Revista Ciência Agronômica, v. 54, e20218176, 2023
Centro de Ciências Agrárias - Universidade Federal do Ceará, Fortaleza, CE
www.ccarevista.ufc.br

Scientific Article
ISSN 1806-6690

Gas exchange in forage cactus cultivars of genera *Opuntia* and *Nopalea* (Cactaceae)[1]

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ABSTRACT - Forage cactus species are cultivated in northeaster Brazil for feed, mainly during dry periods, as cacti are xerophytes well adapted to drought. Gas exchange studies have elucidated the physiological mechanisms underlying plant adaptation to ecosystems with low water availability. Here, we evaluated the variability between and within cactus forage genera *Opuntia* and *Nopalea* with respect to gas exchange behaviour. Twenty-one cultivars were used, 16 of which belonged to genus *Opuntia*, while six belonged to genus *Nopalea*, particularly, *O. cochenillifera*. Gas exchange was evaluated in the secondary cladode at 00:00 hours using a portable infrared gas analyser. Net CO_2 assimilation rate, stomatal conductance, CO_2 intercellular concentration, transpiration rate, and leaf temperature were evaluated. Additionally, instantaneous water use efficiency, intrinsic water use efficiency, and instantaneous carboxylation efficiency were calculated. Boxplots were used to assess value dispersion between the genera prior to submitting the data to multivariate analysis of principal components and cultivar-based grouping, and subsequently organizing the species studied in a dendrogram. Variability between the two genera and among cactus forage cultivars was detected for gas exchange. Cultivars were classified into three groups and two main components were identified. Cultivars 'Verdura' and 'Orelha de Elefante Mexicana' showed higher photosynthetic performance.

Key words: Cactaceae. Photosynthesis. Crassulacean acid metabolism. Semiarid

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DOI: 10.5935/1806-6690.20230035
Editor-in-Chief: Prof. Salvador Barros Torres - sbtorres@ufersa.edu.br

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Received for publication in 26/08/2021; approved in 22/12/2021

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INTRODUCTION

The Cactaceae family comprises approximately 94 genera and 1,150 species (CHRISTENHUSZ *et al*., 2017). In northeastern Brazil, 26 cactaceous genera and 113 species have been identified (GUERRERO *et al*., 2018). Cultivation of *Opuntia ficus-indica* (forage palm) is predominant in the semiarid region of northeastern Brazil. The genus is native to the Americas but is widely distributed in diversity of habitats, such as tropical deciduous forests and temperate forests, although it is more abundant in the Caatinga ecosystem (MIGUEL-TALONIA; TÉLLEZ-VALDÉS; MURGUÍA-ROMERO, 2014), showing an remarkably high water use efficiency (WUE). Currently, millions of hectares are cultivated with cactus forage for various uses (food, forage, or dye production), especially in Mexico (3 million ha), Brazil (500,000 ha), Peru (10,000 ha), Argentina (1,650 ha), and Chile (1,000 ha) (INGLESE *et al*., 2017).

In northeaster Brazil, *Opuntia ficus-indica* and *O. cochenillifera* (formerly *Nopalea*) (MAJURE *et al*., 2012) are the most cultivated species for feeding livestock, due to their high adaptability to extreme water deficit, high temperature, and high solar radiation intensity (ALVES *et al*., 2017). Forage cacti have developed adaptation strategies to these extreme environments through anatomical, morphological, physiological, and biochemical changes that allow them to maintain cell turgor, concomitantly with minimal water loss (SILVA *et al*., 2014).

Anatomical adaptations in cacti include thick cuticles, few stomata, and small openings close to the lower and upper surfaces of the cladodes (BARTWAL *et al*., 2013). Among morphological adaptations, the presence of branched roots stands out, reaching several meters in length (RAMAKRISHNA; RAVISHANKAR, 2011). In turn, physiological adaptations include stomatal opening at night to fix CO_2, thereby preventing excessive water loss during daytime, when evaporative demand is high. Finally, biochemical adaptations are related to the production and accumulation of primary and secondary metabolites to maintain turgor, stabilising proteins, and cell membranes in plants exposed to conditions of water deficit, salinity, and high temperature stress, to which plants in semiarid regions are subjected on a daily basis (RODZIEWICZ *et al*., 2014).

Understanding the factors that affect gas exchange is of paramount importance for optimising photosynthetic carbon assimilation and controlling water loss, as it allows the adaptation and stability of plant performance in extreme ecosystems. The reduction in crop growth and productivity may be related to a reduction in photosynthetic activity, which is limited by abiotic factors intrinsic to the cropping environment (REIS; CAMPOSTRINI, 2011).

The objective of this study was to evaluate the variation in gas exchange among different species of forage cacti belonging to the genera *Opuntia* and *Nopalea*, currently called *O. cochenillifera*.

