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Impact of weather and soil conditions on *Opuntia stricta* and *Nopalea cochenillifera* growth and forage yield in the Brazilian dryland

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ABSTRACT

Opuntia and *Nopalea* (Cactaceae) are plants well-adapted to a semi-arid environment and can be utilized for multiple purposes. However, weather and soil conditions can influence their morphophysiology and growth. Understanding these effects is essential for developing management practices that enhance production efficiency. This study was conducted under real-world conditions at 12 locations in Brazil to investigate morphophysiological traits, forage production, and water use efficiency of two species: *Opuntia stricta* [Haw.] Haw. cultivar 'Orelha de Elefante Mexicana' (OEM) and *Nopalea cochenillifera* (L.) Salm-Dyck cultivar 'Miuda'. No significant differences were observed between species for forage yield (average 13,587 kg dry matter (DM) ha⁻¹), water use efficiency (2.11 g DM kg H₂O⁻¹), or forage accumulation (38.8 kg DM ha⁻¹d⁻¹). However, morphological differences were noted, with *N. cochenillifera* exhibiting a greater number of cladodes (16.9 per plant) and *O. stricta* developing larger cladodes (0.04 kg DM) and a higher cladode leaf area index (1.15 m² m⁻²). Forage yield was positively associated with rainfall and soil organic carbon ($r=0.39$, $p<0.001$; $r=0.34$, $p<0.01$). Conversely, electrical conductivity and sodium content were inversely related to both the forage accumulation rate ($r = -0.43$, $p<0.001$; $r = -0.36$, $p<0.001$) and water use efficiency ($r = -0.32$, $p<0.01$; $r = -0.27$, $p<0.05$). The soil bulk density also showed a negative correlation to forage yield and forage accumulation rate ($r = -0.32$, $p<0.01$; $r = -0.35$, $p<0.001$). Rainfall variability and soil organic carbon were important key factors influencing *O. stricta* and *N. cochenillifera* morphology and productivity, while the high soil bulk density, electrical conductivity, and sodium content were detrimental to forage production.

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Introduction

Drylands are comprised of arid, semi-arid and dry sub-humid areas covering 41% of Earth's terrestrial landmass (Millennium Ecosystem Assessment Board 2005). These regions are characterized by prolonged water deficit periods throughout the year (Ruppert et al. 2015). As global food demand continues to rise due to population growth, the development of more efficient, environmentally sustainable, and resilient food systems has become increasingly important, particularly in dryland areas (Robinson et al. 2015).

Livestock systems play a vital role in the socioeconomic development of dry regions. In this context, Cactaceae, which are drought-tolerant plants, emerge as a multipurpose resource that is particularly valuable as a forage crop. These plants can provide both feed and water for animals during dry seasons, contributing to food security and mitigating the impacts of prolonged drought (Pereira et al. 2020, 2021).

In the Brazilian semi-arid region, the cultivation and use of *Opuntia* and *Nopalea* (Cactaceae), commonly referred as cactus or spineless cactus, for livestock feed is considered technically and economically viable (Cardoso et al. 2019; Inácio et al. 2020). The species *Opuntia stricta* [Haw.] Haw. and *Nopalea cochenillifera* (L.) Salm-Dyck, particularly the cultivars Orelha de Elefante Mexicana (OEM) and Miuda have been among the most important genotypes due to their resistance to *Dactylopius opuntiae* (Cockerell) (Lopes et al. 2024).

Although these species exhibit satisfactory productive performance, their forage yields vary across locations (Edvan et al. 2020; Jardim et al. 2021). Environmental factors, such as temperature (Drennan and Nobel 1998) and rainfall, affect soil water availability, significantly influencing their growth and productivity. Under rainfed conditions, the soil water content is a primary regulator of *Opuntia* growth, but elevated temperatures have been associated with reduced carbon assimilation (Scalisi et al. 2016). Considering the three daily temperature metrics (minimum, average, and maximum temperature), the optimal values for growth have been reported as 13°C (Medina-García et al. 2021), 18°C–23°C (Inglese, Liguori, and De La Barrera 2017), and 28.5°C–31.5°C (Silva et al. 2017), respectively.

Soil characteristics also play a critical role in the plant development. A high soil electrical conductivity, which is indicative of salinity (Franco-Salazar and Veliz 2007) or the sodium concentration (sodicity), and bulk density (Bariagabre et al. 2016) have been negatively associated with growth. Soil pH can influence nutrient solubility and availability, and potassium is among the macronutrients taken up in larger quantities by *Opuntia* (Donato et al. 2017b). Soil organic carbon, a major component of organic matter, enhances nitrogen mineralization, serves as a nutrient reservoir, and improves the soil structure (Camelo et al. 2021).

Under field conditions, the extent to which weather and soil characteristics influence plant morphology, water use efficiency, and forage production of these species remains insufficiently understood. These responses are critical for developing effective management practices to enhance crop productivity.

We hypothesize that lower minimum, average, and maximum temperatures and increased rainfall enhance the forage yield, forage accumulation rate, and water use efficiency of *O. stricta* and *N. cochenillifera*. An increased bulk density, electrical

conductivity, and sodium concentration will negatively impact forage yield and water use efficiency. Higher levels of soil organic carbon, increased potassium content, and a less acidic pH are expected to improve both forage production and water use efficiency for these species.

This study presents a novel approach for the evaluation of these two species under large-scale, multi-location field conditions, considering both local weather patterns and soil properties. Unlike previous research, this work aimed to identify key environmental drivers associated with morphological traits, forage productivity, and water use efficiency. The objective was to evaluate the effects of meteorological factors, including temperature and rainfall, and soil conditions, bulk density, soil organic carbon, potassium and sodium contents, electrical conductivity, and pH on the morphological traits, forage yield, and water use efficiency of *O. stricta* and *N. cochenillifera* in a multi-site field study in Brazil. These findings will contribute to practical recommendations for optimizing their cultivation in dryland environments.

Materials and methods

Species

Two species were evaluated: *O. stricta* [Haw.] Haw., cultivar Orelha de Elefante Mexicana (OEM), and *Nopalea cochenillifera* (L.) Salm-Dyck, cultivar Miuda.

Resistance to *D. opuntiae* (Silva et al. 2022; Vasconcelos et al. 2009) was the primary criterion for selecting the cultivars used in this study. This trait, combined with their forage production potential has supported the expansion of their cultivation in the Brazilian semiarid region (Araújo Júnior et al. 2025), where the pest is widely distributed (Soares et al. 2024). These cultivars offer alternatives for areas where susceptible genotypes have experienced significant losses and serve as a preventive strategy in regions with low or no current pest incidence, reinforcing the importance of their inclusion in multi-site studies.

Although both species are used as animal feed, they differ in chemical composition. *N. cochenillifera* has higher concentrations of dry matter and soluble carbohydrates and is considered to have superior nutritional value compared to *Opuntia* (Dubeux et al. 2021). From an agronomic perspective, *O. stricta* has lower nutrient requirements and greater drought tolerance than *N. cochenillifera* (Inácio et al. 2020). In addition, there are notable morphological and structural differences: *N. cochenillifera* has smaller and lighter cladodes, as well as a greater number of cladodes per plant compared to *O. stricta*. While *N. cochenillifera* exhibits predominantly vertical growth, *O. stricta* grows in a more horizontal form (Ramos et al. 2021).

