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Influence of irrigation on leaf water relations and dry matter production in coconut palms

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Summary. The effect of different frequencies of irrigation on the leaf water relations and dry matter production of the West Coast Tall coconut palms (*Cocos nucifera* L.) was studied during two growing seasons. Irrigation was applied in amounts of 60 mm at a ratio of irrigation water to cumulative pan evaporation (I/E) of 1.0, 0.75, 0.50 and 0.0. Measurements were made of stomatal resistance, leaf water potential and epicuticular wax content, and vegetative and reproductive dry matter production. Irrigation treatments resulted in a four-to five-fold increase in the soil water deficit at I/E ratios of 0.5 and 0.0 as compared to 1.0. Coconut palms experienced severe moisture stress at an irrigation level of 0.50, resulting in a greater stomatal resistance (111%) and epicuticular wax content (32%) and reduced transpiration rate (10%), leaf water potential (68%), and reproductive dry matter production (22%), compared with well watered palms. Based on the relationship between the soil water deficit and the stomatal resistance, the critical soil water deficit for irrigation scheduling was deduced to be 110 mm. However vegetative dry matter production was reduced at much lower soil water deficits than this value.

In India the major coconut belt lies on the West Coast with Kerala State accounting for 60% of the total area of the countries 1.01 m ha of coconuts. At Kasaragod (12°30′ N, 70°00′ E, 11 m MSL) the total rainfall averages 360 cm, of which 85% is received during the South-west monsoon (June to September), 7.5% during the North-east monsoon (October–November) and 8.5% as non-seasonal rainfall. Thus, the rainless period ranges from 5 to 8 months due either to early cessation of the S.W. monsoon or failure of the N.E. monsoon and non-seasonal rains. Occasionally both can fail, as happened in 1982–1983. Total sunshine hours range from 6 to 9 h per day during dry months and 3 to 4 h per day during rainy months. Typically maximum temperatures vary between 29 °C to 34 °C with a minimum temperature of 20 °C. Solar radiation ranges from 165 W m^{-2} to 330 W m^{-2} with a vapour pressure deficit of 1.1 to 3.0×10^{-3} MPa. The mean monthly pan evaporation ranges from 2.3 to 3.6 mm day^{-1} during the rainy months and from 4.1 to 5.2 mm day^{-1} during the dry months. In most years, December to April is the rainless period with February and

March being the peak dry season. A major portion of the soil is a coastal sandy or sandy loam resulting in poor water retention. Thus during the dry months both soil and atmospheric droughts exist to varying degrees necessitating irrigation. As the palms are an important oil crop, which greatly influences the economy of not only the farmers but the entire state, their efficient management is of paramount significance.

Although traditionally, coconut is a rainfed crop, the positive influence of summer irrigation on nut production had been well established (Padmanabhan 1973; Venkitesan 1973; Bhaskaran and Leela 1978; Nelliat and Padmaja 1978). However, the critical level of soil moisture at which the crop experiences stress and reduces nut yield has not been studied for any of the coconut soils. Information is lacking on the relationship between the soil water deficit and the development of stress in coconut. This information, essential for irrigation scheduling, requires studies on plant water relations and soil water depletion. With this in view, the objective of the present work was to study the changes in stomatal resistance, leaf water potential, epicuticular wax content and dry matter production of palms with different levels of irrigation and soil water depletion.

Materials and methods

Growing conditions. Coconut palms (*Cocos nucifera* L. var. West Coast Tall) were planted in 1966 in the Institute Farm as part of a larger fertilizer and irrigation trial. The original experiment consisted of water applied (I) in amounts of 20, 40 and 60 mm at each irrigation at three frequencies based on the cumulative pan evaporation (E) between irrigations. The frequency of irrigation was varied to give treatments based on I/E ratios of 1.0 (T_1), 0.75 (T_2), 0.50 (T_3) or 0.0 (T_4), which were combined with three levels of fertilizers to give a 3^3 factorial confounded design with two replications of four palms each, at a spacing of 7.5 m × 7.5 m. This monocrop experiment existed on a red sandy loam soil. Fertilizers were applied in split doses and irrigation by sprinklers with perforated spray pipes (6 m long, 50 mm i.d. and 40 perforations on two lateral sides) placed horizontally in between the rows of palms to wet the basins.

Preliminary studies on water relations indicated no significant difference in the stomatal resistance of palms irrigated at rates of 20, 40 and 60 mm of water at a frequency equal to the rate of pan evaporation (I/E) ratio of 1.0. When water applied was 0.75 and 0.50 of E, moisture stress effects on coconut palms were more discernible at the 60 mm rate of application at each irrigation than the other two depths. Hence, this study was carried out with all irrigation amounts of 60 mm depth at different irrigation frequencies using the I/E ratios of 1.0 (T_1), 0.75 (T_2) and 0.50 (T_3). Palms maintained under rainfed conditions served as the control (T_4).

