ALEXANDRE MANIÇOBA DA ROSA FERRAZ JARDIM

ENERGY AND CARBON FLUXES IN BRAZILIAN SEMI-ARID LANDSCAPES: HOW THE ESTABLISHMENT OF CACTUS PLANTATIONS CAN MITIGATE THE ADVANCE OF DESERTIFICATION

Recife

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ADVANCE OF DESERTIFICATION

Thesis submitted to the Agricultural Engineering Graduate Program of the Federal Rural University of Pernambuco in partial fulfillment of the requirements for the degree of Doctor in Agricultural Engineering.

Advisor: Prof. Dr. Thieres George Freire da Silva.
Co-Advisors: Prof. Dr. Luciana Sandra Bastos de Souza, and Dr. José Edson Florentino de Morais.

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Thesis presented to the Federal Rural University of Pernambuco, as partial fulfillment of the requirements for the Graduate Program in Agricultural Engineering, to obtain the title of Doctor in Agricultural Engineering.

DEFENDED and APPROVED on January 25, 2023.

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"To everything there is a season,
and a time for every purpose under heaven".
- Ecclesiastes 3:1.

"If I have seen further than others,
it is by standing upon the shoulders of giants".
- Isaac Newton.

DEDICATION

I dedicate this thesis work to my loving parents, Iamí Maniçoba da Rosa Ferraz Jardim and Valdomiro Ferraz Jardim Filho (*in memoriam*), and my sister Camila. Everything I am today is because of you.

I also dedicate this thesis to God Almighty, the creator who gives us wisdom, knowledge and understanding, and all Scientists (science only real when shared).

$\int_{\heartsuit}^{\infty}$ My love for you all can never be quantified.

God bless you.

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SUMMARY

GENERAL ABSTRACT

Vegetated surfaces are considered important in controlling environmental degradation processes and improving water, carbon, and energy fluxes on the Earth's surface. Dry forests and cacti crops are common vegetation in arid and semi-arid environments. Therefore, Caatinga and cactus areas were investigated using techniques such as energy balance through meteorological tower data, eddy covariance, and satellite images emphasizing hyperspectral vegetation monitoring. In addition, data on cacti's physiological, photochemical, and morphometric responses in a semi-arid environment were explored. This study was divided into eight chapters emphasizing meteorological variations, energy, water, and carbon flux responses in Caatinga and cacti (*Opuntia* and *Nopalea*) in the Brazilian semi-arid region. The use of methods that integrate data from climate monitoring towers and remote sensing products helps to improve the accuracy of determining energy fluxes on a global scale. In dry forest areas, woody species can store large amounts of carbon (C) in their biomass above and below ground. The significant increase in agricultural areas resulted in the progressive reduction of the Caatinga biome. Furthermore, the phases of the El Niño-Southern Oscillation directly influenced the rainfall variability in the Pernambuco study. The values for the effective quantum yield of PSII and changes in photochemical quenching was higher in the 'Orelha de Elefante Mexicana' cactus clone. In cactus clones, there was a difference in non-photochemical quenching. In general, cactus cultivation showed significantly higher net radiation (R_n) during the wet season, being on average 14% higher than during the dry season and transitions. There was no difference in evapotranspiration during the wet or dry seasons, but there was a 40% reduction during the dry-wet transition. The H/R_n ratio showed a decreasing behavior from the dry to the wet season, with a reduction of 36.90% in *Nopalea* and 14.04% in *Opuntia*. The Normalized Difference Vegetation Index (NDVI) varied from 0.19 to 0.67 (*Nopalea*) and from 0.17 to 0.70 for *Opuntia*, similar to the Chlorophyll Index, which maintained the seasonality of the NDVI. Overall, spatial patterns for the Photochemical Reflectance Index were found from −0.01 to 0.14 for *Nopalea* and *Opuntia*. Under the same conditions, *Opuntia* showed the highest growth and net assimilation rates. The average water content of the cladode was 86.01% in *Nopalea* and 88.91% in *Opuntia*. Biomass and water use efficiency was higher in *Opuntia* (56.01 Mg ha^{-1} and 7.54 kg m^{-3}, respectively). These comparisons indicate greater sensitivity in *Nopalea* and more meaningful quantification of surface energy balance in *Opuntia*. The radiation use efficiency of the wet season was 81.48% higher than in the dry season. Clearly, these comparisons indicate that the cactus is a potential year-round carbon sink (net ecosystem CO_2 exchange [NEE]: −4,517 g C m^{-2}; gross primary production [GPP]: 2,352 g C m^{-2}). The results help us to understand that most of the R_n energy is used in the sensible heat flux (58% ratio).

Keywords: flux partitioning, surface energy balance, cacti, Caatinga, climate change, photosynthesis, desertification

GENERAL INTRODUCTION

With the large emissions of greenhouse gases and the influence of meteorological factors, the semi-arid regions of the planet are expected to become even drier (Bao et al., 2022; Dass et al., 2018). For decades, vegetation in a semi-arid climate has been experiencing interannual variability in the absorption of carbon dioxide (CO_2), a decrease in rainfall, and an increase in temperature, which has triggered serious environmental problems. In terrestrial ecosystems, grasslands cover approximately 30–40% of the land surface and forests approximately 30%; these environments are responsible for providing a carbon sequestration from the atmosphere of approximately 20% to 90% (Balasubramanian et al., 2020; Besnard et al., 2018). When the ecosystem is disturbed, there is a tendency for increased heterotrophic respiration due to the increase in above-ground biomass from litter, while gross primary production suffers problems due to reduced leaf area, thus increasing the net release of CO_2 into the atmosphere (Besnard et al., 2018). This type of imbalance can cause problems in the carbon balance on vegetated surfaces since the global net carbon balance is the difference between the gains and losses of this element. Basically, ecosystems assimilate carbon through photosynthesis and the same can be lost in the form of CO_2 through the respiration of organisms (autotrophs and heterotrophs) and volatilization of organic compounds (Viglizzo et al., 2019). C4 photosynthesis and crassulacean acid metabolism (CAM) plants are responsible for covering important ecological niches in grasslands, tropical forests, and arid ecosystems, with 25% of terrestrial primary production represented by C4 plants in grasslands, while CAM plants represent 50% of plant biomass in arid and semi-arid regions (Hartzell et al., 2018).

CAM photosynthesis is an ancient adaptation of the C3 pathway, being more efficient due to the control of stomatal opening, commonly performed during the night. The resultant of this photosynthetic process provides water use efficiency three to six times higher compared to the photosynthetic species C4 and C3, respectively, and, consequently, a potential increase in the net absorption of CO_2 (Niechayev et al., 2019). Cacti of the genera *Opuntia* and *Nopalea*, holders of the CAM pathway, are important plants of the Cactaceae family, which stand out due to their survival in environments considered inhospitable for several agricultural species, presenting high efficiency in the use of water and carbon, and

adapting well to high temperatures and low water availability (Nobel, 1991; Nobel and Zutta, 2008; Winter and Smith, 2022). In addition, cacti are great producers of biomass and can be used in animal and human food.

Globally, climate change threatens to increase the frequency, duration and geographic distribution of droughts. In this way, the interest in expanding studies and techniques that help in the evaluation of the behavior of ecosystems is of great relevance. Monitoring the volume and spatialization of rainfall events, changes in the energy and carbon balance of vegetation, and understanding the morphophysiological behavior of plants can be a way to mitigate how environmental conditions influence the performance of species. Thus, techniques such as energy balance using meteorological tower data, eddy covariance, satellite images with emphasis on hyperspectral monitoring of vegetation, physiological and photochemical responses using chlorophyll fluorescence and morphometric data were used in this study to quantify responses of cactus vegetation and Caatinga in a semi-arid environment. This study was divided into eight chapters with an emphasis on meteorological variations, energy, water and carbon flux responses in the Caatinga, as well as in cacti (*Opuntia* and *Nopalea*) in the Brazilian semi-arid region.

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1 **CHAPTER 1**

2

3 Understanding interactive processes: a review of CO_2 flux, evapotranspiration, and energy

4 partitioning under stressful conditions in dry forest and agricultural environments

5

6 **Abstract**

7 Arid and semiarid environments are characterized by low water availability (e.g., in soil and

8 atmosphere), high air temperature, and irregularity in the spatio-temporal distribution of

9 rainfall. In addition to the economic and environmental consequences, drought also causes

10 physiological damage to crops and compromises their survival in ecosystems. The removal

11 of vegetation is responsible for altering the energy exchange of heat and water in natural

12 ecosystems and agricultural areas. The fluxes of CO_2 are also changed, and environments

13 with characteristics of sinks, which can be sources of CO_2 after anthropic disturbances. These

14 changes can be measured through methods such as e.g., sap flow, eddy covariance, remote

15 sensing, and energy balance. Despite the relevance of each method mentioned above, there

16 are limitations in their applications that must be respected. Thus, this review aims to quantify

17 the processes and changes of energy fluxes, CO_2, and their interactions with the surfaces of

18 terrestrial ecosystems in dry environments. Studies report that the use of methods that

19 integrate data from climate monitoring towers and remote sensing products helps to improve

20 the accuracy of the determination of energy fluxes on a global scale, also helping to reduce

21 the dissimilarity of results obtained individually. Through the collection of works in the

22 literature, it is reported that several areas of the Brazilian Caatinga biome, which is a

23 Seasonally Dry Tropical Forest have been suffering from changes in land use and land cover.

24 Similar fluxes of sensible heat in areas with cacti and Caatinga can be observed in studies.

25 On the other hand, one of the variables influenced mainly by air temperature is net radiation.

26 In dry forest areas, woody species can store large amounts of carbon in their biomass above

27 and below ground. The use of cacti can modify the local carbon budget when using tree crops

28 together. Therefore, the study highlights the complexity and severity of land degradation and

29 changes in CO_2, water, and energy fluxes in dry environments with areas of forest, grassland,

30 and cacti. Vegetation energy balance is also a critical factor, as these simulations are helpful

31 for use in forecasting weather or climate change. We also highlight the need for more studies

that address environmental conservation techniques and cactus in the conservation of degraded areas.

Keywords: Eddy covariance, gross primary productivity, energy balance method, semiarid, dry forest.

Introduction

The environments that have deficient climatic conditions, quite common to be seen in arid and semiarid locations in the world, are under increasing pressure, mainly due to climate change and anthropic factors. These areas are sensitive to climate vulnerabilities and are also prone to drought and land degradation events, and, in addition, water scarcity is a factor that significantly worsens the resilience of terrestrial ecosystems (Seidl et al., 2016; Spinoni et al., 2021). The processes of environmental degradation cause serious problems in the survival of plants and threaten food security. In addition, changes in land use/land cover can promote invaluable losses in biodiversity and affect natural resources. The main consequences of these disturbances mentioned above are the increase in the emission of greenhouse gases and the biogeochemical and biogeophysical changes in the landscapes (Ribeiro et al., 2016; Silva Junior et al., 2020; Guillen-Cruz et al., 2021; Jardim et al., 2022).

On a global scale, inappropriate land use and occupation practices in forest areas resulted in a decrease of 420 million hectares between 1990 and 2020. In addition, forests can store about 55% of environmental carbon due to species efficiency (Ahirwal et al., 2021), and one-third of all anthropogenic carbon emissions are a consequence of land use and land cover practices (Lai et al., 2016).

On the other hand, an important carbon sink in ecosystems is the soil (Rossel et al., 2014), and according to Menezes et al. (2021), when it comes to dry tropical forest, considering areas with dense Caatinga and sparse Caatinga (open vegetation) this carbon stock can vary from 72 to 76%, respectively. Furthermore, with changes in land use/land cover, the decrease or increase in agricultural and forest areas can impact available energy, carbon dioxide (CO_2) flux, surface albedo, and evapotranspiration (Bright et al., 2017; Liu et al., 2021b; Li et al., 2022). In addition to these factors, when there is a decrease in the leaf area of landscapes, there is a reduction in evapotranspiration and latent heat flux, resulting in

63 greater energy for heating the air and soil (Bright et al., 2017), which becomes an
64 environment of stressful conditions.

65   The interaction of the land surface with the boundary layer of the atmosphere
66 promotes energy gain and loss changes and, consequently, regulates climates through
67 biogeochemical and biophysical processes. The presence of different types of surfaces found
68 in biomes and ecosystems can significantly change the energy budget and, e.g., impact the
69 dissipation of heat and water in these locations (Huang et al., 2018). Forest species are
70 responsible for transferring 60 to 80% of soil water to the atmosphere through
71 evapotranspiration (Schlesinger & Jasechko, 2014; Hu et al., 2018). In addition to
72 evapotranspiration, variables such as net radiation, CO_2, sensible, latent, and soil heat fluxes
73 are essential for understanding energy feedback in ecosystems. However, partitioning the
74 energy, water, and CO_2 budget on a space-time scale in ecosystems often becomes onerous
75 and with some uncertainties (Baldocchi, 2003; Valayamkunnath et al., 2019). Methods such
76 as e.g., sap flow, eddy covariance, remote sensing, and energy balance (Maltese et al., 2018;
77 Dhungel et al., 2021; Chandel et al., 2021) are fundamental for determining mass and energy
78 fluxes in these areas.

79   In Seasonally Dry Tropical Forests such as the Caatinga (exclusive Brazilian biome),
80 due to its richness of endemic, arboreal, shrubby, herbaceous, and cactus species, several
81 studies are concentrated in this biome with stressful climatic conditions and high water deficit
82 (Teixeira et al., 2008; Silva et al., 2017; Campos et al., 2019; Santos et al., 2020). Such
83 interest may also be related to the loss of biodiversity resulting from prolonged droughts over
84 the years and anthropic disturbances (Campos et al., 2019; de Jesus et al., 2022). According
85 to the results of these studies (e.g., Schulz et al., 2016; Araújo Filho et al., 2018; Pereira et
86 al., 2020; de Oliveira et al., 2021), even under severe drought conditions, the Caatinga biome
87 remains an important carbon sink; however, prolonged drought and drier soil conditions can
88 cause aridification and, thus, reduce net primary production (NPP) levels and decrease the
89 carbon assimilation of its vegetation. In addition, changes in the energy exchange of soil-
90 vegetation-atmosphere interactions can change turbulent heat flux and thermal energy in the
91 soil. For example, during the dry season, Silva et al. (2017), in the Caatinga area (northeastern
92 region of Brazil), observed average net radiation and latent heat flux of 19.6 MJ m^{-2} day^{-1}
93 and 2.3 MJ m^{-2} day^{-1}, respectively. However, in the vegetation of cactus (*Opuntia ficus-*

94 *indica*), in a semiarid region of Italy, Consoli et al. (2013a) reported net radiation of 19 MJ

95 m^{-2} day^{-1}, partitioned into sensible and latent heat fluxes (9.3 MJ m^{-2} day^{-1} and 6.2 MJ m^{-2}

96 day^{-1}, respectively). Therefore, detailed knowledge of the responses of vegetation mass and

97 energy fluxes in interaction with meteorological conditions and terrestrial ecosystems on a

98 seasonal and annual scale is necessary.

99 The different photosynthetic metabolism (e.g., C3, C4, and CAM—crassulacean acid

100 metabolism) present in Caatinga biome species can influence carbon capture, gas exchange,

101 and energy balance (Silva et al., 2017; Hartzell et al., 2018; de Oliveira et al., 2020). In a

102 semiarid environment, C4 plants are predominant in pastures, because tropical grasses

103 commonly have a C4 photosynthetic pathway—assisting in the survival and cycling of water

104 and nutrients; on the other hand, CAM plants are present in pasture and forest areas, thus

105 representing 6% of vascular plants worldwide (Morgan et al., 2011; Holtum et al., 2016;

106 Nichols et al., 2016; Hartzell et al., 2018). However, despite significant carbon sequestration

107 and water use efficiency, CAM plants in agriculture are still neglected (Hogewoning et al.,

108 2021).

109 Thus, motivated by the existing gaps in the literature and anthropic influences on

110 energy and mass fluxes in deficient environments, we carried out this review work to

111 substantiate and quantify the energy balance in Caatinga and cactus areas in dry

112 environments. The objective of this review was to quantify the processes and changes of

113 energy fluxes, CO_2, and their interactions with the surfaces of terrestrial ecosystems in dry

114 environments.

115

116 **Literature review**

117 In this review article, we compiled and synthesized 152 peer-reviewed articles

118 published from 1983 to 2022 (Fig. 1). Our literature selection criterion was through keyword

119 combinations for each section described in the review: ("forest" OR "dry forest") AND

120 ("land-use" OR "pasture land-use") AND ("litterfall" OR "litter") AND ("climate" OR

121 "climate change") AND ("flux" OR "flux density") AND ("eddy covariance" OR "sonic

122 anemometer") AND ("CO2 fluxes" OR "CO2") AND ("CAM photosynthetic pathway" OR

123 "CAM pathway" OR "Crassulacean acid metabolism") AND ("trees" OR "shrubs" OR

124 "grassland") AND ("C4 plant", "C3 plant" OR "CAM plant") AND ("semiarid" OR

125   "semiarid landscape") AND ("cacti" OR "cactus"), "agricultural systems", "livestock",

126   "environmental   modeling",   "transpiration",   "photosynthesis",   "respiration",

127   "evapotranspiration", "sap flow", "energy balance", "carbon sink", "carbon source", AND

128   "remote sensing". In the present study, the literature search was performed using databases

129   from Google Scholar, ScienceDirect, Web of Science, and Scopus.

130
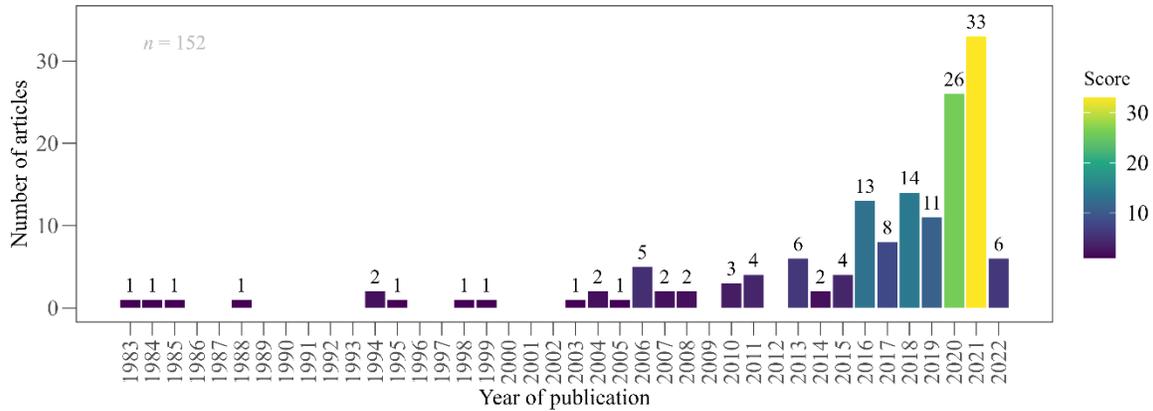
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132   **Fig. 1** Number of articles per year used in this study

133

134   We then created the sections that we will discuss throughout this review. Here, we

135   reviewed the broader set of literature to discuss Energy and mass fluxes in dry forest

136   environments. The next section deals with Methods of measuring fluxes in ecosystems, while

137   the last section reports on Carbon allocation and partitioning in ecosystems.

138

139   **Energy and mass fluxes in dry forest environments**

140   The arid and semiarid climates regions are characterized by low water availability

141   (e.g., in the soil and the atmosphere), high air temperature, and irregularity in the spatio-

142   temporal distribution of rainfall. These mentioned factors are key elements for the

143   understanding of climate change predicted for the coming decades (IPCC, 2021), and with

144   the increase of the global population, the demand for food grows, and the exploitation of

145   natural resources will be intensified, causing greater environmental damage. Furthermore, in

146   agricultural and/or forest ecosystems, abiotic factors such as, for example, drought and heat

147   are the main causes of death and deleterious damage to species, promoting a decrease in yield

148 and low photosynthetic performance, which leads to a reduction in food resources (Cook et
149 al., 2016; Esquivel-Muelbert et al., 2017; Ray et al., 2019; Rocha et al., 2020).

