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PHOTOSYNTHETIC CHARACTERS IN DIFFERENT SHAPES OF COCONUT CANOPY UNDER IRRIGATED AND RAINFED CONDITIONS

S. NARESH KUMAR*[1] AND K.V. KASTURI BAI

Central Plantation Crops Research Institute, Kasargod, 671 124, Kerala, India

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SUMMARY

The details about the gas exchange parameters in leaves of coconut canopy in three different types of canopy shapes, viz. (i) oval shaped (ii) X- shaped and (iii) semi circle shape under rainfed and irrigated conditions are discussed. Mean photosynthesis rate (Pn), stomatal conductance (gs), internal CO_2 concentration (Ci) and transpiration rate (E) were significantly higher in irrigated palms. However, rainfed palms had significantly higher WUE. The Pn rates were higher in leaves from 2nd to 10th leaf from top and then gradually declined with increase in age of the leaf. Similar trends were observed for gs and E. The relationship between the deviations of Ci/gs and Pn indicated two types of relationship, (i) asymptotic negative relationship in irrigated condition and (ii) low relationship under rainfed conditions. The Pn rates positively correlated with specific leaf weight in irrigated condition while negatively in rainfed conditions. Four general types of leaves were found in coconut canopies, viz. (i) leaves with higher Pn and WUE than mean performance of canopy leaves, (ii) leaves with higher Pn and lower WUE, (iii) leaves with lower Pn and higher WUE and (iv) leaves with lower Pn and lower WUE (lower leaves). Oval shaped canopy is more suitable for higher photosynthesis efficiency, WUE and productivity as compared to X-shaped and semi circle shaped canopies. These results indicate that canopy shape plays a role in the overall performance of photosynthesis and water use efficiencies and productivity in coconut. Results also indicate coconut as a source-limited plant.

Key words: **Canopy, coconut, gas exchange characters, photosynthetic rates, water use efficiency**

INTRODUCTION

Coconut is a tropical perennial plantation generally grown either in irrigated or rainfed conditions, with higher yields in irrigated condition. Plant productivity is related to its photosynthetic efficiency. Coconut palm had lower photosynthetic rates among the C_3 crops (Escbach *et al.* 1982, Jayashekara *et al.* 1996, Naresh Kumar *et al.* 2002). Since coconut palms are source limited, it is essential that more understanding about photosynthetic efficiency is warranted in order to improve the productivity of these palms.

Crop productivity is mainly dependent on interception efficiency of PAR and conversion efficiency of light energy to produce dry matter. In a canopy, light interception is considered to be the most important factor in determining the gas exchange rates. The leaf of coconut is compound in nature and is called 'frond' and in this article it is referred as leaf. Thirty to forty leaves are present in a canopy. Leaves are arranged either in spiral or anti spiral arrangement and each leaf is separated by 142° from other, thus proving opportunity for all the leaves for proper light interception (Menon and Pandalai 1960). The mean light interception by coconut

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*Corresponding author, E-mail: nareshkumar.soora@gmail.com, [1]Current address: National Professor Unit, Division of Environmental Sciences, Indian Agricultural Research Institute, New Delhi-110 012 canopy though out the year was around 72 per cent under well managed conditions (Moss 1992). One leaf is emerged at almost monthly interval. In a canopy 28 to 40 leaves are present depending on the management. In general, three types of canopy shapes viz., i) oval shaped ii) X- shaped and iii) semi circle shape, are found in coconut. The photosynthetic rates and related gas exchange parameters were studied in coconut in relation leaf ontogeny (Jayashekara *et al.* 1996) but without any consideration to shape of canopy or other details such as inflorescence bearing leaves, rainfed or irrigated conditions, etc. Earlier studies indicated that photosynthetic rates were low in rainfed coconut palms (Naresh Kumar *et al.* 2002), while soil moisture conservation resulted in higher photosynthetic rates and thus higher yields (Naresh Kumar *et al.* 2006).

In coconut, measurements on photosynthetic rates and related gas exchange parameters are done in intact leaves for *in situ* estimations (Braconnier 1998, Rajagopal *et al.* 2000) and in detached leaves (Rajagopal *et al.* 1987, Jayashekara *et al.* 1996, Naresh Kumar *et al.* 2002 and 2006). Measuring photosynthetic rates in intact leaves require elevated platform as coconut palms are very tall (Gomes *et al.* 2002 a and b). This makes intact estimations more tedious, tiresome, time taking and unsafe. The gas exchange parameters did not vary significantly from intact leaf with in 150 s of detachment (Rajagopal *et al.* 1987, Braconnier 1998, Naresh Kumar *et al*. 2002, Siju Thomas *et al.* 2008). Thus, for making rapid and more number of measurements, detached leaf method is more suitable. This approach will also reduce the errors due to less number of observations that are possible while taking observations in intact leaves. Hence, in this investigation, measurements were made in detached leaves within 60 seconds of detachment. This paper gives details about the gas exchange parameters in different leaves of coconut canopy in three types of canopy shapes under rainfed and irrigated conditions.