MATERIAL AND METHODS

Experimental location and protocol

The experiments reported herein were conducted in a greenhouse at the Department of Plant Science and Environmental Sciences of the Federal University of Paraíba, Areia, Paraíba, Brazil. Cladodes were collected at the Arcoverde Experimental Station of the Agronomic Institute of Pernambuco, in the municipality of Arcoverde. After collection, the cladodes were kept in a shaded environment for 10 days to facilitate the loss of some water as well as to heal the wounded area. These cladodes were then planted in 12 kg containers filled with regolithic neosoil substrate and placed in a greenhouse for two years. The growth medium was watered so as to increase soil moisture to 60% of field capacity. To maintain field capacity, eight pots were weighed before irrigation to verify the amount of water needed to reach the required moisture level. Control of carmine mealybug (*Dactylopius opuntiae*) and scale mealybug (*Diaspis echinocacti*) was performed manually using water and plant loofah.

Plant material

The species used in the experiments were divided into two groups. Group 1 was composed of varieties belonging to the old genus *Nopalea* and group II was comprised of varieties that were already part of the genus *Opuntia* (Table 1). Analyses were performed on the secondary cladodes.

Variables analysed

The evaluations was performed between 00:00 and 01:00 (ALVES *et al*., 2018) using an infrared gas analyser (IRGA, LI-6400XT, LI-COR®, Nebraska, USA) with an airflow of 300 mL min^{-1}. The following variables were measured: CO_2 net assimilation rate (A, μmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}), intercellular CO_2 concentration (C_i, μmol CO_2 m^{-2} s^{-1}), transpiration rate (E, mmol H_2O m^{-2} s^{-1}), leaf temperature (T_{lea}, °C), instantaneous water use efficiency (WUE_i = A/E), intrinsic water use efficiency (WUE_{in} = A/gs), and instantaneous carboxylation efficiency (CE_i = A/Ci).

Statistical analysis

Data were subjected to dispersion analysis (boxplot) and then multivariate analysis of principal components (PCA) and clustering based on cultivar groups (MINGOTI, 2005) were applied. The criterion

Table 1 - List of forage cactus cultivars used in gas exchange analysis

Species	Varieties	Identification
	Grupo 1	
Nopalea O. cochenillifera	‘F21 Sementes’	1
	‘IPA – Sertânia’	2
	‘F1 Cultura de Tecido – 6’	3
	‘Miúda’	4
	‘F1 Cultura de Tecido – 13’	5
	Grupo 2	
O. ficus-indica	‘Copena’	1
	‘Redonda’	2
	‘IPA Clone 20’	3
	‘IPA 98/T26’	4
	‘IPA 98/T51’	5
	‘IPA 98/T23’	6
O. stricta	‘Orelha de Elefante Mexicana’	1
	‘Orelha de Elefante Mexicana – Lisa’	2
	‘Orelha de Elefante Mexicana – Espinho’	3
O. undulata	‘Orelha de Elefante Africana – Clone 9’	1
	‘Orelha de Elefante Africana’	2
O. atropes	‘F24’	1
	‘F8’	2
Opuntia sp.	‘Algerian’	1
	‘ChillyFruit’	2
	‘Verdura 23’	3

used to classify the variables in the components was based on the relation 0.5 ($\lambda^{-0,5}$), where λ is the eigenvalue of the component (OVALLES; COLLINS, 1988). Subsequently, a dendrogram was prepared to separate the cultivars studied, ordering the values from highest to lowest following the sequence (Red/orange/ice). Statistical analysis was performed using the R software version 3.5.2.

