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Effect of Water Stress on Coconut (*Cocos nucifera* L.) Seedlings Under Different Soil Types and Compaction Levels

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ABSTRACT. *The impact of water stress on coconut (Cocos nucifera L.) seedlings grown in different soil types viz. sandy (Weliketiya series), loamy (Wilpattu series) and clayey (Mavillu series) with two different soil that were compacted to bulk densities of 1.3 and 1.6 Mg* m^{-3} *was studied in a pot experiment under plant house environment. Changes in physiological parameters namely, transpiration, stomatal diffusive resistance, leaf water potential, rate of photosynthesis, vapour pressure deficit and leaf temperature were monitored. Among these parameters diffusive resistance and rate of photosynthesis appeared as reliable measures to determine drought stress in coconut.*

Water stress decreased net assimilation by enhancing stomatal diffusive resistance to conserve water. Leaf temperature was increased significantly in the absence of transpirational cooling and consequently enhanced the break down of chlorophyll leading to reduction in the rate of photosynthesis. These effects were more prominent in sandy and clayey soils. However, loamy soils with relatively high water holding capacity compensated many adverse effects of moisture stress. In high soil compaction the seedlings responded to stress by reduced root growth.

The results indicated significant interactions between water, soil type and soil compaction in relation to physiological measurements of coconut seedlings grown under different levels of moisture stress. These factors should be considered in replanting of coconut seedlings under different environments.

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INTRODUCTION

Coconut (*Cocos nucifera* L.) is the largest plantation crop in Sri Lanka which occupies about 25% of the national agricultural land (Perera, 1990). It is mainly grown for production of nuts despite a minor proportion being tapped for toddy. Frequent drought conditions prevailing in coconut growing areas greatly affect its growth and yield due to restricted carbon metabolism. The impact of drought on growth of young and adult coconut palms varies according to variety, intensity and duration of the drought and management of the land. Seedlings, especially being highly vulnerable to water stress, find it more difficult to establish and survive under water limiting environments.

The wide variation of soil types, existing in the main coconut growing area further complicates the situation in addition to modifications posed by the degree of soil compaction (Somasiri *et al.*, 1994). Water deficit conditions coupled with soil type and degree of compaction trigger stomatal regulation, which in turn modifies other physiological and biochemical processes related to growth (Jayasekara *et al.*, 1993; Blum, 1996). Morphological, anatomical, physiological and/or biochemical adaptations are common features of arresting moisture stress in plants (Kramer, 1983). Morphologically, rooting pattern and leaf area development and anatomically, cuticular thickness and structural variations in epidermal and guard cells play an important role in complying with water stress (Parsons, 1979). Physiological characters such as stomatal regulation and leaf water potential components (Milburn and Zimmermann, 1977), and biochemical parameters such as accumulation of proline (Christine *et al.*, 1996) and abscisic acid (Alvim *et al.*, 1979) are important measures of drought resistance.

The response of palms to water stress depends on the nature of the soil and its degree of compaction. A clear understanding of the interactive effects of water, soil type and soil compaction on the growth and the establishment of coconut seedlings is a need to assess the effects of drought on coconut. Hence, this experiment was aimed at investigating the influence of soil water stress on water relations, carbon assimilation, shoot and root growth and some biochemical aspects in seedlings of the commercial coconut cultivar CRIC 60 (*Tall* × *Tall*).

MATERIALS AND METHODS

Planting material

Six month old, open pollinated CRIC 60 (*Tall* × *Tall*) coconut seedlings were used in the experiment. The primary selection for their uniformity was made on growth parameters of the seedlings namely, height, girth at collar and the total number of leaves at the commencement of the experiment.

Soil and preparation of pots

Three soil types representing main soil textural groups *viz.* sandy (Weliketiya series), loamy (Wilpattu series) and clayey (Mavillu series) (Somasiri *et al.*, 1994) were collected from Puttalam area. Large galvanized iron pots (33 cm diameter x 85 cm height) were used in the experiments. The pots were filled with dry soil, in layers of 12.5 cm in height, up to 75 cm height amounting to a total volume of 0.067 m^3 per pot. The appropriate masses of dry soil were calculated based on the relevant bulk densities[1]. The soils were compacted to *in situ* bulk densities which were 1.3 and 1.6 Mg m^{-3}. Each soil layer was compressed with an equal number of hammerings using a weight of 750 g. When filling the top portion of the pot with soil, a soil mass equivalent to the volume of the seed nut was excluded. Seedlings were planted in pots and allowed to grow for a period of six weeks in the glass house environment before imposing water treatment.

