

## LEAF GAS EXCHANGE OF 20 PALM SPECIES UNDER FIELD CONDITIONS

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**WILLIS, L.E., MARLER, T.E. & HUBBUCH, C. 1998. Leaf gas exchange of 20 palm species under field conditions.** Leaf gas exchange variables of 20 palm species were determined under field conditions in Miami, Florida during June 1994 in order to establish a comparison among the six palm subfamilies. Diurnal variation in net CO<sub>2</sub> assimilation (A) and stomatal conductance to H<sub>2</sub>O (g<sub>s</sub>) was measured on leaves of *Sabal causiarum* on a representative mostly sunny day for the season. Pinnae A and g<sub>s</sub> rapidly increased following sunrise to a maximum by 0900 h, followed by a slow decline throughout the day. Moderate recovery of A occurred during late afternoon, but g<sub>s</sub> did not follow this pattern. Dark respiration of *S. causiarum* was 5.3% of maximum A. Based on these data, measurements on the 20 species were made during the morning hours when gas exchange was maximal. Net CO<sub>2</sub> assimilation ranged from 5.5 μmol m<sup>-2</sup>s<sup>-1</sup> for *Ravenea rivularis* to 16.9 μmol m<sup>-2</sup>s<sup>-1</sup> for *Bismarckia nobilis*. The range of g<sub>s</sub> was 121 mmol m<sup>-2</sup>s<sup>-1</sup> for *Phytelephas macrocarpa* to 582 mmol m<sup>-2</sup>s<sup>-1</sup> for *B. nobilis*. Mean transpiration (E) ranged from 1.9 to 6.2 mmol m<sup>-2</sup>s<sup>-1</sup>. Values of A, g<sub>s</sub>, and E were lowest for Calamoidae and Phytelephantoidae species, lowest to mid-range for Arecoideae and Ceroxyloideae species, mid-range for the only Nypoidae species, and mid-range to highest for the Coryphoidae species. Values for gas exchange variables of these palm species were within the range to be expected for evergreen woody plants.

Key words: Palms - photosynthesis - stomatal conductance

**WILLIS, L.E., MARLER, T.E. & HUBBUCH, C. 1998. Pertukaran gas daun bagi 20 spesies palma di bawah keadaan ladang.** Pemboleh ubah pertukaran gas daun bagi 20 spesies palma ditentukan di bawah keadaan ladang di Miami, Florida pada Jun 1994 untuk mengkaji perbezaan di antara enam subfamili palma. Variasi harian dalam asimilasi CO<sub>2</sub> bersih (A) dan pengaliran stoma kepada H<sub>2</sub>O (g<sub>s</sub>) disukat pada daun

*Sabal causerianum* pada hari yang mewakili hari yang cerah dalam musim tersebut. Puncak  $A$  dan  $g_x$  naik dengan cepat selepas matahari terbit hingga ke maksimum pada 0900 h, dan berkurangan secara perlahan di sepanjang hari tersebut. Pemulihan sederhana bagi  $A$  terjadi pada lewat petang, tetapi  $g$  tidak mengikut pola ini. Respirasi gelap bagi *S. causerianum* ialah 5.3 % daripada nilai  $A$  maksimum. Berdasarkan data ini, sukatan bagi 20 spesies berikut dibuat pada waktu pagi semasa pertukaran gas maksimum. Asimilasi  $CO_2$  bersih berjulat dari  $5.5 \mu mol m^{-2} s^{-1}$  bagi *Ravenia rivularis* kepada  $16.9 \mu mol m^{-2} s^{-1}$  bagi *Bismarckia nobilis*. Manakala julat  $g_x$  ialah  $121 mmol m^{-2} s^{-1}$  bagi *Phytelephas macrocarpa* kepada  $582 mmol m^{-2} s^{-1}$  bagi *B. nobilis*. Purata transpirasi ( $E$ ) berjulat daripada 1.9 hingga  $6.2 mmol m^{-2} s^{-1}$ . Nilai-nilai  $A$ ,  $g_2$  dan  $E$  didapati terendah bagi spesies Calamoidae dan spesies Phytelephantoidae, terendah hingga ke julat pertengahan bagi spesies Arecoideae dan spesies Ceroxyloideae, julat pertengahan bagi spesies Nypoidae tunggal dan julat pertengahan hingga tertinggi bagi spesies Coryphoidae. Nilai pemboleh ubah pertukaran gas spesies palma ini adalah dalam julat yang dijangkakan bagi tumbuhan berkayu malar hijau.

