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Photosynthesis and water relations of peach palms (*Bactris gasipaes* Kunth) under soil water deficit

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Abstract The Amazonian peach palm is presently the main species of heart-of- palm producer in many Brazilian regions. Here we evaluated the effects of soil water deficit and rewatering on leaf water potential (ψ_{leaf}), gas exchange and chlorophyll fluorescence emission in peach palms. Plants were grown in 80 L-plastic pots under greenhouse conditions. Water deficit was imposed by water withdrawing for 13 days, when irrigation was re-established for 8 days more. ψ_{leaf} was measured at 5:30 a.m. and 1:30 p.m. Gas exchange measurements were performed at 8:00 a.m. and at 2:00 p.m., after chlorophyll *a* fluorescence evaluations. The minimum ψ_{leaf} value observed at predawn was − 1.6 MPa, when net CO_2 assimilation (P_N) was zero on the 13th day of water deficit, thus showing mesophytes characteristics. The sharp P_N decrease of 94%, 6 days after the beginning of treatments, demonstrated the drastic effect of the soil water deficit. After rewatering, a rapid recuperation of ψ_{leaf} was observed, whereas P_N, transpiration rate (E) and stomatal conductance (g_s) recovered more slowly, reaching values exhibited by the control plants only 7 days after rewatering. The lower maximal quantum yield of photosystem II (PSII) (F_V/F_M) values in the midday for plants under water deficit indicated dynamic photoinhibition of PS II to excessive PPFD. These results suggest a drought tolerance of peach palm plants, showing stomatal control of water losses and P_N limitation, whereas the photosynthetic apparatus was maintained by photoprotection processes.

1 Introduction

The peach palm native to Amazonian is presently the main species of heart-of- palm producer in many Brazilian regions. According to data from the Brazilian Institute of Statistics and Geography (IBGE) (2016), São Paulo State (SP) stands out as one of the main Brazilian heart-of-palm producers. About 80% of the production is concentrated in the region named Vale do Ribeira-SP (LUPA 2008). Due to the tradition in heart-of-palm production and mainly to the climatic conditions (rainfall of 1600 mm year^{-1}, with regular rainfall distribution throughout the year) this region presents ideal characteristics for rain-

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fed cultivation. However, an increase in peach palm plantations in non-traditional production regions, generally under water restriction (rainfall index below 1400 mm year^{-1}, with rainfall concentrated in the spring/summer and dry winter seasons) requires the use of irrigation.

The soil water availability plays a crucial role in the production of peach palm because 90% of the heart-of-palm is composed of water (Ferreira and Graner 1982), and most of its roots occupy the upper soil layer (Bovi et al. 1999). According to Clement and Bovi (2000), due to the precocity and abundant tillering of the species, which allow constant cuts of heart-of-palms, the clump is always in vegetative stage. Abiotic factors, such as light, temperature, water and fertilizers should be optimized to maximize yield and to increase the useful economic life of the crop. With the expansion of the crop area and its migration to drought-prone areas, there is a high probability that, at least during certain periods of the year, water deficit situations will occur, causing production losses. In this context, it seems necessary to know the effects of soil water deficit on the physiology of this species and, consequently, to provide technical knowledge for peach palm irrigation.

There is an intricate relationship between rainfall and air temperature and, on the other hand, between photosynthesis (P_N), stomatal conductance (g_s), leaf water potential (ψ_{leaf}), chlorophyll fluorescence emission, which have influence on crop yields (Ball et al. 1994). Differently to what occurs in native habitats, in the state of São Paulo the peach palm experiences a climate seasonality with consequences for P_N and vegetative growth. Regarding the later, Tucci et al. (2007) observed lower growth rates in the winter and higher ones in the summer; additionally, P_N was lower in winter months (Tucci et al. 2010), what was attributed to low night temperatures throughout the winter.

In comparison to other palms of economic importance, such as coconut palm (Gomes and Prado 2007) and oil palm (Dufrêne and Saugier 1993; Suresh et al. 2012), little is known about gas exchange in peach palms (Tucci et al. 2010) and even less under soil water deficit conditions. A study addressing gas exchange in peach palm seedlings under water deficit conditions was performed on still biphid-leaves (Oliveira et al. 2002), but it is known that the stomatal frequency of biphid-leaves differs from those of adult,

pinnate leaves of this species (Tucci et al. 2000). In addition, there are few studies using other heart-of-palm producers under soil water deficit, such as açaí palm (*Euterpe oleracea* Mart.; Calbo and Moraes 2000) and buriti palm (*Mauritia vinifera* Mart.; Calbo and Moraes 1997). More recently, others palms native to Brazil, such as *Syagrus coronata* (Mart.) Becc. (Arecaceae), showed robust stomata control and no photochemical damage under soil water deficit, and after rehydration it showed a rapid photosynthetic capacity recovery (Medeiros et al. 2015). Under field conditions, this same species exhibited lower sensitivity to drought, showing higher P_N and water use efficiency during the dry season of the Northeastern semi-arid region of Brazil (Oliveira et al. 2016).

We investigated the photosynthetic performance of the peach palm, native to the Amazonian region, when cultivated under water deficit conditions at subtropical environment. The effects of soil water deficit on leaf water potential, gas exchange, chlorophyll fluorescence, as well as the performance of the species throughout the rewatering period were evaluated.