Experimental conditions and treatments

The experiments were carried out in the plant house of the Coconut Research Institute (CRI), Lunuwila, Sri Lanka. The conditions in the plant house were; photosynthetically active radiation (PAR) ranging from 600 to 950 µmol m^{-2} s^{-1}, day and night temperatures from 30-34℃ and 28-30℃, respectively, and relative humidity of 25-45% during day and 14-27% during night. The treatments consisted of two stress regimes namely, W_1 (watered to field capacity) and W_2 (continuous withholding of water for 8 weeks), three soil textural classes namely, S_1 (sandy), S_2 (loamy) and S_3 (clayey), and two compaction levels namely, C_1 (Bulk density of 1.3 Mg m^{-3}) and C_2 (Bulk

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[1] Dry mass of the soil (g) = Volume covered by the soil (cm^3) × Bulk Density (g cm^{-3}).

density of 1.6 Mg m^{-3}). The experiments were carried out as a three factor factorial in a completely randomized design with six replicates.

Measurements

Weekly measurements of the rate of stomatal diffusive resistance (s cm^{-1}) and transpiration (μg cm^2 s^1) were taken using Li–1600 steady state porometer (LI–COR Inc., Lincoln, Nebraska, USA) and leaf water potential was measured using Scholander type pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, USA). All measurements were taken during the period of 9:00 a.m. to 10:30 a.m. during which parameters concerned showed minimum diurnal variation (Jayasekara *et al.*, 1996). At all instances the youngest, fully expanded, sun lit leaf was used for measurements. Entire set of seedlings were used for measurements, hence, there were six measurements per treatment combination.

The rates of photosynthesis (μmol m^{-2} s^{-1}), vapour pressure deficit (mb) and leaf temperature (°C) were measured using Li–6200 Portable Photosynthesis System (LI–COR Inc., Lincoln, Nebraska, USA). Three consecutive measurements were taken from each replicate per treatment combination.

Gypsum resistance blocks prepared at CRI according to Wellings *et al.* (1985) and calibrated under same soils and compactions were used for the measurement of soil moisture with 5910–A Soil Moisture Meter (Soil Moisture Equipment Corp., Santa Barbara, USA).

The total chlorophyll content of leaves (mg cm^{-2}) was measured (Arnon, 1949) using the UV–160 A, UV–VIS Recording Spectrophotometer (Shimadzu Corporation, Kyoto, Japan). Three fresh leaf disks with the diameter of 7 mm were crushed using Ultra Turrax T–25 (F.G. Bode & Co. GmbH, West Germany) with 5.0 ml of 80% Acetone for 1 min and centrifuged for 10 min at 3500 r.p.m. Chlorophyll content in the supernatant was measured by the absorbance at 645, 652 and 663 nm wave lengths. Measurements were done in duplicate. The same youngest, fully expanded, sun lit leaf was used for measurements throughout the experiment except once where a new leaf of seedlings was used at the beginning of the recovery period.

Data were analysed by the procedure of Analysis of Variance (ANOVA) using the Statistical Analysis System (SAS) computer package.

RESULTS AND DISCUSSION

The results of the analysis of variance explaining the effects of the treatments on the physiological parameters at the end of the drying period are shown in Table 1. There were significant interactions between water stress, soil type and soil compaction on transpiration rate and diffusive resistance.The effects of different levels of the main factors on rate of photosynthesis, vapour pressure deficit and the chlorophyl content were significant.

Water relations

The rate of transpiration declined with the increasing water deficit conditions in coconut seedlings (Figure 1). The variability in transpiration at the onset of treatments is mainly due to the differences in number of functional stomata in developing leaves. However, the rates of transpiration were similar during the first week of drying where seedlings were still under field capacity. This is a consequence of the rapid increase in the stomatal diffusive resistance (SDR) as observed during the imposed drying period (Figure 2) to conserve available water by the stomatal regulation.