## Introduction

Palm trees are prevalent or dominant members of most undisturbed or disturbed tropical forests. The palm family contains numerous species of value in international commerce, while many more species are of local use as sources of food, building materials, medicines and many other raw products (Blombery & Rodd 1982, Uhl & Dransfield 1987).

Despite the importance of palms historically, ecologically and in forestry, little research has been devoted to the physiology of these species. Chazdon (1986) reported the influence of daily light variation on photosynthesis for *Geonoma cuneata*, *Asterogyne martiana* and *Geonoma congesta* in the lowlands of Costa Rica. Hogan (1988) reported the influence of several leaf characteristics on photosynthesis of *Scheelea zonensis* and *Socratea durissima* on Barro Colorado Island, Republic of Panama. To date, there have been no comparisons of any leaf physiology characteristic among a wide range of palm species.

Leaves continuously balance water loss, net  $CO_2$  import, maintenance of adequate leaf temperature and other functional aspects. Simultaneous measurements of photosynthesis, stomatal conductance, transpiration and other components of leaf physiology give us useful information for studying the response of plants to the environment.

This study was conducted to establish a general description of several gas exchange variables of 20 palm species growing at the same location. The influence of time of day on gas exchange was determined for *Sabal causerianum*. Gas exchange variables of the 20 species were measured and compared only for the time of day in which gas exchange was maximal for *S. causerianum*. This list of species included members of every described palm subfamily (Uhl & Dransfield 1987).

## Materials and methods

### *Plant materials*

Twenty taxonomically-distinct palm species were selected for this study in order to include representatives from each of the recognised palm subfamilies (Table 1). The plants from which measurements were made were well-established, field specimens growing on the grounds of The Montgomery Foundation or Fairchild Tropical Garden in Miami, Florida (25.8 N, 80.2 W). Climate of the experimental site is semi-tropical, and the measurements were made in early summer. Accession numbers for the included taxa are presented in Table 1. The soil classification for measurements taken on *Mauritia flexuosa*, *Acoelorrhaphes wrightii*, *Bismarckia nobilis* and *Nypa fruticans* was coarse-silty, carbonatic, hyperthermic Typic Fluvaquents. For all other species sampled, soil was classified as sandy, siliceous, hyperthermic Lithic Udorthents with rock outcrop. The plants were fertilised twice annually with a 12N - 2P - 10K granular fertiliser at the rate of 0.7, 2.0 or 4.8 kg per small, medium or large plant respectively. To ensure that moisture was not limiting, the soil moisture was raised to field capacity one to two days prior to measurements either by rainfall or irrigation.

### *Gas exchange measurements*

Pinnae gas exchange was measured with a CIRAS-1 portable photosynthesis system (PP Systems, Stotfield, Hitchin, Herts, U.K.). This system is designed with four independent infrared gas analysers, and is operated as an open system. The cuvette exposed 2.5 cm<sup>2</sup> of pinnae surface, and air was supplied to the cuvette at the rate of 300 ml min<sup>-1</sup>. Measurements were confined to recently expanded leaves. Natural orientation of pinnae was approximately perpendicular to the vertical, but during measurements the cuvette was oriented perpendicular to the sun. An initial survey of gas exchange from the base to the apex of leaves within each species provided the zone of maximum flux within each leaf. This zone was not consistent among the species, but was consistent within a species. Measurements were confined within this zone for each species. Pinnae width of *Calamus* sp., *Chamaedorea cataractarum*, *Pseudophoenix sargentii* and *Ravenea rivularis* leaves was more narrow than that of the cuvette. For these species, two pinnae were inserted parallel to each other with no gap or overlap in order to fill the 2.5 cm<sup>2</sup> opening of the cuvette.

Measurements were made on two *S. causiarius* plants about every two hours throughout the photoperiod on 26 June 1994. Ten measurements, five for each plant, were made per time interval beginning at about 0545 h and terminating at about 2100 h. Sky conditions were representative for the season, and sunrise and sunset were 0630 and 2015 h on this day.