MATERIALS AND METHODS

Three coconut palms of West Coast Tall cultivar with different types of canopy grown in irrigated and rainfed conditions were selected for the study. Palms were maintained under uniform management except for irrigation. Palms are of comparable age group of about 25 years with stabilized yielding phase. One set of palms were grown under rainfed conditions while the other set was provided with basin irrigation @ 200L/palm once in 4 days during January-May period. The gas exchange parameters on coconut leaves was estimated using portable photosynthetic system (Li COR 6400 fitted with leaf chamber of 6 cm^2 area and light source –LED source 6400-02). Before making estimations the analyzer was calibrated for CO_2 and H_2O concentrations. The leaf chamber was provided with block temperature control and the light was provided using LED light source at 1500 mmol m^{-2} s^{-1} PAR levels. In coconut photosynthesis saturates at around 1400 mmol m^{-2} s^{-1} PAR levels (Jayashkara *et al.* 1996). All other microclimatic parameters which influence the gas exchange parameter such as RH, chamber or block temperature, PAR levels are kept uniform throughout the measuring period. Flow rate was fixed at 200 mmol s^{-1}. The boundary layer was kept typically and the stomatal ratio was zero as the coconut leaflets are hypostomatus (Naresh Kumar *et al.* 2000). The gas exchange measurements were made between 9 AM to 11.30 AM keeping in view of the diurnal fluctuations (Rajagopal *et al.* 2000). The estimations were made in detached leaflets with in 60 sec. of detachment. One leaflet was detached at a time for taking measurements. In LiCOR 6400 leaf chamber is integrated with infrared gas analyzers so the stabilization is very fast for making measurements. With in 6-8 seconds of detachment the leaflet was clamped to the leaf chamber and measurements were logged till 50th second at every 2 seconds interval after stabilization of Ci. Thus, for a leaflet at least 15 readings were logged. In each leaf measurements were made at least on four leaflets form the middle of the leaf, the mean of these values formed one observation. Same leaflets were used for estimating the specific leaf weight (SLW). For this the leaflets were cut into pieces of known area and then were oven dried at 65 ^oC to constant dry weight and SLW was computed as the leaf dry weight/leaf area ratio. Observations were taken for two consecutive years during peak summer month of April. Six years mean nut yield was also collected to estimate the yield levels of experimental palms. Data were subjected to statistical analysis in GLM for finding the significance of difference using SPSS (v10.) package.

RESULTS AND DISCUSSION

In coconut population, generally three canopy shapes are found (Plate 1). The leaf orientation is well suitable for proper light interception by all leaves in oval shaped canopy. But, in X-shaped canopy the upper and middle leaves are well exposed to light leaving a congested inclination for lower leaves. Whereas, in semi circle shaped canopy, which had generally less number of eaves, lower leaves also get ample light.