150   As a result of the increase in the frequency of occurrence and magnitude of drought
151 events in Brazil and the world, plant species have a high susceptibility to a decrease in leaf
152 area and/or death of individuals, which compromises their assimilation and allocation of
153 carbon (C) (Feldpausch et al., 2016; Rocha et al., 2020). In addition, the cumulative effects
154 of drought also cause physiological damage to crops that compromise their survival in
155 ecosystems (Feldpausch et al., 2016). Among natural phenomena with high complexity and
156 damage capacity, drought is one of the most dangerous, characterized by long water deficit
157 periods (Xu et al., 2019; Ding et al., 2021). Droughts can be subdivided into (i)
158 meteorological drought; (ii) hydrological drought; (iii) agricultural drought; and (iv)
159 socioeconomic drought (Yao et al., 2020; Ding et al., 2021) (Fig. 2).

160
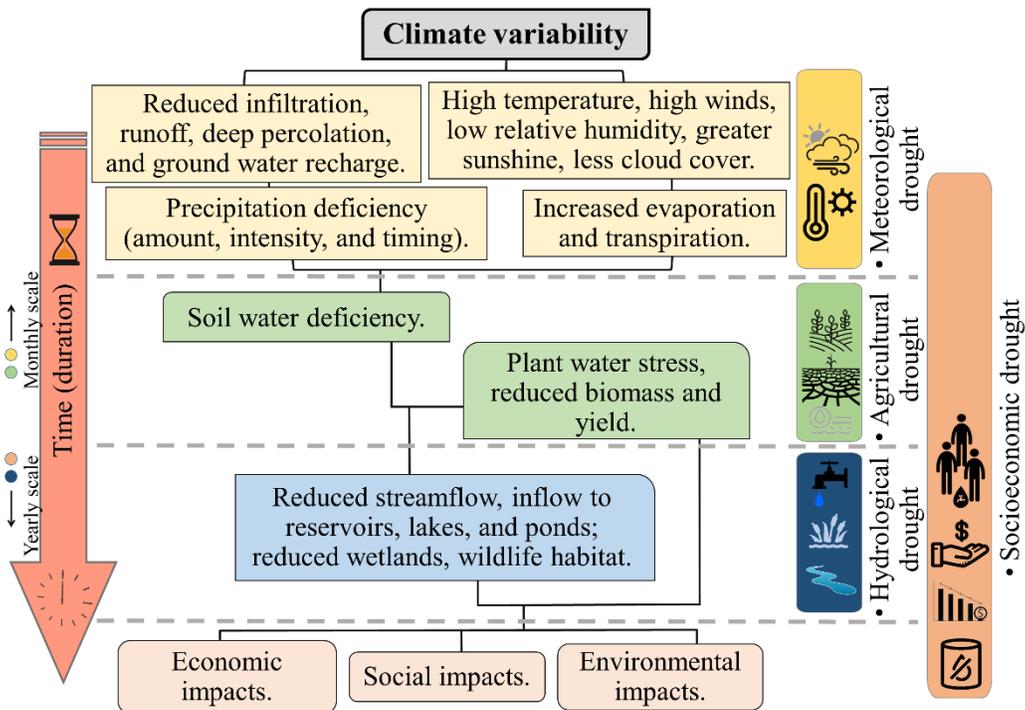
161
162 **Fig. 2** Flowchart of the four types of drought and their main intrinsic relationships to social
163 and environmental impacts

164

165   The damage from droughts becomes more aggravating, and this occurs mainly due to
166   lower availability and access to water, even when the years are not of climatic anomalies.
167   When there is a prolonged water shortage, a meteorological drought can become a
168   hydrological drought, consequently causing agricultural and socioeconomic damage to the
169   population (Xu et al., 2019; Guo et al., 2020; Noorisameleh et al., 2020). In low-latitude
170   forests with hostile climates (i.e., arid and semiarid), heat stress and drought cause changes
171   in atmospheric water demand, causing species to change their transpiration capacity (Liu et
172   al., 2013; Hu et al., 2018) and, consequently, changes in the net productivity of the ecosystem
173   (Cavaleri et al., 2015).

174   Particularly, species from forest ecosystems are responsible for transferring 60 to 80%
175   of the water from the soil to the atmosphere by evapotranspiration (Schlesinger & Jasechko,
176   2014; Hu et al., 2018); however, these quantities are smaller when reporting to areas of dry
177   forest—Caatinga. Low-latitude tropical forests play a key role in the planet's vegetation cover
178   rates (15% of the Earth's surface) and, in addition, contribute significantly to soil carbon
179   stocks and atmospheric carbon fluxes (Cavaleri et al., 2015). The mass and energy fluxes in
180   these environments undergo changes in the rainy and dry seasons, mainly controlled by
181   weather and vegetation conditions, respectively (Silva et al., 2017).

182   Places with arid and semiarid climates undergo changes both in the distribution and
183   in the amount of rainfall. In particular, these climates occur in different parts of the world
184   and have high water scarcity and economic losses (Mady et al., 2020). The Brazilian semiarid
185   region is characterized as one of the most populous semiarid areas worldwide (Lindoso et al.,
186   2018). In northeastern Brazil, a region that covers a large part of the Brazilian semiarid region
187   and, consequently, the Caatinga biome, there is significant rainfall variation in rainfall events
188   (500 to 2,000 mm year^{-1}). This is because the region suffers from meteorological phenomena,
189   e.g., El Niño-Southern Oscillation (ENSO), Sea Surface Temperature (SST) anomalies, and
190   Inter-Tropical Convergence Zone (ITCZ) (Nobre et al., 2006; Marengo & Bernasconi, 2015;
191   Marengo et al., 2020). In addition, it has a high air temperature, an aridity index of up to 0.5,
192   a risk of drought above 60%, and a high incidence of solar radiation, causing a decrease in
193   soil moisture, and increasing the possible levels of stress for the species (Nobre et al., 2006;
194   Marengo & Bernasconi, 2015; Marengo et al., 2020). The Caatinga biome has 6,053 species
195   in its flora (Jacob et al., 2020), of which 4,657 are angiosperms, and 913 are endemic

196   (Bonatelli et al., 2021). Its ecophysionomy consists of xerophilous plants with different
197   growth habits and succulent and deciduous plants, which provides tolerance to environmental
198   stresses (Jacob et al., 2020; Bonatelli et al., 2021).

199   Furthermore, in areas of Caatinga (Brazilian Seasonally Dry Tropical Forest), the
200   relationship with the vegetation surface and the atmospheric conditions, e.g., in the rainy and
201   dry season, cause instability to close the surface energy balance. However, in this type of dry
202   forest, when partitioning the energy balance components in the rainy season, the results are
203   more satisfactory, and an excessive conversion of net radiation into sensible heat flux (H) is
204   common (Teixeira et al., 2008; Silva et al., 2017; Campos et al., 2019; Santos et al., 2020).

205   In rainy periods with low values of the vapor pressure deficit, the vegetation increases
206   its evapotranspiration due to the atmospheric gradient that helps in greater stomatal openings.
207   In this way, the meteorological conditions control the fluxes (Silva et al., 2017; Campos et
208   al., 2019), making the vegetation respond to water availability in the soil-atmosphere system
209   (Marques et al., 2020). In dry seasons, there is a leaf fall (i.e., caducifolia—leaf habit of
210   perennial or deciduous species) in most of the species that make up the Caatinga. This type
211   of adaptive mechanism helps in the resistance and resilience of the ecosystem, drastically
212   reducing gas exchange and water consumption (Silva et al., 2017; Santos et al., 2020;
213   Marques et al., 2020) since tropical forests are commonly exposed to long periods of water
214   deficit (Tan et al., 2019; Borges et al., 2020).

215

Methods of measuring fluxes in ecosystems

217   The vegetation removal and environmental disturbances are responsible for altering
218   heat and water's energy exchange in natural ecosystems and agricultural areas. For example,
219   anthropogenic actions have caused the massive removal of native forests, transforming them
220   mainly into agricultural cultivation areas. This type of practice alters the biophysical
221   exchanges with the atmosphere, making it necessary to measure the magnitude of these
222   changes to understand the process better (Antongiovanni et al., 2020). Among the various
223   methods of measuring and/or estimating mass and energy flows in the literature, the
224   following stand out: (1) sap flow, (2) eddy covariance, (3) remote sensing, and (4) energy
225   balance (Maltese et al., 2018; Dhungel et al., 2021; Chandel et al., 2021). All these methods

226 are essential for determining evapotranspiration (ET) from natural/artificial forest
227 ecosystems and irrigated/rainfed agricultural areas.

228

229 *Sap flow method*

230   Sap flow is a technique often used in conjunction with another method, e.g., eddy
231 covariance. The application of the sap flow method consists of measuring transpiration of the
232 species by thermal dissipation probes. For this, soil evaporation data must also be quantified
233 with mini-lysimeters and, thusly, the evapotranspiration of the system is determined. Probes
234 are inserted into the xylem in the trunk or stem region and quantify the sap velocity and heat
235 pulses. The probes are similar to needles, which are inserted in parallel into the trunk/stem
236 of trees at breast height (~1.30 m) or above the buttress roots (i.e., roots exposed above the
237 soil surface) (Fig. 3).

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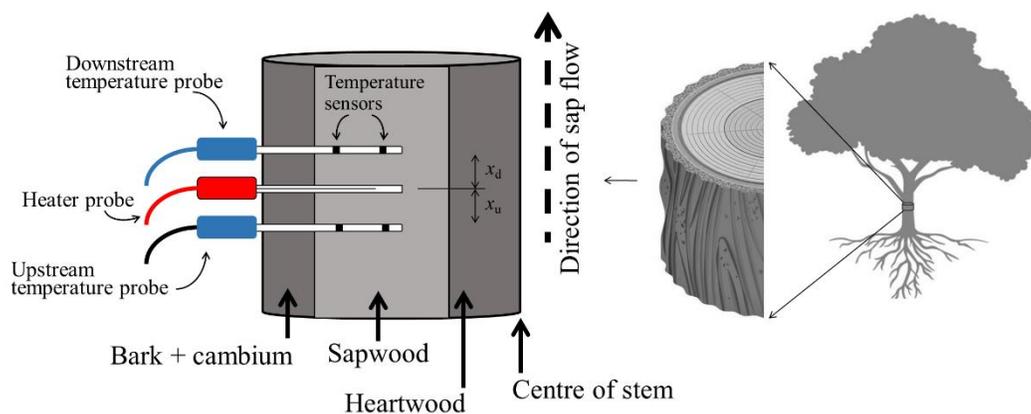
239

240 **Fig. 3** Diagram of the sap flow meters and heat-pulse probes implanted radially into a stem.
241 The upstream temperature sensor is installed at a distance x_u below the heater, and the
242 downstream sensor at a distance x_d above the heater

243

244   Despite being a usual method, some care should be taken, such as sensor calibration
245 for the studied species (Williams et al., 2004; Consoli & Papa, 2013; Fuchs et al., 2017; Link
246 et al., 2020). The tangential and axial distances of the sensors are crucial since they are
247 inserted in the equations for quantifying the flows. When opening a fissure in the trunk to
248 install the probe in the sapwood, one must avoid obstruction of the flow at the site and not
249 excessively damage the fibers (Barrett et al., 1995; Moore et al., 2010; Wullschleger et al.,

250 2011; Vandegehuchte & Steppe, 2013). According to Barrett et al. (1995), damage caused in

251 the installation of the sensor alters the axial direction of the flow; and in the short and long

252 term, these injuries can cause problems in the dissipation of heat flow in the wood (Moore et

253 al., 2010; Wullschleger et al., 2011). This is also caused by disruption of xylem vessels,

254 causing anatomical changes and negatively influencing physiological processes such as

255 transpiration.

256 The sap flow has an intimate connection between the water and hydraulic

257 relationships of plants with the atmosphere. This energy gradient promotes the transpiration

258 flow of species and contributes to the hydrological cycle. About 45,000 km^3 of water per

259 year is transpired by terrestrial vegetation (Poyatos et al., 2021). Mathematically, the sap

260 flow density can be determined by equations that relate heat and humidity in the sapwood

261 region (Equations 1 and 2) (Granier, 1985; Vandegehuchte & Steppe, 2013). Thus, to

262 consolidate the plant's water relationships, the daily water use per tree (kg day^{-1}) can be

263 applied to understand water consumption by multiplying the sap flow density by the sapwood

264 area (Kotowska et al., 2021).

265

266
$$SFD = \frac{\rho_d}{\rho_s} + \left(MC + \frac{c_{dw}}{c_s} \right) \cdot V_h \qquad (1)$$

267
$$F_d = \alpha \cdot K^{\zeta} \qquad (2)$$

268

269 where SFD and F_d are the sap flux densities (m^3 m^{-2} s^{-1} and g m^{-2} s^{-1}, respectively), ρ_d is the

270 dry density of the sapwood (kg m^{-3}), ρ_s is the density of the sap (assumed to be the density

271 of water of 1,000 kg m^{-3}), MC is the sapwood water content (i.e., considering the weight of

272 water over dry weight of wood), c_{dw} is the specific heat capacity of the woody matrix (1,200

273 J kg^{-1} K^{-1} at 20 ºC), c_s is the specific heat capacity of the sap (using the water, 4186 J kg^{-1}

274 K^{-1} at 20 ºC), V_h is the heat velocity (m s^{-1}), α and ζ are the coefficients dependent on the

275 amount of heat applied proposed by Granier (1985), and K is the dimensionless sap flow

276 index (i.e., $K = \frac{(\Delta T_o - \Delta T)}{\Delta T}$, where ΔT_o is the maximum temperature difference (ºC) between the

277 two sensor needles, when there is no sap flow or minimum sap flow, and ΔT is the

278 temperature difference at a given time).

279

280   Particularities between sap flows were observed by Kotowska et al. (2021), where
281   species with higher hydraulic efficiency have significantly higher flow. In addition, medium-
282   sized plants in the same area had no direct effect on this efficiency, and the environment was
283   an expressive controller of the hydraulic gradient, with these characteristics being
284   differentiated in wet and dry forests. Goldsmith (2013) encourages that the analysis of this
285   variable and the observations in the soil-plant-atmosphere system should be correlated due
286   to the intrinsic relationships between them.

287

288   *Eddy covariance method*

289   Another widely used method, with several monitoring towers worldwide, is the eddy
290   covariance method, capable of directly measuring vertical turbulent flows from different
291   surfaces. This method quantifies the fluxes of energy and gases, e.g., methane (CH_4), nitrous
292   oxide (N_2O), carbon dioxide (CO_2), and water vapor, between the biosphere and the
293   atmosphere (Moffat et al., 2007; Rannik et al., 2016). At the canopy-atmosphere interface,
294   the sensor daily, on a daytime and night-time scale, quantifies the net exchange of CO_2 in the
295   ecosystem employing an infrared gas analyzer. Despite its expressive use in several
296   agricultural and forestry land areas, the method is criticized due to errors or uncertainty of
297   fluxes not fully accounted for within and below the sensor field, and horizontal advection,
298   which makes it difficult to interpret the fluxes (Baldocchi, 2003; Loescher et al., 2006; Xu et
299   al., 2018b; Levy et al., 2020) (Fig. 4).

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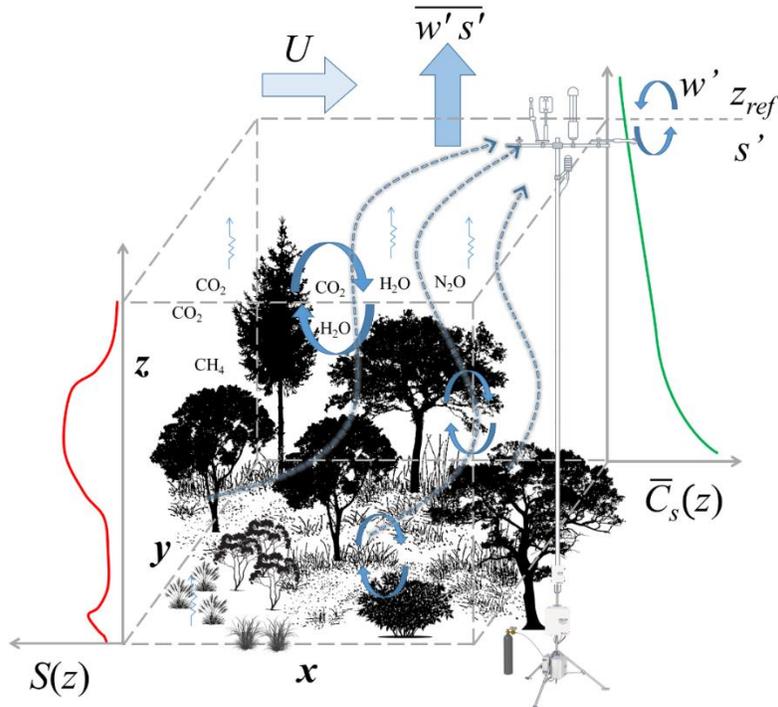
Fig. 4 Schematic view of a monitoring tower with eddy covariance. Local-scale measurements of flows are made directly in situ

In Fig. 4 the vertical turbulent flux of mass and energy is quantified at the reference height (z_{ref}), referring to all sources and sinks [$S(z)$] in the ecosystem of the study area (i.e., range area represented by the grey dotted line), which can be calculated by integrating $\overline{w's'}(z_{ref}) = - \int_{z=0}^{z_{ref}} S_s(z)$, where $\overline{w's'}$ is the covariance between wind speed fluctuations and the corresponding perturbations in a scalar concentration. The correlated eddies of vertical wind speed (w') and scalar concentration (s') are responsible for transporting mass and energy vertically. $\overline{C}_s(z)$ is the schematic concentration profile of the area (Baldocchi, 2003; Loescher et al., 2006; Xu et al., 2018b; Levy et al., 2020).

As with any method of quantifying energy and mass fluxes, this one has pros and cons. Among the several existing advantages, the main ones are: it is not a destructive method (i.e., it does not cause disturbances in vegetation and soil), which thus demands a lower workload and can be used on large scales, in addition to being a method independent. However, when applied in places with unstable atmospheric conditions and uneven terrain, the readings have low accuracy and/or coherence (Billesbach, 2011; Yuan et al., 2019),

mainly due to absent advection fluxes and energy instability surface, which is considered a disadvantage (Baldocchi et al., 1988), given that quantifying this flow is a difficult task, as it requires having several towers in the same site (Xu et al., 2020; Matthews and Schume, 2022).

However, in the last two decades, the eddy covariance technique has still been one of the most important in determining fluxes in arid, semiarid, and humid ecosystems. Studies carried out in riparian cottonwood forests in Lethbridge, Alberta, Canada by Flanagan et al. (2017) and Flanagan et al. (2021) have indicated that the energy budget of latent and sensible heat fluxes was satisfactory and with good results. According to the authors, such flux variations were driven by the availability of energy in the ecosystem and acted as CO_2 sinks in the growing season. In this season, the energy consumed by plants for their physiological activities increases; on the other hand, the net energy present in the environment decreases (Xue et al., 2021).