Irrigation treatments were initiated in the month of December and continued until May (1983–1984 and 1984–1985). As the irrigation schedule depended on E, the treatments T_1, T_2 and T_3 received irrigation once about every 12, 16 and 24 days respectively. This worked out to about 15, 10 and 7 cycles of irrigation during the months of December to May. Thus the total water applied through irrigation was 900 mm, 600 mm and 450 mm respectively for the three treatments. The effective rainfall during the year (average of two years) was 1396 mm. On the basis of discharge of water through the holes of the sprinkler system, the time required to achieve the desired depths of application was calculated and followed routinely.

The experiments were conducted during February and March for two consecutive years (1984 and 1985). All the measurements were taken between 10.00 and 12.00 h, the optimum period for monitoring the response to the physiological parameters.

Light, temperature and relative humidity were recorded near the experimental palms using the portable steady state porometer (Li-Cor 1600, Lambda Instruments, Nebraska, USA). Data on pan evaporation was obtained with USWB class A pan at the Institute's climatological station.

Soil moisture content was determined at four depths viz. 0–30, 30–60, 60–90 and 90–120 cm, in the basins of two palms per replication for each treatment, employing the Troxler neutron probe (model 3222, USA). This was done one day prior to irrigation for each treatment and repeated thrice during the first year and twice during the second year. From the soil moisture content data obtained, the soil water deficit (SWD) was calculated based on the field capacity at different depths.

The stomatal resistance and transpiration rate were determined using the steady state porometer with excised leaves from the middle whorl as described earlier (Rajagopal et al. 1986). Briefly, the method consisted of determination of leaf diffusive resistance and transpiration in two leaflets on the abaxial surface (hypostomatic type) of the lamina at five positions along the length on either side of the midrib. Thus ten measurements were made quickly on each palm and average of six palms per treatment was given in the table. Stomatal resistance is expressed as s cm^{-1} and transpiration rate as μg cm^{-2} s^{-1}.

Leaf water potential ψ was determined on the leaflets opposite to those used for stomatal resistance, using a Scholander pressure chamber, plant water console (model 3000, Soil Moisture Co., USA), according to the method of Milburn and Zimmermann (1977) and Rajagopal et al. (1987). ψ values are expressed as MPa.

The epicuticular wax content, ECW was extracted from the leaflets used for the above determinations by the method described by Ebercon et al. (1977). Segments 3 × 1 cm were cut from the leaflets and 20 segments were plunged into 15 ml chloroform and vigorously shaken for 15 to 20 s and decanted. This procedure extracts the wax from both the surfaces of leaflets. The colour developed with dichromate was read at 590 nm using the Perkin-Elmer spectrophotometer and ECW content was expressed as μg cm^{-2}.

Estimation of vegetative dry matter production and observations of the annual increment in stem growth, number of leaf scars and number of leaves produced per year were recorded. For the estimation of stem dry matter increment, the base just below the crown was marked by a red colour band during September. After 12 months, the increase in height of palms was measured. Number of leaf scars from this portion of the stem was counted. As there was high correlation (based on destructive sampling of 10 adult palms) between the height of leaf scar segment of the stem and dry weight ($r^2=0.8307$) from the measured annual height as well as the number of leaf scars, height of three leaf scar segment was estimated. Incorporating this in the regression equation $Y=-113.44+93.67\,x$, where x is the height of the segment, the annual dry matter increment in the stem was calculated. Leaf dry weight was determined by destructive sampling of six leaflets from the middle portion of the leaf and drying to constant weight at 80 °C. Using the regression equation $Y=-3.438+0.0197\,x_1+0.0202\,x_2$, where x_1 = dry weight of six leaflets and x_2 = number of leaflets, the dry weight of a single leaf was obtained. By multiplying this with the total number of leaves produced in a year, the annual dry matter production was calculated. For the reproductive dry matter, weight of nuts and bunches produced during the two year period (computing the data at each harvest time) was calculated by oven drying the samples at 80 °C to constant weight.

Water use efficiency, WUE was calculated by dividing the total vegetative plus reproductive dry matter produced during the year by the total water used (mm), including the effective rainfall, for each treatment (Yusuf et al. 1979). As all coconut plant parts are of economic value (nuts for oil, husk for the coir, stem as timber, leaves as thatch, spathes and spikelets as fuel) the total biomass produced was taken into consideration rather than only the nuts. According to Hillel (1972) estimation of WUE on the basis of total amount of water would be of more practical use to irrigationists and engineers.

