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Ecophysiology of the tall coconut growing under different coastal areas of northeastern Brazil

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ABSTRACT

Coconut palm is an important crop explored as a rich source of oil, fiber, milk, and water in most tropical areas. Brazil is the fifth largest producer in the world, and extensive coastal areas of Northeastern Brazil are planted with tall coconut. However, the sustainability of these coconut plantations can be affected by different abiotic stresses, including drought, mineral nutrition, and salinity. So, the objective of the present study was to evaluate the ecophysiological responses of tall coconut (*Cocos nucifera* L.) adult plants in cultivated and semi-extrativist areas on coast of Ceará state, in Northeastern Brazil. The study was carried out in four areas: Irrigated, Rainfed, *Foreiro* (coconut trees on coastland owned by the Navy and temporarily rented to private individuals) and *Preamar* (coconut trees in high-tide areas owned by the Navy). The evaluations (leaf gas exchanges, Na^+ on leaf surfaces, leaf concentrations of soluble carbohydrates, N, K, P, and Na, soil moisture, and soil electrical conductivity) were carried out in the dry and rainy seasons, between 2015 and 2017. Our results indicated that tall coconut palms were subjected to abiotic constraints in three of the four evaluated areas. Salinity and waterlogging were evident in Preamar plants; water deficit in Rainfed plants; and nutritional stress limited the crop yield in Rainfed, Preamar, and Foreiro areas. Coconut plants that grew in Foreiro area, despite the proximity to the ocean, were not subjected to salt stress, and the higher moisture in lower soil layers significantly reduced the effect of the dry season on photosynthetic rates. Seawater spray caused accumulation of Na^+ on coconut leaf surfaces, mainly in the areas close to the sea. The repeated salinity stress and waterlogging in high-tide area caused a permanent hindrance for carbon assimilation rate, limiting the capacity of fruit production by plants. Current climatic changes leading to the elevation of sea level and intrusion of sea water enhance the general concern on how to maintain these coconut plantations as source of fiber and nutrition to future generations.

1. Introduction

The coconut palm trees (*Cocos nucifera* L.) has as its origin centers the southeast and southern part of the Asian continent, according to genetic evidences and patterns of occurrence in the world (Gunn et al., 2011). Its dispersion occurred naturally, carried by oceanic currents from Southeast Asia to the Pacific and Indian oceans, and by human migration (Ribeiro et al., 2010). Considered as one of the main crops of the humid tropics, coconut is cultivated by 11 million farmers worldwide (Naresh Kumar, 2011), and its commercial exploitation is evident in approximately 93 countries, with an annual production of 60.3 million tons of fruit in about 12.3 million hectares (FAOSTAT, 2018). The top five producing countries are India, Philippines, Indonesia, Sri Lanka and Brazil. These countries show the best climatic conditions for this crop, including intense solar radiation and relatively high annual rainfall.

Coconut palm trees have been growing in Brazil for more than 450 years. Nowadays, the species is distributed along the coast, from the equator to the Tropic of Capricorn (approximately 23°26'17" south of the Equator), with the majority of the plants located on the Northeastern coast (Ribeiro et al., 2010). The Brazilian Northeastern coastline presents favorable conditions to coconut cultivation, such as sandy soils, high solar radiation balance, and precipitation above 1100 mm (Azevedo et al., 2006; Ribeiro et al., 2010). In this region it is

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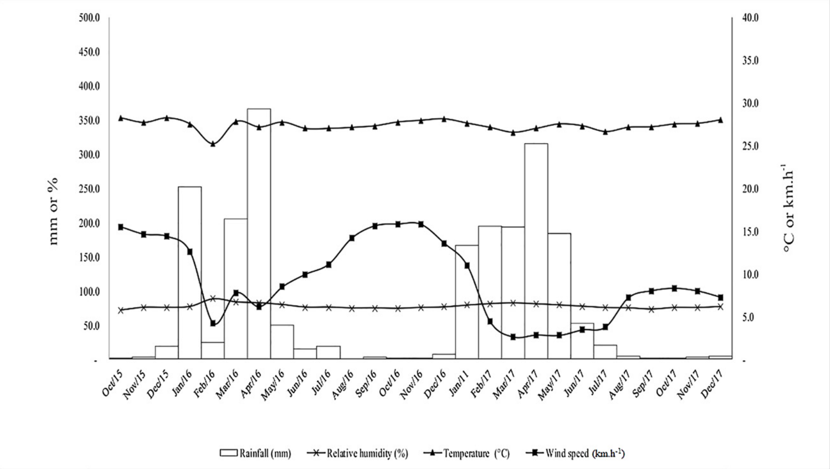

Fig. 1. Total monthly rainfall, mean air temperature, relative air humidity, and wind speed at 2.0 m height, from October 2015 to December 2017 on the coast of the State of Ceará, Brazil.

possible to find rainfed and irrigated areas cultivated with different types of coconut, i.e., tall, green dwarf, and hybrids. In addition, large areas of coconut plantation can be found close to the beaches, where the activity is considered as semi-extractive. Tall coconut predominates in rainfed and beach areas, being more rustic and tolerant to the adverse environmental factors, especially to water deficit, in relation to the hybrid and green dwarf types (Cintra et al., 2009; Ribeiro et al., 2010),

The coconut has a high water requirement (Cintra et al., 2009; Carr, 2011), each plant of tall coconut may consume from 100 to 150 L per day in irrigated areas of Northeast Brazil (Crisostomo and Naumov, 2009). On the other hand, in rainfed areas of this region the plants are subjected to many periods of water deficit throughout the year, which affect their development and production. However, this species presents a variety of morphophysiological, anatomical, and metabolic changes in response to drought, which includes: accumulation of osmoregulatory compounds, changes in leaf area and root system, presence of stomata only on the abaxial leaf surface, strong stomatal control, thick cuticle, hypodermic cell layer, epicuticular wax deposition, among others (Rillo et al., 1972; Rajagopal et al., 2005; Gomes and Prado, 2007; Gomes et al., 2010; Solangi et al., 2010; Silva et al., 2016). All these responses help plants to tolerate longer periods of water stress, but their productivity is much lower than that observed in irrigated areas, associated in many cases with the low supply of nutrients such as N, P and K (Ferreira Neto et al., 2014).