Currently, some flux networks can be accessed to acquire energy budget data between the biosphere and atmosphere, e.g., the National Observatory of Water and Carbon Dynamics in the Caatinga Biome (NOWCDCB), AmeriFlux, FluxNet, CarboEuroFlux, FluxNet-Canada, among others. The towers for monitoring the variables of turbulent fluxes of CO_2, sensible heat, and latent heat, are equipped with an eddy covariance system. Installed in towers above the surface, e.g., forest canopy and cropland, the basic equipment is an open-path, infrared gas analyzer—IRGA (for quantification of CO_2 and water vapor) and three-dimensional sonic anemometer (i.e., to quantify wind direction and speed), connected to a datalogger (Niu et al., 2021). It is worth mentioning that installing other micrometeorological sensors is of paramount importance for quantifying environmental variables. For example, in Brazil, NOWCDCB has ensured monitoring in several areas of the Caatinga biome, providing data on carbon stocks and fluxes from this ecosystem (e.g., Mendes et al., 2020, 2021; Menezes et al., 2021; Costa et al., 2022).

The absorption of energy by the surface in the layers close to the ground is one of the factors responsible for generating the turbulent movements of the energy flux. The upward and downward movement of air that forms inside and above the canopy carries particles with different vertical speeds up and down in the form of eddies (Fig. 4). On a diurnal scale, CO_2 fluxes are represented by the net exchange of carbon from photosynthesis (i.e., consumption

350   of CO_2) and ecosystem respiration (i.e., the release of CO_2 to the environment). In respiration,

351   a process that occurs mostly at night, autotrophic (e.g., roots, stems, leaves) and heterotrophic

352   respiration (e.g., soil-dwelling microorganisms) predominate, occurring simultaneously.

353   Thus, knowing the concentration of CO_2 and the vertical velocity of the air parcels, we can

354   determine the vertical flux (Equation 3) (Burba and Anderson, 2010; Velasco & Roth, 2010).

355

356
$$F = \overline{c' \cdot w'} = \frac{1}{n} \sum_{i=1}^{n} \left(w_i' \cdot c_i' \right) \tag{3}$$

357

358   where F is the turbulent vertical flux of CO_2, $\overline{c'}$ is the covariance between the instantaneous

359   deviations of the CO_2 concentration, $\overline{w'}$ is the covariance between the instantaneous

360   deviations from the vertical wind speed, and n is the number of samples during the averaging

361   time. For example, F is expressed in units of mass per area and time (g m^{-2} s^{-1}) or equivalent

362   units, with mass being expressed in micromoles ($\square$mol), grams of CO_2 (g), or grams of

363   carbon (g C), the area in m^2, ha or km^2, and the time in seconds, hours, days or years.

364

365   It is important to emphasize that the footprint (i.e., part of the surface that contains

366   the source and sinks elements that contribute to the vertical flux) of the constituent gases in

367   the atmosphere in which it is intended to be analyzed must contain a large and homogeneous

368   surface. According to Grimmond and Oke (1999), it can be 100 to 300 times the height of

369   the analyzed surface in urban areas (e.g., with buildings); in a forested area, Rebmann et al.

370   (2005) reported minimum requirements of 50 to 100 m roughness lengths. In an agricultural

371   field, Arriga et al. (2017) used a measurement height of 2.35 m above the canopy, whose

372   vegetation had a height of 1.0 m. This characteristic helps the dataset, not present

373   inconsistency problems, also known as noise (Velasco & Roth, 2010). Hence, other methods

374   can be applied to measure fluxes in ecosystems.

375

376   *Remote sensing-based surface energy balance*

377   On a space-time scale, remote sensing data are applied to quantify fluxes in forest and

378   agricultural areas. This tool, which in different spatial resolutions has open access to images

379   and is very useful for quantifying energy balance components; as well as their interactions

380 with water scarcity phenomena in the atmosphere and soil. The spectral monitoring of the

381 canopy and the unification of meteorological variables are essential data for model inputs

382 (Saleska et al., 2016; Liu et al., 2021a). Models such as SEBAL (Surface Energy Balance

383 Algorithm for Land), METRIC (Mapping EvapoTranspiration at high Resolution with

384 Internalized Calibration), and SEBS (Surface Energy Balance System) are the main

385 algorithms used in remote sensing to quantify energy fluxes (Allen et al., 2011; Wagle et al.,

386 2017; Mokhtari et al., 2021). With the images in hand, the principle consists of identifying

387 cold and hot pixels, and through interactive methods, the fluxes on the surface are determined

388 (Allen et al., 2011).

389   The application of remote sensing techniques in the determination of fluxes has been

390 gaining strength over the years due to the practicality and low cost of application. For the

391 determination of turbulent flows on the surface, the technique is based on the use of auxiliary

392 surface parameters (e.g., albedo, emissivity, relief, vegetation cover index, leaf area index,

393 land surface temperature, among others), as well as, latent heat fluxes, sensible heat, soil heat

394 flux and evapotranspiration can be determined (Shang et al., 2020; Nisa et al., 2021). Using

395 observational data from FLUXNET, Bodesheim et al. (2018) were able to quickly and

396 accurately determine the global latent heat flux through remote sensing. In addition, recent

397 studies have reported that the use of methods that integrate data from towers and remote

398 sensing products can help to improve the accuracy of energy flux determination on a global

399 scale and that they also help to reduce the dissimilarity of results obtained individually

400 (Bodesheim et al., 2018; Xu et al., 2018a; Shang et al., 2020).

401   In a study carried out by de Oliveira et al. (2022), using data from the Moderate

402 Resolution Imaging Spectroradiometer (MODIS), for the application of remote sensing,

403 together with data monitored by in situ flux towers over Caatinga areas, were fundamental

404 for the quantification of gross primary production (GPP). Also, according to the authors, the

405 MODIS products, i.e., GPP and ET, showed high accuracy (about 60%) on a vegetated

406 surface with Caatinga. Since this biome has intrinsic characteristics and endemic species,

407 monitoring the GPP helps to understand the behavior of CO_2 exchanges in this ecosystem

408 (Costa et al., 2022). Furthermore, carbon and water fluxes vary across most surfaces; for

409 example Costa et al. (2022) observed more intense seasonal changes in GPP in sites with

410 Caatinga and Pantanal than in Amazon and Cerrado (Brazilian Savanna). Due to this,

411 monitoring vegetation with high frequency and low cost in different parts of the world makes
412 MODIS a widely used sensor (MacBean et al., 2018). On the other hand, there are advantages
413 and disadvantages to MODIS. As a disadvantage, it has a large resolution, and, as an
414 advantage, it has daily periodicity and spectral sensitivity, which helps in the application of
415 energy balance, analysis of vegetation indices, and quantification of GPP (Wu et al., 2008;
416 MacBean et al., 2018; Yao et al., 2018).

417   The surface energy balance can be measured independently using sensors or
418 estimated using equations on an ecosystem scale. The energy components of this application
419 result in net radiation (R_n), from which the latent heat flux (LE), sensible heat flux (H), and
420 soil heat flux (G) are partitioned (Wagle et al., 2017; Mauder et al., 2020). However, the
421 instrumentation used to measure mainly the LE component is not always applicable or
422 accessible. Thus, this variable was quantified in several studies by the simplified energy
423 balance residue, i.e., $LE = R_n − G − H$ (Wagle et al., 2017; Chen and Liu, 2020; Mauder et
424 al., 2020; Castellví et al., 2020). In addition, there are other terms linked to energy
425 represented in the canopy and energy used in the process of photosynthesis, but no more than
426 2% in these types of ecosystems (Heilman et al., 1994; Allen et al., 1998). The LE is the
427 energy associated with water vaporization and evapotranspiration; R_n is the energy from the
428 atmosphere and the surface of the soil-canopy system (i.e., converted into thermal energy or
429 long-wave and short-wave heat); G is the soil heating energy, and H is the energy available
430 for heating the air. These parameters mentioned above are fundamental for the occurrence of
431 gas exchange in plants (Fig. 5).
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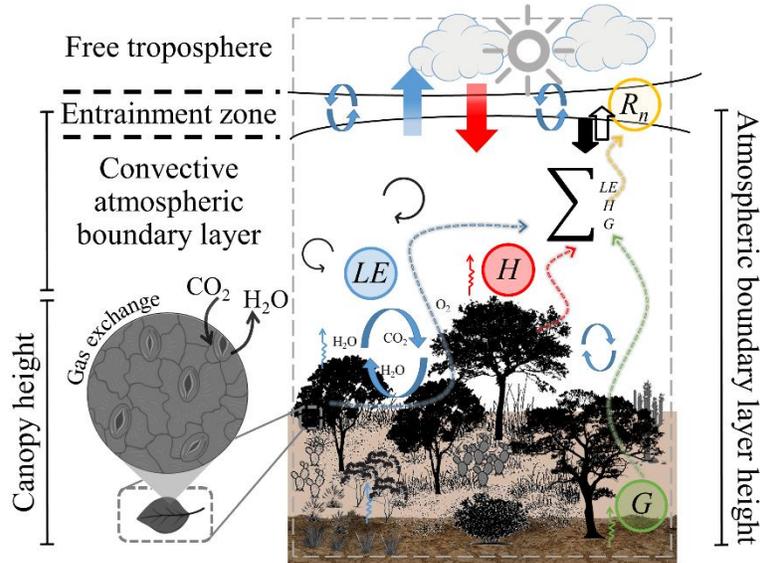
Fig. 5 Diurnal interactions between latent heat fluxes (*LE*), sensible heat (*H*), soil heat (*G*),
and net radiation (R_n) in a Brazilian Seasonally Dry Tropical Forest (Caatinga). The dashed
arrows in blue, red, and green colors are contributors to the energy balance. Note: in this
flowchart, we do not show the influence of horizontal advection, which also affects the
atmospheric boundary layer.

439

In the transfer of energy from surfaces, there are variations in heat fluxes according
to vegetation, soil exposure, and local humidity (Faridatul et al., 2020). In areas with Caatinga
and agriculture, net radiation presents lower results (< 20%) when compared to areas of
exposed soil, in which this variation ranges from 25 to 30%. On vegetated surfaces, energy
transfer to the atmosphere during the day is slower, conserving it for a longer time (Lima et
al., 2021). One of the variables that mostly contributes to air temperature variation is net
radiation due to the energetic contribution of *LE* and *H*. According to Oliveira et al. (2006),
values lower than 25 MJ m^{-2} day^{-1} of global solar radiation were observed at times with
milder temperatures (~24 ºC), and 28.5 MJ m^{-2} day^{-1} when the temperature was higher
(above 30 ºC), in the Caatinga area. In contrast, Silva et al. (2017) found R_n values in the
Caatinga of 19.6 MJ m^{-2} day^{-1}, soil heat flux ranging from 0.01 to 1.07 MJ m^{-2} day^{-1}, and
in the dry and rainy season, the average *LE* was 2.3 MJ m^{-2} day^{-1} and 4.8 MJ m^{-2} day^{-1},
respectively.

453   Unfortunately, in areas with expressive vegetation of cactus species, this information

454   is still developing in the literature. Under arid conditions in the Atacama Desert, Kalthoff et

455   al. (2006) evaluated the heat fluxes of mixed areas, with the presence of irrigated agriculture

456   (e.g., viticulture), shrub, and cacti. Also, according to the authors, sensible heat throughout

457   the year was more prominent than latent heat, with sensible heat being the largest dominant

458   energy sink during the day. In the semiarid region, in *O. ficus-indica* cultivation (Consoli et

459   al., 2013a), they observed net radiation of 19 MJ m^{-2} day^{-1}, part of which was destined for

460   *H* (9.3 MJ m^{-2} day^{-1}) and *LE* (6.2 MJ m^{-2} day^{-1}), corresponding to 49 and 33%, respectively.

461   Furthermore, Consoli et al. (2013b) reported that the heat flux in the soil during the cactus

462   growth period presented very low values, close to zero. Interestingly, this energetic partition

463   is similar to the Caatinga, perhaps due to resistance to water deficit and stomatal regulation.

464   In cacti, the sensible heat flux may also be higher due to atmospheric instability, causing

465   convection to become efficient and transfer more energy to this component (Consoli et al.,

466   2013b).

467   The variability of available energy is notorious, whether in Caatinga ecosystems or

468   with cacti. In Caatinga, greater expressiveness was reported throughout the year for sensible

469   heat flux (Teixeira et al., 2008; Borges et al., 2020), and in cactus, this similarity of flux

470   occurs in cactus—*Opuntia* (Consoli et al., 2013b), as well as in columnar cactus—*Carnegiea*

471   *gigantea* (Flanagan and Flanagan, 2018). Although, the sensible heat flux has greater

472   magnitudes in the rainy season; this caveat is also valid for the soil heat flux (Teixeira et al.,

473   2008; Consoli et al., 2013b; Flanagan and Flanagan, 2018).

474   Among the components of the simplified surface energy balance, the soil heat flux

475   (*G*) is an often neglected constituent (Heusinkveld et al., 2004). However, this variable is

476   closely related to plants and the atmosphere. Under arid climate conditions, Saito et al. (2006)

477   pointed out that the bare soil has its heat and water fluxes affected. In forest areas, the

478   variability of flows may be linked to soil characteristics, canopy density of species and root

479   biomass heterogeneity, factors that mainly alter the flux of carbon dioxide in the soil

480   (Kulmala et al., 2019; Palmroth et al., 2019). In addition, changes in land use and land cover

481   can modify the local hydrological dynamics, as well as influence ecosystem services.

482

483 **Carbon allocation and partitioning in ecosystems**

484   In vegetated areas, despite advances in monitoring and carbon partitioning of
485 ecosystems, there are still uncertainties related to these processes. Carbon emission and/or
486 capture have a significant relationship with the global carbon balance in terrestrial
487 ecosystems. One of the most relevant variables in the carbon balance is the net ecosystem
488 CO_2 exchange (NEE), which is simply determined through gross primary productivity (GPP)
489 and ecosystem respiration (R_{eco}) (Table 1). The NEE can be quantified independently of the
490 photosynthetic metabolism of the species (e.g., C3, C4, and CAM—crassulacean acid
491 metabolism; see Fig. 6); however, each metabolism has its particularities. Furthermore, as it
492 is a CO_2 balance, NEE must be measured on a day and night scale since there is a daytime
493 CO_2 uptake from C3 and C4; however, in CAM, there is a predominance of nocturnal uptake
494 of atmospheric CO_2. Thus, the GPP corresponds to photosynthesis (i.e., it is the amount of
495 carbon absorbed by the vegetation), and the R_{eco} refers to the sum of carbon efflux from the
496 respiration of autotrophic and heterotrophic organisms (Zanotelli et al., 2015; Campioli et
497 al., 2016; Schimel & Schneider, 2019).

498

499 **Table 1** List of equations for estimating the carbon balance in ecosystems and relevant
500 components

Equation	Source
$NEE = -GPP + R_{eco}$	(Schimel & Schneider, 2019)
$GPP = NPP + R_a$	(Campioli et al., 2016)
$R_{eco} = R_a + R_h$	(Campioli et al., 2016)
$NEP = GPP - R_{eco} = NPP - R_h$	(Campioli et al., 2016)
$NECB = NEP + OF - FH$	(Zanotelli et al., 2015)
$CUE = \dfrac{NPP}{GPP}$	(Zanotelli et al., 2015)

where NEE is the net ecosystem CO_2 exchange, GPP is the gross primary production, R_{eco} is the ecosystem respiration, NPP is the net primary production (quantified above- and belowground), R_a is the autotrophic respiration (quantified above- and belowground), R_h is the heterotrophic respiration from soil and coarse woody debris, NEP is the net

ecosystem production, NECB is the net ecosystem carbon balance, *OF* are the organic fertilizers, *FH* is the fruit harvest, and CUE is the carbon use efficiency.

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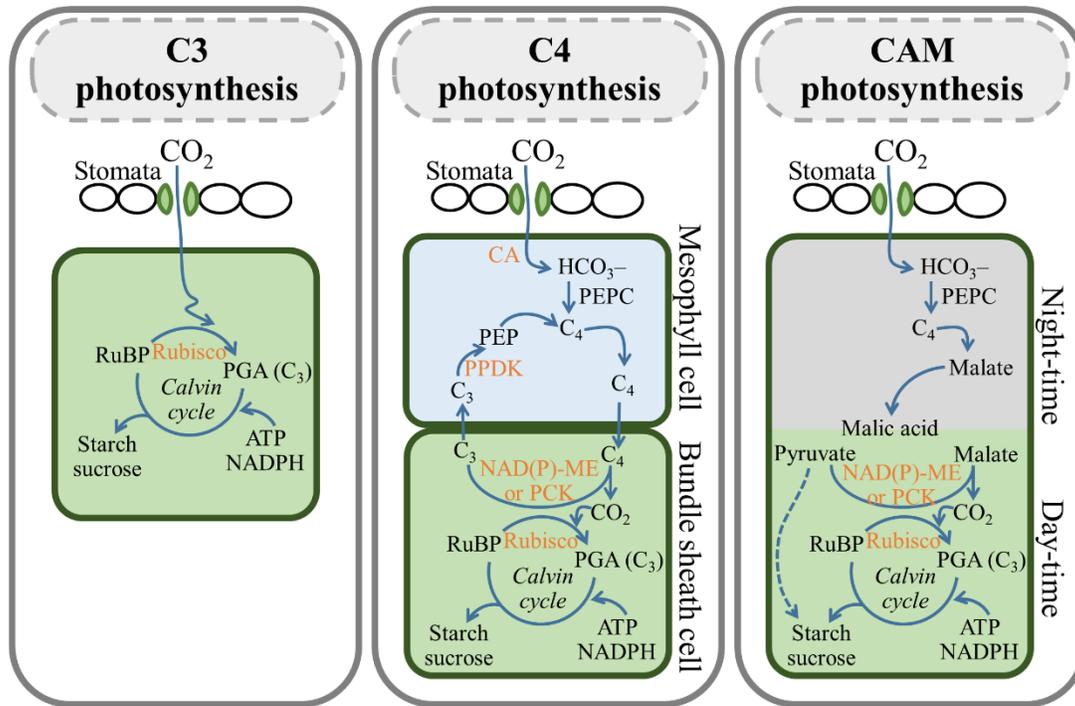
502

503 **Fig. 6** Carbon pathway in the photosynthetic metabolism of C3, C4, and CAM plants
504 (crassulacean acid metabolism)

505

506   The carbon assimilation carried out by the species is fundamental for determining the
507 productivity of the crop or biome. With the plant's carbon budget, we can determine the net
508 biome production (i.e., $NBP = -NEE - Yield - \varepsilon$), where Yield is harvested crop yield, and
509 ε is the carbon losses caused by disturbances, e.g., fires. Net biome production (NBP) results
510 are positive and negative scale, indicating that the environment can be a carbon source or
511 sink (Pecchioni et al., 2020; Zhou et al., 2021). In pasture areas under semiarid conditions,
512 biotic and abiotic factors can compromise the carbon balance. For example, water deficit and
513 air and soil temperature cause heat stress on plants and soil microorganisms, negatively
514 altering the carbon exchange capacity of the ecosystem (Wang et al., 2019).
515   Major differences exist between the photosynthetic and transpiration rates of C3, C4,
516 and CAM plants. CAM species have substantially higher efficiency in carbon assimilation

than species performing C3 or C4 photosynthesis. However, even with high carbon utilization, CAM plants in agriculture are still neglected (Hogewoning et al., 2021). On the other hand, cactus cultivation goes beyond the use of fruits and cladodes to feed humans and animals. In environmental and economic matters, the stock of carbon in the soil has been an efficient alternative (Bautista-Cruz et al., 2018), and it is worth noting that on average, 36.2% of the cladode of *Opuntia* is composed of carbon, with one adult plant is capable of fixing 8.29 kg of CO_2 per year (Gomez-Casanovas et al., 2007). Considering 1 hectare of *Opuntia ficus-indica*, carbon fixation can reach 63.25 kg day^{-1} (Andreu-Coll et al., 2020). These carbon fixation values may vary depending on environmental conditions, agricultural practices, the number of cladodes per plant, and cultivation density. The carbon present in the *Opuntia* structures can be used to produce substrate for bacteria that help in the fermentation of biomass to produce biogas (Quiroz et al., 2021). Despite the high capture and use of CO_2, cactus cultivation can be stimulated for agricultural areas as a carbon credit. However, there are still uncertainties about the carbon balance in areas cultivated with these plants.

