



Revista Ciência Agronômica

ISSN: 0045-6888

ISSN: 1806-6690

Universidade Federal do Ceará

Barbosa, Marcela Lúcia; Silva, Thieres George Freire da; Zolnier, Sérgio;
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Revista Ciência Agronômica, vol. 49, no. 3, July-September, 2018, pp. 399-408
Universidade Federal do Ceará

DOI: 10.5935/1806-6690.20180045

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Environmental variables influencing the expression of morphological characteristics in clones of the forage cactus¹

Variáveis ambientais condicionando a expressão de características morfológicas de clones de palma forrageira

Marcela Lúcia Barbosa², Thieres George Freire da Silva^{3*}, Sérgio Zolnier², Sérvulo Mercier Siqueira e Silva⁴ and Williams Pinto Marques Ferreira⁵

ABSTRACT - The environmental factors that affect the morphological characteristics of different genera of cacti are little known. The aim of this study therefore was to analyse the contribution of environmental variables to growth in cladodes and plant of forage cactus clones of the genera *Nopalea* and *Opuntia*. The data used in this study were obtained from an experiment conducted in Serra Talhada, Pernambuco, Brazil, between 2012 and 2013, where the clones 'IPA Sertânia' (*Nopalea*), 'Miúda' (*Nopalea*) and 'Orelha de Elefante Mexicana' (*Opuntia*) were submitted to different irrigation depths (2.5, 5.0 and 7.5 mm) and fixed irrigation intervals (7, 14 and 28 days). Morphological characteristics of the cladodes and plants and weather variables were obtained over time. Pearson's correlation, followed by multicollinearity, canonical and path analysis were applied. The minimum temperature, maximum and minimum relative humidity, wind speed and solar radiation were the variables that most affected growth in the cactus. The genus *Opuntia* showed less sensitivity to variations in air temperature compared to the genus *Nopalea*. The higher intensities of global solar radiation affected clones of the genus *Nopalea* more than the genus *Opuntia*. It can be concluded that there are different environmental requirements between forage cacti of the genera *Nopalea* and *Opuntia*.

Key words: Statistical analysis. *Nopalea* sp. *Opuntia* sp. Weather variables.

RESUMO - Os fatores ambientais que afetam as características morfológicas de distintos gêneros de cactáceas são pouco conhecidos. Assim, objetivou-se analisar a contribuição de variáveis ambientais para o crescimento dos cladódios e da planta de clones de palma forrageira dos gêneros *Nopalea* e *Opuntia*. Os dados usados nesse estudo foram adquiridos de um experimento conduzido em Serra Talhada, Pernambuco, entre os anos de 2012 e 2013, onde os clones 'IPA Sertânia' (*Nopalea*), 'Miúda' (*Nopalea*) e 'Orelha de Elefante Mexicana' (*Opuntia*) foram submetidos a distintas lâminas (2,5; 5,0; e 7,5 mm) e intervalos fixos de irrigação (7; 14 e 28 dias). Características morfológicas dos cladódios e das plantas, e variáveis meteorológicas foram obtidas ao longo do tempo. Correlação de Pearson, seguida de análises de multicolinearidade, canônica e trilha foram aplicadas. Temperatura mínima, umidade relativa máxima e mínima, velocidade do vento e radiação solar foram as variáveis que mais afetaram o crescimento da palma. O gênero *Opuntia* revelou menor sensibilidade à variação da temperatura do ar quando comparado ao gênero *Nopalea*. As maiores intensidades de radiação solar global afetaram mais os clones do gênero *Nopalea* do que do gênero *Opuntia*. Conclui-se que há uma exigência ambiental diferenciada entre os gêneros *Nopalea* e *Opuntia* de palma forrageira.

Palavras-chave: Análise estatística. *Nopalea* sp.. *Opuntia* sp.. Variáveis meteorológicas.

DOI: 10.5935/1806-6690.20180045

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Received for publication 06/06/2016; approved 16/08/2017

¹Parte da Dissertação de Mestrado da primeira autora apresentada no Programa de Pós-graduação em Meteorologia Agrícola

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INTRODUCTION

Knowledge of the interaction between plants and the environment is an aid to understanding the influence of weather elements on species growth, development and productivity (SENTELHAS; MONTEIRO, 2009). These elements influence the dynamics of plant metabolism, interfering directly or indirectly in processes such as stomatal activity, photosynthesis, morphology, and the duration of phenological phases, among others (JIA *et al.*, 2015; LLORENS *et al.*, 2015; MOTSA *et al.*, 2015).

