

Diurnal and seasonal variation in photosynthesis of peach palms grown under subtropical conditions

M.L.S. TUCCI^{*,†}, N.M. ERISMANN^{**}, E.C. MACHADO^{**}, and R.V. RIBEIRO^{**}

Section of Tropical Plants, Center for Research and Development in Horticulture, Instituto Agronomico, P.O. Box 28, 13012-970, Campinas/SP, Brazil^{*}

Section of Plant Physiology, Center for Research and Development in Ecophysiology and Biophysics, Instituto Agronomico, P.O. Box 28, 13012-970, Campinas/SP, Brazil^{**}

Abstract

The Amazonian peach palm (*Bactris gasipaes* Kunth) has been grown for heart-of-palm production under subtropical conditions. As we did not see any substantial study on its photosynthesis under Amazonian or subtropical conditions, we carried out an investigation on the diurnal and seasonal variations in photosynthesis of peach palms until the first heart-of-palm harvest, considering their relationship with key environmental factors. Spineless peach palms were grown in 80-L plastic pots, under irrigation. Gas exchange and chlorophyll fluorescence emission measurements were taken in late winter, mid spring, mid summer and early autumn, from 7:00 to 18:00 h, with an additional chlorophyll fluorescence measurement at 6:00 h. The highest net CO₂ assimilation (P_N), observed in mid summer, reached about 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which was about 20% higher than the maximum values found in autumn and spring, and 60% higher than that in winter. The same pattern of diurnal course for P_N was observed in all seasons, showing higher values from 8:00 to 9:00 h and declining gradually from 11:00 h toward late afternoon. The diurnal course of stomatal conductance (g_s) followed the same pattern of P_N , with the highest value of 0.6 $\text{mol m}^{-2} \text{s}^{-1}$ being observed in February and the lowest one (0.23 $\text{mol m}^{-2} \text{s}^{-1}$) in September. The maximal quantum yield of photosystem II (F_v/F_m) was above 0.75 in the early morning in all the months. The reversible decrease was observed around midday in September and October, suggesting the occurrence of dynamic photoinhibition. A significant negative correlation between the leaf-air vapour pressure difference ($\text{VPD}_{\text{leaf-air}}$) and P_N and a positive correlation between P_N and g_s were observed. The photosynthesis of peach palm was likely modulated mainly by the stomatal control that was quite sensible to atmospheric environmental conditions. Under subtropical conditions, air temperature (T_{air}) and $\text{VPD}_{\text{leaf-air}}$ impose more significant effects over P_N of peach palm than an excessive photosynthetic photon flux density (PPFD). The occurrence of dynamic photoinhibition indicates that under irrigation, peach palms appeared to be acclimated to the full-sunlight conditions under which they have been grown.

Additional key words: *Bactris gasipaes*; chlorophyll fluorescence; gas exchange; stomatal conductance; vapour pressure deficit.

Introduction

Growing the Amazonian peach palm (*Bactris gasipaes* Kunth) for heart-of-palm production has been an important alternative to decrease the predatory exploitation of the native palm *Euterpe edulis* Mart. from the Atlantic forest, which in recent decades has been included

among the species threatened by extinction. The area used for cultivating peach palm in São Paulo State, Brazil, corresponds to approximately 3,900 ha (Anefalos *et al.* 2007), and is expanding.

In their natural habitats peach palms are under tropical

Received 15 March 2010, accepted 2 July 2010.

[†]Corresponding author; fax: +55-1932877530, e-mail: tucci@iac.sp.gov.br

Abbreviations: AGR – absolute growth rate; C_i – intercellular CO₂ concentration; ETR – apparent electron transport rate; F – instantaneous fluorescence of light-adapted state; F_0 – minimal fluorescence yield of dark-adapted state; F_m – maximal fluorescence of dark-adapted state; F_m' – maximal fluorescence of light-adapted state; F_v – variable fluorescence of dark-adapted state; F_v/F_m – maximal PSII quantum yield; g_s – stomatal conductance; P_N – net CO₂ assimilation; PPFD – photosynthetic photon flux density; PSII – photosystem II; T_{air} – air temperature; T_{leaf} – leaf temperature; VPD_{air} – air vapour pressure deficit; $\text{VPD}_{\text{leaf-air}}$ – leaf-to-air vapour pressure difference; ΔF – variable fluorescence of light-adapted state; $\Delta F/F_m'$ – effective PSII quantum yield; Ψ_{leaf} – leaf water potential.

Acknowledgments: The authors gratefully acknowledge the Fundação de Amparo à Pesquisa do Estado de São Paulo (Fapesp, Brazil) for financial support (n° 00/02782-6). E.C. Machado and R.V. Ribeiro are also grateful to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil) for the fellowship granted.

climate conditions throughout the year, while in São Paulo State the species has been cultivated under subtropical conditions. At latitude above 21°S, the plants face large seasonal variation of environmental conditions, mainly in temperature and rainfall, with consequences to their photosynthesis. In addition, peach palms naturally occur in disturbed ecosystems principally along river beds and in primary forest gaps, while cultivated peach palms have grown under full sunlight (Mora-Urpí *et al.* 1997). Thus, it is necessary to understand the physiological responses of the peach palms grown under subtropical conditions in order to evaluate the effects of the new habitat on their growth and crop yield. Peach palm growth has been well studied both under Amazonian (Yuyama and Silva 2003) and subtropical conditions (Clement and Bovi 2000, Vega *et al.* 2004), over the last decades. Recently, Tucci *et al.* (2007) showed that although under subtropical conditions peach palms were growing all year round, lower growth rates were noticed in winter, and a positive correlation between the main stem height and the average maximum, medium, and minimum temperatures of the 60 days before each evaluation was observed.