Factors controlling variation in carbon dioxide efflux from surface litter

In forested areas, woody species can store large amounts of carbon in their above- and below-ground biomass. Therefore, the implementation of forests as a CO_2 sequester has low costs between 10 USD to 68 USD t CO_2-eq (López-Pacheco et al., 2021). In the Caatinga area under semiarid conditions, Silva et al. (2017) reported uptake of 2.82 t C ha^{-1} year^{-1}, and in pasture 3.62 t C ha^{-1} year^{-1}. In pastures in the Cerrado, results of 842 g C m^{-2} year^{-1} were observed (Arruda et al., 2016), and according to Ferreira et al. (2020) in Caatinga, it is 4.63 g CO_2 m^{-2} day^{-1} (is equal to 461 g C m^{-2} year^{-1}, for reference, 1 g C = 0.083 mol CO_2 = 3.664 g CO_2). The lowest values of CO_2 uptake generally occur in the dry season in the Caatinga, this is due to the fall of leaves, a phenomenon that does not occur in pastures. On the other hand, deciduous leaves do not occur in the cactus, giving the plant absorption of CO_2 throughout the year, keeping the carbon stored efficiently.

In the interaction of the soil-plant system, one of the main contributors to the natural return of carbon to the soil is litterfall. The litter material comes from the forest and crops debris, which, in turn, are deposited on the soil and subsequently decomposed by soil-

548 dwelling microorganisms, jointly aided by environmental conditions (Fig. 7). In this way,

549 carbon is maintained in the soil, and plants benefit by supporting vegetative growth (Fang et

550 al., 2015; Riutta et al., 2021). However, the quantity and quality of these deposited materials

551 are crucial for the carbon balance. As reported by Fang et al. (2015), the greater the litterfall

552 inflows into forest areas, there is an increase in the loss of litter mass and constituted carbon.

553 This type of characteristic may be due to the accelerated decomposition of the material and

554 available nutrients, increasing soil respiration and, consequently, CO_2 emission.

555
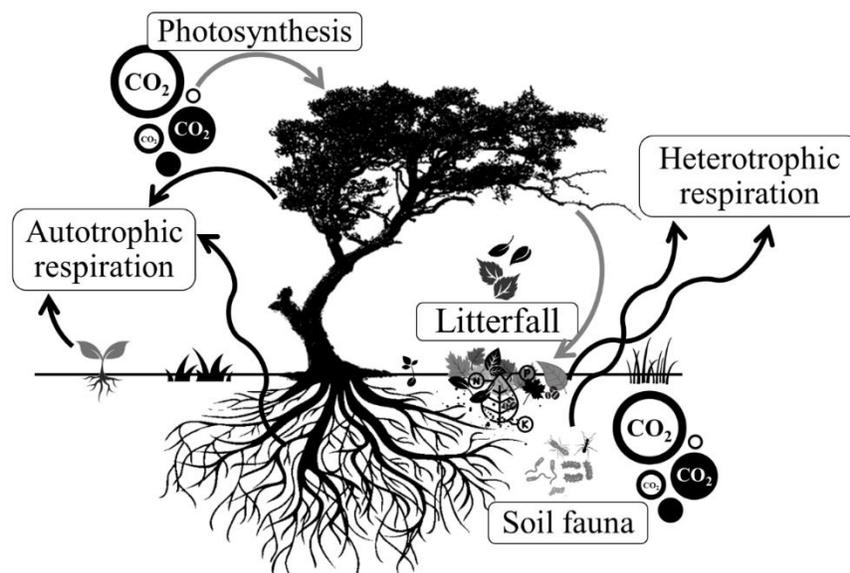
556

557 **Fig. 7** Conceptual diagram illustrating litter components and carbon dioxide (CO_2) emissions

558 through autotrophic and heterotrophic respiration in a forested area

559

560 Therefore, whether in planted or natural forest areas, the losses of litter mass and

561 carbon contained in it are differentiated. In addition, not only due to debris deposited in the

562 soil, but environmental conditions exert seasonality in the emission of CO_2 and respiratory

563 flux of the ecosystem. Fang et al. (2015) observed that in seasons with warm-wet conditions,

564 there were higher soil respiration rates when compared to cool-dry seasons. In areas with

565 cactus and legume agroforestry systems, variations in carbon content and soil respiration

566 were also observed (Camelo et al., 2021). Also, according to the authors, climatic conditions

567 influence these variables, and plants with CAM metabolism, despite the lower contribution

568 with canopy debris, help deposition plant material from the root system (De León-González

569   et al., 2018; Camelo et al., 2021). In addition, this root system in rainy periods helps rapidly

570   capture carbon and decreases CO_2 emission from soil respiration (De León-González et al.,

571   2018). Air temperature and soil moisture are variables that contribute to the carbon balance

572   in cactus areas, and, in addition, carbon and calcium from cladodes are fundamental in the

573   decomposition of cactus litterfall (Bilderback et al., 2021).

574   While there is much evidence in a forested landscape, for example, comparing

575   Atlantic forest, Amazon forest, and Cerrado savanna biomes, Tonin et al. (2017) observed

576   variations in litter inputs on a space-time scale as a function of rainfall and water depth

577   through regression model (Fig. 8). The findings highlighted an increase in litter storage with

578   annual precipitation and water depth. Moreover, temporal patterns of litterfall were

579   consistently different among biomes. Techniques such as cutting management in Caatinga

580   forest species can help in the deposition and decomposition rate of litter (Barreto-Garcia et

581   al., 2021; Matos et al., 2021). According to Barreto-Garcia et al. (2021), the use of clear

582   cutting and selective cutting by diameter in species of the Caatinga biome, in the short term,

583   negatively influences soil microbial activity because soil carbon suffers greater losses in the

584   form of CO_2. To help understand litter deposition, variables such as global solar radiation,

585   soil heat flux, precipitation, vapor pressure deficit, and Normalized Difference Vegetation

586   Index are factors that control the deposition of this material in the soil (Queiroz et al., 2019).

587   In addition, the maintenance of carbon in the litter soil is essential for the release of nutrients

588   such as nitrogen and thus will assist in the survival and maintenance of Caatinga species

589   (Queiroz et al., 2019; Menezes et al., 2021; Silva et al., 2021).

590
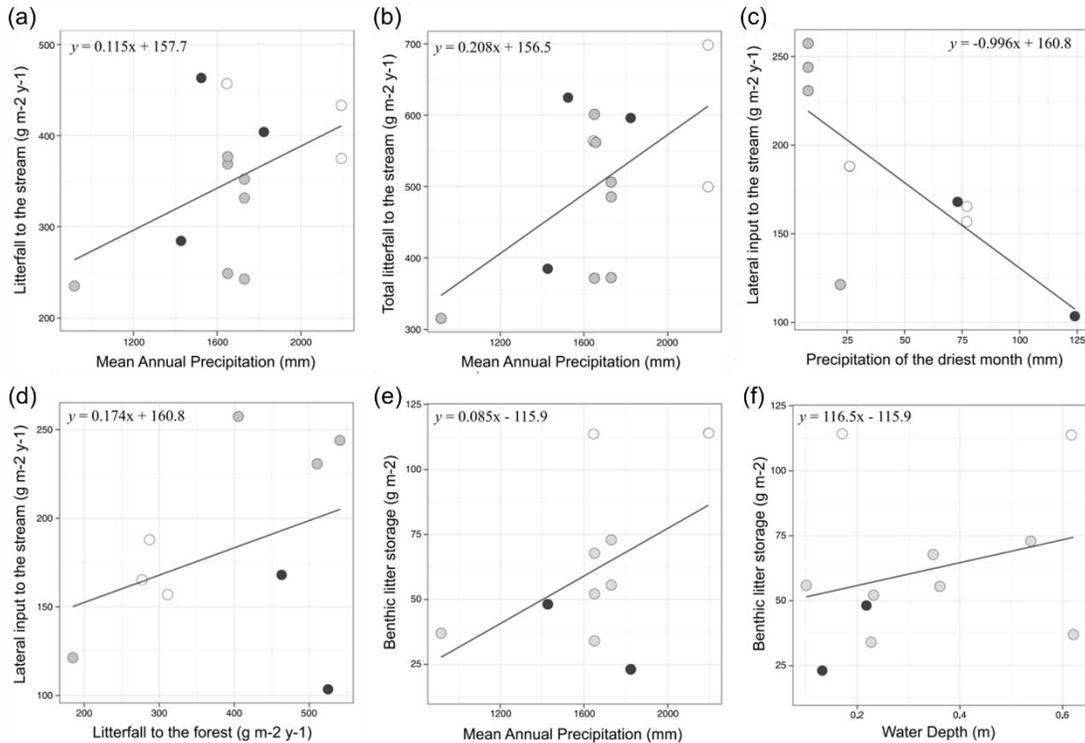
Fig. 8 Relationships between litter inputs, benthic storage and their predictors in Atlantic forest (black circles), Amazon (white circles), and Cerrado streams (grey circles): (a) litterfall vs. mean annual precipitation; (b) total litterfall vs. mean annual precipitation; (c) lateral inputs vs. precipitation of the driest month; (d) lateral inputs vs. litterfall to the forest; (e) storage vs. mean annual precipitation; and (f) storage vs. water depth. More details can be found in Tonin et al. (2017)

Factors affecting respiration from soil, litter, and soil organic matter

One of the biggest drivers of carbon efflux in terrestrial ecosystems is soil respiration. This variable ranks at approximately 75 to 100 Pg C year^{-1} on the terrestrial sphere and deserves significant attention as far as CO_2 emissions from fossil fuels (Riutta et al., 2021). In areas with buildings, the search for urban green landscapes is constant. Thus, in arid regions, the use of cacti, together with xerophilous tree and shrub species, contributes to the regulation of biogeochemical cycles, in addition to maintaining carbon for a longer time fixed in the soil (Guillen-Cruz et al., 2021). In areas of the Caatinga, carbon is not significantly released into the atmosphere in the wet season, and in the dry season, the vegetation can still act as a carbon sink, with low respiration rates (Mendes et al., 2020). Then also, according

to the authors, the respiration of the ecosystem in 2014 was higher and more significant ($p <$ 0.01) than in 2015, both in the dry season and wet season (Table 2). However, these results are low when compared to Amazon, Cerrado, and Atlantic forest due to low organic carbon in relation to humid regions. Although the measurement of carbon dynamics in vegetated areas is important information for society and the academic community, many uncertainties are raised due to interactive processes and autotrophic and heterotrophic soil respiration changes.

Table 2 Seasonal variation and annual net ecosystem CO_2 exchange (NEE), gross primary production (GPP), ecosystem respiration (R_{eco}) and ecosystem carbon-use efficiency (NEP/GPP ratio) fin the study period. Source: (Mendes et al., 2020)

Year	Variable	Statistics	Dry-wet transition	Wet season	Wet-dry transition	Dry season	Annual
	NEE	Mean	**−0.50 ± (0.05)**	−0.70 ± (0.33)	−0.25 ± (0.04)	**−0.26 ± (0.03)**	**−0.46 ± (0.03)**
		Sum	**−45.9**	−84.0	−14.9	**−24.2**	**−169.0**
	GPP	Mean	**−1.20 ± (0.08)**	**−1.68 ± (0.10)**	−0.73 ± (0.06)	**−0.64 ± (0.04)**	**−1.14 ± (0.06)**
2014		Sum	**−110.6**	**−200.8**	−44.3	**−59.0**	**−414.7**
	R_{eco}	Mean	**0.70 ± (0.04)**	**0.98 ± (0.04)**	0.48 ± (0.03)	**0.39 ± (0.01)**	**0.68 ± (0.03)**
		Sum	**64.7**	**117.0**	29.4	**34.7**	**246.0**
	NEP/GPP	Ratio	**0.41**	0.42	0.34	**0.41**	0.41
	NEE	Mean	**−0.28 ± (0.03)**	−0.63 ± (0.07)	−0.30 ± (0.03)	**−0.36 ± (0.01)**	**−0.40 ± (0.02)**
		Sum	**−17.9**	−56.0	−27.1	**−44.0**	**−145.0**
	GPP	Mean	**−0.79 ± (0.03)**	**−1.43 ± (0.08)**	0.78 ± (0.04)	**−0.71 ± (0.02)**	**−0.92 ± (0.04)**
2015		Sum	**−49.0**	**−127.0**	72.0	**−86.0**	**−334.0**
	R_{eco}	Mean	**0.51 ± (0.02)**	**0.80 ± (0.04)**	0.49 ± (0.02)	**0.34 ± (0.02)**	**0.52 ± (0.02)**
		Sum	**30.9**	**71.3**	44.8	**42.0**	**189.0**
	NEP/GPP	Ratio	**0.36**	0.44	0.38	**0.51**	0.43

Bold values are significantly different between each season in 2014 and its correspondent season in 2015 at the 0.05 level ($p < 0.05$).

The results are given in the form mean ± standard deviation (g C m^{-2} year^{-1} or g C m^{-2}).

Thus, as a way of decreasing the efflux of CO_2 in the ecosystem, the use of CAM plants can modify the local carbon budget when tree crops are used together (Owen et al., 2016). For Guevara-Escobar et al. (2021), cacti may not be highly expressive in decreasing the nocturnal CO_2 source when exposed to other cultures of C3 and C4 metabolism. However, it is known that cacti of the species *O. ficus-indica* under fields with a high density of individuals have expressive nocturnal assimilation of CO_2. Nevertheless, when exposed to extreme droughts, the net uptake of CO_2 shows an extreme reduction (Acevedo et al., 1983;

628　Nobel & Hartsock, 1984). Indeed, not only due to environmental and climatic circumstances,
629　but the age of the cladodes and the plant influence the preference for CO_2 uptake, as cladodes
630　with initial weeks of emergence can open their stomata during the daytime and capture CO_2
631　(Acevedo et al., 1983). In summary, *Opuntia*, when exposed to high CO_2, absence of water
632　stress, and favorable temperature (i.e., 25 ℃ during the day and 15 ℃ at night), significantly
633　increases the production of biomass, thickness, and the number of cladodes (Nobel & Israel,
634　1994; Neupane et al., 2021).

635

636　**Conclusions**

637　　　In the present study, we carried out a survey of studies focusing on carbon and energy
638　fluxes in terrestrial ecosystems. We emphasize that deforestation can cause serious problems
639　in the energy and carbon balance, and areas with Caatinga can suffer significant damage due
640　to the composition of species with different photosynthetic metabolism, considering that
641　plants with crassulacean acid metabolism (CAM) can work efficiently in low water vapor
642　and CO_2. However, more intense anthropic disturbances and the increase in aridity, predicted
643　by climate simulations, could significantly negatively affect large species. Thus,
644　understanding the energy balance of vegetation is also a critical factor, as these simulations
645　are helpful for use in weather forecasting or climate change prediction. In this context, due
646　to the findings in this review, future research may be encouraged on:

647　　　(1) Water use and carbon allocation above and below ground.

648　　　(2) Plant responses under extreme growing conditions, particularly to long periods of
649　drought.

650　　　(3) Climate simulations in cactus and Caatinga agricultural areas.

651

652　**Statements and Declarations**

653　All authors have read and understood the statement of policy of interests.

654

655　**Ethical Responsibilities of Authors**

656　The authors declare no competing interests.

657

658　**Data availability**

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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CHAPTER 2

A systematic review of energy and mass fluxes, and biogeochemical processes in seasonally dry tropical forests and cactus ecosystems

Abstract

Regions with arid and semi-arid climates are characterized by hostile climatic conditions of high water deficit in the soil-atmosphere system. Local landscapes with climates of low rainfall and relative humidity, and high air temperature, such as regions of sub-humid, semi-arid, and arid zones, cover approximately 45.4% of the entire land surface of the planet, to which the biomes with dry forests occupy a total area of 1079×10^4 km^2. Thus, this review aims to quantify the processes and changes in energy, water, and carbon fluxes, and their interactions with the surfaces of terrestrial ecosystems of Caatinga and cacti in semi-arid environments. Studies report that forests in arid and semi-arid environments show resilience to local diversity, prominent in the interrelationship of species, which favors the survival of individuals with changes in the ecological niche. One of the main modifications in land occupation and land use in dryland landscapes is the implementation of agriculture. Furthermore, carbon and energy fluxes in terrestrial ecosystems undergo significant changes with the removal of native vegetation. Therefore, the damage caused by deforestation can cause serious problems in the energy and carbon balance, compromising species' survival. Finally, we emphasize that CAM photosynthesis plants can be an alternative in places with high environmental degradation problems.

Keywords: carbon stocks, energy balance, deforestation, cacti, Caatinga

1. Introduction

The Earth's surface is composed of a diversity of landscapes and scenarios that cover the regions of the planet in their different edaphoclimatic conditions. Arid and semi-arid climate regions are characterized by hostile climatic conditions of high water deficit in the soil-atmosphere system, significantly affecting the fauna and flora populations that inhabit these locations (Huang et al. 2016). In a region of flora with shrubby and herbaceous

32 vegetation, climate change associated with land use influences natural processes, as well as

33 future perspectives related to species survival (Schulz et al. 2016; Silva et al. 2018, 2020;

34 Fischer 2018). With the growing demand for food, the disturbances caused in the soil-

35 vegetation-atmosphere system lead to losses in biodiversity and compromise fragile

36 landscapes in semi-arid regions (Althoff et al. 2018; Weiler et al. 2020). The Caatinga biome

37 is a typical Brazilian ecosystem that covers areas with high water deficits. The seasonally dry

38 tropical forest known as Caatinga is diverse and characterized by various endemic species of

39 fauna and flora (Althoff et al. 2018). Among the numerous families of plants that mostly

40 occur in this region, cacti (Cactaceae Juss.) are the species that stand out (Moura et al. 2016),

41 both from the point of view of tolerance and for their importance in local ecosystem services.

42   As a result of environmental degradation processes, which include pollution on both

43 the land and the atmosphere, deforestation, soil salinization, burning and greenhouse effect,

44 plant species are primarily threatened by environmental degradation processes in Brazilian

45 semi-arid conditions. In addition to disrupting the dynamics of plant species reproduction

46 and the survival of the biome, it has detrimental effects on local natural resources as well as

47 the population residing in these regions. Cactus (*Opuntia* spp. and *Nopalea* spp.) is one of

48 the most promising species for cultivation in arid and semi-arid regions and can also be used

49 in areas with the presence of environmental degradation (e.g., erosion and deforestation)

50 (Alary et al. 2007). In addition to climate and land use changes, poor management of

51 environmental resources contributes massively to the productive decline of these species,

52 altering the dynamics of vegetation, physical, chemical, and biological properties of soils, as

53 well as the fluxes of energy, carbon and of water in the soil-plant-atmosphere system (Moura

54 et al. 2016; Chazdon et al. 2016a; Nanni et al. 2019).

55   The need to maximize agricultural and livestock systems is one of the key points in

56 terms of exploration and land use change (Fernandes et al. 2020b). The fact that vegetated

57 surfaces assume the role of important sinks of carbon dioxide—CO_2 (Schulz et al. 2016), soil

58 exposure in hostile environments brings consequences such as the reduction of soil and air

59 moisture, in addition to increasing the sensible heat flux (Rotenberg and Yakir 2011; Brugger

60 et al. 2019). Soil moisture content is a vital bridge for plants as a source of water recharge

61 (Cheng et al. 2021), contributing to plant thermoregulation through transpiration. The water

62 stored by crops in their vegetative structures mitigates thermal and water stress, preventing

63 plants from excessively losing water to the atmosphere (Cheng et al. 2021). The native

64 species of the Caatinga, including cactus, are tolerant to water stress and high air

65 temperatures. However, although cactus plants do not have deciduous leaves (i.e., perennial

66 or deciduous foliar habits), like the tree and shrub species of this biome, they present other

67 alternatives, such as physiological and anatomical ones, for storing and balancing water in

68 the driest periods (Dória et al. 2016; Ricardo et al. 2018). These adaptive anatomical and

69 morphophysiological features are: crassulacean acid metabolism (CAM), aquiferous

70 parenchyma, leaves modified into spines, succulent cladode-shaped roots, and stems.