Depending on the interaction with environmental variables, the plants can undergo processes of phenotypic plasticity in order to develop characteristics for adaptation to the growth environment (LOUW *et al.*, 2015). An example of this is the acid metabolism of the crassulaceae (CAM), which allows the plants to tolerate conditions of water stress at high ambient temperatures as found in arid and semi-arid regions. CAM plants open their stomata to capture the CO₂ necessary for their metabolism, especially at night, when ambient temperatures and water losses to the atmosphere are lower. Photosynthesis takes place during the day through photochemical stimulus of the solar radiation; however, the stomata remain closed (LÜTTGE, 2010).

Among CAM species, the cactus (*Opuntia* sp. and *Nopalea* sp.) is important due to its use as a source of food and water for animals during periods of drought. In this species, the leaves are atrophied and only spines remain in their place, so that the photosynthetic tissue is located in the cladodes, which in addition to storing water and CO₂ for photosynthesis, convert light energy into chemical energy (AZEVEDO *et al.*, 2013).

Despite having the same photosynthetic type, cactus clones differ in their morphological characteristics as they have different cladode sizes and structures. These characteristics reflect differences in the photosynthetic structures and in the architecture of the plant canopy, resulting in different methods of water extraction and storage in the cladodes (SILVA *et al.*, 2008; SILVA *et al.*, 2014).

Multivariate analysis, such as canonical correlation, is an aid to understanding these characteristics, since they evaluate the interrelationships between two groups of variables. Many studies have used these techniques for forage cactus. Peña-Valdivia *et al.* (2008) correlated the vegetative characteristics of the cladodes with those of clones of the genus *Opuntia*. Pinheiro *et al.* (2014) studied the interrelation between the cladode area index and the morphogenic and productive characteristics of clones of the genera *Opuntia* and *Nopalea*. Silva *et al.* (2010) and Neder *et al.* (2013) identified the morphological

characteristics that contribute most to the productivity of different forage cactus clones.

Based on the above, it is expected to answer the following questions: How do environmental variables affect expression of the morphological characteristics of the forage cactus? Although belonging to the same photosynthetic group (CAM), do clones of different genera respond differently to environmental variables? The aim of this study therefore was to analyse the contribution of environmental variables to the expression of morphological characteristics in plants and cladodes of clones of the genera *Nopalea* and *Opuntia* in a semi-arid environment.

MATERIAL AND METHODS

The experiment was carried out at the Agronomic Institute of Pernambuco (IPA), in the district of Serra Talhada, in the semi-arid region of the State of Pernambuco, Brazil (PE). The local climate characteristics are determined by the average annual temperature of 24.8 °C, relative humidity of 62% and rainfall of approximately 642 mm year⁻¹, with a more concentrated distribution from January to April. The soil of the experimental area is classified as a eutrophic Red Yellow Argisol with a sandy loam texture, and the climate, according to the Köppen classification, is type BSh.

Three forage cactus clones were evaluated, one of the genus *Opuntia* ('Orelha de Elefante Mexicana', OEM) and two of the genus *Nopalea* ('Miúda', MIU and 'IPA-Sertânia', IPA), during the second production cycle (after the 1st cut), giving a total of 532 days from March 2012 to August 2013. The spacing used was 1.6 x 0.2 m, with the crop rows planted in a system of terraces.

The design was of randomised blocks in a 3x3x3+3 factorial arrangement, with three replications and one control for each clone. Using a drip irrigation system (emitters spaced 0.40 m apart) three fixed irrigation depths [2.5 mm (D2.5), 5.0 mm (D5.0) and 7.5 mm (D7.5) - plots] were applied to replenish the water in the soil, at three irrigation frequencies [every 7 days (F7), 14 days (F14) and 28 days (F28) - subplots]. The three clones (IPA, OEM and MIU) made up the sub-subplots. The experiment had 90 sub-subplots, each comprising 4 rows of 20 plants, giving a total of 80 plants with an area of 25.6 m² and a working area of 11.52 m². The working area consisted of 32 plants located in the two central rows.

During the experimental period, the three clones received the equivalent of 756 (D7.5 F7), 672 (D5.0 F7), 622 (D7.5 F14), 586 (D2.5 F7), 579 (D5.0 F14), 555 (D7.5 F28), 536 (D2.5 F14), 535 (D5.0 F28), 514 (D2.5 F28) and 493 mm year⁻¹ (Control).

Fertilisation was carried out monthly, with an application of 50 kg ha⁻¹ NPK formulation 14-00-18, as recommended by the Agronomic Institute of Pernambuco. Throughout the experimental period, crop treatments, such as weeding and the application of herbicides, were carried out to eliminate weeds; disease control was carried out whenever necessary.