RESULTS AND DISCUSSION

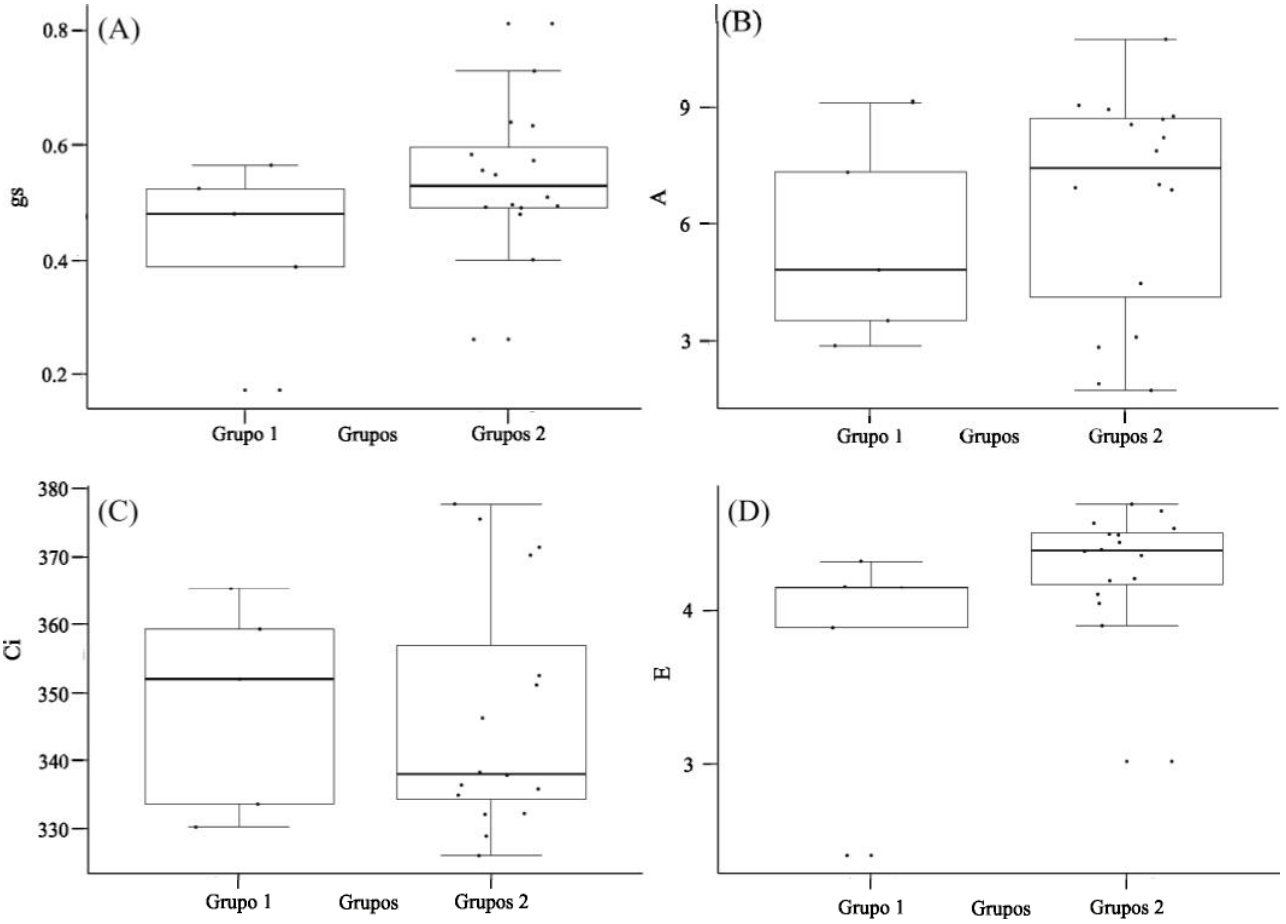
Group dispersion

Scattering of stomatal conductance (g_s) values for the cultivars belonging to the two cactaceous groups tested herein are shown in Figure 1A. There were four *Opuntia* cultivars (group 2), with contrasting values and two in group 1 (*Nopalea*). The four *Opuntia* cultivars were within the upper quartile (Q3), which comprised 75% of the highest values measured. With respect to net CO_2 assimilation (A), the greatest range amplitude of the data was observed for the cultivars that were already part of the *Opuntia* genus (Figure 1B). Some of the cultivars within genus *Opuntia* showed higher stomatal conductance (g_s), which may be a species-specific characteristic. Cultivars with higher g_s values commonly show high photosynthetic rates and low C_i values likely due to the greater flow and assimilation of CO_2 during photosynthesis (DALASTRA *et al*., 2014).

These four cultivars fell into the lower quartile (Q1). The top quartile (Q3) contained all four cultivars. As for Ci, in both groups, only one cultivar was inserted in the second quartile (Q2) with 50% of the cultivars (Figure 1C). In *Opuntia* (group 2), out of 50%, 25% of the cultivars were in Q1, and the other 25% were in the lower limit.

Some cultivars belonging to the *Opuntia* and *Nopalea* genera showed a low E values and were located at the lower limit (Figure 1D). *Opuntia* and *Nopalea* showed some peculiarities, such as the occurrence of cultivars located below the lower limit (Li) and a low E, due to a lower g_s, which is a beneficial behaviour, especially in the northeastern region of Brazil, as it minimises transpirational water loss.

