycads in any of their 13 morphological/ecological groups would be difficult. For example, cycads could not be considered universally succulent, herbaceous, or woody. To date, no description of any aspect of cycad leaf gas exchange has been compiled. Moreover, no such description could be reviewed at this time to compare with the data of Körner et al. (1979) since the only published values we found are for photosynthesis from a single species (Fetcher et al., 1994). These authors reported a range of 2.5 to 3.5 μmol·m^{-2}·s^{-1} for maximum photosynthesis of *Zamia skinneri* Warscz. ex A. Dietr. at La Selva, Costa Rica; values of which are among the very low end of the range for all neotropical trees and understory shrubs at the same location.

Cycads are sometimes called living fossils due to fossil records that date these plants to the Permian period (Crane, 1988). Cycads survived the mass extinctions during the Mesozoic, and some are commonly found as landscape specimens today. Despite the importance of cycads ecologically, horticulturally, and especially historically, surprisingly little organismal research has been devoted to the group. Investment in photosynthetic machinery is of critical importance in natural selection (Field, 1991), and cycads have survived millions of years of natural selection relatively unchanged [e.g., one estimate of the age of *Zamia pumila* is 60 million years (Walters and Decker-Walters, 1991)] and are successful as contemporary plants (Norstog, 1987). Thus, a comparison of cycad gas exchange characteristics with the range known for other contemporary plants would be of interest to many plant scientists.

Field measurements of gas exchange among studies are notoriously variable. The cultural inputs before measurements integrate with natural preconditioning characteristics to influence leaf gas exchange. In addition, conditions during measurement of gas exchange are quite variable among studies from different geographic regions or seasons. These instantaneous and preconditioning characteristics render comparison of gas-exchange data obtained from different studies difficult (Andersen, 1989; Flore and Lakso, 1990). As a result, field measurements from one location using plants receiving the same cultural and environmental inputs may provide the most reliable data for comparison among the plants.

This study was conducted to establish a general description of leaf gas-exchange characteristics for cycads growing at the same location in an *ex situ* research collection, focusing on 16 species

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that we feel are fairly representative of the Cycadales. We also included a description of leaf gas-exchange characteristic of *Bowenia serrulata* (W. Bull) Chamberlain, but these data were not included in the survey comparisons since the plants were growing under glasshouse conditions. Taxonomists are engaged in debate concerning the number of cycad genera. Currently, there are 10 (e.g., Kaufman et al., 1989) or 11 (e.g., Jones, 1993; Stevenson, 1990) recognized cycad genera, *Chigua* D. Stevenson being the one in dispute. With the inclusion of *Bowenia serrulata*, this study incorporates representatives from all four cycad families and all 10 undisputed genera. We compare the range of data for the group with that described for all plant species, the range of data among the field-grown species, the range of data among each geographic zone from which the species are endemic, and the range of data between the largest arborescent species and the smallest species with subterranean axes or short, bulbous stems. In addition, the influence of time of day on gas exchange of *Zamia furfuracea* was determined to compare this diurnal pattern for a representative cycad with the diurnal pattern reported for other perennial species. *Zamia furfuracea* was selected for these measurements because it is a popular landscape species in southern Florida.

Materials and Methods

Sixteen cycad species were selected for this study based on current taxonomic treatments of Cycadales, geographic regions from which they are endemic, and growth forms (Table 1). Included in this field study were one to two species from nine of the ten undisputed cycad genera. Plants representing each of the species except *Zamia pumila* L. were well-established cultivated specimens growing on the grounds of the Montgomery Foundation in Miami, Fla. (25.8 N lat.). The plants were fertilized two times annually with 12N–2P–10K granular fertilizer at the rate of 0.45, 1.4, or 3.2 kg per small, medium, or large plant, respectively, and had been growing in the landscape of the Montgomery Foundation for at least 4 years.

Zamia pumila is native to Florida, and wild plants growing in open habitats on the Montgomery Foundation were selected for use in the study. These plants were growing in competition with other shrub species. For comparative purposes, measurements were made on a stand of cultivated *Zamia pumila* plants in the landscape of Fairchild Tropical Garden, located about 3 km from the Montgomery Foundation. These plants were grown in the absence of competition with other species and were periodically fertilized and irrigated.