2 Materials and methods

2.1 Plant material and cultivation conditions

The experiment was carried out at Instituto Agronômico (IAC), Campinas, SP, Brazil (SP), at 22°54′S; 47°05′W, 674 m of altitude above sea level. One-year-old peach palm, *Bactris gasipaes* Kunth (Arecaceae), obtained from seeds of the Yurimaguas region, Peru, were transplanted, under greenhouse conditions, to 80 L-plastic pots (0.7 m in height, 0.4 m in diameter; 115 kg of substrate), where they were irrigated daily and grew for nine months. The pots, with one plant each, were arranged in four lines of ten plants each, with 2 m between lines and 1 m between plants on lines. Evaluations were carried out in plants of the central lines. A mixture of soil, cattle manure and sand (1:1:1) was used as substrate, and the plants were fertilized according to both the results of the chemical analysis of substrate and to recommendations by Bovi and Cantarella (1996). A more detailed description of substrate, fertilization and plant nutritional status evaluations are described by Tucci et al. (2007). At the beginning of the experiment, plants averaged

171.3 cm in height. The measurements were performed for 21 days, during April, 2002.

2.2 Greenhouse environmental conditions

Temperature and relative humidity conditions inside the greenhouse were monitored by temperature sensors, LI-1000-16, and data were stored by a data logger LI-1000, both from LI-COR Inc., Lincoln, NE, USA. Average data were recorded every 30 min. The maximum photosynthetic photon flux density (PPFD), monitored by a quantum sensor (LI-190, LI-COR Inc., Lincoln, NE, USA), was 1400 µmol m^{-2} s^{-1}. It is worth mentioning that throughout the experiment the days were clear and sunny. The nighttime period was of 11:30 h (7:00 p.m. until 06:30 a.m). Air temperature (T_{air}) measured with a dry- and a wet-bulb thermometer and data were used for calculating the air vapor pressure deficit (VPD_{air}) (Buck 1981), whereas the vapor pressure difference between the leaf and the air ($VPD_{leaf–air}$) was measured using the relative humidity and T_{leaf}, both measured with an infrared gas analyzer.

2.3 Experimental design and water regimes

The experiment was arranged in a completely random design with five control plants and five plants submitted to soil water deficit. The five control plants were well-irrigated daily so as to allow the soil to remain at field capacity of water retention. Water deficit was imposed by withdrawing water until the 13th day of study, when leaves were wilted on this day irrigation was re-established (to field capacity of water retention) for 8 days more.

2.4 Soil and plant water status

Soil water content was evaluated throughout the experiment at 10:00 a.m. by time domain reflectometry (TDR) using the soil moisture analyzer Trase System I (SoilMoisture Equipment Corp., Goleta, CA, USA). Soil water content was transformed into soil water potential (ψ_{soil}) by means of calibration curves established in the same pots, full of substrate, according to Arruda et al. (2002). Measurements were taken at 0.3 m depth in pots of both treatments.

Plant water status was monitored by leaf water potential (ψ_{leaf}) at 5:30 a.m. and 1:30 p.m., using a

pressure chamber (PMS mod. 1002, PMS Instrument Co., Albany, USA). Measurements were performed on sunlit leaves, on the terminal portion of leaflets from the medium part of the third younger completely-expanded leaf (+3 leaf), according to Tomlinson's criteria (Tomlinson 1990).

2.5 SPAD readings

Soil and plant analyses development (SPAD) values were evaluated by means of a chlorophyll meter SPAD-Meter, Minolta 502, Japan. The equipment provides data corresponding to the intensity of the green color of the leaves, that is, an estimation of the total chlorophyll content of leaves. Measurements were performed twice, being the first at the imposition of treatments and the second at 13 day of study, corresponding to the maximum water deficit, always measured at 4 p.m. These measurements were performed in the middle of the +2 leaf, the second fully-expanded leaf from the top of the plant. On each leaflet, the SPAD readings were performed in the middle, and also on the proximal and distal part of it.

2.6 Gas exchange

The following variables were evaluated by means of a portable IRGA equipment model LCA-4 working in connection with the module Leaf Microclimate Control System, both from ADC, BioScientific Ltd., England: net CO_2 assimilation (P_N), transpiration rate (E), stomatal conductance (g_s) and intercellular CO_2 partial pressure (C_i). The water use efficiency (P_N/E) and apparent carboxilation efficiency (P_N/C_i) were calculated. The chamber was coupled to the portable light unity, which allows the measurements to be performed at a fixed photosynthetic photon flux density (PPFD). Gas exchange measurements were performed every 2 days at the beginning of the experiment, and daily after the 1st week, twice a day: at 8:00 a.m. and at 2:00 p.m., under natural T_{air} and CO_2 partial pressure of 36.0 ± 0.7 Pa, under a constant PPFD of 1400 µmol m^{-2} s^{-1}, which corresponded to the maximum PPFD observed inside the greenhouse. Measurements were performed on the medium portion of +2 leaves. Five plants per treatment were evaluated.