Table 1. **Effect of water stress on different physiological parameters as revealed by analysis of variance.**

Source	Trans.	Dif. res.	Photo	VPD	Chl
Water	***	***	***	***	***
Soil	***	*	*	**	**
Comp	***	***	**	**	***
W*S	***	NS	NS	NS	NS
W*C	***	*	NS	*	NS
S*C	**	*	NS	NS	NS
W*S*C	**	*	NS	NS	NS
CV%	29.30	37.17	31.70	10.45	17.78

* $P<0.05$ ** $P<0.01$ *** $P<0.001$ NS - Not significant
Trans - transpiration rate; Dif. Res - diffusive resistance; Photo : rate of photosynthesis; VPD - vapour pressure deficit; Chl - chlorophyl content

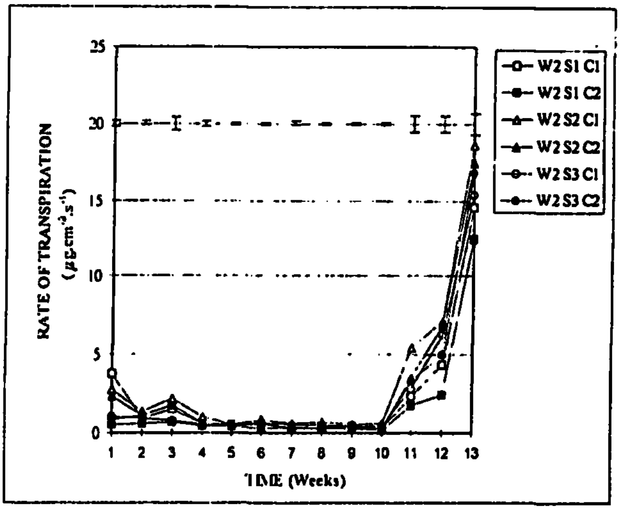

Figure 1. **Changes in rate of transpiration with water stress under different soil types and compaction levels.**

[Note: S1–Sandy, S2–Loamy, S3–Clayey, C1–Low compaction, C2–High compaction, W2 - Water treatment : Week 1–Field capacity, Weeks 2-9 : Drying, Weeks10-13:Rewatering. * Vertical bars indicate the standard error of the means.]

Coconut seedlings being relatively hardy, did not respond quickly to rewatering like a herbaceous plant. However, transpiration was increased with simultaneous decrease of stomatal resistance within a week after watering. In contrast a gradual increase in transpiration with decreasing diffusive resistance was observed in seedlings which were regularly watered (Figures 3 and 4). However, the expected increase in transpiration was not observed. This may be due to the relatively low number of stomata per unit area and higher boundary layer resistance created within the plant house although a continuous circulation of air was maintained using three exhaust fans to control the temperature and to simulate the field conditions. Under low water stress, the transpiration rate was high in loamy soil and low in sandy soil. Since the water readily percolates through largely available macro pores in sandy soil resulting in low water holding capacity, coconut seedlings experienced moisture stress within a short period of time.

The SDR increased and conversely transpiration rate is decreased with the increasing levels of compaction indicating poor absorption of water