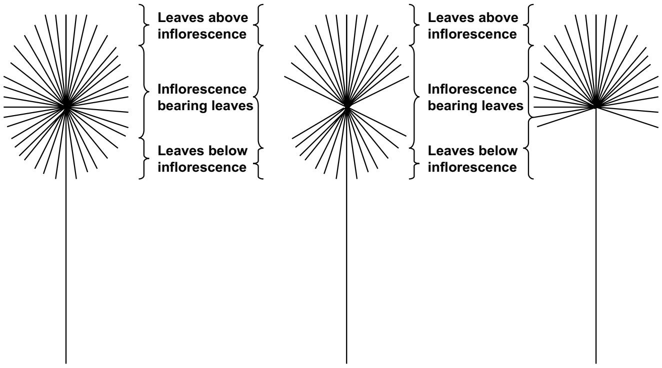

Plate 1. Three types of coconut canopy shapes

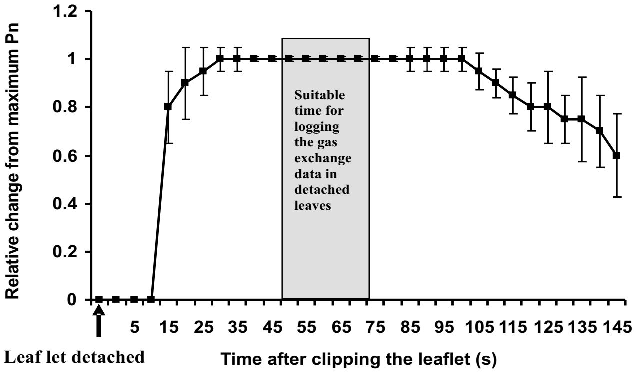

Fig. 1. Relative change in net photosynthetic rate (Pn) with time in detached coconut leaftlet. Each value represents mean of 400 observations taken at different times of a day, month and year. The X axis indicates time after clipping the leaflets and clamping to the leaf chamber of portable IRGA (LiCOR-6400). Y axis indicates change in Pn from respective maximum Pn rates at different times of measurements. Values ranged from 0-1 with 1 indicating maximum Pn. The shaded area indicates proper time for logging the gas exchange data as the Ci values are stable during this period

The stand-out experiment on stability of photosynthetic rates in detached coconut eaves indicated that the Ci gets stabilized in about 35 seconds after clamping the leaf chamber of IRGA (LiCOR-6400). Thus, in coconut adult palms, it is possible to get the values of Pn almost similar to that of intact leaf with in 70 s after detachment (Fig. 1). However, it is advisable to log the data between 45-55 s after clamping the leaf chamber as Ci is stable as also Pn and other gas exchange parameters during this period.

The photosynthetic rates in irrigated palms were significantly higher than in rainfed palms (Fig. 2a). The Pn rates were higher in leaves from 2nd to 10th leaf from top and then gradually declined with increase in age of the leaf till 18th leaf. From 19th leaf to 22nd leaf it increased and then shown a general declining trend in the lower leaves of the canopy. Generally, 16th to 22nd leaf subtend rapidly developing coconut bunch, thus causing a sink-driven increase in photosynthesis in these leaves. Younger leaves have higher Pn rates than in older leaves, thus optimizing the efficiency of light use (Lawlor 1995). In rainfed palms all leaves had lower Pn rates. Similar trends were observed for gs and E (Fig. 2b and c). Results indicate that water stress inhibited Pn rates in coconut canopy. Even though photosynthesis is insensitive to dehydration down to 50 to 70% relative water content, under long term water stress coupled with full sun-light, photo-inhibition of photosynthesis takes place. Internal carbon dioxide (Ci) concentrations were almost stable around 200 to 250 up to 26th leaf and then it increased in lower leaves (Fig. 2d). Stomatal closure caused the increased Ci in lower leaves. On the other hand in rainfed palms, even at very low gs, the Ci was maintained around 250 to 280 ppm up to 18th leaf then after it declined. This indicates that under severe water limited conditions stomatal closure causes lowering in Ci in lower leaves against the expected increase as was found in the lower most leaves where Ci shot up above 300 ppm due to reduced carboxylations rates and increased photorespiration (Oliver 1998). Water use efficiency (WUE) in irrigated palms was almost stable and similar up to the 26th leaf then after it increased in the lower leaves (Fig. 2e). On the contrary, the WUE did show fluctuations in rainfed palms up to 19th leaf. There after it increased before finally decreasing in the lower leaves. Earlier work also indicated that irrigated

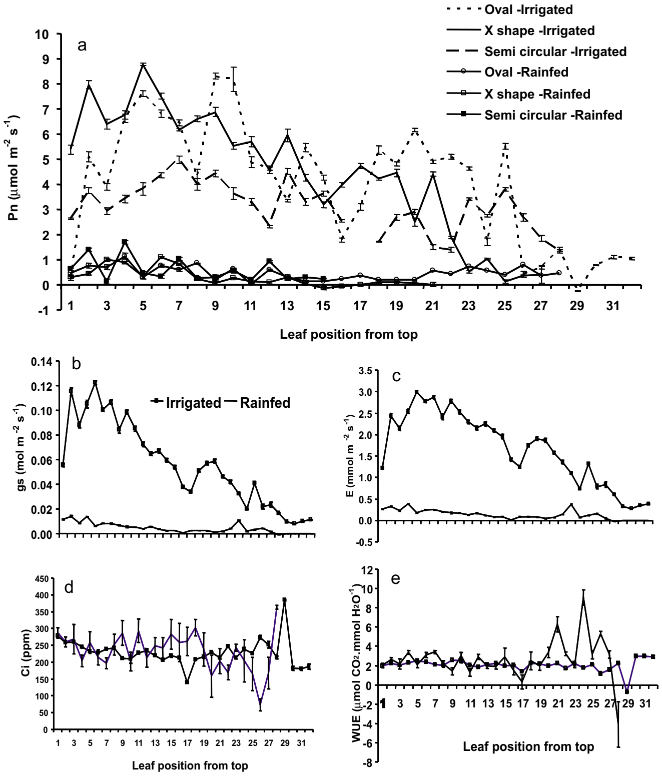

Fig. 2. Gas exchange parameters in leaves of progressive age in coconut canopy under irrigated and rainfed conditions, (a) net photosynthetic rate, (b) stomatal conductance, (c) transpiration rate, (d) water use efficiency (a- each point is a mean of 200 observations; b-e- each data point is the mean of over 600 observations)

palms had higher Pn rates than the rainfed ones (Naresh Kumar *et al.* 2002).