The statistical significance of treatment differences was examined by analysis of variance.

Results

Agroclimatic conditions. Dry weather prevailed during the experimental period. When measured between 11.00 h and 12.00 h, the light intensity varied between 1,350 and 1,650 μ*E* cm^{-2} s^{-1}, with high mid-day temperatures in the range of 31.0 °C to 40.8 °C (Table 1). The vapour deficit, VPD, was between 2.9 and 5.0×10^{-3} MPa whereas daily pan evaporation varied between 5.0 and 6.9 mm. All the parameters indicated 1985 to be drier than 1984.

Table 1. Agroclimatic conditions near the experimental palms on the days when other observations were also recorded. Measurements were taken between 10.00 and 12.00 h. Values are means of six observations

Date of experiment	Light $\mu E\ m^{-2}\ s^{-1}$	Air temp. °C	VPD $\times 10^{-3}$ MPa	Daily pan evaporation mm
23 Feb 1984	1470	33.6	3.6	5.0
25 Feb 1984	1350	31.0	3.0	5.3
2 March 1984	1540	35.2	3.7	5.1
7 March 1984	1380	31.8	3.0	5.8
18 March 1984	1330	30.8	2.9	5.9
19 Feb 1985	1560	32.6	3.4	6.0
22 Feb 1985	1600	36.8	4.0	6.3
26 Feb 1985	1530	33.4	3.5	6.6
5 March 1985	1550	32.2	3.0	6.5
14 March 1985	1650	40.8	5.0	6.9

Table 2. Soil water deficit (mm) prior to irrigation in the coconut basins under different levels of irrigation. Values are averages of two basins per treatment and five determinations

Treatments	Soil depth, cm				Total profile
	0–30	30–60	60–90	90–120	
T_1	9	5	6	1	21
T_2	9	14	5	0	28
T_3	14	27	28	42	113
T_4	18	31	38	50	137
Field capacity (mm)	39	90	145	192	

Table 3. Leaf water relation characteristics in coconut palms under different levels of irrigation. *rs* – stomatal resistance, *Tr* – transpiration rate, ψ – leaf water potential, ECW – epicuticular wax content. Values are mean of six palms

Treatments	*rs* $s\ cm^{-1}$	*Tr* $\mu g\ cm^{-2}\ s^{-1}$	ψ MPa	ECW $\mu g\ cm^{-2}$
T_1	3.6	4.1	−0.9	85.2
T_2	5.0	4.1	−1.1	97.4
T_3	7.6	3.7	−1.3	112.8
T_4	15.2	1.7	−1.4	116.8
C.D. (5%)	2.0	1.3	0.2	12.3

Soil water deficit. When determined one day prior to the imposition of irrigation, the SWD was relatively low (21 mm for the total profile) in T_1 and increased in other treatments (Table 2). When irrigated with I/E ratio of 0.75 (T_2), the SWD was only 34% of that under T_1, while it was as high as 434% and 548% under T_3 and T_4. Depthwise, SWD was low below 60 cm in T_1 and T_2, increasing several-fold in the other two treatments.

Table 4. Vegetative and reproductive dry matter and water use efficiency in coconut palms under different levels of irrigation. Values are means of six palms

Treatments	Vegetative dry matter kg palm^{-1} year^{-1}	Reproductive dry matter kg palm^{-1} year^{-1}	WUE kg palm^{-1} mm^{-1} water used
T_1	52.6	93.7	0.0637 (11.1)*
T_2	44.7	74.9	0.0600 (10.5)*
T_3	43.3	73.1	0.0631 (11.0)*
T_4	42.7	66.4	0.0781 (13.7)*
C.D. (5%)	6.1	8.2	

* Values in parenthesis indicate WUE kg ha^{-1} mm^{-1} water used on the basis of 175 palms ha^{-1}

Irrigation treatments had a significant effect on the plant water relations of coconut palms. With normal irrigation (T_1) leaves had low leaf diffusive resistance, high transpiration rate and high ψ (Table 3). Reducing irrigation water by 50% (T_3) resulted in 111% increase in stomatal resistance and 10% decrease in the transpiration rate as compared to T_1. These changes in stomatal regulation resulted in a reduced ψ, from -0.9 MPa in T_1 to -1.1 MPa and -1.3 MPa in T_2 and T_3 respectively. The leaves of palms under T_1 had relatively low ECW, while imposition of stress enhanced the content, for instance, by 32% in T_3 as compared to the former. In the unirrigated palms (T_4) the stomata almost closed, as revealed by a more than four-fold increase in diffusive resistance, with drastic reduction in transpiration rate. Further decrease in ψ and a marginal increase in ECW were observed in these palms.