**Table 1.** Description of 20 palm species growing in southern Florida, used in a survey for determining the range in value for gas exchange variables

Species	Subfamily	Accession number	Origin
<i>Acoclorraphye wrightii</i> (Griseb. & H. Wendl.) H. Wendl. ex Becc.	Coryphoidae	79338A	C. America
<i>Bactris gasipaes</i> H.B.K.	Arecoideae	66342A	C. America
<i>Bismarckia nobilis</i> Hildebr. & H. Wendl.	Coryphoidae	9338A	Madagascar
<i>Calamus</i> sp.	Calamoidae	64129	Australia
<i>Caryota mitis</i> Lour.	Arecoideae	92487C	Asia
<i>Chamaedorea calaractarum</i> Mart.	Ceroxyloideae	7685	Mexico
<i>Cocos nucifera</i> L.	Arecoideae	935N	undetermined
<i>Elaeis guineensis</i> Jacq.	Arecoideae	7845	Madagascar, C. America
<i>Hyophorbe verschaffellii</i> H. Wendl.	Ceroxyloideae	9335B	Rodriquez Is., Mascarenes
<i>Hyphaene coriacea</i> Gaertn.	Coryphoidae	91434B	Trop. Africa
<i>Mauritia flexuosa</i> L.f.	Calamoidae	87457	C. America
<i>Nypa fruticans</i> Wurm	Nypoidae	82473A	Trop. Asia
<i>Phoenix loureirii</i> Kunth	Coryphoidae	76853F	Asia
<i>Phytelephas macrocarpa</i> Ruiz & Pav.	Phytelephantoidae	70279	S. America
<i>Pseudophoenix sargentii</i> Sarg.	Ceroxyloideae	82441E	Caribbean, C. America
<i>Ptychosperma microcarpum</i> (Burret) Burret	Arecoideae	81605A	Papua New Guinea
<i>Ravenea rivularis</i> Jum. & Perr.	Ceroxyloideae	9337	Madagascar
<i>Sabal carisiarum</i> (O.F. Cook) Becc.	Coryphoidae	86305	Caribbean
<i>Wodyetia bifurcata</i> Irvine	Arecoideae	9334C	Australia
<i>Zombia antillarum</i> (Descourt. ex B.D. Jacks.) L.H. Bailey	Coryphoidae	X13118F	Caribbean

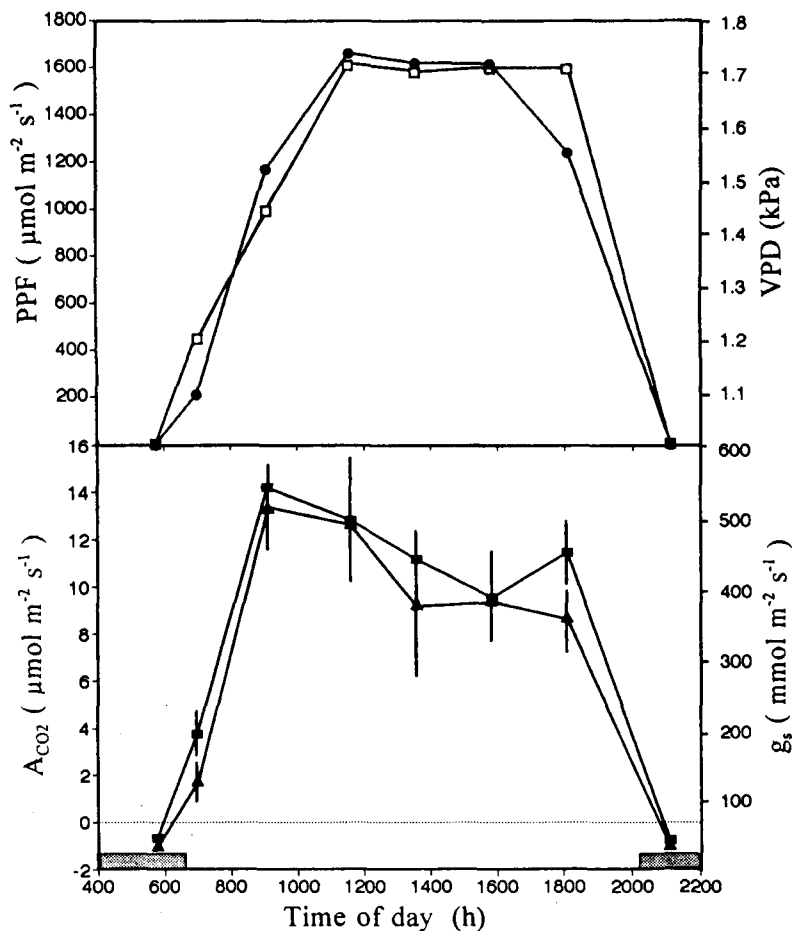
Gas exchange measurements for species comparisons were made from about 0900 until 1130 h during sunny to mostly sunny conditions from 25 to 29 June 1994. Eleven measurements were made for each species. Conditions during the periods of field data collection were: photosynthetic photon flux density (PPFD), 1250 to 1790  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; external  $\text{CO}_2$ , 340 to 350  $\mu\text{l l}^{-1}$ ; air temperature, 31 to 33°C; vapor pressure deficit (VPD), 1.48 to 1.83 kPa.

