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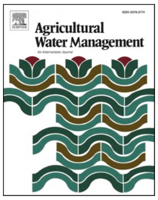

Energy balance, water use efficiency, and photochemistry of two globally cultivated rainfed cactus species

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ABSTRACT

Linking knowledge of energy fluxes and evapotranspiration (ET) in cacti is useful for understanding plant growth, which acts as an extremely important feed source for dairy farming. However, there is little quantitative understanding of the latent (*LE*) and sensible (*H*) heat fluxes in drylands of cactus. We therefore investigated the feedback from plants of *Nopalea* and *Opuntia* on an interannual and seasonal scale, of the surface energy balance (SEB) components, morphophysiological parameters, biomass, water relations and photochemical relationships during the wet and dry seasons of 2018–2021 in the semi-arid region of Brazil. To analyse the data, four periods were selected (dry season, wet season, and dry-wet and wet-dry transitions). Our results showed that the *LE* (105.26 W m^{-2}) of *Opuntia* was 77 % greater than that of *Nopalea.* In all seasons, *H* was the SEB component with the highest energy consumption in the two cacti, with *LE* the second most affected. Under *Nopalea*, the soil heat flux increased at the surface (112 %) during the wet and dry seasons (a mean of 1.61 MJ m^{-2} day^{-1}). The mean ET of *Nopalea* and *Opuntia* was 1.71 and 1.96 mm day^{-1} respectively. The H/R_n ratio showed decreasing behaviour from the dry to the wet season, with a reduction of 37 % in *Nopalea* and 14 % in *Opuntia.* The NDVI ranged from 0.19 to 0.67 (*Nopalea*), and 0.17–0.70 for *Opuntia,* similar to the Chlorophyll Index, which maintained the seasonality of the NDVI. Overall, we found spatial patterns for the Photochemical Reflectance Index of −0.01 to 0.14 for *Nopalea* and *Opuntia.* Under the same conditions, *Opuntia* showed a higher growth rate and net assimilation rate. The mean cladode water content was 86 % in *Nopalea* and 89 % in *Opuntia.* Biomass and water use efficiency were greater in *Opuntia* (56.01 Mg ha^{-1} and 7.54 kg m^{-3} respectively). We also found that these comparisons indicate greater sensitivity in *Nopalea*, and more-significant quantification of the SEB in *Opuntia*.

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1. Introduction

It is believed that climate change over many decades will have a negative impact on the performance of many poorly adapted plant species (Yao et al., 2020; Shahzad et al., 2021). Around 41 % of the Earth's surface consists of drylands, while another 30 % is covered by pasturelands. These pasturelands play a crucial role in the global energy exchange within the land-vegetation-atmosphere system (Kumar et al., 2021; Tai et al., 2021; Yao et al., 2020; Yue et al., 2018). However, not all plants that make up these ecosystems have adapted; among vascular species, approximately 6 % have developed crassulacean acid metabolism (CAM), this photosynthetic pathway being well-adapted to the most hostile of climate conditions (Borland et al., 2011; Nobel and De La Barrera, 2003; Nobel and Zutta, 2008; Winter and Smith, 2022). The CAM pathway is an enhancement of C3 photosynthesis, an evolutionary result of 20–30 million years (Hartzell et al., 2018; Winter and Smith, 2022). Family Cactaceae Juss. includes an example of xerophytic species considered models of the CAM photosynthetic pathway, such as the cacti of genera *Nopalea* and *Opuntia,* specialists in assimilating carbon dioxide (CO_2) at night, thereby promoting a significant improvement in water use efficiency—WUE (Borland et al., 2011; Jardim et al., 2021; Nobel, 1991; Winter and Smith, 2022). CAM plants typically have a higher WUE than do C3 and C4 pathway plants, up to six and three times greater, respectively (Jardim et al., 2021; Winter and Smith, 2022). In response to the high WUE, the cactus has a water demand of approximately 20 % of the total demand of traditional crops (Neupane et al., 2021).

The cactus (*Nopalea cochenillifera* and *Opuntia stricta*) is commonly planted in arid and semi-arid environments of low water availability (250–450 mm $year^{-1}$) and high temperatures, which are generally unfavourable conditions for cultivating various C3 and C4 species (Kumar et al., 2022; Nobel, 1991; Winter and Smith, 2022). Countries such as Mexico and Brazil lead the world in areas planted with cactus, with approximately three million hectares and nine hundred thousand hectares, respectively (Ciriminna et al., 2019). The cactus is an important forage, food, and medicinal crop, and can be consumed by humans and animals (Acharya et al., 2019; Tenorio-Escandón et al., 2022). In addition to its powerful metabolic pathway, its anatomical adaptations, such as a modified succulent stem—known as cladode (flattened stem), spiny body, developed vacuole, impermeable epidermis, mucilaginous cells, and prominent root system make this crop adept at tolerating environments under abiotic stress (Santos-Díaz et al., 2019; Scalisi et al., 2016; Tenorio-Escandón et al., 2022). According to Nobel and De La Barrera (2003), cacti (*Nopalea* and *Opuntia*) can survive in regions with a high thermal amplitude (−6°C to 65°C) and high vapour pressure deficit (VPD), although the excess light and heat can cause problems in dissipating photochemical energy (Adams et al., 1989; Jardim et al., 2021). Part of the downward global solar radiation interacts with the plant canopy and with the soil, promoting changes in the energy balance and evapotranspiration (Alves et al., 2022; Chen et al., 2022; Dhungel et al., 2021). One way of understanding the response of plants to imposed environmental conditions is by quantifying turbulent fluxes, growth and photochemical parameters.

So far, there have been few studies quantifying turbulent fluxes by means of the energy balance in ecosystems with cacti (Flanagan and Flanagan, 2018; Guevara-Escobar et al., 2021; Lewis et al., 1977) - only some with *Opuntia* (Consoli et al., 2013a, 2013b; Unland et al., 1996; Jardim et al., 2023a) and one with *Nopalea* (Jardim et al., 2023b). However, the aforementioned studies employed different methods to quantify turbulent fluxes, such as eddy covariance (EC), surface renewal (SR), and the Bowen ratio-energy balance (BREB). Generally, each method has its limitations and uncertainties. The BREB method, in particular, may lead to underestimations of latent heat flux (*LE*) at high VPD (Shi et al., 2008), errors due to sensor height (Stannard et al., 2004), and uncertainties in the Bowen ratio during the night (Perez et al., 1999).

The energy balance is a promising method for quantifying energy exchanges originating from the net radiation (R_n) and partitioned into elements for heating the water, air and soil (Campos et al., 2019; Chen et al., 2022; Irmak and Kukal, 2022). In addition to being a fairly robust method, it can be applied in various ecosystems, from arid to humid (Jung et al., 2019; Unland et al., 1996; Yue et al., 2018). For example, Consoli et al. (2013a) observed changes in the *LE* and sensible heat flux (*H*) in irrigated *O. ficus-indica* in relation to the time of year and the physiological state of the plants, in a cultivated area in western Sicily in the semi-arid region of Italy. Furthermore, according to the authors, during the growth period of the cactus, SEB evapotranspiration was fairly accurate when compared with microlysimeters. In terms of water and energy fluxes, Pierini et al. (2014) reported higher values for *H* compared to *LE* in an ecosystem with *O. spinisior* and *O. engelmannii* in the Sonoran Desert. Consoli et al. (2013b) also used the energy balance to determine evapotranspiration, where they found a high WUE in plants of *O. ficus-indica* under the Mediterranean climate of Italy.

In agricultural ecosystems, the interaction between the biogeochemical cycle and the vegetation is fundamental for understanding energy partitioning and the way changes occur in the distribution of turbulent fluxes (i.e., *LE* and *H*) and the soil heat flux (*G*) on the surface (Alves et al., 2022; Bezerra et al., 2022; Chen et al., 2022; Dhungel et al., 2021). These elements, together with climate and environmental factors, can cause changes in evapotranspiration (ET) during the plant growing season. Overall, ET is a variable of great importance in the hydrologic cycle, comprising the physical processes of evaporation and transpiration that transfer a mass of water and energy to the atmosphere (Chen et al., 2022; Irmak and Kukal, 2022). Generally, this variable can be accurately determined by weighing-lysimeter and eddy covariance techniques, despite being high-cost methods of determining flux (Dhungel et al., 2021; Jung et al., 2019; Pokhariyal and Patel, 2021). Here, we highlight the Bowen ratio-energy balance method, which quantifies the energy equivalent of ET, i.e., the latent heat flux using the R_n, air temperature, humidity and *G*, employing accurate sensors at a lower cost (Bowen, 1926; Ortega-Farias et al., 1996; Yue et al., 2018). These measurements are valuable for understanding the water status of plants and, consequently, their levels of climate adaptation.

Integrating micrometeorological variables, such as vegetation indices (e.g., Normalised Difference Vegetation Index), physiological responses (e.g., Chlorophyll Index; Photochemical Reflectance Index), and growth rates can help as early indicators of plant response to abiotic stress (Jardim et al., 2023c; Perez-Priego et al., 2015; Sanchez et al., 2022; Chen et al., 2025), since these variables can serve as indicators of biomass production, the photosynthetic pigment pool and growth performance. Therefore, our hypothesis is that (i) cactus species can maintain their performance for energy fluxes, ecophysiological fluxes and evapotranspiration fluxes even under conditions of stress. Although the hypothesis tested here may be true, we believe that (ii) *O. stricta* presents better adaptation and, consequently, higher yield, and spectral, photochemical and hydric responses compared to *N. cochenillifera*, being an important piece of information for understanding the contribution of cactus species to ecosystem services in arid and semi-arid areas.

Based on the above, the aim of this study was to compare the feedback from cactus plants (*Nopalea* and *Opuntia*) on an interannual and seasonal scale, of surface energy balance components, morphophysiological parameters, biomass yield, water relations and photochemical relationships during the wet and dry seasons in a semi-arid environment. To achieve this goal, we quantified the heat fluxes, partitioned the net radiation, and calculated growth rates, plant spectral responses, and cladode succulence. The arguments presented here are based on four years observing surface fluxes, and six years analysing the growth of cacti. This is also the first study to measure energy fluxes in the simultaneous cultivation of *Nopalea* and *Opuntia*.

2. Materials and methods

2.1. Description of the experimental sites

We used experimental data from two micrometeorological towers located on the 'Várzea Alegre' farm (8°17' S, 36°53' W, at an altitude of 792 m above sea level), in the district of Pesqueira in Pernambuco, Brazil (Fig. 1). According to Köppen, the climate is classified as hot semi-arid (BShw) (Beck et al., 2018) with irregular rainfall from January to July. The mean annual rainfall and air temperature are 607 mm and 26°C, respectively. Table 1 shows the physical and chemical data of the soil from the experimental sites.

The experiment was conducted from January 2015 to December 2021 with the cacti *Nopalea cochenillifera* (hereafter called *Nopalea*, clone 'IPA Sertânia') and *Opuntia stricta* (hereafter called *Opuntia*, clone 'Orelha de Elefante Mexicana'), both species resistant to the carmine mealybug [*Dactylopius opuntiae* (Cockerell); Hemiptera: Dactylopiidae]. The soil was initially prepared by ploughing, harrowing and furrowing. The cladodes were then planted in January 2015, inserting 50 % of their height into the soil. The two experimental sites comprised a planted area of approximately 27 ha of *Nopalea* and 36 ha of *Opuntia* (Fig. 1). The linear distance between the sites was 2.4 km. All the plants were arranged in single rows, at a spacing of 1.5 × 0.2 m. For every nine rows of cactus (i.e., plant rows with no bare areas) there was an uncultivated area of 3 m (i.e., areas of bare soil), this was repeated until reaching a total density of 27,273 plants ha^{-1} (Fig. 2). The cropping treatments included manual weeding, with herbicide and insecticide applied as necessary to avoid competition with weeds and promote full growth of the crop. Throughout the experimental period, the cacti were grown under rainfed conditions. All field management practices were the same at both sites.

In this study, to investigate the effects of rainfall availability on the vegetation, we evaluated the hydrological periods in four seasons (wet, wet-dry transition, dry, and dry-wet transition) from 2018 to 2021 (Table 2), based on the start and end of the rainfall (Leite-Filho et al., 2019; Salack et al., 2016). For instance, a dry season was defined as a period where the cumulative rainfall over the 30 days before or after the day being examined is below 20 mm, and there are fewer than five days with rain. Conversely, if during the same time frame, there are five or more days with rainfall exceeding 20 mm, it is categorised as a wet season. When none of these criteria are met, it is referred to as a transition season. If this transition season follows a dry season, it is termed a dry-wet transition season, while if it follows a wet season, it is termed a wet-dry transition season.

Table 1
Physical and chemical properties of the soil at the experimental sites.