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2.7 Chlorophyll *a* fluorescence

Chlorophyll *a* fluorescence emission was evaluated on the same leaflets at 7:00 a.m. and 1:30 p.m. A portable modulated fluorometer was used (PAM-2000, Heinz Walz GmbH, Effeltrich, Bayern, Germany), following the saturation pulse method (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 maximum (F_M) and the minimum (F_0) fluorescence signals, measured at 7:00 a.m., after overnight dark-acclimation, and after 30 min of dark-acclimation during diurnal period. The minimum initial fluorescence (F_0) was determined under non-photosynthetic conditions under a low-intensity measuring beam. Five plants per treatment were measured.

2.8 Statistics

The experiment was arranged in a completely randomized design and data was subjected to the analysis of variance (ANOVA), considering the treatments as the source of variation. Regression analyses and curve fitting were done with the program Origin 6.0 (OriginLab Corp., Northampton, USA).

3 Results

3.1 Environmental conditions

During the study, air temperature in the greenhouse varied from 17.8 to 22.3 °C in the morning period and from 28.6 and 34.2 °C at 2:00 p.m. Leaf temperature varied from 30.2 to 34.6 °C in the morning period for plants under water deficit and from 29.4 to 32.5 °C for control plants. At 2:00 p.m. it varied from 34.5 and 41.0 °C for plants under water deficit and from 34.3 to 40.2 °C for control plants (Fig. 1a, b). The minimum air temperature during the experiment was observed on the 6th day at 6:30 a.m. corresponding to 16.7 °C (data not shown).

VPD$_{air}$ varied from 0.08 to 0.24 kPa in the morning (Fig. 1c, d). At 2:00 p.m. it was slightly higher, varying from 0.64 to 1.50 kPa, whereas VPD$_{leaf–air}$ varied from 1.73 to 3.15 kPa for plants under water deficit and from 1.86 to 2.89 kPa for control plants. At 2:00 p.m. VPD$_{leaf–air}$ varied from 2.20 to 3.83 kPa for

plants under water deficit and from 1.94 to 3.51 kPa for control plants (Fig. 1c, d).

3.2 Soil and plant water status

For the control plants, the average ψ_{soil} value was − 0.016 MPa (Fig. 2). On the other hand, soil under water deficit showed ψ_{soil} of − 0.21 MPa 3 days after the beginning of water withdrawing and − 0.63 MPa on the day of maximum water deficit, and after rewatering values reached values close to those exhibited by the control.

Predawn ψ_{leaf} of control plants varied from − 0.3 to − 0.2 MPa, whereas plants under soil water deficit showed the lowest ψ_{leaf} at the 13th day of experiment, corresponding to − 1.6 MPa. Twelve hours after rewatering this value reached − 0.6 MPa, when leaves had already recovered their turgidity. In the following 24 h ψ_{leaf} recovered the value observed at predawn for control plants (Fig. 3a).

ψ_{leaf} of control plants was lower at 1:30 p.m. than at 5:30 p.m., varying from − 1.4 to − 0.8 MPa. ψ_{leaf} decreased over water deficit period, being lower than those of the control plants, reaching − 1.7 MPa 13 days after water withdrawal. Nevertheless, ca. 20 h after rewatering ψ_{leaf} reached − 0.5 MPa, indicating rehydration in relation to the control plants, which showed a ψ_{leaf} of − 1.2 MPa. Thereafter, at 1:30 p.m., ψ_{leaf} of control plants remained lower than those that had been under water deficit (Fig. 3b).

3.3 SPAD readings

Initially, plants of both treatments showed SPAD values of 62.0 and 61.9, respectively. On the day of maximum water deficit, SPAD values were 62.7 e 58.8 for control and water deficit plants, respectively, with no significant difference between them.

3.4 Gas exchange

On the first day of experiment P_N was ca. 11 µmol m^{-2} s^{-1} for both treatments. In the morning period, 3 days after water withdrawal, P_N of plants that had been submitted to water deficit decreased to 3.9 µmol m^{-2} s^{-1}, reaching values close to zero on the 10th day, maintaining these values until the day of maximum water deficit (Fig. 4a). After rewatering, P_N increased gradually, reaching 52% of the control