Soil was classified as sandy, siliceous, hyperthermic Lithic Udorthents with rock outcrop. To ensure that moisture was not limiting, the soil moisture was raised to field capacity by rainfall or irrigation 1 to 2 d before measurement.

Pinnae gas exchange was measured with a CIRAS-1 open system (PP Systems, Stotfield, Hitchin, Herts, U.K.). The cuvette exposed 2.5 cm^2 of pinnae surface. Pinnae width of *Cycas chamberlainii*, *Dioon edule* Lindley, *Dioon merolae* De Luca, Sabato & V-Torres, *Macrozamia communis* L.A.S. Johnson, *Microcycas calocoma* (Miq.) A.DC., and *Zamia pumila* plants were narrower than the diameter of the cuvette. Two to three pinnae were inserted side by side, with no gap or overlap, in the cuvette to achieve measurements on these species. All of these species exhibited pinnae with parallel margins lacking inflexed or reflexed characteristics (Stevenson, 1981), which made this approach possible. Based on measurements from several species that indicated that fully expanded but light green, immature foliage had lower gas-exchange values than more mature dark foliage, only plants with dark green foliage were used. This additionally ensured the lack of temporary increased sink activity due to expansion of immature reproductive or vegetative structures. For example, Hanson et al. (1988) reported that, during the expansion of a new flush of *Quercus rubra* L. stem growth, gas exchange of the

Table 1. Family and accession number[z] of sixteen cycad species selected for inclusion in a survey of gas-exchange characteristics. Subheadings indicate the geographic region where the species are endemic[y].

Species	Family	Accession no.
	Africa	
Encephalartos bubalinus Melville	Zamiaceae	64570
Encephalartos hildebrandtii A. Br. & Bouche	Zamiaceae	64575
Stangeria eriopus (Kunze) Nash	Stangeriaceae	651325
	Australia	
Lepidozamia hopei Regel	Zamiaceae	71468A
Lepidozamia peroffskyana Regel	Zamiaceae	59883C
Macrozamia communis L.A.S. Johnson	Zamiaceae	651326D
Macrozamia lucida L.A.S. Johnson	Zamiaceae	59691
	Caribbean	
Microcycas calocoma (Miq.) A. DC.	Zamiaceae	82277B
Zamia pumila L.	Zamiaceae	Wild plants
	Mexico	
Ceratozamia hildae G. Landry & M. Wilson	Zamiaceae	88339
Ceratozamia latifolia (Miq.) D. Stevenson	Zamiaceae	8544
Dioon edule Lindley	Zamiaceae	6132C
Dioon merolae De Luca, Sabato V-Torres	Zamiaceae	76461A
Zamia furfuracea L. fil. in Aiton	Zamiaceae	94464A
	Pacific Islands	
Cycas chamberlainii W.H. Brown & Keinholz	Cycadaceae	77963F
Cycas seemannii A. Br.	Cycadaceae	66636A

[z] From the *ex situ* research collection at the Montgomery Foundation, Miami, Fla., accession system is that of Fairchild Tropical Garden.
[y] According to Stevenson et al. (1990).

preexisting leaves on the same stem increased due to sink activity of the new flush. An initial survey of gas exchange for pinnae located from the base to the apex of leaves provided the zone of maximum flux within each leaf for each species. This zone was inconsistent among the species but consistent within each species, and measurements were confined within this zone for each species.

All gas-exchange measurements were made from 0900 until 1130 HR on sunny to mostly sunny days from 16 to 26 June 1994. Measurements were made on each species during at least 2 separate days for a total of 20 measurements from each species.

Gas-exchange characteristics selected for comparison were A_{CO2}, E, g_s, water-use efficiency (WUE; A_{CO2}/E), ΔT (leaf temperature – air temperature), and C_i:C_a (intercellular CO_2/external CO_2). Several comparisons were made.

a) A general comparison among the species was accomplished by calculating least significant difference ($P \leq 0.05$) based on pooled error variance with equal replications of 20.

b) The geographic region defining the endemic zone for each cycad genus is fairly narrow (exception for *Cycas* L.). The *Cycas* selected for inclusion were *Cycas chamberlainii* from the Philippine Islands and *Cycas seemannii* from Fiji. We defined this zone as Pacific Island species, and thus had five geographic regions to compare (Table 1). A comparison among these regions was accomplished by calculating least significant difference ($P \leq 0.05$) based on a pooled error variance with among species nested within geographic zones and unequally replicated means.