Description	Site	Site
Physical attributes (0–0.40 m)	*Nopalea cochenillifera*	*Opuntia stricta*
Sand (g kg^{-1})	714.88	738.20
Silt (g kg^{-1})	216.86	235.64
Clay (g kg^{-1})	68.26	26.16
Bulk density (g cm^{-3})	1.66	1.64
Total porosity (%)	34.57	35.51
Soil texture	Sandy loam	Loamy sand
Chemical attributes (0.0–0.40 m)	*Nopalea cochenillifera*	*Opuntia stricta*
EC_e (dS m^{-1})	0.70	0.66
pH	5.13	5.40
P (mg dm^{-3})	25.03	53.50
K^+ ($cmol_c$ dm^{-3})	0.26	0.21
Na^+ ($cmol_c$ dm^{-3})	0.09	0.11
Ca^{2+} ($cmol_c$ dm^{-3})	4.43	4.38
Mg^{2+} ($cmol_c$ dm^{-3})	1.09	1.25
H+Al ($cmol_c$ dm^{-3})	2.75	2.15
CEC ($cmol_c$ dm^{-3})	8.60	8.10
Base saturation (%)	63.83	72.90

EC_e is the electrical conductivity of the saturated soil paste extract; pH in H_2O at a ratio of 1:2.5 v/v; CEC is the cation exchange capacity.

2.2. Measurements and instrumentation

Meteorological measurements were obtained from January 2018 to December 2021, from two towers, 3 m in height, installed in the centre of each experimental area, above the cactus canopy. Each tower comprised the same type of sensors for measuring flux. To measure the net radiation (R_n), closed-cell thermopile-type sensors were used (NR-Lite, Kipp & Zonen, Delft, Netherlands). The two radiometric balance sensors were installed 2.8 m above the canopy. The soil heat flux (G) was

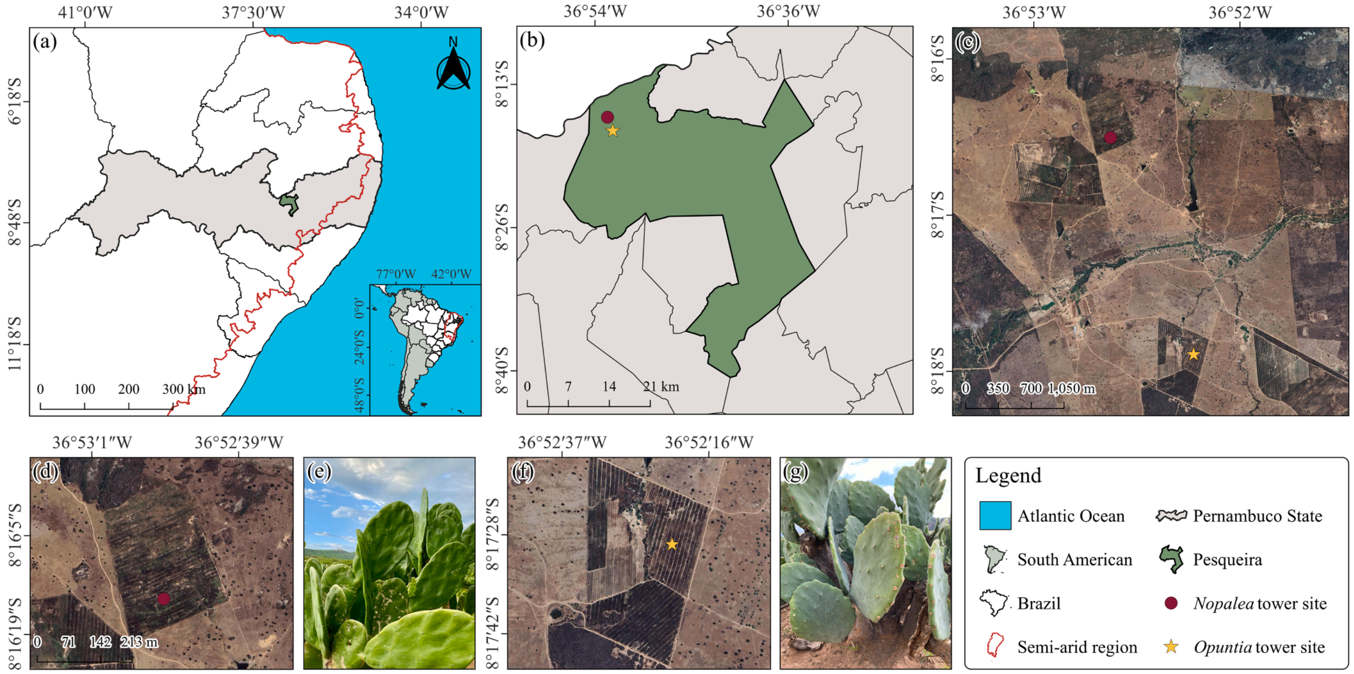

Fig. 1. Geographic location of the study areas in the Pesqueira district, Pernambuco, semi-arid region of Brazil (a–b). Overview of the two experimental fields (c). Zoom-in panels for location of the micrometeorological towers in the cultivated sites of *Nopalea* (d–e) and *Opuntia* (f–g).

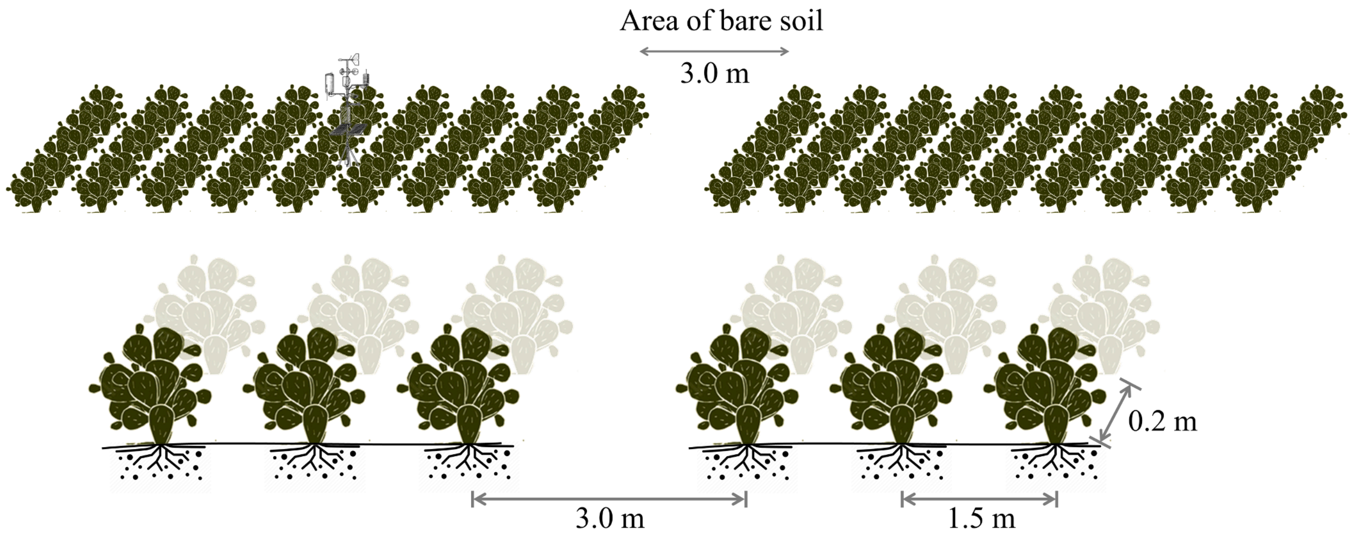

Fig. 2. Schematic diagram showing the planting patterns for *Nopalea* and *Opuntia*. Distances between rows and plants (1.5 × 0.2 m) are indicated. There was a distance of 3.0 m between nine rows of cacti.

Table 2
Delimiting dates for the seasons based on the start and end of the rainfall, from 2018 to 2021.

Dry season		Dry-wet transition		Wet season		Wet-dry transition	
Start date	End date	Start date	End date	Start date	End date	Start date	End date
01/01/2018	20/01/2018	21/01/2018	20/02/2018	21/02/2018	27/05/2018	28/05/2018	01/07/2018
02/07/2018	08/01/2019	09/01/2019	15/02/2019	16/02/2019	02/08/2019	03/08/2019	14/09/2019
15/09/2019	23/12/2019	24/12/2019	02/02/2020	03/02/2020	06/07/2020	07/07/2020	30/08/2020
31/08/2020	27/09/2020	28/09/2020	14/03/2021	15/03/2021	10/05/2021	11/05/2021	06/09/2021
07/09/2021	27/11/2021	28/11/2021	28/12/2021	29/12/2021	31/12/2021	-	-

Note: Dates are in dd/mm/yyyy format.

quantified using heat flux plates (HFT3, REBS, Hukseflux, Delft, Netherlands) buried close to the rows of cactus at a depth of 0.05 m. Air temperature and relative humidity were determined with the aid of two thermo-hygrometers (HMP155A, Campbell Scientific, Logan, Utah, USA), creating a vertical profile of 0.5 and 1.5 m above the surface of the plant canopy. Rainfall data were quantified using an automatic rain gauge (AeroCone, Rain Collect, Hayward, CA, USA), installed 3 m above the canopy. In this study, a fetch to height ratio of more than 100:1 was obtained, an acceptable value when measuring the Bowen ratio (Heilman et al., 1989). The dataset was recorded every 60 seconds (CR1000, Campbell Scientific Inc., Logan, Utah, USA), with a storage interval of 10 minutes. Measurements were collected continuously throughout the day and night.

2.3. Calculation of the surface energy balance and parameters

In this study we used the simplified version of the surface energy balance method. This method is based primarily on the principle of conservation of energy (Eq. 1). According to Bowen (1926), the Bowen ratio (β) (Eq. 2) can be calculated using the sensible heat flux (H) to latent heat flux (LE) ratio. This ratio is closely linked to the vertical gradients of air temperature and humidity; we therefore assume similarity of equality between the turbulent transfer coefficients of sensible heat and water vapour suggested by Gavilán and Berengena (2007). LE and H were estimated by combining the available energy from the energy balance and the Bowen ratio (Eqs. 3 and 4). The flux data used in applying the BREB method were considered on a daytime scale, from sunrise to sunset only. This is because during the night and before sunrise, when the temperature/humidity gradients are small, they can cause the quantification of erroneous data and inconsistent fluxes (e.g., with β generally close to -1 or tending to infinity). Each dataset is referred to in local time (i.e., GMT-3).

$$R_n - G = LE + H \tag{1}$$

$$\beta = \frac{H}{LE} = \left(\frac{P_a \times c_p}{\lambda \times \varepsilon} \times \frac{\Delta T}{\Delta e} \times \frac{K_h}{K_w}\right) \tag{2}$$

$$LE = \frac{R_n - G}{1 + \beta} \tag{3}$$

$$H = \frac{\beta}{1 + \beta} \times (R_n - G) \tag{4}$$

where R_n is the net radiation (W m^{-2}); G is the soil heat flux (W m^{-2}); LE is the latent heat flux (W m^{-2}); H is the sensible heat flux (W m^{-2}); β is the Bowen ratio (dimensionless); P_a is the atmospheric pressure (kPa); c_p is the specific heat capacity of air (1004.67 J kg^{-1} ºC^{-1}); λ is the latent heat of vaporisation (2.454 MJ kg^{-1} at 20ºC); ε is the ratio of the molecular weights of the air and water vapour (0.622); ΔT is the air temperature difference between two heights (ºC); Δe is the vapour pressure difference between two heights (kPa); K_h is the eddy diffusivity of heat (m^2 s^{-1}); K_w is the eddy diffusivity of water vapour (m^2 s^{-1}).

The energy from metabolic activities, heat storage in the plant tissue and canopy, and horizontal advection, were considered insignificant. As such, these energy components were not included in our energy balance algorithm (Eq. 1) (Hu et al., 2014; Pokhariyal and Patel, 2021). After determining LE (W m^{-2}), we converted this variable into evapotranspiration (ET), dividing the LE by the latent heat of vaporisation of water in J kg^{-1} (Tang et al., 2014). In this way, the hourly values of ET are integrated, giving the daily values in mm day^{-1}.

2.4. Criteria for selecting data for the energy balance method

For the acceptance and/or rejection criteria of the data collected by the BREB method, we used the approach proposed by Perez et al. (1999), which parameterises the criteria for using variables in composing the method. This is because the Bowen ratio depends on measuring temperature and vapour pressure gradients. That said, abnormal data is seen when the available-energy heat flux is very small ($R_n - G$), or negative ($R_n - G < 0$). In this way, errors can occur in applying the energy balance using the Bowen ratio (β), later triggering physical inconsistency in the data. Here, we summarise some of the information that results in errors in the results of the Bowen ratio method: (1) when the sensor resolution is inadequate to resolve the gradient in ΔT and Δe; (2) stable atmospheric conditions, e.g., at dawn and dusk, cause β values close to -1, resulting in evapotranspiration tending to infinity, which is clearly inconsistent; and (3) when conditions change abruptly, they induce measurement errors (Hu et al., 2014; Ortega-Farias et al., 1996; Perez et al., 1999; Unland et al., 1996).

