

Day Time Fluctuations in Photosynthetic Parameters and Water Relations in Juvenile Coconut Palms Grown Under Rainfed and Irrigated Conditions

V. Rajagopal, S. Naresh Kumar*, K. V. Kasturi Bai and R. H. Laxman

Division of Plant Physiology, Biochemistry and Post Harvest Technology, Central Plantation Crops Research Institute, Kasargod 671 124, India

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Day time (7 h to 18 h) fluctuations in photosynthetic parameters (net photosynthetic rate, P_n ; stomatal conductance, g_s ; internal CO_2 concentration, C_i); water relations (leaflet water potential, Ψ_{leaf} ; transpiration rate, E) and weather parameters (photosynthetically active radiation, PAR; leaflet temperature, T_{leaf} ; air vapor pressure deficit, VPD) were estimated in juvenile palms of coconut grown under rainfed and irrigated conditions. Variations in values and day time fluctuations in photosynthetic parameters and water relations were observed between palms grown under rainfed and irrigated conditions, P_n , E and g_s were maximum between 09:00 and 11:30 and 15:00 and 16:00 h. C_i and Ψ_{leaf} were least during mid-day. Mid-day slump in P_n and g_s was observed. T_{leaf} , PAR and VPD were maximum between 09:00 and 16:00 h. E and VPD were positively correlated. Rainfed palms had higher T_{leaf} , C_i , C_i/C_a and leaf to ambient temperature difference (ΔT) and lower P_n , Ψ_{leaf} and E compared to the irrigated palms. Instantaneous and intrinsic water use efficiency increased under mild water-deficit conditions. It is apparent that under rainfed conditions the carbon assimilation efficiency was low compared to irrigated condition. VPD and ΔT influenced g_s and water relations during day time which predominantly determined the variations in photosynthetic efficiency of coconut under irrigated and rainfed conditions.

Keywords: Diurnal course, VPD, transpiration, photosynthesis, drought, WUE, stomatal conductance, water relations, gas exchange parameters.

Introduction

Carbon assimilation efficiency during the day determines plant growth and productivity. This efficiency is a compound effect of net photosynthetic rate and photosynthate partitioning. In several field crops, the diurnal variation in photosynthetic rates and their depression during mid-day has been reported (Kalt-Torres *et al.*, 1988; Singh *et al.*, 1988; Dufrene and Saugier, 1993). The weather parameters influence/cause these variations (Maroco *et al.*, 1997). Ball and Berry (1982) have suggested that stomatal conductance of plants is regulated in such a way that internal CO_2 concentration (C_i) and atmospheric CO_2 concentration (C_a) ratio lies between 0.5 and 0.9 for C_3 plants. Direct effect of leaf to air vapour pressure deficit (VPD) on stomatal regulation

was reported in many woody crops (Flore and Lakso, 1989).

Coconut (*Cocos nucifera* L.) is grown both under rainfed and irrigated conditions. It is shown that the rainfed palms produce less dry matter and hence the nut yields are lower in them (Kasturi Bai *et al.*, 1997). Since the dry matter production is a direct result of the photosynthetic efficiency of the plant, it is important to understand the photosynthetic patterns during day time. Photosynthesis is a dynamic process that is highly influenced by the water relations of the plant. In turn both photosynthesis and water relations are highly influenced by the ambient microclimatic conditions. The day time variations in photosynthetic rates, transpirational rates, etc. were studied by Jayasekara *et al.* (1996) in coconut during summer and rainy seasons. They found that net photosynthetic rate (P_n), transpiration rate (E) and stomatal conductance (g_s) were higher during wet

*For correspondence. (e-mail: nksoora_66@yahoo.com)

season. However, the VPD and leaf to air temperature difference (ΔT) factors were not taken into consideration. The relationship between weather parameters and diurnal changes in photosynthesis and water relation parameters and their inter-relationships were not studied in coconut. In the present study emphasis is laid on the day time variation in water relations and photosynthetic parameters in relation to weather conditions and also their inter-relationships in rainfed and irrigated juvenile palms in a given day.