In comparison with other palms of economic importance, such as coconut palm (Gomes *et al.* 2002a, 2002b, Gomes *et al.* 2007, Passos *et al.* 2009) and oil

palm (Corley 1983, Dufrêne and Saugier 1993, Lamade and Setiyo 1996, Suresh and Nagamani 2006), photosynthesis of the peach palm has been less studied, even under the natural Amazonian conditions. A low P_N of peach palm was reported in Willis *et al.* (1992), however neither experimental conditions, nor the ontogeny of the leaves was documented. Another study under glasshouse conditions (Oliveira *et al.* 2002) addressed the gas exchange in peach palm seedlings, however, the leaves were still biphids and it is known that the stomatal frequency on biphid leaves differs from that of the adult, pinnate leaves (Tucci *et al.* 2000).

Over the last two decades, the importance of carrying out experiments concerning the peach palm physiology has been emphasized (Clement *et al.* 1988), and Mora-Urpí *et al.* (1997) had indentified several important issues for future research on peach palms, including the relationship among environmental and physiological variables, growth, and yield.

This work was carried out to investigate the diurnal and seasonal variation in photosynthesis of peach palms grown under subtropical conditions until the first heart-of-palm harvest, considering their relationship with plant growth and with the variation of key environmental factors.

Materials and methods

Growth conditions: Spineless peach palms from Yurimaguas (Peru) population were grown at Campinas Experimental Center, of Instituto Agronomico (IAC), in Campinas, São Paulo State, Brazil, at 22°54'S; 47°05'W, 674 m a.s.l. The climate, according to the Köppen System, is humid subtropical (Cwa), characterized by hot, humid summers and cool winters. According to the Campinas, São Paulo State, monthly climate normals (Ortolani *et al.* 1995), a warm and rainy season is observed from October to March, with mean T_{air} ranging from 22 to 24°C and 1,057 mm precipitation; and a drier and cooler season occurs from April to September, with mean T_{air} ranging from 18 to 22°C, 325 mm precipitation.

The seedlings were grown under greenhouse conditions for one year according to recommendations of Bovi (1998). Thereafter, plants were transplanted to 80-L plastic pots (115 kg substrate), with holes in the bottom to allow water drainage. The substrate was a mixture 1:1:1 (v/v) of soil, sand, and cattle manure. This was sufficient to maintain nutrient levels within the range suitable to the species (van Raij and Cantarella 1996). Details of the substrate, fertilization, and plant nutritional status evaluations have been given previously (Tucci *et al.* 2007). Plants were grown spaced 2 × 1 m, disposed in four lines of ten plants each. Due to plant growth, it was necessary to build a wooden deck between the central lines to allow the evaluations towards the end of the experiment.

The height growth of peach palms was evaluated according to Tucci *et al.* (2007). Growth data were adjusted by Boltzmann's function and the absolute growth rate (AGR) was calculated by the first derivative of the growth function. At the time of the first gas-exchange measurements, peach palms were 15 months old. Throughout the experiment the plants had 5 to 7 leaves and 11–12 offshoots.

After transplanting, the plastic pots were irrigated daily, until drainage. The substrate water status was evaluated by Time Domain Reflectometry (TDR), by means of the soil moisture analyzer *Trase System 1* (SoilMoisture Equipment Corp., Goleta, CA, USA). The substrate was irrigated throughout the experiment according to Tucci (2004). Plant water status was monitored on eight plants by measuring the leaf water potential (Ψ_{leaf}) at 5:30 and 13:00 h, using a pressure chamber (*PMS 1002*, PMS Instrument Co., Albany, OR, USA). Measurements were performed on the terminal portion of a leaflet from the medium portion of sunlit leaves in which gas exchange was measured.

Gas-exchange and environmental measurements: Gas-exchange measurements were taken throughout a year (September, October, 2001, and February, April, 2002), aiming to evaluate such physiological traits in a range of environmental conditions. P_N , g_s , intercellular CO_2 concentration (C_i), leaf temperature (T_{leaf}) and PPFD

were evaluated under natural T_{air} and CO_2 concentration [$360 \pm 7 \mu\text{mol}(\text{CO}_2) \text{ mol}^{-1}$], with a portable infrared gas analyzer (*LCA-4*, *ADC BioScientific Ltd.*, Great Amwell, Herts, England), operated at $200 \mu\text{mol s}^{-1}$ flow rate. Measurements were always taken under natural PPFD, on the adaxial surface of a sunlit leaflet with the leaf chamber facing the sunlight (90°), on the medium part of the younger completely expanded leaf (leaf +1), according to Tomlinson (1990). Throughout the experiment, leaves of the same ontogeny were evaluated on 8 plants, every two hours from 7:00 to 18:00 h. Each measurement took about 2 min.

Environmental data were monitored with a meteorological station located 300 m from the experimental area. The air vapour pressure deficit (VPD_{air}) and the $\text{VPD}_{\text{leaf-air}}$ were evaluated from relative humidity by using vapour pressure equations (Buck 1981).

Chlorophyll *a* fluorescence emission was evaluated on the same leaflets and at the same time as gas-exchange measurements, with an additional measurement at 6:00 h. A portable modulated fluorometer was used (*PAM-2000*, *Heinz Walz GmbH*, Effeltrich, Bayern, Germany), following the saturation pulse method, under field conditions (Bilger *et al.* 1995). Maximal quantum yield (F_v/F_m , where $F_v = F_m - F_0$) of photosystem II (PSII) was calculated from the maximal (F_m) and the minimal (F_0)

fluorescence signals, measured at 6:00 h (after overnight dark-acclimation) and after 30 min of dark-acclimation during diurnal period. The minimal initial fluorescence (F_0) was determined in nonphotosynthetic conditions under a low-intensity measuring beam. The effective quantum yield of PSII ($\Delta F/F_m'$) was determined on leaflets continuously exposed to natural variation of PPFD, from the maximal (F_m') and instantaneous (F) fluorescence signals, where $\Delta F = F_m' - F$. Both F_m and F_m' were measured after a light saturation pulse [$\lambda < 710 \text{ nm}$, PPFD $\sim 10,000 \mu\text{mol m}^{-2} \text{ s}^{-1}$, 0.8 s]. The apparent electron transport rate (ETR) was calculated as $\text{ETR} = \text{PPFD} \times \Delta F/F_m' \times 0.5 \times 0.84$ (Krall and Edwards 1992). In addition, the ETR/P_N ratio was determined as an estimate of the number of electrons transported through PSII per CO_2 fixed (Krall and Edwards 1992).