c) Cycads vary in growth habit from large, columnar, arborescent stems as high as 3 m to small, subterranean stems (Stevenson, 1990). Some genera are restricted to one growth form, and others have species representing either growth form or intermediate characteristics. Arborescent stems are composed of a massive parenchymatous pith and cortex and secondary vascular tissue (Stevenson, 1990), so great disparity in sink strength may exist among the growth forms. To determine the influence of growth form on gas exchange, we compared characteristics of the four distinctly large arborescent species (*Cycas chamberlainii*, *Lepidozamia hopei* Regel, *Lepidozamia peroffskyana*, and *Microcycas calocoma*) with the three distinctly small species exhibiting either subterranean or short, bulbous stems [*Ceratozamia latifolia* (Miq.) D. Stevenson, *Stangeria eriopus* (Kunze) Nash, and *Zamia pumila*]. Mean comparisons were accomplished as described for among geographic zones.

d) Leaf gas-exchange characteristic of wild versus cultivated *Zamia pumila* plants were compared using a *t* test.

No field-grown specimens of *Bowenia serrulata* were in the collection; therefore, measurements were made on containerized specimens growing under glasshouse conditions. Plants were growing in 15-L containers with peat-based medium under 78% shade supplied by wavelength-neutral shadecloth. Plants were drenched two times per month with a solution of Peters 20N–10P–17K (W.R. Grace & Co., Fogelsville, Pa.), Liquid Green (Atlantic Fertilizer, Homestead, Fla.), Sequestrene 138Fe (Ciba-Geigy,

Table 2. Net CO_2 assimilation (A_{CO2}), stomatal conductance to H_2O (g_s), water-use efficiency (WUE), leaf temperature – air temperature (ΔT), and the ratio internal CO_2 concentration/external CO_2 concentration (C_i : C_a) of sixteen cycad species growing under field conditions in Miami, Fla.; n = 20.

Species	A_{CO2} (µmol·m^{-2}·s^{-1})	g_s (mmol·m^{-2}·s$^{-1)}$)	WUE (A_{CO2}/transpiration)	ΔT (°C)	C_i:C_a
			Africa		
Encephalartos bubalinus	5.8	88	3.5	1.1	0.60
Encephalartos hildebrandtii	9.4	335	2.0	0.4	0.77
Stangeria eriopus	7.1	119	2.2	1.1	0.71
Mean	7.4	181	2.6	0.9	0.70
			Australia		
Lepidozamia hopei	5.4	123	2.1	1.2	0.72
Lepidozamia peroffskyana	4.9	86	2.5	1.4	0.67
Macrozamia communis	7.6	191	2.3	0.7	0.73
Macrozamia lucida	7.4	142	2.1	1.0	0.71
Mean	6.3	136	2.2	1.1	0.71
			Caribbean		
Microcycas calocoma	7.4	143	3.4	1.2	0.68
Zamia pumila	9.4	293	2.2	0.3	0.75
Mean	8.4	218	2.8	0.7	0.71
			Mexico		
Ceratozamia hildae	6.7	152	2.5	1.4	0.65
Ceratozamia latifolia	6.9	132	2.5	1.1	0.68
Dioon edule	7.2	155	2.5	0.9	0.68
Dioon merolae	7.8	194	2.3	0.6	0.73
Zamia furfuracea	10.1	235	2.4	0.4	0.69
Mean	7.7	173	2.4	0.9	0.69
			Pacific Islands		
Cycas chamberlainii	5.4	103	3.3	1.1	0.69
Cycas seemannii	5.8	85	3.4	1.6	0.61
Mean	5.6	94	3.3	1.4	0.65
$LSD_{0.05}$ among geographic zones	1.0	53	0.5	0.4	0.05
$LSD_{0.05}$ among species	0.9	42	0.4	0.1	0.05

Greensboro, N.C.), and Stem (W.R. Grace & Co.) at 1.12 g, 1.47 g, 0.81 g, and 1.47 g·L^{-1}, respectively. No direct comparisons were made with the field-grown species due to the contrasting conditions of the glasshouse. Data are presented as means ± standard error.

