

THE INFLUENCE OF VAPOUR PRESSURE DEFICIT ON LEAF WATER RELATIONS OF *COCOS NUCIFERA* IN NORTHEAST BRAZIL

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SUMMARY

Daily courses of leaf gas exchange and leaf water potential (Ψ_{leaf}) of green dwarf coconut palm (*Cocos nucifera*) were measured in irrigated plantations on the wet coastal plateau and in a dry semi-arid area of northeast Brazil. At both sites, significant correlations were obtained between stomatal conductance (g_s) and vapour pressure deficit (VPD_{air}), Ψ_{leaf} and VPD_{air} , leaf transpiration (E) and g_s , and $E-\Psi_{\text{leaf}}$. Despite these similar relationships between sites, stronger correlations involving $g_s-\text{VPD}_{\text{air}}$ and $E-\Psi_{\text{leaf}}$ were found at the semi-arid site, where whole-plant hydraulic conductance (g_p) was correlated significantly with VPD_{air} . In addition, at the semi-arid site, only, the net photosynthesis (P_N) was not correlated with E and Ψ_{leaf} , and the intrinsic water use efficiency (WUE_i) was disconnected from VPD_{air} and Ψ_{leaf} . The different behaviour of leaf gas exchange and Ψ_{leaf} between sites was probably caused by low g_s in response to high VPD_{air} at the semi-arid site. Our results indicate potential for significant alterations in the pattern of leaf gas exchange during future climatic changes with increasing temperature and concomitant increases in VPD_{air} . The atmospheric water stress will probably reinforce the strength of connection among water relation variables (E , Ψ_{leaf} , g_s , g_p , and VPD_{air}), but it will disrupt the linear relationship between net CO_2 assimilation and leaf water relations such as P_N-E , $P_N-\Psi_{\text{leaf}}$, $\text{WUE}_i-\text{VPD}_{\text{air}}$ and $\text{WUE}_i-\Psi_{\text{leaf}}$.

INTRODUCTION

There are many irrigated fields along the São Francisco River in northeast Brazil that make the commercial planting of coconut palm (*Cocos nucifera*) possible on the coastal plateau of Sergipe state and in the semi-arid regions of Pernambuco and Bahia states. In northeast Brazil, coconut is obtained principally from the green dwarf cultivar, which is grown for the great palatability of its liquid albumen. The climate on the coastal plateau and at the inland semi-arid sites is considered suitable for cultivating coconut palm, but dry spells and seasonal drought necessitate irrigation. Drought is considered more severe in the semi-arid area than on the coastal plateau site due to the lower rainfall and higher air vapour pressure deficit (VPD_{air}).

The water balance of *C. nucifera* is strongly influenced by the atmospheric water content (Gomes and Prado, 2007). Monthly average values of air relative humidity lower than 60% are considered risky to the water balance of the coconut palm due to the excessive transpiration (Ochs, 1977). Stomatal conductance to water vapour

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(g_s) of *C. nucifera* usually decreases with VPD_{air} under controlled and field conditions (Gomes and Prado, 2007). Kasturibai *et al.* (1988) observed a progressive decrease of g_s with VPD_{air} in a study of tall coconut palms in the dry season in northeast Kerala, on the southwestern coast of India. In addition, Gomes *et al.* (2002) pointed out the strong influence of VPD_{air} on g_s using mathematical models in dwarf coconut palm in both humid and semi-arid sites in the northeast of Brazil.

Different responses of g_s , net photosynthesis (P_N) and leaf transpiration (E) in dwarf (Passos *et al.*, 2005) and in tall (Prado *et al.*, 2001) cultivars of coconut palm have been found during the dry and wet seasons on the coastal plains, northeast Brazil. However, there are no studies on the seasonal or daily leaf gas exchange and leaf water status of coconut palm in semi-arid sites. Dry areas could impose significant restrictions on g_s and P_N and different patterns of water use efficiency, even in irrigated plantations, by reason of the close relationship between VPD_{air} and leaf water relations in dwarf coconut palm (Gomes *et al.*, 2002; Gomes and Prado, 2007). Because high VPD_{air} results in low g_s in dwarf coconut palm (Gomes and Prado, 2007), the long-term influence of VPD_{air} could change the pattern of leaf gas exchange. For example, dwarf coconut palm grown under high values of VPD_{air} , as in semi-arid sites, could be more responsive to dry air, having a particular behaviour of leaf gas exchange and leaf water potential (Ψ_{leaf}) during the course of the day. Ronquim *et al.* (2006) highlighted the influences of contrasting VPD_{air} on daily leaf gas exchange of *Coffea arabica* through daily-integrated values of P_N , g_s , and E . Moreover, different patterns of leaf gas exchange among tall *C. nucifera* cultivars were revealed integrating P_N , g_s , and E on a daily basis (Prado *et al.*, 2001). Therefore, daily-integrated leaf gas exchange of dwarf coconut palm could indicate significant differences of P_N and water relations under different VPD_{air} regimes in the northeast of Brazil.