The shape of the canopy influenced the photosynthetic patterns in successive leaves (Fig. 1a). Results indicated that the Pn rates on top most opened leaf is lower in all shapes of canopy probably due to less chlorophyll and under-developed photosynthetic apparatus in this leaf. From the second leaf on wards till 10th leaf which form the upper whorl of canopy, Pn rates were higher. The oval shaped and X-shaped canopies had significantly higher Pn and E rates in irrigated palms while they were higher in oval shaped and semi-circular shaped canopies in rainfed conditions (Table 1). Water use efficiency was higher in semicircular and oval shaped canopies. Mean Pn rates, gs, Ci and E rates were significantly higher in irrigated palms. Gas exchange parameters varied also based on whether the leaf is bearing inflorescence or not (Table 2). Results indicate that oval shaped canopy is more suitable for higher photosynthetic efficiency and productivity in coconut as indicated by higher Pn rates, more number of leaves and also nut yield (Fig. 7) in both irrigated and rainfed conditions.

In coconut, each leaf axial has one inflorescence and thus one can get progressively growing nuts in successive bunches. In irrigated conditions, palms with oval shaped and X- shaped canopy had just opened inflorescence in the axil of 10th leaf while in semi circle shaped canopy and it was in the axial of 8th leaf. In rainfed palms, just opened inflorescence was found in the axil of 7th leaf in oval shaped and semi circular shaped canopies while in

Table 1. Mean gas exchange rates and WUE leaves of different shapes of coconut canopy under irrigated and rainfed conditions

Canopy shape/ condition	**Gas exchange characteristics**				
	Pn (µmol m^{-2} s^{-1})	**WUE (Pn/E) (µmol CO_2 mmol H_2O^{-1})**	**gs (mol m^{-2} s^{-1})**	**Ci (ppm)**	**E (µmol m^{-2} s^{-1})**
Oval -Irrigated	4.0±0.4	2.1±0.1	0.065±0.007	234.2±7.4	1.9±0.19
X shape -Irrigated	4.5±0.5	1.8±0.1	0.074±0.009	237.0±6.1	2.3±0.21
Semi circular -Irrigated	3.1±0.2	2.4±0.1	0.046±0.004	222.3±6.8	1.3±0.07
Irrigated	3.5±0.3	2.0±0.1	0.056±0.006	228.9±7.1	1.7±0.15
Oval -Rainfed	0. 5±0.1	2.6±0.4	0.005±0.001	224.8±11.8	0.2±0.02
X shape -Rainfed	0.3±0.1	2.1±0.4	0.005±0.001	267.6±12.6	0.2±0.03
Semi circular -Rainfed	0.6±0.1	3.1±0.3	0.007±0.001	229.0±14.3	0.2±0.03
Rainfed	0.4±0.1	2.6±0.4	0.004±0.001	203.6±16.7	0.1±0.02

Table 2. Mean gas exchange rates and WUE of leaves from different whorls in coconut canopy under irrigated and rainfed conditions