71 With the instability of the leaf area, in periods with the presence of vegetation, the

72 balance of energy and water present changes throughout the year between the dry and rainy

73 seasons. These changes modify the behavior of the energy balance, where the heat fluxes

74 when interacting with the environment's surface can be accounted for and distinguished

75 (Santos et al. 2020a). Methods for determining the energy balance, e.g., eddy covariance and

76 Bowen ratio, have the quantification of evapotranspiration as a product, in addition to being

77 well-known methods in the literature (Wagle et al. 2020; Longo et al. 2020; Ferreira et al.

78 2020). However, these methods are not commonly characterized and applied in

79 Caatinga/cactus areas. This energy available in the environment can be used in organic matter

80 decomposition processes (e.g., litter) (Queiroz et al. 2019), thus making nutrients available

81 to plants (Zhu et al. 2021).

82 Therefore, with the differentiation of ecosystem surfaces and species of type C3, C4,

83 and CAM, we carried out a systematic review to investigate the patterns of energy-water-

84 carbon fluxes in ecosystems of cacti and Caatinga aiming at understanding the contributions

85 of the Caatinga with litter deposition, its nutrient stocks, and decomposition. For this, several

86 papers were accessed online and used according to their theme and relevance.

87

88 **2. Methodology**

89 First, we conducted a literature search from 1973 to 2021 for the construction of this

90 systematic review. Search results were limited to journal articles. In addition, search strings

91 were constructed using online databases sourced from Scopus, Web of Science, Google

92 Scholar, and Science Direct with keywords related to ecosystems, soil, dry land, dry forest,

93 C4 plant, C3 plant, CAM plant, environmental modeling, evapotranspiration, tree, cactus,

94　energy balance, eddy covariance, sonic anemometer, litterfall, litter, mineralization, carbon,

95　water, Land-Use/Cover Change, LUCC, turbulent flows, climate change, arid and semi-arid.

96　Boolean operators "AND" and "OR" were used to combine the keywords described above.

97　Finally, we used 77 articles for the construction of this review article (Figure 1).

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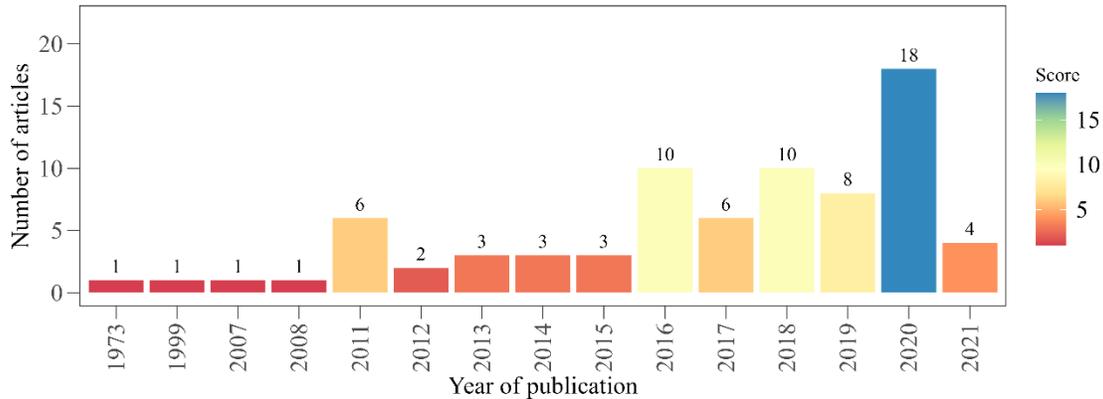
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100　**Figure 1.** Distribution of selected publications by year.

101

102　**3. Literature review**

103　*3.1. Seasonally dry forest and cactus ecosystems in semi-arid regions*

104　　　Landscapes in places with climates of low rainfall and relative humidity, and high air

105　temperature (e.g., regions of sub-humid, semi-arid and arid zones) cover approximately

106　45.4% of the entire land surface of the planet, to which the biomes with dry forests occupy a

107　total area of 1079×10^4 km^2. Despite the hostile climate of these regions, they are densely

108　populated, and these areas are facing the processes of climate change and land use, negatively

109　compromising biodiversity and species habitat (Almeida et al. 2011; Prăvălie 2016; Bastin

110　et al. 2017). It is estimated that by the end of the 21st century, climate change will cause the

111　expansion of semi-arid lands to an extent equivalent to half the land surface of the globe

112　(Huang et al. 2016).

113　　　These environmental changes and anthropic influences provide a reduction in rainfall

114　volumes and an increase in air temperature. Tropical vegetation landscapes have undergone

115　drastic changes over the years in terms of their coverage due to fires and loss of biodiversity

116　caused by the invasion of exotic species, and bad practices in land use, influencing the future

117　perspectives of these areas (Schulz et al. 2016; Silva et al. 2018, 2020; Fischer 2018).

118   The main impacts on biodiversity loss in semi-arid regions of Brazil are related to
119   exacerbated disturbances in land use, prominent from the expansion of agricultural activities
120   (Bogoni et al. 2018; Weiler et al. 2020). These growing anthropic pressures are driven by the
121   high demand for food, the exploration and expansion of pasture areas to feed beef cattle, and
122   the constant extraction of wood. Thus, these actions lead to a reduction in the capacity for
123   regrowth and regeneration of natural species, compromising the resilience of the local
124   vegetation and, as a consequence, declining the vitality of the local biome (Althoff et al.
125   2018; Milliken et al. 2018). One of the biomes with high susceptibility to these impacts and
126   historically neglected is the Caatinga. This biome is composed of a dry tropical forest of high
127   expressiveness in the Northeast region of Brazil (Mariano et al. 2018; Fernandes et al. 2020a),
128   with an area of approximately 912 thousand km^2, comprising a high richness of flora and
129   fauna (Marinho et al. 2019; Ledru et al. 2020). However, despite the significant territorial
130   extension of this biome, about 45% of its total area is already deforested and compromised,
131   with only 7.8% protected by law (Pacheco et al. 2018).

132   In the Caatinga areas, plant species may vary in height and canopy characteristics
133   (i.e., canopy projection and leaf density), varying according to edaphoclimatic conditions,
134   mainly due to water availability in the soil. Some plants can reach 15 to 20 m in height, with
135   significant leaf density in the canopy and biomass. However, most plants in this complex
136   ecosystem are 5–10 m in height and have low soil cover, forming forest fragments with open
137   spaces similar to Savanna (Moura et al. 2016). In addition to tree and shrub species, the
138   Caatinga has plants that make up the herbaceous stratum and are dependent on the growth
139   dynamics of larger individuals, as well as soil moisture and climate conditions (Moura et al.
140   2016; Moraes et al. 2020).

141   Furthermore, in the Caatinga, the herbaceous stratum is quite rich and diverse,
142   presenting several phylogenetic groups of species with high resilience and tolerance to
143   edaphoclimatic disturbances (Carrión et al. 2017). Among the individuals present in the
144   Caatinga, the species of the Cactaceae family are in great expression (Moura et al. 2016) due
145   to their adaptability, being one of the most diverse with 1480 species recognized in the
146   Neotropics (Goettsch et al. 2015). The cactus (*Opuntia* spp. and *Nopalea* spp.), despite being
147   an exotic species, is widely cultivated and widespread in arid and semi-arid environments for
148   forage production, living fences, composition in the diet of animals and humans, and

149 recovery of areas undergoing degradation processes (Carrión et al. 2017; Lemos et al. 2021).

150 In addition to being a highly resilient and promising crop in dry lands, its agricultural

151 cultivation and/or spontaneous growth in native vegetation of Caatinga forest can effectively

152 contribute to improving soil carbon sequestration and ecosystem enrichment (Figure 2).

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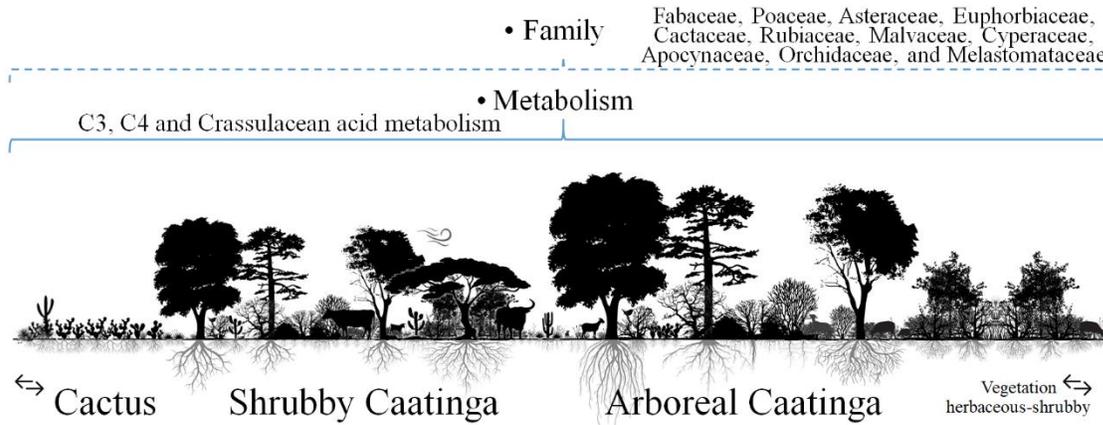
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155 **Figure 2.** Scheme of the main plant families that make up the Caatinga biome. Note:

156 Illustration with observations of canopy cover transitions, with tree, shrub and herbaceous

157 species.

158

159 The Caatinga, with distinct floristic vegetation because they are located in the region

160 known as the dry diagonal (Figure 3), is marked by seasonal stresses arising from climatic

161 factors (latitude, altitude, sea conditions, sea currents, vegetation, air masses, relief, and

162 other) (Gomes et al. 2019b), and soil management. A significant part of this biome is in a

163 fallow state for natural regeneration, due to extensive activities such as cattle raising and

164 reduced soil fertility, leaving it exposed to weathering agents. These sites are considered

165 environmental hotspot areas, these sites deserve attention due to vegetation changes (mainly

166 deforestation and reforestation), global biogeoclimatic and ecological dynamics, and carbon

167 fluxes (Chazdon et al. 2016b; Moura et al. 2016; Nanni et al. 2019).

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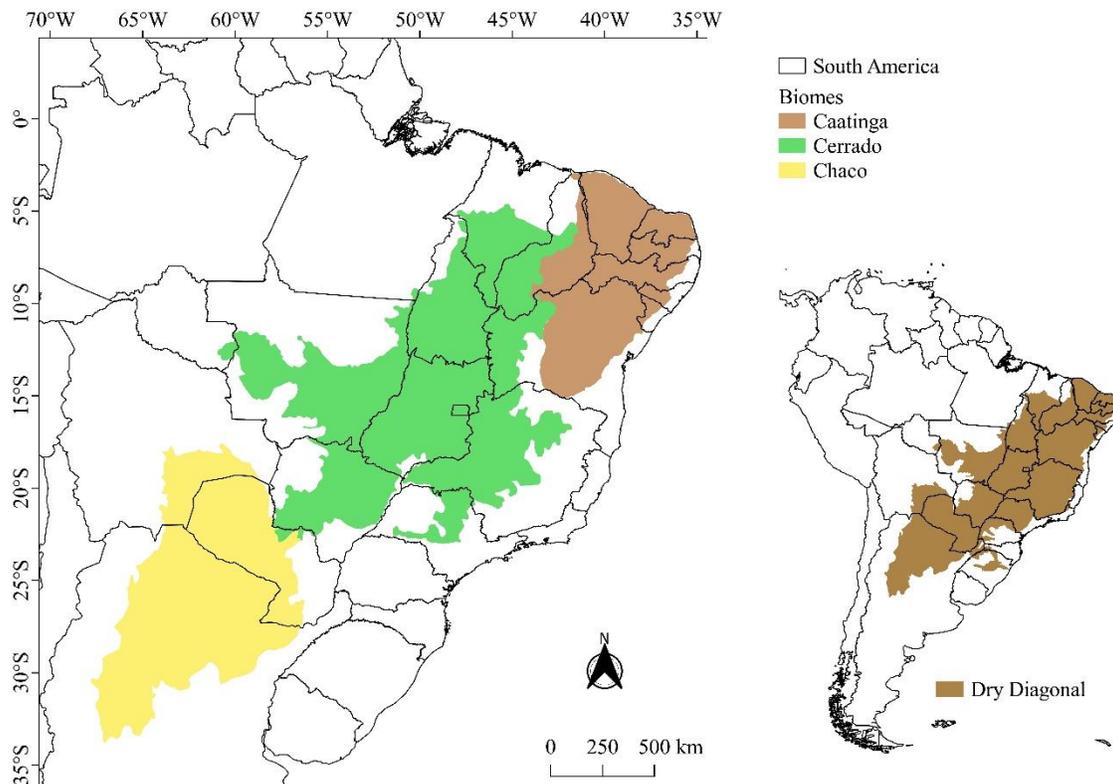
Figure 3. Geographic representation of dry diagonal distribution in South America. Note:
The forests included in this ecosystem are Caatinga (seasonally dry tropical forest), Cerrado
(Savanna) and Chaco biomes.

Although anthropic alterations, such as the removal of native vegetation through
deforestation for the exploitation of agricultural crops, and together with climatic conditions
result in significant environmental changes, this type of environment can compromise the
dry seasonal forests inserted in these biomes (Figure 3). This type of environment does not
only have xeromorphic species. Furthermore, its floristic composition is quite diversified,
showing biogeographic affinities, which make up 11,392 species in the Cerrado (Savanna),
4,322 species in the Caatinga (seasonally dry tropical forest), and 3,400 species in the Chaco
(Forzza et al. 2012; Collevatti et al. 2020). All these ecosystems with dry, semi-arid, and arid
climatic conditions have peculiarities in the composition of flora and fauna, which are altered
by the problems of climate change and land use. Based on climate similarities, the Chaco
differs from the Cerrado and the Caatinga due to winter frosts (Werneck 2011).

186 **4. Land use and land cover changes on the dry diagonal**

187   Forests in arid and semi-arid environments show resilience to local diversity,

188 prominent in the interrelationship of species, which favors the survival of individuals with

189 changes in the ecological niche (Filazzola and Lortie 2014). Vegetation resilience is linked

190 to the adaptive capacity of species and/or systems to resume their original functions after

191 suffering environmental disturbances (Holling 1973; Lin 2011; Anderson and Bollig 2016),

192 and when this is not achieved, stand failures and loss of diversity occur of the vegetation.

193 Due to the loss of biodiversity and adaptive inability, the transitions of the vegetation cover

194 of forested areas are often altered due to the intensification of agricultural activity, a factor

195 that still generates many uncertainties for the environment (Wilson et al. 2017), since, even

196 with the insertion of vegetation cover of crops on the soil, abrupt losses occur due to the

197 reduction in species diversity (Figure 4) (Beuchle et al. 2015; Chazdon et al. 2016a).

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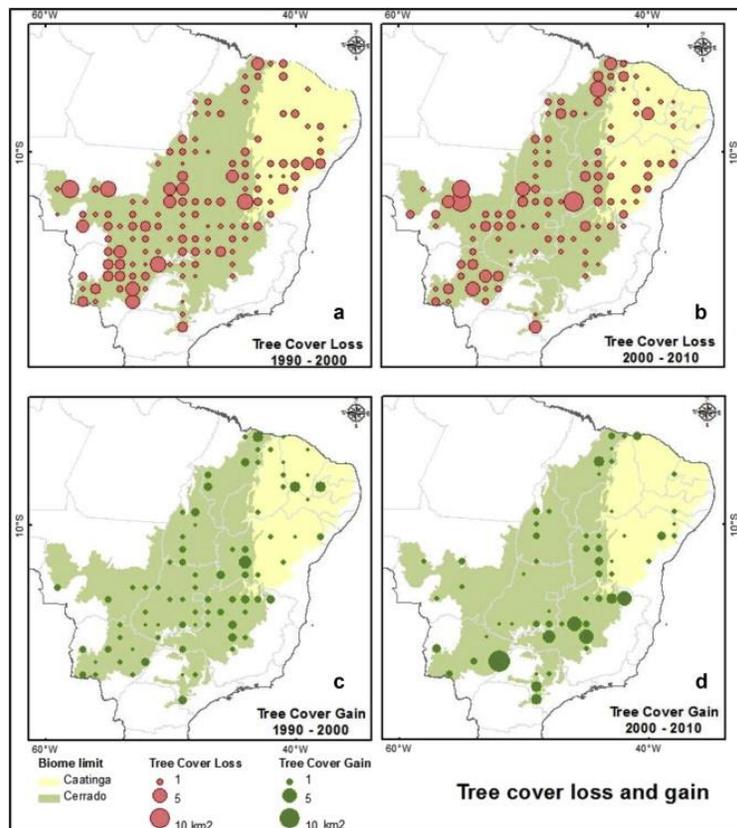
200 **Figure 4.** Gross tree cover loss and gain per sampling unit of the Caatinga and Cerrado

201 biomes during 1990–2010. (a) tree cover loss from 1990 to 2000, (b) tree cover loss from

202 2000 to 2010, (c) regrowth/afforestation from 1990 to 2000, and (d) afforestation from 2000

203   to 2010 (Beuchle et al. 2015).

204

205   Deforestation has been a common practice for hundreds of years (Pinheiro Junior et

206   al. 2019), and in recent decades the practice has been intensifying in tropical forests in dry

207   regions. Worldwide, Brazil is the second largest holder of gross losses of forested areas

208   (Hansen et al. 2013), and damage to these vegetation and biomes is caused by increases in

209   agricultural frontiers, driven by the exploitation of commodity crops, availability of labor

210   and favorable climatic conditions (Fehlenberg et al. 2017), causing substantial damage to

211   natural vegetation (Hansen et al. 2013). Approximately 28.6 million people depend on the

212   resources of these forests, and losses from deforestation ecosystem services' disruption cause

213   catastrophic global damage (Tabarelli et al. 2018).

214   Forested areas, when deforested, take decades to regenerate secondary forest

215   vegetation; however, this last type of vegetation does not present the same floristic diversity

216   as the original forest. With the changes in land use and land cover, in 2017 approximately 1

217   million hectares of forest were lost in Brazil. This was a key factor for the increase in the

218   emission of greenhouse gases into the atmosphere since the country is the seventh largest

219   emitter of carbon dioxide equivalent (Le Quéré et al. 2015; Fernandes et al. 2020b).

220   The balance in carbon (C) emission is fundamental for understanding anthropogenic

221   disturbances in ecosystems (Le Quéré et al. 2015). The emission of fossil fuels and changes

222   in land use contribute to the emission of 10 Pg C year^{-1} (Poulter et al. 2014). One of the main

223   changes in the occupation and use of land in dryland landscapes is the implementation of

224   agriculture (Fernandes et al. 2020b). Because these sites play a significant role as CO_2 sinks,

225   modifications to these environments alter CO_2 fluxes in the soil-plant-atmosphere system

226   (Schulz et al. 2016).

227

228   **5. Energy and mass fluxes**

229   Agricultural and industrial activities emit the most greenhouse gases (carbon dioxide,

230   methane, and nitrous oxide) into the atmosphere. The agricultural sector is responsible for

231   approximately 10 to 12% of this emission, and due to this magnitude, Federal Law No.

232   12,187 of December 29, 2009, proposed incentives for low-carbon agriculture in Brazil

233   (Figueirêdo et al. 2013). The interaction of biotic factors and anthropogenic interventions can

234   change the emission dynamics of these gases, mainly in the CO_2 flux in forest and agricultural

235   ecosystems. Because it is a constituent gas of the atmosphere and quite dynamic, its

236   production and concentration can change in time and space, whether in aquatic or terrestrial

237   ecosystems (Stets et al. 2017).

