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FULL-LENGTH RESEARCH ARTICLE

Soil Class, Mechanical Impedance and Irrigation: Impact on Physiological Performance in Green Dwarf Coconut

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Abstract The objective of this study was to assess the physiological aspects of young green dwarf coconut cultivated in greenhouse as a function of soil class and different compaction levels and moisture conditions. The experiment was carried out in a greenhouse, using a randomized complete block design with nine replications and with 32 treatments in a $2 \times 4 \times 4$ factorial scheme, with two soil classes—Typic Kandiudult and Umbric Dystrochrept, four compaction levels and four soil moisture conditions. Leaf predawn water potential (Ψ_w), net photosynthetic (A), stomatal conductance (gs), transpiration rates (E) and growth traits were higher in coconut grown in Umbric Dystrochrept soil. Moreover, these plants showed the highest values of maximum quantum yield of photosystem II (F_v/F_m) and leaf 'greenness' (SPAD reading) was higher, but only in the lowest soil moisture condition, when compared with Typic Kandiudult. Higher soil moisture led to a higher Ψ_w for both soil classes. Close relationship between SPAD reading and the increase in soil moisture as well as between F_v/F_m and the increase in soil moisture for coconuts grown in Typic Kandiudult soil was observed. Furthermore, good correlations were observed between Ψ_w and the increase in soil moisture in coconuts grown in both soil classes as well as between F_v/F_m and the increase in soil density in coconuts grown in Typic Kandiudult soil. Effects of soil compaction were not observed on other physiological variables. Overall, green dwarf coconut trees grown in Umbric Dystrochrept soil allowed the higher water storage, which may contribute to increases in circumference, plant height, leaf area and dry weight (leaves, stem and root) linked to high photosynthetic rates.

Keywords *Cocos nucifera* · Gas exchange · Soil density · Soil moisture · Water potential · Photosynthetic rate · Stomatal conductance · Transpiration rate

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Introduction

Coconut (*Cocos nucifera* L.) palm is of great social and economic importance for millions of people in the tropics and subtropics [20]. The coconut contributes to the livelihoods of millions of people in the developing world, not only through its production but also through employment generated by the many associated industries. It is one of the most economically important palm of the wet tropics, being found mainly in coastal areas between latitudes 20°N and 20°S of the equator [7].

In Brazil, the expansion of coconut tree cultivation to regions not conventionally cropped has resulted in a series of technological problems, most of which are still under study. Those related to soil include the occurrence of cohesive layers on the Coastal Tablelands ("*Tabuleiros Costeiros*") or compacted layers (typical of degraded areas), so that crop grows under water scarcity condition, poor aeration and mechanical resistance to root penetration unlike those that are found on the coastal plain. Mechanical impedance to root growth is one of the most important factors determining root elongation and proliferation within a soil profile [3, 13]. High levels of soil compaction can harm water absorption by the plants [6, 35] and can reduce the growth and development of the dwarf green coconut tree. Decreases in water absorption by roots formed in compacted soils can be associated with a high suberization of these roots [10]. Actually, mechanical impedance reduces the rate of extension and increases root diameter immediately below the root tip [22]. One study showed root thickening was caused by an increase in the diameter of the cortex which was, in turn, brought about by an increase in the diameter of individual cells rather than an increase in cell number [2].

The decrease in root and canopy growth and reduced stomatal conductance due to high soil mechanical resistance have been reported in several species, namely wheat [31], tomato [24], soybean [4], corn [23, 39] and papaya [6]. However, in some of these experiments, the indirect consequences of compaction (e.g., water shortage and low oxygen supply) were artificially suppressed, so that the true effect could be attributed only to the variations in the mechanical resistance imposed by the treatments. This fact shows that soil compaction can cause alterations in the growth and gas exchange besides those factors related to water availability and root respiration. Moreover, phytohormonal and nutritional imbalances may be associated with these alterations [26]. In fact, compaction can resulted in reduced nutrients and solutes concentrations in shoot and e roots, respectively, as well as increase the amount of recently assimilated dry weight required to produce new root [22, 26].

Stomatal closure associated with increased air vapor pressure deficit (VPD_{air}) may be exacerbated by water shortage in the soil caused by compaction. Stomata close in response to leaf turgor decline due to the elevated VPD_{air} in the atmosphere or to root generated chemical signals, the latter being a common response pattern of plant to drought [9]. Water stress effects on photosynthesis can be direct, as the decreased CO_2 availability caused by diffusion limitations through the stomata and the mesophyll [17, 18] or alterations of photosynthetic metabolism caused by decreased ATP and RuBP synthesis [28] or they can arise as secondary effects, especially oxidative stress [8]. In other situations, water availability and soil compaction levels can affect plant physiological performance thought alterations in leaf photosynthetic pigments content [42] or/and chlorophyll *a* fluorescence [1, 5].