Materials and methods

Juvenile palms (3 years old after field planting) of coconut were selected for the study. These palms were grown in red laterite soils of CPCRI experimental fields (~ 17 m above sea level) under recommended agronomic practices and have received recommended dose of fertilizers (N:P:K; 330:240:810 g/palm/year). One set of juvenile palms (six palms/set in CRD) was maintained under assured basal irrigation to field capacity (twice a week) and other set was maintained under rainfed conditions. The irrigated palms were watered continuously for a week prior to measurements. Measurements on gas exchange characteristics and water potentials in the irrigated and rainfed palms (six palms/set; 2 readings/palm) were simultaneously taken during day in mid-April, 1995–97.

P_n , g_s , C_i , E and photosynthetically active radiation (PAR) incidence on the leaf surface and leaf surface temperature were recorded using a portable IRGA (ADC LCA-4, UK). Before the use of instrument, zero settings for H_2O and CO_2 were made. The boundary layer resistance to vapour (r_b) was typically $0.8 \text{ m}^2 \text{ s}^{-1} \text{ mol}^{-1}$. Air was drawn into the instrument from an air probe at the height of 3 m above ground surface. The air pumped into the system was dried using anhydrous calcium sulphate. The gas flow to leaf chamber was maintained at $300 \pm 2 \mu\text{mol s}^{-1}$. All measurements were made in middle leaflets of the third leaf from top (including spindle leaf) and care was taken to keep the position of angle of leaflet as naturally occurred.

Water potentials of leaflets were measured using the Pressure Chamber model 3000 (Soil Moisture Equipment Corp, Santa Barbara, USA). Water po-

tential of the leaflet was determined within 15 sec of detachment. The water potential measurements were made in the leaflets adjacent to those used for gas exchange measurements.

All the measurements on gas exchange and water potential parameters were done simultaneously at the quickest possible time. The data were statistically analysed using general linear model and the means and their SEM were expressed to compare the data.

Results and discussion

Net photosynthesis and weather parameters

The PAR gradually increased from 07:00 to 18:00 h, was maximum at 12 noon and then declined (Figure 1). Ambient temperature (T_{amb}) was also maximum at 12 noon. The VPD increased till 13:00 h. The leaf surface temperature also was significantly higher in rainfed palms from 10:00 to 16:00 h. The leaf to air temperature differences (ΔT) indicate that the coconut palm conserves water by closing the stomata, thus its leaflet temperatures are maintained higher than the ambient temperature. This increase in ΔT was significantly higher in rainfed palms. Also, increase ΔT was maximum at 12 noon. Reduced transpiration rates in rainfed palms due to closure of stomata, as feedback response to high temperature-related high VPD, limited the thermoregulatory capacity of leaflets, leading to increase in ΔT by 3°C over the irrigated ones.

The day time trends in P_n rate show two peaks, one at 09:00 and another at 15:00 h under rainfed condition (Figure 2). However, under irrigated condition, the peaks were less distinct but had higher values at 10:00 and 14:00 h. The irrigated palms maintained significantly higher P_n rates. However, in rainfed palms the P_n rates were significantly higher between 08:00 and 09:30 h over irrigated ones. Stomatal conductance was significantly higher in irrigated palms compared to rainfed palms. The g_s also had two peaks in rainfed palms with maximum at 09:00 and 15:00 h. In irrigated palms also the g_s was maximum at 10:00 and then maintained at a steady state between 13:00 and 17:00 h. The C_i and C_i/C_a were significantly higher in rainfed palms compared to irrigated palms and they were higher at early and late hours of the day and also at mid-day, when stomata