Canopy shape/ condition	Gas exchange characteristics					
	Pn (μmol m^{-2} s^{-1})	WUE (Pn/E) (μmol CO$_2$ mmol H$_2$O^{-1})	gs (mol m^{-2} s^{-1})	Ci (ppm)	E (μmol m^{-2} s^{-1})	Ci/Ca
Oval -Irrigated						
Leaves above inflorescence	5.5±0.8	2.0±0.2	0.101±0.014	252.8±9.9	2.54±0.34	0.71±0.03
Inflorescence bearing leaves	4.7±0.5	2.1±0.1	0.071±0.007	222.3±4.9	2.25±0.18	0.61±0.01
Leaves below inflorescence bearing ones	1.7±0.6	2.0±0.4	0.024±0.007	234.0±20.9	0.75±0.20	0.64±0.05
X shape -Irrigated						
Leaves above inflorescence	6.9±0.3	2.2±0.1	0.124±0.008	234.7±2.5	3.29±0.21	0.64±0.01
Inflorescence bearing leaves	4.5±0.3	1.9±0.1	0.065±0.005	214.6±5.4	2.33±0.13	0.60±0.01
Leaves below inflorescence bearing ones	0.5±0.2	0.8±0.1	0.014±0.004	290.4±7.9	0.56±0.11	0.78±0.02
Semi circular -Irrigated						
Leaves above inflorescence	3.7±0.3	2.5±0.2	0.0700.007	251.9±11.7	1.55±0.13	0.70±0.04
Inflorescence bearing leaves	3.2±0.2	2.5±0.1	0.043±0.005	211.5±7.5	1.36±0.11	0.54±0.05
Leaves below inflorescence bearing ones	2.3±0.3	2.2±0.2	0.031±0.003	212.7±13.8	1.10±0.09	0.59±0.03
Oval -Rainfed						
Leaves above inflorescence	0.7±0.1	2.8±0.3	0.010±0.001	235.8±16.6	0.24±0.03	0.68±0.04
Inflorescence bearing leaves	0.3±0.1	3.3±1.2	0.005±0.001	237.8±13.3	0.17±0.02	0.64±0.04
Leaves below inflorescence bearing ones	0.5±0.1	2.0±0.2	0.003±0.001	198.7±28.8	0.11±0.04	0.55±0.07
X shape -Rainfed						
Leaves above inflorescence	0.7±0.1	2.2±0.3	0.011±0.001	250.6±15.8	0.32±0.03	0.71±0.04
Inflorescence bearing leaves	0.1±0.02	2.4±0.4	0.002±0.001	287.6±13.7	0.08±0.02	0.79±0.04
Leaves below inflorescence bearing ones	0.09±0.01	1.5±0.5	0.0009±0.0001	126.8±5.6	0.009±0.0002	0.44±0.09
Semi circular -Rainfed						
Leaves above inflorescence	0.8±0.3	2.7±0.6	0.010±0.002	250.6±27.3	0.24±0.05	0.68±0.09
Inflorescence bearing leaves	0.4±0.1	3.3±0.4	0.005±0.001	214.6±14.8	0.13±0.02	0.60±0.04
Leaves below inflorescence bearing ones	0.2±0.04	1.6±0.4	0.001±0.0003	165.0±10.2	0.09±0.02	0.60±0.03

X- shaped canopy it was found in the axil of 8th leaf. Accordingly, in irrigated conditions, fully mature bunches were found in the leaf axils of 22nd leaf in palms with oval shaped and X-shaped canopy and 20th leaf in palms with semi-circle canopy. In rainfed conditions, fully mature bunches were found in the leaf axils of 19th leaf in palms with oval shaped and semi-circle canopy and 18th leaf in palms with X-shaped canopy. Interestingly, it was noted that the second, but lower peak in Pn rates was found in leaves with nuts of the age from 6th month to 11th month. This indicates that in irrigated palms photosynthetic rates in leaves having rapidly developing nuts in their axil are 'sink driven', as indicated by increase in Pn rates in these leaves. This increase is coincided with the rapid growth phase of nuts. On the other hand, no such distinct peak was observed in case of rainfed palms. This indicates that in rainfed conditions, no such 'sink driven spurt' in Pn rates can be seen mainly due to less sink demand (less number of nuts which are developing) in rainfed palms. Most assimilates for fruit development are translocated from the subtending leaves where fruits are attached (Rallo and Suarez 1989; Proietti and Tombesi 1996). The presence of active sink demand in the form of developing fruits stimulates the Pn rates (Daie 1985, Dickson 1991).

Further analysis by transforming data on WUE and Pn indicated four general relationships that existed in coconut canopies (Fig. 3) i) leaves with higher Pn and WUE than mean performance of canopy leaves ii) leaves with higher Pn and lower WUE iii) leaves with lower Pn and higher WUE and iv) leaves with lower Pn and lower WUE. The rainfed palms have more number of leaves with high WUE but low Pn rates. Lower leaves were falling in the category of low Pn with low WUE in both conditions. The oval shaped canopy had higher number of leaves with higher Pn than the mean performance of canopy rates and high WUE under both irrigated and rainfed conditions. On the other hand, X-shaped and semi circle shaped canopies had more number of leaves with low Pn rates and low WUE. These results indicate that canopy shape had played a role in the overall performance of canopy for photosynthetic and water use efficiencies.

The relationship between intrinsic water use efficiency (Pn/gs) and Pn (Fig. 4) indicated that rainfed palms had more number of leaves with high Pn/gs over mean performance of canopy. The relationship between Pn/Ci and Pn deviations had significantly positive trends under irrigated and rainfed conditions (Fig. 5a). However, the relationship between the deviations of Ci/gs and Pn (Fig. 5b) indicated two types of relationship i) asymptotic negative relationship in irrigated condition and ii) low relationship under rainfed conditions.