Data of global solar radiation (Rg, MJ m⁻² day⁻¹), mean (Tm, °C), maximum (Tx, °C) and minimum (Tn, °C) temperatures, and mean (RHm,%), maximum (RHx,%) and minimum (RHn,%) relative humidity, wind speed (u, m s⁻¹) and rainfall (R, mm) were obtained daily from an automatic weather station of the National Weather Institute - INMET, located 1.7 km from the experimental area.

The morphological characteristics of plant and cladode growth were recorded in 13 campaigns: 24/07/2012 - DAC 146, 22/08/2012 - DAC 175, 19/09/2012 - DAC 203, 27/10/2012 - DAC 241, 24/11/2012 - DAC 269, 22/12/2012 - DAC 297, 26/01/2013 - DAC 332, 2/23/2013 - DAC 360, 03/23/2013 - DAC 388, 04/27/2013 - DAC 423, 05/25/2013 - DAC 451, 06/07/2013 - DAC 493 and 07/27/2013 - DAC 514.

The experimental data were arranged in three groups of response and/or explanatory variables according to the interest under study, as follows.

The group known as 'Environment' consisted of weather and soil water supply (SWS) data, which were obtained by integrating the values for precipitation and irrigation; the latter depending on the treatments of irrigation depths and frequencies. Data of the weather elements, as well as those of SWS, were considered for the intervals between the recording campaigns of the morphological characteristics. Daily mean values for air temperature, relative humidity and wind speed data were determined. On the other hand, integration of the global solar radiation data and the sum of the precipitation data was carried out daily.

The 'Plant' group consisted of morphological characteristics, represented by plant height (PH, from the soil surface to the highest cladode) and plant width (PW, at the widest part), obtained with the aid of a tape measure. The total number of cladodes in each plant (TNC) was also counted in order of cladode appearance (NC1, the first units to emerge from the basal cladode) to the fourth order (NC2, NC3, NC4), depending on the clone. The cladode area index (CAI) was determined by the ratio between total cladode area and plant spacing (1.6 x 0.2 m).

The 'Cladode' group comprised the morphological characteristics of the cladodes, which consisted of measurements of the basal cladodes up to the fourth order of appearance on a representative branch of the plant.

These measurements included cladode length (CLB, CL1, CL2, CL3 and CL4), width (CWB, CW1, CW2, CW3 and CW4), and thickness (CTB, CT1, CT2, CT3 and CT4) from the basal cladodes to the fourth order, which were measured with a tape measure and callipers. In addition, values for cladode area were calculated for all orders (CAB, CA1, CA2, CA3 and CA4), using statistical models adjusted by Silva *et al.* (2014) for the clones, based on the data of cladode length and width.

The 'Environment' group was considered an explanatory variable, and the 'Plant' and 'Cladode' groups considered response variables.

The data from each group were submitted to tests of normality and analysis of variance, and of the interrelationships between the explanatory and response characteristics of the clones and the crop environment as described above. First, the Pearson correlation matrix was prepared, in which the existence, direction and intensity of the linear relationship between the groups of variables was evaluated. The significance of the coefficients was evaluated by Student's t-test.

The response and explanatory variables that presented significant correlations were submitted to the multicollinearity test. This was done for the data of each group, with the aim of identifying the existence and intensity of the correlation between the variables.

Only the variables that showed weak multicollinearity were used in the canonical correlation analysis, and evaluated for associations between groups of variables. The canonical axes were established from the number of variables of the smallest group. The canonical correlations were tested using the chi-square test.

Path analysis was applied in the breakdown of the correlation coefficient, allowing the degree of the effect of an explanatory variable on the response variable to be determined by means of the path coefficient. In this analysis, the partial correlation coefficient between two variables was calculated, disregarding the effect of the remaining variables. The significance of the partial correlation adopted was the same as used in the Pearson correlation.

All statistical analyses followed the procedures suggested by Toebe and Cargnelutti Filho (2013), and were carried out using the GENES statistical software (CRUZ, 2006).

RESULTS AND DISCUSSION

Despite belonging to different genera, expression of the morphological characteristics of the plant and

cladodes in the forage cactus clones was influenced by the environmental variables. Pinheiro *et al.* (2014), Neder *et al.* (2013) and Silva *et al.* (2010) also reported morphological differences between clones that may influence the different responses to the growth environment.