2.5. Yield measurements

Biomass yield was determined annually, considering the weight of four randomly chosen representative plants from each site. The biomass above the basal cladode (a vegetative structure planted directly in the soil) was fully harvested and weighed on an electronic balance to quantify the fresh matter (g FM plant^{-1}), and then dried in a forced air circulation oven at 55°C to constant weight. We determined the dry matter weight per plant (g DM plant^{-1}), and the annual increase in productivity of the cacti (Mg ha^{-1}) was then estimated, considering a final density of 27,273 plants ha^{-1}.

2.6. Allometry and measurements of plant growth

Every three months we collected morphometric and biomass data of the plants. During the evaluations, four plants from each site were measured to comprise the morphometric data, and another four plants were collected to analysis the biomass over time. For each plant, we quantified morphometric variables of the cladodes and of the plant. The length, width and perimeter of the cladodes were measured, and the number of cladodes determined by order of appearance on the plant (i.e., first order, second order, third order and so on); the total number of cladodes was then determined. To measure plant height, we considered the vertical distance from the ground to the apex of the canopy; plant width was measured as two widths of the top of the canopy. The collected samples were then used to quantify the morphophysiological indices of the cacti. Using the morphometric data, the cladode area—CA (Eq. 5) and cladode area index—CAI (Eq. 6) were determined (Pinheiro et al., 2014; Silva et al., 2014). In addition, from the dry matter yield and cladode parameters, we calculated the morphophysiological indices of the cacti using a three-parameter sigmoid model (Eq. 7) (Jardim et al., 2023c).

$$\mathrm{CA} = \begin{cases} 1.6691 \times \left[\dfrac{1 - e^{(-0.0243 \times \mathrm{CP})}}{-0.0243}\right] & \text{for } \textit{Nopalea} \\ 0.7086 \times \left[\dfrac{1 - e^{(-0.000045765 \times \mathrm{CL} \times \mathrm{CW})}}{0.000045765}\right] & \text{for } \textit{Opuntia} \end{cases} \tag{5}$$

$$\mathrm{CAI} = \left[\sum_{n}^{i=1} (\mathrm{CA}) \middle/ \frac{10,000}{(\mathrm{S1} \times \mathrm{S2})}\right] \tag{6}$$

$$y = \frac{a}{1 + e^{\left(-\frac{x - x0}{b}\right)}} \tag{7}$$

where CP is the cladode perimeter (cm); CL is the cladode length (cm); CW is the cladode width (cm); i is the observation number; n is the total number of observations; 10,000 is the conversion factor from cm^2 to m^2; S1 × S2 is the spacing between the rows and plants of each cactus (i.e., 1.5 × 0.2 m), respectively. The parameters for the morphophysiological analysis were: y - the response variable (e.g., cladode dry matter, cladode area index, and number of cladodes); a - the maximum value for the rate (i.e., the distance between the two asymptotes); x - the accumulated days; $x0$ - the number of days necessary for the plant to express 50 % of the maximum rate (i.e., the inflection point of the curve), and b - the number of days necessary for the start of the rate.

We then quantified the absolute growth rate—AGR (Mg ha^{-1} day^{-1}), relative growth rate—RGR (Mg Mg^{-1} day^{-1}), net assimilation rate—NAR (Mg ha^{-1} day^{-1}), and specific cladode area—SCA (Mg^{-1} day^{-1}) (Jardim et al., 2023c; Khapte et al., 2022). The AGR represents the increase in dry biomass per unit of time, and the RGR the increase in dry biomass adjusted by the accumulated biomass per unit of time. NAR represents the dry mass produced per cladode area per unit of time; this variable is commonly used to represent the net photosynthetic rate of the plants. The SCA represents the cladode area used in photosynthesis (Jardim et al., 2023c). All the growth rates were calculated during the experimental period, from 2015 to 2021.

2.7. Plant water status: cladode water content, succulence, and water use efficiency

The water status of the plants was measured using biomass data and morphometric variables. To this end, the cladode water content (CWC) and cladode succulence (CS) were calculated for the two cacti. The cladodes were removed from the plants and immediately weighed to quantify the fresh weight. They were then identified and left to dry in an oven at 55°C to constant weight. We calculated the cladode water content (%) from the fresh matter (FM) and dry matter (DM) weight of the samples (Eq. 8). Cladode succulence (g cm^{-2}) was determined by subtracting the dry from the fresh weight of the samples and dividing by the cladode area—CA (Eq. 9) (Corrado et al., 2020; Ho et al., 2019).

$$\mathrm{CWC} = \left(\frac{\mathrm{FM} - \mathrm{DM}}{\mathrm{FM}}\right) \times 100 \tag{8}$$

$$\mathrm{CS} = \left(\frac{\mathrm{FM} - \mathrm{DM}}{\mathrm{CA}}\right) \tag{9}$$

The water use efficiency (WUE) was calculated using the ratio between the annual biomass yield of the crop and the evapotranspiration (Eq. 10) (Kai Zhang et al., 2022).

$$\mathrm{WUE} = \frac{\mathrm{DMY}}{\mathrm{ET}} \tag{10}$$

where DMY is the annual dry matter yield (kg ha^{-1}); ET is the total annual evapotranspiration (m^3 ha^{-1}).

2.8. Indices of environmental and physiological stress

To assist in understanding the plant responses to environmental stress, we used spectral reflectance indices, e.g., the Normalised Difference Vegetation Index (NDVI), Photochemical Reflectance Index (PRI) and the Chlorophyll Index (CI), with discussions and mathematical formalisms provided by Gitelson and Merzlyak (1994); Perez-Priego et al. (2015) and Sanchez et al. (2022). These indices were calculated using images from the Sentinel-2 MultiSpectral Instrument (MSI), which offers different spatial resolutions (i.e., 10, 20, and 60 m) available from the United States Geological Survey (USGS, https://www.usgs.gov/). Here, we use reflectances of 800 and 670 nm for the NDVI, 531 and 570 nm for the PRI, and 750 and 705 nm for the CI (Gitelson and Merzlyak, 1994; Perez-Priego et al., 2015; Sanchez et al., 2022). The images were acquired from 16 January 2018 to 31 December 2021 under

< 10 % cloud cover. All the image processing and calculations were carried out using the Google Earth Engine (GEE) platform. In addition, we applied a pixel quality attribute mask to the images, masking clouds, cloud shadow and water, using the CFMask algorithm (Foga et al., 2017; Hurni et al., 2019).

2.9. Data analysis

We used the cladode area index and dry matter data to determine the growth rates of the plants using nonlinear sigmoid models. The models were evaluated and chosen based on significance ($P < 0.05$; using the F-test), and a coefficient of determination greater than 0.85. To test the difference between the energy balance components, i.e., R_n, *LE*, *H*, and *G*, as well as ET, and VPD during the four seasons under study (i.e., wet season, dry season, wet-dry and dry-wet transitions) in the two species of cactus, we used Student's *t*-test and set a significance of $P < 0.01$. We also included box and whisker plots, showing the median, interquartile range and 1.5 times the interquartile range for the data related to cladode water content, succulence, energy balance, ET and VPD. To examine the interrelationships between the plant parameters and environmental conditions, principal component analysis (PCA) was applied. This type of analysis is used to reduce variables or a large dataset using orthogonal transformation, generating linearly uncorrelated variables (Lamichhane et al., 2021), allowing the identification of the correlation between groups of response and explanatory variables and, therefore, the contributions of the explanatory variables to the phenomena studied (e.g., growth dynamics, energy and water exchanges, dry matter accumulation, physiological processes, among others). In this way, we constructed a PCA of twenty variables (R_n, *LE*, *H*, *G*, LE/R_n, H/R_n, G/R_n, VPD, NDVI, PRI, CI, ET, DMY, WUE, CWC, CS, AGR, RGR, NAR and SCA). In addition, it should be noted that before carrying out the analysis, each response variable was standardised using the z-transform, with zero mean and unit standard deviation. Finally, the significant principal components were selected based on the Kaiser criterion, considering only eigenvalues greater than 1.0 (Jardim et al., 2021; Kaiser, 1960; Lamichhane et al., 2021). The data were processed and analysed using the R software (R Core Team, 2024).

3. Results

3.1. Daytime variation in the energy fluxes

Fig. 3 shows the daytime surface energy balance for the four seasons (dry season, dry-wet transition, wet season, and wet-dry transition) from January 2018 to December 2021 on an hourly scale. The sites cultivated with *Nopalea* (Fig. 3a–d) and *Opuntia* (Fig. 3e–h) had respective mean values of 249.19 and 245.60 W m^{-2} for net radiation (R_n). The mean latent heat flux (*LE*) for *Opuntia* was 105.26 W m^{-2}, 77 % higher than at the site cultivated with *Nopalea*. During the dry-wet transition season, *Opuntia* had the highest *LE* (117.36 W m^{-2}), ranging from 0.34 to 217.87 W m^{-2}, with a peak from 10:30–12:30 local time (Fig. 3f). For *Nopalea*, the highest *LE* (90.53 W m^{-2}) was seen during the wet season, varying throughout the day from 1.21 to 165.22 W m^{-2}, with a peak from 09:30–12:30 (Fig. 3c). The sensible heat flux (*H*) was the most contrasting variable at both sites, with the highest energy consumption in each season. In *Opuntia*, the greatest value for *H* was seen during the dry season, with a mean of 183.33 W m^{-2} (Fig. 3e), 2 % higher than in *Nopalea*, which occurred during the dry-wet transition season (Fig. 3b). In both of the cactus crops, the soil heat flux (*G*) was greater during the dry season (Figs. 3a and 3e), with 28.45 W m^{-2} in *Nopalea* and 16.65 W m^{-2} in *Opuntia*. During the dry season, greater values for *G* in *Nopalea* were clearly seen at dawn, with peaks between 11:00 and 12:30 in both cacti. Interestingly, the lowest values for *G* were seen during the wet-dry transition season, with a mean of 8.25 W m^{-2} (*Nopalea*) and 10.21 W m^{-2} (*Opuntia*). Furthermore, during the same wet-dry transition season, the R_n of the sites cultivated with *Opuntia* (218.75 W m^{-2}) and *Nopalea* (216.56 W m^{-2}) were the lowest for the entire study period.

3.2. Seasonal and interannual characteristics of the energy fluxes

Our results for temporal variation in energy and water flux for two agroecosystems of *Nopalea* and *Opuntia* cacti are shown in Fig. 4. On average, the values of R_n during the months under evaluation varied between 12.76 and 12.64 MJ m^{-2} day^{-1} for *Nopalea* (interquartile range 11.54–14.07) and *Opuntia* (interquartile range 11.85–13.76), respectively. At both sites, the lowest and highest values of R_n occurred in June

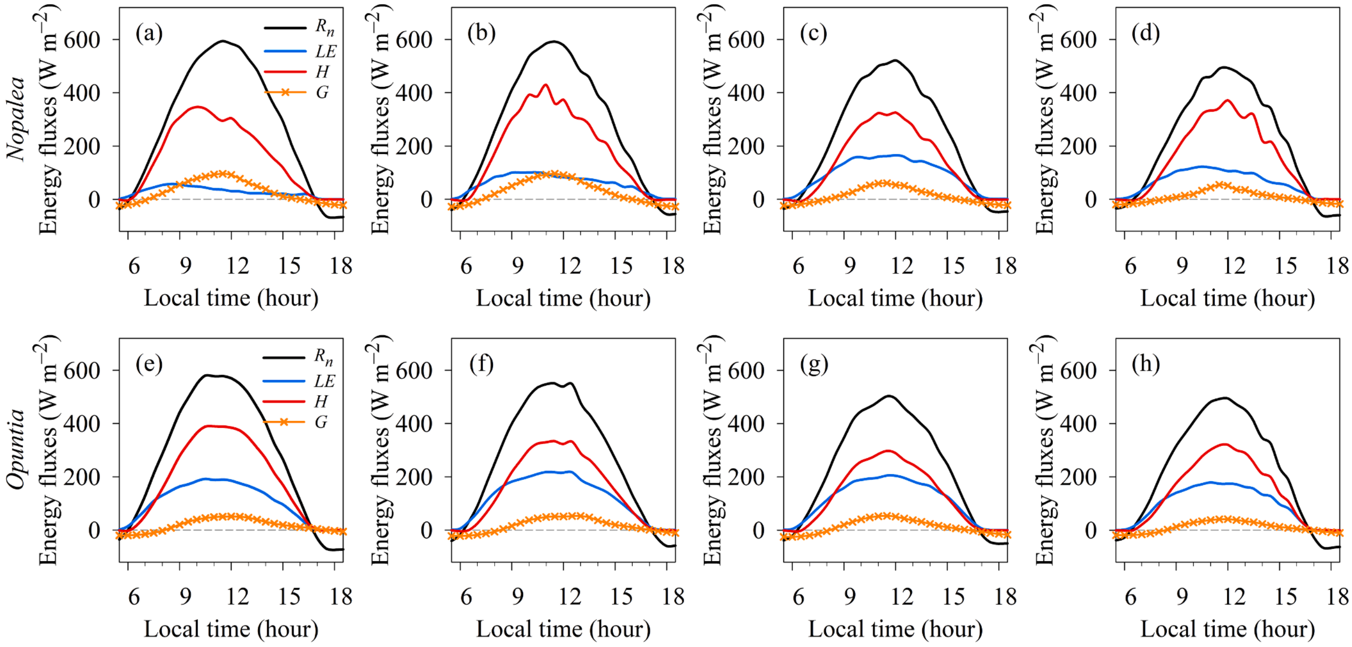

Fig. 3. Mean daytime evolution of the surface energy balance components (net radiation—R_n, latent heat flux—*LE*, sensible heat flux—*H*, and soil heat flux—*G*) between the two experimental sites, with *Nopalea* (a–d) and *Opuntia* (e–h). The measurements were taken during the dry season (a and e), dry-wet transition season (b and f), wet season (c and g), and wet-dry transition season (d and h), from 2018 to 2021.