Figure 1 - Boxplot of the dispersion of stomatal conductance – g_s values (A), net CO_2 assimilation – A (B), intercellular concentration of CO_2 – C_i (C), and transpiration – E (D) in forage cactus cultivars of genera *Opuntia* and *Nopalea*



The range amplitude of the CE_i data did not vary among groups (Figure 2A). However, for some cultivars that were already part of the genus *Opuntia*, there were scattered values, with four cultivars below the lower limit. Only in *Nopalea* was there a cultivar with a value above the median. In the genus *Opuntia*, four cultivars showed T_{leaf} above 23.5 °C, and they were located at the upper limit (Figure 2B). However, no *Nopalea* cultivar was located above the upper Quartile (Q3) with T_{leaf} ranging from 22.8 to 23.5 °C. Transpiration is the main mechanism involved in leaf temperature regulation; however, due to the characteristically smaller stomatal openings of cacti, transpiration is reduced, which may result in the increase of T_{leaf}, whereby heat energy dissipation through heat irradiation plays a crucial role in maintaining physiological T_{leaf} levels (FIGUEIREDO *et al*., 2019). However, we did not observe such response in this study.

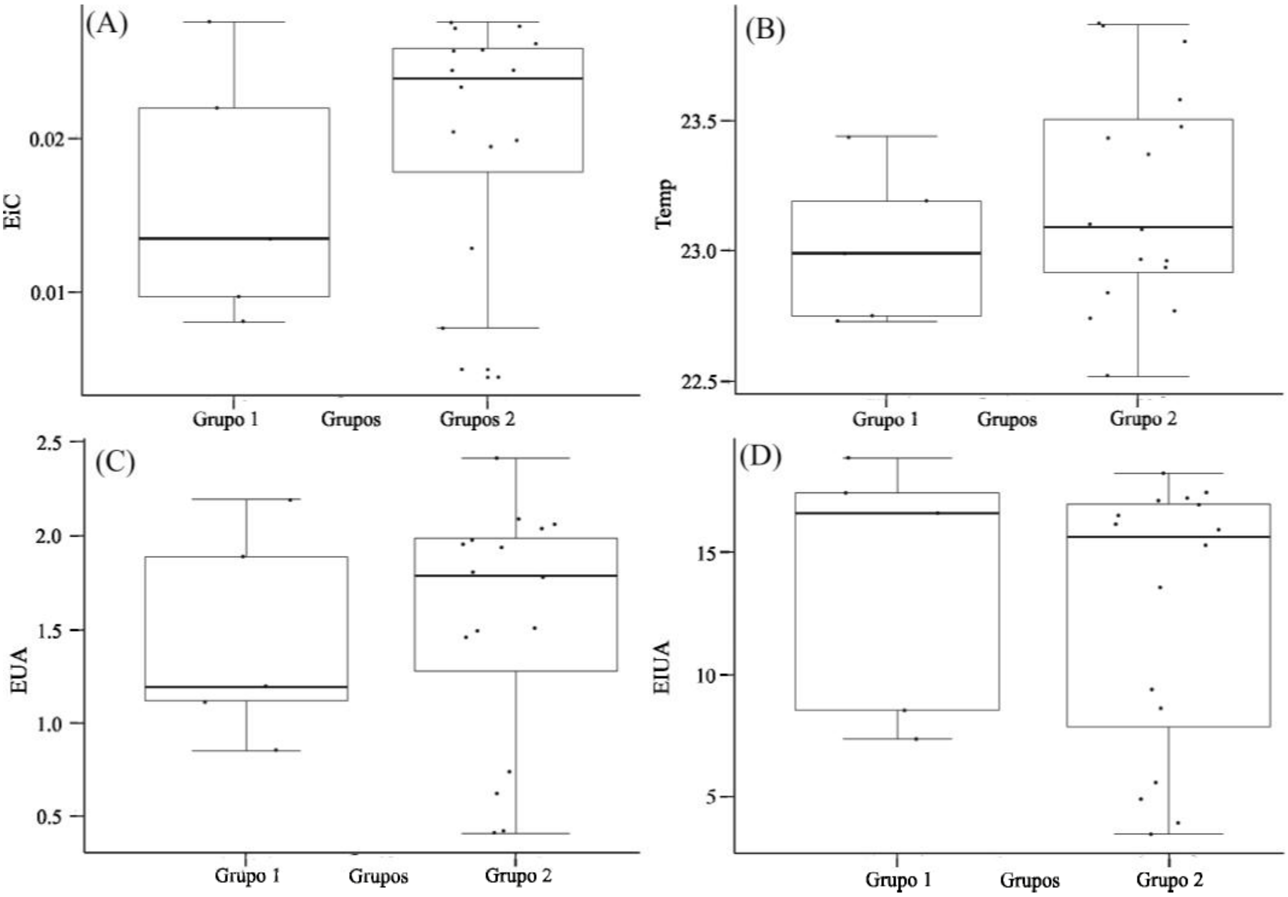
With respect to WUE_i, *Opuntia* cultivars showed a greater range amplitude for the data, as they were located in the lower (Q1) and upper (Q3) quartiles. Only one *Nopalea* cultivar was located within the upper limit. WUE_i followed the same trend as that of WUE (Figure 2D).