The large areas of coconut palms in the coastal areas are also subjected to seasonal water deficit, but to a lesser degree in comparison to areas far from the coast, due to the higher total annual precipitation and shallow water table. However, in these areas near to ocean the plants are subjected to the effects of salty spray or tidal elevation. This may promote salt stress in the plants, impacting plant production due to the osmotic stress, that reduces the water absorption by the roots, and specific ionic effects that interfere in the absorption of nutrients and cause toxicity (Taiz et al., 2015). The high occurrence of coconut palm trees in the coastal regions around the world leads many to believe that coconut would be a halophyte - a native plant of saline environments. However, experimental data obtained with seedlings and adult plants indicate that the coconut is a salt-tolerant glycophyte, with small reductions in growth and yield when irrigated with water of an electrical conductivity up to 5.0 dS m^{-1} (Marinho et al., 2006; Ferreira Neto et al., 2007; Lima et al., 2017).

Considering the different environments and systems of tall coconut cultivation in the coastal areas of Northeastern Brazil, it is possible to infer that plants can be subjected to a combination of different abiotic constraints (Mittler, 2006), such as water deficit, salinity and nutritional deficiency. Our hypothesis is that physiological responses can be used as indicators of the sensitivity of these cropping systems, allowing the identification of abiotic factors that contribute most to low crop yield. It is worth mentioning that little is known about the ecophysiology of tall coconut palm under conditions of water and salt stresses imposed on adult plants in these environments. Because it is a crop with long life span (60–80 years), the study of coconut ecophysiology becomes of great importance in understanding the maintenance of production under conditions of seasonal or intermittent stresses. The analysis of ecophysiological responses may also provide insights into the future of these coconut plantations in the coastal areas, which may be impacted by climate changes and sea level elevation (Renaud et al., 2015; Kheir et al., 2019). So, the objective of the present study was to evaluate the ecophysiological responses of adult plants of tall coconut palm trees (*Cocos nucifera* L.) in irrigated, rainfed and semi-extractive areas on the coast of the state of Ceará, in the northeastern region of Brazil.

2. Material and methods

2.1. Characterization of the experimental areas

The study was conducted on the coast of the state of Ceará, in the district of Icaraí de Amontada, municipality of Amontada (3°1′40″S; 39°38′57″W), CE, Brazil, from October 2015 to April 2017. The climate of the region according to Köppen's classification is Aw type (rainy tropical climate), with rainy season in summer and autumn, from January to May, and dry season from June to December. The average annual rainfall of the region is 1300 mm. The climatic data from October 2015 to December 2017 were collected by the company Ducoco Litoral SA, with an automatic meteorological station located in the municipality of Itarema (2°58′28.78″S; 39°47′31.57″W) with average distance of 15.34 km of the studied environments. The Fig. 1 shows the existence of two well-defined seasons, the rainy season (from January to May) and the dry season (from June to December), with variations in total rainfall between 2016 and 2017.

The study was carried out in different environments and systems of exploration of tall coconut on the coast of the state of Ceará, characterized as:

Irrigated System - Area located 3.5 km from the Atlantic Ocean with coordinates 3°2′20.41″S; 39°41′14.30″W, elevation 22 m;

Rainfed System - Area located 3.6 km from the Atlantic Ocean with the following coordinates: 3°2′41.29″S; 39°41′5.12″W, with an elevation of 24 m;

Foreiro area – Area near the Atlantic Ocean, located 70 m from the maximum level of the tide, with coordinates 3°1′23.12″S; 39°38′41.7″ W. It is a coastland area owned by the Navy and temporarily rented to private individuals.

Preamar area - Coconut trees in high-tide areas owned by the Navy, with the following coordinates: 3°1′24.09″S; 39°38′45.32′W. The tides of the region are semidiurnal, with interval of 12 h and 25 min between two levels of high tide, and have mean amplitude of -0.20 m at low tide to 3.2 m at high tide in relation to the current average sea level. Wave patterns are predominantly of the sea type, with the largest swell wave-type waveform records in the months of March to May. This distribution is related to the displacement of the Intertropical Convergence Zone to the south of the Equator during the first months of the year.

The Irrigated and Rainfed areas belong to the COHIBRA Company (Comércio de Cocos Hybridos do Brasil Ltda). Irrigation was performed daily, using a micro sprinkler system with a flow rate of 4.0 L h^{-1}, and applying a total of 220 L per plant day^{-1}.Water from a small dam with low electrical conductivity (ECw = 0.8 dS m^{-1}) was used for all events of irrigation. In Rainfed, Preamar and Foreiro areas the water supply for coconut plants was provided only by rainfall, as shown in Fig. 1.

The soil of the four areas was classified as Arenosols, according to World Reference Base for Soil Resources (FAO, 2015) or Quartzipsamments as per Brazilian System of Soil Classification (EMBRAPA, 2013). Soil samples of the 0–30 and 30 − 60 cm layers indicated that all areas present sandy texture, with 93.6–95.4 % of sand, 3.1–3.9 % of silt, and 1.5–2.5 % of clay. The soil moisture percentage (on weight basis) at field capacity (-0.01 MPa) and permanent wilting point (-1.5 MPa) ranged from 6.1-7.2% and 0.9–1.2 %, respectively. All areas presented low cation exchange capacity (mean value of 3.15 $cmol_c$ dm^{-3} at 0 − 30 cm soil layer) and no aluminum toxicity problems. The mean values of pH and electrical conductivity of 1:1 soil water extract ($EC_{1:1}$) were, respectively: 7.1 and 0.29 dS m^{-1} for the Irrigated area; 6.4 and 0.16 dS m^{-1} for the Rainfed area; 8.2 and 0.35 dS m^{-1} for the Foreiro area; and 8.3 and 1.8 dS m^{-1} for the Preamar area.

2.2. Selection and initial characterization of plants

In each of the evaluated systems, ten tall coconut plants (*Cocos nucifera* L.) were randomly selected. The data collection started in the dry season of 2015, when biometric measurements (plant height, trunk diameter, and leaflets per leaf) of the selected plants were carried out (Table 1). According to information from COHIBRA Company and farmers, the evaluated plants are aged between 30 and 40 years, within their peak production stage (Aragão et al., 1999).

The other soil and plant samplings were carried out in two distinct seasons, dry and rainy, for two years, in October 2015, May 2016, September 2016 and April 2017. All plant evaluations were performed on the leaf 14 (counting from the apex), located in the middle of the coconut canopy, being considered as the reference leaf for mineral nutrition studies of coconut (Frémond et al., 1966; Ferreira et al., 1997). For analysis whole leaves were collected with the aid of a metal stick.

2.3. Soil moisture and salinity

At each evaluation period, soil samples were collected in different depths (0–30, 30–60, 60–90 and 90–120 cm) to determine the soil moisture and salinity. Soil moisture was determined by gravimetric method. The electrical conductivity of the soil was estimated in a soil:water (1:1) extract ($EC_{1:1}$), being the readings obtained directly in the suspension in a conductivimeter (model MA521, Marconi) with automatic temperature compensation. All soil sampling were performed in the morning, between the first daily low and high tides.