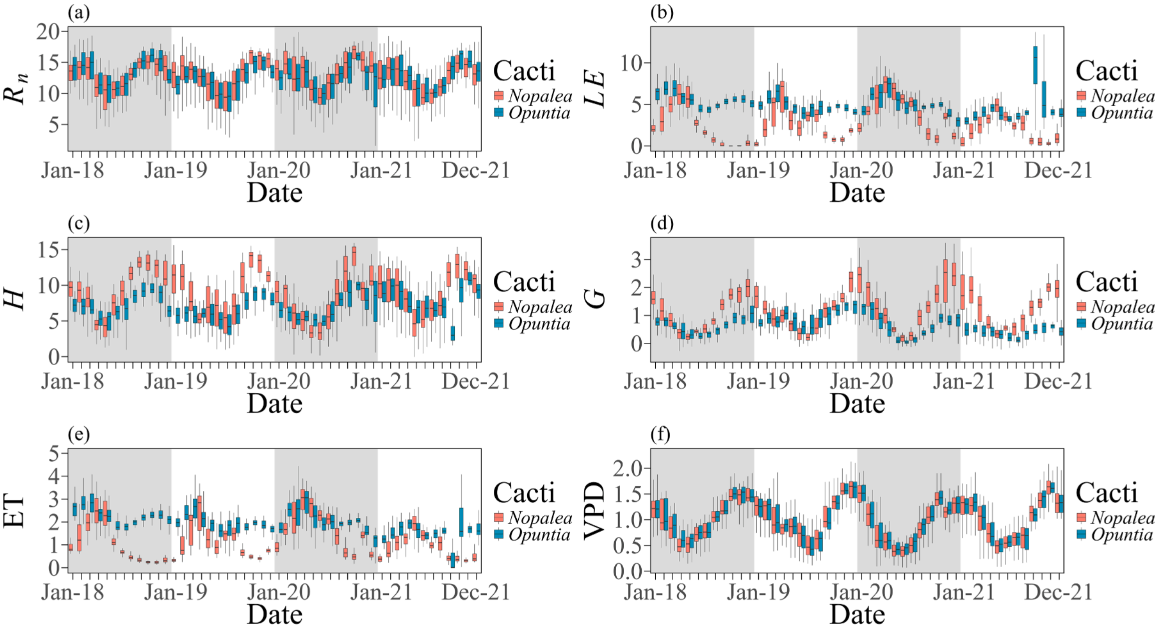

Fig. 4. Temporal variation in energy flux (i.e., net radiation—R_n (a), latent heat flux—LE (b), sensible heat flux—H (c), and soil heat flux—G (d), expressed in MJ m^{-2} day^{-1}) and water (i.e., evapotranspiration—ET (e) and vapour pressure deficit—VPD (f), expressed in mm day^{-1} and kPa, respectively) in two species of cactus from 2018 to 2021. The boxplots denote the median, 25th, 50th, and 75th percentiles, the whiskers indicate 1.5 times the interquartile range. The shaded areas represent year boundaries.

and October, respectively (Fig. 4a). In general, R_n patterns remained quite stable throughout the period under evaluation (2018–2021). There were clearly significant variations in LE between the sites cultivated with *Nopalea* and *Opuntia* (Fig. 4b); for *Nopalea*, we found minimum and maximum mean values for LE ranging from 0.62 to 5.71 MJ m^{-2} day^{-1}, with an overall mean value of 2.76 MJ m^{-2} day^{-1} (interquartile range 1.24–3.77), while LE for *Opuntia* was 80 % greater than for *Nopalea* during the evaluated period. Our results show a seasonal variation in LE, with higher values from January to June, and falling off from July to December. On the other hand, we clearly saw greater resistance in *Opuntia*, maintaining the LE during periods of greater deficiency. For example, whereas *Nopalea* experienced a significant reduction in LE when the vapour pressure deficit (VPD) was high (~1.22 kPa), *Opuntia* maintained a stabilised LE, with less significant reductions. With the exception of November 2020, *Nopalea* had the lowest value for LE from September to November (0.69 MJ m^{-2} day^{-1}), while during the same period the value for *Opuntia* was higher (5.37 MJ m^{-2} day^{-1}). As a result, H had a mean value of 8.84 MJ m^{-2} day^{-1} (interquartile range 6.36–10.86) in *Nopalea*, with a mean of 7.04 MJ m^{-2} day^{-1} (interquartile range 6.01–7.53) in *Opuntia* throughout the period (Fig. 4c). In both cacti, the range of results for H was broader, and the results higher, between September and December.

Corresponding to the turbulent fluxes from the vegetated surfaces, Fig. 4d shows the variations in G for the cacti. Notably, we found higher values for G in *Nopalea*, ranging from 0.36 to 2.08 MJ m^{-2} day^{-1}, with a mean of 1.16 MJ m^{-2} day^{-1}. The results showed differing patterns between surfaces, with *Nopalea* 82 % greater than *Opuntia*. The highest values, and the most-pronounced variation in G occurred from October to February: 1.78 MJ m^{-2} day^{-1} in *Nopalea* and 0.86 MJ m^{-2} day^{-1} in *Opuntia*. In addition, on average, when compared to the other months under analysis, a reduction can be seen for G between April and August, of 66 % in *Nopalea* and, to a lesser extent in *Opuntia* (48 %) (Fig. 4d), the results being consistent with the location and time of year. The results for evapotranspiration (ET) also showed significant variations over the years at sites with *Nopalea* and *Opuntia* (Fig. 4e). Both cacti kept the ET synchronous with the VPD (Fig. 4f) and turbulent fluxes (i.e., LE and H). Under these conditions, the ET ranged from 0.43 to 2.30 mm day^{-1} in *Nopalea* (mean 1.71 mm day^{-1}, interquartile range 0.61–1.53), and 1.65–2.46 mm day^{-1} in *Opuntia* (mean 1.96 mm day^{-1}, interquartile range 1.71–2.13). Although the VPD at both sites is similar, we found a strange variation in ET for *Nopalea* in relation to *Opuntia*, with a mean reduction of 40 % when comparing water lost to the atmosphere. Similarly, during the last four months of each year (2018–2021), the decline in ET in *Nopalea*, in relation to the overall mean ET, was more marked (53 %), in contrast to *Opuntia* (7 %). The sharpest decline in ET occurred predominantly in October and December in *Nopalea* and *Opuntia*, respectively.

Fig. 5 shows the energy balance components, ET and VPD, during the dry season, dry-wet transition, wet season, and wet-dry transition. Only during the wet-dry transition season was there any highly significant difference in R_n between the two species of cactus ($P < 0.001$) (Fig. 5a). We also found the mean value of R_n to be 3 % higher for *Opuntia* during the wet-dry transition (median 11.33 MJ m^{-2} day^{-1}, interquartile range 9.47–13.20) compared to *Nopalea* for the same period. The LE was significantly higher in *Opuntia* during the dry season (513 %), with an interquartile range of 4.30–5.51 MJ m^{-2} day^{-1} (Fig. 5b). During each of the seasons under evaluation, there was a significant difference in LE, H, G, ET and VPD between the cacti. The lowest values for LE in *Nopalea* were during the dry season (0.85 MJ m^{-2} day^{-1}), whereas for *Opuntia* it was during the wet-dry transition season (4.22 MJ m^{-2} day^{-1}). Our results further show that, on average, during the wet season, the difference in LE between *Opuntia* and *Nopalea* was relatively low (0.55 MJ m^{-2} day^{-1}).

During the dry season and the dry-wet transition, H was higher and more significant in *Nopalea*, respectively 45 % and 29 % higher than in *Opuntia* for the same seasons (Fig. 5c). This resulted in similar behaviour between the surfaces for the other fluxes, with G in *Nopalea* 139 % higher than *Opuntia* during the dry-wet transition season, followed by 86 % higher during the dry season ($P < 0.001$, Fig. 5d). Although the sites generally have similar weather conditions, there were also differences between the surfaces for ET and VPD (Fig. 5e–f). For *Nopalea*, the ET ranged from 0.49 to 1.92 mm day^{-1}, in contrast, *Opuntia* maintained ET at its most stable throughout the four seasons, ranging from 1.67 to 2.17 mm day^{-1}.

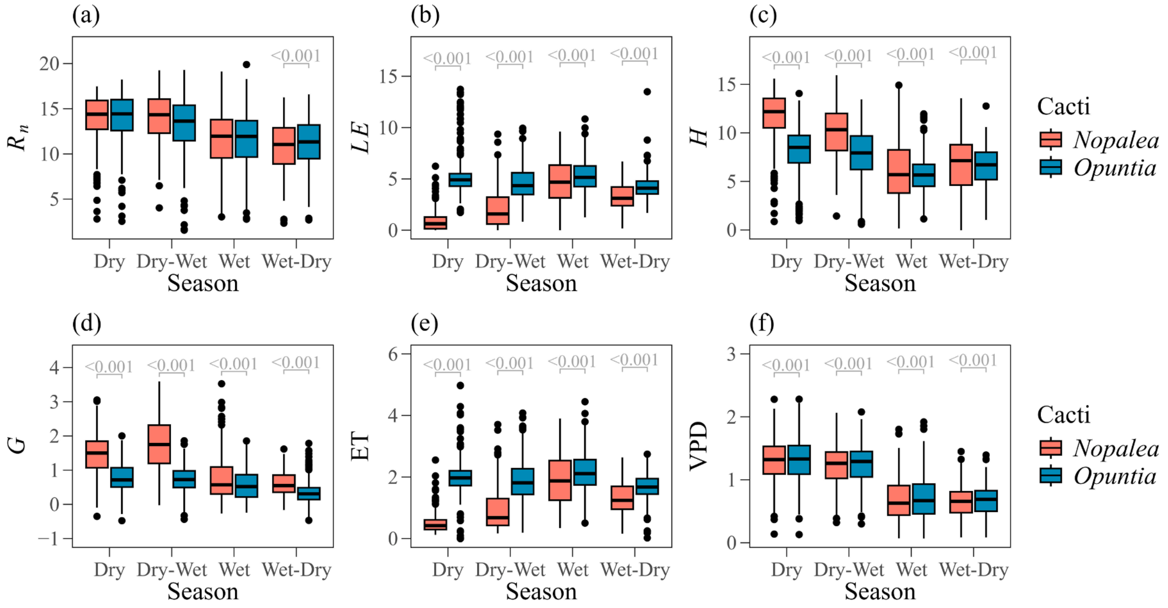

Fig. 5. Boxplot showing energy flux components and water exchange in two species of cactus (*Nopalea cochenillifera* and *Opuntia stricta*) during the wet and dry seasons, and the dry-wet and wet-dry transition seasons. The *P* value was calculated using Student's *t*-test ($P < 0.01$). R_n is the net radiation in MJ m^{-2} day^{-1} (a), *LE* is the latent heat flux in MJ m^{-2} day^{-1} (b), *H* is the sensible heat flux in MJ m^{-2} day^{-1} (c), *G* is the soil heat flux in MJ m^{-2} day^{-1} (d), ET is the evapotranspiration in mm day^{-1} (e), and VPD is the vapour pressure deficit in kPa (f). The boxplots denote the median, 25th, 50th, and 75th percentiles, the whiskers indicate 1.5 times the interquartile range and individually plotted outliers.

3.3. *Changes in energy partitioning for surfaces with cacti*

Fig. 6 shows the seasonal changes in energy partitioning during the four seasons for both cacti. Despite the similarity of energy inputs previously shown by R_n (Fig. 5a), interaction with the two vegetated surfaces significantly alters energy partitioning (Fig. 6). The H/R_n ratio in the area of *Nopalea* was the highest in each season (a mean of 0.69), 22 % higher than the mean H/R_n ratio in *Opuntia*. Although the mean value of H/R_n is lower in *Opuntia* (18 %), it is obvious that *H* was the main consumer of R_n in both areas of cacti, heating the air. We observed decreasing behaviour in H/R_n from the dry to the wet season, with a partition ratio 37 % lower in *Nopalea* and 14 % in *Opuntia*. During the same seasons, i.e., wet and dry, the LE/R_n ratio was highly variable in *Nopalea*, and at both sites *LE* was inversely proportional to the seasonal variations in *H*. The G/R_n ratio was equal to 0.10 and 0.12 in *Nopalea* during the dry and dry-wet transition seasons, however, during the dry season and dry-wet transition, *Opuntia* was, respectively, 40 % and 50 % lower.