Statistics: The experiment was arranged in a completely random design and data were subjected to the analysis of variance, considering the evaluation dates as the source of variation. When significance was detected, mean values were submitted to *Newman Keuls* multiple range test ($p \leq 0.01$). Correlation analysis was performed by Pearson's method (Steel and Torrie 1980) at 5% and 1%. Regression analysis and curve fitting as well as data integration were conducted with *Origin 6.0* (*OriginLab Corp.*, Northampton, MA, USA).

Results

Environmental conditions: Higher T_{air} up to 30°C were observed at 16:00 h in April (Fig. 1D). Actually, this month was atypical, reaching higher temperatures and lower rainfall than the historic series of climate data (Alfonsi *et al.* 2002). On the other hand, the lowest T_{air} was recorded in September (Fig. 1A), with early morning values below 15°C . In fact, predawn T_{air} was around 13°C at this evaluation. Sun-exposed-leaves temperature reached 35°C in September, October and February, and around 32°C in April (Fig. 1A-D). Higher VPD_{air} of 2.5 and 3 kPa were observed at mid afternoon in October and April, respectively. As for the $\text{VPD}_{\text{leaf-air}}$, the highest values were observed in September, October and February, varying from 4 and 4.5 kPa.

Plant growth and leaf water potential (Ψ_{leaf}): Upon measuring the gas-exchange parameters, the main stem of peach palms had a height of 110, 117, 177, and 200 cm in September, October, February, and April, respectively (Fig. 2). Growth was more intensive in warmer months, with a maximum AGR of around 0.48 cm d^{-1} in December/January. Ψ_{leaf} throughout the experiment was maintained within the range of -0.1 to -0.3 MPa at predawn, and of -0.8 to -1.1 MPa at midday (detailed data not shown).

Diurnal course and seasonal variation of leaf gas exchange: All seasons showed maximum PPFD (Fig. 3A) from 10:00 to 12:00 h. In February, the photoperiod was longer with PPFD remaining above $1,300 \mu\text{mol m}^{-2} \text{ s}^{-1}$ until 17:00 h. In April, due to the presence of clouds around 14:00 h, PPFD declined to about $400 \mu\text{mol m}^{-2} \text{ s}^{-1}$, a level below light saturation for the species, of 800 to $900 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Tucci 2004).

The same pattern of diurnal course of P_N was observed in all seasons, with values higher at 8:00 to 9:00 h and declined gradually from 11:00 h toward late afternoon (Fig. 3B). P_N was higher in February, differing significantly from the other months ($p \leq 0.001$). In fact, the maximum P_N values were about $15 \mu\text{mol m}^{-2} \text{ s}^{-1}$, which was 20% higher than the maximum values found in April and October. Considering the maximum P_N values in September, which was around $9 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at 9:00 h, a reduction of 60% was verified as compared to February evaluations.

The diurnal-integrated P_N differed among seasons and showed correspondence to those of maximum P_N values. The P_N values integrated over the entire diurnal period were higher in February, with plants showing CO_2 fixation of $360 \text{ mmol m}^{-2} \text{ d}^{-1}$. Intermediate values were observed in April and October, being around 71% of

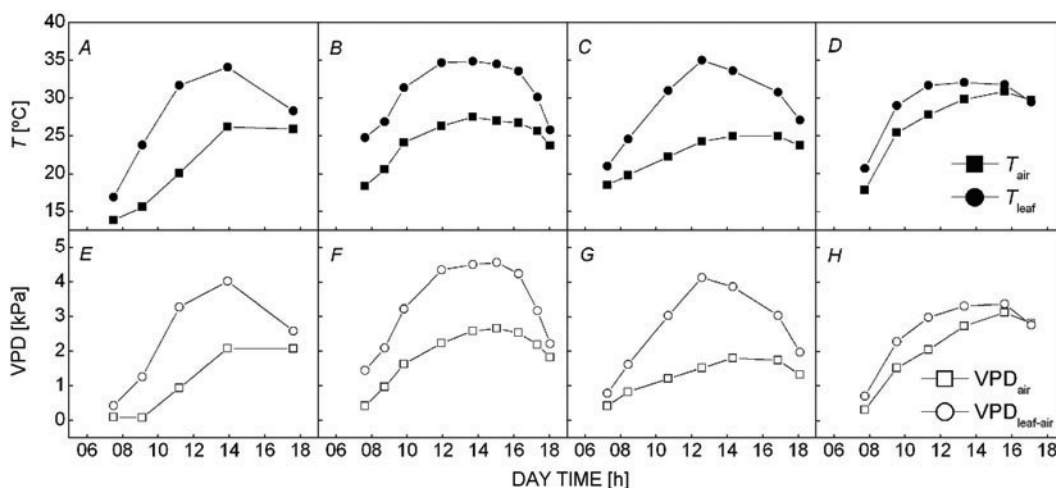


Fig. 1. Diurnal course of average air temperature (T_{air}), leaf temperature (T_{leaf}), air vapour pressure deficit (VPD_{air}) and leaf-air vapour pressure difference ($\text{VPD}_{\text{leaf-air}}$) on September, 13 (A,E) and October, 25 (B,F), 2001, and on February, 25 (C,G) and April, 25 (D,H), 2002. Campinas, SP, Brazil.

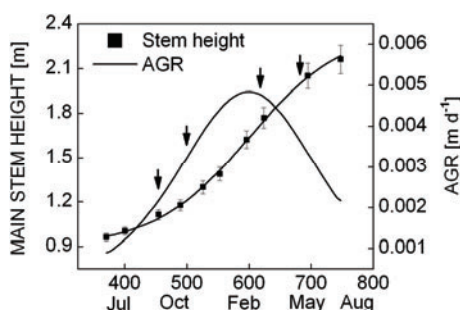


Fig. 2. Seasonal variation of growth and absolute growth rate (AGR) in height of the main stem of peach palms growing under subtropical conditions. Arrows indicate days of photosynthesis evaluation. Each symbol represents the mean value of 16 plants ($\pm$ SE).

those found in February. The lowest diurnal-integrated P_N values were observed in September, being around $164 \text{ mmol m}^{-2} \text{ d}^{-1}$ and representing only 46% of those values noticed in February.