Measurements were also made on *Zamia furfuracea* plants about every 2 h throughout the photoperiod on 26 June 1994. Ten measurements per time interval were performed. Measurements were started at 0545 HR and terminated at 2100 HR. Sky conditions were typical for the season, and sunrise and sunset were 0630 and 2015 HR on this day. Data are presented and means ±standard error.

Results and Discussion

Conditions during the periods of field data collection were as follows: photosynthetic photon flux (PPF), 1450 to 1930 μmol·m^{-2}·s^{-1}; external CO$_2$, 340 to 355 μL·L^{-1}; air temperature, 31 to 34 °C; and vapor pressure deficit (VPD), 2.0 to 2.5 kPa. Mean A_{CO2} varied about 2-fold among the 16 cycad species measured under field conditions, with the Australian *Lepidozamia peroffskyana* Regel exhibiting the lowest (4.9 ± 0.2 μmol·m^{-2}·s^{-1}) and the Mexican *Zamia furfuracea* exhibiting the highest (10.1 ± 0.2 μmol·m^{-2}·s^{-1}) values (Table 2). Mean g_s was more variable, with almost a 4-fold difference among the species (from 85 ± 4 mmol·m^{-2}·s^{-1} for *Cycas seemannii* to 335 ± 27 mmol·m^{-2}·s^{-1} for *Encephalartos hildebrandtii*). Transpiration is not included in Table 2, but values can be calculated from A_{CO2} and WUE. A 2.8-fold difference in transpiration was apparent among the species, from 1.7 ± 0.1 mmol·m^{-2}·s^{-1} for *Cycas chamberlainii* to 4.8 ± 0.3 mmol·m^{-2}·s^{-1} for *Encephalartos hildebrandtii*. WUE was less variable among the species. The greater range in E was more controlling of WUE than was the more narrow range in A_{CO2}. For instance, *Encephalartos hildebrandtii* and *Zamia furfuracea* exhibited the highest values in A_{CO2} but had WUE values toward the lower end of the range. Transpiration was so controlling of WUE that A_{CO2} and WUE were not correlated ($r = 0.46^{NS}$). The 5-fold difference in ΔT depended on the range in g_s. The three species that were able to maintain pinnae temperature to within 0.4 °C of air temperature (*Encephalartos hildebrandtii*, *Zamia furfuracea*, *Zamia pumila*) exhibited the three highest values of g_s among the group. *Cycas seemannii* leaves exhibited the lowest value of g_s and the highest values of ΔT (1.6 °C). The least variable characteristic was $C_i : C_a$, with a range from the lowest to highest values representing only 22% of the highest value.

The range in values of A_{CO2} and g_s from these cycads are positioned with the two lowest ranking groups of Körner et al. (1979), succulents and evergreen conifers. The relatively low values for cycads may be partly attributed to the longevity of photosynthetic surface and the potential for maintaining carbon acquisition throughout the year. Except for *Stangeria*, which produces one leaf at time, cycads have a flushing growth habit where a new set of leaves develops in a relatively short period of time, followed by a longer period where no visible growth occurs at the meristem (Stevenson, 1981). As with many other evergreen species, cycads retain functional leaves for more than one growing season [e.g., 4 years for *Zamia skinneri* median leaf longevity (Clark et al., 1992)].

The two Caribbean species exhibited leaf gas-exchange characteristics that were greater than those from the Australian and Pacific Island species (Table 2). Other than this, differences among the geographic regions were not apparent. Moreover, the range in values within the geographic regions was high. For example, the two African *Encephalartos* species were either the extremes or close to the extremes for the range of values for A_{CO2}, E, and WUE.

Every cycad genus except *Cycas* (Kaufman et al., 1989) and *Zamia* (Jones, 1993) is naturally restricted to a small geographic region. Accurate comparison of gas-exchange characteristics of all nine genera in the survey would not be possible in their native habitat. We have tried to minimize the influence of instantaneous and preconditioning variables by standardizing edaphic, climatic, and cultural preconditioning and by confining conditions during measurements to narrow ranges of PPF, temperature, VPD, and time of day. These methods were possible only because of the extensive *ex situ* collection of cycads at the Montgomery Foundation.