Location, conditions, and geographical coordinates

Twelve field experiments were conducted from 2017 to 2020 across different locations in Brazil, all under rainfed conditions. Eleven of these experiments were located in the Brazilian semi-arid region, while one was conducted in the Cerrado biome. Both species were grown in all 12 locations. According to Köppen classification,

the predominant climate is the BSh type in the Brazilian semi-arid region (Borges et al. 2020) and the Aw type in the Cerrados (Oliveira et al. 2024).

The geographical coordinates and elevations of the experimental sites and their respective regions are shown in Table 1, and the locations of the experimental sites in Brazil are shown in Figure 1.

The experimental locations were strategically selected to capture environmental variability across the study region. The goal was to include at least one site within each federative unit located in the Brazilian semi-arid zone, including the state of Maranhão, which contains municipalities officially classified within this region.

Priority was given to areas relevant to livestock production, as *O. stricta* and *N. cochenillifera* cultivation in this study was primarily intended for forage use. Since the experiments were conducted under real-world conditions on commercial properties, practical considerations also influenced site selection. This included accessibility, the

Table 1. Locations, regions, geographical coordinates, and elevation for the 12 experimental sites in Brazil that were cultivated with *Opuntia stricta* and *Nopalea cochenillifera*.

Location	Region	Coordinates	Elevation, m
Baixa Grande, BA	Semi-arid	11°57'57"S/40°17'39"W	397
Batalha, AL	Semi-arid	9°40'09"S/37°08'25"W	394
Carlos Chagas, MG	Semi-arid	17°41'03"S/40°47'53"W	160
Fortuna, MA	Cerrados	5°45'30"S/44°08'46"W	225
Ibaretama, CE	Semi-arid	4°48'14"S/38°45'10"W	92
Ipirá, BA	Semi-arid	12°09'28"S/39°44'13"W	330
Itapetinga, BA	Semi-arid	15°15'41"S/40°14'27"W	293
Lajes, RN	Semi-arid	5°42'29"S/36°13'55"W	173
Montes Claros, MG	Semi-arid	16°44'06"S/43°51'42"W	648
São João, PE	Semi-arid	8°49'26"S/36°25'24"W	710
São Raimundo Nonato, PI	Semi-arid	9°05'06"S/42°42'57"W	361
Tenório, PB	Semi-arid	7°00'37"S/36°40'23"W	598

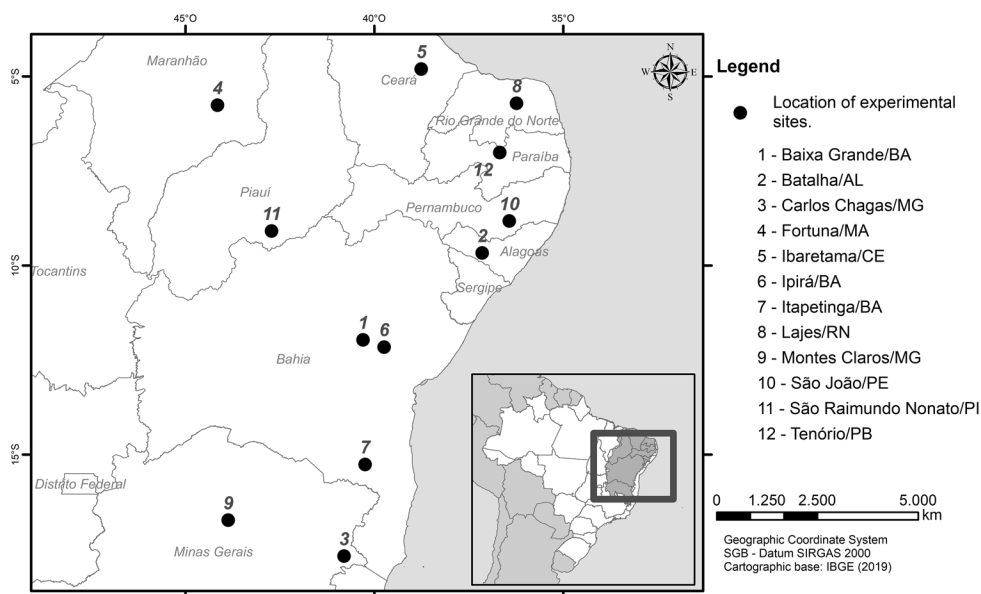


Figure 1. Locations of the 12 experimental sites in Brazil where this study was conducted.

availability of fenced areas for crop protection, and adequate infrastructure for sample processing and storage.

Soil data

Soil samples were collected approximately 1 month prior to planting, which occurred from October 2017 to September 2018, following the agricultural calendar specific to each location. Sampling was conducted by collecting individual samples in the 0–20 cm soil layer throughout the entire plot. Due to the small plot size, these samples were combined into a single composite sample per location and subsequently sent for laboratory analysis.

Chemical analyses were conducted to determine the pH, electrical conductivity (1:1 soil water ratio), sodium and potassium contents determined by Mehlich-1 (0.0125 mol L⁻¹ H₂SO₄ and 0.05 mol L⁻¹ HCl) using a flame photometer. Soil organic carbon was determined using the method of Walkley and Black (1934). Physical analysis to determine the bulk density used the graduated cylinder method. The soil analysis procedures were carried out in accordance with Teixeira et al. (2017).

Weather data

Minimum, average, and maximum temperatures and rainfall were recorded daily by weather stations installed in each area. As the crop cycles differed depending on the region, the cumulative rainfall in a crop cycle for each location was divided by the growth time to estimate the daily average rainfall (mm d⁻¹). Solar radiation data were obtained from the NASA-POWER system (<https://power.larc.nasa.gov>) (NASA, 2022). The weather data considered in the analysis refer to the period from planting to the first harvest and from the first to final harvest, representing two crop cycles at each location.

Experimental design, plots, and planting density

The experimental design was a completely randomized block with two replicates. Each plot was 5 m long and 4 m wide (20 m²) and consisted of 5 rows with 16 plants, totaling 80 plants. There was 1.0 m between rows and 0.25 m between plants, resulting in a planting density of 40,000 plants ha⁻¹.

Soil preparation, fertilization, and crop management

The experimental area was enclosed with fencing, and the preparation of the soil was carried out through plowing, harrowing, and furrowing. In most areas, fertilization was performed on the day of planting or one day afterward. In Itapetinga, BA, fertilization occurred 24 days before planting due to the need for replanting, while in Ipirá, BA, it was conducted 31 days after planting due to heavy rainfall shortly after planting.

Although a combination of both organic (cured cattle manure) and mineral fertilization is recommended, organic fertilization was implemented in only five areas due

to limited availability in some locations. In São João, PE, mineral fertilization at planting was not performed due to the unavailability of fertilizers at the time of planting. Based on the availability of fertilizer sources, either nitrogen, phosphorus, and potassium (NPK), phosphorus, and potassium (as in Baixa Grande, BA) or only P (as in Carlos Chagas, MG) were applied.

The fertilizer sources used included single superphosphate (18% phosphorus pentoxide; P_2O_5), potassium chloride (58% potassium oxide; K_2O), and urea (45% nitrogen). Post-harvest topdressing fertilization was also carried out, depending on rainfall occurrence and the availability of fertilizers. In these cases, either NPK- or nitrogen-only fertilization was applied, using urea, single superphosphate, and potassium chloride as nutrient sources.