Mechanical impedance can induce the abscisic acid (ABA) accumulation imitating a plant response to water stress. For instance, the decrease in the photosynthesis activity due to reduced stomatal conductance of tomato plants in compacted soils can be attributed to a chemical messenger (ABA) produced in the root tips under mechanical stress [30] and carried to the leaves through the transpiration stream [12, 39]. In compacted soil, the leaf growth rate of corn was inhibited and showed good correlation with the abscisic acid concentration in the xylem sap, coinciding with a reduction in the leaf water potential and the turgor pressure [23]. Additionally, the increase in soil mechanical resistance negatively affected gas exchange of papaya genotypes, restricting stomatal conductance, net photosynthetic rate, internal carbon dioxide concentration, and rise in leaf temperature compared to plants grown in an area without mechanical restriction [6].

Although studies considering the effect of soil mechanical resistance on coconuts plants are lacking, ABA accumulation in leaflets from coconut palms grown under drought conditions occurred before there were significant changes in predawn leaf water potentials and remained high even after 8 days of rewatering [21]. Moreover, under mild stress stomatal conductance was controlled by ABA accumulated in the leaflets, while at greater stress levels it was controlled by the leaf water status [21]. These results indicate that coconut is able to transport stomata-closing signal to the leaves when soil water depletion occurs in the rootzone [20]. Therefore, it seems reasonable to hypothesize that coconuts plant growing in the soil with higher compaction can reduce photosynthetic rates linked to stomatal closure. That said, the objective of the present study was to assess the physiological aspects of young green dwarf coconut cultivated in greenhouse as a function of soil class and different compaction levels and moisture conditions. Better understanding of genotypic responses to specific environmental factors (soil class, mechanical impedance and water stress) will contribute to improving agroclimatic zoning for coconut cultivations.

Materials and Methods

The experiment was performed at Empresa de Pesquisa Agropecuária do Estado Rio de Janeiro—PESAGRO, Campos dos Goytcazes, RJ (21°75′46″S, 41°32′42″W) in a greenhouse covered with plastic (80% transmission of the photosynthetically active radiation, maximum PAR of 1300 μmol m^{-2} s^{-1}) (Fig. 1) in 2007. The treatments were arranged in a 2 × 4 × 4 factorial design, two soil classes contrasting in mechanical impedance (e.g., Typic Kandiudult soil having increased density in the subsurface soil and Umbric Dystrochrept soil with low density), four compaction levels (increase in relation to the minimum density of 0, 30, 60 and 90% of the variation amplitude of the soil density "Δsd," the Δsd value corresponded to the difference between the maximum density—obtained in the Proctor Normal tests according to [38]), and four moisture conditions (level 2 = field capacity; levels 1, 3 and 4 were established by maintaining soil moisture at + 0.04, − 0.04 and − 0.08 m^3 m^{-3} compared to level 2—Table 1). A complete randomized design was used with nine block totalizing 96 plots, each one corresponding to a plastic pot (0.4 m × 0.6 m) with 100 L volume. An approximately 12-week-old green dwarf coconut tree with three or four leaves and 0.3–0.5-m trunk circumference was planted in the center of each pot on 15 March 2006. Urea and KCl were applied according to [37]. Weeds were controlled by hand, and spraying with acaricide and insecticide was