In general, the diurnal course of g_s followed the same pattern of P_N (Fig. 3C). In all seasons maximum g_s values occurred in the early morning and significant differences were observed only between September and February ($p \leq 0.05$). The highest g_s reached $0.60 \text{ mol m}^{-2} \text{ s}^{-1}$ in February, followed by $0.45 \text{ mol m}^{-2} \text{ s}^{-1}$ in April, $0.33 \text{ mol m}^{-2} \text{ s}^{-1}$ in October and $0.23 \text{ mol m}^{-2} \text{ s}^{-1}$ in September. A similar diurnal pattern of C_i (Fig. 3D) was observed among evaluation dates, with two exceptions. In September, a reduction of C_i was observed around midday, when the lowest C_i value of $101 \mu\text{mol mol}^{-1}$ was observed. In April, there was an increase in C_i to about $260 \mu\text{mol mol}^{-1}$ at 15:00 h. This increase in C_i was caused by low P_N as PPFD had a sharp decrease due to the presence of clouds (Fig. 3A).

Linear correlations among photosynthetic variables

and key environment factors (Table 1) indicate high negative correlations ($p \leq 0.01$) between P_N and $\text{VPD}_{\text{leaf-air}}$ ($r = -0.61$). Among photosynthetic variables, positive correlations ($p \leq 0.01$) between P_N and g_s ($r = 0.73$), P_N and C_i ($r = 0.64$), g_s and C_i ($r = 0.73$) should be mentioned, due to their relevance. Whereas the relationship between P_N and g_s average values could be better explained by an exponential function (Fig. 4A), the best P_N response function to $\text{VPD}_{\text{leaf-air}}$ was linear (Fig. 4B).

Diurnal course and seasonal variation of photochemical activity: The highest F_v/F_m values (Fig. 5A) were found in early mornings were higher than 0.75 in all evaluations. During the daytime, F_v/F_m decreased to a significant ($p \leq 0.001$) midday minimum of 0.54 in October, being the lowest value found. In all seasons, F_v/F_m resumed the early morning values in late afternoon. Regarding $\Delta F/F_m'$ (Fig. 5B), in September and April, there was an intense decrease of $\Delta F/F_m'$ from early morning, reaching minimum values of 0.2 in September and 0.3 in April. In October and February, $\Delta F/F_m'$ decreased from 8:00 h, remaining relatively constant until late afternoon, and reaching the lowest values below 0.2 in October.

The diurnal course of ETR (Fig. 5C) revealed minimum values in the early morning, increasing henceforth with the PPFD and then decreasing in late afternoon. Maximum ETR values, in a range from 150 to $230 \mu\text{mol m}^{-2} \text{ s}^{-1}$, were observed in all evaluation dates, except in October, when ETR values were lower and maintained a plateau around $120 \mu\text{mol m}^{-2} \text{ s}^{-1}$ from 10:00 to 15:00 h. Average values of ETR/P_N , considering evaluations from 9:00 to 15:00 h varied between $41 \mu\text{mol mol}^{-1}$ (in September) and $17 \mu\text{mol mol}^{-1}$ (in October, February, and April).

Discussion

Although grown under irrigation, the peach palms showed differences in P_N among evaluation dates. Therefore, environmental influences other than soil water availability regulated both diurnal and seasonal variations in gas exchange. The highest P_N values were in accordance to Larcher (2000), who suggests for woody C_3 plants a P_N between 10 and 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$. In addition, Jayasekara and Jayasekara (1995) mentioned that palms have low to moderate photosynthetic capacity, with maximum P_N under 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$. One important aspect is that sunlight is not a limiting factor in the tropical and subtropical regions where most of palm plants inhabit (Tomlinson 2006). Regardless evaluation dates PPFD remained above the peach palm light saturation, around 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Tucci 2004), during most part of the day.

The diurnal course of gas-exchange (Fig. 3) followed the pattern mentioned by Kozłowski and Pallardi (1997) for tropical trees, that is, P_N was low in the early morning and coupled with low PPFD, increased sharply and reached a maximum around midday. Afterwards, the decrease in P_N until late afternoon may be related to the higher afternoon T_{leaf} and $\text{VPD}_{\text{leaf-air}}$ (Fig. 1). Similar patterns were shown by other palms such as coconut (Prado *et al.* 2001, Passos *et al.* 2009), as well as by other tree species like citrus (Machado *et al.* 2002) and eucaliptus (Prior *et al.* 1997, Eamus and Cole 1997). In the afternoon, the decrease in g_s was related to the increase in $\text{VPD}_{\text{leaf-air}}$ (Fig. 1), a response also observed in citrus (Machado *et al.* 2002, Ribeiro *et al.* 2009a) to prevent excessive shoot dehydration. Even under low g_s in the afternoon, the higher $\text{VPD}_{\text{leaf-air}}$ caused increased transpiration (data not shown), and then decreased Ψ_{leaf} from -0.2 MPa at 5:30 to -0.9 MPa at 13:00 h. Therefore, the reduction of g_s in the afternoon might be related to a drop in Ψ_{leaf} as well as to the high $\text{VPD}_{\text{leaf-air}}$.

Higher maximum P_N and g_s as well as higher integrated P_N values occurred in February, when VPD_{air} was below 2 kPa and moderate T_{air} (reaching 25°C) was noticed. This temperature is close to the optimum for P_N (Tucci and Machado, unpublished result). In this study, P_N reached 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in February. In other well-studied palms of economic importance, such as dwarf coconut plants, P_N values reached up to 14–17 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Gomes *et al.* 2002a, 2002b, 2007, Passos *et al.* 2009).