The present work evaluated the influence of VPD_{air} on leaf gas exchange and Ψ_{leaf} of green dwarf coconut palm growing on irrigated fields under contrasting climate in northeast Brazil. Despite abundant water availability in the rhizosphere provided by irrigation, we expected that the short- and long-term influences of high VPD_{air} on leaf gas exchange and on Ψ_{leaf} would appear clearly at the semi-arid site. We supposed that the intrinsic water use efficiency (P_N/g_s) should be higher in the semi-arid than in the coastal plateau site, because the low g_s in dry sites is usually more limiting to water loss than it is to CO_2 transfer from the atmosphere into leaves. Other features might also be modified by contrasting VPD_{air} between study sites. At semi-arid sites green dwarf coconut palm could change the strength of the connection between P_N and the components of leaf water relations (E , g_s , Ψ_{leaf}). Furthermore, the relationships between P_N with leaf water relation variables and between P_N - VPD_{air} could play a pivotal role in carbon and water balances of *C. nucifera* under future climatic change with increasing temperature and concomitant increases in VPD_{air} .

MATERIALS AND METHODS

Plant material, study sites and growth conditions

Leaf gas exchange and Ψ_{leaf} were determined in adult dwarf coconut palms (cultivar Jiqui Green Dwarf) distributed in an equilateral triangular space (7.5 m) on irrigated

commercial plantations (150 l per plant day⁻¹). The irrigation water was delivered during the day by two sprinklers placed at 0.8 m from the coconut palm stem. One study site was on the coastal plateau in Neópolis municipality (10°17'S, 36°30'W, 75 m asl), in Sergipe state, northeast Brazil. The climate in the coastal plateau is wet tropical with dry summers. The total annual rainfall and mean air temperature are 1159 mm and 25 °C, respectively. Rainfall occurs mainly between April and September. The other study area was in Petrolina municipality (09°09'S, 42°22'W, 387 m asl), located in an inland semi-arid area of Pernambuco state, also in northeast Brazil. The climate in Petrolina is semi-arid with rainfall concentrated between January and May. The total annual rainfall and mean air temperature in Petrolina are 536 mm and 26 °C, respectively. The types of soil in the coastal plateau and in the semi-arid sites are Ultisol and Oxisol, respectively.

Period of study and monthly meteorological data

The daily courses of leaf gas exchange and Ψ_{leaf} were measured seasonally at both sites in December 2002 (summer), March 2003 (autumn), June 2003 (winter) and September 2003 (spring), resulting in one daily course for each season for each site. The monthly meteorological data (rainfall, air temperature and air relative humidity) was acquired from meteorological stations inside plantations in coastal plateau and in semi-arid sites. The monthly mean air temperature was calculated using the average daily values resulted from the sum of maximum and minimum air temperatures. Monthly values of air relative humidity (RH) were obtained through mean daily values of RH, which was calculated by adding the values obtained at 07:30 and at 15:00 hours, and two times the value recorded at 21:00 hours. Daily and monthly values of air vapour pressure deficit (VPD_{air}) were obtained with the corresponding mean values of air temperature and air RH using an equation proposed by Jones (1992).

Leaf physiological and micrometeorological determinations

The daily courses of leaf gas exchange and micrometeorological determinations were measured every three hours during the course of the day (from 08:00 to 17:00 hours) using a portable infrared gas analyzer (IRGA) model LCA-2 (Analytical Development Company [ADC], Hoddesdon, UK). The LCA-2 was connected to a narrow Parkinson leaf chamber (PLCN-2, ADC) and to a data logger (DL-2, ADC). The IRGA worked as an open system (Prado and Moraes 1997; Prado *et al.*, 2001). The leaf chamber was equipped with a Peltier cooler (ADC), which made it possible to maintain natural micrometeorological conditions inside PLCN-2 throughout the day, following the air temperature outside. The air temperature and the air relative humidity outside the leaf chamber were determined in shade by a regular thermometer and opened PLCN-2 without a leaflet, respectively. Air temperature and air RH were measured before every leaf gas exchange determinations during the course of the day. The IRGA determined, simultaneously, P_N , g_s , E and the incident photosynthetic photon flux density (PPFD) on a leaflet.

The selected adult individuals for leaf physiological determinations were growing near the centre of the coconut plantation. Physiological determinations were carried out on leaf number 14 (counted from the apex) nearly parallel to the horizon and inserted on the stem at 2.7 m height. The height from the soil surface up to the insertion of the first leaf on stem was 1.70 and 2.00 m in Neópolis and Petrolina, respectively. Four plants at the coastal plateau site and five plants at the semi-arid site were marked for leaf physiological determinations. Four leaflets at the coastal plateau site and five leaflets at the semi-arid site, i.e. one leaflet per plant, were utilized at each time in order to obtain the corresponding mean value of P_N , g_s , E and PPFD during the course of the day. Leaf physiological and micrometeorological determinations were carried out at 08:00, 11:00, 14:00 and 17:00 hours in a diurnal course in each season. The leaflet in the middle of the leaf number 14 was detached at its base and gas exchange was determined under full solar irradiance in less than two minutes as indicated by several authors (Braconnier, 1998; Passos and Da Silva, 1990; Passos *et al.*, 1999; 2005; Prado *et al.* 2001). The gas exchange determinations on detached leaflets were possible because the detached and attached leaflets of green dwarf coconut did not show significant differences between mean values of g_s up to two minutes under VPD_{air} of 1–2 kPa (Gomes and Prado, 2007). The thick midrib of leaflet was avoided during gas exchange determinations. Therefore, only half of the area of PLCN-2 was useful for determining the leaflet gas exchange (Dufrene and Saugier, 1993; Passos *et al.*, 2005; Prado *et al.*, 2001).