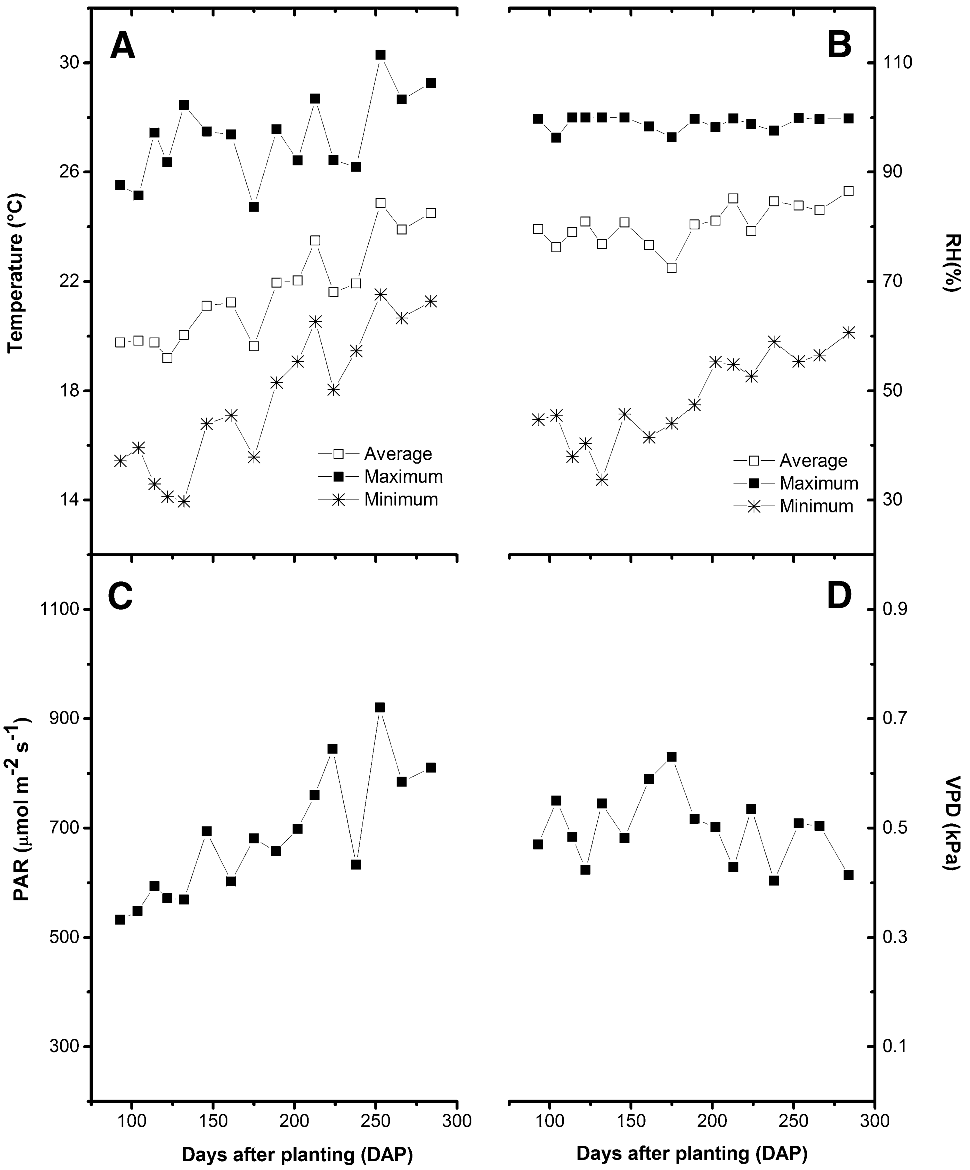

Fig. 1 Seasonal trends of air temperature (**a**), relative humidity—RH (**b**), photosynthetically active radiation (PAR) and air vapor pressure deficit—VPD inside the greenhouse during experimental time[1])

Table 1 Soil moisture and aeration porosity after implementing four moisture conditions (irrigation 1, 2, 3 and 4) on the Typic Kandiudult (PAdx) and Umbric Dystrochrept (CXbd) soils at the four compaction levels (cp1; cp2; cp3; and cp4)

Sol	Soil moisture (m^3 m^{-3})				Aeration porosity (m^3 m^{-3})			
	cp1	cp2	cp3	cp4	cp1	cp2	cp3	cp4
Irrigation 1								
PAdx	0.34	0.36	0.37	0.39	0.28	0.19	0.14	0.04
CXbd	0.41	0.42	0.43	0.44	0.18	0.14	0.07	0.03
Irrigation 2								
PAdx	0.30	0.32	0.33	0.35	0.32	0.23	0.18	0.08
CXbd	0.37	0.38	0.39	0.40	0.24	0.18	0.11	0.07
Irrigation 3								
PAdx	0.26	0.28	0.29	0.31	0.36	0.27	0.22	0.12
CXbd	0.33	0.34	0.35	0.36	0.26	0.22	0.15	0.11
Irrigation 4								
PAdx	0.22	0.24	0.25	0.27	0.40	0.31	0.26	0.16
CXbd	0.29	0.30	0.31	0.32	0.30	0.26	0.19	0.15

Increase in relation to the minimum density of 0, 30, 60 and 90% of the variation amplitude of the soil density "Δsd"

carried out whenever necessary. The temperature and relative humidity were measured using a WatchDog datalogger (Spectrum Technologies, USA), and VPD was calculated according to [25] (Fig. 1).

The physiological characteristics were determined in the 40th week (280 days after planting, DAP). The predawn water potential (Ψ_w) was determined with a Scholander pressure chamber at predawn [34], between 4 and 6 am, using the leaflets of the mid-region of developed leaves (leaf 3 or 4). Net photosynthetic rate (A), stomatal conductance (gs), transpiration (E) and leaf-to-air vapor pressure difference ($\mathrm{VPD_{leaf\text{-}air}}$) were performed between 08:00 and 10:00 am, using a portable close-system infrared gas analyzer (LI-6200, LICOR, Lincoln, NE, USA). The physiological measurements from 96 plants were taken on three consecutive days. Gas exchange measurements were made on middle leaflets from leaf number 3 and 4 (counting from the top, taking the spindle as zero) of three different plants randomly selected at each time from each treatment. The infrared gas analyzer chamber was equipped with an artificial irradiance red source (Red light LEDs, 800 μmol m^{-2} s^{-1}). The CO_2 flux was adjusted to maintain a concentration of 390 μmol m^{-2} s^{-1} inside the chamber.