Table 1
Mean values of plant height (PH), stem diameter (SD) and number of leaflets per leaf of tall coconut trees (*Cocos nucifera* L.) in different production areas.

Areas	PH (m)	SD (cm)	Leaflets per leaf
Irrigated	9.01 ± 0.30	27.32 ± 0.62	222.06 ± 1.95
Rainfed	8.43 ± 0.23	25.61 ± 0.61	214.60 ± 1.77
Foreiro	12.22 ± 0.17	25.88 ± 0.77	201.43 ± 3.38
Preamar	11.52 ± 0.41	26.24 ± 0.98	183.53 ± 3.14

*values represent the mean ± standard error of the mean. n = 10.

2.4. Leaf gas exchange

Measurements of the CO_2 assimilation rate (*A*, μmol m^{-2} s^{-1}), transpiration (*E*, mmol m^{-2} s^{-1}), stomatal conductance (g_s, mol m^{-2} s^{-1}), and internal concentration of CO_2 (*Ci*, μmol mol^{-1}) were performed in six plants of each area on leaflets of the medial region of leaf 14, fully expanded. An infrared gas analyser (IRGA, model LI-6400XT, Li-Cor, USA) was used, and the readings were performed between 8:00 am and 11:00 am, under saturating photosynthetically active radiation (1600 μmol m^{-2} s^{-1}), air flow rate of 500 μmol s^{-1}, concentration of CO_2 of 380 μmol mol^{-1}, and environmental conditions of humidity and air temperature. These measurements were carried out in two distinct seasons, dry and rainy, for two years, in October 2015, May 2016, September 2016 and April 2017.

2.5. Sodium accumulation on leaf surface

In order to evaluate the effect of the sea water spray, samples of the same leaves used for leaf gas exchange measurements were collected and immediately washed in distilled water, using similar samples size and volume of water. In the aqueous extract the Na^+ concentration was determined using a flame photometer (model 910 M, Analyser), according to Malavolta et al. (1997), and the amount accumulated on the leaf surface was estimated and expressed in mg kg^{-1} of leaf dry matter.

2.6. Mineral nutrients and soluble carbohydrates

Samples of six intact leaflets from the central part of the leaf 14 were collected, eliminating the edges. Each sample was wrapped in aluminum foil, and immediately frozen in liquid nitrogen (-196 °C). After freeze dried, the samples were ground and used in the preparation of the extracts (sulfuric acid for N, nitric perchloric acid for P, K, and Na, and aqueous for soluble carbohydrates). In these materials, N, P, K and Na concentrations were determined according to Malavolta et al. (1997). Nitrogen was determined after distillation using a micro-Kjeldahl device (model TE0363, Tecnal) followed by titration. Na and K were determined using a flame photometer (model 910 M, Analyser), and a spectrophotometer (model UV-1650PC, Shimadzu) was used for P determination. Total soluble carbohydrates were determined according to Dubois et al. (1956)), using a spectrophotometer (model UV-1650PC, Shimadzu).

2.7. Statistical analysis

The data were subjected to the Kolmogorov-Smirnov normality test, as a prerequisite for analysis of variance by F test. Then, the data were submitted to a two-way analysis of variance. The means were compared by the Tukey's test ($p < 0.05$), using statistical software ASSISTAT (Silva and Azevedo, 2016). The Pearson's correlation matrix and Principal Component Analysis (PCA) were performed using SPSS software v.16. To assess the adequacy of the sample, the Kaiser-Meyer-Olkin (KMO) and Bartlett's sphericity tests were used. For the correlation analyzes, average soil moisture and salinity data up to 60 cm were used, since they were available at all seasons and collection sites.

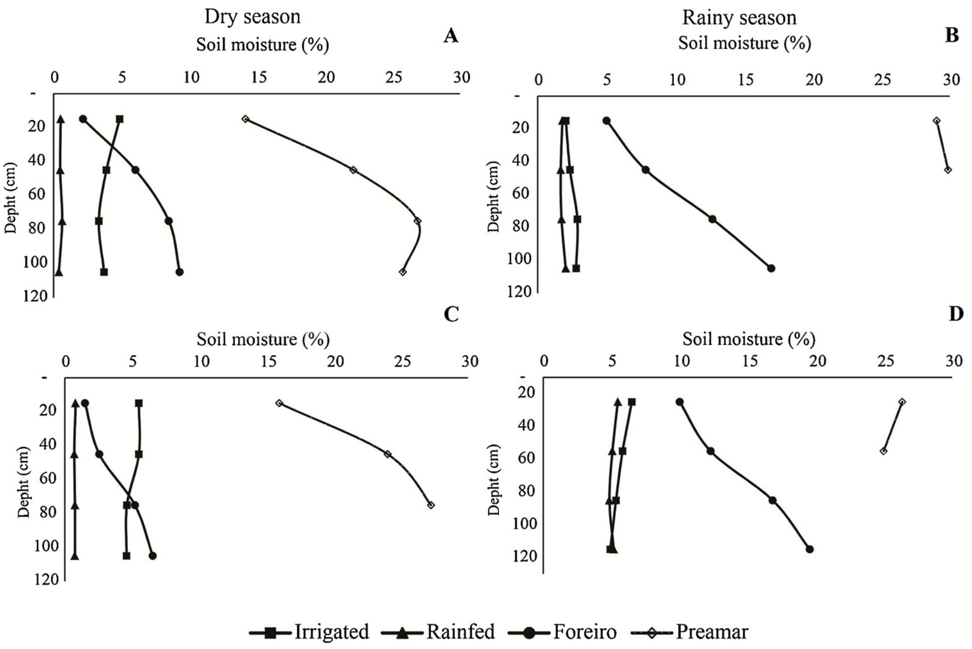

Fig. 2. Soil moisture profile in the dry and rainy seasons of the Irrigated, Rainfed, Foreiro and Preamar areas, planted with tall coconut (*Cocos nucifera* L.). A - October 2015 (dry season); B - May 2016 (rainy season); C - September 2016 (dry season); D - April 2017 (rainy season). n = 6.

3. Results

3.1. Profile of soil moisture and salinity

The percentage of soil moisture in the irrigated area was around 6.0 % in the 0 − 30 cm layer and 4.8 % in the 90 − 120 cm layer, with small differences between the dry and rainy seasons (Fig. 2). On the other hand, the soil of the Rainfed area presented the lowest values of moisture content in the measurements performed in the dry season, with averages around 0.6 % in the whole soil profile (Fig. 2A and C). In the rainy season, mean value of soil moisture content in this area was 3.6 % and 7.2 %, respectively for 2016 and 2017 (Fig. 2B and D).