The Ψ_{leaf} was also measured on leaflets from leaf number 14 soon after gas exchange determination. Ψ_{leaf} measurements were carried out on leaflets from the opposite side of those leaflets detached for measuring gas exchange (Kasturibai *et al.*, 1988). The Ψ_{leaf} was measured by a pressure chamber model 3001 (Santa Barbara Soil Moisture, Santa Barbara, USA). The mean value of Ψ_{leaf} was obtained after five and four measurements in coastal plateau and semi-arid sites, respectively, using one leaflet per plant for each day during the daily courses.

Data analysis

Instantaneous transpiration efficiency (ITE) and intrinsic water use efficiency (WUE_i) were calculated as P_N/E and P_N/g_s , respectively (Nogueira *et al.*, 2004). The mean values of g_s as a function of VPD_{air} were adjusted through the equation of first order exponential decay. The correlation coefficient (r) and associated probability (p) were used to analyse the relationship among leaf gas exchange, Ψ_{leaf} , and VPD_{air} . The correlation between paired variables was considered not significant for $p > 0.05$. The values of leaf gas exchange and the PPFD throughout the daily courses were integrated to obtain the corresponding rates per day at each season (Kikusawa *et al.*, 2004; Prado *et al.*, 2001; Ronquim *et al.*, 2006). The soil water potential in rhizosphere was considered virtually zero during the gas exchange and Ψ_{leaf} determinations, since green dwarf coconut palms were growing on irrigated plantations in both sites with abundant water (150 l per plant day⁻¹, Azevedo *et al.*, 2006) during the daily courses. Therefore, the hydraulic water flow per unit of leaf surface (E , mmol H₂O m⁻² s⁻¹)

and driving force (Ψ_{leaf} , MPa) were utilized to estimate the whole-plant hydraulic conductance (gp, $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$). In this approach, it is assumed that, under steady state conditions, the flow of water from soil to leaf can be expressed following the Ohm's law analogy, often referred to as van der Honert's equation (Lhomme, 1998):

$$E = (\Psi_{\text{soil}} - \Psi_{\text{leaf}})/r_{\text{soil-leaf}} \quad (1)$$

where E = leaf transpiration; Ψ_{soil} = effective soil water potential, representing an average value of soil water potential, virtually zero in this work because of full irrigation during daily courses; Ψ_{leaf} = average leaf water potential; $r_{\text{soil-leaf}}$ = effective bulk resistance to water transfer from soil to leaf. The inverse of $r_{\text{soil-leaf}}$ was considered the effective bulk conductance from soil to leaf, which represents here the whole-plant hydraulic conductance (gp).

RESULTS

Monthly meteorological data

Differences in rainfall, RH and VPD_{air} were found between sites during leaf physiological measurements (Figure 1). Rainfall was 100 mm or more at the coastal plateau site between March and August 2003. Contrastingly, at the semi-arid site, rainfall was higher than 100 mm only in January 2003. Monthly mean values of VPD_{air} were always higher at the semi-arid than the coastal plateau site, but the opposite occurred for RH. The mean air temperature was higher at the coastal than the semi-arid site only between December 2002 and February 2003. When monthly rainfall was greater than 30 mm at the semi-arid site (January–May 2003), the mean values of VPD_{air} , air temperature and RH were similar between sites.

Daily courses of leaf physiological and micrometeorological determinations

Figure 2 shows local micrometeorological (VPD_{air} and PPF) and leaf physiological (P_{N} , g_{s} , E , Ψ_{leaf}) mean values during the course of the day at both study sites in each season for 2002–2003. PPF was usually lower in the semi-arid than the coastal plateau site because of recurrent clouds during the course of the day, except in June 2003. It occurred mainly in December 2002 (summer), when VPD_{air} at the coastal plateau was abnormally higher than at the semi-arid site. On the other hand, comparing the sites, the daily VPD_{air} was similar in March (autumn), but higher at the semi-arid than at the coastal plateau site in June (winter) and in September (spring). P_{N} was usually similar at both sites, but in September it was higher at the coastal plateau site, especially around midday. Irrespective of the differences of VPD_{air} and PPF between sites, g_{s} and E were frequently lower at the semi-arid site, especially when E peaked at the coastal plateau site before midday. Contrastingly, Ψ_{leaf} was lower at the coastal plateau site, mainly before midday.