Fig. 1 Average air (T_{air}) and leaf temperatures (T_{leaf}) (**a, b**), vapor pressure deficit (VPD_{air}) and leaf–air vapor pressure difference ($VPD_{leaf–air}$) (**c, d**) for control and treated plants at 8:00 a.m. (**a, c**) and 2:00 p.m. (**b, d**). Day 0: all plants irrigated; days 1–13: plants submitted to water deficit. Arrows indicate the day of rehydration
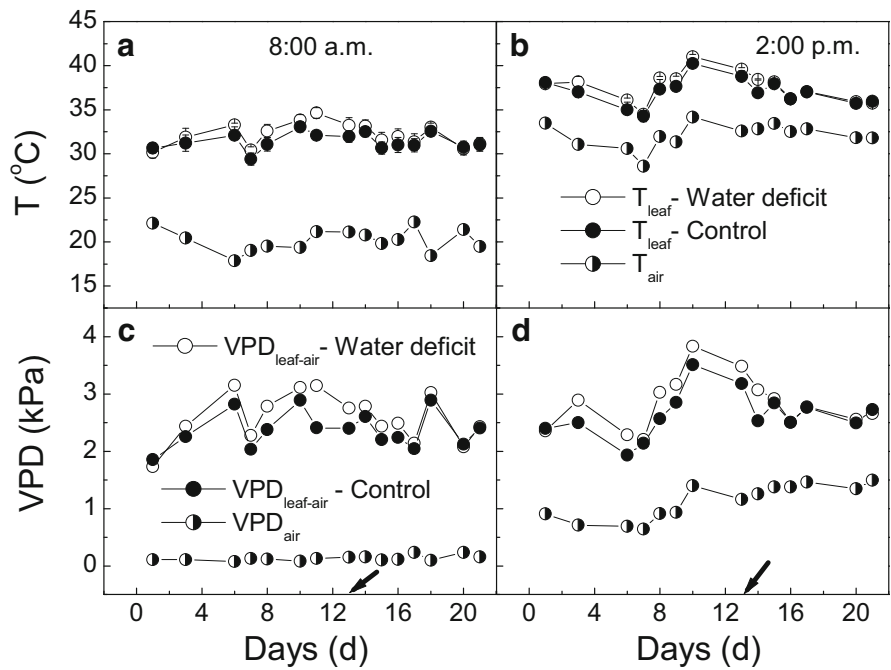
Fig. 2 Soil water potential (ψ_{soil}, MPa) for control and treated plants at 9:00 a.m. Day 0: all plants irrigated; days 1–13: plants submitted to water deficit. Arrows indicate the day of rehydration. Each symbol represents the mean value of five plants ($\pm$ SE)
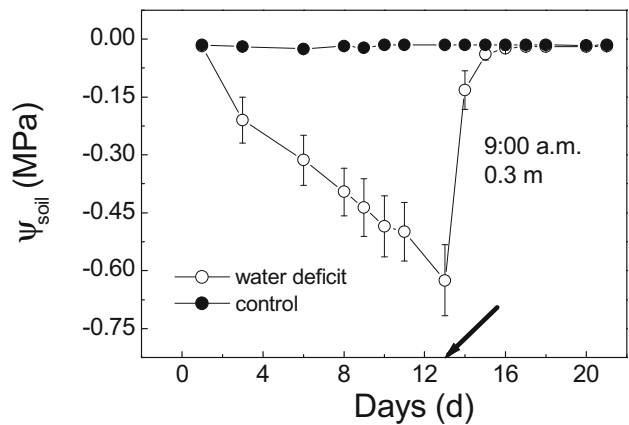
Fig. 3 Leaf water potential (ψ_{leaf}, MPa) for control and treated plants at 5:30 a.m (**a**) and at 1:30 p.m. (**b**). Day 0: all plants irrigated; days 1–13: plants submitted to water deficit. Arrows indicate the day of rehydration. Each symbol represents the mean value of five plants ($\pm$ SE)
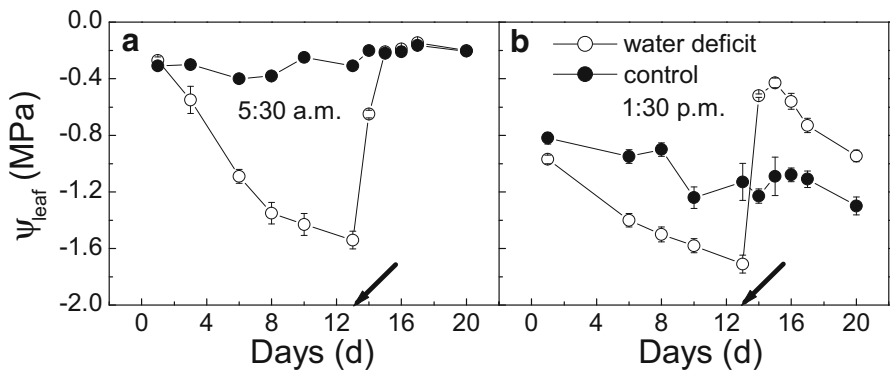
Fig. 4 CO_2 assimilation rate (**a**, **b**), stomatal conductance (**c**, **d**), transpiration rate (**e**, **f**) and intercellular CO_2 partial pressure (**g**, **h**) for control and treated plants at 8:00 a.m. (**a**, **c**, **e**, **g**) and 2:00 p.m (**b**, **d**, **f**, **h**). Day 0: all plants irrigated; days 1–13: plants submitted to water deficit. Arrows indicate the day of rehydration. Each symbol represents the mean value of five plants (± SE)
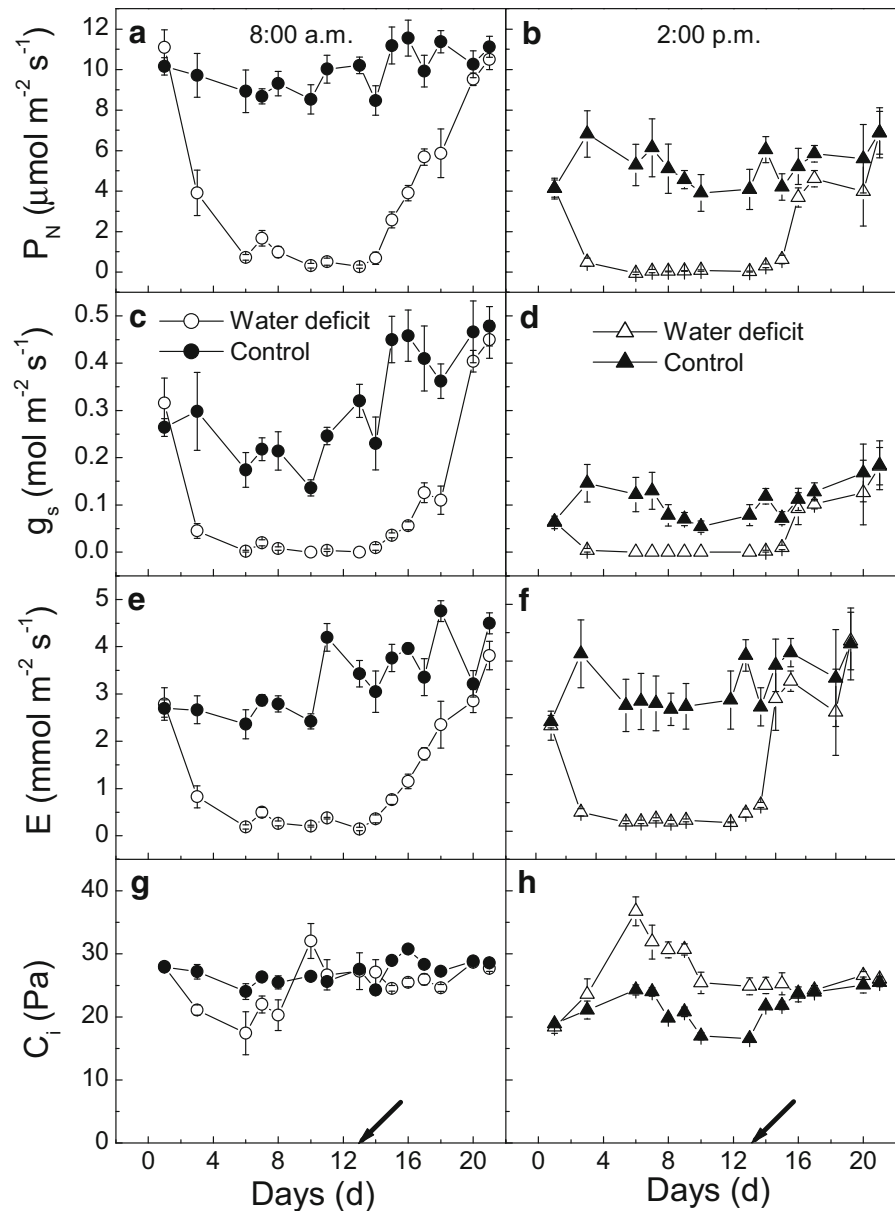
4 days after rewatering and the same values exhibited by the control plants after 3 days more. Significant differences between treatments (P < 0.01) were observed from the third day after water suppression until the 6th day after rewatering. At 2:00 p.m., the control plants showed P_N varying from 4.1 to 6.8 μmol m^{-2} s^{-1}, whereas plants submitted to water deficit showed P_N values of 4 μmol m^{-2} s^{-1} at the beginning of the study; after 3 days, P_N of plants submitted to water deficit decreased to nearly zero until the 2nd day after rewatering (Fig. 4b). After the