The soil moisture content in the Foreiro area in the dry seasons was lower than that of the Irrigated area only in the superficial layer (Fig. 2A) or up to 60 cm depth (Fig. 2C). In the rainy seasons, the moisture content in Foreiro area was higher than in the Irrigated area across the soil prolile (Fig. 2B and D). On the other hand, there was a higher percentage of soil moisture in the Preamar environment, ranging from 14.2%–25.8% along the soil profile in the dry season (Fig. 2A and C), and 22.3%–27.3% in the rainy season (Fig. 2B and D).

In general, values of soil electrical conductivity ($EC_{1:1}$) showed slight variations in soil profile (Fig. 3). The values of electrical conductivity of the soil of the Preamar area stand out as the highest observed, followed by the Foreiro, Irrigated and Rainfed areas (Fig. 3). Additional data collected on high and low tide show clear difference also in water salinity and water table depth in the Preamar area. On high tide, the water depth is closer to the soil surface (34.7 ± 2.1 cm) and the salinity level of the water that reaches the roots of tall coconut plants is much higher (12.9 ± 1.7 dS m^{-1}) than the values observed during the low tide (64.7 ± 2.4 cm and 1.1 ± 0.1 dS m^{-1}, respectively). The Foreiro area, despite the proximity to sea, bears little resemblance to Preamar in terms of soil (Fig. 3) and water salinity (data not shown).

3.2. Concentrations of Na^+ on the leaf surfaces

The accumulation of Na^+ on leaf surfaces varied according to the season and the growing environment (Table 2), but no influence of the interaction between factors was observed. The Na^+ accumulation on leaf surfaces were higher in the dry season, independent of the area, and decreased in the rainy season because of frequent washing with rainwater (data not shown). The proximity to the sea resulted in higher values of Na^+ on the leaf surfaces, with the highest averages verified in the Preamar area (Fig. 4A).

3.3. Mineral and carbohydrates content in the leaves

Concentrations of N, P, K and Na^+/K^+ ratio in leaf of tall coconut palm trees were significantly influenced by the growing environment, but effect of the interaction between the factors were not significant (Table 2). The Foreiro area presented low K concentration (Fig. 4E), while the Preamar areas showed the lowest nutrient concentrations and the highest values of Na^+/K^+ ratio (Fig. 4B). The highest levels of N (Fig. 4C) and P (Fig. 4D) were observed in the Irrigated area, and the highest levels of K (Fig. 4E) were observed in the Irrigated and Rainfed areas.

Leaf concentrations of total soluble carbohydrate were significantly influenced by the growing environments and season (Table 2). The highest values of total soluble carbohydrates were observed in the measurement performed in the rainy season of 2016, with no difference among other periods (data not shown). The plants of Irrigated area presented the lowest concentration of these solutes in the leaves (Fig. 4F).

3.4. Leaf gas exchange parameters

In the evaluations of the photosynthetic rate, stomatal conductance, transpiration and internal CO_2 concentration, there was influence of the isolated factors (growing area and season) as well as of the interaction (Table 2). The plants in the Irrigated area presented the high values and lowest variations of A (Fig. 5A), g_s (B), and E (C).

The Rainfed system, as expected, showed the highest variations and response to the water factor, with the photosynthetic rate varying from 3.75 μmol m^{-2} s^{-1} in the dry season of 2016 to 11.83 μmol m^{-2} s^{-1} in the rainy season of 2017 (Fig. 5A). On the contrary, it was verified that plants in the Foreiro area, despite not receiving irrigation, presented similar results to those of irrigated area, with lower values of A (Fig. 5A) and g_s (Fig. 5B) only in the dry season of 2016. On the other

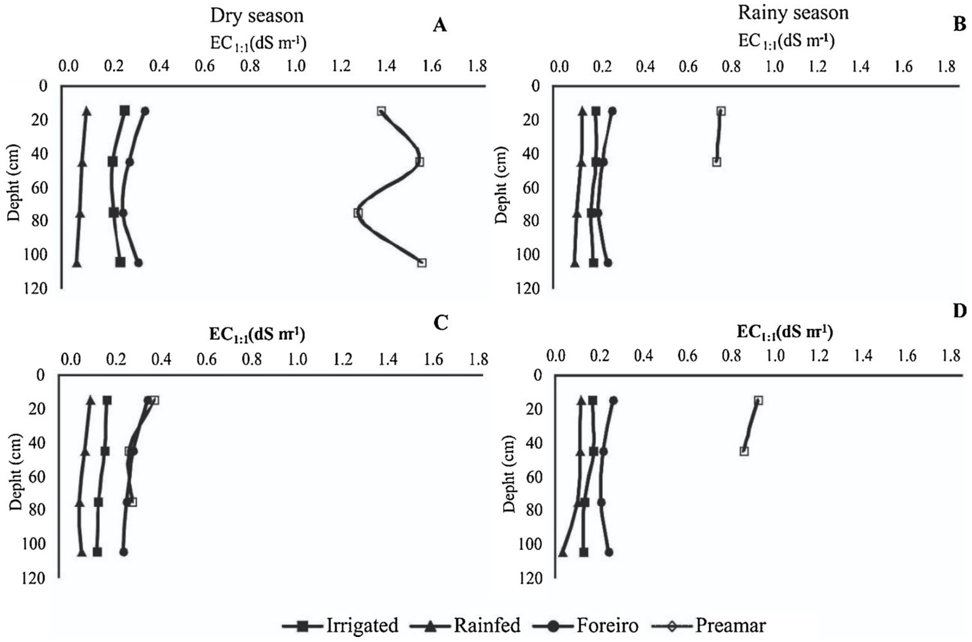

Fig. 3. Soil electrical conductivity ($EC_{1:1}$) profile in the dry and rainy seasons of the Irrigated, Rainfed, Foreiro and Preamar environments, planted with tall coconut (*Cocos nucifera* L.). A - October 2015 (dry season); B - May 2016 (rainy season); C - September 2016 (dry season); D - April 2017 (rainy season). n = 6.

hand, the plants in the Preamar showed lower values of *A* and g_s, but similar or higher values of *Ci* (Fig. 5D), in relation to the other growing environments.