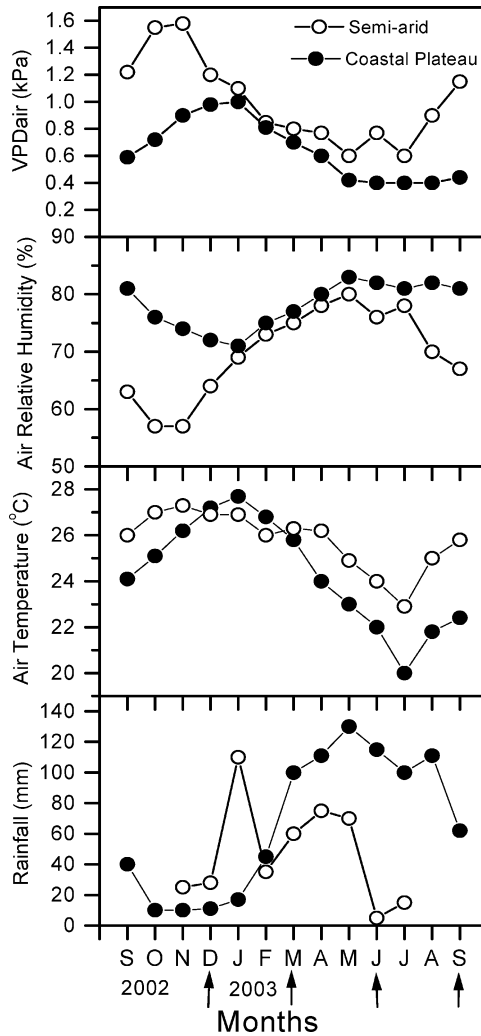


Figure 1. Monthly mean values of vapour pressure deficit (VPD_{air}), air relative humidity, air temperature, and the monthly total rainfall from September 2002 to September 2003 at coastal plateau (●) and inland semi-arid (○) sites in northeast Brazil. Arrows indicate when daily courses of leaf gas exchange and leaf water potential were measured at both sites.

Leaf gas exchange, Ψ_{leaf} , and VPD_{air}

The average values of g_s decreased exponentially with increasing VPD_{air} at both sites (Figure 3). Nevertheless, the correlation between g_s - VPD_{air} was weaker at the coastal plateau than at the semi-arid site, where g_s was usually lower than $0.11 \text{ mol m}^{-2} \text{ s}^{-1}$. On the other hand, a similar linear negative correlation was obtained at both sites between Ψ_{leaf} and VPD_{air} (Figure 3). The relationship between E and g_s was equivalent at both study sites, but E decreased less steeply with Ψ_{leaf} in semi-arid site, where E - Ψ_{leaf} correlation was stronger than at the coastal plateau site (Figure 4).