4th day of re-irrigation, P_N values increased to those exhibited by the control plants.

Both g_s and E (Fig. 4c–f) showed a response pattern that was similar to P_N. At 8:00 a.m., it was possible to observe significant difference in g_s between treatments (P < 0.05) from the third day after water suppression to the 6th day after rewatering (Fig. 4c). At 2:00 p.m., g_s values of control plants were lower than those measured in the morning, remaining below 0.18 mol m^{-2} s^{-1} (Fig. 4d).

At 8:00 a.m., C_i was lower for water deficit plants than the control up to the 8th day after water suppression and also soon after rewatering (Fig. 4g). In contrast, at 2:00 p.m., C_i of water deficit plants remained higher than that of control plants from the 6th day after water suppression up to when water was replaced (Fig. 4h).

At 8:00 a.m., water use efficiency (P_N/E) (Fig. 5a) was higher ($P \leq 0.05$) for plants under water deficit 3 days after water suppression, then it decreased to values that were lower than the control plants from the 10th to the 14th day. At 2:00 p.m., P_N/E of plants submitted to water deficit remained lower than that exhibited by the control plants until 3 days after rewatering (Fig. 5b).

At 8:00 a.m., values of the apparent carboxylation efficiency (P_N/C_i) of control plants varied from 0.42 to 0.32 μmol m^{-2} s^{-1} Pa^{-1}, whereas plants under water deficit showed significant decrease ($P \leq 0.05$) 3 days after water suppression, reaching values of 0.01 μmol m^{-2} s^{-1} Pa^{-1} from the 10th day after water suppression until the end of the water withdrawal. After rewatering, values of P_N/C_i increased and reached values exhibited by the control plants 7 days after rewatering (Fig. 5c). At 2:00 p.m., control plants showed values of P_N/C_i that were lower than those observed in the morning (Fig. 5d). In plants under water deficit, P_N/C_i remained near zero

throughout the days of water suppression, recovering to the values shown by the control plants 3 days after rewatering.