Gas exchange variables selected for comparison were net  $\text{CO}_2$  assimilation (A), transpiration (E), stomatal conductance to  $\text{H}_2\text{O}$  ( $g_s$ ), water use efficiency (A/E) and the ratio intercellular  $\text{CO}_2$  concentration / external  $\text{CO}_2$  concentration. Data are presented as means  $\pm$  standard error.

## Results

### Daily changes

Net CO<sub>2</sub> assimilation of *S. causerium* pinnae increased rapidly after sunrise to a maximum (Figure 1). This period was followed by a gradual decline to a lower value during mid-afternoon, which was about 70% of the morning maximum. Net CO<sub>2</sub> assimilation recovered to about 80% of the morning maximum during late afternoon, then declined rapidly parallel to PPFD. The pattern of g<sub>s</sub> was in close synchrony with that of A; however, there was no evidence of partial recovery during late afternoon prior to the decline in PPFD (Figure 1).



**Figure 1.** Photosynthetic photon flux (PPFD, ●), vapor pressure deficit (VPD, □), net CO<sub>2</sub> assimilation (A, ■), and stomatal conductance (g<sub>s</sub>, ▲) of *Sabal causerium* pinnae as influenced by time of day. Data were from 26 June 1994 in Miami, Florida, and shaded bars at base of figure represent before sunrise and after sunset. Data points are mean ± standard error, n = 10. Symbols are larger than standard error bars for dark respiration.

Species differences

The species belonging to the Ceroxyloideae and Arecoideae subfamilies exhibited a wide range in values of A, with some species exhibiting high values relative to the survey group as a whole and other species exhibiting relatively low values (Figure 2). The species belonging to the Calamoidae and Phytelephantoidae subfamilies exhibited relatively low values of A, in the range of 5.8 to 7.2  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . *Nypa fruticans*, the sole species in the Nypoidae subfamily, had moderate A value of 12.7  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . Species within the Coryphoidae subfamily had the highest A as a group, ranging from moderate to high values relative to the group as a whole.

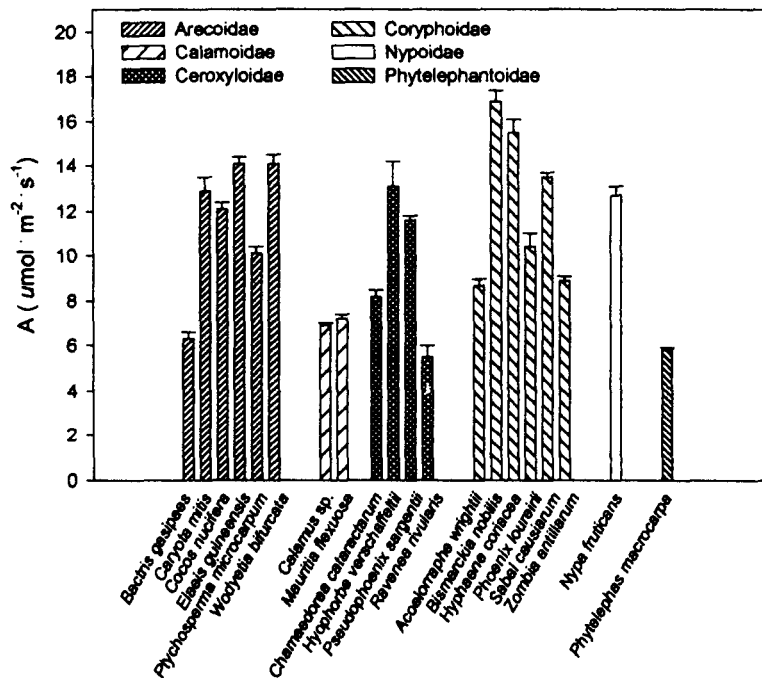


Figure 2. Net CO<sub>2</sub> assimilation (A) of 20 palm species growing under field conditions in Miami, Florida. Bars represent mean  $\pm$  standard error.