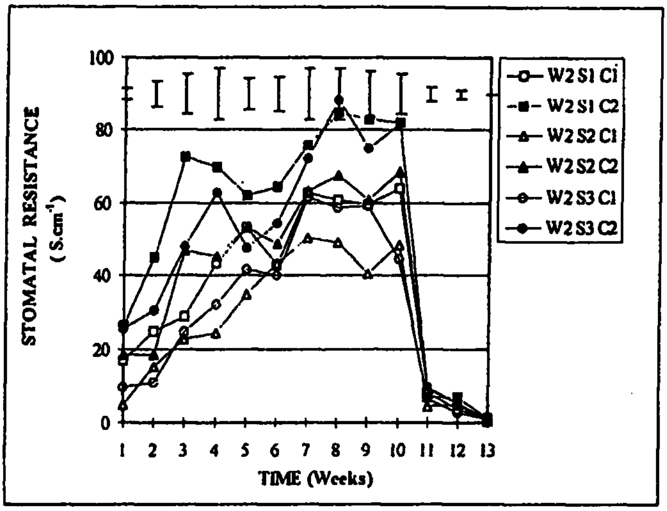

Figure 2. **Changes in stomatal diffusive resistance with water stress under different soil types and compaction levels.**
[Note: S1–Sandy, S2–Loamy, S3–Clayey, C1–Low compaction, C2–High compaction, W2 - Water treatment : Week 1 : Field capacity, Weeks 2-9 : Drying, Weeks 10-13: Rewatering. * Vertical bars indicate the standard error of the means.]

from highly compacted soil. This is supported by observations on root growth (data not shown) where the root growth was found to be retarded with the increase of compaction in all soil categories. Compaction is a barrier for water movements within the soil and root growth. The decrease in the volume of soil explored by the root system and the root surface area for water absorption under high compaction, contribute to the rapid development of stress and related changes. Possibly, the signals originating in the roots which are in stress, result in synthesis and transport of agents such as abscisic acid (ABA) which prepares the plant to arrest the situation by increasing the diffusive resistance (Walton *et al.*, 1976; Cornich and Zeevaart, 1985; Anders *et al.*, 1996).

The SDR of coconut seedlings in loamy soils with high compaction compares well to that of seedlings in sandy and clayey soils with low compaction. In sandy and clayey soils with limited available water, compaction further enhanced stress in seedlings. However, in loamy soils the high water holding capacity compensated the impact of compaction to a greater extent and the seedlings were less affected by compaction (Table 2).

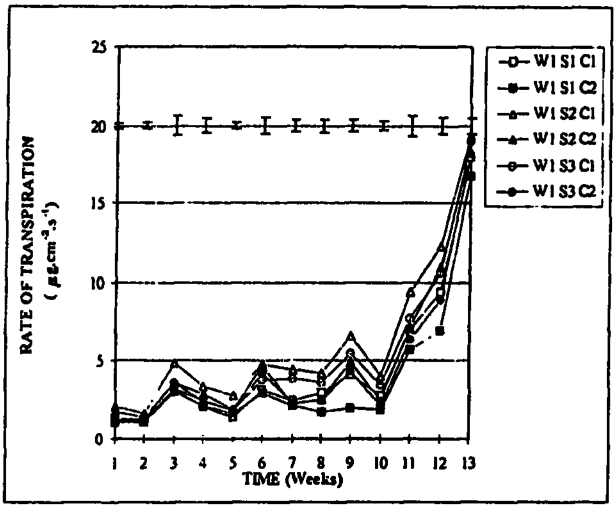

Figure 3. Changes in rate of transpiration with regular watering under different soil types and compaction levels.

[Note: S1–Sandy, S2–Loamy, S3–Clayey, C1–Low compaction, C2–High compaction, W1 : Regular watering * Vertical bars indicate standard error of the means.]

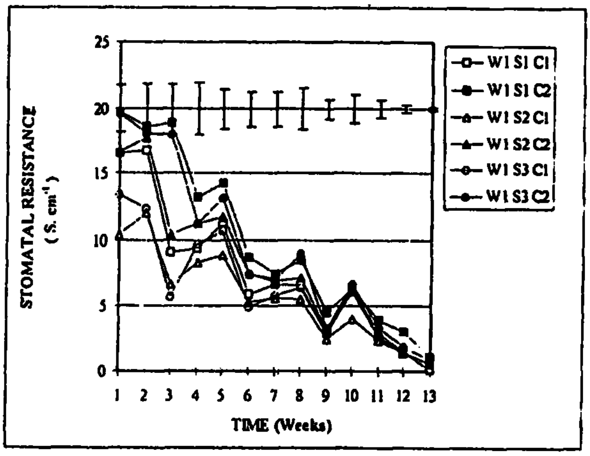

Figure 4. Changes in stomatal diffusive resistance with regular watering under different soil types and compaction levels.

[Note: S1–Sandy, S2–Loamy, S3–Clayey, C1–Low compaction, C2–High compaction, W1 - Regular watering * Vertical bars indicate the standard error of the means.]