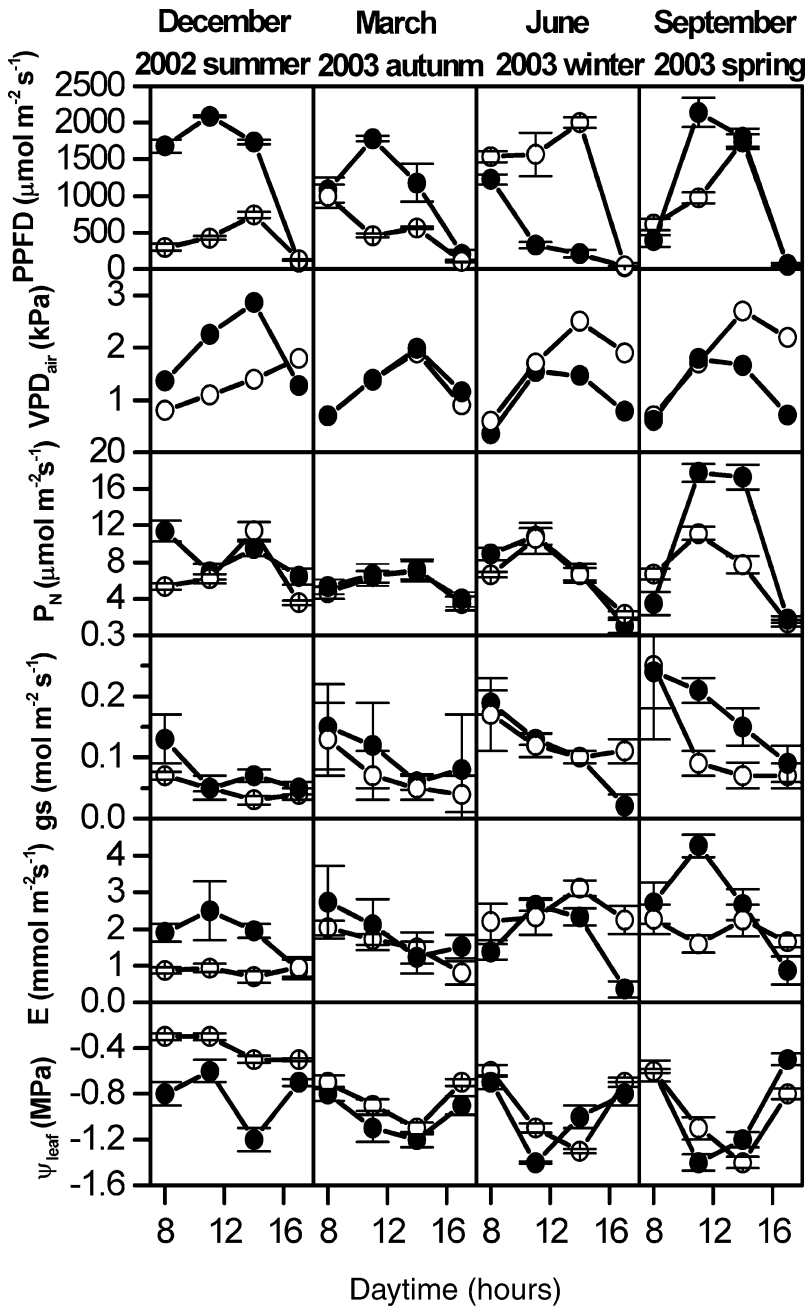


Figure 2. Mean values (symbols) and standard error (bars) of photosynthetic photon flux density (PPFD), air vapour pressure deficit (VPD_{air}), net photosynthesis (P_N), stomatal conductance (g_s), leaf transpiration (E), and leaf water potential (Ψ_{leaf}) during daily courses over the year in green dwarf coconut palm growing at coastal plateau (●) and inland semi-arid (○) sites in northeast Brazil. For each quantity, excluding VPD_{air} , $n = 4$ at the coastal plateau and $n = 5$ at the semi-arid site.

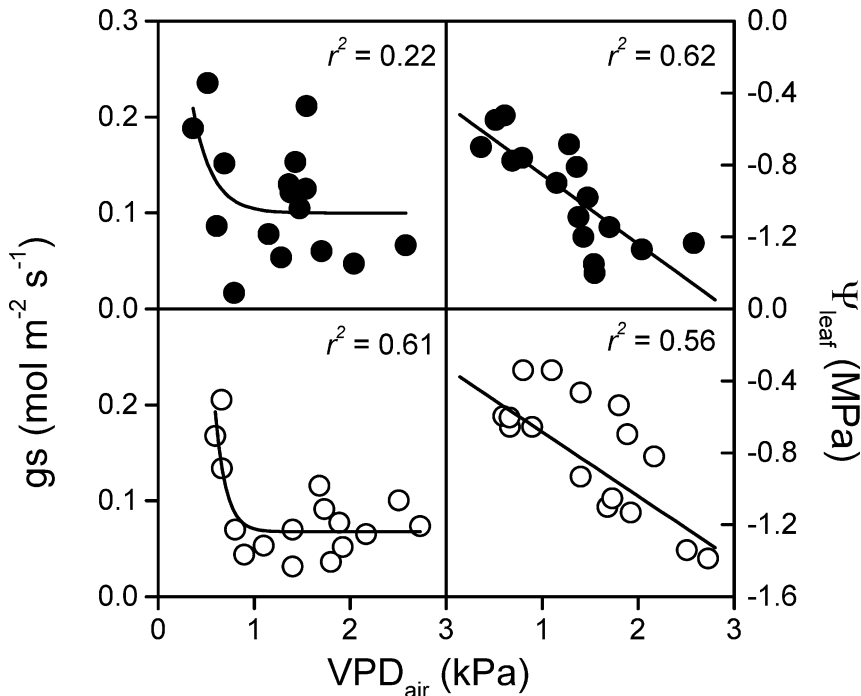


Figure 3. Mean values (symbols) of stomatal conductance (g_s) and leaf water potential (Ψ_{leaf}) as a function of vapour pressure deficit (VPD_{air}). Data were obtained seasonally under field conditions during daily courses on leaves of green dwarf coconut palm growing at coastal plateau (●) and inland semi-arid (○) sites in northeast Brazil. For each quantity $n = 4$ in coastal plateau and $n = 5$ in semi-arid site.

The whole-plant hydraulic conductance ($E/-\Psi_{\text{leaf}}$ under soil water potential in the rhizosphere near 0.0 MPa) was correlated significantly with VPD_{air} only at the semi-arid site (Figure 5). Contrastingly, at the coastal plateau site only, P_N was correlated with E and Ψ_{leaf} , and WUE_i with VPD_{air} and Ψ_{leaf} (Figures 6 and 7, respectively). One average value of WUE_i was out of range ($362 \mu\text{mol mol}^{-1}$) and is not shown for the semi-arid site (Figure 7). The relationships g_s -PPFD, g_s - P_N , and g_s - Ψ_{leaf} were not significant at either site.