The relationship between P_N and g_s (Fig. 6a) was explained by an exponential function ($R^2 = 0.99$), whereas the relationship between P_N and P_N/C_i was explained by a linear equation ($R^2 = 0.98$) (Fig. 6b). It is worth mention that both relationships were fitted to data from morning and afternoon periods both for control and under deficit plants. The relationships between P_N and ψ_{leaf} at 5:30 a.m. ($R^2 = 0.64$), and between P_N and VPD$_{leaf-air}$ ($R^2 = 0.43$) were adjusted by linear functions only for morning data (Fig. 6c, d) for plants under water deficit.

3.5 Chlorophyll *a* fluorescence

The average values of maximal quantum yield (F_V/F_M) of PSII for control plants were 0.83 at 7:00 a.m. and 0.81 at 1:30 p.m. (Fig. 7a, b). At 7:00 a.m. values of F_V/F_M for plants under water deficit decreased from the 7th day, reaching 0.78 on the 14th day of experiment, then it increased to values that were similar to those exhibited by the control plants at the end of the study. At 1:30 p.m., on the day of maximum water deficit, F_V/F_M reached 0.76, and after 4 days


Fig. 5 Values of water use efficiency (**a**, **b**) and apparent carboxylation efficiency (**c**, **d**) for control and treated plants at 8:00 a.m. (**a**, **c**) and 2:00 p.m. (**b**, **d**). Day 0: all plants irrigated; days 1–13: plants submitted to water deficit. Arrows indicate the day of rehydration. Each symbol represents the mean value of five plants (± SE)
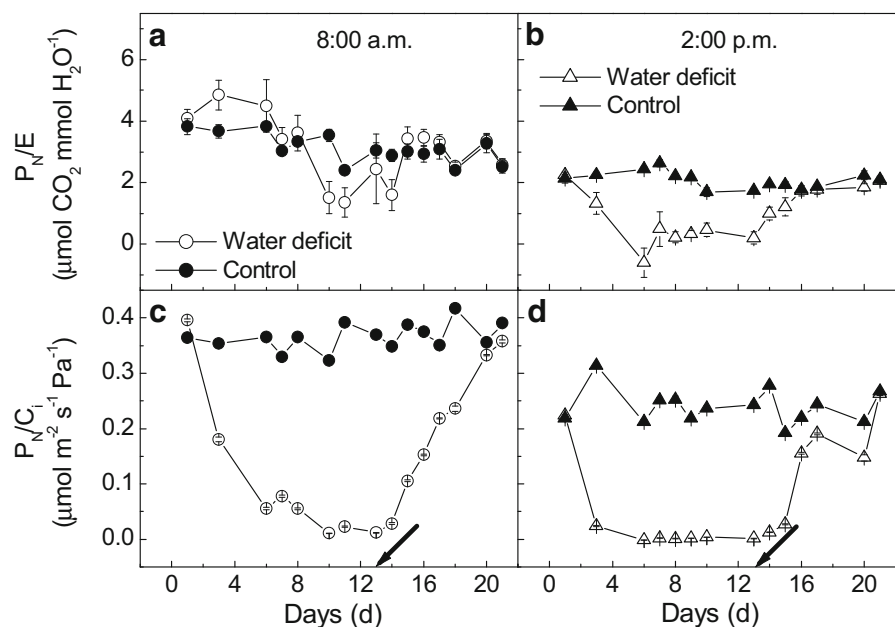
Fig. 6 Relationships between CO_2 assimilation rate and stomatal conductance in (a) ($R^2 = 0.99$**; $n = 58$) and apparent carboxilation efficiency (P_N/C_i) (b) ($R^2 = 0.98$**; $n = 58$); and leaf water potential at 5:30 a.m. (ψ_{leaf}) (c) ($R^2 = 0.64$**; $n = 15$); and leaf–air vapour pressure difference ($VPD_{leaf–air}$) (d) ($R^2 = 0.43$**; $n = 11$) for control and treated plants at 8:00 a.m. (a, c) and 2:00 p.m. (b, d). In c and d only P_N data of 8:00 a.m. were included. Each symbol represents the mean value of 5 plants ($\pm$ SE)
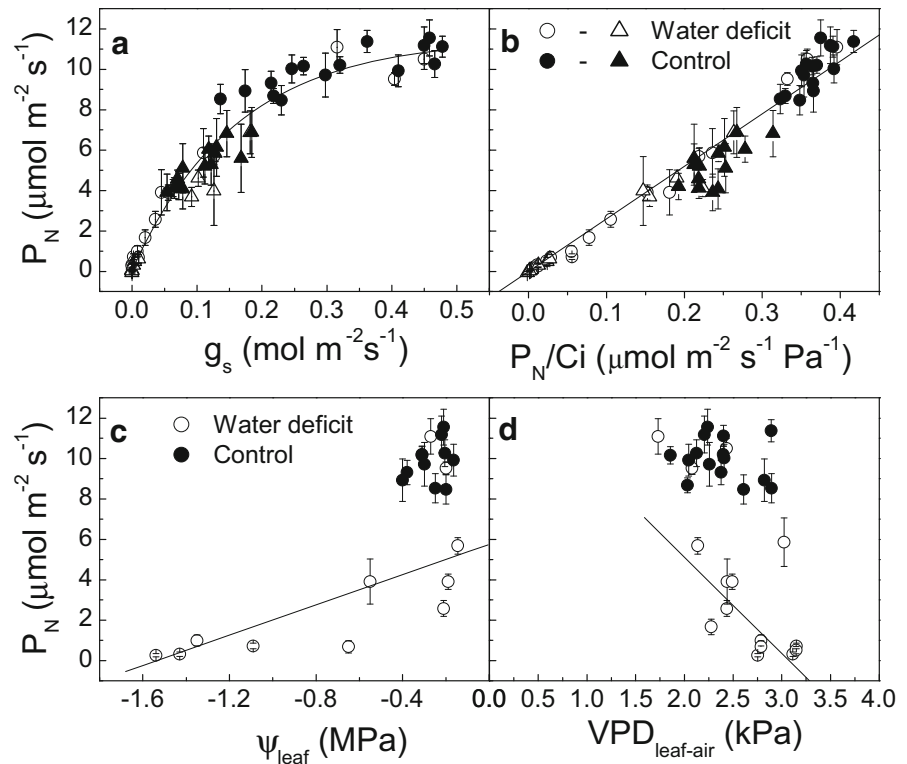
Fig. 7 Maximal quantum yield (F_V/F_M) of PSII for control and treated plants at 7:00 a.m. (a) and 1:30 p.m. (b). Day 0: all plants irrigated; days 1–13: plants submitted to water deficit. Arrows indicate the day of rehydration. Each symbol represents the mean value of five plants ($\pm$ SE)
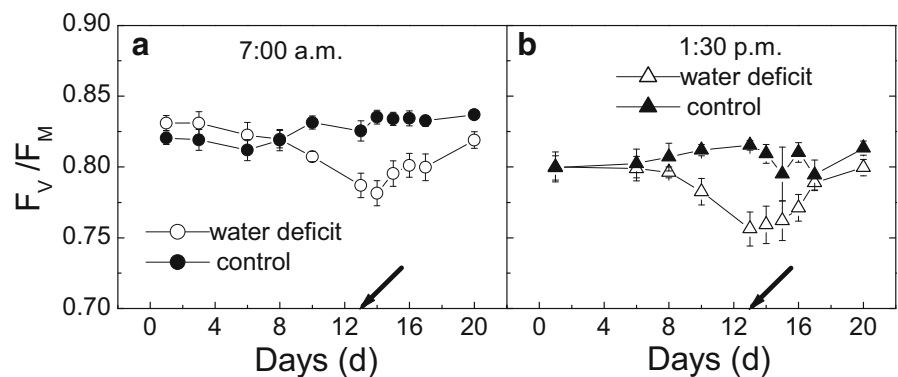
of rewatering values were similar to those shown by the control plants (Fig. 7b).