238   In vegetation of semi-arid environments, low soil cover, exposure to high-intensity

239   solar radiation, and low water availability alter the CO_2 flux and, consequently, contribute to

240   considerable effects on the sensible heat flux of the environment. These conditions affect

241   convective activities and decrease air humidity, making the environment more hostile

242   (Rotenberg and Yakir 2011; Brugger et al. 2019). The accumulation of energy in the canopy

243   makes the plant need to dissipate heat to the environment through transpiration (i.e., cooling

244   process). However, due to the low water availability in the root zone, such physiological

245   output becomes costly (Kröniger et al. 2018).

246   Shrubby vegetation generally has lower water requirements when compared to large

247   tree species. In semi-arid environments, surrounding shrubs play a crucial role in dissipating

248   sensible heat flux, transferring energy to overlying layers and, subsequently, to the

249   atmosphere (Rotenberg and Yakir 2011). Vegetation with adequate density in semi-arid

250   zones helps to maintain water bodies and soil moisture due to the interception of rain by the

251   canopy and retention by the roots, making water available to the species and helping to

252   dissipate energy by latent heat flux (Cheng et al. 2021).

253   The heat fluxes (latent—LE, sensible—H, and soil—G), which are partitioned into

254   net radiation (R_n), are elements of the energy balance and result from the interaction of energy

255   with surfaces that alter the local ET (Santos et al. 2020a). Quantifying energy exchange with

256   the environment can be performed using methods, such as eddy covariance and Bowen ratio

257   (Wagle et al. 2020; Longo et al. 2020; Ferreira et al. 2020). The process of water loss through

258   plant transpiration causes their stomata to open, transfer water to the atmosphere, and capture

259   CO_2 (Figure 5). In environments where water availability is restricted, like arid and semi-

260   arid regions, species have high water extraction efficiency through deep root systems,

261   seeking moisture where non-adapted species commonly cannot reach (Abdallah et al. 2020).

262   These characteristics are noticeable in Caatinga species due to adaptations and morphological

263   modifications.

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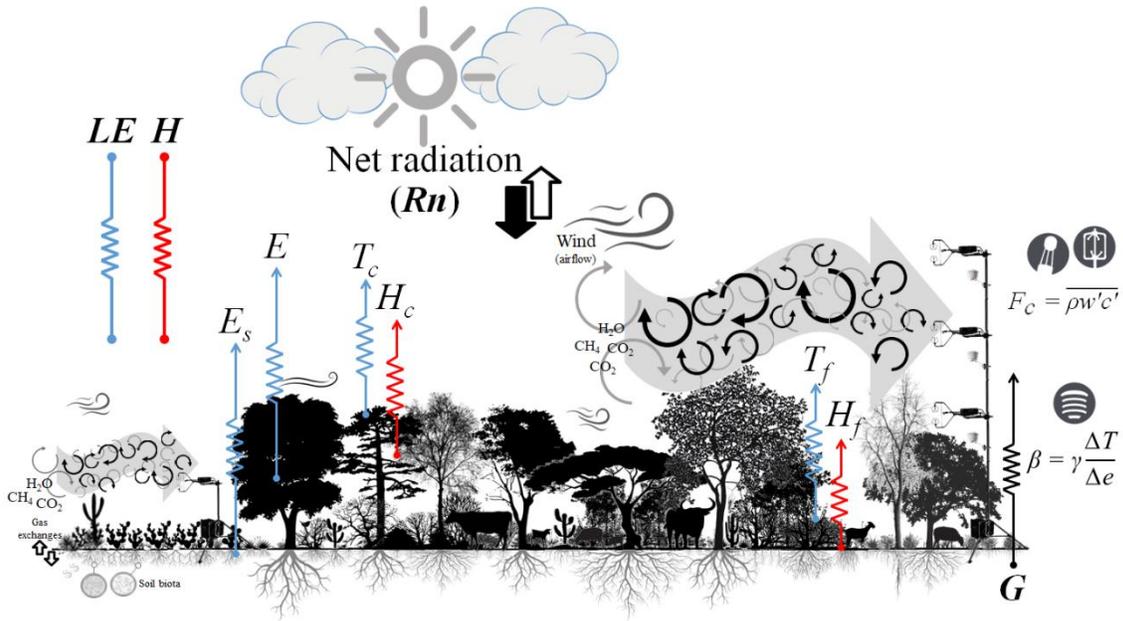
Figure 5. Schematic view of the diurnal energy balance in an ecosystem. Net radiation (R_n) is balanced by sensible (H), latent (LE) heat fluxes, and soil heat flux (G). The constituents for LE are surface evaporation (E) and transpiration (T). The subscript letters c, f, and s are assigned to the canopy, forest floor and soil, respectively. Flow measurements can be made using the Bowen ratio (β) and eddy covariance methods, as represented in the diagram on the right.

The heat exchange and mass of dryland ecosystems are governed by water availability. When water is restricted, damage to the ecosystem's gross primary productivity is often more severe than ecosystem respiration, causing these sites to shift from sinks to carbon sources (Biederman et al. 2017; Nosetto et al. 2020). Understanding these phenomena in sink-source dynamics helps understand carbon stocks in ecosystems (Nosetto et al. 2020). Furthermore, in dry forest areas, like Caatinga, there is a multispecific floristic composition, which in conjunction with the different metabolisms (e.g., C3, C4 and CAM), drives biophysical resources and carbon use by plants (Oliveira et al. 2020).

6. Storage: interaction and stocks of biophysical elements in dry forest ecosystems

Soil is a reservoir of nutrients, ions, water and carbon. In addition, it is also the habitat of several microorganisms that play an essential role in the ecosystem. In the biosphere, the

285 soil is of fundamental importance in organic carbon stocks and is a significant sink of
286 atmospheric carbon dioxide (CO_2). However, the ability to store organic carbon in the soil is
287 governed by some factors, e.g., climatic conditions, soil type and local vegetation (Gomes et
288 al. 2019a). Despite the soil's carbon storage capacity, the soil respiration process releases
289 CO_2 into the environment, basically due to three factors: metabolism of microorganisms,
290 respiration of macro- and micro-fauna, and roots (Santos et al. 2020b).

291 The dry tropical forest has relevant storage of nutrients in the soil (e.g., carbon,
292 nitrogen, and phosphorus) when compared to those contained in the vegetation biomass
293 (Medorio-García et al. 2020). In tropical ecosystems, about 30 to 60% of carbon is stored in
294 the soil (Don et al. 2011), contributing to its fertility and decreasing erosion processes and
295 susceptibility to desertification (Farina et al. 2020).

296 About 471 Pg of C is stored in organic form in tropical forests (Pan et al. 2011).
297 However, when forests are cleared, the carbon that is stored in the soil layers, and above the
298 surface, like in plant biomass, is released into the atmosphere (Baccini et al. 2012). Although
299 semi-arid vegetation is not very dense, this type of environment makes a significant
300 contribution to carbon retention (Poulter et al. 2014). CO_2 plays several important roles in
301 plants, including the main substrate for photosynthesis and enhancing the carboxylation rate
302 when in favorable concentrations (Piao et al. 2019).

303 As semi-arid environments are deficient in water, the increase in CO_2 concentration
304 favors stomatal regulation, keeping plants with their stomata partially closed, that is reducing
305 excessive water loss. This implies an improvement in the efficiency of water use of the
306 species and the photosynthetic capacity (Keenan et al. 2013; Piao et al. 2019). Trees in these
307 environments, when subjected to water limitations, can outline three adaptive strategies, such
308 as (i) drought prevention; (ii) drought resistance capacity; and (iii) drought tolerance, all of
309 which are linked to physiological mechanisms (Chaturvedi et al. 2020). However, under these
310 conditions, nutrient absorption becomes reduced.

311 Plants benefit from the minerals and organic matter present in the soil, as well as their
312 characteristics, such as humidity, topography, and mineral constituents, that alter the
313 maintenance and fixation of carbon (Zong et al. 2021). This type of material can be
314 maintained with the deposition of Caatinga leaves in the soil, which provides nutrients such
315 as nitrogen, phosphorus, and potassium, and after mineralization, become indispensable for

316   the development of plants.

317

7. Nutrient cycling

319   The climate is an abiotic component that contributes significantly to regulating the

320   biogeochemical activity of terrestrial ecosystems. Vegetation, in turn, is a biotic constituent

321   that plays a key role in the availability of finite resources for soils. An important nutrient

322   replenisher for the soil is the litter (Moura et al. 2016), which comes from constituent

323   materials of plants (i.e., branches, dry leaves, flowers, fruits, seeds) and, when decomposed,

324   releases nutrients and organic compounds, helping in the composition of soil organic matter,

325   as well as in maintaining the microbiota (Farina et al. 2020). In addition to the return of

326   nutrients to the soil, the soil is less exposed to incident solar radiation after the mineralization

327   of the biomass made available by the litter. Consequently, there is a sudden attenuation of

328   the thermal amplitudes (Figure 6). In areas of the Caatinga, the excessive elevation of soil

329   temperature alters the dynamics of nitrogen and oxygen, increasing soil anaerobiosis and,

330   therefore, increasing the emission of nitrous oxide (N_2O) in the atmosphere. However, even

331   with these observations, the Caatinga has low emissions of harmful gases compared to other

332   biomes (Ribeiro et al. 2016).

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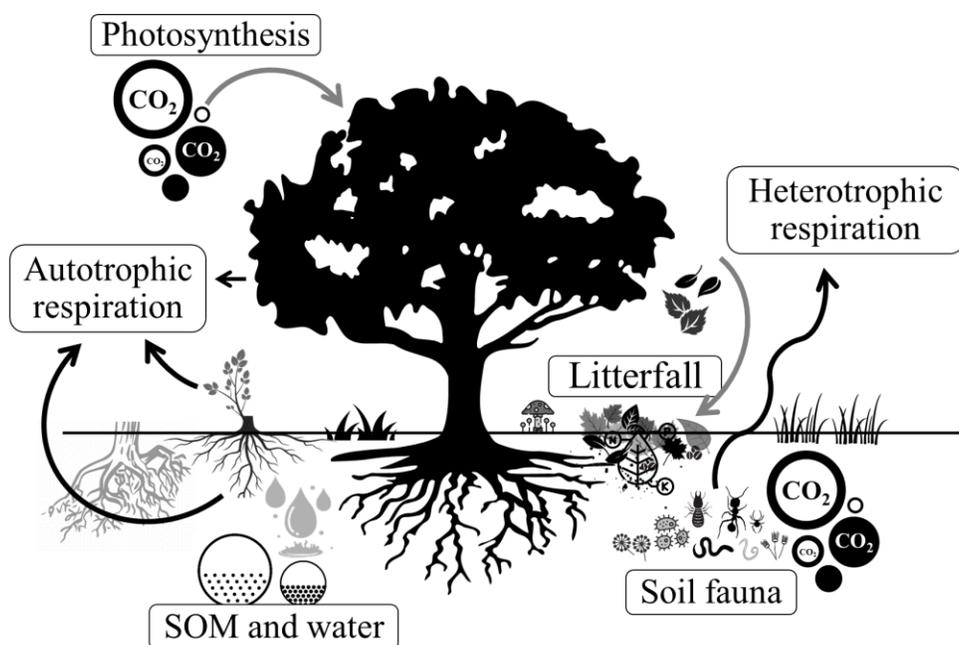
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335   **Figure 6.** Schematic illustration of litter deposition in soil and its interaction with soil

336 organisms and plants. SOM is the soil organic matter.

337

338   The heterotrophic organisms active in the cycling of nutrients have as energy source
339 precursors the elements made available by the litter (Rai et al. 2016). This nutrient
340 availability in dry forests in semi-arid regions has an ecological footprint for maintaining
341 plant growth. The deposition of debris in the soil is not only a factor governed by climatic
342 conditions, but also by the characteristics of the canopy of plant species (Carrera et al. 2008;
343 Rai et al. 2016). The constituents and their quality, e.g., nitrogen content, C/N ratio, and
344 lignin percentage, influence the decomposition capacity of the material and, mainly, the
345 speed of decomposition (Jamaludheen and Kumar 1999).

346   The species with higher concentrations of nitrogen in the vegetative structures present
347 a more accelerated decomposition rate. In this way, the litter commonly presents a
348 decomposition listed in some phases, being, initially (i) a deposition phase, later there is (ii)
349 a faster release of nutrients and, the final phase, characterized by (iii) deceleration in the
350 release of compounds (Carrera et al. 2008). The seasonality of environmental conditions and
351 the low and/or high deposition of debris in the soil can change the rate of decomposition of
352 the material (Queiroz et al. 2019).

353   Several nutrients are found in litter, in addition to carbon, hydrogen, and oxygen, the
354 primary (N, P, and K) and secondary macro (Ca, Mg and S) and micronutrients (Fe, Cu, Zn,
355 Mn, Ni, B, Cl, and Mo). Macronutrients are part of essential molecules and are needed in
356 large amounts, having a structural function in plants, while micronutrients are needed in
357 smaller amounts and have a regulatory function. Thus, cycling processes favor the storage of
358 these nutrients, as well as their availability to plants in gross primary production through this
359 recycling (Carrera et al. 2008; Queiroz et al. 2019; Zhu et al. 2021). Costly nutrients such as
360 nitrogen, phosphorus, and potassium in forest ecosystems are made available to plants
361 through the litter in a high percentage of return, favoring the production of biomass and
362 helping in metabolic processes and tolerance to stress (biotic and abiotic) due to plants being
363 well nourished (Zhu et al. 2021).

364

365 **8. Conclusion**

366   This review reveals that carbon and energy fluxes in terrestrial ecosystems undergo

367　significant changes with the removal of native vegetation. The damage caused by
368　deforestation implies serious problems in the energy and carbon balance, compromising the
369　survival of species. Plants with CAM photosynthesis can be an alternative in places with high
370　environmental degradation problems. In addition, the use of these plants can be a tool to
371　make ecosystems more resilient due to the high efficiency in the use of water and CO_2. Due
372　to the importance of cactus and Caatinga ecosystems, future research is needed to understand
373　carbon deposition in the soil and species' survival.

374

382

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619

CHAPTER 3

2

3   Spatiotemporal climatic analysis in Pernambuco State, Northeast Brazil

4

5   **Abstract**

6   The main factors responsible for the greatest natural disasters are related to extreme weather

7   events for which no country is really well-prepared, particularly in Latin America, and

8   specifically in Brazil. This research was developed to determine the spatiotemporal climatic

9   similarities of municipalities along a longitudinal gradient from the east to north-east of

10   Pernambuco State, in northeastern Brazil, from 1993 to 2018, based on applied statistics. The

11   daily meteorological database (rainfall, air temperature, humidity, pressure, wind and

12   evaporation) registered at eight manual meteorological stations of the National Institute of

13   Meteorology, with a historical period of 26 years. The meteorological data were subjected to

14   descriptive statistics, the cluster analysis (CA), and the principal components analysis (PCA),

15   to identify which components are most affected in the climatic patterns. This study also

16   carried out investigations into the influence of the possible dynamic causes of the El Niño-

17   Southern Oscillation (ENSO) phases on the rainfall patterns of the municipalities. The

18   eigenvalues of the three PCAs > 1. PC 1 and PC 2 showed a total variance of 59.50%. The

19   variables rainfall and relative humidity presented a higher correlation with the municipalities

20   of Recife and Triunfo (group G_1). The municipalities of Petrolândia, Cabrobó and Ouricuri

21   were grouped according to the variables evaporation, air temperature and atmospheric

22   pressure (group G_2). The CA was able to indicate the cluster of municipalities with similar

23   climatic characteristics. The ENSO phases directly influence the variability of rainfall in both

24   homogeneous groups identified in the study. Based on multivariate statistical analysis, it is

25   possible to determine the meteorological seasonality between the different regions of the

26   State of Pernambuco - northeastern Brazil. Such an analysis is important for the population

27   in the eight municipalities, since it makes it possible to improve the productivity of economic

28   activities, especially crop cultivation and livestock rearing.

29

30   **Keywords:** Meteorological variables, ENSO, Cluster Analysis, Principal Component

31   Analysis, Vulnerability

32

1. Introduction

The main factors responsible for the greatest natural disasters in urban and rural areas are climate extremes (droughts and floods), earthquakes, forest-fire, and some associated with climate change. These events have become common in several regions of the globe (de Lima et al., 2013; Pereira et al., 2018; Nogueira et al., 2020; Singh et al., 2020) and particularly in the north-east of Brazil (Cavalcanti, 2012; Costa et al., 2020). Climatic changes in several countries, occurring over decades, are negatively affecting human development and activities, decreasing biodiversity and causing degradation of agricultural land worldwide (Zarei et al., 2019; Rega et al., 2019; Singh et al., 2020).

Northeastern Brazil (NEB) is characterized by presenting distinct climatic conditions throughout its territory, encompassing places with low and high spatiotemporal variability of rainfall and a wide extent of semi-arid lands, which corroborates climate vulnerability (Martins et al., 2019; Comin et al., 2020; Costa et al., 2021), and accentuates its high social vulnerability, with emphasis on worse Human Development Indexes (HDI) - (Marengo et al., 2018; Lyra et al., 2017; IBGE, 2019; Feindouno et al., 2020). Places with an arid and semi-arid climate present a great challenge for the management of water resources, whether in cities or agricultural areas (Sadeghi et al., 2016).

Multiple factors can cause spatiotemporal variations in meteorological variables (e.g., rainfall, air temperature, relative humidity, wind speed, and solar radiation), such as elements linked to topography, the proximity of large water bodies, among others, thus compromising the management of water resources (Raz1ei, 2018; Santos et al., 2020). This collection of meteorological information and temporal variations is decisive—ideally for applying statistical models and understanding climate risks in a region (de Lima and Lovejoy, 2015; Comin et al., 2020; Diez-Sierra and del Jesus, 2020). Anthropic actions in the environment have a significant effect on climate change by changing local weather conditions and so compromising agriculture and the environment (Herath et al., 2018).

Agro-ecological zoning and the characterization of homoclimatic regions, based on meteorological variables, have become necessary for planning actions aimed at economic, social and environmental activities. Marumbwa et al. (2019) used the technique of grouping meteorological data in arid and semi-arid environments and observed changes in the rainfall

63 events of the biomes, which allowed decisions to be taken on adapting to climate change and
64 alternatives for ecosystem conservation. In this context, the use of classical statistics makes
65 it possible to explain the relationship of up to two variables; however, the application of
66 multivariate statistics allows us to explain a set of two or more variables. Therefore, the use
67 of multivariate statistics associated with climatic data has grown over the years, to infer
68 clustering information based on its meteorological similarity (Saraçli et al., 2013; Raziei,
69 2018; Silva et al., 2021).

70   The State of Pernambuco located in the East part of NEB (ENEB) exhibits great
71 spatial and temporal variability of the rainfall regime, due to the diversified geography of the
72 region and the proximity to the Atlantic ocean. In this context, the climate is characterized as
73 tropical-humid (coastal strip) and semi-arid as a result of the shape and morphology of the
74 state, and especially because of the active atmospheric systems (Silva et al., 2017; Jardim et
75 al., 2019; Leal et al., 2020; Comin et al., 2020; Silva et al., 2021). The region is influenced
76 by several meteorological systems that operate more precisely on the synoptic and sub-
77 synoptic scale; there are Frontal Systems (FS), Intertropical Convergence Zone (ITCZ), East
78 Waves Disturbances (EWD), Upper Tropospheric Cyclonic Vortices (UTCV), and South
79 Atlantic Subtropical High (SASH); in mesoscale are the Instability Lines (IL), Mesoscale
80 Convective Complexes (MCC), mesoscale circulation (sea-land and valley-mountain
81 breezes); and on a microscale are small convective cells, orographic circulation, these being
82 major factors in the modification of air mass flow on a vertical and horizontal scale (Molion
83 and Bernardo, 2002; Reboita et al., 2010, 2012; Lyra et al., 2014; Utida et al., 2019). In
84 addition, in the ENEB region, there are modes of climatic variability that interfere with
85 climatic variability and the dynamics of the region's biomes (Correia Filho et al., 2019), for
86 example, El Niño-Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO) and
87 Atlantic interhemispheric sea surface temperature gradient (AITG) - (Lyra et al., 2017;
88 Erfanian et al., 2017).