The planting was performed manually using a single cladode, of which 50% of the pad was below ground. All plants in each plot were harvested, which was conducted manually by cutting the plant at the intersection between the basal and first cladodes, with only the basal cladode remaining after harvest.

In each location, both species were harvested and evaluated in two crop cycles for all 12 sites for a total of 24 growing seasons that were evaluated. The first crop cycle or growing season corresponded to the period from planting to the first harvest, and the second cycle or growing season corresponded to the period from the first to the second harvest. The period from planting to the second harvest date ranged from 633 to 999 days. On average, each crop cycle was 360 days, ranging from 303 to 632 days, depending on the location (Table 2).

Pest management for *Diaspis echinocacti* (Bouché) and other pests, such as ants, and weed control were conducted based on occurrence and necessity.

Variable selection and categorization

To characterize the soil conditions, three parameters indicative of fertility were selected: pH, soil organic carbon, and potassium content. The soil pH was included due to its direct influence on nutrient solubility and availability. Potassium was selected because of its high accumulation in plant tissues, and soil organic carbon is considered a key indicator of nutrient and water retention capacity, microbial activity, and overall soil health.

To account for soil salinity, two parameters were included: electrical conductivity and sodium content. In addition, bulk density was chosen to represent the physical conditions of the soil, reflecting compaction and porosity.

Local weather conditions were assessed using variables that reflected rainfall, temperature, and solar radiation. These included average daily rainfall and minimum, average, and maximum daily temperatures. Elevation was also considered due to its potential effect on local climatic conditions.

Plant response variables were selected to capture both morphological and productive characteristics. Morphological traits included plant height, plant width, number of cladodes per plant, average cladode weight, and cladode area index, an integrative measure related to biomass productivity. Productive responses included forage yield and forage accumulation rate, and water use efficiency was used to evaluate the relationship between biomass production and water use.

Table 2. Crop management practices applied to the *opuntia stricta* and *nopalea cochenillifera* grown at 12 experimental locations.

Location	Planting date	First harvest date	Final harvest date	Fertilization date	Amount of fertilizer
Baixa Grande, BA	12/26/2017	12/30/2018	12/31/2019	12/26/2017	12,000 kg DM ha ⁻¹ *
				12/26/2017	10 kg ha ⁻¹ P
				12/26/2017	30 kg ha ⁻¹ K
				01/04/2018	50 kg ha ⁻¹ N
				03/23/2019	30 kg ha ⁻¹ N
Batalha, AL	02/15/2018	12/27/2018	11/29/2019	02/15/2018	18 kg ha ⁻¹ P
				02/15/2018	75 kg ha ⁻¹ K
				04/12/2018	45 kg ha ⁻¹ N
				04/12/2018	42 kg ha ⁻¹ K
				05/15/2018	45 kg ha ⁻¹ N
Carlos Chagas, MG	10/01/2017	10/13/2018	10/19/2019	07/10/2019	50 kg ha ⁻¹ N
				10/01/2017	95 kg ha ⁻¹ P
				02/01/2018	65 kg ha ⁻¹ N
				10/28/2018	32 kg ha ⁻¹ N
				12/08/2018	32 kg ha ⁻¹ N
Fortuna, MA	11/21/2017	09/29/2018	09/27/2019	11/21/2017	20 kg ha ⁻¹ N
				11/21/2017	70 kg ha ⁻¹ P
				11/21/2017	40 kg ha ⁻¹ K
				03/01/2018	40 kg ha ⁻¹ N
				02/03/2019	45 kg ha ⁻¹ N
Ibaretama, CE	01/03/2018	12/20/2018	11/01/2019	02/03/2019	30 kg ha ⁻¹ P
				02/03/2019	50 kg ha ⁻¹ K
				05/06/2019	45 kg ha ⁻¹ N
				05/06/2019	30 kg ha ⁻¹ P
				05/06/2019	50 kg ha ⁻¹ K
Ipirá, BA	09/20/2018	10/11/2019	10/30/2020	10/21/2018	120 kg ha ⁻¹ N
				10/21/2018	100 kg ha ⁻¹ P
				10/21/2018	40 kg ha ⁻¹ K
				11/26/2019	120 kg ha ⁻¹ N
				11/26/2019	100 kg ha ⁻¹ P
Itapetinga, BA	03/05/2018	02/20/2019	12/29/2019	11/26/2019	40 kg ha ⁻¹ K
				09/04/2018	60 kg ha ⁻¹ P
				09/04/2018	30 kg ha ⁻¹ N
				09/04/2018	90 kg ha ⁻¹ K
				02/17/2019	50 kg ha ⁻¹ N
Lajes, RN	01/02/2018	09/26/2019	09/27/2020	01/02/2018	12,000 kg DM ha ⁻¹ *
				01/07/2020	15 kg ha ⁻¹ N
				01/07/2020	45 kg ha ⁻¹ P
				01/07/2020	30 kg ha ⁻¹ K
				10/04/2017	20 kg ha ⁻¹ P
Montes Claros, MG	10/04/2017	08/21/2018	06/20/2019	10/04/2017	48 kg ha ⁻¹ K
				10/04/2017	20 kg ha ⁻¹ N
				10/21/2018	65 kg ha ⁻¹ N
				02/04/2018	8000 kg DM ha ⁻¹ *
				03/16/2019	30 kg ha ⁻¹ K
São João, PE	02/04/2018	02/03/2019	02/21/2020	03/16/2019	10 kg ha ⁻¹ P
				03/16/2019	23 kg ha ⁻¹ N
				01/02/2018	8,000 kg DM ha ⁻¹ *
				01/02/2018	70 kg ha ⁻¹ P
				02/21/2018	8000 kg DM ha ⁻¹ *
São Raimundo Nonato, PI	01/02/2018	11/07/2018	11/16/2019	02/21/2018	20 kg ha ⁻¹ N
				02/21/2018	60 kg ha ⁻¹ P
				02/21/2018	30 kg ha ⁻¹ K
				03/02/2019	60 kg ha ⁻¹ P
				03/02/2019	20 kg ha ⁻¹ N
Tenório, PB	02/21/2018	02/23/2019	12/27/2019	03/02/2019	30 kg ha ⁻¹ K

*Manure (0.9% nitrogen, 0.3% phosphorus, and 0.24% potassium), dry weight basis. N=nitrogen, P=phosphorus, K=potassium, DM=dry matter.

The inclusion of average rainfall and forage accumulation rates accounted for variations in harvest intervals across locations, ensuring more consistent and accurate estimates of the evaluated parameters.

Morphological traits, cladode weight, and cladode area index

Structural measurements were carried out on five plants from each plot at each harvest time. Plant height and width were measured using a tape measure, and the number of cladodes per plant was counted. All cladodes on each plant were measured using a tape measure to determine their length, width, and thickness.

The cladode area (CA) of OEM and Miuda were estimated according to Silva et al. (2014) using the following equations:

$$CA_{OEM} (cm^2) = 0.7086 \times \left(\frac{1 - e^{(-0.000045765 \times CL(cm) \times CW(cm))}}{0.000045765} \right) \quad (1)$$

$$CA_{MIUDA} (cm^2) = 0.7198 \times CL(cm) \times CW(cm) \quad (2)$$

where CL and CW are the cladode length and cladode width, respectively.