Mean leaf A_{CO2}, g_s, and E for the four large species with arborescent growth form (5.8 μmol·m^{-2}·s^{-1}, 114 mmol·m^{-2}·s^{-1}, and 2.2 mmol·m^{-2}·s^{-1}, respectively) were less than for the three small species with subterranean or short, bulbous growth form (7.8 μmol·m^{-2}·s^{-1}, 181 mmol·m^{-2}·s^{-1}, and 3.3 mmol·m^{-2}·s^{-1}, respectively). The highest mean value for A_{CO2} in this study was obtained from *Zamia furfuracea* (10.1 μmol·m^{-2}·s^{-1}). Growth form of this species is a short bulbous stem, and the relative size of the stem and leaves is intermediate among all cycads (Jones, 1993). The larger amounts of chemical energy, carbohydrates, and other substances needed for growth and maintenance of the vegetative structures in the larger species compared with the smaller species may be provided by the greater amount of photosynthetic surface of larger leaves, rather than from a higher rate of carbon gained per unit of leaf surface.

Gas-exchange characteristics of the wild *Zamia pumila* plants (Table 2) were not different from those obtained from plants under cultivation (A_{CO2} = 9.2 ± 0.4 μmol·m^{-2}·s^{-1}; g_s = 268 ±35

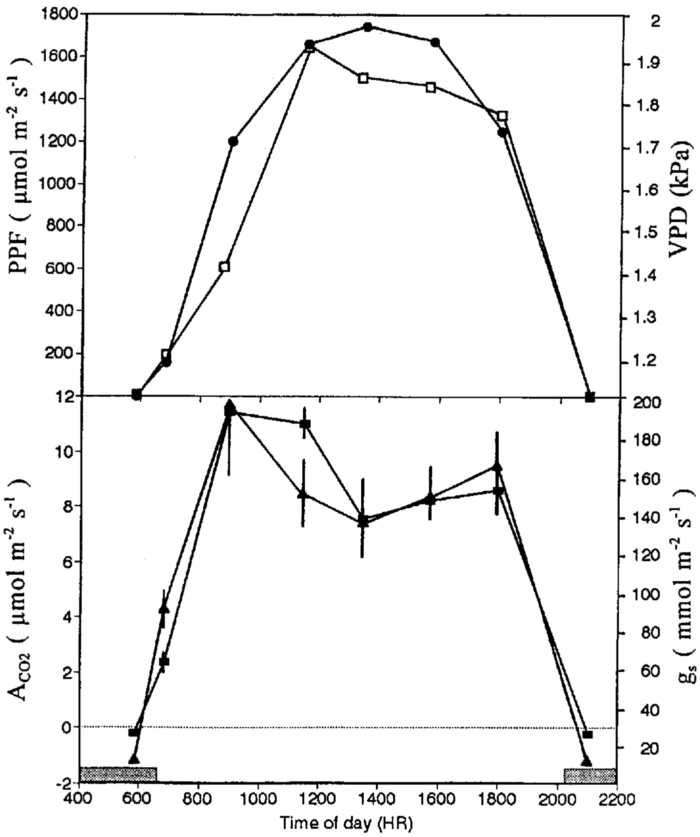

Fig. 1. Photosynthetic photon flux (PPF, ●), vapor pressure deficit (VPD, ☐), net CO$_2$ assimilation (A_{CO2}, ▲), and stomatal conductance (g_s, ■) of *Zamia furfuracea* pinnae as influenced by time of day. Data were obtained on 26 June 1994 in Miami, Fla. Data points are mean ± SE, n = 10.

mmol·m^{-2}·s^{-1}; E = 4.2 ± 0.3 mmol·m^{-2}·s^{-1} for the cultivated plants). Reduced competition for resources from neighboring plants and periodic irrigation and fertilization of the cultivated plants apparently did little to influence capacity for carbon gain. Thus, we presume it also exhibited little influence on investment in photosynthetic machinery. This may have been due to the symbiosis that *Zamia pumila* and other cycads develop with nitrogen-fixing cyanobacteria (Lindblad, 1990).

Bowenia serrulata pinnae had A_{CO2} of 4.3 ± 0.2 µmol·m^{-2}·s^{-1} and g_s of 115 ± 10 mmol·m^{-2}·s^{-1} under the following glasshouse conditions: PPF, 425 to 450 µmol·m^{-2}·s^{-1}; external CO_2, 340 to 345 µL·L^{-1}; air temperature, 30 to 31 °C; and VPD, 1.0 to 1.2 kPa. *Bowenia serrulata* is an Australian forest understory species, and the value of A_{CO2} is similar to the 3.5 µmol·m^{-2}·s^{-1} reported for *in situ* plants of *Zamia skinneri*, a neotropical forest understory species (Fetcher et al., 1994).