3.4. *Changes in the vegetation, photochemical and pigment indices*

Variations in the Normalised Difference Vegetation Index (NDVI), Photochemical Reflectance Index (PRI), Chlorophyll Index (CI) and rainfall for the sites cultivated with *Nopalea* and *Opuntia* are shown in Fig. 7. The results show that the NDVI for *Nopalea* ranged from 0.19 to 0.67 (mean ± standard deviation: 0.36 ± 0.13), only slightly different to *Opuntia*, with values between 0.17 and 0.70 (a mean of 0.37 ± 0.11) (Fig. 7a). Furthermore, we found that during the wet season the results for the NDVI were higher in both species. This was also true for the CI (Fig. 7c). The best results for NDVI and CI were clearly between April and May, with a mean of 0.52 and 0.33, respectively, for *Nopalea*, whereas, for *Opuntia,* during the months in question, the respective values were 5 % and 6 % lower.

The photosynthetic responses of the plants under environmental

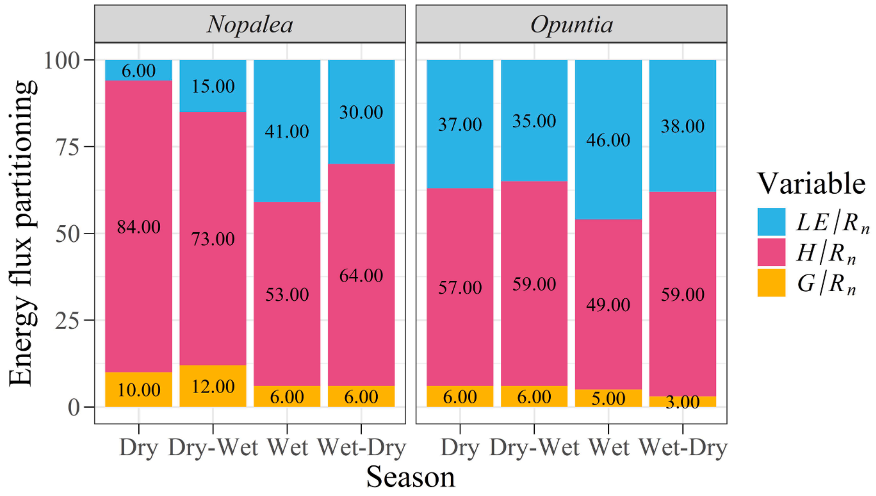

Fig. 6. Surface energy partitioning in two agroecosystems with cacti (*Nopalea cochenillifera* and *Opuntia stricta*).

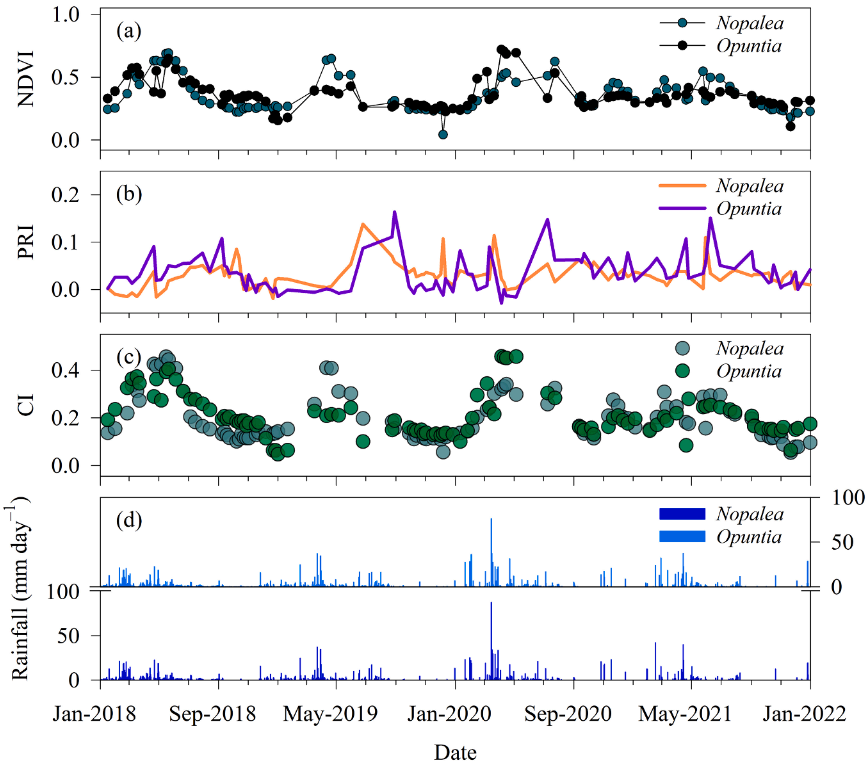

Fig. 7. Normalised Difference Vegetation Index—NDVI (a), Photochemical Reflectance Index—PRI (b), Chlorophyll Index—CI (c), and rainfall (d) in two areas of cactus (*Nopalea cochenillifera* and *Opuntia stricta*), from January 2018 to December 2021.

conditions resulted in values for the PRI that ranged from −0.01 to 0.14 over the time series under evaluation. A joint assessment of the relationships between the NDVI, PRI, CI and rainfall, showed an increase in the PRI in the period following the rainy season, that is, during the wet-dry season (Fig. 7d). In particular, when the NDVI and CI were drastically reduced by the plants, the values of the PRI were higher. These clear changes in the vegetation indices relative to the photosynthetic indices help clarify the photochemical efficiency and pigment pools of the plants. In addition, when the PRI showed no sudden variations relative to the NDVI or CI (November 2018 to Ma 2019 and November 2020 to Ma 2021), the cacti presented a reduced photosynthetic response despite a lack of stress conditions. The temporal pattern of the rainfall was very similar at both sites: *Nopalea* (mean 494.9 mm year^{-1}, total 1979.8 mm) and *Opuntia* (mean 512.8 mm year^{-1}, total 2051.2 mm), with 2020 the wettest year (Fig. 7d). It is important to note that a brief 4 % greater difference in water availability in the area of *Opuntia* may have been one of the causes of the changes in the PRI, CI and NDVI at the end of the experiment in 2021.

3.5. *Rates of plant growth, morphology, and physiology*

Fig. 8 shows the seasonal variation in absolute growth rate (AGR), relative growth rate (RGR), net assimilation rate (NAR), and specific cladode area (SCA) for the two species under study. We measured morphometric variables in both cacti from 2015 to 2021 to assess plant growth performance. During this period, one cycle of *Nopalea* and two cycles of *Opuntia* were evaluated. For the latter, the first cycle was harvested on 12 December 2018 (day of year [DOY] 1428), and the second cycle on 31 December 2021 (DOY 1115). The *Nopalea* was harvested on the same date, but 2543 days after planting. The absolute growth rate curves for *Nopalea* in the first cycle (Fig. 8a), and *Opuntia* in the second cycle (Fig. 8c), were very similar, however, the performance of the AGR in *Opuntia* averaged 0.10 Mg ha^{-1} day^{-1} (a peak of 0.14 Mg ha^{-1} day^{-1}), with 0.02 Mg ha^{-1} day^{-1} (a peak of 0.03 Mg ha^{-1} day^{-1}) in *Nopalea*. When examining the AGR in *Opuntia* in more detail during the first cycle, we found far higher values compared to *Nopalea* (380 %). Similarly, the AGR in *Opuntia* during the first cycle was 11 % higher compared to the second cycle.

In the present study, the results of the relative growth rate (RGR) ranged from 0.001 to 0.0043 Mg Mg^{-1} day^{-1} for *Opuntia*, with lower values for *Nopalea*, ranging from 0.0001 to 0.0015 Mg Mg^{-1} day^{-1} (Fig. 8d–f). In addition, the RGR was notably higher during the initial growth period in both species, gradually falling until reaching minimum values. During the first cycle of *Opuntia*, we clearly saw a prolongation of the high values for RGR, which started to fall in October 2017 (DOY 1000) (Fig. 8e). Overall, the RGR during the first *Opuntia* cycle was higher than during the second cycle, as well as higher than that of *Nopalea*, with a value greater than 0.004 Mg Mg^{-1} day^{-1}. Similarly, the high values for AGR in *Opuntia* produced an expressive response in the NAR, with a mean of 17.60 Mg ha^{-1} day^{-1} during the first cycle, and 175.15 Mg ha^{-1} day^{-1} during the second cycle (Fig. 8h–i); whereas for *Nopalea*, the mean value for NAR was 23.57 Mg ha^{-1} day^{-1} (Fig. 8g). Our results for NAR therefore show that species *Nopalea*, despite a high NAR throughout the cycle, did not show greater photosynthetic capacity than *Opuntia*.

To further explore the contributions of environmental factors to the variation in plant growth rates, we analysed the behaviour of the SCA (Fig. 8j–l). During the first cycle, *Opuntia* exhibited a mean SCA of 0.19 ha Mg^{-1}, ranging from 0.04 to 0.34 ha Mg^{-1}. These results afforded a percentage superiority for the SCA in *Opuntia*; when compared to *Nopalea* and to *Opuntia* in the second cycle the values were, respectively, 293 % and 155 % higher. Despite the high values of the SCA in *Opuntia* during the first cycle, there was a strong, almost linear reduction over time (Fig. 8k). During the single cycle of *Nopalea* and the second cycle of *Opuntia*, there was a peak in the SCA (humped curve) following the start of evaluations; results observed around DOY 1175 and 450, respectively.

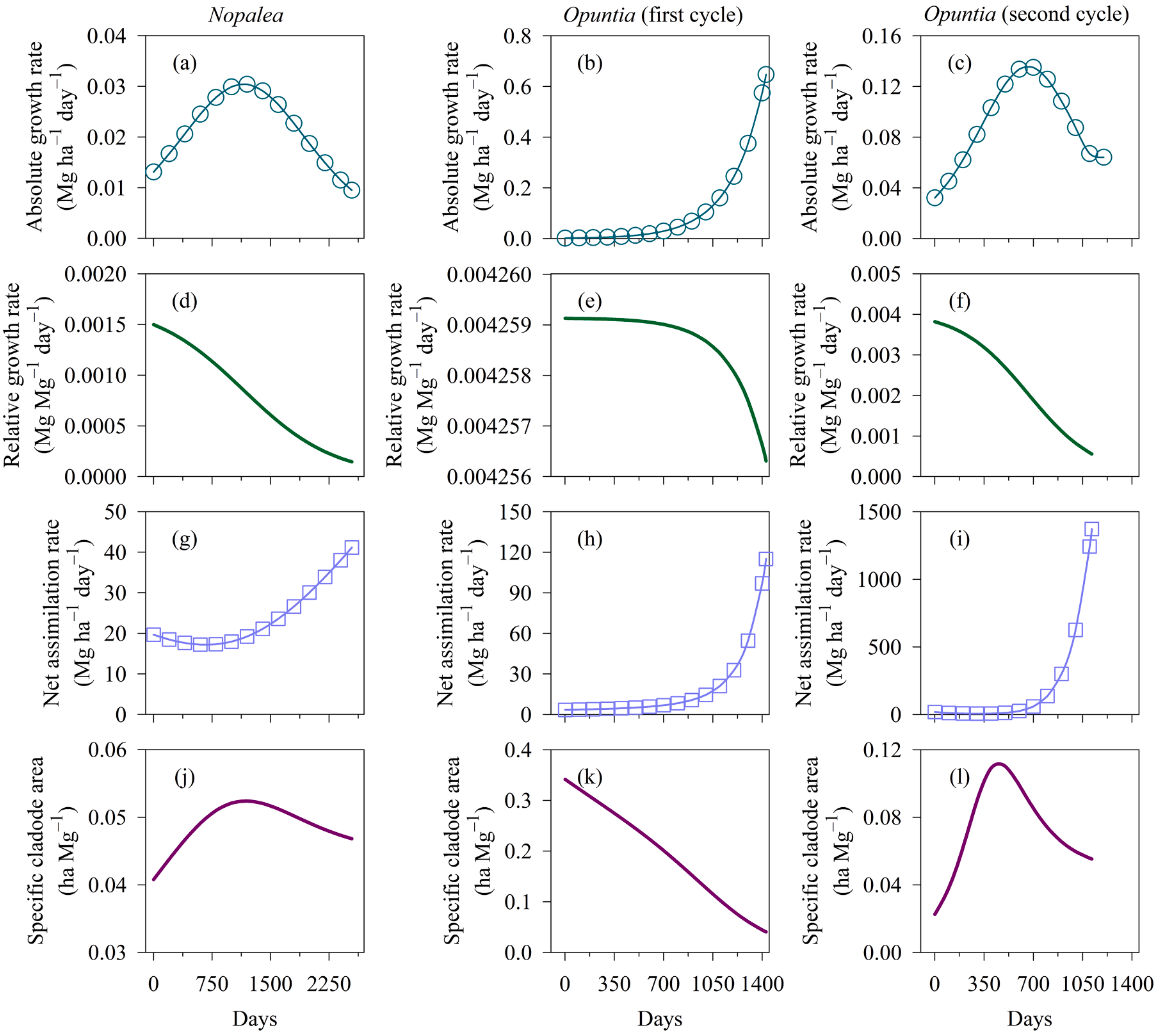

Fig. 8. Seasonal changes in absolute growth rate (a–c), relative growth rate (d–f), net assimilation rate (g–i), and specific cladode area (j–l) in two species of cactus (*Nopalea cochenillifera* and *Opuntia stricta*) measured over a period of seven years (2015–2021).