The cladode area index (CAI, $m^2 m^{-2}$) represented by the total photosynthetic area per unit soil area occupied by the plant was estimated from CA and plant spacing, considering the following equation, according to Pinheiro et al. (2015):

$$CAI (m^2 m^{-2}) = (CA (cm^2)) / 10,000 / (S1 \times S2 (m)) \quad (3)$$

where CA (cm^2) corresponds to the area per cladode; 10,000 is the conversion factor from cm^2 to m^2 , and S1 and S2 are the spacings between rows and plants, respectively.

Five plants per plot were harvested to determine the mass per plant, which were individually weighed. Fresh forage material was dried in a forced-air oven at $55^\circ C$ until a constant weight to determine the dry mass. The dry mass ($kg plant^{-1}$) was divided by the number of cladodes per plant to estimate the average weight per cladode.

Forage yield, forage accumulation rate, and water use efficiency

Forage yield ($kg dry mass ha^{-1}$) was estimated by multiplying the average plant dry mass by the number of plants ha^{-1} . The forage accumulation rate ($kg DM ha^{-1} day^{-1}$) was determined by dividing the forage yield by the number of days of the cycle or growing season. The water use efficiency ($g DM kg H_2O^{-1}$) was estimated by dividing the forage yield ($g DM$) by the amount of rainfall converted from mm to $kg H_2O$.

Data preparation and statistical analysis

The evaluation of morphological and yield responses included two species, two growing seasons or crop cycles, and 12 locations, totaling 48 observations. For each species, mean values for productive and morphological traits were calculated based on two replicates per plot. Within each plot, measurements from five plants were

averaged, and the resulting means from the two plots per species were subsequently averaged.

Local weather data were summarized for each site based on the corresponding growing season, resulting in 24 weather datasets (12 locations $\times$ 2 seasons). The same weather data were applied to both species at each location, as they were grown simultaneously under the same conditions.

Soil data were collected once before planting, yielding 12 soil datasets, 1 per location. These values were used for both species and cultivation cycles, since the objective was to evaluate the influence of initial soil conditions on plant responses over time.

Descriptive statistics were used to characterize weather and soil variables and to present measures of central tendency and variability for the morphological and productive traits of species across the 12 study sites. For each species descriptive statistics for morphological traits and productive responses were based on data collected from 12 locations across two seasons, totaling 24 observations.

Given the variability in management practices among locations as planting, harvesting and fertilization dates and amount of fertilizers, Pearson's correlation analysis was used to examine potential relationships among variables as well as the direction and strength of associations.

All descriptive statistics and correlation analyses were performed using the PROC MEANS and PROC CORR procedures in SAS software. Comparisons of morphological and productive traits between species were conducted using Tukey's test via PROC GLM, with statistical significance determined at $p < 0.05$.

Results

Morphological traits and agronomic responses

On average, the species had a forage yield, water use efficiency, and forage accumulation rate of 13,587 kg DM ha⁻¹, 2.11 g DM kg H₂O⁻¹, and 38.8 kg DM ha⁻¹ day⁻¹, respectively (Table 3). The observed values for productivity and water use efficiency in this study are consistent with those reported by Léo et al. (2019). Similarly, the cladode area index values align with the findings reported by Alves and dos Santos (2024), indicating that the results are within the expected range under similar environmental conditions.

A comparison of the means for the measured traits showed a similar plant height and width, forage yield, forage accumulation rate, and water use efficiency for both species ($p > 0.05$). However, *N. cochenillifera* had more cladodes per plant, a lower cladode area index, and lower weight per cladode than *O. stricta* ($p < 0.05$) (Table 4).

Plant height was positively correlated to the plant width and cladode area index for both species. In addition, the cladode area index was also positively correlated with the number of cladodes. Plant width increased with the cladode weight for *O. stricta* and *N. cochenillifera*, while the weight per cladode had a negative correlation with the number of cladodes for *O. stricta* (Table 5).

Morphological traits (plant height and width, cladode weight, and cladode area index) were positively correlated with forage yield, water use efficiency, and forage accumulation rate. The positive correlation coefficients for the cladode area index

Table 3. Cladode area index, forage yield, water use efficiency, and forage accumulation rate of species *Opuntia stricta* cultivar 'orelha de elefante Mexicana' (OEM) and *Nopalea cochenillifera* cultivar 'Miuda' grown at 12 experimental sites over two crop cycles.

Location	Cladode area index (m ² m ⁻²)			Forage yield (kg DM ha ⁻¹)			Water use efficiency (g DM kg H ₂ O ⁻¹)			Forage accumulation rate (kg DM ha ⁻¹ day ⁻¹)		
	Mean	Miuda	OEM	Mean	Miuda	OEM	Mean	Miuda	OEM	Mean	Miuda	OEM
Baixa Grande, BA	1.54	1.40	1.68	16,009	14,778	17,240	2.47	2.43	2.51	43.6	40.3	46.9
Batalha, AL	0.85	0.65	1.05	9320	7980	10,660	1.63	1.41	1.85	28.5	24.4	32.5
Carlos Chagas, MG	0.88	0.70	1.05	17,078	19,520	14,635	1.73	1.96	1.49	45.2	52.3	38.1
Fortuna, MA	1.48	1.28	1.68	17,431	17,108	17,753	2.10	2.06	2.13	51.8	51.1	52.4
Ibaretama, CE	0.91	0.83	0.98	6458	6833	6083	1.31	1.35	1.26	19.8	20.8	18.7
Ipirá, BA	0.82	1.03	0.60	12,530	16,755	8305	2.10	2.86	1.34	32.6	43.6	21.6
Itapetinga, BA	1.54	1.80	1.28	22,475	26,040	18,910	3.56	4.41	2.70	67.4	76.1	58.7
Lajes, RN	0.72	0.75	0.68	7634	8390	6878	1.23	1.35	1.11	16.1	17.7	14.5
Montes Claros, MG	1.37	1.13	1.60	17,647	19,310	15,983	2.29	2.54	2.04	56.5	62.1	50.9
São João, PE	1.08	0.95	1.20	9878	12,825	6930	1.24	1.59	0.88	26.4	34.0	18.7
São R. Nonato, PI	0.64	0.60	0.68	11,340	10,110	12,570	1.97	1.79	2.14	32.2	29.1	35.3
Tenório, PB	1.05	0.80	1.30	15,240	14,160	16,320	3.63	3.31	3.94	45.2	41.6	48.7
Average	1.07	0.99	1.15	13,587	14,484	12,689	2.11	2.26	1.95	38.8	41.1	36.4
Standard deviation	0.33	0.33	0.38	4819	5675	4737	0.81	0.92	0.84	15.4	17.4	15.3

DM: dry matter.

Table 4. Descriptive statistics and least square means for morphological characteristics (plant height, width, cladodes per plant, cladode area index, and cladode weight) of *Opuntia stricta* cultivar 'orelha de elefante Mexicana' (OEM) and *Nopalea cochenillifera* cultivar 'Miuda' and grown at 12 experimental sites over two crop cycles ($n = 48$).

Variable	Miuda				OEM				SEM	p value
	Average	Standard deviation	Min.	Max.	Average	Standard deviation	Min.	Max.		
Plant height (m)	0.54a	0.10	0.32	0.72	0.54a	0.13	0.34	0.75	0.017	0.90
Plant width (m)	0.66a	0.17	0.32	0.91	0.63a	0.15	0.32	1.07	0.023	0.43
Cladodes per plant (n)	16.9a	6.40	6.0	35.0	9.4b	3.12	4.0	18.0	0.76	<0.0001
Cladode area index (m ² m ⁻²)	0.94b	0.39	0.40	1.80	1.14a	0.51	0.40	2.50	0.067	0.047
Cladode weight (kg dry matter)	0.02b	0.011	0.007	0.062	0.04a	0.016	0.013	0.083	0.002	<0.0001

Within a row, means followed by a different lowercase letters are significantly different according to the Tukey test ($p < 0.05$).

ranged from 0.52 to 0.69 for productive responses (forage yield and forage accumulation rate) and water use efficiency.