Zamia furfuracea plants exhibited a two-peaked pattern of gas exchange under these field conditions (Fig. 1). Mean A_{CO2} increased rapidly after sunrise to a maximum that lasted several hours, then declined to a midday minimum that was about 65% of the morning maximum. During middle to late afternoon, A_{CO2} recovered to about 75% of the morning maximum, then declined coincident with sunset. The pattern of g_s was in close synchrony with that of A_{CO2} (Fig. 1).

The two-peaked pattern of A_{CO2} resulting from the midday depression is commonly found over a range of environments and for many species (Schulze and Hall, 1982). High temperature, high VPD or low humidity, high light stress, decreased g_s, decreased leaf water status, or diurnal changes in hormones have been implicated as causal for this midday depression (Flore and Lakso, 1990; Marler et al, 1994; Roy and Mooney, 1982; Schulze and Hall, 1982; Sinclair et al., 1984; Tenhunen et al., 1984). VPD was highest during midday on 26 June 1994; however, conditions were mild with a peak of only 1.9 kPa. Moreover, the afternoon recovery of A_{CO2} and g_s began before any substantial decline in VPD in late afternoon. Stomatal conductance declined in parallel with A_{CO2} during midday; however, we found no consistent pattern with internal CO_2 concentration. It is therefore doubtful that the midday decline in A_{CO2} was due to g_s limitation. Air temperature remained at about 34 °C throughout the middle portion of the photoperiod, and leaf temperature peaked at 35.6 °C, so heat stress could have been partially responsible for the midday decline in A_{CO2}. However, leaf temperature was above 35 °C until about 1600 HR, well after A_{CO2} began to recover. Factors such as leaf water status, photochemical efficiency, or diurnal hormonal relations were not measured in this study.

Dark respiration was measured on *Zamia furfuracea* before sunrise and after sunset, and values were only 4% of the maximum A_{CO2} (Fig. 1). Carbon loss from dark respiration can be up to 20% of maximum A_{CO2} (Flore, 1994), and total respiratory losses of the carbon fixed through photosynthesis may be as high as 50% (Amthor, 1989). Therefore, the value for this species is relatively low. If further study resolves that this characteristic is representative of cycads as a group, a low proportional loss of carbon may be one means of maintaining favorable leaf carbon balances despite the relatively low values of A_{CO2}.

In summary, the gas-exchange characteristics of 16 cycad species were measured under homogeneous field conditions in southern Florida. These data indicate that the range in gas-exchange characteristics among these representative cycad species is in the lower range previously reported for all described species. The two Caribbean species exhibited higher gas exchange than the Australian and Pacific Island species. However, the values within geographic regions were highly variable. Leaf gas exchange for the three cycads with the smallest growth form was greater than that for the four cycads with largest growth form. *Zamia furfuracea* plants exhibited a typical two-peaked diurnal variation of A_{CO2} and g_s, and dark respiration represented on 4% of the maximum A_{CO2} during the photoperiod.

Literature Cited

Amthor, J.S. 1989. Respiration and crop productivity. Springer-Verlag, New York.

Andersen, P.C. 1989. Leaf gas exchange characteristics of eleven species of fruit crops in north Florida. Proc. Fla. State Hort. Soc. 102:229–234.

Clark, D.B., D.A. Clark, and M.H. Grayum. 1992. Leaf demography of a neotropical rain forest cycad, *Zamia skinneri* (Zamiaceae). Amer. J. Bot. 79:28–33.

Crane, P.R. 1988. Major clades and the relationships in the "higher" gymnosperms, p. 218–272. In: C.S. Bech (ed.). Origin and evolution of the gymnosperms. Columbia Univ. Press, New York.

Fetcher, N., S.F. Oberbauer, and R.L. Chazdon. 1994. Physiological ecology of plants, p. 128–141. In: L.A. McDade, K.S. Bawa, H.A. Hespenheide, and G.S. Hartshorn (eds.). La Selva: Ecology and natural history of a neotropical rain forest. Univ. of Chicago Press, Chicago.