Leaf water potential (ψ_L) did not indicate significant differences between moisture regimes or soil types or soil compaction levels. This is somewhat uncharacteristic of ψ_L since it is a very sensitive parameter of assessing water status in many herbaceous plants. In previous studies that have been conducted to assess moisture stress in young and adult coconut palms, ψ_L has also not shown any notable responses to drought stress conditions (Rajagopal *et al.*, 1993). This may be related to the hardy structure of the coconut leaves and the high stomatal regulation which causes early stomatal closure preventing further water loss and maintaining the water status of seedlings. This is supported by the extremely low values of ψ_L observed in palms only when they are severely affected by leaf scorch decline which creates a very high water stress situation within the palm (Jayasekara *et al.*, 1989).

Table 2. Mean stomatal diffusive resistance (s cm^{-1}) (Mean±standard error) in different soil types with different compaction levels and water levels at the last week of drying period.

Soil Category	C1		C2	
	W1	W2	W1	W2
Sandy	2.85±0.22	59.10±0.72	13.47±3.05	74.63±5.70
Loamy	2.48±0.22	59.58±3.84	3.12±0.33	60.75±5.20
Clayey	3.03±0.04	40.36±4.25	3.26±0.13	82.95±2.06

$P < 0.05$ Least Significant Difference = 8.37

C_1–Low compaction C_2–High compaction

W_1–Regular watering W_2–Drying for 8 weeks

Net assimilation and chlorophyll content

The net photosynthetic rate of coconut seedlings declined with increasing water stress in both levels of compaction in each soil. The average net photosynthetic rate declined from about 7 to 2 μmol m^{-2} s^{-1} at the end of the drying period (Figure 5) while regularly watered seedlings showed a gradual increase (Figure 6). The higher compaction level of all soil categories

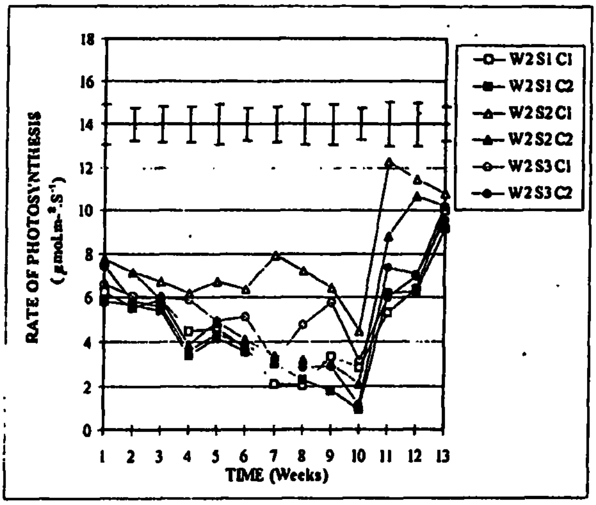

Figure 5. Changes in the rate of photosynthesis with water stress under different soil types and compaction levels.

[Note: S1–Sandy, S2–Loamy, S3–Clayey, C1–Low compaction, C2–High compaction, W2 - Water treatment : Week 1–Field capacity, Weeks 2-9 : Drying, Weeks10-13:Rewatering. * Vertical bars indicate the standard error of the means.]

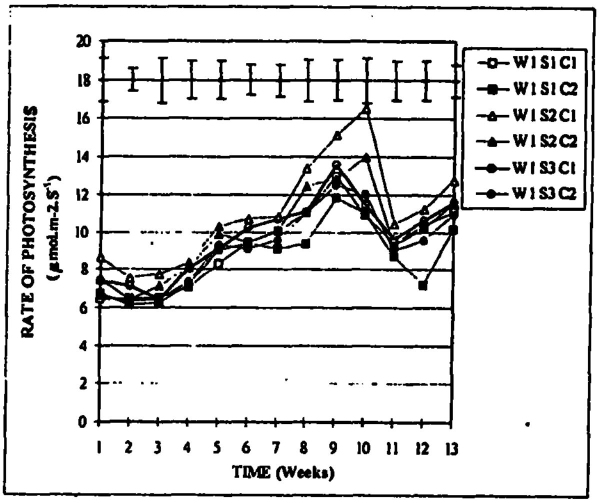

Figure 6. Changes in the rate of photosynthesis with regular watering under different soil types and compaction levels.