4 Discussion

The fact that T_{leaf} of water deficit plants was higher than control ones could be due to the cooling effect of the higher E in control plants. As expected, ψ_{leaf} of control plants were more negative in the midday than in the predawn. Because control plants were maintained at soil field capacity, their ψ_{leaf} values being more negative than those measured in the afternoon (− 1.3 to − 0.8 MPa; Fig. 3b) could be due to the increase in T_{air} and T_{leaf}.

The linear relationships between P_N and ψ_{leaf} in the predawn (Fig. 6c) and between P_N and $VPD_{leaf–air}$ (Fig. 6d) observed only for plants under water deficit suggest higher sensitivity of P_N to water deficit in the soil as well as in the air, in relation to control plants.

High differences between predawn ψ_{leaf} and ψ_{soil}, as observed in this study for water deficit plants

has already been reported in the literature. In addition to differences associated with the methods used for the estimation of ψ_{leaf} and ψ_{soil}, when roots are under dry soil conditions, the discrepancies might be likely due to soil moisture heterogeneity, low soil and plant hydraulic conductivity and also poor soil-root hydraulic continuity (Richter 1997; Donovan et al. 2001). Other mechanisms that could contribute to predawn differences between ψ_{leaf} and ψ_{soil}, even in plants growing in well-watered homogenous soils are nighttime transpiration, putative apoplastic solutes in intercellular spaces, and growth (Donovan et al. 2001).

The sharp decrease of P_N 6 days after the beginning of treatments (Fig. 4a) demonstrates the drastic effect of the soil water deficit on the peach palm photosynthetic activity. A P_N decrease of 94% was observed in the morning when the ψ_{leaf} reached − 1.1 MPa at predawn, whereas at midday, ψ_{leaf} reached − 1.4 MPa (Fig. 3). On the other hand, P_N and g_s showed values that were close to zero in the midday.

Regarding plants submitted to soil water deficit, a very interesting situation could be observed after rewatering. On the next day after rewatering, ψ_{leaf} reached − 0.5 MPa at midday, that is, leaves measured at midday were more hydrated than those measured at predawn on the same day (− 0.6 MPa), and also when compared to the control plants measured at midday (− 1.2 MPa). From then until the end of the experiment, control plants maintained more negative ψ_{leaf} at midday when compared to those submitted to water deficit. The fact that ψ_{leaf} still recovered during the morning hours, instead of reaching a plateau value, could suggest a very low soil-leaf hydraulic conductance, that is, one night after rehydration was not sufficient to completely recover the plant water status (Donovan et al. 2001).