The increase in g_s and A, concomitant with a reduction in E, which leads to higher CE_i and WUE, reportedly provides greater carbon availability at the Rubisco activity site (MUIR *et al*., 2014). However, the higher cladode temperature in some cultivars may be a limiting factor for enzyme activity (YAMORI *et al*., 2012).

Multivariate analysis of the main components

The variability among forage cactus species/ cultivars of the genera *Opuntia* and the clade *O. cochenillifera*, former genus *Nopalea*, can be explained by two principal components that accounted for 85.07% of total variance (Table 2). Principal component 1 (PC1) was responsible for 56.45%, while PC2 was responsible for 28.62% of the total data variation. Approximately 70% of the total variance was explained by the first principal components (RENCHER; CHRISTENSEN, 2012), corroborating the values obtained in this study. The

Figure 2 - Boxplot of the dispersion of values for instantaneous carboxylation efficiency – CE_i (A), leaf temperature – T_{leaf} (B), instantaneous water use efficiency – WUE_i (C), and intrinsic water use efficiency – WUE_{in} (D) in cactaceous cultivars of genera *Opuntia* and *Nopalea*



reduced number of cultivars with low or high values of E and g_s may occur because neither E nor g_s are not part of PC1. As the variables present in PC1 are also defined as the most important, they contribute the most to the total variation found in the original data.

Eigenvectors with values equal to or greater than 0.2352 and 0.3304 for PC1 and PC2, respectively, were considered relevant. The variables WUE, A, WUE_i, CE_i, and C_i had discriminatory power for PC1. On the other hand, the last main components will be responsible for variables that are not associated with greater variability (HONGYU; SANDANIELO; OLIVEIRA JUNIOR, 2015). Cladode temperature did not fit into any of the main components, indicating that there was no variability among cultivars for this parameter (STRAPASSON; VENCOVSKY; BATISTA, 2000).

Cultivar scattering

According to principal component analysis, PCA, the 21 cultivars of forage cactci studied clustered into three groups, 16 of which were represented by the genus *Opuntia* sp. and five by genus *Nopalea* (Figure 3). Group 1 (red) was represented by the cultivars with the highest values for CE_i, A, WUE, and WUE_i. This group included 11 cultivars, one belonging to *Opuntia* sp., two to *O. atropes*, and three to *O. ficus-indica*. All cultivars of *O. stricta* belonged to this group. With respect to *Nopalea*, IPA Sertânia stood out as being closer to the WUE variable, together with *O. atropes* and *O. stricta*. Thus, it appears that the cultivars of the two genera respond differently to tests involving CE_i and A with WUE and WUE_i, which are perfectly separated in axis 2 (PC2) and explain 28.6% of the variance. However, PC1 (56.4 %) had a high score for the variables studied.