3.5. Pearson correlation matrix and PCA

Pearson correction coefficients (Table 3) show that soil moisture and soil electrical conductivity correlated positively with each other. These two soil variables showed high negative correlation with nutrient leaf concentration and leaf gas exchange, and correlated positively with Na accumulation on leaf surfaces and with Na^+/K^+ ratio in leaves. Photosynthesis rates showed positive correlation with N leaf concentration and negative correlation with Na^+ accumulation on leaf surface and leaf Na^+/K^+ ratio. High positive correlations were also observed between g_s, *A* and *E*.

The PCA allowed obtaining two main components with eigenvalue higher than 1.0, which explain about 65 % of the evaluated data (Fig. 6). The component 1 (eigenvalue of 4.59) showed a strong association between EC (0.618), soil moisture (0.747), leaf Na^+/K^+ ratio (0.911), and Na^+ accumulation on leaf surface (0.818). This component also showed a second group of variables with negative loadings: N (-0,704), K (-0,726), P (-0,485). Leaf gas exchange also showed negative loadings ranged from -0.233 (*A*) to -0,143 (*E*). On the other hand, component 2 (eigenvalue of 1.91) basically shows the strong association between photosynthesis rate (0.867), stomatal conductance (0.968) and transpiration (0.919).

4. Discussion

In our study the Irrigated area is, of course, the reference system, where plants are not subjected to substantial levels of abiotic constraints. The soil of this area does not present problems of salinity (Fig. 3) and sea water spray is not a relevant constraint (Fig. 4). Plants received fertilization according to the recommendations, and as a consequence presented high levels of P, K, and N in the leaves (Fig. 4). The water management (irrigation depth and scheduling) was satisfactory as indicated by the values of soil moisture (Fig. 2), close to those observed for field capacity, and by high values of leaf gas exchanges (Fig. 5). The maintenance of soil moisture at suitable levels also favors the nutrient acquisition by mass flow and diffusion,

Table 2
Summary of two-way analysis of variance (F and p values) for physiological responses of tall coconut plants (*Cocos nucifera* L.) at different seasons (S) and growing environments (Env).

Source of variation	Na^+ (mg kg^{-1})		N (g kg^{-1})		P (g kg^{-1})		K (g kg^{-1})		Na^+/K^+	
	F	p	F	p	F	p	F	P	F	p
S	28.95	0.0001	8.27	0.0014	0.29	0.8343	6.43	0.0046	0.07	0.9336
Env	6.68	0.0003	29.99	0.0001	20.87	0.0001	41.73	0.0001	42.21	0.0001
S x Env	0.65	0.7556	1.34	0.2383	0.91	0.5266	1.02	0.4377	0.80	0.6215

	A (μmol m^{-2} s^{-1})		gs (mol m^{-2} s^{-1})		E (mmol m^{-2} s^{-1})		Ci (μmol mol^{-1})		Carbo (μmol g^{-1})	
	F	p	F	p	F	p	F	P	F	p
S	34.87	0.0001	49.47	0.0001	38.98	0.0001	62.20	0.0001	9.44	0.0007
Env	38.09	0.0001	26.72	0.0001	15.73	0.0001	19.88	0.0001	9.19	0.0001
S x Env	5.21	0.0001	10.40	0.0001	11.55	0.0001	13.91	0.0001	1.33	0.2491

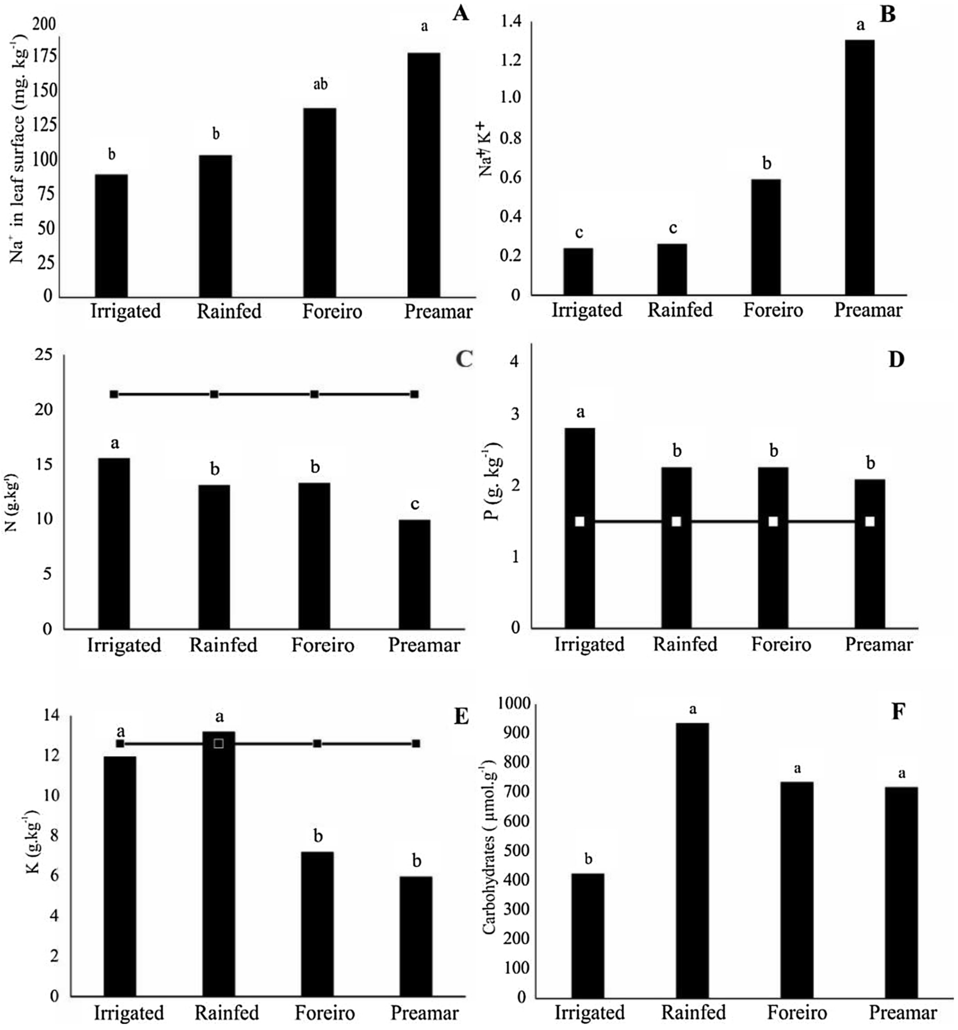

Fig. 4. Sodium accumulation on leaf surface (A), leaf Na^+/K^+ ratio (B), and concentrations of N (C), P (D), K (E), and carbohydrates (F) in leaf 14 of tall coconut plants (*Cocos nucifera* L.) growing in different environments. Means followed by the same letter do not differ by Tukey's test ($p < 0.05$). Solid line indicates the optimum level of nutrient according to Saldanha et al. (2014). $n = 6$.

especially in fertile or fertilized soils (Marschner, 2012). These conditions ensure adequate nutrition and high yields of irrigated coconut (Valicheski et al., 2011).