The greatest range in stomatal conductance occurred within the Arecoideae and Coryphoidae subfamilies, ranging from about 200 to 600  $\text{mmol m}^{-2}\text{s}^{-1}$  (Figure 3). In comparison, the species in the remaining subfamilies exhibited relatively low stomatal conductance.

Net CO<sub>2</sub> assimilation varied more than three-fold among the 20 palm species measured under field conditions; *Ravenea rivularis* showed the lowest and *Bismarckia nobilis* the highest values (Figure 2). The range in values of stomatal

conductance or transpiration were 4.8-fold or 3.3-fold respectively (Figure 3, Table 2). Water use efficiency exhibited a smaller range, from 2.4 to 3.9  $\mu\text{mol CO}_2$  per  $\text{mmol H}_2\text{O}$  for the group (Table 2). The ratio internal  $\text{CO}_2$  / external  $\text{CO}_2$  exhibited the smallest range among the species and subfamilies, with a 22% difference from the smallest to the largest value (Table 2).

**Table 2.** Transpiration, water use efficiency (net  $\text{CO}_2$  assimilation / transpiration), and the ratio of internal to external  $\text{CO}_2$  for 20 palm species growing under field conditions in Miami, Florida. Table subheadings are names of subfamilies. n = 11.

Species	Transpiration ( $\text{mmol m}^{-2} \text{ s}^{-1}$ )	Water use efficiency ( $\mu\text{mol mmol}^{-1}$ )	Internal $\text{CO}_2$ / external $\text{CO}_2$
Arecoideae			
<i>Bactris gasiphaea</i>	2.1 $\pm$ 0.1	3.0 $\pm$ 0.1	0.67 $\pm$ 0.02
<i>Caryota mitis</i>	3.9 $\pm$ 0.2	3.4 $\pm$ 0.1	0.70 $\pm$ 0.01
<i>Cocos nucifera</i>	4.0 $\pm$ 0.1	3.1 $\pm$ 0.1	0.71 $\pm$ 0.01
<i>Elaeis guineensis</i>	4.9 $\pm$ 0.3	2.9 $\pm$ 0.1	0.77 $\pm$ 0.01
<i>Ptychosperma microcarpum</i>	2.7 $\pm$ 0.1	3.7 $\pm$ 0.2	0.68 $\pm$ 0.01
<i>Wodyetia bifurcata</i>	3.9 $\pm$ 0.2	3.6 $\pm$ 0.1	0.68 $\pm$ 0.01
Calamoidae			
<i>Calamus</i> sp.	2.6 $\pm$ 0.1	2.7 $\pm$ 0.1	0.72 $\pm$ 0.01
<i>Mauritia flexuosa</i>	2.6 $\pm$ 0.1	2.8 $\pm$ 0.1	0.73 $\pm$ 0.02
Ceroxyloideae			
<i>Chamaedorea cataractarum</i>	2.7 $\pm$ 0.2	3.1 $\pm$ 0.2	0.71 $\pm$ 0.01
<i>Hyophorbe verschaffeltii</i>	3.4 $\pm$ 0.3	3.9 $\pm$ 0.3	0.63 $\pm$ 0.03
<i>Pseudophoenix sargentii</i>	2.9 $\pm$ 0.1	4.1 $\pm$ 0.2	0.65 $\pm$ 0.02
<i>Ravenea rivularis</i>	1.9 $\pm$ 0.2	3.0 $\pm$ 0.4	0.70 $\pm$ 0.03
Coryphoidae			
<i>Acoelorrhaphe wrightii</i>	3.4 $\pm$ 0.2	2.6 $\pm$ 0.1	0.72 $\pm$ 0.01
<i>Bismarckia nobilis</i>	6.2 $\pm$ 0.4	2.8 $\pm$ 0.1	0.78 $\pm$ 0.02
<i>Hyphaene coriacea</i>	5.0 $\pm$ 0.6	3.1 $\pm$ 0.1	0.75 $\pm$ 0.01
<i>Phoenix loureirii</i>	4.4 $\pm$ 0.3	2.4 $\pm$ 0.1	0.80 $\pm$ 0.01
<i>Sabal causiarum</i>	4.5 $\pm$ 0.1	3.0 $\pm$ 0.1	0.77 $\pm$ 0.01
<i>Zombia antillarum</i>	2.9 $\pm$ 0.1	3.1 $\pm$ 0.1	0.69 $\pm$ 0.01
Nypoidae			
<i>Nypa fruticans</i>	3.5 $\pm$ 0.2	3.7 $\pm$ 0.2	0.64 $\pm$ 0.02
Phytelephantoidae			
<i>Phytelephas macrocarpa</i>	2.2 $\pm$ 0.1	2.7 $\pm$ 0.1	0.71 $\pm$ 0.01