89   In recent years, several climatological studies have been carried out at ENEB with an
90 emphasis on climate variability (Moscati and Gan, 2007; Correia Filho et al., 2019), climate
91 projections (Utida et al., 2019; Marengo et al., 2020), among others. However, few studies
92 have characterized climatic similarity in the ENEB region (Marinho et al., 2020; Medeiros
93 et al., 2020). The objective of this paper was to determine the spatiotemporal climatic

94 similarities of municipalities along a longitudinal gradient from the east to north-east of
95 Pernambuco State, Brazil, in the period 1993 to 2018.
96

97 **2. Material and methods**
98 *2.1 Study area and data used*
99   The study region comprises the Pernambuco State, with an area of 98,937 km^2, which
100 covers eight municipalities (Ouricuri, Cabrobó, Petrolânida, Triunfo, Arcoverde, Garanhuns,
101 Surubim and Recife), from the *Sertão* mesoregion to the *Zona da Mata* (Figure 1a). The
102 characteristic climates in the state's mesoregions, according to the Köppen classification are
103 "BSh" (semi-arid in low latitude and altitude), "As" (tropical with dry summer) and "Am"
104 (tropical monsoon) that influence a proportion of 61.4%, 32.7%, and 4.9% of their territory,
105 respectively (Alvares et al., 2013). The smaller coastal region (metropolitan area) with "Am"
106 climate, and the *Sertão* region and zone of transition of the state with "BSh" and "As" climate
107 (Medeiros et al., 2018) showing in those places, high seasonal and interannual variability of
108 rainfall (Rodrigues et al., 2020). According to the Brazilian Institute of Geography and
109 Statistics (IBGE), the total population of the eight studied municipalities is approximately
110 2,080,424 inhabitants (IBGE, 2019). The state presents a transition of vegetation starting
111 from the longitudinal axis from east to west, represented by 'Atlantic Forest' to 'Seasonal
112 Dry Tropical Forest' (known as *Caatinga*) - (Correia Filho et al., 2019; Queiroz et al., 2020a).
113

114
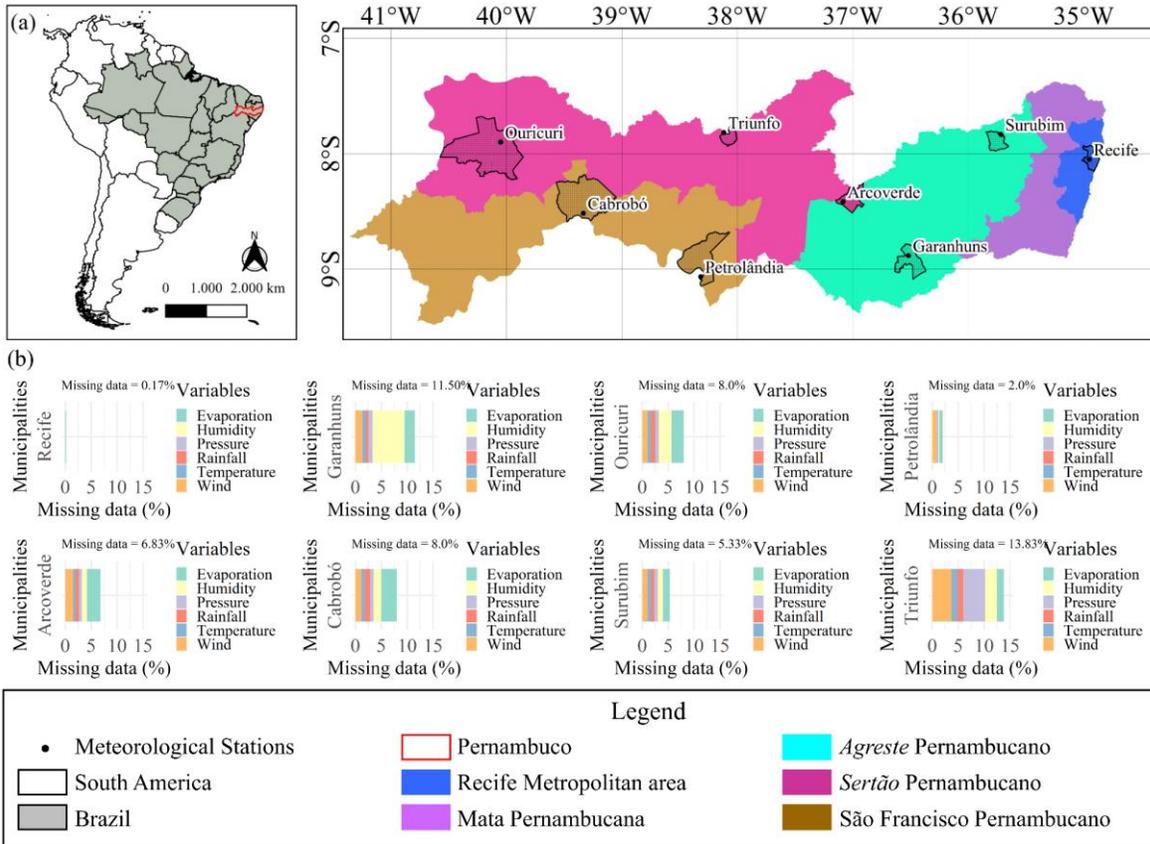
Fig. 1. The geographic location of the eight municipalities in the State of Pernambuco, Brazil (a); and (b) missing data from meteorological stations. Note: Variable not shown in the graph indicates contains no missing data in that municipality.

We first examined the database from eight conventional (manual) meteorological stations in a historical series of 26 years (1993 to 2018) of daily data, belonging to BDMEP (Meteorological Database for Teaching and Research), from the National Institute of Meteorology (INMET, 2019). With the data series, data consistency analysis was performed (average, data inference and identification of outliers), in spreadsheets, which considered the years with complete data, for better quality (minimum of missing data in the respective years) - (Figure 1b). We performed a boxplot analysis to identify outliers and statistical properties, i.e. three percentiles (median and interquartile range), and the minimum and maximum values (whisker, represented by the small vertical [upper-lower] lines of the standard boxplot) constituting the five-number summary of all meteorological parameters used in our study

97

129 (see Figure 2). This type of analysis of climatological consistency helps to flag suspicious

130 values (Lima et al., 2021).

131
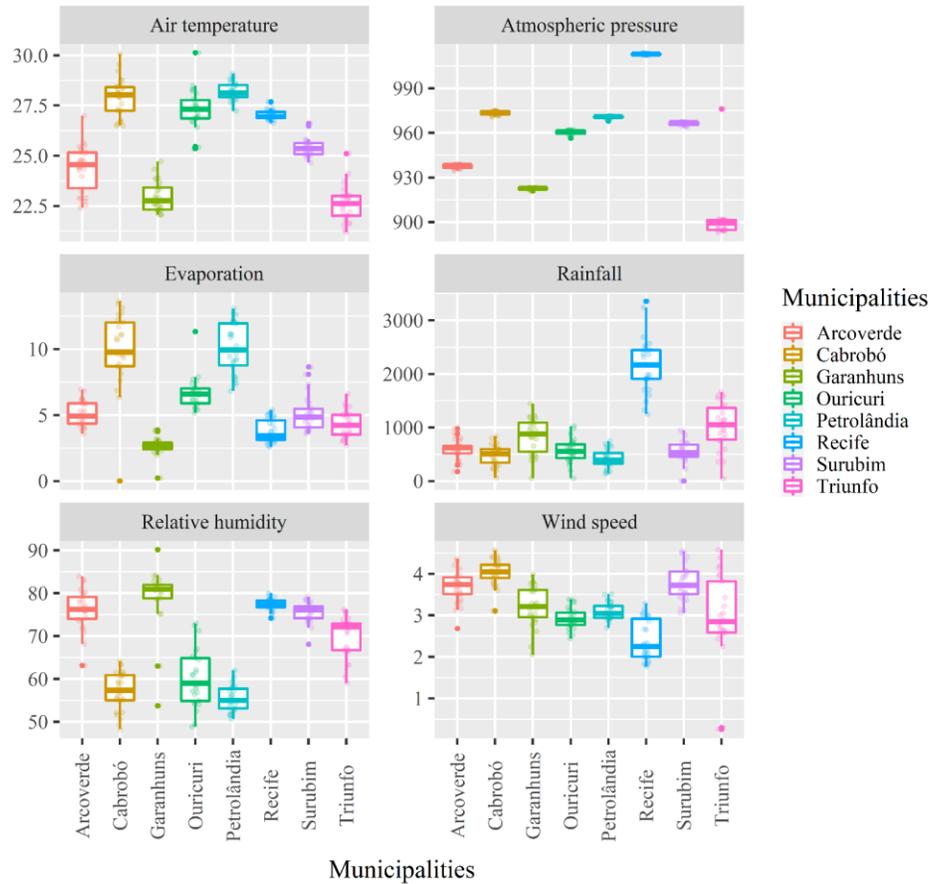
132

133 **Fig. 2.** Boxplots of yearly meteorological data sets (air temperature - ºC year^{-1}, atmospheric

134 pressure - hPa year^{-1}, evaporation - mm year^{-1}, rainfall - mm year^{-1}, relative humidity - %

135 year^{-1}, and wind speed - m s^{-1} year^{-1}) in the period 1993–2018 of the eight municipalities in

136 the State of Pernambuco, Brazil. Note: Lines were used to indicate the boundaries of the

137 adjusted boxplot.

138

139 *2.2 Data analysis and statistical techniques used*

140   The meteorological data of each municipality were subjected to descriptive statistics

141 (boxplots), to identify the spatial distribution of these analyzed parameters. In the cluster

142 analysis and principal component analysis, all the meteorological variables were

143 standardized, since their measurement units differ from each other, trying to ensure that they

144   have the same score reliability (i.e., to eliminate the scale effect). After standardization,

145   cluster analysis (CA) was performed by the dendrogram, using Ward's aggregation method

146   and employed at Euclidean distance (Ward, 1963). In general, this method is regarded as very

147   efficient when it comes to climate data and considers the squared Euclidean distance as a

148   measure of dissimilarity or similarity to clustering (Wilks, 2011; Lima et al., 2021).

149   The similarities were attributed to the meteorological variables (rainfall - mm,

150   average air temperature - °C, average relative humidity - %, evaporation - mm, average wind

151   speed - m s^{-1}, and atmospheric pressure - hPa), by calculating the Euclidean distance (d_{ij}) and

152   by the hierarchical method of Ward (indicated for analysis of climatic data and demonstrating

153   more realistic results) between two objects (*i* and *j*), in which, the shorter their distance, the

154   greater the quantitative similarity between individuals (Ward, 1963; Lyra et al., 2014), as

155   described in Equations 1 and 2, respectively.

156

157    $$d_{ij} = \sqrt{\sum_{k=1}^{n} (x_{ik} - x_{jk})^2} \qquad (1)$$

158

159   where, d_{ij} is the Euclidean distance; x_{ik} and x_{jk} are the data observed at the meteorological

160   stations of municipalities *i* and *j*, respectively.

161

162    $$W = \left[\sum_{i=1}^{n} x_i^2 - \frac{1}{n} \left(\sum_{i=1}^{n} x_i \right)^2 \right] \qquad (2)$$

163

164   where, *W* is the minimum intergroup variance by Ward's hierarchical method; *n* is the number

165   of elements; x_i is the *i*-th member of the group.

166

167   Subsequently, principal component analysis (PCA) was used to identify which

168   components are most affected by the climatic patterns of the municipalities. This method

169   allows statistical parameters to reduce orthogonal and non-correlated variables, which

170   explain most of the total variation (Xie et al., 2019; Jardim et al., 2021). When faced with a

171   very large data set we apply this analysis to reduce its size, while minimizing any loss of

172 information, and expanding the interpretation of the variability data explained. In the
173 application of the analysis, diverse components are created; however, the first component
174 will be the most important, as it explains the highest percentage of the data variance, while
175 the later components created in the analysis represent a lower variation of the data. Moreover,
176 we also performed the Pearson correlation test for the six meteorological variables in the
177 eight municipalities, to observe the strongest associations between the variables, with a
178 significance level at p-value ≤ 0.05.

179   The Kaiser criterion was used, considering eigenvalues (λ) above 1.0. Nevertheless,
180 when above 1.0 they generate components with a relevant amount of information contained
181 in the original data, discarding components with eigenvalues below 1.0 (Kaiser, 1960). In the
182 PCA, the eigenvalue corresponds to the variance of each principal component (PC),
183 therefore, it is an important measure to explain the variation of the data (Jolliffe, 1990).

184   We conducted the PCA following four fundamental steps to build the analysis. In the
185 first step, we perform the standardization of the dataset (i.e., the entire data to have zero mean
186 and unit standard deviation). The second step consisted of calculating the covariance matrix
187 to identify the possible correlation between the variables in the data set sampled in this study.
188 In the third step, we calculate the eigenvalues (Equation 3) and eigenvectors (Equation 4) for
189 the covariance matrix to thus determine the principal components of the data. Later, in the
190 fourth step, we constructed a characteristic vector matrix (A) containing the principal
191 components (PCs), which includes the eigenvalues selected greater than the unity ($\lambda > 1$).
192 The new data sets are formed by multiplying the matrix of the vector of transposed
193 characteristics (A^{T}) by the standardized data matrix (E). The principal component analysis is
194 a decomposition of an $m \times w$ matrix X, with m measurements performed and w variables
195 (Equation 5).

196

197     $|(C - \lambda \cdot I)| = 0$ (3)

198

199     $|(C - \lambda \cdot I)| \cdot v = 0$ (4)

200

201     $X = A^{\mathrm{T}} \cdot E$ (5)

202

203 where C is the covariance matrix; I is the identity matrix of the same dimension; v is the

204 eigenvector; A is the data matrix that contains the loadings (i.e., matrix $A \in \Re^{w \times r}$); superscript

205 T denotes matrix transposition; E is the data matrix that contains the scores (i.e., matrix $E \in$

206 $\Re^{m \times r}$); and r is the dimension of number independent columns in X and is bounded by the

207 minimum of m and w.

208

209   The entire data set was standardized to obtain a better physical interpretation of the

210 variables, and to maximize the correlation of the variables and components (Nehrani et al.,

211 2020). All analyses were performed using R software version 4.0.1 (R Core Team, 2020).

212

213 *2.3 Classification dataset for ENSO warm and cold episodes*

214   Information on climatic fluctuations in the occurrence of ENSO was obtained from

215 the database of the National Oceanic and Atmospheric Administration and Climate

216 Prediction Center - NOAA/CPC (NOAA/CPC, 2020). ENSO is a phenomenon that results

217 from the atmosphere-ocean interaction that affects the global climate (Patra et al., 2020). The

218 years of El Niño, La Niña, and neutral from 1993 to 2018, were based on a limit of $\pm$ 0.5 ºC

219 of the sea surface temperature (SST) of the equatorial Pacific ocean and the Oceanic Niño

220 Index (ONI), with a minimum of five consecutive 3-month averages seasons overlapping in

221 the Niño 3.4 region (5º N–5º S, 120º–170º W, calculated based on the ERSST.v5 dataset) –

222 (Huang   et   al.,   2016).   Data   used   was   found   at   the   following   website:

223 http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml.

224 We consider the major La Niña and El Niño phenomena regarding the occurrence of negative

225 and positive anomalies, respectively. Such anomalies are presented on the NOAA/CPC

226 online open-access platform, defined as the continuous average of three months and classified

227 as warm (red) and cold (blue) according to NOAA/CPC (2020). Thus, this type of

228 investigation of ENSO contributes to understanding rainfall variability in the NEB

229 (Ndehedehe et al., 2020; Medeiros and Oliveira, 2021).

230

231 **3. Results and discussion**

232   Table 1 shows the principal components of the meteorological variables with their

233 respective loadings, eigenvalues, the total variance of each component, and the accumulated

total variance. The eigenvalues for the first three PCs were greater than 1.0, and thus considered relevant according to the criterion of Kaiser (1960). However, only components 1 (PC 1) and 2 (PC 2) were used for two-dimensional graphic projection, as they carry the highest rate of total variance for explaining the variables, about 59.50%.

Table 1. Summary of principal component analysis, consisting of loadings, eigenvalues and percentages (%) of the variance of meteorological variables of the eight municipalities in the State of Pernambuco.

Variables	PC 1	PC 2	PC 3
Rainfall	0.659	–0.566	0.087
Temperature	–0.747	–0.486	0.092
Humidity	0.581	0.038	0.644
Pressure	–0.306	–0.616	0.515
Wind	–0.309	0.627	0.617
Evaporation	–0.847	0.007	0.016
Eigenvalues	2.239	1.333	1.079
Variance (%)	37.30	22.20	18.00
Cumulative variance (%)	37.30	59.50	77.50

PC – is the principal component.

Similar results corroborate the present study (e.g., Darand and Daneshvar, 2014; Braga et al., 2012; Raziei, 2018). Darand and Daneshvar (2014), for example, analyzed a historical series of rainfall from 1951 to 2007, seeking to regionalize rainfall regimes in Iran, and obtained eigenvalues for the first three principal components above 1.0 and total variance of 70.98%, for the first two PCs. Raziei (2018) evaluated the monthly rainfall time series of 155 meteorological stations distributed in Iran (1990 to 2014) and obtained a total variance of 70.70% for PC 1 and PC 2, agreeing with results obtained in this study. Braga et al. (2012) identified three PCs that explain 94.0% of the total monthly rainfall variance in Rio Grande do Norte, NEB. The studies by Farrokhi et al. (2020) and El Alaoui El Fels et al. (2020), using climatic data, also demonstrated the relevance of applying the principal component

254 analysis technique and highlighted a better understanding of the meteorological phenomena,

255 as well as the high response of the total variance to explain the data by the components.

256 Figures 3a and 3b respectively show the principal components and Pearson's

257 correlation matrix of the environmental variables for the eight studied municipalities. The

258 variables of rainfall and relative air humidity presented greater relations with Recife and

259 Triunfo, explained by PC 1 (37.30%) with loadings of 0.659 and 0.581, respectively,

260 denoting a strong and positive relationship in this principal component for the variables

261 mentioned above. Even though Recife is close to the coastal environment, and Triunfo is in

262 the inland *Sertão*, the two municipalities have similar climatic conditions due to the

263 orography and influence of oceanic air masses, causing thermal gradients and providing the

264 greater expression of these variables. These two municipalities are the ones that have the

265 largest record of annual rainfall and relative humidity (see Figure 2). To explore this question,

266 we emphasize that there was a significant positive correlation between rainfall and humidity

267 (see Figure 3b) with the value of 0.375 ($p < 0.001$).