Meteorological conditions versus morphological traits and agronomical responses

The rainfall recorded during the evaluated crop cycles, each spanning approximately one year, was consistent with one of the key criteria for defining Brazil's semi-arid region: annual precipitation not exceeding 800 mm (Barbosa et al. 2024). Although the average minimum temperature during the study period was slightly below regional values, the average and maximum temperatures were consistent with those reported

Table 5. Pearson correlation coefficients for morphological traits (plant height, plant width, cladodes per plant, cladode area index, and cladode weight) and productive responses (forage yield, water use efficiency, and forage accumulation rate for *Opuntia stricta* cultivar 'orelha de elefante Mexicana' (OEM) and *Nopalea cochenillifera* cultivar 'Miuda' from 12 areas over two crop cycles ($n=48$).

Morphological traits	Plant height	Plant width	Cladodes per plant	Cladode area index	Cladode weight
Plant height	1.00	Corr. 0.68*** Miuda 0.71*** OEM 0.66***	Corr. 0.28** Miuda 0.28 OEM 0.54***	Corr. 0.51*** Miuda 0.41** OEM 0.60***	Corr. 0.15 Miuda 0.40** OEM 0.05
Plant width	Corr. 0.68*** Miuda 0.71*** OEM 0.66***	1.00	Corr. 0.32*** Miuda 0.37* OEM 0.30	Corr. 0.44*** Miuda 0.39** OEM 0.56***	Corr. 0.61*** Miuda 0.59*** OEM 0.72***
Cladodes per plant	Corr. 0.28** Miuda 0.28 OEM 0.54***	Corr. 0.32*** Miuda 0.37* OEM 0.30	1.00	Corr. 0.47*** Miuda 0.90*** OEM 0.80***	Corr. -0.47*** Miuda -0.28 OEM -0.31*
Cladode area index	Corr. 0.51*** Miuda 0.41** OEM 0.60***	Corr. 0.44*** Miuda 0.39** OEM 0.56***	Corr. 0.47*** Miuda 0.90*** OEM 0.80***	1.00	Corr. 0.13 Miuda -0.123 OEM 0.127
Cladode weight	Corr. 0.15 Miuda 0.40** OEM 0.05	Corr. 0.61*** Miuda 0.59*** OEM 0.72***	Corr. -0.47*** Miuda -0.28 OEM -0.31*	Corr. 0.13 Miuda -0.12 OEM 0.13	1.00
Forage yield	Corr. 0.49*** Miuda 0.54** OEM 0.46***	Corr. 0.57*** Miuda 0.55*** OEM 0.58***	Corr. 0.388*** Miuda 0.46** OEM 0.46**	Corr. 0.59*** Miuda 0.57*** OEM 0.68***	Corr. 0.46*** Miuda 0.64*** OEM 0.52***
Water use efficiency	Corr. 0.47*** Miuda 0.47** OEM 0.47**	Corr. 0.59*** Miuda 0.54*** OEM 0.59***	Corr. 0.31** Miuda 0.43** OEM 0.27	Corr. 0.52*** Miuda 0.55*** OEM 0.54***	Corr. 0.39*** Miuda 0.45** OEM 0.49***
Forage accumulation rate	Corr. 0.53*** Miuda 0.59*** OEM 0.48**	Corr. 0.61*** Miuda 0.63*** OEM 0.58***	Corr. 0.39*** Miuda 0.48*** OEM 0.46**	Corr. 0.61*** Miuda 0.58*** OEM 0.69***	Corr. 0.44*** Miuda 0.59*** OEM 0.49***

Corr = correlation coefficient considering both species; Miuda and OEM = correlation coefficient for each species ($n=24$).
*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

by Curado et al. (2023), who identified typical values for the Brazilian semi-arid northeast as 21.7°C (minimum), 26.4°C (average), and 32.2°C (maximum). This region encompasses most of the Brazilian semi-arid zone. Solar radiation levels during crop cycles were also marginally lower than the typical averages for the region (Jean and Brasil Junior, 2022).

Among the four high-productivity locations, cumulative rainfall during the cultivation cycle ranged from 734 to 1003 mm, with an average rainfall exceeding 2.45 mm d⁻¹. Maximum temperatures ranged from 30.6°C to 33.8°C. In contrast, the four lowest productivity locations recorded average rainfall between 1.37 and 2.12 mm d⁻¹ with a mean of 1.71 mm d⁻¹, and maximum temperatures ranging from 31.0°C to 33.5°C (Table 6).

Plant height and cladode weight were not correlated to the meteorological conditions or elevation. However, plant width was positively correlated to elevation and negatively to maximum temperature; the cladode area index was negatively correlated to the average temperature and positively to the average daily rainfall (Table 7).

The correlation analysis for meteorological conditions with agronomical responses revealed that the minimum, average, and maximum temperatures were not significantly correlated with forage yield, water use efficiency, or the forage accumulation rate. Both forage yield and the forage accumulation rate increased with an increase in average daily rainfall (mm day⁻¹), and they were not affected by solar radiation. Additionally, water use efficiency for *O. stricta* was reduced with the increase in solar radiation and was increased with elevation.

Table 6. Minimum, average, and maximum daily temperature, cumulative and daily average rainfall, and average daily total solar radiation recorded at the experimental sites.

Location	Minimum temperature (°C)*	Average temperature (°C)*	Maximum temperature (°C)*	Cumulative rainfall (mm)*	Average daily rainfall (mm d ⁻¹)*	Solar radiation (MJ m ⁻² d ⁻¹)*
Baixa Grande, BA	19.3	25.6	31.9	627	1.92	19.8
Batalha, AL	20.9	25.6	33.5	548	1.62	20.8
Carlos Chagas, MG	18.2	24.1	32.0	1003	2.68	19.4
Fortuna, MA	19.6	27.8	33.8	829	2.51	22.1
Ibaretama, CE	18.7	26.8	31.0	580	1.71	19.2
Ipira, BA	19.8	26.2	32.3	644	1.67	20.7
Itapetinga, BA	18.9	23.4	32.1	734	2.22	19.1
Lajes, RN	21.4	26.8	33.5	738	1.37	23.1
Montes Claros, MG	20.7	25.0	30.6	784	2.49	21.6
São João, PE	20.5	23.7	30.6	788	2.12	23.0
São Raimundo Nonato, PI	22.1	27.7	35.0	536	1.59	19.9
Tenório, PB	21.4	24.5	31.5	446	1.29	19.5
Statistical summary of meteorological conditions						
Mean	20.2	25.8	32.4	666	1.88	20.7
Standard deviation	1.20	1.4	1.40	181	0.47	1.50
Minimum	17.8	23.1	29.9	337	1.11	19.1
Maximum	22.2	28.1	35.5	1043	2.81	23.9

*Average of two growing seasons per location.