In consonance with above discussion, the irrigated tall coconut produced during the two years of study on average 97 fruits plant^{-1} year^{-1}, with estimated productivity of 6.7 t ha^{-1} (information provided by COHIBRA Company), a high yield for this type of coconut (Fontes et al., 2003, 2015). On the other hand, the average productivity in the Rainfed system was 20 fruits plant^{-1} year^{-1}, with estimated productivity of 1.3 t ha^{-1}. For the other environments where the exploration is semi-extractive production data are not available. However, according to COHIBRA Company and farmers' information crop yields are similar (Foreiro) or much lower (Preamar) in relation to Rainfed area. According to Fontes et al. (2003), the most part of coconut plantations in coastal areas of Northeastern Brazil do not produce more than 30 fruits plant^{-1} year^{-1}, and these include basically semi-extractives and rainfed plantations with tall coconut. These low yields are due to several factors such as environment constraints, pests, diseases, and inadequate or nonexistent crop management. Taking into account the environmental conditions, important questions are raised: What abiotic factors contribute most to the low productivity of tall coconut in these areas? Physiological responses can give us insights related to this first question?

The Pearson correlation matrix and Principal Component Analysis can give some important answers for these questions. First, soil electrical conductivity showed positive correlation with soil moisture (Table 3), with high levels of salinity observed in the site with high level of soil moisture. These soil variables promoted decrease in the leaf concentration of N and K, inhibited the leaf gas exchange, and increased the leaf Na^+/K^+ ratio. There was also high positive correlation between soil variables and Na^+ accumulation on leaf surface. This last correlation does not indicate a direct cause-effect relationship between them, since Na^+ on leaf surface is related to sea water spray, but demonstrates that these problems are intensified by the proximity to the ocean, in the Preamar area.

PCA shows the separation of two components (Fig. 6). The first component summarizes the variables related to the Preamar environment, forming a group of variables with positive and strongly related loadings (EC, soil moisture, leaf Na^+/K^+ ratio, and Na^+ on leaf surfaces) in contrast to a group of variables with negative loadings, related to mineral nutrition (N, K, and P) of plant. This component also shows negative effects of soil variables on leaf gas exchange, but with lower loadings.

Variation of tidal height results in changes of soil moisture and salinity in the root zone in the Preamar plants, allowing the occurrence of transient stress due to both waterlogging and high salinity, especially under high tide. The semidiurnal character of the tides indicates that these stresses recur many times throughout the year in this area. On the

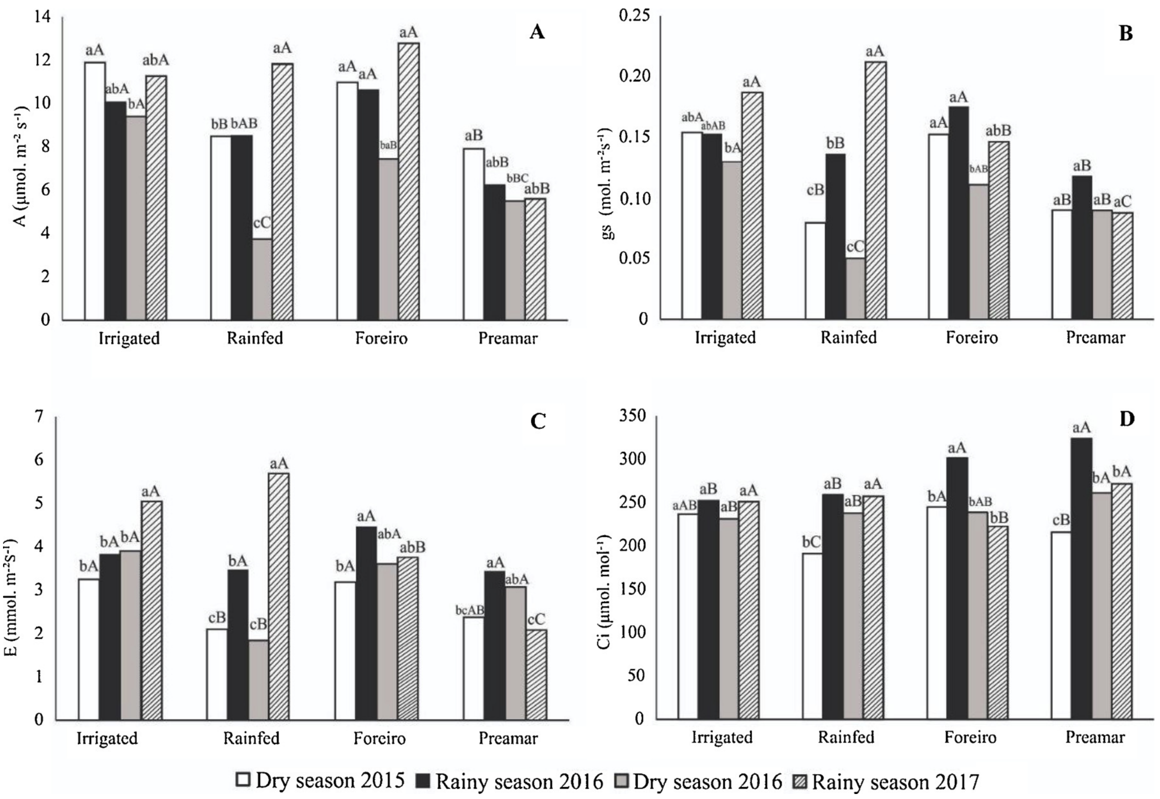

Fig. 5. Photosynthetic rate - *A* (A), stomatal conductance - g_s (B), transpiration – *E* (C), and internal CO_2 concentration - *Ci* (D) in leaf 14 of tall coconut plants (*Cocos nucifera* L.) at different seasons and growing environments. Means followed by the same lowercase letter (Seasons) and uppercase letter (environments) do not differ by the Tukey's test ($p < 0.05$). n = 6.

other hand, during the rainy season there is an elevation of the water table, which can intensify the stress due to saturation of soil, but it can relieve salt stress, since groundwater accumulated in the aquifers advance towards the sea and cause the salt dilution.