Field, C.B. 1991. Ecological scaling of carbon gain to stress and resource availability, p. 35–65. In: H.A. Mooney, W.E. Winner, and E.J. Pell (eds.). Response of plants to multiple stresses. Academic press, San Diego, Calif.

Flore, J.A. 1994. Stone fruit, p. 233–270. In: B. Schaffer and P.C. Andersen (eds.). Handbook of environmental physiology of fruit crops. vol. 1: Temperate fruits. CRC Press, Boca Raton, Fla.

Flore, J.A. and A.N. Lakso. 1990. Environmental and physiological regulation of photosynthesis in fruit crops. Hort. Rev. 11:111–157.

Hanson, P.J., J.G. Isebrands, R.E. Dickson, and R.K. Dixon. 1988. Ontogenetic patterns of CO_2 exchange of *Quercus rubra* L. leaves during three flushes of shot growth. I. Median flush leaves. For. Sci. 34:55–68.

Jones, D.L. 1993. Cycads of the world. Smithsonian Inst. Press, Washington, D.C.

Kaufman, P.B., T.F. Carlson, P. Dayanandan, M.L. Evans, J.B. Fisher, C. Parks, and J.R. Wells. 1989. Plants: Their biology and importance. Harper & Row, New York.

Körner, C., J.A. Scheel, and H. Bauer. 1979. Maximum leaf diffusive conductance in vascular plants. Photosynthetica 13:45–82.

Kozlowski, T.T., P.J. Kramer, and S.G. Pallardy. 1991. The physiological ecology of woody plants. Academic Press, San Diego, Calif.

Lindblad, P. 1990. Nitrogen and carbon metabolism in coralloid roots of cycads. Memoirs of the New York Botanical Garden 57:104–113.

Long, S.P. and J.-E. Hällgren. 1985. Measurement of CO_2 assimilation by plants in the field and the laboratory, p. 62–94. In: J. Coombs, D.O. Hall, S.P. Long, and J.M.O. Scurlock (eds.). Techniques in bioproductivity and photosynthesis. 2nd ed. Pergammon Press, New York.

Marler, T.E., B. Schaffer, and J.H. Crane. 1994. Developmental light level affects growth, morphology, and leaf physiology of young carambola trees. J. Amer. Soc. Hort. Sci. 119:711–718.

Norstog, K. 1987. Cycads and the origin of insect pollination. Amer. Scientist 75:270–279.

Roy, J. and H.A. Mooney. 1982. Physiological adaptation and plasticity to water stress of coastal and desert populations of *Heliotropium curassavicum* L. Oecologia 52:370–375.

Schaffer, B. and P.C. Andersen. 1994. Handbook of environmental physiology of fruit crops. vol. II. Sub-tropical and tropical crops. CRC Press, Boca Raton, Fla.

Schulze, E.-D. and A.E. Hall. 1982. Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments, p. 181–230. In: A. Pirson and M.H. Zimmerman (eds.). Encyclopedia of plant ecology. II. Water relations and carbon assimilation. Springer-Verlag, New York.

Sinclair, T.R., C.B. Tanner, and J.M. Bennett. 1984. Water-use efficiency in crop production. BioScience 34(1):36–40.

Stevenson, D.W. 1981. Observations on ptyxis, phenology, and trichomes in the Cycadales and their systematic implications. Amer. J. Bot. 68:1104–1114.

Stevenson, D.W. 1990. Morphology and systematics of the Cycadales. Memoirs of the New York Botanical Garden 57:8–55.

Stevenson, D.W., R. Osborne, and J. Hendricks. 1990. A world list of cycads. Memoirs of the New York Botanical Garden 57:200–206.

Tenhunen, J.D., O.L. Lange, J. Gebel, W. Beyschlag, and J.A. Weber. 1984. Changes in photosynthetic capacity, carboxylation efficiency and CO_2 compensation point associated with midday stomatal closure and midday depression of net CO_2 exchange of leaves of *Quercus suber*. Planta 162:193–203.

von Caemmerer, S. and G.D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153:376–387.

Walters, T.W. and D.S. Decker-Walters. 1991. Patterns of allozyme diversity in the West Indies cycad *Zamia pumila* (Zamiaceae). Amer. J. Bot. 78:436–445.