Table 7. Pearson correlation coefficients for morphological traits and productive responses for *Opuntia stricta* cultivar 'Orelha de Elefante Mexicana' (OEM) and *Nopalea cochenillifera* cultivar 'Miuda' with meteorological factors (minimum, average, and maximum daily temperatures, solar radiation, average daily rainfall, and elevation) for 12 experimental sites in Brazil ($n=48$).

Morphological traits	Minimum temperature	Average temperature	Maximum temperature	Solar radiation	Average daily rainfall	Elevation
Plant height	Corr. -0.12	Corr. -0.10	Corr. -0.08	Corr. -0.10	Corr. 0.13	Corr. 0.02
	Miuda -0.15	Miuda -0.11	Miuda -0.06	Miuda -0.16	Miuda 0.26	Miuda -0.04
	OEM -0.10	OEM -0.10	OEM -0.10	OEM -0.10	OEM 0.02	OEM 0.07
Plant width	Corr. -0.02	Corr. -0.18	Corr. -0.34**	Corr. 0.01	Corr. 0.13	Corr. 0.35***
	Miuda -0.03	Miuda -0.19	Miuda -0.40**	Miuda 0.02	Miuda 0.21	Miuda 0.41***
	OEM -0.01	OEM -0.12	OEM -0.26	OEM -0.01	OEM 0.04	OEM 0.27
Cladodes per plant	Corr. -0.14	Corr. -0.13	Corr. -0.13	Corr. 0.16	Corr. 0.20	Corr. 0.11
	Miuda 0.29	Miuda -0.25	Miuda -0.23	Miuda 0.13	Miuda 0.22	Miuda 0.12
	OEM -0.06	OEM -0.06	OEM 0.06	OEM 0.17	OEM 0.30*	OEM 0.03
Cladode area index	Corr. -0.23*	Corr. -0.20	Corr. -0.16	Corr. -0.01	Corr. 0.25*	Corr. 0.156
	Miuda -0.27	Miuda -0.19	Miuda -0.13	Miuda 0.10	Miuda 0.21	Miuda 0.09
	OEM -0.21	OEM -0.21	OEM -0.20	OEM -0.07	OEM 0.31*	OEM 0.25
Cladode weight	Corr. -0.20	Corr. -0.18	Corr. -0.12	Corr. -0.18	Corr. 0.10	Corr. 0.07
	Miuda -0.18	Miuda -0.16	Miuda -0.13	Miuda -0.14	Miuda 0.24	Miuda 0.04
	OEM -0.07	OEM -0.09	OEM -0.16	OEM -0.18	OEM 0.24	OEM 0.18
Forage yield	Corr. -0.19	Corr. -0.12	Corr. -0.05	Corr. -0.08	Corr. 0.38***	Corr. 0.20
	Miuda -0.26	Miuda -0.20	Miuda -0.14	Miuda 0.03	Miuda 0.42**	Miuda 0.18
	OEM -0.12	OEM 0.06	OEM 0.06	OEM -0.24	OEM 0.35*	OEM 0.22
Water use efficiency	Corr. 0.09	Corr. 0.03	Corr. -0.04	Corr. -0.25*	Corr. -0.15	Corr. 0.30**
	Miuda -0.01	Miuda -0.06	Miuda -0.11	Miuda -0.16	Miuda -0.11	Miuda 0.35
	OEM 0.17	OEM 0.15	OEM 0.14	OEM -0.35*	OEM -0.19	OEM 0.34*
Forage accumulation rate	Corr. -0.19	Corr. -0.12	Corr. -0.08	Corr. -0.11	Corr. 0.41***	Corr. 0.25*
	Miuda -0.24	Miuda 0.18	Miuda -0.17	Miuda 0.02	Miuda 0.45**	Miuda 0.24
	OEM -0.13	OEM -0.05	OEM 0.01	OEM -0.27	OEM 0.37*	OEM 0.26

Corr = correlation coefficient considering both species; Miuda and OEM = correlation coefficient for each species ($n=24$).*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Effects of soil condition on morphological traits and agronomic responses

On average, soils across the study did not exhibit high electrical conductivity or sodium concentrations, except in Lajes, RN, where elevated salinity and sodium levels were observed. The soil pH in most locations was below the optimal range for *Opuntia* cultivation (5.6–6.3), and the potassium content was generally low (Donato et al. 2017a). Bulk density values across sites were below the critical thresholds known to restrict root growth (USDA – NRCS, 1996). However, soil organic carbon levels were low in most locations (Musinguzi et al. 2013), with the exception of Fortuna, MA (Table 8).

Notably, three locations with the highest forage yield, Itapetinga, BA, Montes Claros, MG, and Fortuna, MA, shared similar soil characteristics: low electrical conductivity and sodium concentrations, low bulk density, and the highest levels of soil organic carbon among all locations. In contrast, Lajes, RN, which recorded the lowest forage accumulation rate and water use efficiency for both species, was characterized by high electrical conductivity and sodium levels.

An increase in soil bulk density reduced the plant height and decreased the plant width and cladode weight for both species. The soil organic carbon content increased the number of cladodes per plant and the cladode area index for *O. stricta* and *N. cochenillifera*, while electrical conductivity and sodium content reduced the cladode area index for both species (Table 9).

The soil pH and potassium content were not significantly correlated with the forage yield, water use efficiency, or forage accumulation rate. The forage yield was reduced by the increase of electrical conductivity, sodium content, and bulk density, but electrical conductivity mainly affected *O. stricta*. Bulk density mainly influenced *N. cochenillifera*. In contrast, soil organic carbon increased the forage yield for both species.

Table 8. Average electrical conductivity, pH, potassium and sodium contents, bulk density, and organic carbon content of soils cultivated with *Opuntia stricta* cultivar ‘Orelha de Elefante Mexicana’ (OEM) and *Nopalea cochenillifera* cultivar ‘Miuda’ at the 12 experimental locations.

Location	Electrical conductivity (mS cm ⁻¹)	pH	Potassium content (cmol _c dm ⁻³)	Sodium content (cmol _c dm ⁻³)	Bulk density (kg dm ⁻³)	Soil organic carbon (dag dm ⁻³)*
Baixa Grande, BA	0.55	5.1	0.45	0.08	1.44	0.60
Batalha, AL	0.51	5.8	0.26	0.05	1.38	1.40
Carlos Chagas, MG	0.72	4.7	0.22	0.21	1.25	1.00
Fortuna, MA	0.13	5.1	0.07	0.65	1.33	2.61
Ibaretama, CE	0.76	4.8	0.38	0.04	1.49	0.60
Ipira, BA	0.26	5.3	0.12	0.46	1.33	0.50
Itapetinga, BA	0.32	4.8	0.22	0.18	1.38	1.60
Lajes, RN	7.36	6.1	0.07	7.20	1.37	0.50
Montes Claros, MG	0.21	5.9	0.30	0.19	1.13	1.60
São João, PE	1.30	4.8	0.20	0.14	1.62	1.16
São Raimundo Nonato, PI	0.18	4.7	0.16	0.18	1.56	0.53
Tenório, PB	0.25	5.2	0.22	0.07	1.50	0.50
Statistical summary of soil conditions						
Mean	1.01	5.21	0.22	0.78	1.40	1.03
Standard deviation	1.93	0.47	0.12	1.93	0.13	0.66
Minimum	0.13	4.70	0.07	0.04	1.13	0.50
Maximum	7.36	6.10	0.45	7.20	1.62	2.61

dag = decagram per cubic decimeter.