The correlation analysis between Pn rates and specific leaf weight indicated positive trends in irrigated condition while negative trends in rainfed conditions (Fig. 6). The initial effect of increase in Ci is the activations of RuBiSCO and subsequently there is almost linear response of assimilation rate to Ci (Farquhar and Sharkey 1982) as could be seen in irrigated palms where Pn rates were much higher than in the rainfed palms even at similar Ci. The results indicated that stomatal limitation of Pn is grater in rainfed palms while in irrigated ones it

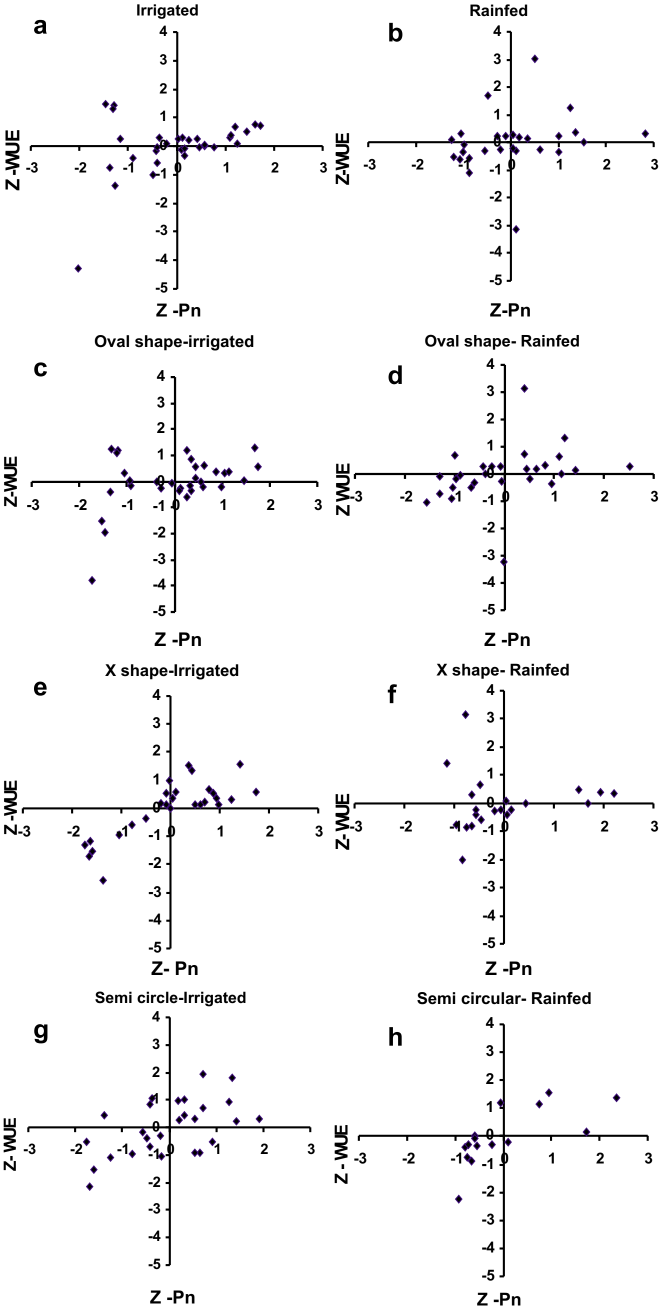

Fig. 3. Water use efficiency (WUE) in relation to net photosynthetic rates (Pn) in leaves with progressive age in three shapes of coconut canopy under irrigated and rainfed conditions (Z-WUE and Z-Pn are transformed Z- standardized values). Each point is a mean of 600 observations in a and b and over 200 observations in c to h