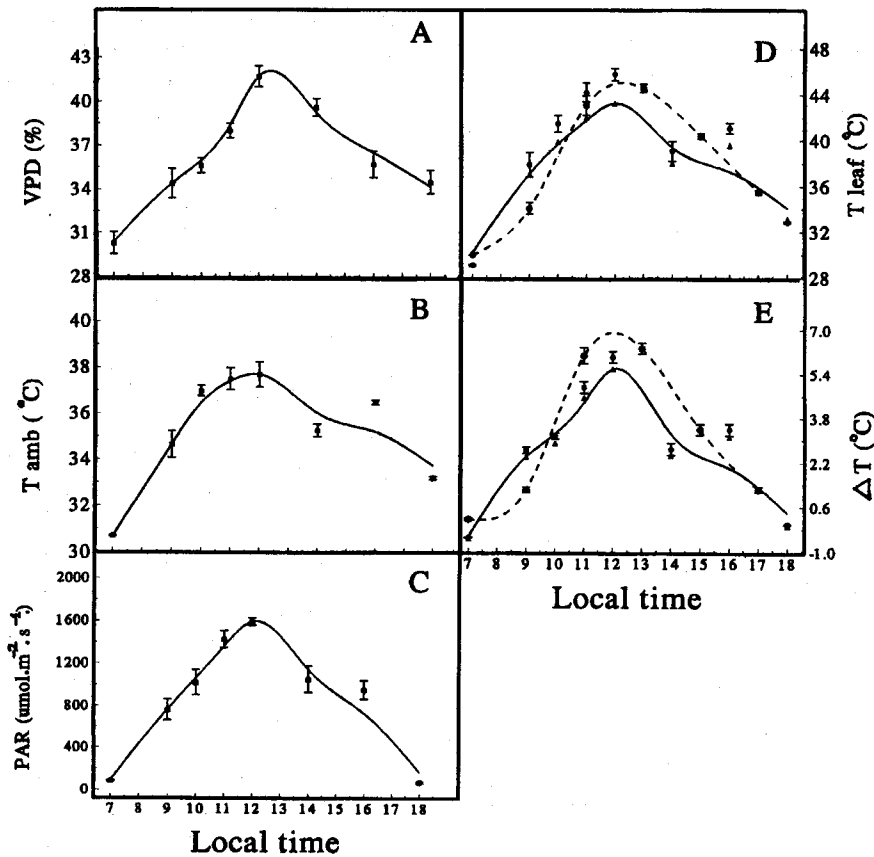


Figure 1. Diurnal changes in leaf to air vapour pressure deficit, VPD (A), ambient temperature, T_{amb} (B), photosynthetically active radiation, PAR (C), leaf temperature, T_{leaf} (D) and leaf to air temperature difference, ΔT (E) in leaflets of coconut juvenile palms grown under irrigated (—) and rainfed (-----) conditions (means of 3 years data measured in April). Vertical bars indicate standard error of means ($n = 36$).

are closed. High C_i in rainfed palms indicates the predominance of nonstomatal inhibition of P_n rates. Increased photorespiration under stress conditions might have inhibited the P_n and thus increased the C_i under stress conditions (Scheyermann *et al.*, 1991). The release of CO_2 by photorespiration and its re-fixation within the leaf also lead to dissipation of absorbed light energy under stress conditions when the stomatal conductance is low (Stuhlfauth *et al.*, 1990). This inhibition of P_n and increase in C_i was also probably due to impaired chloroplast functioning (Gunasekera and Berkowitz, 1992) or lower Hill activity due to water deficiency. High ΔT in rainfed leaflets also contributed to reduced P_n rates. Increase in C_i/C_a when stomata are closed also indicates the nonstomatal limitation of P_n . The results indicate that under rainfed conditions, factors other than PAR

largely decrease the P_n rates (Table 1). However, photo-inhibition of photosynthesis under rainfed conditions can be one of the reasons. The inverse relationship between C_i/C_a and instantaneous WUE indicate that during rainfed situations nonstomatal limitations reduce the P_n rates compared to irrigated conditions.

Water relations

Leaf water potentials (Ψ_{leaf}) were maintained significantly higher in irrigated palms compared to rainfed ones particularly from 10:00 h onwards. Ψ_{leaf} was higher at the beginning and towards the end of the day. Transpiration rates (E) were significantly higher between 9:00 and 13:00 h in irrigated palms, whereas in rainfed ones it had two peaks, one at