One canonical axis for IPA Sertânia - IPA ($p < 0.001$, $\chi^2 = 34$, degree of freedom = 15) and another for 'Miúda' - MIU ($p < 0.001$, $\chi^2 = 39$, degree of freedom = 25) showed the relationship of the 'Plant' group with the environmental variables. In both cases, the minimum temperature (Tn), maximum (RHx) and/or minimum (RHn) relative humidity, and wind speed (u) in that order, explained 96.8% and 97.8% of the changes in the morphological characteristics of the plants.

In terms of the cladodes, there were two significant canonical axes for IPA ($p < 0.001$, $\chi^2 = 130/57$, degree of freedom = 40/28) and three for MIU ($p < 0.001$, $\chi^2 = 141/56/31$, degree of freedom = 40/28/18), showing a relationship with the 'Environment' group. On these axes, the environmental variables RHx, RHn, u and Rg, explained 99.9% and 99.8% of cladode growth in the IPA clone, while Tn, RHn and u were responsible for 99.9%, 99.7% and 98.7% in the MIU clone.

For the 'Orelha de Elefante Mexicana' - OEM, there was no significant canonical axis for the morphological characteristics of the 'Plant' and 'Cladode' groups with the 'Environment' group, showing that its elements explained the growth variables differently.

From the breakdown of the Pearson correlation between the morphological characteristics and the environmental variables, a direct (0.830) and indirect effect via u (-0.535) from Tn was seen on the appearance of first-order cladodes in the IPA clone (Table 1). On the other hand, in the MIU clone, Tn exerted an indirect negative effect via u on plant width (PW) (-0.598) (Table 2).

No effect from Tn was seen in the OEM clone, (Table 3). The data show that clones of the genus *Opuntia* supposedly have a lower sensitivity to variations in air temperature. In the literature, it is stated that *Opuntia ficus-indica* requires a night-time to daytime temperature ratio of 1.7 (25/15 °C) for full growth. These conditions favour CO₂ capture and therefore the accumulation of biomass (NOBEL, 2001). There are no records for the influence of temperature on clones of the genus *Nopalea*. In the present study, maximum and minimum temperatures varied between 30-36 (33) °C and 18-23 (21) °C, in that

Table 1 - Breakdown of the Pearson correlation coefficient into direct and indirect effects between variables of the 'Plant' response group (plant structural characteristics), with variables of the 'Environment' explanatory group (environmental variables) in the IPA Sertânia clone - IPA, under irrigated conditions in a semi-arid environment in the district of Serra Talhada, PE, Brazil

Variable	Effect	PW	NC1	NC3
Tn	Direct effect Tn	-	0.830	-
	Indirect effect via RHx	-	-0.143	-
	Indirect effect via RHn	-	-0.209	-
	Indirect effect via u	-	0.095	-
	Indirect effect via Rg	-	0.007	-
	Total	-	0.581	-
RHx	Direct effect RHx	-	-	0.408
	Indirect effect via Tn	-	-	-0.083
	Indirect effect via RHn	-	-	0.319
	Indirect effect via u	-	-	0.044
	Indirect effect via Rg	-	-	-0.005
	Total	-	-	0.683
RHn	Direct effect RHn	0.529	-	0.361
	Indirect effect via Tn	0.123	-	-0.066
	Indirect effect via RHx	-0.178	-	0.360
	Indirect effect via u	0.104	-	0.055
	Indirect effect via Rg	-0.002	-	-0.002
	Total	0.575	-	0.709

Continuation Table 1

<i>u</i>	Direct effect <i>u</i>	-0.823	-0.148	-0.437
	Indirect effect via Tn	0.161	-0.535	-0.087
	Indirect effect via RHx	0,020	-0.023	-0.041
	Indirect effect via RHn	-0,067	-0.054	-0.046
	Indirect effect via Rg	0,047	0.028	0.029
Total		-0.662	-0.732	-0.582
Coefficient of determination		0.923	0.805	0.871

Where: 'Environment' group: Tn - minimum air temperature, RHx - maximum relative humidity, RHn - minimum relative humidity, *u* - wind speed; 'Plant' group: PW: plant width, NC1 - number of first-order cladodes, NC3 - number of third-order cladodes. "-" indicates that the environmental variable showed no correlation with any of the variables of the 'plant' group

Table 2 - Breakdown of the Pearson correlation coefficient into direct and indirect effects between variables of the 'Plant' response group (plant structural characteristics), with variables of the 'Environment' explanatory group (environmental variables) in the 'Miúda' clone - MIU, under irrigated conditions in a semi-arid environment in the district of Serra Talhada, PE, Brazil