Chlorophyll *a* fluorescence was measured on the same attached leaflets used for the gas exchange measurements, using the non-modulate plant efficiency analyzer fluorimeter (plant efficiency analyzer (PEA) Hansatech Ltd., Norfolk, UK). The LEDs are focused via lenses onto the leaf surface to provide even illumination over the area of leaf exposed by the leaf clip (4 mm diameter). The leaflets were dark-adapted for 30 min before an increase in the actinic light from 0 to 3500 μmol m^{-2} s^{-1}, and then F_0 (represents emission by excited chlorophyll *a* molecules in the antennae structure of Photosystem II) and F_v/F_m (widely used to indicate the maximum quantum efficiency of Photosystem II) were obtained. The green leaf color intensity ('leaf greenness') was determined by a portable chlorophyll meter (model SPAD-502, Minolta, Japan), on the same region of the leaflets shortly after measuring fluorescence. Ten leaflets were used in each plant.

Forty weeks after planting (at the end of the experiment), circumference, plant height and leaf area per plant were measured using a ruler and a LI-3100 area meter (LICOR, USA), respectively. To determine the shoot dry weight, the plants leaves and stem were oven-dried at 80 °C for 48 h.

The analysis of variance of the physiological attributes was carried out by the SAS program. The differences between the soils were identified by the F test, and the Tukey test was used to obtain the significant minimum difference at 5% probability. Differences among the compaction levels or between moisture conditions were assessed by linear polynomial or quadratic regression models fitted using the "PROJ.LIN" matrix function of the Excel electronic spreadsheet.

Results

The average temperature in the days of measurements was 24 °C with a maximum of 29 °C and minimum of 21 °C (Fig. 1a), while the average relative humidity was 85%

with a minimum of 60% (Fig. 1b). The average vapor pressure deficit (VPD) at 280 days after planting was around 0.42 kPa (Fig. 1d).

Since there were no differences among compaction and irrigation levels, only results for soil classes are shown. Coconut trees grown in Umbric Dystrochrept soil showed higher Ψ_w values (ca. 37% more) than those grown in Typic Kandiudult soil (Fig. 2a). Coconut trees grown in Umbric Dystrochrept soil presented higher s *A* (ca. 29%) and g_s values (ca. 25% than their counterparts grown in Typic Kandiudult soil (Fig. 2b, c). High g_s value observed in coconut trees grown in the Umbric Dystrochrept soil increased the transpiration rate (ca. 20%) and caused leaf cooling, reducing $\text{VPD}_{\text{leaf-air}}$ (ca. 9%) (Fig. 2d, e). Good correlation was observed between Ψ_w and the increase in soil moisture (Fig. 3a), while an excellent correlation ($r^2 = 0.96$) was observed between SPAD reading and the increase in soil moisture for coconut trees grown in Typic Kandiudult soil (Fig. 3b).

Regarding the F_v/F_m ratio, although the Umbric Dystrochrept soil had no effect on the irrigation level (general mean 0.81), for the Typic Kandiudult soil the response to soil moisture was fit to a quadratic function ($r^2 = 0.99$) with a maximum value of 0.82 (obtained when the increase in moisture was 0.03 $m^3\ m^{-3}$) and a minimum value of 0.76 (obtained at the lowest soil moisture) (Fig. 4a).

The separation of the compaction × moisture interaction showed that the irrigation level reduced F_v/F_m of the green dwarf coconut trees only at the lowest compaction (level 4, e.g., 4, − 0.08 $m^3\ m^{-3}$), fitting a quadratic function (Fig. 4b). The maximum value of 0.81 was obtained at irrigation water level 2, and this was similar to the value reported for the mean of the other compaction levels (Fig. 4b).