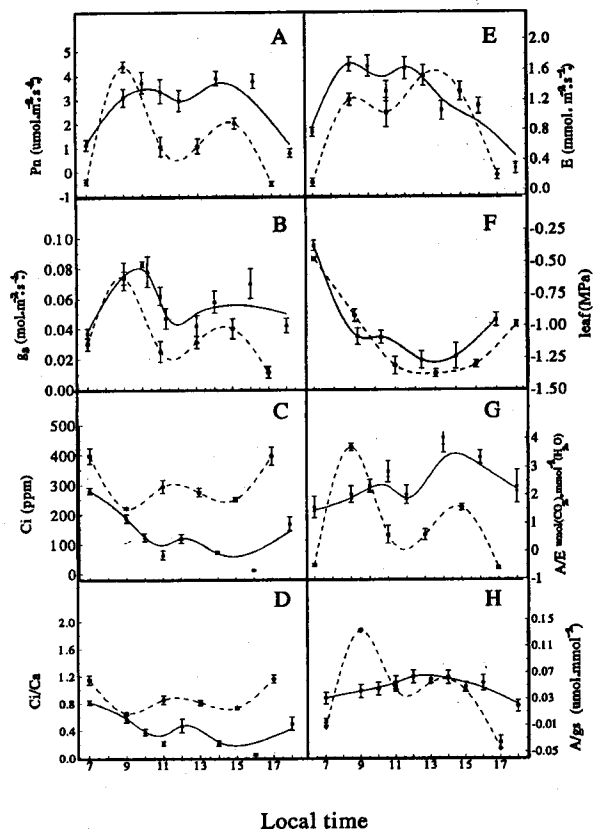


Figure 2. Diurnal changes in net photosynthetic rates, P_n (A), stomatal conductance, g_s (B), internal CO_2 concentration, C_i (C), ratio between internal CO_2 concentration and atmospheric CO_2 concentration, C_i/C_a (D), transpiration rate, E (E), leaflet water potential, Ψ_{leaf} (F), instantaneous water use efficiency, A/E (G), and intrinsic water use efficiency, A/g_s (H) in leaflets of coconut juvenile palms grown water irrigated (—) and rainfed (-----) conditions (means of 3 years data measured in April). Vertical bars indicate standard error of means ($n = 36$).

09:00 and the other at 14:00 h with the second one being higher. The E values were significantly higher in irrigated palms up to 13:00 h closely following the VPD. But from 13:00 h to 16:00 h they were significantly high in rainfed palms.

The instantaneous WUE (A/E) also had two peaks during the day in rainfed palms, one at 09:00 h and the other at 15:00 h of the day, with the first one being higher. In irrigated palms, A/E was significantly higher than rainfed ones from 10:00 h onwards. However, between 08:00 and 09:30 h it was signifi-

cantly higher in rainfed palms. The intrinsic WUE (A/g_s) also had almost similar trends. A/g_s under irrigated conditions gradually increased till 13:00 h and then slightly declined towards the dusk.

The results indicate that very high VPD causes stomatal closure, reducing the g_s , thereby reducing the E , which otherwise closely followed VPD. This consequently reduced the Ψ_{leaf} as indicated by the negative correlation of E with Ψ_{leaf} (Table 1). Such VPD- g_s relationships were noted in many plant species (Schulze, 1986). Photosynthetic rates were higher at mild VPD conditions, when the g_s was sufficient enough to maintain required C_i . In irrigated condition where E was very high relatively to P_n from 08:00 to 10:00 h, thus lowering the WUE during this period compared to the rainfed palms. During the moderate water-deficit periods, WUE is maintained high as the decrease in E was more than the decrease in P_n . Such mild stress increasing the WUE was also reported in oil palm (Dufrene and Saugier, 1993). However, when VPD increased further, the stomata started closing, decreasing P_n rates and increasing C_i and E , thus the WUE reduced drastically under such situations (11:30 to 14:30 h). This impact is much more in rainfed palms. It also occurred due to rise in leaf temperature and resulted in almost 5–7°C increase in ΔT . Stomatal regulation seems to be the first line of defensive mechanism of coconut to withstand the water-deficit conditions.