After rewatering, P_N, E and g_s recovered slowly, nevertheless reaching values shown by the control plants only 7 days after rewatering. At both times of the day, P_N recover was g_s-dependent (Fig. 4a–d), reinforcing the strong stomatal control of P_N usually exhibited by many species (Pinheiro and Chavez 2011). The atypical higher ψ_{leaf} values of rewatered plants at midday deserves further studies but could be partially explained by the incomplete recovery of g_s and E in the morning (Figs. 3, 4), leading to conservation of water in rewatered plants, similar to an isohydric behavior (Tardieu and Simonneau 1998; Tardieu et al. 2010). Nevertheless, after 7 days of rewatering, gas exchange values recovered to those exhibited by the control plants, although ψ_{leaf} at 1:30 p.m. had not recovered yet. These midday ψ_{leaf} differences between treatments observed at the end of the experiment could be due to the following hypothesis: once gas exchange measurements were performed only at 8:00 a.m. and 2:00 p.m., it is possible that g_s of rewatered plants might have decreased at midmorning.

The slow recovery of g_s after rewatering could be attributed to ABA accumulation in leaves symplast throughout the water deficit period, extending the stomatal closing effects, once its redistribution to the guard-cells is dependent on pH gradients in different leaf compartments (Wilkinson and Davies 2002; Tardieu et al. 2010). Gomes et al. (2009) found out that ABA accumulates in dwarf coconut leaflets throughout water withdraw periods and did not decrease completely to levels exhibited by control plants after 8 days of rewatering. In orange trees, Gomes et al. (2004) also found that the soil water deficit increased leaf ABA content with consequent stomatal closure when ψ_{leaf} was lower than − 1.0 MPa, at 2:00 p.m.

The minimum ψ_{leaf} value observed at predawn was − 1.6 MPa, when P_N was near zero at 8:00 a.m. on the 13th day of water deficit. In this respect, the peach palm can be considered a species showing mesophyte characteristics as far as drought tolerance is concerned, once it reaches P_N zero in ψ_{leaf} between − 1.1 and − 2.5 MPa (Larcher, 2000). In other palm species under water deficit, minimum values of ψ_{leaf} when P_N was close to zero were reported at the same mentioned range, varying from − 1.2 MPa for dwarf coconut (*Cocus nucifera* var. *nana*; Gomes et al. 2009) to more negative values than the observed in the present research, such as − 2.1 and − 2.5 MPa for buriti palm (*Muritia vinifera*; Calbo and Moraes 1997) and açaí palm (*Euterpe oleracea*; Calbo and Moraes 2000), respectively. Peach palm seedlings exhibiting biphid-leaves submitted to water deficit a showed a minimum value of ψ_{leaf} of − 1.9 MPa (Oliveira et al. 2002).

The importance of stomatal P_N limitation during water deficit can also be verified by the P_N exponential response to g_s (Fig. 6a), which in the present study presented a more pronounced P_N drop when g_s values were lower than 0.1 mol m^{-2} s^{-1}, reinforcing stomatal limitation of P_N under water deficit as observed for many species (Flexas et al. 2009; Pinheiro and

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Chavez [2011]). In peach palms Tucci et al. ([2010]) also reported a similar relationship between P_N and g_s, under conditions of seasonal variation of gas exchange.

On the other hand, the relationship between P_N and P_N/C_i was linear (Fig. [6]b) indicating no additional increases in the apparent limitation of carboxylation under water deficit. Restriction of CO_2 diffusion to the mesophilic carboxylation sites, with decreases in g_s as well as in mesophyll conductance could be contributing to the down-regulation of P_N and, consequently, to the decrease of P_N/Ci values in low P_N, as also reported for different plant species (Flexas et al. [2009]; Pinheiro and Chavez [2011]). In a study of gas exchange response to irradiance with *Citrus* species, P_N/Ci values of 0.7 µmol m^{-2} s^{-1} Pa^{-1} decreased linearly to zero in response to g_s, as stomata close under darkness (Machado et al. [2005]), pointing out the g_s regulation of P_N and P_N/Ci.

F_V/F_M of control plants was between 0.82 and 0.83 (Fig. [7]) in early morning, which is in the range (between 0.78 and 0.83) observed by Osmond ([1994]) for most species. Control plants showed a midday decrease in F_V/F_M, reflecting photosynthetic regulatory responses to excessive PPFD. On the other hand, plants submitted to water deficit showed a minimum F_V/F_M value of 0.76 on the day of maximum deficit at in. After 4 days of rewatering, F_V/F_M values reached those exhibited by control plants. It is important to note that this minimum F_V/F_M value was not lower than 0.72, thus not characterizing chronic photoinhibition (Critchley [1998]). The lower F_V/F_M values measured at midday in plants submitted to water deficit recovered to values ≥ 0.78 in the following morning, which indicate that a photoprotection or dynamic photoinhibition process has occurred (Osmond [1994]), probably due to PPFD values above saturation and high air temperatures associated with the absence of P_N.

In conclusion, the physiological responses of the peach palms to soil water deficit suggest a tolerance to drought, showing characteristics of mesophytes, that is, moderate decrease of ψ_{leaf}, stomatal control of water losses and consequent P_N limitation, whereas the photosynthetic apparatus was maintained by photoprotection processes.

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