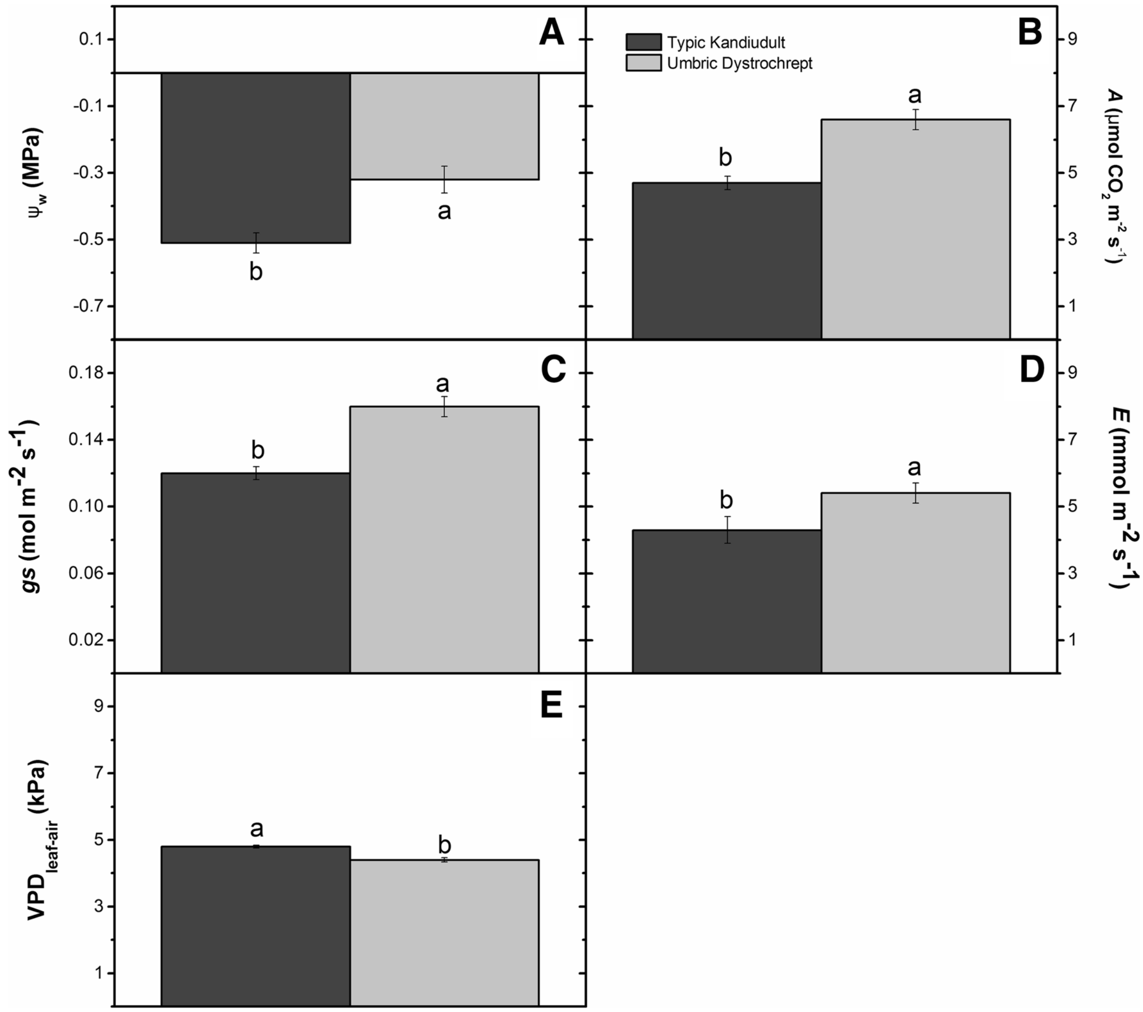

Fig. 2 Variation in the predawn leaf water potential (Ψ_w), net photosynthesis rate (*A*), stomatal conductance (*gs*), transpiration (*E*) and water vapor pressure deficit between the leaf and the air ($\text{VPD}_{\text{leaf-air}}$) in coconut trees grown in either Typic Kandiudult or Umbric Dystrochrept soil. Each value represents the mean ± SE ($n = 9$); different letters indicate significant differences between soil classes for Tukey test at 5% probability

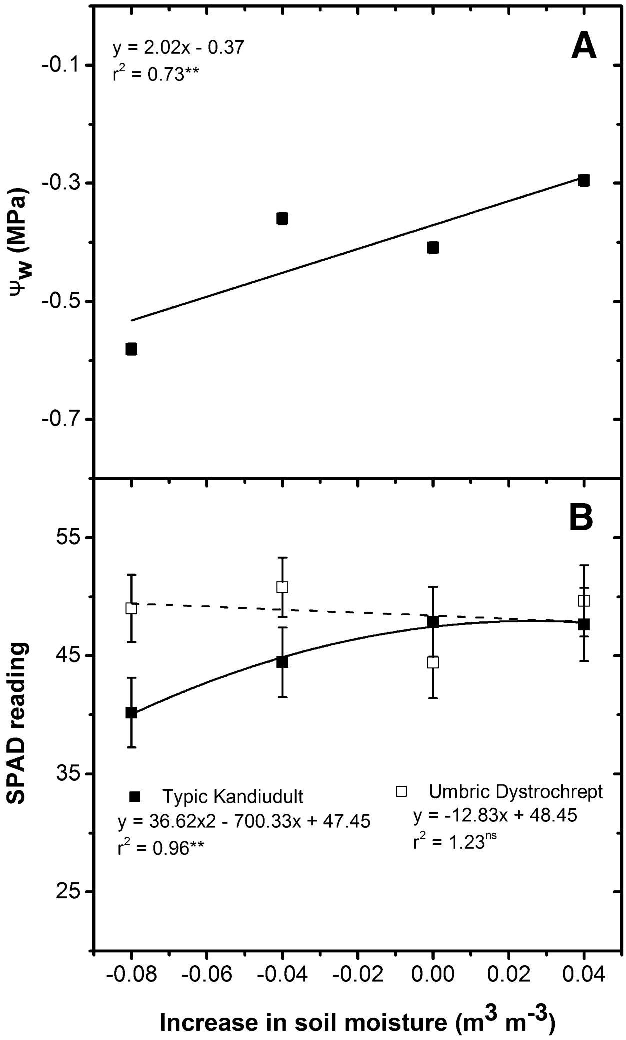

Fig. 3 Relationships between predawn leaf water potential (Ψ_w) and the increase in soil moisture (**a**) and SPAD reading and increase in soil moisture (**b**) in coconut trees grown in either Typic Kandiudult or Umbric Dystrochrept soil. Each value represents the mean ± SE ($n = 9$)

Growth was significantly affected by soil type (Fig. 5). The coconut plants grown in soil Umbric Dystrochrept had the greatest circumference (0.215 cm), height (1.43 m), leaf area (1.07 m^2) and dry weight (1,80 g) values.