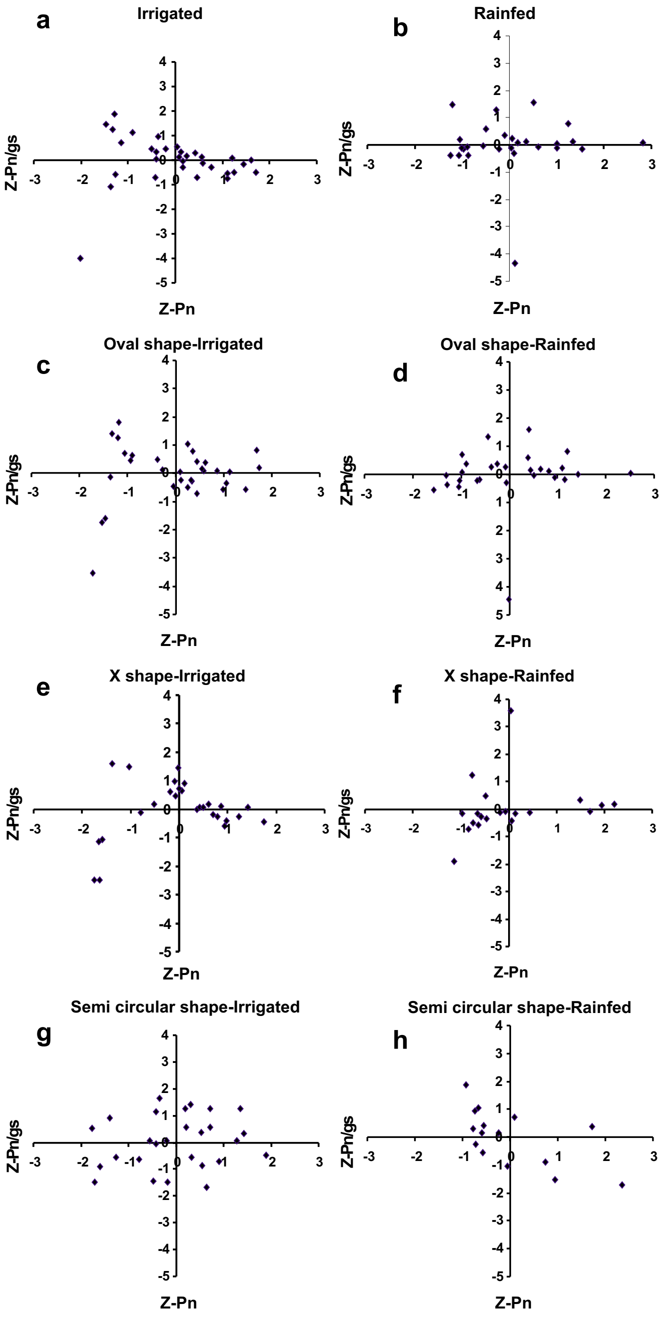

Fig. 4. Pn/gs in relation to net photosynthetic rates (Pn) in leaves with progressive age in three shapes of coconut canopy under irrigated and rainfed conditions (Z-A/gs and Z-Pn are transformed Z- standardized values). Each point is a mean of 600 observations in a and b and over 200 observations in c to h

is the non-stomatal limitation which predominates in limiting Pn. These non-stomatal limitations may be due to higher temperatures, high irradiances and mesophyll limitations. Reductions in net photosynthetic rates in water stress usually have been related to stomatal limitations due to stomatal closure (Chaves and Rodrigues 1987, Rodriguez *et al.* 1993, Delgado *et al.* 1995). However, above non-stomatal factors also may contribute towards reduction of Pn in rainfed palms.