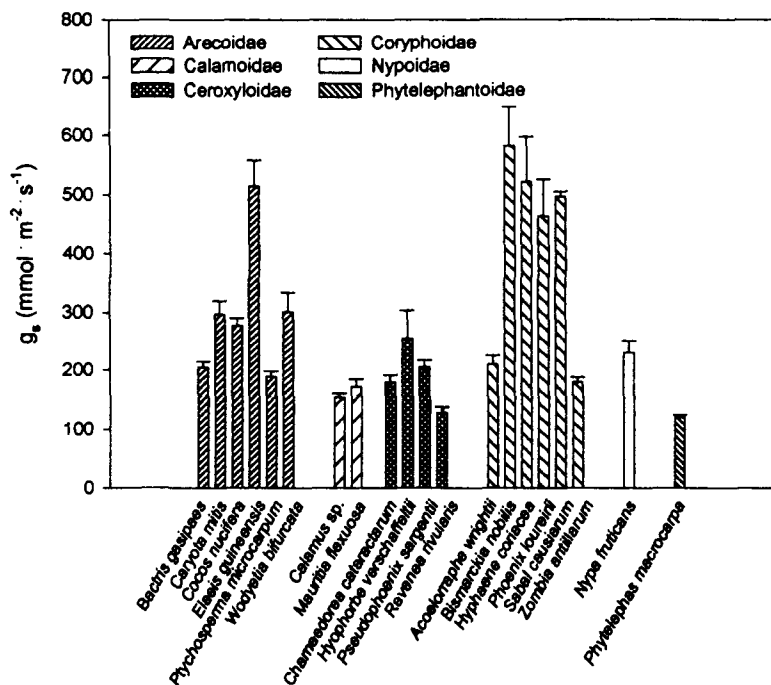


Figure 3. Stomatal conductance ( $g_s$ ) of 20 palm species growing under field conditions in Miami, Florida. Bars represent mean  $\pm$  standard error.

## Discussion

### *Methodological aspects*

Some of the palm species included in this study are common forestry species throughout the tropics, while others are restricted naturally to forests in small geographic regions. For example, *Cocos nucifera* is pantropic in distribution, but *Zamia antillarum* is little known outside of its native Hispaniola habitat. Accurate comparison of gas exchange variables of these 20 species under field conditions was thus only possible because of the extensive *ex situ* collection of palms at The Montgomery Foundation and adjoining Fairchild Tropical Garden. We have attempted to minimise the influence of instantaneous and pre-conditioning variables by standardising climatic and cultural pre-conditioning, and by confining conditions during which measurements were made to narrow ranges of PPFD, temperature, VPD and time of day.



Determining the response of gas exchange to single variables under laboratory conditions has not translated to naturally contrasting field conditions adequately (Schulze & Hall 1982). However, field measurements of gas exchange are notoriously variable among sites, seasons or experiments. The cultural inputs prior to measurements integrate with natural pre-conditioning characteristics to influence gas exchange measurements. These instantaneous and pre-conditioning characteristics render comparison of gas exchange data obtained from different studies difficult (Andersen 1989, Flore & Lakso 1990). We presume that the methods used in this field study were as accurate as possible for comparing the measured variables among the 20 palm species.