The stomatal sensitivity to environmental fluctuations is an important element on the modulation of peach palm gas exchange. This sensitivity to water deficit was evaluated by Oliveira *et al.* (2002), who observed a 54% decrease in stomatal conductance in biphid-leaf peach palm seedlings after five days without watering. However, little is known about the stomatal regulation of photosynthesis in peach palm plants under Brazilian subtropical conditions. In February, the maximum g_s values were observed, being around 2-fold higher than g_s

values reported for coconut plants (Passos *et al.* 2005, 2009).

Regarding the lower P_N and g_s found in September, it is interesting to examine the minimum T_{air} , a common environmental characteristic in the winter season. Minimum temperatures usually occur at night and T_{air} of 13°C was observed around 5:00 h in September. An optimum temperature of 23°C for P_N was observed for biphid-leaf peach palms seedlings under controlled conditions (Tucci and Machado, unpublished results). We may suppose that low night temperatures in winter caused low P_N and g_s in September, which were observed in mango plants (Allen

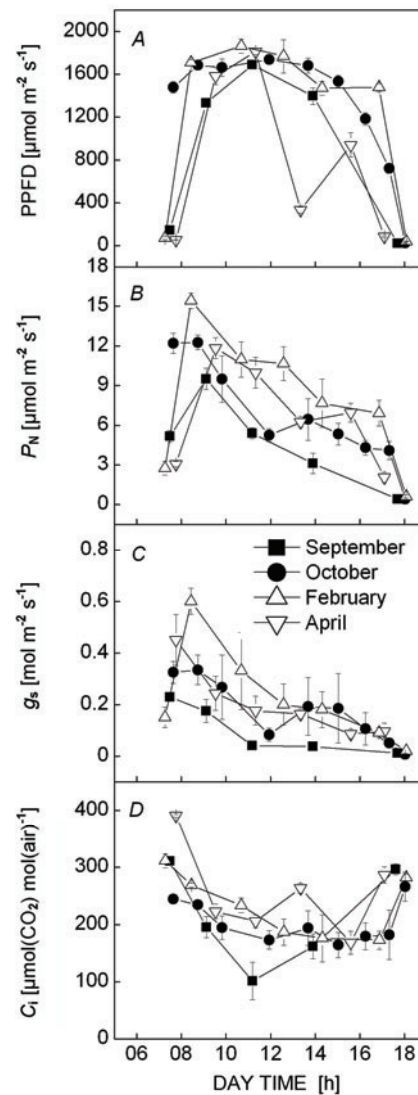


Fig. 3. Diurnal courses of photosynthetic photon flux density (PPFD, A), leaf CO_2 assimilation (P_N , B), stomatal conductance (g_s , C), and intercellular CO_2 concentration (C_i , D) on a typical day in the end of winter (September), in mid spring (October), mid summer (February) and early autumn (April). Each symbol represents the mean value of eight replications ($\pm$ SE).

Table 1. Linear correlations among photosynthetic variables and environmental factors. Only values of photosynthetic photon flux density (PPFD) above peach palm light saturation were considered for calculations. *, ** significant at 5 and 1%, respectively; ns - not significant. $n = 114$.

	P_N	g_s	C_i	F_v/F_m	$\Delta F/F_m'$
P_N [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	–				
g_s [$\text{mmol m}^{-2} \text{s}^{-1}$]	0.73**	–			
C_i [$\mu\text{mol (CO}_2\text{) mol}^{-1}$]	0.64**	0.73**	–		
F_v/F_m	0.37**	ns	0.20*	–	
$\Delta F/F_m'$	ns	ns	ns	0.27**	–
T_{air} [$^{\circ}\text{C}$]	–0.43**	–0.29**	–0.26**	–0.24**	ns
VPD_{air} [kPa]	–0.52**	–0.34**	–0.32**	–0.38**	ns
T_{leaf} [$^{\circ}\text{C}$]	–0.58**	–0.38**	–0.43**	–0.45**	–0.21*
$\text{VPD}_{\text{leaf-air}}$ [kPa]	–0.61**	–0.36**	–0.43**	–0.55**	–0.22*

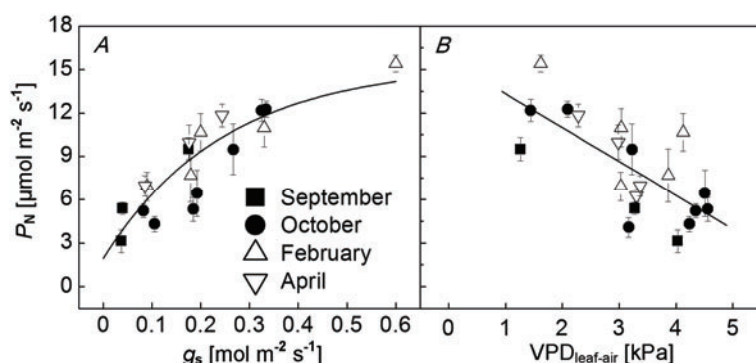


Fig. 4. Relationship between A: net CO_2 assimilation (P_N) and stomatal conductance (g_s), and B: leaf-air vapour pressure difference ($\text{VPD}_{\text{leaf-air}}$), in peach palms. Evaluations were taken in September and October 2001, and February and April 2002. Only data registered above photosynthetic photon flux density (PPFD) of $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ were considered. Each symbol represents the mean value of eight replications ($\pm$ SE).

et al. 2000) and citrus plants (Ribeiro *et al.* 2009a, 2009b), and were considered by Allen *et al.* (2000) as a result of a stomatal limitation of P_N due to an altered guard cell sensitivity to CO_2 . No reference about the low-temperature effects on palms P_N was found. In addition, we should also consider the effects of phenological status on P_N . Peach palms presented seasonal growth (Fig. 2), showing higher AGR from October to April. We may argue that at this period, plants had high sink demand for photoassimilates. In fact, the possible response of P_N to source:sink relationship was pointed out by Foyer and Galtier (1996).