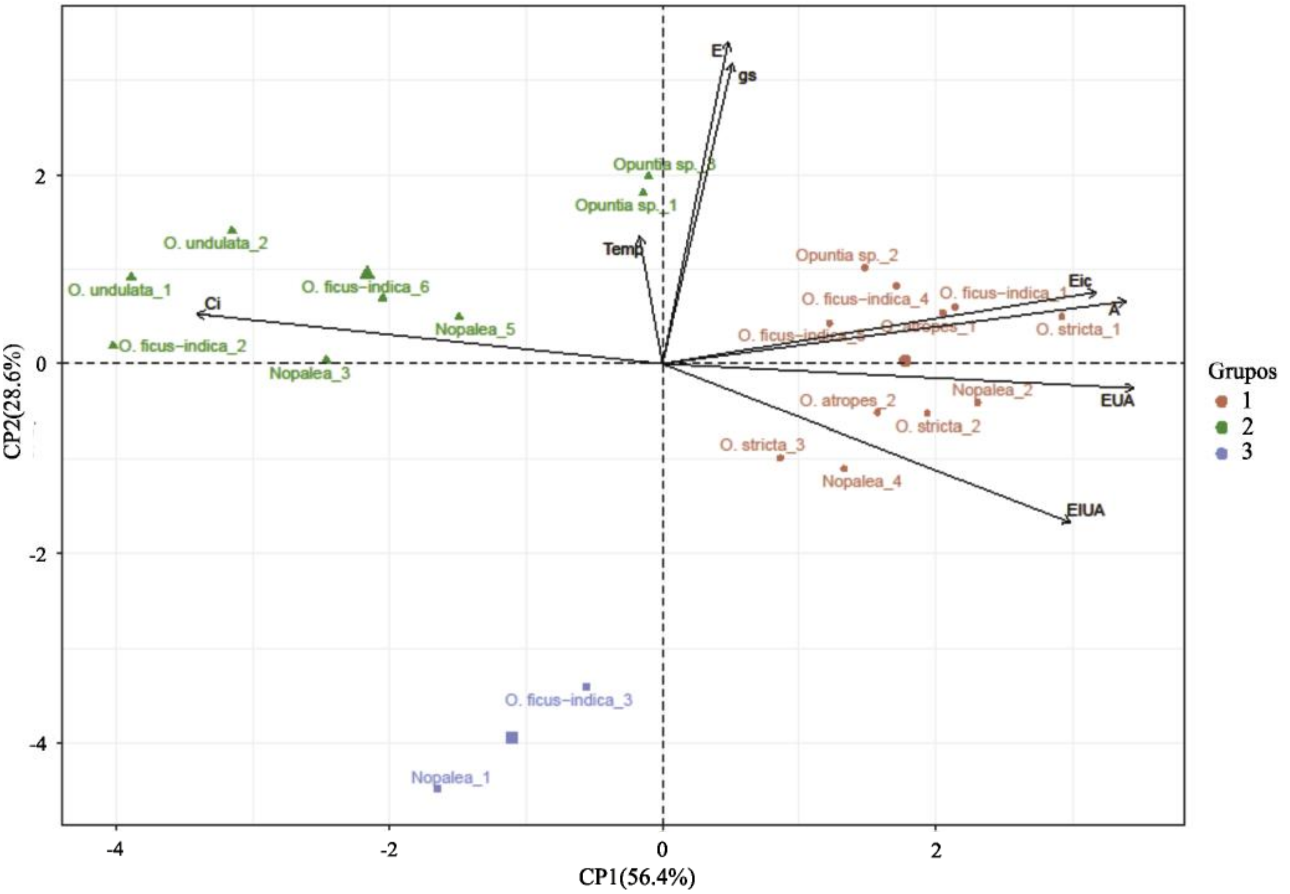
The second group (green) consisted of eight cultivars: six with higher C_i and two with higher E and g_s values. Among the cultivars that showed the highest C_i, the following stand out: two cultivars of *Nopalea*, two cultivars of *O. ficus-indica*, and two cultivars of *O. undulata*. In the second group, the two cultivars that showed higher E and g_s values were the *Opuntia* sp. species. Group three (blue) is represented by one cultivar of *O. ficus-indica* and one cultivar of *Nopalea*.

Table 2 - Matrix of eigenvalues and eigenvectors of two principal components (PC1, PC2) of variables related to gas exchange in forage cactus cultivars belonging to genera *Opuntia* and *Nopalea*

	PC1	PC2
Eigenvalue (l)	4.52	2.29
Explained variance (%)	56.45	28.62
Accumulated variance (%)	56.45	85.07
	Eigenvectors[1]	
T_{leaf}	-0.0231	0.2562
QUE	0.4667	-0.0492
Gs	0.0692	0.6048
A	0.4593	0.1257
WUEi	0.4044	-0.0318
CEi	0.4298	0.1440
Ci	-0.4618	0.1002
E	0.0651	0.6710

[1] Representative variables of the component based on the module of the relation 0,5 ($\lambda^{-0,5}$), highlighted in bold (OVALLES; COLLINS, 1988)

Figure 3 - Scattering of gas exchange variables in forage cactus cultivars belonging to the genera *Opuntia* and *Nopalea*. Intercellular concentration of CO_2 – C_i; Leaf Temperature – T_{leaf}; Transpiration Rate – E; Stomatal Conductance – g_s; Instant Efficiency of Carboxylation – CE_i; Net Assimilation CO_2 – A; Instantaneous Water Use Efficiency – WUE_i, and Intrinsic Water Use Efficiency –WUE_{in}



Dendrogram distribution

In the analysis of gas exchange in forage cacti, variation among cultivars was observed for all variables studied (Figure 4). The differentiation of cultivars into groups is of great importance for the genetic improvement of forage cactus, allowing the breeder to determine the photosynthetic characteristics of each material used. Variability among cactus cultivars is common; this distinction is normal in cacti due to differences in plant biometry, such as width, cladode thickness, cuticle thickness, and genetic differences.