Dry matter production. Irrigation treatment at T_1 resulted in the annual production of 52.6 kg and 93.7 kg of vegetative and reproductive dry matter per palm per year respectively (Table 4). Exposure of palms to moisture stress for 16 or 24 days (T_2 and T_3) led to reductions of 15% and 18% in the vegetative dry matter and 20% and 22% reductions in the reproductive dry matter production as compared to those palms under T_1, whereas rainfed palms exhibited a reduction of 19% and 29% respectively.

Discussion

During the experimental period there was high evaporative demand, as shown by the environmental parameters listed in Table 1, consequently SWD varied according to the irrigation treatments. The existence of both the soil and atmospheric droughts was thus apparent. The soil water characteristics of red sandy loam soil indicated that the field capacity (corresponding to 0.03 MPa) varied from 13.5% to 18.5% volumetric moisture content from the upper to lower soil depths (0 to 120 cm), while the permanent wilting point (-1.5 MPa) varied from 7.5% to 10.9% (Joshi 1986). From this it could be deduced that the SWD ranged from 21 mm to 137 mm between T_1 and T_4. From the soil water content : potential curve (Joshi 1986), it was seen that the treatments T_1 and T_2 had soil water potentials between -0.03 and -0.09 MPa. Irrigating the palms at T_3 resulted in increased SWD corresponding to soil water potentials between −0.5 to −0.75 MPa. There was further reduction in the soil water potential of rainfed plots. The relationship between the changes in soil water potential and plant response is well established (Slatyer 1967; Turner 1974; Blum 1974). Changes in the soil water potential affects ψ and related physiological and biochemical processes (Turner 1979; Levitt 1980) and it has been shown (Hsiao 1973; Jones 1979) that stomatal regulation is the most sensitive parameter affected by stress conditions.

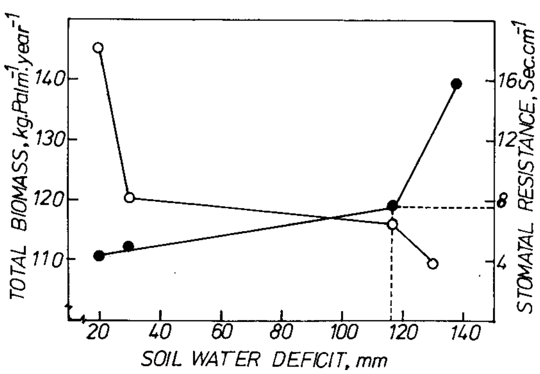
Coconut palms irrigated at an I/E ratio of 1.0 maintained normal water relations, i.e. low stomatal resistance and high ψ, while a change in the ratio to 0.5 resulted in a high degree of stress (Table 3) which could be attributed to high SWD causing low soil water potential (−0.50 to 0.75 MPa). Palms under rainfed conditions (T_4) with soil water potential less than −1.0 MPa exhibited a more than four-fold increase in stomatal resistance as compared to those under T_1. Thus, when moisture stress, caused by both atmospheric and soil droughts increases, coconut palms tend to regulate their water balance through stomatal closure to conserve water (Milburn and Zimmermann 1977). This has been reported with other crops (Turner 1974; Blum 1974), including coconut which shows differences between drought tolerance and susceptible genotypes (Rajagopal et al. unpublished).

Leaf water potential is an important parameter in the study of water relations of crop plants (Slavik 1974). When SWD increased the soil water potential to between −0.5 and −1.0 MPa (T_3 and T_4), ψ was lowered considerably. Turgid leaves of T_1 treatment had a ψ of −0.9 MPa which was reduced to −1.4 MPa in the stressed leaves of T_4. The influence of low soil water potential on stomatal resistance and ψ was reported in sorghum, maize and tobacco (Turner 1974). Present data supports the earlier findings that stomata play an important role in the regulation of water balance in coconut palms (Milburn and Zimmermann 1977; Kasturibai et al. 1988).