Plants of Preamar environment showed the lowest means of N and K (Fig. 4), with contents representing less than half that required for adequate coconut nutrition. The lowest levels of N in the leaf 14 of the Preamar environment are consistent with the visual observations of leaf chlorosis and with data collected in the year 2017 that showed that the relative chlorophyll index in the tall coconut leaves of Preamar area was about half of the value observed in Foreiro plants (data not shown). These reductions in N and chlorophyll content may be indicative of the leaf senescence process, which can be induced by the intermittent stresses associated with high salinity and waterlogging (Taiz et al., 2015; Ren et al., 2016; Medeiros et al., 2018).

The higher Na^+/K^+ ratio in the Preamar area is due to the accumulation of Na^+ (data not shown) and the reduction in K^+ content (Fig. 4E), being an evidence of effect of the competition between these two ions on the membrane absorption sites of the root cells (Lacerda et al., 2003; Marschner, 2012). The value of this ratio was higher than 1.0, being a strong indicator of toxicity level for glycophytes species (Tester and Davenport, 2003), as evidenced by the inhibition of photosynthesis in coconut plants in this area (Fig. 5).

Plants of the Preamar area showed lower rates of photosynthesis than the plants of the Irrigated and Foreiro areas, in both dry and rainy seasons. In addition, the values observed in the plants of Preamar area during the rainy season were similar or lower than those observed in the dry season, with the highest mean values observed in the dry season of 2015 (Fig. 5A). The positive correlation observed for *A* x N and negative correlations observed for *A* x leaf Na^+/K^+ ratio and *A* x soil

Table 3
Pearson correlation matrix for soil variables and plant measurements.

	EC0-60	SM0-60	N	P	Na	K	Na/K	Carb	A	gs	E	Ci
EC0-60	1											
SM0-60	0.408**	1										
N	−0.404**	−0.516**	1									
P	−.210	−0.381**	0.500**	1								
Na	0.449**	0.600**	−0.487**	−0.242*	1							
K	−0.380**	−0.425**	0.380**	0.294**	−0.469**	1						
Na/K	0.478**	0.629**	−0.553**	−0.285*	0.885**	−0.719**	1					
Carb	−0.066	0.003	−0.291**	−0.365**	−0.194	0.139	−0.137	1				
A	−0.196	−0.314**	0.432**	0.192	−0.317**	0.230*	−0.321**	−0.142	1			
gs	−0.237*	−0.321**	0.269*	0.200	−0.289**	0.235*	−0.260*	−0.089	0.842**	1		
E	−0.242*	−0.287**	0.219	0.159	−0.307**	0.179	−0.254*	−0.054	0.687**	0.918**	1	
Ci	−0.004	0.202	−0.393**	−0.110	0.190	−0.194	0.306**	.109	−0.204	0.243*	0.279*	1

**and * Correlation is significant at the 0.01 and 0.05 levels, respectively; Carb = carbohydrates; EC0-60 = mean electrical conductivity for 0 to 60 cm soil layer; SM0-60 = mean soil moisture for 0–60 cm soil layer.

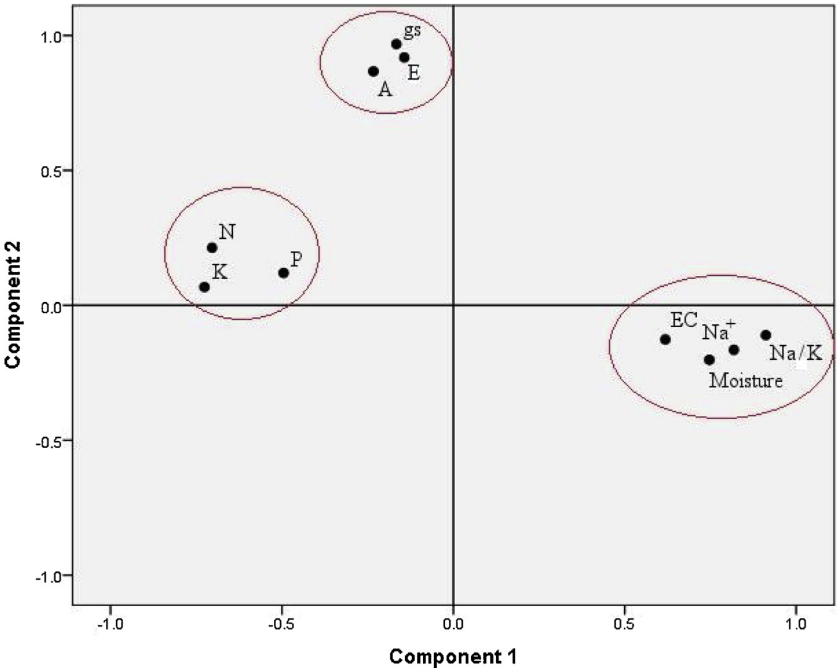

Fig. 6. Principal Component Analysis PCA for soil variable and tall coconut plant response. KMO test: 0.681; Bartlett's test: 45.

moisture (Table 3). can explain, largely, the inhibition of photosynthesis observed in all evaluations in the Preamar.

A relevant issue in this paper was the unusual observation of a negative correlation between soil moisture and leaf gas exchange (Table 3; Fig. 6). This result is explained by the waterlogging condition found in the Preamar area that results in low rates of photosynthesis, even during the rainy season, indicating permanent damage to the photosynthetic apparatus, as observed for other plant species (Ren et al., 2016). For Foreiro and Rainfed environments, seasonal water deficit conditions were observed in the $0-60$ cm soil layer, but the impacts on leaf gas exchange were temporary and less significant. Noteworthy, leaf gas exchange data in plants of Foreiro were similar to those of the Irrigated area (Fig. 5), except in the dry season of 2016. It is important to note that the year 2016 represented the end of a five years period of drought in the region (Marengo et al., 2017), which resulted in the lowering of the water table, even in coastal areas, evidenced by low soil moisture content up to 60 cm depth in Foreiro area (Fig. 2). For the other periods, the maintenance of high photosynthesis rate in this area is justified by the maintenance of high soil moisture and low salinity throughout the soil profile.

Brazilian Northeast coast has a sub-humid tropical climate, but most of its basin, including its fresh water sources, is inserted in the climatic domain of the semiarid. This fact leads to the perception that the water flow upstream of the fluvial-marine plain has an intermittent regime, and the permanence of its drainage is directly influenced by rainy season. The moisture content in the soil profile in the Foreiro area largely explains the existence of large plantations of tall coconut near to the beaches, since the high values in the sub-surface layers throughout the year (Fig. 2) favors the development of plants in this environment, where the roots seek water from deeper soil layers, especially during the dry season (Vincke and Thiry, 2008). It is worth noting that the tall coconut variety has a greater tolerance to water deficit (Cintra et al., 2009; Fontes et al., 2015), which ensure their survival in these areas, even in periods of moderate lowering of the water table levels.