3.6. Water relations, increase in annual biomass yield, and water use efficiency

Fig. 9 shows the cladode water content and cladode succulence for the two species of cactus. There was a significant difference in the cladode water content during the sampling periods (Fig. 9a). We found more-pronounced dehydration in samples 4, 8, 10 and 13, with a mean of 81 % and 82 % for *Nopalea* and *Opuntia*, respectively. In addition, the cladode water content ranged from 73 % to 94 %, with a mean of 86 % in *Nopalea*, and, in contrast, a mean of 88.91 % in *Opuntia*, reaching values between 79 % and 96 %. Our results show a similar albeit not significant trend for cladode succulence in *Nopalea* and *Opuntia* (Fig. 9b). The minimum and maximum values obtained in both species ranged from 0.22 to 0.84 g cm^{-2} in *Nopalea* and 0.11–0.70 g cm^{-2} in

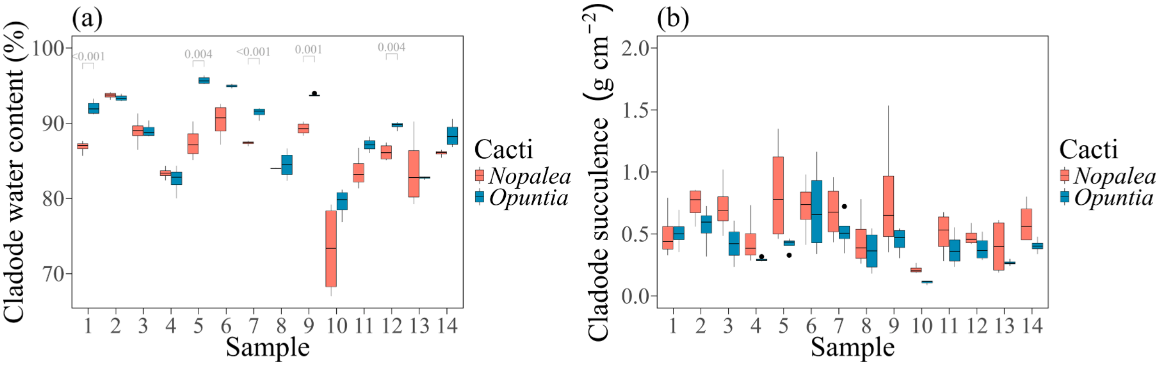

Fig. 9. Variation in cladode water content (a) and cladode succulence (b) in two species of cactus (*Nopalea cochenillifera* and *Opuntia stricta*) from 2018 to 2021 in a semi-arid environment. The boxplots denote the median, 25th, 50th, and 75th percentiles, the whiskers indicate 1.5 times the interquartile range and individually plotted outliers. Student's *t*-test was used to examine the difference between the two species for each sampling period ($P < 0.01$).

Opuntia. In fact, regardless of the sampling period, cladode succulence in *Nopalea* was on average 40 % greater than in *Opuntia*. Although both have succulent cladodes, the high value for cladode succulence in *Nopalea* was probably due to the smaller cladode area promoting greater succulence.

Both species of cactus showed variations in dry matter yield—DMY and water use efficiency—WUE over time (Table 3). For each year under evaluation, the mean annual increase in DMY in *Nopalea* was 0.32 Mg ha^{-1}, reaching a maximum value in 2018 (0.55 Mg ha^{-1}), since with the final samples in 2021 the increase in biomass yield was reduced by 78 %. On the other hand, the mean increase in DMY in *Opuntia* was 56.01 Mg ha^{-1}, ranging from 23.39 to 118.03 Mg ha^{-1} during the years under evaluation (2018–2021). These high biomass yields in *Opuntia* clearly follow the highest WUE presented by the species. Our results show a mean WUE of 7.54 kg m^{-3} for *Opuntia*, with significantly lower values found in *Nopalea*, a mean of 0.08 kg m^{-3}. For the final sampling period, WUE in *Nopalea* was 99 % lower than *Opuntia* for the same year. This shows that, over time, both species have variations in water use capacity and biomass conversion. Here it should be noted that *Nopalea* showed greater sensitivity to environmental conditions due to poorer performance compared to *Opuntia* (Table 3).

3.7. Associations between variables

To examine patterns or trends in the sampled data, we applied principal component analysis (PCA) for the two species of cactus (Fig. 10). We used the first two principal components (PC1 and PC2) to explain the total variance of the data. This criterion was chosen, as the principal components present eigenvalues greater than 1 (Kaiser, 1960). Fig. 10a shows the scores of PC1 (~71 %) and PC2 (~20 %) for *Nopalea*, responsible for explaining 91.71 % of the total accumulated variation. There was a clear difference between the wet season (with respective PC1 and PC2 scores of 1.76 and −1.46), the dry season (with respective PC1 and PC2 scores of −1.75 and 0.03), the wet-dry transition (with respective PC1 and PC2 scores of 0.86 and 2.22) and the wet-dry transition (with PC1 and PC2 scores of −0.87 and −0.79), in relation to the plant and environmental variables. In fact, in PC1, the plant growth variables, such as SCA, AGR, RGR and WUE presented higher negative loadings (−0.56, −0.56, −0.59 and −0.61, respectively) during the dry season and dry-wet transition (Fig. 10b–c). This may indicate that the species has less growth during wetter periods. In contrast, the variables NAR, NDVI and CI showed positive grouping during the wet season (Fig. 10b), with strong positive loadings in PC1, and values of 0.52, 0.62 and 0.62, respectively (Fig. 10c). Furthermore, ET, *LE* and the LE/R_n ratio presented loadings greater than 0.6 during the same season in the above PC. We found high loadings, ranging from −0.52 to −0.62 for *G*, *H*, VPD, R_n, H/R_n and G/R_n during the seasons with less water availability and in PC1. For *Nopalea*, the most significant variables in PC2 were CWC (−0.62) and PRI (0.60) (Fig. 10d).

The PCA results for *Opuntia* are shown in Fig. 10e–h, where the first two components contributed with 85 % of the total variance. PC1 separated the wet season from the other seasons, thereby contributing with 46 % of the total variance. On the other hand, PC2 explained 39 %, and was represented by the dry season and dry-wet transition (Fig. 10e). The variables NAR (0.52), LE/R_n (0.52), NDVI (0.50), ET (0.48), CI (0.46), CWC (0.45) and CS (0.42) had the highest positive loadings in PC1 (Fig. 10f–g). SCA and RGR had the highest contributions with negative loadings (−0.54 and −0.60, respectively) in PC1. We clearly saw higher NDVI and CI loadings when *H* and VPD were lower (Fig. 10f). During the dry season and dry-wet transition, both more strongly inserted in PC2 (scores of 1.23 and 1.08, respectively), the most positively significant variables were G/R_n, *G*, R_n and VPD, with respective loadings of 0.62, 0.62, 0.55 and 0.54. Here, we found that both *Nopalea* and *Opuntia* showed similar groupings during the wet season, but with different loadings and contributions.

Table 3
Increase in annual biomass yield, and water use efficiency in two species of cactus (*Nopalea cochenillifera* and *Opuntia stricta*), during 2018–2021.

Variable	Cacti	Year 2018	2019	2020	2021
DMY (Mg ha^{-1})	*Nopalea*	0.55	0.39	0.23	0.12
	Opuntia	118.03	23.39	45.97	36.66
WUE (kg m^{-3})	*Nopalea*	0.14	0.10	0.04	0.04
	Opuntia	14.31	3.28	6.18	6.39

DMY is the dry matter yield and WUE is the water use efficiency.

4. Discussion

4.1. Energy balance and partitioning

The analyses presented here show that vegetation type can easily promote changes in the surface energy fluxes (i.e., turbulent, radiation and ground heat), on a daily and seasonal scale. We found that species of family Cactaceae, i.e., *Nopalea cochenillifera* and *Opuntia stricta*, afford marked changes in the turbulent energy fluxes and available energy, even under similar environmental conditions (Figs. 3 and 4). Changes in energy availability and turbulent fluxes on a daily scale and across seasons have also been reported by several studies (Alves et al., 2022; Chen et al., 2022; Dhungel et al., 2021; Jardim et al., 2022). In the present study, on an hourly daytime scale, R_n and *H* were the most prominent variables for the two surfaces (Fig. 3). Over the year, these variations may even be similar (Rahman et al., 2019), but generally undergo changes in magnitude and value over the course of each season due to energy availability and the response of the vegetation (Bezerra et al., 2022; Rahman et al., 2019; Souza et al., 2021). In addition, this type of behaviour is well supported by research in semi-arid environments (Souza et al., 2021), being due to deficiencies and low water availability. The sensible heat flux and net radiation gradually increase between 09:00 and 15:00, with considerably higher peaks at noon in response to the greater absorption of surface energy (Bezerra et al., 2022).

During the dry season, the combined effect of a high R_n and high *H*, together with a low *LE* are conditions that can lead to a water deficit (Rahman et al., 2019). This is because during the dry season, R_n is mainly converted into sensible heat flux (Zhang et al., 2022). *G* also showed behaviour typically linked to the seasons and to humidity (e.g., rainfall and VPD), considering that the thermal conditions of the soil are greater during the day due to insolation, and can vary with the water availability, VPD, and physical characteristics of the soil. Loss of energy contained in the soil surface can also occur due to the rainfall, which partially helps to absorb this energy (Yang et al., 2022). In general, all hourly flux components of the energy balance showed parabolic behaviour, synchronous with changes in the R_n (Fig. 3).

We found that during the early hours of the day (06:00–08:00) the plants, in response to the environmental conditions, showed a high *LE* over the course of each season, with maximum values between the hours of 11:00 and 13:00, being more marked during the wet season and slightly lower during the dry season (Fig. 3). During the dry season, even with low water availability, the *LE* was positive around dawn in the areas of cactus, attesting to the high gas exchange activity of these plants (Guevara-Escobar et al., 2021). Due to the crassulacean acid metabolism (CAM) of the plants, they ideally open their stomata at night and/or even during the day if the VPD is low; this phenomenon is seen during CAM phase II, for carboxylation via ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO) (Andrade and Nobel, 1997; Heyduk, 2022; Nobel, 1991; Winter and Smith, 2022). We believe that this was one of the reasons for the higher *LE* during this period of the day. According to Zhang et al. (2022), *LE* may be closely linked to plant transpiration, which, as the rainfall increases, can rise rapidly due to evaporation, transpiration and the energy contained in the exchange of water vapour