Discussion

Higher CO_2 assimilation observed in coconut trees grown in Umbric Dystrochrept soil was probably due to the higher values of leaf water potential and stomatal conductance (Fig. 2). Indeed, a previous study reported that during the rainy season, g_s showed maximum values in tall coconut genotypes around 0800 h (0.25–0.30 mol m^{-2} s^{-1}) and decreased thereafter, following the reduction in ψ_w, despite the increase in irradiance toward midday [33]. In addition, the curvilinear relationship between *A* and *gs* [21] indicates stomatal limitation of *A* (by decreasing C_i) below *gs* of 0.2 mol m^{-2} s^{-1} [20]. Stomatal at increased VPD_{air} generally results in a nonlinear increase in the transpiration rate to a plateau and in some cases a decrease at high VPD_{air} [27]. In addition, stomatal responses to increased VPD_{air} generally follow an exponential decrease; however, such response varies considerably within and among species [27]. In fact, VPD_{air} is one of the most important sources of variation of g_s in coconut trees [20].

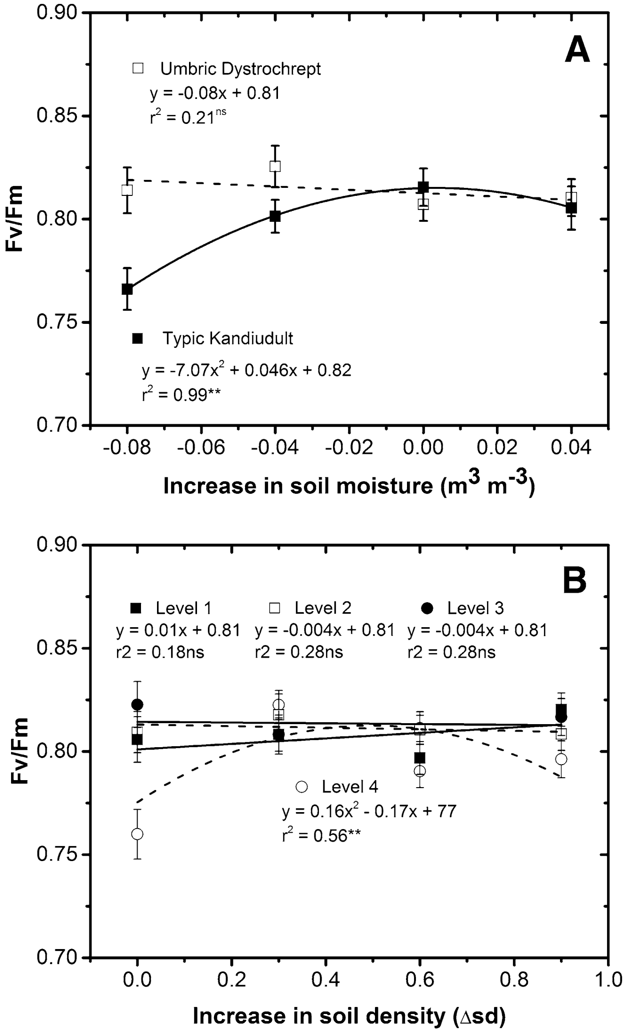

Fig. 4 Relationships between maximum quantum yield of PSII (F_v/F_m) and the increase in soil moisture and F_v/F_m in coconut trees grown in either Typic Kandiudult or Umbric Dystrochrept soil (**a**) and relationships between F_v/F_m and the increase in soil density in coconut trees grown under four irrigation level (level 1 = +0.04; level 2 = 0; level 3 = −0.04 and level 4 = −0.08 m^3 m^{-3}—**b**). Each value represents the mean ± SE ($n = 9$)

Water shortage restricts plant transpiration and can lead to heat stress. When g_s and thus evaporative heat loss decline, leaf temperature increases and causes an increase