[Note: S1–Sandy, S2–Loamy, S3–Clayey, C1–Low compaction, C2–High compaction, Water treatment : Regular watering * Vertical bars indicate the standard error of the means.]

tend to decrease the photosynthesis possibly due to the lowered crop growth and movements of water and nutrients.

The stomatal control to conserve water under drying conditions has a direct effect on rate of assimilation as it disturbs the gaseous exchange and thereby the growth. According to Ramadasan *et al.* (1993) the rate of photosynthesis, number of leaves, chlorophyll content and nitrate reductase activity are significantly and positively correlated with growth and mean yield of coconut. In the present study, the coconut seedlings grown in loamy soil with low compaction performed relatively better maintaining a reasonably high photosynthetic rate even up to seven weeks after introducing stress and this may be due to its high water holding capacity. Generally high compaction tends to reduce photosynthetic rate due to the restricted movements of water and nutrients within the soil.

Similarly chlorophyll content also declined significantly under water stress but the decline was not so prominent in loamy soil with low compaction (Figure 7). The high photosynthetic rate in seedlings grown on loamy soils can be correlated with the chlorophyll content.

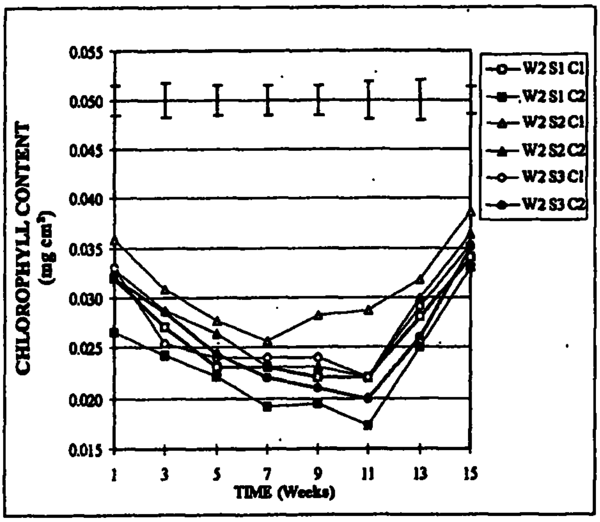

Figure 7. Changes in chlorophyll content per unit area with water stress under different soil types and compaction levels.

[Note: S1–Sandy, S2–Loamy, S3–Clayey, C1–Low compaction, C2–High compaction, W2 - Water treatment : Week 1:Field capacity, Weeks 2-9:Drying, Weeks 10-13: Rewatering. * Vertical bars indicate the standard error of the means.]

The high leaf temperature due to lowering of transpirational cooling effect with the onset of stress probably be attributed to the decline in levels of chlorophyll. The leaf temperature reached maximum of 39°C at the end of dry spell (Figure 8).

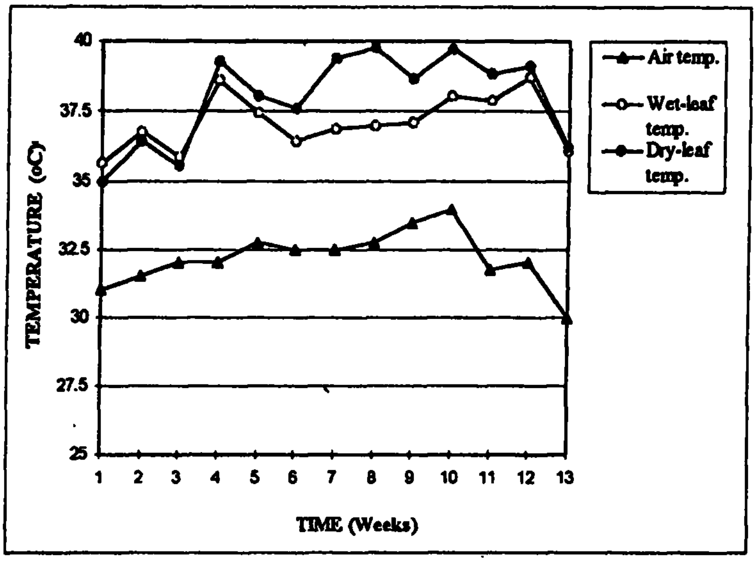

Figure 8. **Changes in temperature of air and leaf temperatures of seedlings with water treatments : Regular watering (Wet) and Drying (Dry).**

Under field capacity the chlorophyll content did not vary significantly between treatments (Figure 9) except the slight decreasing trend which probably is an effect of high temperature which was exceptional during the experimental period.