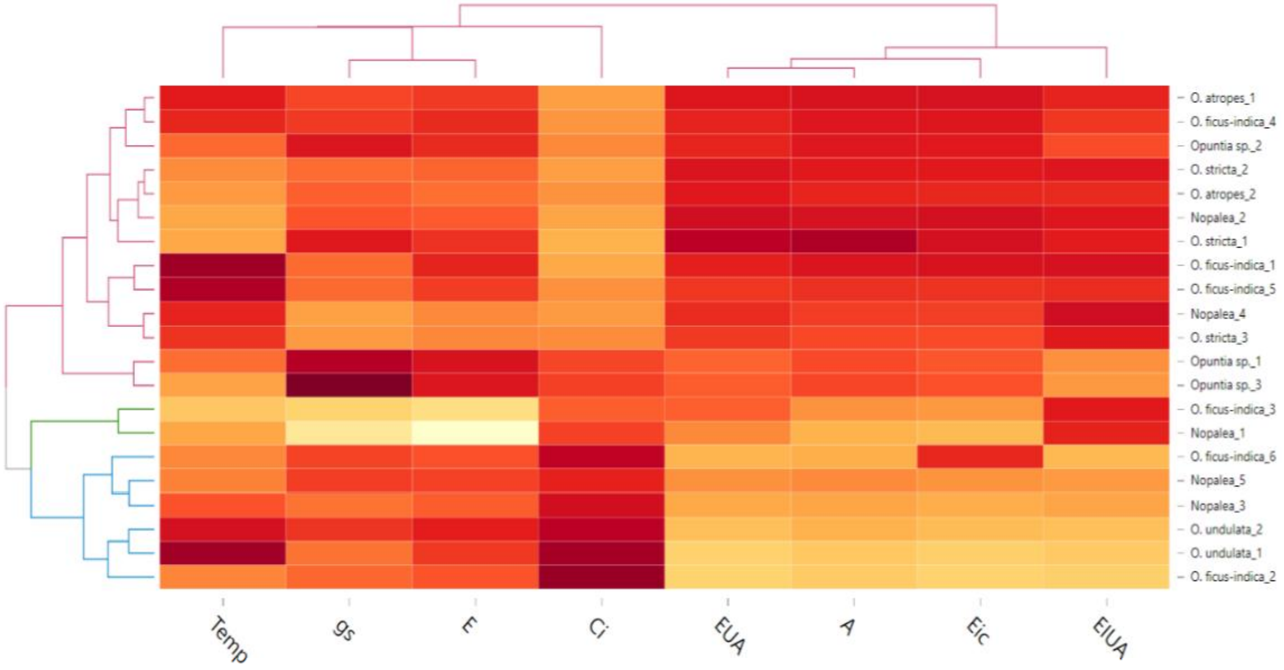
Rosa-Manzano, Flores e Delgado-Sanchez (2016) found similar variability among photosynthetic behaviour of three cactus species, namely, *Turbinicarpus schmiedickeanus*, *Mammillaria zephyranthoides*, and *Echinocactus platyacanthus*. The difference observed in stomatal conductance among cultivars is evident in genus *Nopalea* with cultivars 'F21 Sementes' and in *O. ficus-indica* 'IPA Clone 20', which showed low g_s and consequently, lower A values.

Cladode temperature varied little among cultivars, ranging from 22.5 to 23.8 °C, which is considered an ideal value for cladodes with no energy dissipation through heat irradiation. In contrast, stomatal conductance differed among cultivars, with values ranging from 0.1728 to 0.8120 mol H_2O m^{-2} s^{-1} in *Nopalea* _1 ('F21 Sementes') and *Opuntia* sp._3 ('Verdura'). Cultivars grown under the same environmental conditions showed variability for g_s. These results agreed well with those of Campelo *et al*. (2015), who evaluated gas exchange and photochemical efficiency of PSII in adult gonçalo-alves (*Astronium fraxinifolium*), guanandi (*Calophyllum brasiliens*), yellow ipê (*Handroanthus serratifolius*), ipê-rosa (*Handroanthus impetiginosa*), murapá (*Simarouba amara*), and mahogany (*Swietenia macrophylla*). Furthermore, these authors verified that two species of the same genus (*Handroanthus serratifolius* and *H. impetiginosa*) showed different g_s values ranging from 0.09 and 0.4 mol of H_2O m^{-2} s^{-1}.

Due to the intensity of the colours, there was little variability in E, with the lowest values observed for cultivars 'F21 Sementes' (*Nopalea*_1) and 'IPA Clone 20' (*O. ficus-indica*_3), with rates of 2.40 and 3.01 mmol H_2O m^{-2} s^{-1}, respectively. There is reportedly a direct correlation between g_s and A (LIMA; JARVIS; RHIZOPOULOU, 2003), implying that stomatal opening control directly affects CO_2 diffusion and, consequently, the carboxylation process.

The stomatal-opening control mechanisms are a striking feature in CAM species, whereby, the closing of stomata during the day prevents excess transpirational water loss at the time of maximum evaporative demand, an adaptation of great importance for survival in arid and semi-arid environments in

Figure 4 - Dispersion dendrogram of forage cactus cultivars belonging to the genera *Opuntia* and *Nopalea*. Leaf Temperature- T_{leaf}, Stomatal Conductance- g_s, –Transpiration Rate- E, Intercellular CO_2 Concentration- C_i, Instant Water Use Efficiency- WUE_i, Net Assimilation CO_2- A, Instant Carboxylation Efficiency- CE_i, and Intrinsic Use Efficiency of water- WUE_{in}



which high irradiance levels prevail most of the time (TAIZ *et al.*, 2017). However, stomatal limitations lead to reduced CO_2 diffusion, causing a reduction in net photosynthetic rate (HUSSAIN *et al.*, 2012).