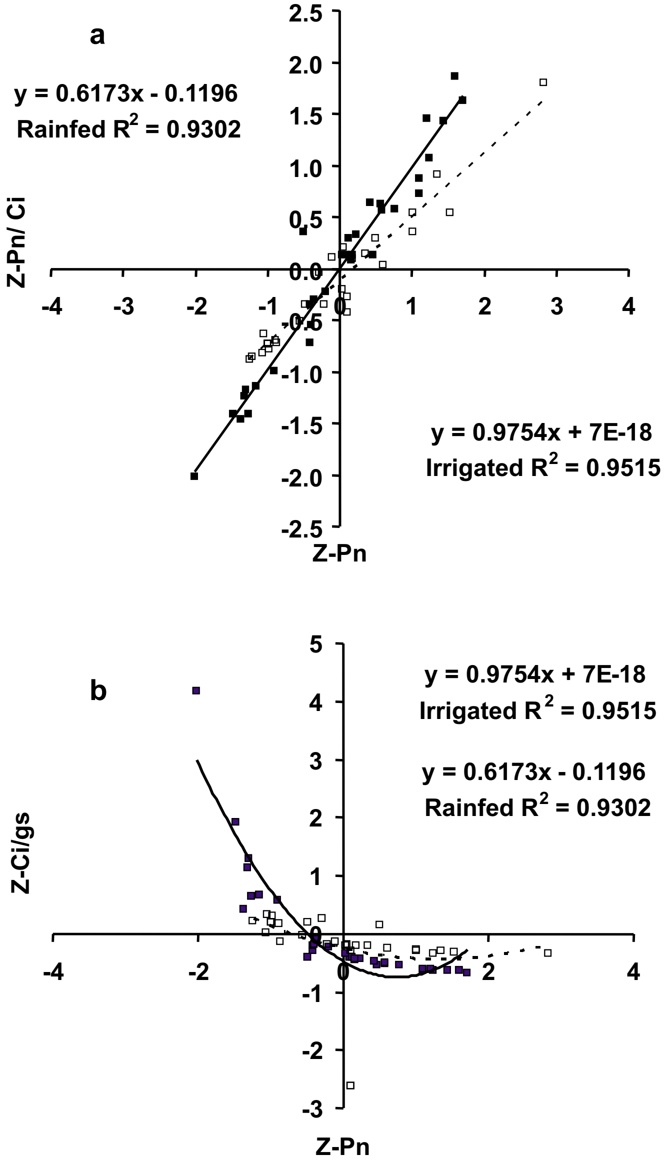

Fig. 5. Pn/Ci and Ci/gs in relation to net photosynthetic rates (Pn) in leaves with progressive age in three shapes of coconut canopy under irrigated and rainfed conditions (Z-Pn/Ci; Z-Ci/gs and Z-Pn are transformed Z- standardized values).■and solid line- irrigated; □ and dashed line- rainfed. Each data point is mean of 600 observations

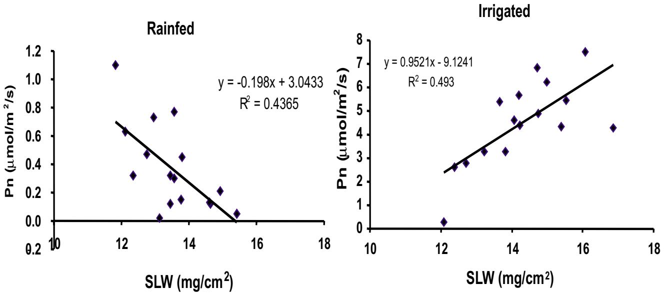

Fig. 6. Correlation between specific leaf weight and net photosynthetic rates (Pn) in leaves with progressive age in three shapes of coconut canopy under irrigated and rainfed conditions. Each data point is the mean of 600 observations

Coconut canopy intercepts 72% of incidental light (Moss 1992) and light saturation of photosynthesis occurs around 1400 mmol m^{-2} s^{-1}, typical to C$_3$ species. The Pn rates increased up to physiological maturation and then declined towards the senescence in many tree species (Hanba *et al.* 2001). However, in this experiment it is very clear that the photosynthetic capacity of leaves decrease after 10th month even after providing PAR at saturating levels. Lower gas exchange rates in rainfed coconuts palms were reported earlier as well (Rajagopal *et al.* 2000, Naresh Kumar *et al.* 2000). Results indicate that the mesophyll limitation is predominating factor in reducing the Pn rates thus contributing to low WUE in lower leaves. Overall Ci was higher in coconut around 250 indicated mesophyll limitation and CO$_2$ flux due to photorespiration particularly in lower leaves and also even in irrigated condition. This indicates coconut as a source-limited plant. Since photosynthesis is essentially related to the dry matter production and yield, high Pn rate along with size and shape of canopy should be important criteria for selection for high-yielding cultivar. In this experiment high Pn rates are in oval shaped canopy and had more number of leaves thus apparently producing more dry matter. These palms also yielded more nuts. Mostly, correlation of Pn with dry matter is via leaf area index and leaf area duration (Lawlor 1995).

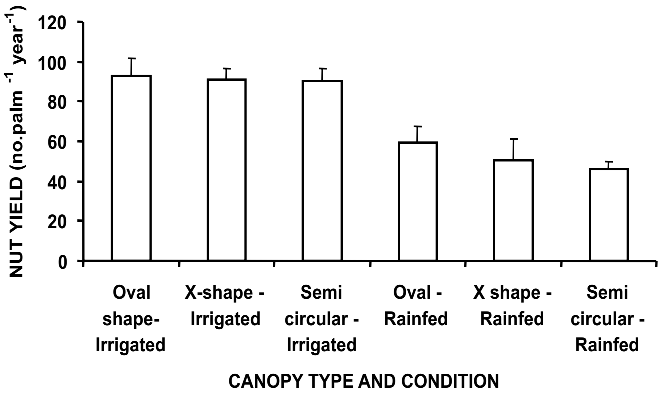

Fig. 7. Mean annual nut yield (no.palm^{-1}) in coconut palms with different canopy shapes under irrigated and rainfed conditions (mean of six years for 10 palms each)

The study revealed the superiority of oval shaped canopy in terms of both unit net photosynthetic rates and water use efficiency under both rainfed and irrigated conditions as compared to the X-shaped and semi circle shaped canopies. This indicates that the oval shaped canopy is suitable for high productivity in coconut.

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