Variable	Effect	PW	NC1	NC3	NC4	CAI
Tn	Direct effect Tn	-	0.070	-	-	-
	Indirect effect via RHx	-	0.475	-	-	-
	Indirect effect via RHn	-	-0.256	-	-	-
	Indirect effect via <i>u</i>	-	0.379	-	-	-
	Indirect effect via Rg	-	0.014	-	-	-
Total		-	0.682	-	-	-
RHn	Direct effect RHn	-	-	-	0.581	-
	Indirect effect via Tn	-	-	-	-0.096	-
	Indirect effect via RHx	-	-	-	0.082	-
	Indirect effect via <i>u</i>	-	-	-	0.056	-
	Indirect effect via Rg	-	-	-	-0.002	-
Total		-	-	-	0,620	-
<i>u</i>	Direct effect <i>u</i>	0.116	-0.587	-0.522	-0.438	-0,887
	Indirect effect via Tn	-0.598	-0.045	-0.189	-0.126	0,230
	Indirect effect via RHx	-0,089	0.078	-0.011	-0.009	0.031
	Indirect effect via RHn	-0,019	-0.066	-0.057	-0.074	-0.062
	Indirect effect via Rg	0,024	0.052	0.040	0.031	0.055
Total		-0.567	-0.568	-0.739	-0.617	-0.633
Coefficient of determination		0.677	0.841	0.903	0.805	0.913

Where: 'Environment' group: Tn - minimum air temperature, RHn - minimum relative humidity, *u* - wind speed; 'Plant' group: PW: plant width, NC1 - number of first-order cladodes, NC3 - number of third-order cladodes, NC4 - number of fourth-order cladodes, CAI - cladode area index. "-" indicates that the environmental variable showed no correlation with any of the variables of the 'plant' group

order, resulting in a daily average of 23-29 (26) °C. Values in parentheses indicate the respective mean values. These data resulted in a thermal ratio of 1.6 (33/21), close to that reported by Nobel (2001) of 1.7.

Scalisi *et al.* (2016) state that air temperature is the variable that most affects the growth dynamics of cladodes when the cactus is grown under conditions of no water restriction. On the other hand, under water limitation,

Table 3 - Breakdown of the Pearson correlation coefficient into direct and indirect effects between variables of the 'Plant' response group (plant structural characteristics), with variables of the 'Environment' explanatory group (environmental variables) in the 'Orelha de Elefante Mexicana' clone - OEM, under irrigated conditions in a semi-arid environment in the district of Serra Talhada, PE, Brazil

Variable	Effec	PH	NC1	CAI
RHx	Direct effect RHx	0.249	-0.656	-
	Indirect effect via RHn	0.409	0.116	-
	Indirect effect via <i>u</i>	0.036	-0.012	-
Total		0.695	-0.551	-
RHn	Direct effect RHn	0.464	-	0.660
	Indirect effect via RHx	0.220	-	-0.082
	Indirect effect via <i>u</i>	0.045	-	0.070
Total		0.729	-	0.648
<i>u</i>	Direct effect <i>u</i>	-	-	-0.555
	Indirect effect via RHx	-	-	0.009
	Indirect effect via RHn	-	-	-0.084
Total		-	-	-0.629
Coefficient of determination		0.668	0.319	0.726

Where: 'Environment' group: RHx - maximum relative humidity, RHn - minimum relative humidity, *u* - wind speed; 'Plant' group: PH - plant height, NC1 - number of first-order cladodes, CAI - cladode area index. "-" indicates that the environmental variable showed no correlation with any of the variables of the 'plant' group

the soil water content is the most determining factor. In the present study, the effect of most of the environmental variables occurred during the rainy season, which may explain why no effect was identified on cactus growth from the water supply. In addition, under ample water availability, the immediate response of the cactus may not be noted due to its high capacity for storing water in the cladodes, low water requirement and low dry-matter conversion (QUEIROZ *et al.*, 2015).

Direct and indirect effects from RHx and RHn were seen in an increase in the number of third-order cladodes; RHn further contributed to the growth in plant width (PW) in the IPA clone. RHn had a direct positive effect on the emergence of higher-order cladodes (NC4) (0.581), while higher values of RHx via Tn contributed to increase the number of first-order cladodes (NC1) (0.475) in MIU. Greater values for RHn favoured PH (0.464) and CAI (0.660) in OEM. In contrast, lower values of RHx did not promote the appearance of new first-order cladodes (NC1) (-0.656).