Peach palms showed a negative correlation between VPD_{air} and P_N , but a correlation of higher magnitude was observed between P_N and $\text{VPD}_{\text{leaf-air}}$ (Table 1), indicating a stomatal regulation in order to cope with high atmospheric demand (Fig. 4A,B). In oil palms, Dufrêne and Saugier (1993) observed that maximum P_N was limited by VPD_{air} above 1.8 kPa, while Lamade and Setiyo (1996) related significant differences among clones in the relationship between P_N and VPD_{air} . Actually, this characteristic is found in palms (Dufrêne *et al.* 1990) and stomatal closure is noticed under VPD_{air} above 1 kPa, even in the absence of soil water deficit. Repellin *et al.* (1997) observed for the first time in palms that stomatal responses in well watered plants were also triggered by VPD_{air} variations, concluding that young coconuts seemed to be acclimated to avoid the effects of atmospheric deficits. In general, stomatal closure in many

species has been considered as a response due exclusively to soil water deficit. It is worth mentioning that, out of its Amazonian habitat, peach palms cultivation has been spread out over a wide range of environmental conditions, including those areas with seasonal water deficit. Therefore further studies should be done to uncover other abiotic effects of the new habitats on the photosynthesis of the species.

As C_i is a variable modulated by stomatal and mesophyll conductance and by the CO_2 demand by photosynthesis, the low C_i in winter suggests that P_N was limited by the atmospheric CO_2 diffusion to the substomatal cavity due to stomatal closure, which was corroborated by the high magnitude correlations observed between g_s and C_i , as well as between P_N and C_i and P_N and g_s (Table 1). In fact, a common curve fit was sufficient to show the last relationship, regardless evaluation dates and highlight the important role of the stomatal control over P_N (Fig. 4A). This could be corroborated by the P_N/g_s (intrinsic water-use efficiency) and P_N/C_i (apparent carboxylation efficiency) ratios (data not shown). While the mid morning P_N/g_s was higher in September, late winter, compared to the other months, P_N/C_i remained at a similar level throughout the year, in accordance to the stomatal limitation discussed by Flexas *et al.* (2001). Positive correlations between P_N and g_s were found also in oil palms (Smith 1989, 1993, Suresh and Nagamani 2006), and in coconut (Repellin *et al.* 1997).

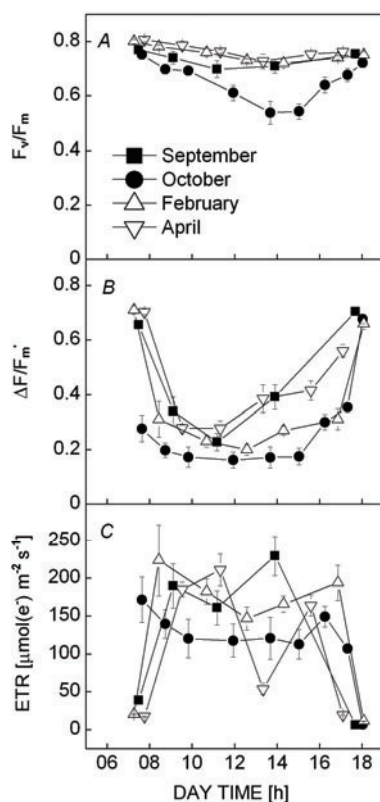


Fig. 5. Diurnal changes in the maximal (F_v/F_m , A) and effective ($\Delta F/F_m'$, B) PSII quantum yield and the apparent electron transport rate (ETR, C) on a typical day in the end of winter (September), in mid spring (October), mid summer (February) and early autumn (April). Each symbol represents the mean value of eight replications ($\pm$ SE).

Peach palms showed predawn F_v/F_m values around 0.8 (Fig. 5), which suggest well acclimated species (Björkman and Demmig 1987, Johnson *et al.* 1993). On the other hand, decreases in F_v/F_m below 0.72, as observed in September and October (Fig. 5), indicate the occurrence of photoinhibition (Critchley 1998). This photoinhibition occurred with plants showing partial stomatal closure and decrease in P_N (Fig. 3B,C). In

October, particularly, a more intensive photoinhibition was observed from 10:00 to 15:00 h, under saturated PPFD, coupled with lower $\Delta F/F_m'$ and ETR, probably caused by the longer exposition of leaves to high $VPD_{\text{leaf-air}}$, above 4 kPa, and T_{leaf} around 35°C. As F_v/F_m resumed the early morning values at late afternoon, we may argue in favour of a dynamic protective photoinhibition (Osmond 1994), which is the PSII response to avoid damage to the functional integrity of photosynthetic machinery under excessive PPFD. This assumption is corroborated by the fact that ETR values remained high during most of the daytime (Fig. 5C). Diurnal and seasonal variations of F_v/F_m as well as dynamic photoinhibition were also observed in eucalyptus (Prior *et al.* 1997), citrus (Medina *et al.* 2002), and many Brazilian 'cerrado' species (Franco and Lüttge 2002).

In September, we noticed a decrease in P_N and g_s probably due to low night temperatures. However this constraining condition did not affect the photochemical processes. In fact, there were nonsignificant changes either in $\Delta F/F_m'$ or in ETR throughout the diurnal period (Fig. 5). As a consequence, a higher ETR/ P_N ratio was observed in September, indicating an increased electron partitioning to alternative process other than photosynthesis. According to Maxwell and Johnson (2000), the main alternative electron sinks are the photorespiration and the reduction of O_2 in PSI, known as Mehler reaction.

In conclusion, the seasonal variation in environmental conditions did not alter the diurnal pattern of photosynthesis in peach palms. Nevertheless, higher maximum P_N and g_s occurred in February under VPD_{air} below 2 kPa and a temperature approaching 25°C, whereas in September, under low night temperatures around 13°C both P_N and g_s showed a significant decline. Actually, the P_N of peach palms was strongly modulated by stomata, which are quite sensitive to atmospheric conditions. Under subtropical conditions, T_{air} and $VPD_{\text{leaf-air}}$ impose more significant effects over P_N than an excessive PPFD. In fact, the occurrence of dynamic PSII photoinhibition, a photoprotective mechanism, indicates that well hydrated peach palms are acclimated to the full sunlight conditions.