The high vapour pressure deficit (VPD) created between leaf interior and the atmospheric air due to the restricted movements through may also reduce photosynthesis under water stress. The VPD was significantly ($P<0.05$) high in sandy soil (44.89 mb) compared to loamy soil (40.61 mb). Under different levels of compaction VPD remains unchanged in field capacity while it changed drastically under stress (Table 3) reducing the rate of photosynthesis.

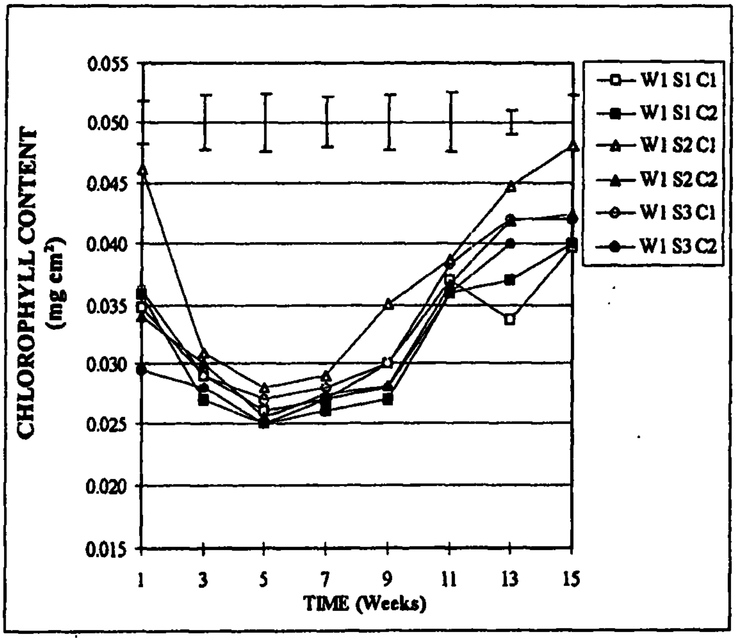

Figure 9. **Changes in chlorophyll content per unit area with regular watering under different soil types and compaction levels.** [Note: S1–Sandy, S2–Loamy, S3–Clayey, C1–Low compaction, C2–High compaction, W1 - Regular watering * Vertical bars indicate standard error of the means.]

Table 3. **Mean vapour pressure deficit (mb) (Mean±standard deviation) in different soil types with different compaction levels and water levels at the last week of drying period.**

	C1	C2
W1	33.20±0.75	34.33±0.86
W2	47.81±1.62	53.47±1.07

$P < 0.05$ LSD = 8.37

C_1–Low compaction C_2–High compaction

W_1–Regular watering W_2–Drying for 8 weeks

CONCLUSIONS

Water greatly affects the growth of coconut seedlings and the stress developed by moisture limitation is modified by the soil characteristics mainly, texture and compaction. Seedlings perform better in loamy soils even under stress with respect to water relation, with high carbon assimilation. The soil compaction affects adversely on the rate of photosynthesis and transpiration causing difficulties for seedlings to establish and survive. The loamy soils can compensate, to a certain extent, to most attributes of stress due to its capacity to hold more water and keeping it available for the coconut seedlings. These information elucidate many interactions between water, soil and soil compaction which are useful factors to be considered in replanting of coconut seedlings in varying environments.

Among the physiological parameters investigated, diffusive resistance and rate of photosynthesis appeared as more reliable measures of drought stress in coconut. The more widely used leaf water potential failed to detect stress accurately in the current experiment. However, more evidence is required to derive a definite conclusion.

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