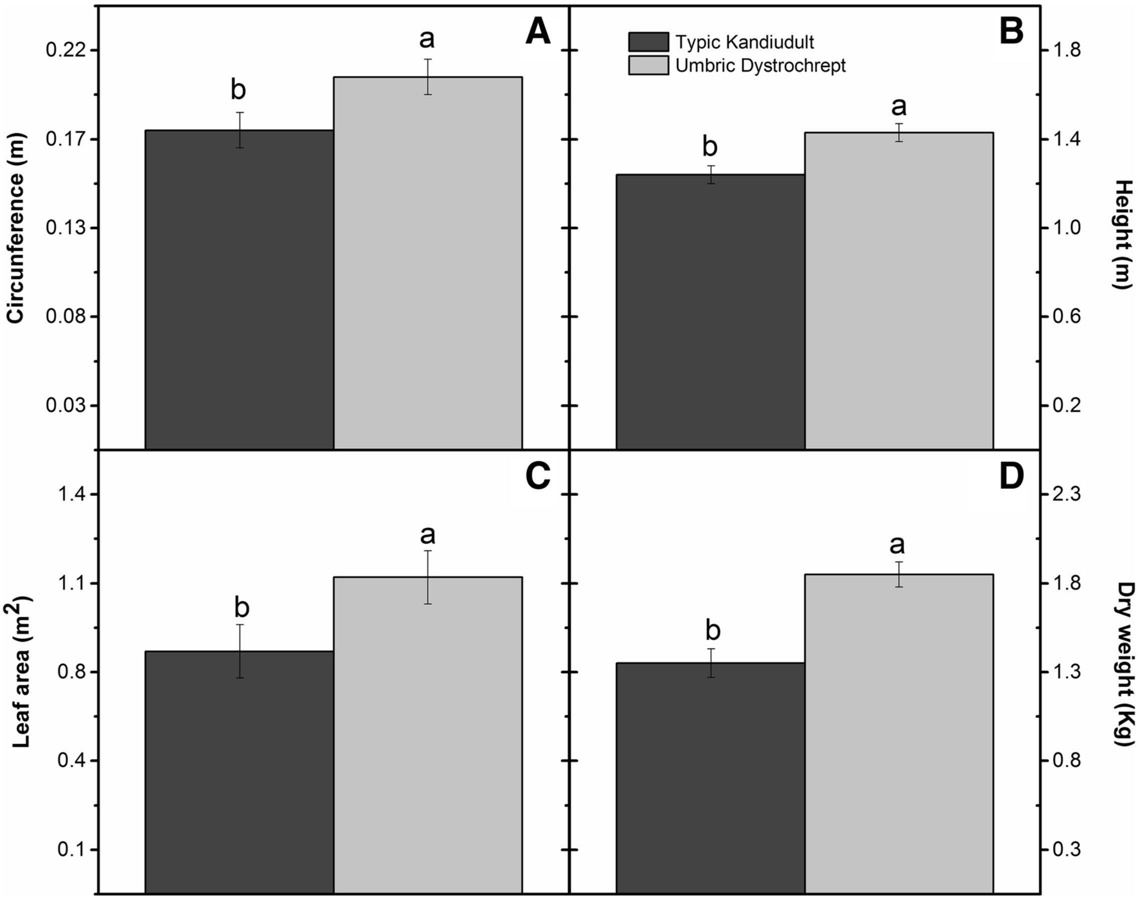

Fig. 5 Variation in the trunk circumference (**a**), height (**b**), leaf area (**c**) and dry weight (**d**) in coconut trees grown in either Typic Kandiudult or Umbric Dystrochrept soil. Each value represents the mean ± SE (n = 9); different letters indicate significant differences between soil classes for Tukey test at 5% probability

in convective heat exchange (by increasing the temperature gradient between leaf and air, e.g., $\mathrm{VPD}_{\text{leaf-air}}$) [27]. Higher heat stress might inhibit photosynthesis, damage protein stability and the membrane function that could result in damage to nutrient absorption and translocation [16, 44]. Higher g_s values found in coconut trees grown in Umbric Dystrochrept soil reduced the $\mathrm{VPD}_{\text{leaf-air}}$ and facilitated CO_2 diffusion to the carboxylation sites, and as a consequence, photosynthesis rates were increased (Fig. 2).

Predawn water potential depends on the soil water status, the root system density and depth as well as the plant height. For instance, mean daily ψ_w values in four giant coconut tree varieties of − 1.87 MPa in the dry period [32], while in the rainy period it was −1.63 MPa. Under drought conditions, ψ_w at the maximum stress point was close to − 1.25 MPa in dwarf green coconut genotypes [21]. However, the ψ_w may not reflect the soil water potential, because of the high solute concentrations in the apoplast [14] and in the xylem sap [11]. Such phenomena may occur in our work, since the treatments imposed (e.g., irrigation water levels and compaction levels) did not result in a significant decrease in ψ_w. Although the leaf water potential is a sensitive indicator of coconut water status, we observed values of ψ_w ranging from − 1.3 MPa (wet soil) to − 2.0 MPa (dry soil) at midday. [7] ψ_w of − 1.2 MPa can result incomplete stomatal closure in coconut trees during the day. Therefore, green dwarf coconut plants studied in this work did not submit the moderate or severe water stress, exhibiting a strong stomatal control of transpiration rate (Fig. 2), resulting in reduced fluctuations in the water status of plant tissues (Fig. 3) [19].

Reductions in ψ_w found in coconut tree leaves (from − 0.25 to − 1.36 MPa) did not greatly affect stomatal conductance (from 0.3 to 0.1 mol m^{-2} s^{-}1) under field conditions [32]. Here, we found great variations in ψ_w (as well as gs (Fig. 2). Therefore, the physiological responses observed (ψ_w, A, gs, E and $\mathrm{VPD}_{\text{leaf-air}}$) resulted from differences among the soil classes and not from the compaction or irrigation water level.