### *Daily changes*

The two-peaked pattern of  $A$  resulting from the decline during late morning and early afternoon has been observed in many environments and for many species (Schulze & 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 a midday decline in  $A$ . Vapor pressure deficit was highest during midday on 26 June 1994; however, conditions were quite mild with a peak of only 1.7 kPa. Moreover, the afternoon recovery of  $A$  occurred in the absence of any decline in VPD in late afternoon. Stomatal conductance declined in parallel with  $A$  during midday; however, the late afternoon recovery of  $A$  was not accompanied by an increase in  $g_s$ . It is therefore doubtful that the decline in  $A$  during the middle of the day was due to  $g_s$  limitation. Air temperature remained between 33 and 34 °C throughout the middle portion of the photoperiod, and leaf temperature peaked at 34 °C (data not shown). Although we do not know the photosynthetic response to temperature for this species, these temperature values are quite high and could have been partially responsible for the midday decline of  $A$ . Moreover, temperature was the only measured variable that changed concomitantly with  $A$  during late afternoon in a manner that correlated with  $A$ . The decline in air temperature during late afternoon was only 0.5 °C; however, leaf temperature dropped below that of air temperature during late afternoon for the first time since the early morning measurement. As a result, leaf temperature declined from 33.8 °C at 1600 h to 32.5 °C at 1800 h. This late afternoon decline in temperature accompanying the increase in  $A$  was so small that temperature probably does not fully explain the decline in  $A$ . We did not obtain any measurements on leaf water status, photochemical efficiency or hormonal changes throughout the day.

Dark respiration in *Sabal causiarum* was 5.3% of the maximum  $A$  (Figure 1). Carbon loss from dark respiration can be up to 20% of the value of  $A$  (Flore 1994), so the value for this palm is relatively low. It is probable that a decrease in the ratio of dark respiration to  $A$  is associated with an increase in vegetative growth (Kozlowski *et al.* 1991), since up to 50% of the carbon fixed through photosynthesis may be lost by respiratory processes (Amthor 1989).

### Species differences

As a group, these data indicate that leaf gas exchange values for members of the Palmae family are in the range for evergreen woody plants (Körner *et al.* 1979). Palms exhibit growth characteristics that are similar to those of many woody evergreen plants. They are relatively slow growing and possess leaves that remain on the plant for extended periods before senescence. For example, Hogan (1988) reports leaf age of two palm species with years as the units of time. Moreover, their evergreen status allows for gas exchange throughout all seasons of the year. It is not surprising that gas exchange tends to fall within the conservative range of other evergreen species.

The influence of natural habitat on the gas exchange variables for these varied palm species (Blombery & Rodd 1982, Uhl & Dransfield 1987) was impossible to discern. For example, *Acoelorrhapha*, *Mauritia* and *Nypa* are adapted to wet and swampy conditions. *Hyphaene*, *Pseudophoenix* and *Zombia* are well-adapted to dry climates. *Phoenix* and *Sabal* typically occur in climates with distinct cycling of wet and dry seasons. The species in each of these groups exhibited a small range in values for gas exchange variables, and these values were within the moderate range when viewed in context of variation in the entire survey. The remainder of the species within the survey occur in wet forest conditions, and this group exhibited the greatest range in gas exchange values. The highest and lowest values of A, for example, were from species within this group. The limited numbers of species representing each of these climates precludes the use of this survey in making conclusions about the relationship of native habitat climate with the value of gas exchange variables.

The species in this survey also included representatives possessing growth characteristics with mature plant size which ranged from small to large stature (Blombery & Rodd 1982, Uhl & Dransfield 1987). *Calamus* and *Chamaedorea*, for instance, were among the species which mature to a relatively small plant size. The gas exchange variables for these species were low to moderate in value. The group of species with more robust mature plant size included those species with the highest values of A within the survey. This characteristic was not universal among these robust species; however, *Mauritia* and *Ravenea* were among this group, and their gas exchange values were toward the lower end of the range of values.

The species included in this survey represent a minor proportion of the 2000-plus palm species. However, this study serves as a foundation for pursuing a further understanding of palm physiology. Our approach has been taxonomic, in order to include representatives from every Palmae subfamily.

In summary, the diurnal variation of net CO<sub>2</sub> assimilation and stomatal conductance for *Sabal causiarum* leaves on a representative summer day in southern Florida followed patterns that are typical for woody perennial plants. The gas exchange variables of 20 palm species were measured under relatively homogeneous field conditions and during the morning when values were at a maximum for *S. causiarum*. This group of palm species exhibited gas exchange values which were within those to be expected for evergreen woody plants. Among the species,

however, the variation in the value of the gas exchange variables was relatively high. Stomatal conductance, for example, varied almost 5-fold among the species.

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