Higher values for RHn and RHx result in a lower vapour pressure deficit, which decreases water loss from the plant to the atmosphere and favours CO₂ uptake (LLORENS *et al.*, 2015; MOTSA *et al.*, 2015). However, the effects also depend on air temperature, which affects several phases of plant metabolism, such as the enzyme action of metabolic processes, respiration and the duration

of phenological phases (BAHUGUNA; JAGADISH, 2015; JIA *et al.*, 2015). In this research, the maximum and minimum values for relative humidity were around 69-86 (78) % and 7-38 (26) %, with a daily average of 41-65 (52) %.

Increases in the number of third-order cladodes (-0.437) and in plant width (-0.823) in the IPA clone occurred at the lower values of *u*. Under this condition, the CAI of the MIU clone did not display much evolution (-0.887); similarly for the CAI of the OEM clone (-0.555). The wind speed varied over time between 2-4 (3) m s⁻¹. Within this range, *u* promotes renewal of the air near the vegetative canopy, aiding in the availability of CO₂. In contrast, higher values contribute to an excessive increase in the processes of transpiration, influencing the stomatal activity of the leaves with a subsequent reduction in photosynthesis (KIM *et al.*, 2014; LOUW *et al.*, 2015). The influence of wind speed in the present research was similar to that seen by Silva *et al.* (2015), who found a direct negative effect on the morphological characteristics of cactus grown under rainfed conditions in the district of Serra Talhada, PE.

For cladode characteristics, it was found that Tn did not affect the IPA clone (Table 4); the same was not seen in the MIU clone (Table 5), which suffered a direct negative effect on growth in the basal cladodes (CLB, CWB), and an indirect effect via RHx on CT4 (0.411). Tn also had a

Table 4 - Breakdown of the Pearson correlation coefficient into direct and indirect effects between variables of the 'Cladode' response group (cladode structural characteristics), with variables of the 'Environment' explanatory group (environmental variables) in the IPA Sertânia clone - IPE, under irrigated conditions in a semi-arid environment in the district of Serra Talhada, PE, Brazil

Variable	Effect	CL1	CL2	CL3	CWB	CW1	CT1	CPB	CP1
HRx	Direct effect RHx	-	-	-0.145	0.127	-	-0.325	-	-
	Indirect effect via Tn	-	-	0.326	-0.204	-	0.474	-	-
	Indirect effect via RHn	-	-	0.413	0.798	-	0.500	-	-
	Indirect effect via <i>u</i>	-	-	0.088	-0.043	-	0.090	-	-
	Indirect effect via Rg	-	-	-0.005	-0.002	-	-0.006	-	-
Total		-	-	0.678	0.678	-	0.733	-	-
HRn	Direct effect RHn	-	-	0.468	0.904	-	0.567	1.499	-
	Indirect effect via Tn	-	-	0.259	-0.162	-	0.377	0.529	-
	Indirect effect via RHx	-	-	-0.128	0.113	-	-0.287	-1.436	-
	Indirect effect via <i>u</i>	-	-	0.110	-0.053	-	0.112	0.090	-
	Indirect effect via Rg	-	-	-0.002	-0.001	-	-0.002	0.000	-
Total		-	-	0.708	0.801	-	0.767	0.682	-
<i>u</i>	Direct effect <i>u</i>	-	-0.655	-	-	-	-	-	-
	Indirect effect via Tn	-	-0.067	-	-	-	-	-	-
	Indirect effect via RHx	-	0.016	-	-	-	-	-	-
	Indirect effect via RHn	-	-0.065	-	-	-	-	-	-
	Indirect effect via Rg	-	0.047	-	-	-	-	-	-
Total		-	-0.724	-	-	-	-	-	-
Rg	Direct effect Rg	-0.615	-	-	-	-0.798	-	-	-0.635
	Indirect effect via Tn	-0.024	-	-	-	0.020	-	-	0.002
	Indirect effect via RHx	0,023	-	-	-	0.001	-	-	-0.007
	Indirect effect via RHn	-0,003	-	-	-	-0.004	-	-	0.003
	Indirect effect via <i>u</i>	-0.043	-	-	-	0.085	-	-	0.055
Total		-0.661	-	-	-	-0.695	-	-	-0.583
Coefficient of determination		0.815	0.896	0.847	0.716	0.819	0.874	0.717	0.748

Where: 'Environment' group: RHx - maximum relative humidity, RHn - minimum relative humidity, *u* - wind speed, Rg - global solar radiation; 'Cladode' group: CL1 - length of the first-order cladode, CL2 - length of the second-order cladode, CL3 - length of the third-order cladode, CWB - width of the basal cladode, CW1 - width of the first-order cladode, CT1 - thickness of the first-order cladode, CPB - perimeter of the basal cladode, CP1 - perimeter of the first-order cladode. "-" indicates that the environmental variable showed no correlation with any of the variables of the 'cladode' group

positive effect on CLB via *u* (0.515). There was also no significant effect from Tn on OEM (Table 6).