Under rainfed conditions palms had lower Ψ_{leaf} due to high VPD-driven E and also due to low water supply from the roots. These two factors led to stomatal closure, consequently reducing the thermoregulatory efficiency leading to increase in ΔT . These conditions adversely affected the photosynthetic efficiency of rainfed palms. This ultimately led to the lower assimilation and production of dry matter and thus resulting in lower nut yield under rainfed conditions. However, irrigation keeps the palm leaflets cooler as the continuous and adequate supply of water from the root system ensure the maintenance of high Ψ_{leaf} . Thus stomata are kept open resulting in high g_s . These conditions resulted in efficient thermoregulation of leaflet as E was maintained to check the increase in ΔT . These situations are favourable for high P_n rates under irrigated conditions. Such observations are supported by the variations in correlations of instantaneous and intrinsic WUE with PAR

Table 1. Correlation analysis between weather parameters (PAR, photosynthetically active radiation; T_{amb} , ambient temperature; VPD, air vapour pressure deficit; T_{leaf} , leaf temperature; ΔT , leaf to air temperature difference), photosynthetic (g_s , stomatal conductance; P_n , net photosynthetic rate; C_i , internal CO_2 concentration; C_i/C_a , ratio between internal CO_2 concentration and atmospheric CO_2 concentration), water relation parameters (Ψ_{leaf} , leaflet water potential; E , transpiration rate) and water use efficiency (WUE-A/E, instantaneous water use efficiency; WUE-A/ g_s , intrinsic water use efficiency) parameters of coconut juvenile palms grown under rainfed (R) and irrigated (I) conditions.

Parameters	Parameters											
	PAR	T_{amb}	VPD	T_{leaf}	ΔT	Ψ_{leaf}	g_s	E	P_n	C_i	C_i/C_a	WUE (A/E)
T_{amb}	0.92	*										
VPD	0.96	0.90	*									
T_{leaf}												
R	0.97	0.98	0.84	*								
I	0.97	0.99	0.83	*								
ΔT												
R	0.99	0.90	0.80	0.97	*							
I	0.98	0.93	0.86	0.98	*							
Ψ_{leaf}												
R	-0.90	-0.99	-0.78	-0.96	-0.87	*						
I	-0.91	-0.89	-0.71	-0.91	-0.88	*						
g_s												
R	-0.06	-0.19	0.40	-0.20	-0.19	0.10	*					
I	0.42	0.57	0.58	0.50	0.40	-0.55	*					
E												
R	0.81	0.74	0.78	0.75	0.71	-0.78	0.49	*				
I	0.75	0.67	0.66	0.72	0.75	-0.71	0.68	*				
P_n												
R	0.20	0.13	0.70	0.10	0.06	-0.24	0.93	0.68	*			
I	0.80	0.73	0.74	0.78	0.73	-0.83	0.77	0.73	*			
C_i												
R	-0.72	-0.63	-0.61	-0.64	-0.62	0.69	-0.61	-0.96	-0.80	*		
I	-0.68	-0.80	-0.59	-0.75	-0.66	0.69	-0.47	-0.24	-0.75	*		
C_i/C_a												
R	-0.71	-0.60	-0.60	-0.62	-0.60	0.67	-0.63	-0.96	-0.81	1.00	*	
I	-0.58	-0.71	-0.58	-0.65	-0.54	0.61	-0.49	-0.16	-0.73	0.99	*	
WUE (A/E)												
R	0.13	0.08	0.65	0.04	-0.01	-0.18	0.94	0.64	1.00	-0.76	-0.78	*
I	0.35	0.38	0.58	0.34	0.25	-0.48	0.28	-0.07	-0.61	-0.80	-0.85	*
WUE (A/ g_s)												
R	0.36	0.19	0.73	0.22	0.24	-0.28	0.90	0.76	0.95	-0.86	-0.87	0.94
I	0.91	0.75	0.58	0.82	0.85	-0.82	0.33	0.64	0.84	-0.68	-0.60	0.54

Values above 0.576 are significant at $P = 0.05$.

and other parameters. This led to higher dry matter production and nut yields under irrigated conditions.