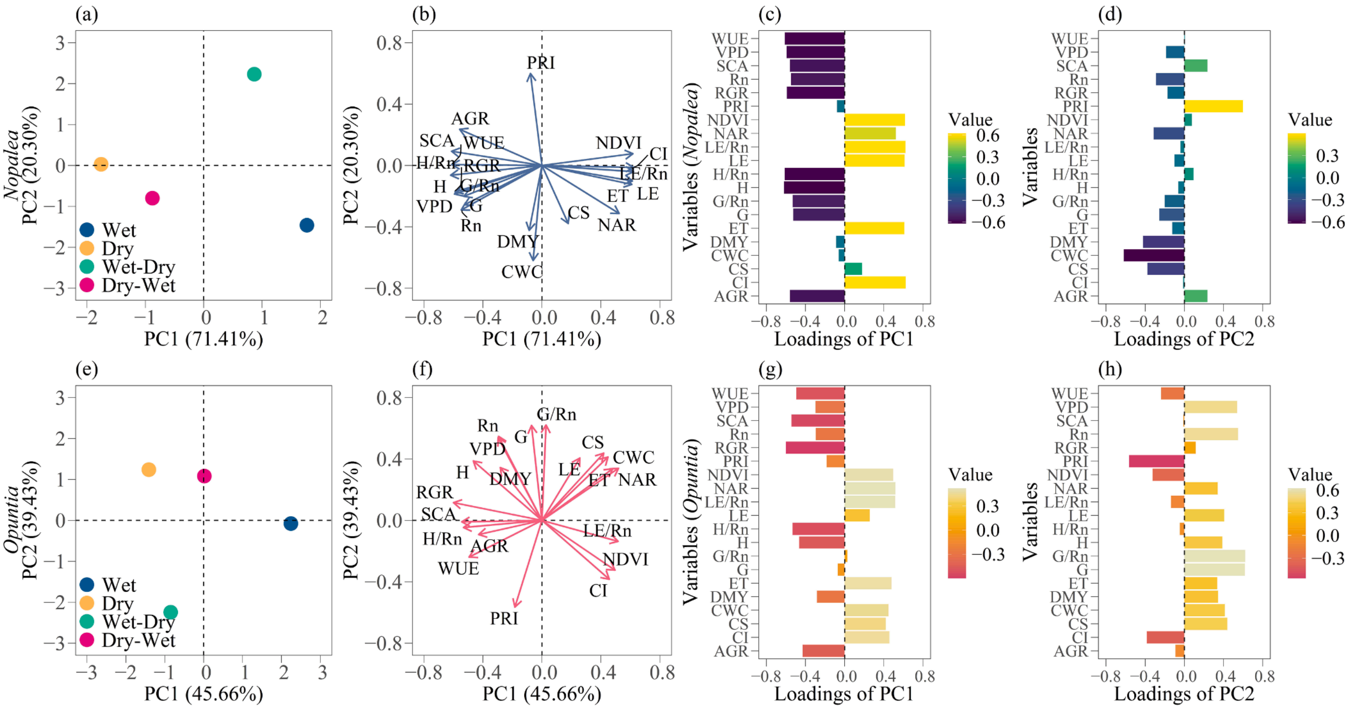

Fig. 10. Key dimensions of the multivariate space of the cactus species (*Nopalea* and *Opuntia*) associated with the seasons, and environmental and plant variables. Biplots with scores from the principal component analysis—PCA (a and e), and loadings of the first two principal components (b and f). The bar graphs with loadings (c–d and g–h) show the contribution for each principal component. Variables: water use efficiency (WUE), vapour pressure deficit (VPD), specific cladode area (SCA), net radiation (R_n), relative growth rate (RGR), Photochemical Reflectance Index (PRI), Normalised Difference Vegetation Index (NDVI), net assimilation rate (NAR), latent heat flux (*LE*), sensible heat flux (*H*), soil heat flux (*G*), evapotranspiration (ET), dry matter yield (DMY), cladode water content (CWC), cladode succulence (CS), Chlorophyll Index (CI), and absolute growth rate (AGR).

(Ma et al., 2022). In the present study, *H* was higher on an hourly scale during each season in both species of cactus. It is to be expected that in areas cultivated with cacti in a semi-arid environment most of the radiant energy would be lost as *H*, and when it rained, the plants would respond after a few days with an increase in transpiration (Unland et al., 1996).

The seasonal variation in R_n was fairly consistent over the years, with lower values in the middle of the year, and higher values at the beginning and end of the year. This behaviour is typical of semi-arid environments at low latitudes (close to the equator), and shows no marked variations. In addition, a high *H* and low *LE* occur at these locations due to the water deficit (Jung et al., 2019). From the middle of each year, when the radiant and surface fluxes were greater, *Opuntia* maintained evapotranspiration and *LE* high compared to *Nopalea*, even with the high VPD of both surfaces (Fig. 4). During periods of greater water availability (lower VPD), the evapotranspiration (ET) rates of *Opuntia* and *Nopalea* species are similar (Fig. 5). However, under drier conditions (higher VPD), the ET of *Opuntia* exceeds that of *Nopalea*. This variation is associated with leaf morphology (SCA), which is related to anatomy, water storage capacity in cladodes (CWC and CS), chlorophyll production and, consequently, photosynthetic performance (NAR) (Silva et al., 2015; Jardim et al., 2021). In dry periods (dry, dry-wet), when VPD is higher, *Opuntia* presents higher ET rates compared to *Nopalea*, due to its higher SCA (i.e., thinner cladode), CWC, CS and CI values, which is also reflected in higher NAR and dry matter accumulation (Fig. 10). Jardim et al. (2021) state that the *Opuntia* specie, clone ‘Orelha de Elefante Mexicana’, presents higher values of maximum quantum yield of photosystem II (ΔF/Fm’), which gives it higher rates of stomatal conductance, that is, transpiration and CO_2 fluxes, and greater capacity to dissipate heat to the environment. Consequently, *Opuntia*, clone ‘Orelha de Elefante Mexicana’ exhibits higher concentrations of total chlorophyll, carotenoids and potassium (K^+) in the cladodes, in addition to having a larger leaf area and dry matter accumulation compared to *Nopalea*, clone ‘IPA Sertânia’. This confirms the hypothesis of adaptability to hostile environments for *Opuntia* as opposed to *Nopalea*.

In addition to the species and environmental factors analysed in this study, other elements can influence energy partitioning, evapotranspiration, and their relationships with crop growth dynamics, such as soil type, pest management, weed control, among others. These factors were not considered because the two cactus fields were grown in the same soil type, both species studied demonstrate resistance to the main pest (*Dactylopius opuntiae*), and the contribution of weeds in agroecosystems is difficult to measure; in addition, their presence is quite common in this cropping system (Owen et al., 2016; Jardim et al., 2023a).

CAM plants in particular, as is the case of these cacti, are specialists in maintaining transpiration under conditions of extreme drought without the loss of turgor pressure (Andrade and Nobel, 1997; Heyduk, 2022; Nobel, 1991; Winter and Smith, 2022). Furthermore, the large plant vacuole can comprise up to 90 % of the cell volume, store water apoplastically in the mucilage and, as a result, increase photosynthetic and transpiration efficiency (Nobel et al., 1992), both more expressive in *Opuntia* (Goldstein and Nobel, 1994). Cacti of genus *Opuntia* are tolerant to variations in temperature (−6°C to 65°C) (Nobel and De La Barrera, 2003; Ojeda-Pérez et al., 2017; Zutta et al., 2011), and have a high photochemical yield and chlorophyll content, which helps their adaptive performance (Arias-Moreno et al., 2017; Jardim et al., 2021).

The soil-vegetation-atmosphere interaction altered both radiant and convective heat transfer at the soil surface. CAM plants are able to cool the soil (Cao et al., 2019; Soares, 2018), with *O. ficus-indica* having the ability to reduce the soil surface heat flux by 50 % (Soares, 2018). In ecosystems with Cactaceae, Flanagan and Flanagan (2018) found a daily mean for *G* of around 2 MJ m^{-2} day^{-1}, varying according to the rainfall pulses; our findings were consistent with this study. Another important factor is the canopy architecture, which possibly favoured a lower incidence of radiation on the surface in the area of *Opuntia*, since each species has a different canopy architecture (Consoli et al., 2013b).

During the growth phase, *O. ficus*-indica (L.) Mill. *G* may present low values, or even values close to zero, where any increase may be influenced by the high values of *H* (Consoli et al., 2013b).

During the wet and dry seasons, variations in R_n are closely linked to such factors as the hydrological season, vegetation and contributions from turbulent fluxes. *LE* can also be quite responsive to rainfall events during the dry season (Mendes et al., 2021), and, as these are non-native species, there may be a reduction in R_n and LE/R_n (Alves et al., 2022). Another factor is the reduced cloud cover, which may increase R_n during the dry season (Malhi et al., 2002). Consoli et al. (2013a), evaluating the cactus *O. ficus-indica* (L.) Mill. in a semi-arid environment in western Sicily, Italy, found a mean value for R_n of ~13 MJ m^{-2} day^{-1}, consistent with our findings of 12.57 MJ m^{-2} day^{-1} over the four seasons (Fig. 5). In seasons with a high moisture deficit, such as the dry season, much of the energy (~70 %) of the R_n is converted into *H* (Campos et al., 2019; Costa et al., 2022). Pierini et al. (2014), in a study with *O. spinisior* and *O. engelmannii*, found greater values for the sensible heat flux compared to the latent heat flux. Thus, for dry-climate vegetation exposed to periods of humidity the conversion of R_n into *LE* and *H* can be very similar (Campos et al., 2019); on the other hand, when partitioned, their contributions differ according to the component and the season. In the present study, the H/R_n ratio during the wet and dry seasons was slightly similar for *Opuntia* (0.57 and 0.49, respectively), and for *Nopalea*, albeit with greater variation (0.84 and 0.53, respectively) (Fig. 6). The *LE* partitioning fluxes in *Nopalea* were far lower, and this may indicate greater sensitivity to a lack of rain and, consequently, lower water availability in the soil. Together with a high VPD and high *H*, plants can trigger physiological controls that reduce stomatal conductance in the leaves and canopy, lowering the *LE* and LE/R_n ratio (Yue et al., 2019). This is clearly noticeable in the daily ET, with a mean of 1.71 mm day^{-1} in *Nopalea*, and 1.16 mm day^{-1} in *Opuntia*, reinforcing the findings of Han and Felker (1997) with *O. ellisiana* under rainfed conditions (1.44 mm day^{-1}). When irrigated, other species of genus *Opuntia* presented an ET greater than 2 mm day^{-1} (Consoli et al., 2013a; Goldstein et al., 1991; Lima et al., 2018). In cactus species, it is common for the largest portion of R_n to be directed to *H*, even during the rainy season (Fig. 6), resulting in higher environmental temperatures. Due to their adaptive mechanisms (morpho-physiological and anatomical) (Nobel and De La Barrera, 2003; Jardim et al., 2021), cacti demonstrate greater tolerance to thermal stress and, even under high temperatures, are able to maintain high growth rates (i.e., SCA, AGR, and RGR) (Fig. 10). However, when temperatures remain persistently outside the ideal range for plants (below 4°C or above 40°C), cactus species show impairment of photochemical parameters, reduction in malic acid consumption, inhibition of the maximum quantum yield of photosystem II (ΔF/Fm') and the photochemical quenching coefficient (qP), in addition to chlorophyll degradation, impairing photosynthetic capacity (Jardim et al., 2021; Zhang e Liu, 2018).

These results are essential for understanding the ecosystem services provided by cactus plantations in arid and semi-arid environments. Maintaining growth (SCA, RGR, and AGR), even during the most inhospitable periods (high temperatures and VPD), ensures provisioning services, allowing their use as forage for animal and/or human consumption, contributing to the local economy (Jardim et al., 2023c). In addition, they offer support services through the maintenance of nutrient cycling, soil fertility (Santos et al., 2024; Stavi, 2022), control of potential pest populations, and conservation of biodiversity and genetic heritage (Stavi, 2022; Ávila-Gómez et al., 2019), among others. Finally, it still maintains regulatory services that include modulating water availability, carbon sequestration, mitigating extreme climate events, maintaining the balance of the hydrological cycle, mitigating desertification, minimizing droughts and controlling critical erosion processes (Louhaichi et al., 2017; Stavi, 2022; Jardim et al., 2023a).

Although this study covers only two species – one from the genus *Nopalea* and the other from the genus *Opuntia* – both genera are widely valued for their forage uses, in Brazil (600,000 ha) and other countries such as Tunisia (230,000 ha), Mexico (150,000 ha), Morocco and Algeria, and 75,000 ha in South American countries (Inglese, 2010; De Waal et al., 2015; Dev et al., 2024). Furthermore, many species present similarities in their genetic, morphological, productive and nutritional variability (Dev et al., 2024). Species of these genera occur in almost all climatic regions of the world, although they are most abundant in arid and semi-arid areas (Inglese, 2010; De Waal et al., 2015).

4.2. *Temporal responses to rain of the NDVI, PRI and CI in the cactus canopy*

We evaluated spectral indices of the cactus vegetation in response to the environmental conditions in order to understand the yield performance and health of the plants, using the NDVI and CI, and, by means of the PRI, their photosynthetic characteristics. In general, the results showed, similar behaviour for the NDVI, ranging from 0.17 to 0.70 for the cacti, with *Opuntia* being slightly higher (Fig. 7). Silva et al. (2021) documented spectral responses of the vegetation of between 0.1 and 0.5 in areas of *N. cochenillifera* and *O. stricta*, in the Agreste region of Pernambuco, Brazil. These findings confirm the high levels of chlorophyll, as well as the photochemical efficiency of the plants, and are consistent with the results of Hartfield et al. (2022) and Jardim et al. (2021). In addition, the NDVI can help in understanding biomass performance and can also be an indicator of stress in the crops (Gerhards et al., 2019). Because of this, we strengthened our investigational analysis of plant stress, applying further indices related to the relevant photosynthetic pigments (e.g., chlorophylls and carotenoids) and the PRI. For Panigada et al. (2014), the PRI has a marked ability for identifying water stress in the aerial part of plants. This is because the PRI is linked to photosynthetic processes, and its sensitivity in identifying xanthophyll pigments reflects photochemical stress in the plants due to increased heat dissipation (Norton et al., 2022; Panigada et al., 2014). As such, the plants, by means of the xanthophyll cycle, increase their spectral emissions and energy dissipation so as not to cause oxidative damage (Gamon et al., 1997). Despite varying results for the PRI, the consistent responses, and its importance, studies reporting its application in the cactus are scarce.