Table 9. Pearson correlation coefficients for morphological traits and productive responses of *Opuntia stricta* cultivar ‘Orelha de Elefante Mexicana’ (OEM) and *Nopalea cochenillifera* cultivar ‘Miuda’ over two crop cycles with soil characteristics (electrical conductivity, pH, potassium and sodium contents, bulk density, and soil organic carbon) from 12 experimental sites ($n=48$).

Morphological traits	Electrical conductivity	pH	Potassium content	Sodium content	Bulk density	Soil organic carbon
Plant height	Corr. -0.18	Corr. 0.10	Corr. 0.09	Corr. -0.12	Corr. -0.41***	Corr. 0.21
	Miuda -0.22	Miuda 0.02	Miuda 0.13	Miuda -0.16	Miuda -0.42**	Miuda 0.25
	OEM -0.15	OEM 0.17	OEM 0.06	OEM -0.09	OEM -0.41**	OEM 0.18
Plant width	Corr. -0.18	Corr. 0.10	Corr. 0.15	Corr. -0.17	Corr. -0.25*	Corr. 0.21
	Miuda -0.26	Miuda 0.02	Miuda 0.19	Miuda -0.25	Miuda -0.23	Miuda 0.24
	OEM -0.09	OEM 0.18	OEM 0.11	OEM -0.07	OEM -0.29	OEM 0.18
Cladodes per plant	Corr. -0.13	Corr. -0.07	Corr. 0.12	Corr. -0.13	Corr. -0.08	Corr. 0.27*
	Miuda -0.20	Miuda -0.13	Miuda 0.22	Miuda -0.21	Miuda -0.08	Miuda 0.32*
	OEM -0.11	OEM -0.03	OEM 0.13	OEM -0.10	OEM -0.18	OEM 0.49***
Cladode area index	Corr. -0.24*	Corr. -0.05	Corr. 0.24*	Corr. -0.22*	Corr. -0.18	Corr. 0.38***
	Miuda -0.17	Miuda -0.04	Miuda 0.17	Miuda -0.14	Miuda -0.19	Miuda 0.30*
	OEM -0.30	OEM -0.05	OEM 0.31*	OEM -0.19	OEM -0.19	OEM 0.45**
Cladode weight	Corr. -0.04	Corr. 0.06	Corr. -0.04	Corr. -0.01	Corr. -0.24*	Corr. 0.04
	Miuda -0.10	Miuda 0.01	Miuda -0.12	Miuda -0.07	Miuda -0.37*	Miuda 0.03
	OEM 0.01	OEM 0.13	OEM 0.02	OEM -0.04	OEM -0.20	OEM 0.04
Forage yield	Corr. -0.33**	Corr. -0.13	Corr. 0.020	Corr. -0.27*	Corr. -0.32**	Corr. 0.344**
	Miuda -0.29	Miuda -0.09	Miuda -0.052	Miuda -0.23	Miuda -0.40**	Miuda 0.297
	OEM -0.38*	OEM -0.18	OEM 0.10	OEM -0.32*	OEM -0.21	OEM 0.401**
Water use efficiency	Corr. -0.32**	Corr. -0.09	Corr. 0.08	Corr. -0.27*	Corr. -0.03	Corr. 0.01
	Miuda -0.30*	Miuda -0.15	Miuda 0.03	Miuda -0.24	Miuda -0.16	Miuda -0.02
	OEM -0.33*	OEM -0.14	OEM 0.14	OEM -0.29	OEM -0.10	OEM 0.05
Forage accumulation rate	Corr. -0.43***	Corr. -0.13	Corr. 0.07	Corr. -0.36***	Corr. -0.35***	Corr. 0.43***
	Miuda -0.40***	Miuda -0.07	Miuda 0.01	Miuda -0.33*	Miuda -0.45**	Miuda 0.39**
	OEM -0.46**	OEM -0.20	OEM 0.13	OEM -0.40**	OEM -0.23	OEM 0.47**

Corr = correlation coefficient considering both species; Miuda and OEM = correlation coefficient for each species ($n=24$).

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Water use efficiency was decreased by increasing electrical conductivity for *O. stricta* and *N. cochenillifera*, and a negative correlation was found between the sodium content and water use efficiency. The forage accumulation rate was negatively influenced by the electrical conductivity, sodium content, and bulk density, while increase of soil organic carbon enhanced the forage accumulation rate for both species.

Discussion

Effect of meteorological conditions on morphological traits and agronomic responses

Despite structural differences, both species exhibited similar potential production and water use efficiency, reflecting distinct growth patterns. Plants with larger, heavier cladodes as *O. stricta* tend to grow horizontally, which is important for supporting their weight, whereas those with smaller cladodes grow vertically, resulting in taller and narrower forms. Although cladode morphology strongly influences the canopy structure and can impact cultural practices, differences in plant architecture between species did not result in increased forage yield, however taller and narrower plants may allow for a denser row spacing.

The increase in plant height and width accompanied by an increase in the cladode area index was expected for both species since the cladode area index is a measure

of the relationship between the total leaf area and the total land area. As the cladode area index increased, forage yield, forage accumulation rate, and water use efficiency also increased. The greater cladode area index represents an increment in the photosynthetic area of the plant (Acevedo et al. 1983), which can increase carbohydrate synthesis and potentially enhance the use of resources, such as nutrients and water, resulting in a larger water use efficiency and favoring plant biomass. Positive correlations between the number of cladodes and plant width with productivity have been reported for 34 genotypes (Ramos et al. 2021), which is consistent with the findings of the present study, suggesting that these two morphological traits, along with the cladode area index, can serve as potential indicators of productivity under field conditions.

Considering meteorological conditions and elevation, the negative correlation of maximum temperature and plant width, especially for *N. cochenillifera* could be due to increased evaporation, which decreases available water and limits plant growth, including lateral expansion. The positive effect of elevation on plant width is attributed to a reduction in the maximum temperature since the elevation was negatively correlated with the maximum temperature ($r = -0.38$; $p < 0.001$), thus improving thermal conditions for both species.

The optimum average temperature range for *Opuntia* reported in the literature ($25^{\circ}\text{C}/15^{\circ}\text{C}$, day/night) (Drennan and Nobel, 1998) or 18°C – 23°C (Inglese, Liguori, and De La Barrera 2017) is confirmed by the present study, as the average temperature observed was 20.2°C , ranging from 17.8°C to 22.2°C across sites, without influencing the agronomic responses or water use efficiency.

Average daily rainfall increased the forage yield and forage accumulation rate, as it refills the amount of water in the soil, increasing the available water for the plant. In this project, we considered 24 crop cycles with an average duration of 360 days. The cumulative rainfall per cycle ranged from 446 to 1003 mm, averaging 688 mm, which is higher than the reported annual amount of rainfall of 400 mm required for *Opuntia ficus-indica* growth (Inglese, Liguori, and De La Barrera 2017). As a result, the observed rainfall contributed to the considerable forage yield in this research. The yields reached in this study, such as in Itapetinga, BA, with $22,075\text{ kg DM ha}^{-1}$ as the average for both species are considered high and are consistent with results reported for *Opuntia stricta* and *Nopalea cochenillifera* in the Brazilian semi-arid region (Rocha Filho et al. 2021).