Integrated (day^{-1}) values of PPFD, leaf gas exchange and whole-plant hydraulic conductance

PPFD was 21% lower at the semi-arid than at the coastal plateau site because of overcast days (Table 1). However, PPFD in both sites was usually between 500 and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ throughout the daily courses (Figure 2), which is enough to saturate 80–100% of P_N on leaves of coconut palm (Gomes *et al.*, 2006). While the integrated values of P_N decreased by 17%, the integrated values of E and g_s were, respectively, 21 and 22% lower at the semi-arid than at the coastal plateau site (Table 1). ITE and WUE_i were higher at the semi-arid than at the coastal plateau site because of more pronounced decrease in integrated E and g_s values. Despite the monthly differences

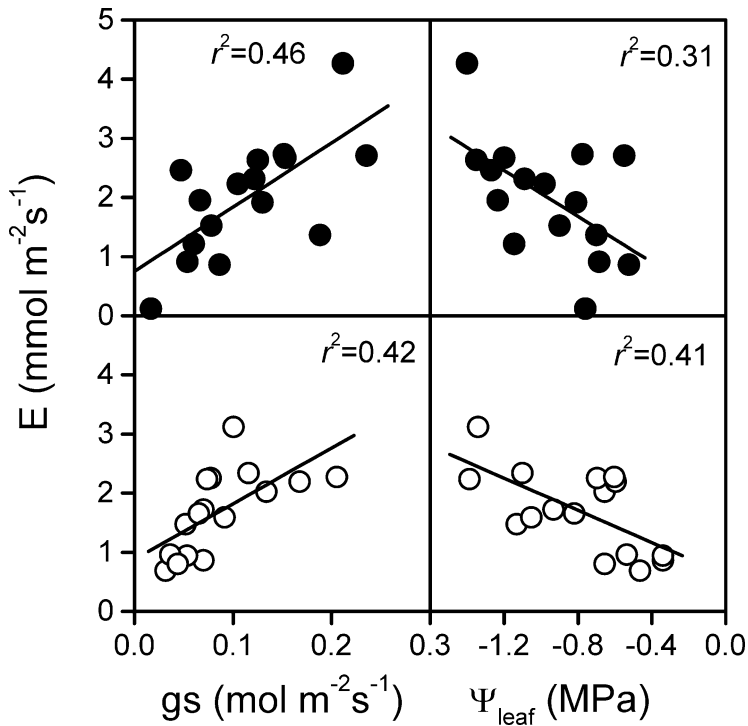


Figure 4. Mean values of transpiration (E) as a function of stomatal conductance to water vapour (g_s) and leaf water potential (Ψ_{leaf}). Data were obtained seasonally under field conditions as for Figure 3.

between sites in integrated components of water relations, including g_p , the total integrated whole-plant hydraulic conductance was similar at both sites (Table 1).

DISCUSSION

Leaf transpiration was usually lower at the semi-arid than the coastal plateau site (Figure 2 and Table 1) keeping the xylem water column under lower tension, especially during the morning (Figure 2). The low leaf transpiration at the semi-arid site resulted in higher Ψ_{leaf} during the course of the day in summer and autumn, and postponed minimum Ψ_{leaf} in winter and spring (Figure 2). Leaf water relations at the semi-arid site were shielded by means of lower E and g_s than on the coastal plateau, resulting in higher Ψ_{leaf} and/or postponed minimum Ψ_{leaf} during the course of the day, in a protective behaviour against atmospheric water stress. This occurred typically in spring, when minimum Ψ_{leaf} was postponed and lower values of g_s and E were found at the semi-arid site (Figure 2). Therefore, depending on atmospheric conditions, it is possible to note the effects of VPD_{air} during the course of the day. On the other hand, it is possible to reveal long-term effects of VPD_{air} on the behaviour of leaf water relations by means of correlations among VPD_{air} , g_s , E, Ψ_{leaf} , and g_p (Figures 3–5).

The exponential decay of g_s with increasing VPD_{air} showed stronger correlation at the semi-arid site (Figure 3). Therefore, stomatal behaviour was directly linked to

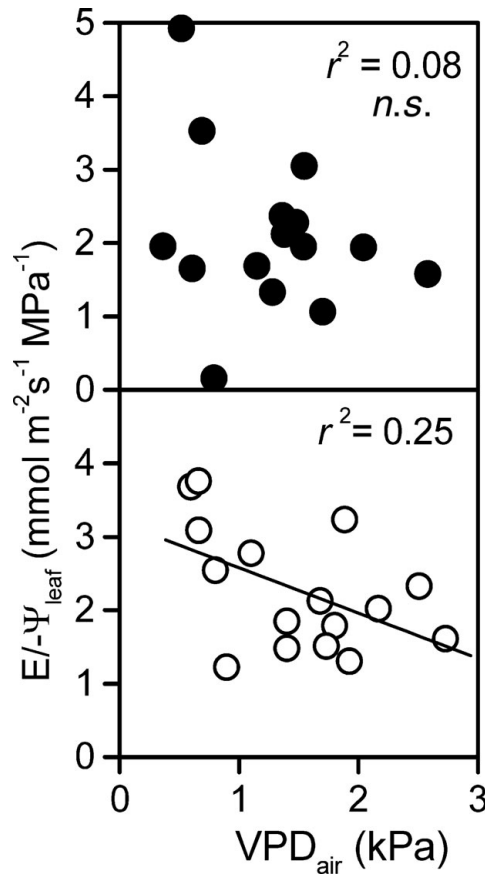


Figure 5. Mean values of whole-plant hydraulic conductance obtained from transpiration (E) per unit of leaf water potential ($-\Psi_{\text{leaf}}$) as a function of vapor pressure deficit (VPD_{air}). Data were obtained seasonally under irrigation ($150 \text{ l per plant day}^{-1}$) and field conditions as for Figure 3.