The data also indicate that during day time E closely follows VPD, thus lowering the Ψ_{leaf} as VPD increased. The rise in ΔT was checked by increased E , thus lowering Ψ_{leaf} . The mid-day closure of stomata due to increased VPD resulted in low g_s and hampered the P_n . The stomatal response to microclimatic variations is suggested to change to maximize the

WUE, particularly under mild water-deficit conditions (Farquhar *et al.*, 1980; Cowan, 1982). Increase in C_i during mid-day-closure of stomata may help plants to avoid photoinhibition by dissipating a part of light energy for CO_2 fixation to maintain P_n rates, even though at lower rates. As VPD increased, instantaneous WUE also increased due to more decrease in g_s than P_n . This is also indicated under rainfed conditions by the increase in instantaneous WUE as VPD increased. The P_n rates and WUE were highly correlated. However, under irrigated

conditions, the proportional increase in P_n rates might be less than the increase in E , as VPD increased, consequently causing lower instantaneous WUE, also indicating the non-stomatal limitation for P_n under these situations. This indicates the limitation of P_n rates at the mesophyll level. Also, at low VPDs the transpiration reduced due to decrease in evaporation-driving forces.

In conclusion, these results indicate that the day time VPD and ΔT influence the photosynthetic characteristics and water relations of leaflets in coconut palms. Instantaneous and intrinsic WUE increased under mild water-deficit conditions. It is apparent that under rainfed conditions, the carbon assimilation efficiency was low compared to irrigated condition. The VPD and ΔT influenced the g_s and water relations during day time which predominantly determined the variations in photosynthetic efficiency of coconut under irrigated and rainfed conditions.

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References

- Ball J T and Berry J A 1982 The C_i/C_a ratio a basis for predicting stomatal control of photosynthesis-Carnegie Fast; *Washington Year Book* **81** : 88-92.
- Cowan I 1982 Regulation of water use in relation to carbon gain in higher plants; in *Physiological plant ecology II. Relations and carbon assimilation* (eds) O L Lange, P S Nobel, C B Osmond and H Ziegler - *Encyclopedia of Plant Physiology*, New Series (Berlin, Springer-Verlag) vol 12B pp 589-614.
- Dufrene E and Saugier B 1993 Gas exchange of oil palm in relation to light, vapour pressure deficit, temperature and leaf age; *Oleagineux* **48** : 347-356.
- Farquhar G D, Schulze E D and Koppers M 1980 Response to humidity of stomata of *Nicotiana glauca* L. and *Corylus avellana* L. are consistent with the optimization of carbon dioxide uptake with respect to water loss; *Aust J Plant Physiol* **7** : 315-327.
- Flore J A and Lakso A N 1989 Environmental and physiological regulation of photosynthesis in fruit crops; *Hortic Rev* **11** : 111-157.
- Gunasekera G and Berkowitz G A 1992 Heterogeneous stomatal closure in response to drought is not a universal phenomenon; *Plant Physiol* **98** : 660-665.
- Jayasekara C, Nainanayake N P A D and Jayasekhara K S 1996 Photosynthetic characteristics and productivity of the coconut palm; *J Plantation Crops* **24** (supplement) : 538-547.
- Kalt-Torres W, Kerr P S, Usuda H and Huber S C 1988 Diurnal changes in maize leaf photosynthesis carbon exchange rate, assimilation export rate enzyme activities; *Plant Physiol* **31** : 320-323.
- Kasturi Bai K V, Rajagopal V, Balasimha D and Gopal-sundaram P 1997 Water relation, gas exchange and dry matter production of coconut (*Cocos nucifera* L.) under unirrigated and irrigated conditions; *Cord* **13** : 45-58.
- Maroco J P, Pereira J S and Manuela Chaves M 1997 Stomatal response to leaf to air vapour pressure deficit in Sahelian species; *Aust J Plant Physiol* **27** : 381-387.
- Scheyermann R, Biehler K, Stuhlfauth T and Fock H P 1991 Simultaneous gas exchange and fluorescence measurements indicate differences in the response of sunflower, bean and maize to water stress; *Photosynth Res* **27** : 189-197.
- Schulze E D 1986 Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil; *Annu Rev Plant Physiol* **37** : 247-274.
- Singh V P, Dey S K and Murthy K S 1988 Diurnal changes in photosynthesis and related characters in rice varieties; *Indian J Plant Physiol* **31** : 320-323.
- Stuhlfauth T, Scheyermann R and Fock H P 1990 Light energy dissipation under water stress conditions; *Plant Physiol* **92** : 1053-1061.