In the present study, the plants were clearly exposed to intense solar radiation due to the semi-arid conditions of the region, with no effect from any interspecific shading other than possible self-shading. Solar radiation can help in the production of starch and the growth of cladodes, with the starch helping osmoregulation and photosynthetic activity (Horibe et al., 2016). In fact, we found that both species stimulated NDVI and CI responses to rainfall. This is because variations in the water potential of the tissues alter chlorophyll synthesis, and change the daily net uptake of CO_2 (Dubeux et al., 2021). As such, the increase in chlorophyll is advantageous for photosynthetic activity, and if water is available, the plants find favourable conditions for development. Even under low water availability, the root system of the cactus is efficient, with the rapid absorption of water influencing the response of the vegetation indices (Ouko et al., 2020).

4.3. *Plant dynamics and growth rate*

Environmental conditions are important factors in the adaptive process of plants, and can cause changes in the morphological and physiological characteristics of both species. As the species are highly adaptable to conditions of stress, the cactus presents physiological plasticity and a slow relative growth rate—RGR (Luo and Nobel, 1993; Martínez-Berdeja and Valverde, 2008). In the present work, we found marked characteristics for the growth rates of both species under study. As previously described by Jardim et al. (2023c) and Araújo Júnior et al. (2021), both *Nopalea* and *Opuntia* generally showed a high growth rate, but with different patterns of development (Fig. 8). Various studies have shown this type of behaviour in *Opuntia* e.g., Araújo Júnior et al. (2021), Jardim et al. (2023c), Scalisi et al. (2016), and Silva et al. (2014), where the higher AGR and RGR, are probably related to the high use of photoassimilates and to leaf expansion, represented by the NAR and SCA. In *Nopalea*, the low values of the net assimilation rate and specific cladode area may serve as an indication that photosynthesis is limiting plant growth. Another possible explanation is that high resistance to desiccation and water stress in *Opuntia* compared to other species, favours its development (Tapia et al., 2019). Han and Felker (1997) reported improvements in the development and yield of the cacti after rainfall, with an increase in the photosynthetic area (analogous to the cladode area index). For Hassan et al. (2020), such factors as light, soil characteristics, temperature and the dry weight of the basal cladodes are essential for growth in the cactus. In the present study, it was observed that the highest NAR values, for both *Opuntia* and *Nopalea*, occurred during the period of greatest water availability, when VPD levels were lower and CI accumulations and ET rates were higher. Since NAR reflects the net photosynthesis of plants, it is clear that, during this period, cacti invested more in the photoassimilate reserve, accumulating them for use in the drier period – evidenced by the lower values of SCA, AGR and RGR (Fig. 10). The higher SCA value (thinner cladodes) suggests the strategy of cacti to maintain their growth during the drier periods, as also stated in other literature (Scalisi et al., 2016; Zhang and Liu, 2018; Jardim et al., 2021).

Among plant growth rates, it should be noted that both the absolute and relative growth rate are indices that help in understanding the efficiency of dry biomass production. That said, the high efficiency was fundamental to the productive performance of the cacti. The results found by Araújo Júnior et al. (2021) show a higher AGR for *O. stricta* (0.0058 Mg ha^{-1} ºCday^{-1}) compared to clones of *N. cochenillifera*, with a mean of 0.0048 Mg ha^{-1} ºCday^{-1} ('Miúda') and 0.0021 Mg ha^{-1} ºCday^{-1} ('IPA Sertânia') conducted under rainfed conditions. Furthermore, according to the authors, the RGR was also higher at the start of the experimental period, with *O. stricta* showing better results (0.0087 Mg Mg^{-1} ºCday^{-1}) than the *Nopalea* clones, which confirms our findings. Using a ground cover of straw, Souza et al. (2022) found an AGR of 0.038 Mg ha^{-1} ºCday^{-1} and AGR of 0.0065 Mg Mg^{-1} ºCday^{-1} in *O. stricta*. On the other hand, in contrast to the studies presented above, our results are superior for AGR, but inferior to those reported for RGR. One possible explanation for the poorer performance of the RGR may be linked to the high AGR and the increased demand for assimilates by the vegetative structures. A high AGR and SCA can cause cladode shading, thereby reducing the RGR (Jardim et al., 2023c; Silva et al., 2014; Souza et al., 2022).

The superior performance of the NAR may be related to a better use of the luminous energy by *Opuntia*. This tactic is related to the rapid growth of the species, where two cycles of *Opuntia* were superior in development to that of the single cycle of *Nopalea* (all evaluated during the same chronological period). The high SCA of the *Opuntia* cactus in both cycles may be a way of the plants better allocating photoassimilates, thereby expressing more-significant growth rates. It is possible that self-shading caused greater problems in the growth rates of *Nopalea* (Jardim et al., 2023c). For Izaguirre-Mayoral and Marys (1996), among species with a CAM pathway, *N. cochenillifera* is not tolerant to shading, and this can cause problems in absorbing CO_2. This characteristic was also seen in *O. ficus-indica* (Luo and Nobel, 1993), but in this study we found a lower performance in *Nopalea*. Plants with significant tolerance to stress have low relative growth rates and short stature (Luo and Nobel, 1993). For example, species of *Nopalea* are morphologically taller, while those of *Opuntia* have smaller individuals (Nobel and Zutta, 2008); this may be a strong key indication of tolerance in the present study.

During the wet season, variables such as WUE, AGR and RGR have lower values, showing that both cacti exhibited less growth and WUE (Fig. 10). On the other hand, the plants showed no signs of stress because the high values of NDVI and CI (i.e., high loadings in PC1). This is because the vectors are in the same direction, showing the strong correlation of the variables with each other, albeit conflicting with the season. The cacti show satisfactory growth responses with the increased water availability (Campos et al., 2021; Lima et al., 2018; Scalisi et al., 2016), however, their growth may vary as shown here. In fact, there were improvements in the photosynthetic efficiency of the plants, since the NAR, NDVI and CI were high. As they are CAM plants, the available rainfall improves the microclimate conditions, resulting in an increase in CO_2 efflux (Campos et al., 2021; Nobel, 1991; Winter and Smith, 2022). Due to the high NAR and low PRI, the high water content of the cladodes shown in our results may have favoured cell turgor and improved photosynthetic activity (Winter and Smith, 2022).

4.4. *Plant water relations and biomass production*

A significant water content was found in the cladodes of both species, especially *Opuntia*, with a mean value of 89 % (± 5 %). This particular trait was not so expressive as to cause any significant difference in cladode succulence (Fig. 9b), probably due to the functional anatomical characteristics of CAM plants, which are able to store large volumes of water in their cells (Borland et al., 2011; Hassan et al., 2020; Nobel, 1991; Nobel et al., 1992; Winter and Smith, 2022). Furthermore, high succulence may be a key feature for maximising biomass production when plants are under a water restriction, helping to maximise the night-time absorption of CO_2 (Borland et al., 2011). This response may explain the expressiveness of the plants of *Opuntia* in relation to those of *Nopalea*. Observations concerning the high cladode water content were also reported by Scalisi et al. (2016) (45–85 %) and Melero-Meraz et al. (2022) (60–95 %). One important explanation for the variation in cladode water content is related to the availability of water in the soil (Melero-Meraz et al., 2022; Scalisi et al., 2016), given that our plants did not undergo long months of drought (see Fig. 7d).

Consistent with earlier literature (Consoli et al., 2013b; Han and Felker, 1997; Lima et al., 2018; Snyman, 2013), the cactus plants showed high WUE, with *Opuntia* higher (7.54 kg m^{-3}) compared to *Nopalea* (0.08 kg m^{-3}) throughout the experiment (Table 3). During the dry season, WUE increased in both species, being greater than 8 kg m^{-3} in *Opuntia* and greater than 0.1 kg m^{-3} in *Nopalea*. Generally, CAM plants have an exceptionally high WUE, around three and six times higher than C4 and C3 plants, respectively (Jardim et al., 2021; Snyman, 2013; Winter and Smith, 2022). In addition, genus *Opuntia* is known for its greater tolerance than other CAM species, which are ideal for arid regions due to their enhanced conversion of water into biomass (Han and Felker, 1997; Ojeda-Pérez et al., 2017). Such characteristics as high WUE and aboveground biomass yield were noticeable in our study. Actually, these results are not enough to report that *Nopalea* plants are more sensitive, but they demonstrate the superiority of *Opuntia* in this environment. A respective WUE of 7.66 and 7.87 kg m^{-3} for *O. robusta* and *O. ficus-indica* were found by Snyman (2013) in Bloemfontein, in the semi-arid region of South Africa. Although the results for WUE found by Snyman (2013) in species of *Opuntia* are similar to those of the present study, the aboveground dry biomass yield was lower, even with the plants receiving 521.75 mm of annual rainfall. Under optimal conditions, dry matter production in C3, C4 and CAM species would be similar; on the other hand, under the deficient conditions of arid and semi-arid climates, CAM plants present greater biomass production (Snyman, 2013).

5. Conclusions

Our analyses provide the first observational evidence of turbulent fluxes and surface energy partitioning in two simultaneous cultivations of *Nopalea* and *Opuntia* cacti in a semi-arid environment. By grouping the data into different water regimes (dry, dry-wet, wet and wet-dry) it was possible to measure the physiological and morphological strategies during the exchange of energy and water with the environment – aspects that would be difficult to identify in analyses of shorter time scales. The results obtained for the succulent species analysed show that, although they present CAM-type photosynthesis, their behaviour in heat exchange and evapotranspiration varies according to the seasons. These findings are extremely relevant for the cactus family, even considering only two species from different genera. Few studies perform simultaneous measurements in different landscapes, and therefore, this research stands out as the only one to integrate microclimatic, physiological, morphological and productive measurements in two cactus agroecosystems. Further analysis revealed that the latent (*LE*) and sensible (*H*) heat fluxes have marked seasonality, with the low *LE* in *Nopalea* occurring during the dry season (0.85 MJ m^{-2} day^{-1}), while for *Opuntia*, during the wet-dry transition season (4.22 MJ m^{-2} day^{-1}). During each season, the *LE* and evapotranspiration (ET) were higher in *Opuntia*. In general, *Nopalea* provides greater *H* and soil heat flux (*G*), even under humid conditions. In both cacti, *H* showed the highest consumption of net radiation (R_n), with *Nopalea* having the highest H/R_n ratio and the lowest LE/R_n ratio (mean 0.23) during each season. Furthermore, the vegetation showed different responses for the spectral, photochemical, chlorophyll and water use efficiency indices, which explains the better yield of *Opuntia* and the greater sensitivity of *Nopalea*. Similarly, the growth rates and biomass of the cacti were different, with *Opuntia* obtaining the greatest increments and adaptive plasticity. Our findings offer new insights, and are fundamental to understanding how biophysical factors influence CAM plants, further demonstrating that their adaptive abilities can change even in individuals of the same family. In conclusion, this study can serve as a valuable baseline for research with cacti in deficient environments. In particular, the findings may also be useful in environmental management and the rehabilitation of degraded areas. One important next step is to assess the potential CO_2 sink of these species for application in agriculture, ecology and hydrology.

CRediT authorship contribution statement

Ometto Jean Pierre Henry Balbaud: Writing – review & editing, Visualization, Supervision, Project administration, Methodology. **Souza Luciana Sandra Bastos de:** Writing – review & editing, Software, Methodology, Formal analysis, Data curation. **Steidle Neto Antonio José:** Writing – review & editing, Visualization, Software, Methodology. **Silva Thieres George Freire da:** Writing – review & editing, Visualization, Supervision, Software, Resources, Methodology, Data curation. **Santos Wilma Roberta dos:** Writing – review & editing, Visualization, Methodology. **de Lima João L.M.P.:** Writing – review & editing, Visualization, Supervision, Project administration. **Souza Carlos André Alves de:** Methodology, Formal analysis. **Araújo Júnior George do Nascimento:** Visualization, Methodology, Data curation. **Marin Fabio Ricardo:** Writing – review & editing, Supervision, Software, Formal analysis. **Silva Gabriel Italo Novaes da:** Writing – review & editing, Visualization, Methodology. **Alves Cléber Pereira:** Writing – review & editing, Visualization, Software, Methodology. **Salvador Kaique Renan da Silva:** Visualization, Software, Methodology. **Jardim Alexandre Maniçoba da Rosa Ferraz:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Leite Renan Matheus Cordeiro:** Visualization, Methodology. **Tang Xuguang:** Writing – review & editing, Visualization, Resources, Methodology, Funding acquisition, Data curation. **Lopes Daniela de Carvalho:** Writing – review & editing, Visualization, Software, Methodology. **Morais José Edson Florentino de:** Writing – review & editing, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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