In the IPA clone, the highest values of RHn promoted an increase in the width (0.904) and perimeter (1.499) of the basal cladode, and an increase in the thickness of the first-order cladodes (0.567) and length of the third-order cladodes (0.468), both directly and indirectly via RHx. In the MIU clone, it was found that RHn contributed directly to increase the thickness of the fourth-order (0.370) and basal cladodes (0.677), while contributing to the growth of the first-order cladodes (CL1, CT1, CP1); RHx favoured

the basal and third-order cladodes (CPB, CT3) in OEM. The growth of the second-order cladodes in IPA occurred at lower values of *u* (-0.655). The higher values of *u* did not favour increases in the width of the first-order (CW1) (0.806) or the second-order cladodes (CP2) in the MIU clone (-0.912), and in OEM did not benefit growth in the older cladodes (CL1) (-0.537). Rg only had an effect on cladode characteristics in clones of the genus *Nopalea*, where the highest intensity reduced the growth of the first-order cladodes in IPA, and decreased the growth of the first- and second-order cladodes in MIU. Over time, this variable presented magnitudes of 17-25 (22) MJ m⁻² day⁻¹.

Solar radiation provides the driving force for photosynthesis; however, in excess, it inhibits growth in species of *Opuntia* sp. (AZEVEDO *et al.*, 2013; LÜTTGE, 2010; NOBEL; HARTSOCK, 1983). Silva *et al.* (2015), in a study carried out with the IPA Sertânia, Miúda and

Mexican Elephant Ear clones under rainfed conditions, found no correlation of solar radiation with most of the morphological characteristics, with the exception of the basal cladodes, where incidence tends to decrease as the plant grows.

Table 5 - Breakdown of the Pearson correlation coefficient into direct and indirect effects between the 'Cladode' response group (cladode structural characteristics), and the 'Environment' explanatory group (environmental variables) in the 'Miúda' clone - MIU, under irrigated conditions in a semi-arid environment in the district of Serra Talhada, PE, Brazil

Variable	Effect	CLB	CL1	CWB	CW1	CTB	CT4	CP1	CP2
Tn	Direct effect Tn	-0.799	-	-1.881	-	-	-	-	-
	Indirect effect via RHx	0,193	-	0.973	-	-	-	-	-
	Indirect effect via RHn	-0,016	-	-0.446	-	-	-	-	-
	Indirect effect via <i>u</i>	-0.066	-	0.639	-	-	-	-	-
	Indirect effect via Rg	0,012	-	-0.005	-	-	-	-	-
Total		-0.677	-	-0.720	-	-	-	-	-
RHx	Direct effect RHx	-	-	-	-	-0.235	-0.169	-	-
	Indirect effect via Tn	-	-	-	-	0.393	0.411	-	-
	Indirect effect via RHn	-	-	-	-	0.589	0.326	-	-
	Indirect effect via <i>u</i>	-	-	-	-	0.066	0.097	-	-
	Indirect effect via Rg	-	-	-	-	-0.006	-0.006	-	-
Total		-	-	-	-	0.807	0.660	-	-
RHn	Direct effect RHn	-	-	0.907	-	0.667	0.370	-	-
	Indirect effect via Tn	-	-	0.925	-	0.313	0.327	-	-
	Indirect effect via RHx	-	-	-1.387	-	-0.208	-0.149	-	-
	Indirect effect via <i>u</i>	-	-	0.126	-	0.083	0.121	-	-
	Indirect effect via Rg	-	-	0.001	-	-0.002	-0.002	-	-
Total		-	-	0.572	-	0.853	0.667	-	-
<i>u</i>	Direct effect <i>u</i>	0.102	-	-	0.806	-	-	-	-0.912
	Indirect effect via Tn	0.515	-	-	-0.173	-	-	-	0.185
	Indirect effect via RHx	0,031	-	-	-0.024	-	-	-	0.070
	Indirect effect via RHn	-0,004	-	-	0.009	-	-	-	-0.053
	Indirect effect via Rg	0,044	-	-	0.047	-	-	-	0.066
Total		0.689	-	-	0.664	-	-	-	-0.644
Rg	Direct effect Rg	-	-0.611	-	-0.504	-	-	-0.748	-0.710
	Indirect effect via Tn	-	-0.006	-	-0.007	-	-	-0.003	0.007
	Indirect effect via RHx	-	0,002	-	0.004	-	-	0.003	-0.010
	Indirect effect via RHn	-	0,001	-	0.000	-	-	0.001	0.002
	Indirect effect via <i>u</i>	-	-0.037	-	-0.075	-	-	-0.044	0.085
Total		-	-0.652	-	-0.582	-	-	-0.791	-0.627
Coefficient of determination		0.778	0.477	0.923	0.722	0.929	0.825	0.889	0.947