Independent of both compaction and water levels, greater water absorption by coconut trees grown in Umbric Dystrochrept soil may have promoted greater nitrogen absorption (that occurs preferentially by bulk flow) and resulted in higher chlorophyll values compared to the coconut plants grown in Typic Kandiudult soil, as reflected by relationships between SPAD reading and increase in soil moisture (Fig. 3b). In fact, a high positive association has been observed among nitrogen levels, leaf chlorophyll content and SPAD reading [15, 40, 41, 45]. SPAD reading values were significant at moisture levels 3 and 4 (− 0.04 and −0.08 m^3 m^{-3}), but not at moisture levels 1 and 2 (+ 0.04 and 0 m^3 m^{-3}) (Figs. 3b, 4). As portable chlorophyll meter (SPAD-502) provides an alternative method for the measurement of relative leaf chlorophyll levels [29, 40, 41], this suggested that the Umbric Dystrochrept soil had effect as a large reservoir, especially under low levels of water availability probably because there was a suitable amount of water and nutrients available to the coconut tree root system [43]. In addition, the lowest SPAD readings in the green dwarf coconut tree in the Typic Kandiudult soil and the lowest irrigation water level treatments were probably due to low water content, and affected nitrogen absorption from the soil, because all the plants in the experiment were fertilized with urea (100 g pot^{-1}).

These results show the Umbric Dystrochrept soil was less stressful to the plants than the Typic Kandiudult soil, presumably because Umbric Dystrochrept soil has a suitable water storage that might have induced less mechanical resistance to root penetration due to the major porosity of these soils. Table 1 shows that although the treatments were proportional for the soils, all the soil moisture for the Umbric Dystrochrept soil was suitable at all the compaction levels imposed. In addition, there are differences in the chemical attributes of the two soils mainly concerning the phosphorus and organic matter (OM) contents in the Umbric Dystrochrept soil (more phosphate and OM contents) (data not shown), which may also contributed to obtaining better physiological responses in the coconut trees cultivated in this soil.

Typic Kandiudult soil dwarf coconut reduced the F_v/F_m at lower irrigation treatments (Fig. 4). This showed the Umbric Dystrochrept soil under experiment conditions maintained a set of attributes favorable to the plants in a wide moisture range. Although the F_v/F_m values found are regarded optimal for many species [5], further decreases in soil moisture may reduce F_v/F_m associated with decreases in SPAD reading. In fact, SPAD readings lower than 40 can indicate early damage to the photosynthetic apparatus (Figs. 3b, 4) [40, 41].

The reduced F_v/F_m values observed in soil of both low compaction and low moisture (Fig. 4) may have been caused by moderate water stress [10]. In fact, an intimate contact between the root surface and the soil is essential for effective water absorption by the root [16]. The coconut trees presented the higher photochemical efficiency where root system did not undergo to mechanical resistance or water shortage, probably linked to higher chlorophyll content, observed by the green leaf color intensity (Fig. 3).

F_v/F_m value ranged from 0.75 up to 0.85 which indicates that coconut trees were not submitted to any type of stress [5]. Therefore, differences among treatments were especially driven by stomatal limitations among the plants for transpiration and carbon assimilation.

Our findings supported our hypothesis. Umbric Dystrochrept soil, which shows lower mechanical impedance, allows plants to maintain greater stomatal opening and transpiration rates, particularity under low moisture availability. Additionally, the higher water storage can reduce mechanical resistance to root [36]. Thus, Umbric Dystrochrept soil probably allowed greater nutrients absorption linked to further soil exploration by large root system and drag of nutrients by the transpiration stream, which may have been contributed to strengthen the photosynthetic apparatus linked to gas exchange. Consequently, the higher carbohydrates content would be available for growth. Indeed, green dwarf coconut trees grown in Umbric Dystrochrept soil showed the higher circumference, height, leaf area and total dry weight (leaves, stem and root) mainly linked to higher photosynthetic performance (Fig. 5).

Conclusions

Under conditions of low moisture availability, the coconut trees in the Umbric Dystrochrept soil treatment presented the highest ψ_w, A, gs, and E values that favored nutrient absorption from the soil and total matter accumulation over time. The leaf 'greenness' was affected by the moisture condition and soil density. There was no difference regarding the physiological responses of the coconut trees to the compaction levels established, except for F_v/F_m values at the lowest irrigation and compaction levels. However, this value showed good efficiency use of the excitation energy in photochemical process. Finally, the greater physiological traits resulted in higher circumference, height, leaf area and total dry weight in green dwarf coconut trees grown in Umbric Dystrochrept soil.

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Author Contributions ALP, CRM and EC were involved in study concept and management.ALP, CRM, EC, RRV, RSB and AT-N conducted the experiments. ALP, CRM, EC, RRV and WPR analyzed and interpreted the data. ALP, CRM, EC, RRV and WPR wrote the manuscript. ALP, CRM, EC, RRV and WPR reviewed the manuscript at the final version.

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