References

- Alfonsi, R.R., Camargo, M.B.P., Bardin, L.: [Water balance from January to December, 2002.] – O. Agron. **54**: 46-47, 2002. [In Port.]
- Allen, D.J., Ratner, K., Giller, Y.E., Gussakovsky, E.E., Shahak, Y., Ort, D.R.: An overnight chill induces a delayed inhibition of photosynthesis at midday in mango (*Mangifera indica* L.). – J. Exp. Bot. **51**: 1893-1902, 2000.
- Anefalos, L.C., Modolo, V.A., Tucci, M.L.S.: [Expansion of the peach palm cultivation in 'Vale do Ribeira', São Paulo State, Brazil, 2002-2006.] – Inf. Econ. **37**: 37-43, 2007. [In Port.]
- Bilger, W., Schreiber, U., Bock, M.: Determination of the quantum efficiency of photosystem II and of non-photochemical quenching of chlorophyll fluorescence in the field. – Oecologia **102**: 425-432, 1995.
- Björkman, O., Demmig, B.: Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. – Planta **170**: 489-504, 1987.
- Bovi, M.L.A.: [Peach palm heart-of-palm: basic information for cultivation.] – Technical Report. Inst. Agron., Campinas 1998. [In Port.]
- Buck, A.L.: New equations for computing vapour-pressure and enhancement factor – J. Appl. Meteorol. **20**: 1527-1532, 1981.
- Clement, C.R., Bovi, M.L.A.: [Standardization of growth and yield measurements in pejiabaye heart-of-palm experiments.] – Acta Amazonica **30**: 349-362, 2000. [In Port.]
- Clement, C.R., Chavez, W.B., Gomes, J.B.M.: [Considerations on peach palm (*Bactris gasipaes* H.B.K.) as a heart-of-palm

- producer.] – Encontro Nac. Pesquisadores em Palmito **1**: 225-247, 1988. [In Port.]
- Corley, R.H.V.: Photosynthesis and age of oil palm leaves. – *Photosynthetica* **17**: 97-100, 1983.
- Critchley, C.: Photoinhibition. – In: RagHAVendra, A.S. (ed.): *Photosynthesis. A Comprehensive Treatise*. Pp. 264-272. Cambridge Univ. Press, Cambridge 1998.
- Dufrêne, E., Ochs, R., Saugier, B.: Oil palm photosynthesis and productivity linked to climatic factors. – *Oléagineux* **45**: 345-355, 1990.
- Dufrêne, E., Saugier, B.: Gas exchange of oil palm in relation to light, vapour pressure deficit, temperature and leaf age. – *Func. Ecol.* **7**: 97-104, 1993.
- Eamus, D., Cole, S.: Diurnal and seasonal comparisons of assimilation, phyllode conductance and water potential, of three *Acacia* and one *Eucalyptus* species in the wet-dry tropics of Australia. – *Aust. J. Bot.* **45**: 275-290, 1997.
- Flexas, J., Gulías, J., Jonasson, S., Medrano, H., Mus, M.: Seasonal patterns and control of gas exchange in local populations of the Mediterranean evergreen shrub *Pistacia lentiscus* L. – *Acta Oecol.* **22**: 33-43, 2001.
- Foyer, C.H., Galtier, N.: Source-sink interaction and communication in leaves. – In: Zamski, E., Schaffer, A.A. (ed.): *Photoassimilate Distribution in Plants and Crops: Source-Sink Relationships*. Pp. 311-340. Marcel Dekker, New York – Basel – Hong Kong 1996.
- Franco, A.C., Lüttge, U.: Midday depression in savanna trees: coordinated adjustments in photochemical efficiency, photorespiration, CO₂ assimilation and water use efficiency. – *Oecologia* **131**: 356-365, 2002.
- Gomes, F.P., Mielke, M.S., de Almeida, A.A.F.: Leaf gas exchange of green dwarf coconut (*Cocos nucifera* L. var. *nana*) in two contrasting environments of the Brazilian north-east region. – *J. Hort. Sci. Biotech.* **77**: 766-772, 2002a.
- Gomes, F.P., Mielke, M.S., de Almeida, A.A.F., Muniz, W.S.: Leaf gas exchange in two dwarf coconut genotypes in the southeast of Bahia State, Brazil. – *Coconut Res. Develop.* **18**: 37-55, 2002b.
- Gomes, F.P., Prado, C.H.B.A.: Ecophysiology of coconut palm under water stress. – *Braz. J. Plant Physiol.* **19**: 377-391, 2007.
- Jayasekara, C., Jayasekara, K.S.: Photosynthetic characteristics of tropical species with special reference to palms. – *Ener. Conver. Manag.* **36**: 919-922, 1995.
- Johnson, G.N., Young, A.J., Scholes, J.D., Horton, P.: The dissipation of excess excitation energy in British plant species. – *Plant Cell Environ.* **16**: 673-679, 1993.
- Kozlowski, T.T., Pallardy, S.G.: *Photosynthesis*. – In: Kozlowski, T.T., Pallardy, S.G.: *Physiology of Woody Plants*. 2nd Ed. Pp. 87-132. Academic Press, San Diego – London – Boston – New York – Sydney – Tokyo – Toronto 1997.
- Krall, J.P., Edwards, G.E.: Relationship between photosystem II activity and CO₂ fixation in leaves. – *Physiol. Plant.* **86**: 180-187, 1992.
- Lamade, E., Setiyo, E.: Variation in maximum photosynthesis of oil palm in Indonesia: comparison of three morphologically contrasting clones. – *Plant. Rech. Dév.* **3**: 429-438, 1996.
- Larcher, W. [The plant under stress.] – In: Larcher, W. (ed.): *Vegetal Ecophysiology*. Pp. 341-378. Rima Artes e Textos, São Carlos 2000. [In Port.]
- Machado, E.C., Medina, C.L., Gomes, M.M.A., Habermann, G.: [Seasonal variation of photosynthetic rates, stomatal conductance and leaf water potential in 'Valência' orange trees.] – *Sci. Agric.* **59**: 53-58, 2002. [In Port.]
- Maxwell, K., Johnson, G.N.: Chlorophyll fluorescence - a practical guide. – *J. Exp. Bot.* **51**: 659-668, 2000.
- Medina, C.L., Souza, R.P., Machado, E.C., Ribeiro, R.V., Silva, J.A.B.: Photosynthetic response of citrus grown under reflective aluminized polypropylene shading nets. – *Sci. Hort.* **96**: 115-125, 2002.
- Mora-Urpí, J., Weber, J.C., Clement, C.R.: Peach Palm (*Bactris gasipaes* Kunth): Promoting the Conservation and Use of Underutilized Crops. – *Inst. Plant Genetics Crop Plant Res., Rome* 1997.
- Oliveira, M.A.J., Bovi, M.L.A., Machado, E.C., Gomes, M.M.A., Habermann, G., Rodrigues, J.D.: [Photosynthesis, stomatal conductance and transpiration in peach palm under water deficit.] – *Sci. Agr.* **59**: 59-63, 2002. [In Port.]
- Ortolani, A.A., Camargo, M.B.P., Pedro Junior, M.J.: [Climate Normals from Instituto Agrônomo Meteorological Stations]. – Instituto Agrônomo, Bol. Téc., Campinas 1995. [In Port.]
- Osmond, C.B.: What is photoinhibition? Some insights from comparisons of shade and sun plants. – In: Baker N.R., Bowyer, J.R. (ed.): *Photoinhibition of Photosynthesis from Molecular Mechanisms to the Field*. Pp. 1-24. BIOS Sci. Publ., Oxford 1994.
- Passos, C.D., Passos, E.E.M., Prado, C.H.B.A.: [Seasonal performance of water potential and gas exchange in four variety of dwarf coconut.] – *Rev. Bras. Frutic.* **27**: 248-254, 2005. [In Port.]
- Passos, E.E.M., Prado, C.H.B.A., Aragão, W.M.: The influence of vapour pressure deficit on leaf water relations of *Cocos nucifera* in northeast Brazil. – *Expl. Agri.* **45**: 93-106, 2009.
- Prado, C.H.B.A., Passos, E.E.M., Moraes, J.A.P.V.: Photosynthesis and water relations of six tall genotypes of *Cocos nucifera* in wet and dry seasons. – *South Afr. J. Bot.* **67**: 169-176, 2001.
- Prior, L.D., Eamus, K., Duff, G.A.: Seasonal and diurnal pattern of carbon assimilation, stomatal conductance and leaf water potential in *Eucalyptus tetrodonta* saplings in a wet-dry savanna in Northern Australia. – *Aust. J. Bot.* **45**: 241-258, 1997.
- Repellin, A., Laffray, D., Daniel, C., Braconnier, S., Zuily-Fodil, Y.: Water relations and gas exchange in young coconut palms (*Cocos nucifera* L.) as influenced by water deficit. – *Can. J. Bot.* **75**: 18-27, 1997.
- Ribeiro, R.V., Machado, E.C., Santos, M.G., Oliveira, R.F.: Photosynthesis and water relations of well-watered orange plants as affected by winter and summer conditions. – *Photosynthetica* **47**: 215-222, 2009a.
- Ribeiro, R.V., Machado, E.C., Santos, M.G., Oliveira, R.F.: Seasonal and diurnal changes in photosynthetic limitation of young sweet orange trees. – *Environ. Exp. Bot.* **66**: 203-211, 2009b.
- Smith, B.G.: The effects of soil water and atmospheric vapour pressure deficit on stomatal behaviour and photosynthesis in the oil palm. – *J. Exp. Bot.* **40**: 647-651, 1989.
- Smith, B.G.: Correlations between vegetative and yield characteristics and photosynthetic rate and stomatal conductance in the oil palm *Elaeis guineensis* Jacq.). – *Elaeis* **5**: 12-26, 1993.
- Steel, R.G., Torrie, J.H.: *Principles and Procedures of Statistics*. – MacGraw-Hill, New York 1980.
- Suresh, K., Nagamani, C.: Variations in photosynthesis rate and associated parameters with age of oil palms under irrigation. – *Photosynthetica* **44**: 309-311, 2006.