Where: 'Environment' group: Tn – minimum air temperature, RHx - maximum relative humidity, RHn - minimum relative humidity, *u* - wind speed, Rg - global solar radiation; 'Cladode' group: CLB - length of the basal cladode, CL1 - length of the first-order cladode, CWB - width of the basal cladode, CW1 - width of the first-order cladode, CTB - thickness of the basal cladode, CT4– thickness of the fourth-order cladode, CP1 - perimeter of the first-order cladode, CP2 - perimeter of the second-order cladode. “-” indicates that the environmental variable showed no correlation with any of the variables of the 'cladode' group

Table 6 - Breakdown of the Pearson correlation coefficient into direct and indirect effects between variables of the 'Cladode' response group (cladode structural characteristics), with variables of the 'Environment' explanatory group (environmental variables) in the 'Orelha de Elefante Mexicana' clone - OEM, under irrigated conditions in a semi-arid environment in the district of Serra Talhada, PE, Brazil

Variable	Effect	CL1	CT1	CT3	CPB	CP1
RHx	Direct effect RHx	0.042	-	0.553	0.584	-
	Indirect effect via RHn	0,491	-	0.054	0.006	-
	Indirect effect via <i>u</i>	0,054	-	0.031	0.007	-
	Total	0.587	-	0.638	0,596	-
RHn	Direct effect RHn	0.556	0.458	0.061	0.006	0,800
	Indirect effect via RHx	0.037	0.031	0.489	0.515	-0,279
	Indirect effect via <i>u</i>	0,068	0.061	0.038	0.008	0.060
	Total	0.661	0.550	0.588	0,530	0,581
<i>u</i>	Direct effect <i>u</i>	-0.537	-	-	-	-
	Indirect effect via RHx	-0.004	-	-	-	-
	Indirect effect via RHn	-0,071	-	-	-	-
	Total	-0.612	-	-	-	-
Coefficient of determination		0.721	0.526	0.499	0.360	0.582

Where: 'Environment' group: RHx - maximum relative humidity, RHn - minimum relative humidity, *u* - wind speed; 'Cladode' group: CL1 - length of the first-order cladode, CT1 - thickness of the first-order cladode, CT3 - thickness of the third-order cladode, CPB - CP1 - perimeter of the basal cladode, CP1 - perimeter of the first-order cladode. "-" indicates that the environmental variable showed no correlation with any of the variables of the 'cladode' group

In general, at times when the minimum temperature was higher, associated with higher maximum and minimum relative humidity and lower intensity wind speeds and global solar radiation, the environmental variables favoured growth in the plant and cladodes of the forage cactus, with an increase in their dimensions. Therefore, when planting this species, it is important to consider the period of the year when these conditions predominate, in order to promote the initial growth of the plants and ensure their establishment. In the Brazilian semi-arid region, such environmental conditions are typical of the transition between summer (December-March) and autumn (March-June), which coincides with the rainy season.

CONCLUSIONS

1. Growth was most favoured in the forage cactus when the minimum temperature and the maximum and minimum relative humidity were increasing, and the intensity of the wind speed and solar radiation were lower;
2. Growth in clones of the genus *Nopalea* was affected by the association of environmental variables, unlike the genus *Opuntia*, which occurred in isolation and depended on morphological characteristics;

3. The variability of the water regime did not significantly explain the seasonality of the growth of the forage cactus, irrespective of clone or genus;
4. The genus *Opuntia* showed a lower sensitivity to variations in air temperature when compared to the genus *Nopalea*;
5. Global solar radiation affected only the morphological characteristics of the cladodes;
6. The highest intensities of global solar radiation affected the clones of the genus *Nopalea* (IPA Sertânia and 'Miúda') more than of the genus *Opuntia* (Mexican Elephant Ear).

ACKNOWLEDGEMENTS

The authors wish to thank FACEPE for their financial assistance (APQ-0215-5.01 / 10) and CAPES for granting the scholarship.

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