An adaptive mechanism which has a key role in the ability of plants to withstand water deficits is the formation of the epicuticular wax layer on the leaf surface (Hall and Jones 1961; Baker 1974). The ECW has been shown to exhibit genotypic variations in crops like sorghum (Ebercon et al. 1977), oat (Bengston et al. 1978), cocoa (Balasimha et al. 1985) and coconut (Rajagopal et al. unpublished data). As an important component in reducing the transpirational loss of water, deposition of wax on the leaf surface correlated with the drought resistance in the above crops. An increase in ECW on leaves of droughted soybeans accompanied by a reduction in transpiration was reported by Clarke and Levitt (1956). In the present study there is a clear indication of a negative relationship between ECW and transpiration rate with increasing water deficit in the T_3 and T_4 treatments. For instance, Table 3 shows that there was a significant increase in ECW (37%) with a concomitant reduction in transpiration rate (60%) in the leaves of rainfed palms as compared to normally irrigated palms. Rajagopal et al. (unpublished) found variations in ECW among coconut genotypes screened for drought tolerance.

Determination of dry matter production in a perennial crop like coconut, with leaf production at the rate of about 12 per annum, an indeterminate flowering habit with continuous nut growth and harvest almost every month, pose immense practical difficulties. Hence, preliminary studies with destructive sampling of palms was undertaken and statistically analysed for correlation with different growth components. Further non-destructive determinations were carried out using the equations as explained under the Materials and methods Section.

Fig. 1. Stomatal resistance in coconut palms (•) as a function of changes in the soil water deficit (right scale). *Horizontal dotted line* indicates $\frac{1}{2}$ max value for the stomatal resistance, while the *vertical dotted line* denote the corresponding level of soil water deficit (i.e. critical level). Relationship between the soil water deficit and total biomass (o) is drawn on the left scale. Each point represents mean of six palms



With the increase in SWD between T_1 and T_4 there was decline in the dry matter production; reproductive dry matter was more affected than the vegetative dry matter (Table 4). It is interesting to note that whereas dry matter production of trees receiving T_2 was affected to the same extent as that of T_3, the SWD in T_2 was increased only by 34% as compared to T_1. That is, although the SWD was considerably lower in T_2 (28 mm) than in T_3 (113 mm) the palms under T_2 also had low production of dry matter. The reason may well be that irrigations of palms could only mitigate soil but not atmospheric drought. Examination of the VPD data showed that the difference between T_1 (2.2×10^{-3} MPa) and T_2 (2.5×10^{-3} MPa) treatments was only 0.3×10^{-3} MPa. Recently Kasturibai et al. (1988) found that a VPD of 2.7×10^{-3} MPa was the critical level for stomatal closure in coconut. The significance of VPD as an important component of atmospheric drought on stomatal regulation had been well established (Schulze et al. 1974; Rajagopal and Sinha 1979). It implies that though stomatal resistance only increased by 39% in T_2 as compared to T_1, the overall photosynthetic activity, responsible for dry matter production, was affected even at T_2 level. Low SWD and low VPD, both favourable for low stomatal resistance might have been the cause of the higher dry matter production in T_1 than those in other treatments, which had both high SWD and high VPD. Thus, the latter situation represented the influence of soil drought magnified by atmospheric drought, whereas under T_1 only atmospheric drought occurred.

The WUE of rainfed coconut palms was higher than those of palms receiving irrigation. This can be attributed to the differences in the production of total biomass, which was low under T_4 as compared to T_1. The WUE trend observed in the coconut under different levels of irrigation is in agreement with that in some of the annual crops (Yusuf et al. 1979, 1980). As a tree crop with continuous vegetative growth and nut production throughout the year, the values of WUE given for coconut should not be taken as absolute but rather as approximate estimates.

The relationship between the SWD and stomatal resistance and that between SWD and the total biomass in coconut is depicted in Fig. 1. Taking 50% of maximum value of stomatal resistance as indicating the onset of stomatal closure, it appears that coconut palms are subject to severe stress when the SWD exceeds a threshold of 115 mm. This can be taken as the critical level for initiating irrigation and planning water application schedules. The total biomass response to SWD implies that coconut palms are highly sensitive to water deficit conditions in terms of overall photosynthetic activity, CO_2 assimilation, dry matter production and partitioning. It is evident that SWD has differential influence on transpiration and photosynthesis (dry matter production) as had been shown in many crops (Parson 1982; Jones 1979; Hsiao 1973).

That the water management of coconut palms during summer months is most beneficial in enhancing the nut yield is an established fact (Nelliat and Padmaja 1978). As the number of nuts produced per palm is enhanced significantly, the irrigation practice has proved to be rewarding in increasing the economic returns of even small land holders. Based on the results obtained with irrigation experiments over the years in the Institute, it has been recommended that the coconut palm should be irrigated between December and May at the rate of 200 to 250 litres of water per palm once in four days and the basins should be mulched with dry coconut leaves (Anonymous 1985). The present paper highlights the impact of moisture stress on coconut palms, and suggests the threshold level of SWD to be adopted for planning irrigation schedules.

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