In addition, Silva et al. (2017) reported an annual total rainfall of 812–1090 mm as the maximum limit for optimum growth, which is higher than the cumulative rainfall per crop cycle in 11 of the 12 locations in this study (446–829 mm), suggesting that there is potential to increase the productive response in the crop cycles with higher rainfall, especially when it is poorly distributed. This positive response to rainfall also suggests that the use of techniques that favor water harvesting and improve the use of rainwater can increase the forage production. Rainfall is a key determinant of the soil water content. Accordingly, the findings of this study agree with those of Scalisi et al. (2016), who reported that under rainfed conditions, the soil water content is a principal factor regulating *Opuntia* growth.

The hypotheses related to the effect of weather conditions on the morphological traits and productive responses were partially confirmed. The average and maximum

temperatures did not influence plant height, plant width, the number of cladodes per plant, or cladode weight for the two species evaluated in this study. However, a lower maximum temperature resulted in wider *N. cochenillifera* plant, but it did not affect forage production or water use efficiency for either species. The increase in average daily rainfall enhanced the forage yield and the forage accumulation rate for *O. stricta* and *N. cochenillifera*.

Effects of soil conditions on morphological traits and agronomic responses

Due to the sensitivity of *Opuntia* to salinity (Berry and Nobel 1985), there was a decrease in the cladode area index and a reduction in forage yield, water use efficiency, and the forage accumulation rate associated with greater electrical conductivity and sodium content. Salinity can decrease photosynthesis and thus CO₂ uptake (Nerd, Karadi, and Mizrahi 1991), inhibiting plant growth (Franco-Salazar and Veliz 2007). According to Silva-Ortega et al. (2008), this can be attributed to a reduction in water availability, sodium ion accumulation, and mineral imbalance, leading to cellular and molecular damage. Furthermore, a high salt or sodium concentration in the soil can decrease soil porosity and permeability (Freire et al. 2018). In this study, one location (Lajes, RN) had both saline and sodic soil (Foronda 2022) (electrical conductivity of saturation extract >4 mS cm⁻¹; exchangeable Na >4 cmol_c dm⁻³, with exchangeable sodium percentage >15%, since the cation exchange capacity was 17 cmol_c dm⁻³), and it had the lowest forage accumulation rate.

The soil pH affects the solubility of many elements essential for plant growth and development, influencing their availability. Less acidic conditions increase the availability of macro- and micronutrients for plants and microbial activities in the soil (Bariagabre et al. 2016). The soil pH recommended by Donato et al. (2017a) to optimize the productive responses of the *Opuntia ficus-indica* ranges from 5.6 to 6.3. Nevertheless, in this study, the pH was somewhat lower, ranging from 4.7 to 6.1. However, it was not significantly correlated to the morphological or agronomical traits of either species, and some locations, such as Carlos Chagas, MG, Itapetinga, BA, and São João, PE, had a pH ranging from 4.7 to 4.8 with a high forage accumulation rate. These locations, however, had a high average daily rainfall that contributed to an increase in forage yield and a reduced potential negative effect of soil pH.

The negative influence of bulk density on morphological traits, such as plant height and cladode weight, forage yield, and forage accumulation rate is because an increase in this characteristic represents soil compaction. It can also reduce litter decomposition (Bariagabre et al. 2016) and the presence of macropores (Ramos et al. 2013). The results of this study indicate that *N. cochenillifera* is more sensitive to increased bulk density than *O. stricta* based on the reduction in forage yield and forage accumulation rate.

Potassium plays essential roles in plant physiology, including participation in osmotic regulation, protein synthesis, pH control, and stomatal function (Cirino et al. 2022). It is also known to accumulate in high concentrations in plant tissues (Donato et al. 2017b). Despite its physiological importance, no significant effects of soil potassium levels were observed on the agronomic performance, water use efficiency, or morphological traits of the studied species.

An exception was found in the cladode area index, which showed a positive response to increasing potassium levels, particularly for *O. stricta*. This result is likely associated with the *O. stricta*'s greater capacity for potassium accumulation compared to *N. cochenillifera* (Jardim et al. 2021).

Of the 12 study locations, 9 site soils had low potassium concentrations ($<30 \text{ mg dm}^{-3}$), while the remaining 3 sites exhibited moderate potassium levels ($30\text{--}60 \text{ mg dm}^{-3}$), as classified by Sobral et al. (2015). Based on these values, potassium fertilization was applied in 10 locations to mitigate the potential negative effects of potassium deficiency on growth and productivity.

A reduction in water use efficiency caused by electrical conductivity and the sodium content can be related to salt accumulation in the soil, which may influence the porosity, permeability, and water infiltration. Moreover, elevation had a negative correlation with electrical conductivity ($r = -0.33$; $p < 0.05$) and sodium content ($r = -0.30$; $p < 0.05$), as the topography is one of the main factors controlling the geographical variation of salts (Bakr and Ali 2019) considering that salts move from surrounding areas and that poor drainage, low permeability, and high evapotranspiration can boost those effects.

The positive effects of soil organic carbon on the structural characteristics (cladode area index and cladodes per plant), forage yield, and forage accumulation rate are due to the role it plays in agricultural systems (Camelo et al. 2021), promoting physical soil condition. In this study, soil organic carbon was also negatively correlated with the bulk density ($r = -0.28$; $p < 0.01$). The responses observed in this study regarding soil organic carbon, a key component of soil organic matter, are consistent with the low productivity in a location with low soil organic matter (Matos et al. 2021).

The hypotheses associated with the effect of soil conditions on morphological traits and productive responses are partially accepted since the electrical conductivity, sodium content, and bulk density reduced forage production, while soil organic carbon increased forage production and the pH. However, the potassium content did not affect forage yield for either species.

Overall, these findings partially confirm our initial expectations, particularly regarding the cladode area index as an important determinant of forage yield, forage accumulation rate, and water use efficiency for both species, and they also underscore the role of rainfall variability and soil organic carbon as key drivers of forage production. Furthermore, the negative impacts of soil electrical conductivity, the sodium content, and bulk density on forage yield were also anticipated and confirmed. In contrast, more pronounced changes in morphological traits and forage production were expected in response to local weather conditions. In contrast to our expectations, a differential response of forage yield between species was not observed, indicating environmental adaptability across the tested locations.

Conclusions

This study showed that rainfall variability is an important determinant of the morphological and productive responses of the species *N. cochenillifera* and *O. stricta* particularly the cultivars Miuda and Orelha de Elefante Mexicana (OEM), respectively. Among the

soil characteristics, soil organic carbon increased the forage yield, while electrical conductivity, sodium content, and soil bulk density were important factors that were associated with a reduction in the forage production. Although this study was only conducted for two crop cycles the results have a theoretical importance by enhancing the understanding of the productivity under variable environmental conditions, particularly regarding how morphology and site-specific factors influence forage yield and water use efficiency. Practically, the results offer guidance for optimizing Cactaceae-based forage production and the need to improve soil health and water management. The influence of rainfall variability highlights the importance of implementing water conservation strategies, such as rainwater harvesting. The impact of soil conditions underscores the need for soil management practices aimed at reducing compaction and maintaining or increasing soil organic carbon. These practices have the potential to improve water retention and infiltration, thereby decreasing drought effects.

These results from this study show that *O. stricta* and *N. cochenillifera* can maintain forage yield and water use efficiency under diverse environmental conditions. The identification of critical soil constraints (e.g., high electrical conductivity, sodium levels, and bulk density) provides knowledge for crop site selection, and practices for improving soil health and water management for optimizing productivity in dry zones.

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Disclosure statement

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