Areas that showed seasonal water deficit (Foreiro and Rainfed) presented 15 % reduction in leaf N concentration, as compared to Irrigated area (Fig. 4), indicating the occurrence of moderate nutritional stress. Although the seasonal water deficit affects the acquisition and transport of N, the lack of fertilization during favorable periods of soil moisture is the most important factor impacting crop yield in these areas. Moreover, in Foreiro it is evident that there is no great water limitation, indicating that the availability of nutrients is the decisive factor for fruit production of coconut plants. The reduction in soil moisture up to 60 cm soil depth during the dry season in this area (Fig. 2) may also limit nutrient uptake by mass flow and diffusion (Marschner, 2012), considering that most of the absorbing roots of tall coconut are located in this soil layer (Lamanda et al., 2008).

In the Rainfed area the leaf concentrations of P and K were not affected (Fig. 4), with values within the adequate range, according to Saldanha et al. (2014). In studies carried out by Sobral (1990) it was verified that in tall coconut palm with low productivity, the foliar analysis can detect high values of K, being this accumulation a consequence of the reduction of the drains. On the other hand, this higher K accumulation in plants under water deficit conditions can also be justified, at least in part, by the increased demand for potassium, contributing to the osmotic adjustment, water absorption, stomatal regulation and detoxification of reactive oxygen species (Wang et al., 2013; Silva et al., 2017, 2018).

The reduction in A in plants under water deficit was clearly observed in the Rainfed area (Fig. 5), where the soil moisture reach value below the permanent wilting point obtained in laboratory (-1.5 MPa). The high correlation between g_s and A (Table 3; Fig. 6) seem to indicate strong stomatal regulation in these coconut plants during the dry season (Passos et al., 2005; Gomes and Prado, 2007; Silva et al., 2017), being a fast and effective response to water loss control, possibly modulated by the synthesis and distribution of abscisic acid (Davies et al., 2002; Gomes et al., 2010)

The second component of PCA (Fig. 6) showed a strong correlation between leaf gas exchange variables (A, g_s, and E), indicating the stomatal limitation of the photosynthetic process. However, the inhibition in the carbon assimilation rate can be also related to non-stomatal causes (Galmés et al., 2007; Taiz et al., 2015), such as reduction of mesophilic conductance and biochemical limitations, especially under severe stress conditions (Galmés et al., 2007). In the present study the correlation of g_s with Ci (Table 3) was much weaker than between g_s and A (Table 3; Fig. 6). In addition, negative and positive correlations were observed, respectively, for Ci x leaf N concentration and Ci x leaf Na^+/K^+ ratio. These results seem to indicate the occurrence of non-stomatal effects, notably in the two most stressful environments, i.e., Preamar and Rainfed. However, different from Preamar area, the increase in soil moisture in Rainfed area (Fig. 2) associated to the rainy season (Fig. 1), allows the recovery of photosynthesis rate, contributing to the seasonal production of fruits by tall coconut plants in this area. These results also show the plasticity of tall coconut palms, with adaptation mechanisms, including changes in root system architecture, for survival and production under severe seasonal water deficit (Gomes and Prado, 2007; Lamanda et al., 2008).

The damage for carbon assimilation capacity of the plants under salt stress occurs mainly by the reduction of leaf area, chlorophyll loss, stomatal closure, and effects on the photochemical and biochemical stages of photosynthesis (Sengar et al., 2013; Taiz et al., 2015). The plants of the Preamar area presented lesser number of leaflets per leaf (Table 1), low levels of N (Fig. 4) that correlate with visual symptoms of chlorosis, low values of A and g_s, and high internal concentration of CO_2 (Fig. 5). These results indicate a severe stress situation caused by waterlogging (Fig. 2) and high salinity (Fig. 3), which acting intermittently through numerous times throughout the year cause permanent hindrance for plants functioning. Occurrence of dead plants in this environment are in line with this observation, which shows the concern with the maintenance of these coconut palm plantations in the future, due to the climatic changes that can result in the elevation of the oceans level (Renaud et al., 2015; Kheir et al., 2019).

The results of our work did not identify a significant correlation (Table 3) between net photosynthesis rate and carbohydrate concentration in the leaves, as was also observed in citrus plants by Ribeiro et al. (2012). A study carried out with African Mahogany under water stress showed a direct relationship between these two variables, with significant reductions in the rate of photosynthesis and carbohydrate content (Albuquerque et al., 2013). Conversely, coconut trees in areas with at least one stress factor (water, salinity and/or nutritional) were those with the highest total soluble carbohydrates (Fig. 4). This supports the idea that this accumulation may be associated with the osmotic adjustment process necessary for the maintenance of the water absorption under water and salt stress conditions (Bai and Rajagopal, 2000; Rajagopal et al., 2005; Gomes and Prado, 2007; Lima et al., 2017). Another possibility is that the differences in the accumulation of carbohydrate in the leaves are related to the variations in size of sources and drains (Alves et al., 2011). Fruit production was much higher in the Irrigated area, so the carbohydrates produced in photosynthesis should be rapidly translocated to fruits (Ribeiro et al., 2012). On the other hand, the absence of strong drains in other environments could lead to the accumulation of carbohydrates in the leaves, as observed in the Rainfed, Preamar and Foreiro areas.

5. Conclusions

Our results indicate different abiotic constraints acting on tall coconut plantations in all evaluated areas, except in Irrigated system. Salt stress and waterlogging affect plants in Preamar area, water deficit impacts on Rainfed coconut, and nutritional stress limits plant responses under Rainfed, Preamar and Foreiro.

Foreiro area, despite the proximity to ocean, does not present problems of soil and water salinity, and the higher soil moisture in subsurface layers of the soil profile significantly reduces the influence of the dry season on the rates of photosynthesis.

The sea spray causes accumulation of Na^+ on the coconut leaf surfaces in all environments, highlighting those close to the sea.

PCA and Pearson correlation analysis indicate that the transient salinity and waterlogging stresses observed in the Preamar area result in lower nitrogen and potassium concentrations in the leaves, and a significant increase in the Na^+/K^+ ratio. These changes cause a permanent hindrance for carbon assimilation rate, limiting the capacity of fruit production by plants. Current climatic changes leading to the elevation of sea level and intrusion of sea water enhance the general concern on how to maintain these tall coconut plantations as source of fiber and nutrition to future generations.

Declaration of Competing Interest

Authors declare that they have no conflict of interest.

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