VPD_{air} in a feedforward response (Farquhar, 1978; Lange *et al.*, 1971; Schulze *et al.*, 1987) at both sites, but it was clearer at the semi-arid site. Particularly at the semi-arid site, a direct response to VPD_{air} probably prevents potential disruption among E , water acquisition capacity by roots, and water-lifting capacity from root to canopy (Saliendra *et al.*, 1995), keeping E - Ψ_{leaf} relationship fasten and less steep under high VPD_{air} . It is consistent with theoretical expectations of a hydraulic model of stomatal regulation, in which pore aperture regulates E , and E is linked with Ψ_{leaf} even in non-saturating light (Oren *et al.*, 1999). Fundamentally, the stomatal closure as VPD_{air} increases was caused by an increase in rate of transpiration and the corresponding decrease of Ψ_{leaf} in both sites, but it was clearer at the semi-arid than at the coastal plateau site. Similar values of whole-plant hydraulic conductance obtained from the summation of all months at both sites corroborate the role of stomata behaviour for maintaining g_p as constant as possible. Therefore, where hydraulic homeostasis is more strongly affected by VPD_{air} such as at the semi-arid site, g_s was lower, thus avoiding high E and the corresponding

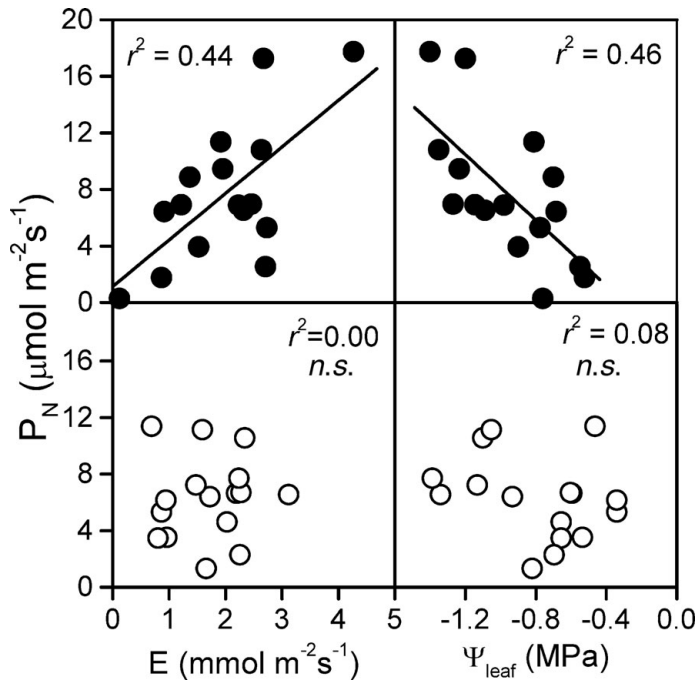


Figure 6. Mean values of net photosynthesis (P_N) as a function of leaf transpiration (E) and leaf water potential (Ψ_{leaf}). Data were obtained seasonally under field conditions as for Figure 3.

Ψ_{leaf} decline (Saliendra *et al.*, 1995). It is recognized that VPD_{air} is one of the most important sources of variation in g_s (Gomes and Prado, 2007; Gomes *et al.*, 2002).

Hence, stomatal apparatus would be more responsive to VPD_{air} during the course of the day at the semi-arid site, where g_s was usually lower than coastal plateau even under heavy irrigation and high VPD_{air} , which indicates stomatal closure. Since the narrower stomatal pore tends to reduce the water loss to a greater extent than the incoming CO_2 in leaves (Nobel, 1999), it resulted in higher integrated ITE and WUE_i at the semi-arid site (Table 1). Stomata closure would be heterogeneous (patchy) when transpiration was reduced at low air humidity (Mott and Parkhurst, 1991). Indeed, the complete closure of stomata in patches can occur at high VPD_{air} (Beyschlag *et al.*, 1992). Combined with stomatal pore narrowing, the heterogeneous stomatal closure could be responsible for disrupting the linear correlations between carbon and water gas exchanges (P_N - E) on leaves at the semi-arid site (Figure 6). Therefore, the out of range mean value obtained about WUE_i ($362 \mu\text{mol mol}^{-1}$, not shown in Figure 7) was probably caused by heterogeneous closure of stomata at the semi arid site.