- Tomlinson, P.B.: The Structural Biology of Palms. – Clarendon Press, Oxford 1990.
- Tomlinson, P.B.: The uniqueness of palms. – Bot. J. Linn. Soc. **151**: 5-14, 2006.
- Tucci, M.L.S.: [Seasonal variation of growth and of gas exchange in peach palm (*Bactris gasipaes* Kunth).] – PhD. Thesis. Univ. Campinas (UNICAMP), Campinas 2004. [In Port.]
- Tucci, M.L.S., Bovi, M.L.A., Machado, S., Spiering, S.H.: Stomatal frequency and size in leaves of peijibaye (*Bactris gasipaes* Kunth). – Acta Hort. **516**: 145-154, 2000.
- Tucci, M.L.S., Bovi, E.C., Spiering, S.H., Machado, E.C.: Seasonal growth variation of peach palms grown in containers under subtropical conditions. – Sci. Agr. **64**: 138-146, 2007.
- van Raij, B., Cantarella, H., Quaggio, J.A., Furlani, A.M.C.: [Fertilizer and Lime Recommendations for the State of São Paulo, Brazil.] – Technical Report. Inst. Agron., Campinas 1996. [In Port.]
- Vega, F.V.A., Bovi, M.L.A., Berton, R.S., Spiering, S.H., Godoy, G., Jr.: [Allometric relations for aerial biomass estimative in peach palm.] – Hort. Bras. **22**: 104-108, 2004. [In Port.]
- Willis, L.E., Marler, T.E., Hubbuch, C.: Leaf gas exchange of 20 palm species under field conditions. – J. Trop. Forest Sci. **10**: 346-356, 1998.
- Yuyama, K., Silva, F.M.S.: Initial growth of peach palm (*Bactris gasipaes*) in monoculture and combined with short cycle crops. – Hort. Bras. **21**: 15-19, 2003. [In Port.]