The results reported herein reveal a plant strategy for regulating water use in environments with restricted water availability based on reduced transpiration and water loss to the environment, a fact that can be verified for the cultivar 'IPA Clone 20'. Similar results were found by Lina and Eloisa (2018), who evaluated three cactus species (*Acanthocereus tetragonus, Melocactus curvispinus*, and *Stenocereus griseus*) in a dry tropical forest in Colombia, and found that species with lower transpiration rates survived longer in that dry environment. Similarly, Huber *et al.* (2018) studied plants of *Carnegiea gigantea* and *Pachycereus pringlei* and concluded that an increase in g_s caused increased transpiration rates, consistently with our findings.

The highest C_i values (375.4820, 371.3704, 377.6440, and 370.2825 μmol CO_2 m^{-2} s^{-1}) were observed in cultivars 'Orelha de Elefante Africana – Clone 9' (*O. undulata*_1), 'Orelha de Elefante Mexicana' (*O. undulata*_2), and *O. ficus-indica*_2 and _6 (' Redonda 'IPA 98/T23'), respectively. However, we observed cultivars showing different C_i values within the same species. The higher C_i values can be explained by the fact that they have a low photosynthetic rate, i.e., a smaller amount of CO_2 is fixed in the carboxylation step. Consistently with this finding, Dalastra *et al.* (2014) reported that C_i decreased owing to the assimilation of carbon by the photosynthetic process.

The highest rate of net CO_2 assimilation was observed in cultivar 'Orelha de Elefante Mexicana' (*O. stricta*_1 with 10.7330 μmol CO_2 m^{-2} s^{-1}), while variability was observed within the same species. In turn, CE_i was lower in *O. ficus-indica*_2 ('Redonda' - 0.0272) and *O. undulata*_1 ('Orelha de Elefante Africana – Clone 9' - 0.0050), and as for WUE_i, cultivar *Nopalea*_4 ('Miúda') showed the highest value (18.8302), followed by *O. ficus-indica*_1 ('Copena'), with 18.2063.

Low CE_i was probably due to the reduction in RubisCO activity, considering that the carboxylation efficiency represents an estimate of the activity of this enzyme. Such a response may occur due to a reduction in photosynthetic rate, which in turn reduces the availability of ATP and NADPH, and the substrate for RubisCO (SILVA *et al.*, 2015).

The highest WUE was observed in cultivar *O. stricta*_1 belonging to 'Orelha de Elefante Mexicana', with a value of 2.4134 calculated by A/E, in contrast to cultivars belonging to *O. ficus-indica*_2 and *O. undulata*_1 ('Redonda' – 0.4085 and 'Orelha de Elefante Africana – Clone 9' – 0. 4283). Cultivar 'Orelha de Elefante Mexicana' showed the highest WUE. Such characteristic behaviour is due to the photosynthetic metabolism of forage cactus (CAM), which allows for higher WUE than that allowed by C3 or C4 photosynthetic metabolism (SNYMAN, 2013). Tatagiba *et al.* (2014) reported that g_s is directly influenced by a reduction in E and the resulting reduced water loss.

In other crop plants, variability among and within species was found to be common, as shown by Dutra *et al.* (2015) for cowpea (*Vigna unguiculata* L.) genotypes BRS Guariba, BR17 Gurguéia, and BRS Marataoã. The variability among cultivars may be a function of genus, species, and cultivation conditions. Research by Cajazeira *et al.* (2018) evaluated gas exchange in white pitaya (*Hylocereus undatus*) plants under the influence of potassium and calcium. They recorded values ranging from 15 to 18.81 μmol CO_2 m^{-2} s^{-1}. In general, cacti show greater WUE than C3 or C4 plants, as in that case, photosynthesis continues at times of water scarcity, enabling cacti to complete their developmental cycle (HOPKINS; HÜNER, 2009).

CONCLUSION

Variability is reported between and within cactaceous genera *Opuntia* and *Nopalea*. Cultivars 'Verdura' (*Opuntia* sp. _3) and 'Orelha de Elefante Mexicana' (*O. stricta*_1) were outstanding in terms of photosynthetic performance, while 'IPA Clone 20' (*O. ficus-indica*_3) and 'F21 Sementes' (*Nopalea*_1) showed the lower transpiration rates, and cultivars 'Orelha de Elefante Mexicana' (*O. stricta*_1), 'Miúda' (*Nopalea*_4), and 'Copena' (*O. ficus-indica*_1) showed the highest water use efficiency, which makes them the most suitable cultivars for cultivation in environments with limited water availability.

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