Concluding, there were two processes driving the stomatal behaviour in green dwarf coconut palm growing in irrigated fields. The first is a simple hydraulic effect of increased transpiration reducing Ψ_{leaf} (Figure 4), ultimately decreasing stomatal pore conductance and g_s when VPD_{air} increases. In this classical feedback processes, peristomatal transpiration and its direct effect on guard cells should not be excluded

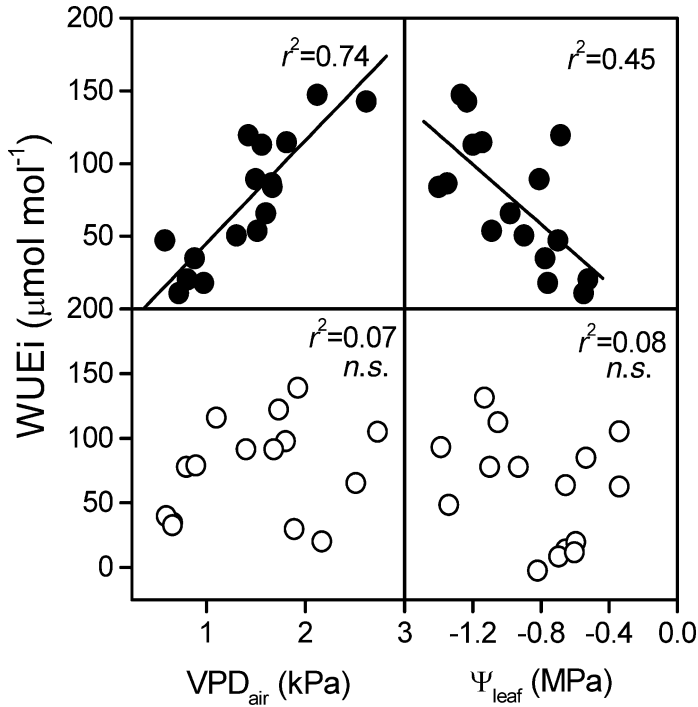


Figure 7. Mean values of intrinsic water use efficiency (WUEi), as a function of vapor pressure deficit (VPD_{air}) and leaf water potential (Ψ_{leaf}). Data were obtained seasonally under field conditions as for Figure 3.

Table 1. Integrated values (day⁻¹) of photosynthetic photon flux density (PPFD), net photosynthesis (P_N), transpiration (E), stomatal conductance (g_s), instantaneous transpiration efficiency (ITE, P_N/E), intrinsic water use efficiency (WUEi, P_N/g_s), and the whole-plant hydraulic conductance (E/−Ψ_{leaf}) of green dwarf coconut palm growing in coastal plateau (CP) and in semi-arid (SA) sites in northeast Brazil. The numbers in parentheses are the percentage (+ or −) of the total in relation to coastal plateau site, which was considered 100%.

Integrated values (day ⁻¹)	December 2002 Summer		March 2003 Autumn		June 2003 Winter		September 2003 Spring		Total Figures in parentheses are % in relation to CP	
	CP	SA	CP	SA	CP	SA	CP	SA	CP	SA
PPFD mol m ⁻²	50.9	14.9	38.9	16.9	12.6	47.0	44.9	32.9	147.3	111.7 (−21)
P _N mmol m ⁻²	273	238	195	190	245	233	390	247	1103	908 (−17)
E mol m ⁻²	63	27	61	50	63	83	94	63	281	223 (−21)
g _s kmol m ⁻²	2.3	1.5	3.2	2.2	3.6	3.9	5.8	4.0	14.9	11.6 (−22)
ITE mmol mol ⁻¹	4.3	8.8	3.2	3.8	3.9	2.8	4.1	3.9	15.5	19.3 (+25)
WUEi mmol kmol ⁻¹	119	159	61	86	68	60	67	61	315	366 (+16)
E/−Ψ _{leaf} mol m ⁻² s ⁻¹ MPa ⁻¹	69	58	57	63	86	57	65	92	277	270 (−3)

(Bunce 1996; Lange *et al.*, 1971). Combined with this feedback mechanism there is the feedforward response revealed by g_s -VPD_{air} relationship at both sites (Figure 3). Feedback and feedforward mechanisms are clearer at the semi-arid than at the coastal plateau site (Figures 3 and 4). Based on the results presented here it is possible to suggest that the future climatic change with increasing temperature and concomitant increases in VPD_{air} will alter significantly the pattern of leaf gas exchange, the relationship among leaf water relations components, and the strength of connection between carbon assimilation and plant water relations. Probably, higher VPD_{air} in the future will reinforce the disruption of linear relationships between P_N and leaf water relations in the coconut palm growing under field conditions, even with full irrigation. On the other hand, high VPD_{air} will increase water use efficiencies and the strength of connection between g_s -VPD_{air} and g_p -VPD_{air}. In this future scenario, P_N could be also affected negatively by lower g_s under higher VPD_{air}, which leads to stomatal closure. Under these new constraints in the future, coconut plantations would not be appropriate in areas with high VPD_{air} such as in the study semi-arid site, even under heavy irrigation regimes.

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