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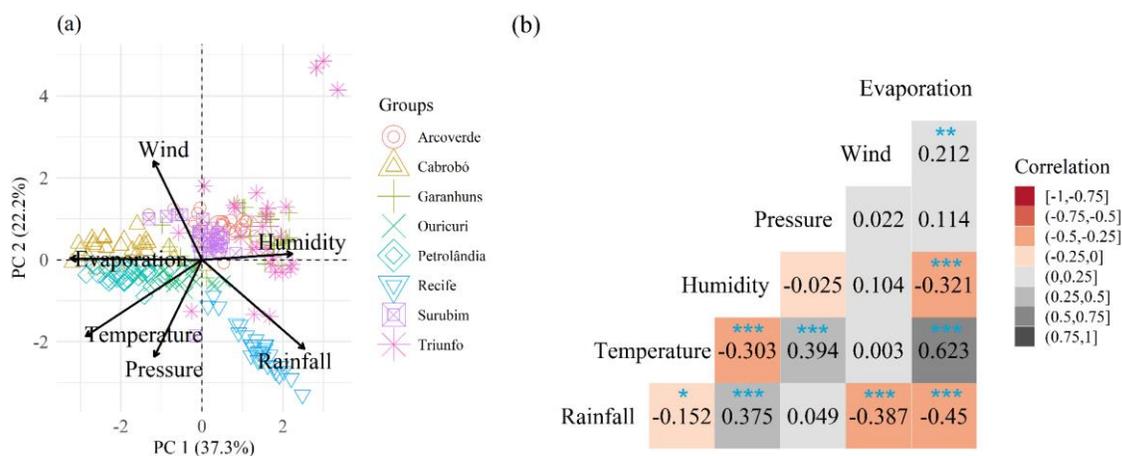
269

270 **Fig. 3.** Principal component analysis, scores plot of the first two principal components (a),

271 and Pearson correlation matrix (b) of the meteorological variables of the eight municipalities

272 in Pernambuco State, Brazil. Note: *, **, and *** correlation is significant at the 0.05, 0.01

273 and 0.001 level, respectively.

274

275 The geographical position is essential to determine the relationship between these two

276 variables. The meteorological station of Recife receives large masses of humid air coming

277 from the Atlantic ocean and therefore records high rainfall indexes; associated with this, the

278   ITCZ, EWD, trade winds, and the circulation of sea breezes act as the most important systems

279   in the rainfall on the coast of NEB (Reboita et al., 2012; Braga et al., 2012; Lyra et al., 2014;

280   Anjos and Lopes, 2019). High air humidity is common in Recife, to the point of causing

281   discomfort, very often in densely populated and urbanized areas (Souza Hacon et al., 2019).

282   In addition, it is important to mention that due to climatic and anthropogenic conditions, the

283   metropolitan region of Recife is affected by the urban heat island (UHI) phenomenon

284   (Monteiro et al., 2021), and it has been reported that the region's annual rainfall has a

285   tendency to increase (Nóbrega et al., 2015).

286   The Triunfo station is at an altitude of more than 1,000 m (see Figure 1), and the most

287   important static factor in determining climate is the relief, which acts as a natural barrier to

288   advancing air masses and so influences the distribution of air humidity and maintenance of

289   air temperature. Also, the microscale effects, such as orographic circulation and small

290   convective cells, provide higher levels of rainfall above 1,000 mm year^{-1} (Molion and

291   Bernardo, 2002; Valadão et al., 2017). According to Slavich et al. (2014) and Sobral et al.

292   (2018) the presence of physiographic factors can influence climate characteristics and local

293   biodiversity, mainly rainfall and wind patterns.

294   The municipalities of Petrolândia, Cabrobó and Ouricuri are grouped according to the

295   variables evaporation, air temperature and atmospheric pressure, explained by PC 1 with

296   negative loadings of –0.847, –0.747, and –0.306, respectively. Inversely proportional to

297   evaporation, temperature and pressure were the variable relative humidity of the air, being

298   higher in the municipalities of Triunfo, Surubim, Arcoverde, Garanhuns and Recife. These

299   results are statistically elucidated in an underlying way through the principal component

300   analysis presented in Figure 3a. Studies by Arraes et al. (2016) also classified these

301   municipalities as places with high relative humidity, since evaporation is not too high,

302   confirming our studies.

303   The wind speed variable was slightly related in the municipalities of Cabrobó,

304   Surubim and Arcoverde. Although Recife is on the coast, with higher rainfall, wind

305   conditions were not very relevant in the analysis. The municipality of Arcoverde receives air

306   masses from the ITCZ in the same way as Cabrobó; however, other mechanisms can directly

307   or indirectly alter the average behavior of local variables, like the eastern winds that transfer

308   moisture to the NEB (Comin et al., 2020).

309   In this context, it is possible that the SASH, an ever-present phenomenon on the NEB

310   coast (Lyra et al., 2014), can strengthen the southeast (SE) trade winds, together with the

311   local effects of a thermal gradient, which acts mainly to intensify or attenuate existing winds

312   (Moscati and Gan, 2007). The influence of the surface characteristics (e.g., relief, soil type,

313   soil cover and presence of water bodies) are equally determining factors for the dynamics of

314   meteorological variables processes. These situations can be noted in the studies developed

315   by Molion and Bernardo (2002) and Souza and Oyama (2017). These researchers verified

316   the connection between the trade winds and the sea breeze, which can penetrate up to 300

317   km inland from the coast. Silva et al. (2016) and Pimenta et al. (2019) confirm that the NEB

318   is notable for high wind speeds, mainly in the coastal region.

319   Atmospheric pressure, too, had little influence on the grouping of municipalities,

320   explained by PC 2 (22.20% and showed a strong negative loading of –0.616). However, it

321   was possible to observe (Figure 3a), that the municipality of Triunfo had the lowest values

322   of atmospheric pressure, due to its altitude, above 1,000 m (Figure 1). Thus, we find that

323   Triunfo has an inverse proportionality to atmospheric pressure (Figure 3a). According to

324   Sumesh et al. (2019), the topography of a locality has a great influence on the cloud system

325   and contributes to the amount and periodicity of rainfall in high places due to the overlapping

326   of hot and cold clouds, which favors the saturation of the atmosphere.

327   Figure 4 shows the dendrogram obtained by Ward's hierarchical method through the

328   Euclidean distance. The cut horizontal line of the Euclidean distance in the dendrogram was

329   considered to be half the greatest distance between the groups with homogeneous

330   characteristics, thus characterizing two large distinct groups.

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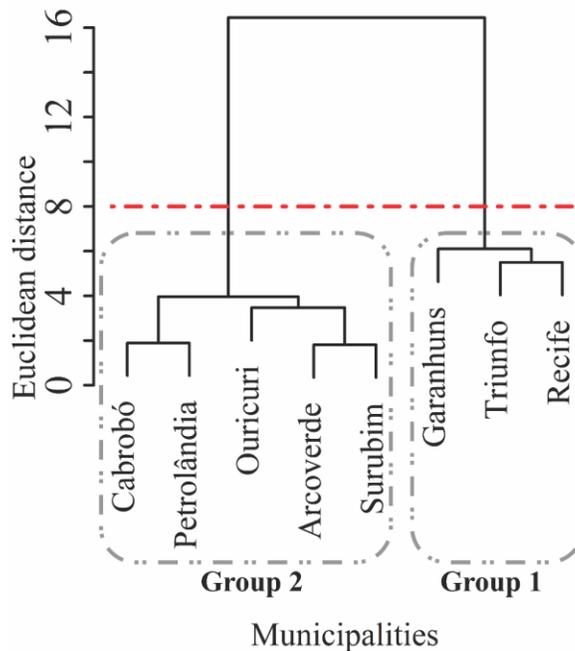
Fig. 4. Dendrogram for the classification of the two groups (G_1 and G_2), formed by Ward's hierarchical method with the Euclidean distance of the meteorological variables for the eight municipalities in the State of Pernambuco, Brazil.

336

In group 1 (G_1), made up of the municipalities of Recife, Triunfo and Garanhuns (Figure 4) - (average Euclidean distance of 5.80), the smallest homogeneous group formed and distributed in the mesoregions *Agreste*, Metropolitan and *Sertão* (see Figure 1), they were grouped by the similarity of the rainfall events, emphasizing the municipalities of Recife and Triunfo, which have normal climatic rainfall above 1,000 mm year^{-1}. Curiously, although Triunfo is located in the semi-arid region of the country, the region has a climate with rainfall ranging from 500 to 800 mm year^{-1}. Therefore, its altitude directly influences the annual rainfall volumes since it is at a higher altitude than the average compared to other municipalities from the semi-arid region (see Figure 2). The region is influenced by the ITCZ, which varies latitudinally, and in the period from February to May, when the position is further south (~4 ºS), it contributes to more intense rainfall events (Utida et al., 2019). This especially affects Recife, which is on the NEB coast and has rainfall above 1,500 mm year^{-1} (Oliveira et al., 2017). The significant influence on rainfall volumes at high altitude locations

350   was also reported by El Alaoui El Fels et al. (2020); however, the authors report an exception

351   due to the influence of the shelter effect, which may not accurately represent the overall

352   rainfall in their region compared to neighboring municipalities.

353   Group 2 (G_2), referring to the municipalities of Surubim, Arcoverde, Ouricuri,

354   Petrolândia and Cabrobó, the largest homogeneous group formed and distributed in the

355   mesoregions of *Agreste*, *Sertão* and São Francisco Pernambucano (Figure 1), shows

356   similarity regarding the climatic variables (evaporation, wind and air temperature), and the

357   Euclidean distances for these municipalities were also similar (Figure 4), with average

358   clustering of 2.78. Environmental factors can also influence the grouping of climatic

359   variables, for example from the interaction between vegetation cover and mesoscale

360   phenomena in the atmospheric circulation (Oliveira et al., 2017). The vegetation of the

361   *Caatinga* biome is related to the local rainfall index, which shows the seasonality of the

362   vegetation, with the municipalities in the semi-arid being characterized by this biome

363   (Ribeiro et al., 2016; Almeida et al., 2019; Correia Filho et al., 2019; Queiroz et al., 2020b).

364   Recently, Marengo et al. (2020) evaluated the projections of vegetative stress conditions from

365   the Vegetation Health Index (VHI) and indicated semi-desert and arid conditions that will

366   replace the *Caatinga* in 2100. This could seriously compromise food security and increase

367   social vulnerability in the NEB. Group 2 (G_2) regions are places with drier environments and

368   located in the central area of the Brazilian semi-arid region, due to the local topography,

369   under the influence of the Serra da Borborema (i.e. a topographic barrier against the

370   atmospheric flow), which deflects the trade winds and the sea breezes that arrive in these

371   regions, leaving the environment with a water deficit (Lyra et al., 2014).

372   A study by Lima et al. (2019) observed variations in the rainfall and air temperature

373   for the NEB region. They indicated that this variability was due to atmospheric phenomena

374   that affect it, such as sea breezes, trade winds, ITCZ, UTCV and FS. It is known that the

375   ENSO climate variability coupled with the sea surface temperature (SST) anomalies interfere

376   with rainfall, air temperature and wind patterns in NEB (Molion and Bernardo, 2002; Braga

377   et al., 2012; Lyra et al., 2017).

378   The distances generated by groups G_1 and G_2 explain the spatiotemporal

379   characteristics of similarity or dissimilarity that each municipality has in its climatic

380   conditions (Saraçli et al., 2013). This supports our understanding of the drier and wetter parts
381   of the country.

382   Based on the CA technique, the G_2 group was formed by the municipalities of
383   Cabrobó and Petrolândia (see Figures 4 and 5). According to the IBGE, both municipalities
384   showed agricultural diversity and high volume production of food through permanent and
385   non-permanent crops; for example, with a range of 14 crops (Cabrobó) and 16 crops
386   (Petrolândia) - (Andrade, 1975; Cierjacks et al., 2016; Hagel et al., 2019; IBGE, 2020). Such
387   diversification and increase production are due to the similar climatic characteristics, which
388   favor the development of a diversity of crops, and further encouraged by the municipalities
389   being located close to the São Francisco River. This ensures the production of irrigated crops
390   at different times of the year (Cierjacks et al., 2016; Santos et al., 2020; Teixeira et al., 2020).
391   Mostly in the semi-arid region, family farming predominates with the cultivation of beans,
392   maize, rice, and cassava. However, when not properly managed, it becomes more vulnerable
393   to the impact of climate variability due to the edaphoclimatic conditions of the region
394   (Rossato et al., 2017).

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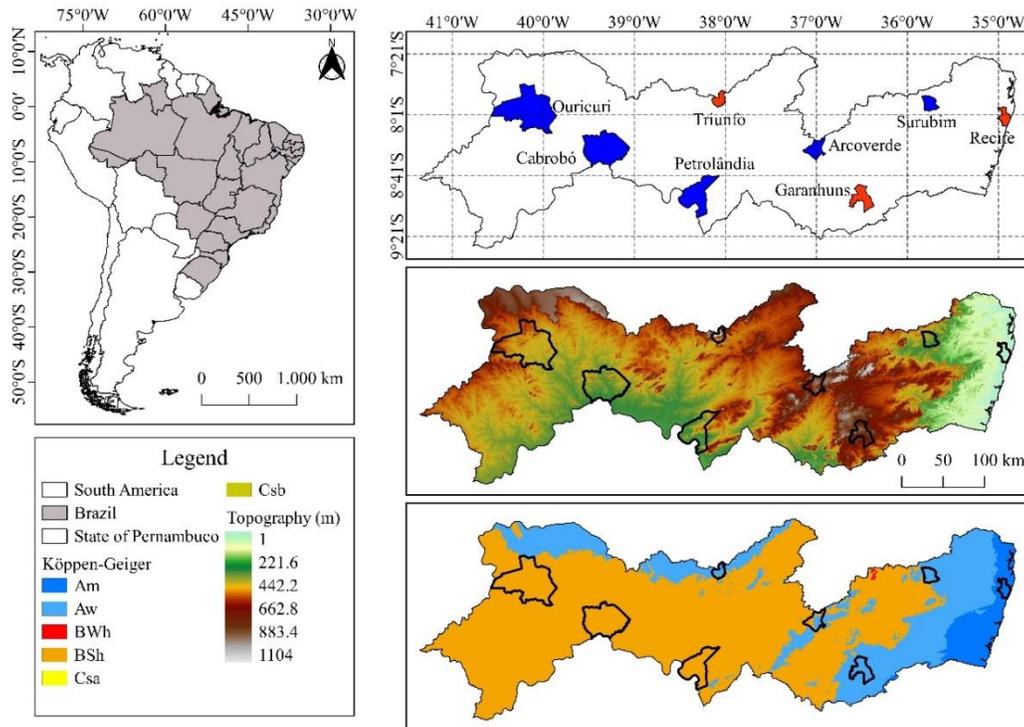
Fig. 5. Map of the clusters of municipalities (Group 1 (G$_1$): Recife, Triunfo and Garanhuns; and Group 2 (G$_2$): Surubim, Arcoverde, Ouricuri, Petrolândia and Cabrobó), topographic elevation and Köppen climate classification for the State of Pernambuco.

The municipalities of Cabrobó and Petrolândia stand out on the axis with the same climatic conditions according to the Köppen classification, categorized as "BSh" (Alvares et al., 2013). The municipalities of Triunfo, Garanhuns and Recife, comprise the G$_1$ group (Figures 4 and 5), regardless of altitude, the municipalities have similar climatic characteristics, being "Am" and "Aw", according to the Köppen classification, like the results obtained previously by Medeiros et al. (2018), with the classification of three climatic regions in the State of Pernambuco. According to Souza et al. (2021), despite the climatic variations in Pernambuco, the performance of the ENSO phases and the variability of the AITG (Lyra et al., 2017) cause interruptions in the grain harvest and crop gathering across the state. The problems caused by the decrease in rainfall because of meteorological droughts hinder the development of crops, causing the agricultural drought (Rossato et al., 2017).

Afterwards, we examined the historical analysis of the meteorological data (Figure 2) to identify the influence of the ENSO phases. Figure 6 shows the study region's annual

414   rainfall data, highlighting the most extreme ENSO phases (i.e., more intense/persistent in El

415   Niño and La Niña phases). All the municipalities evaluated reported intra-annual variations

416   in rainfall records. Such intra-annual variability is due to the ENSO phases (El Niño and La

417   Niña), which cause droughts and rains throughout the state (Jong et al., 2016; Souza et al.,

418   2018; Silva et al., 2019; Rodrigues et al., 2020), where the intra-annual variability is more

419   accentuated in the rainfall in the municipalities that are near the coast (Rao et al., 1993;

420   Rodrigues et al., 2020). However, in the inland, the variations are less accentuated but still

421   existing, caused by meteorological systems and the ITCZ seasonal modulation (Lyra et al.,

422   2014; Gomes and Lima, 2021).

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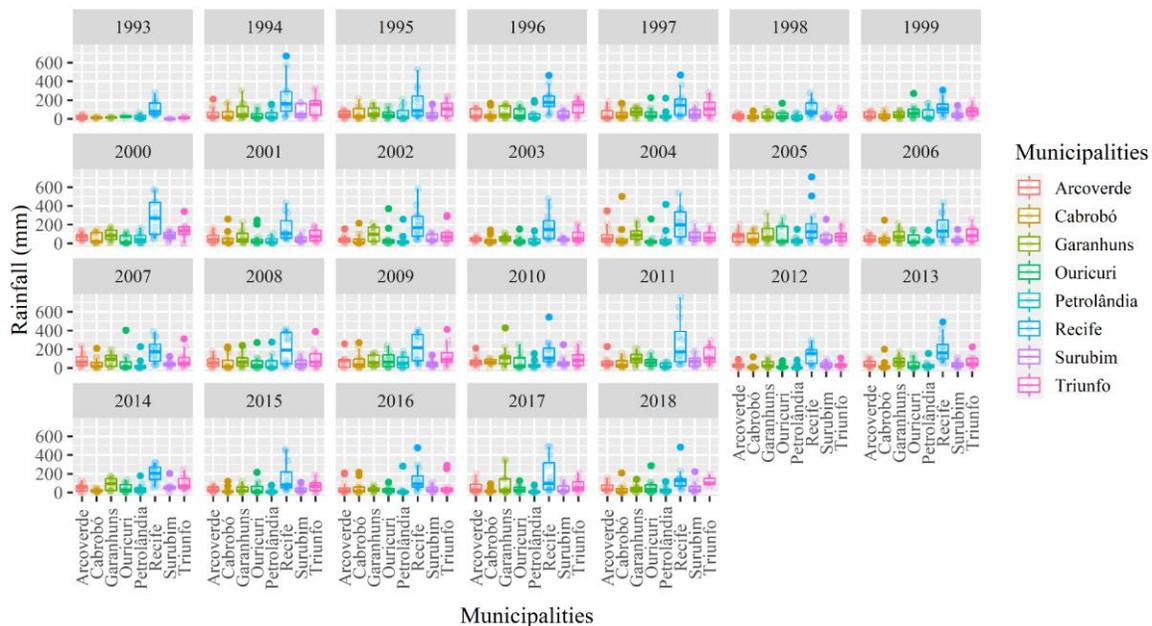
Fig. 6. Boxplot of annual rainfall (mm) of the eight municipalities in the State of
Pernambuco, Brazil, in the period 1993–2018. Note: We highlight the most extreme El Niño-
Southern Oscillation phases (i.e., more intense/persistent in El Niño and La Niña phases) that
occurred in the study period according to NOAA/CPC (2020).

429

430   Lower rainfall was recorded in 1993 under the influence of the ENSO-neutral phase

431   (NOAA/CPC, 2020). Despite being an ENSO-neutral phase year, rainfall volumes were

432   influenced by previous El Niño years (Cavalcanti, 2015). In 1997–1998, under what has been

433   called the El Niño of the century, there was a significant decrease in rainfall for all

municipalities, with approximately 50% of the rainfall recorded in 1998, being below average (see Figure 2), which was caused by a severe drought in the semi-arid region of NEB (Marengo et al., 2013; Correia Filho et al., 2019). The drought events that occurred in this region caused serious problems and threats to the local biome (i.e. *Caatinga*) - (Correia Filho et al., 2019; Pereira et al., 2020) and thus compromised the quality of life of the inhabitants, by causing collapses in subsistence agriculture – commonly practiced by farmers in the region (Justino et al., 2013; Novaes et al., 2013; Pereira et al., 2020). Previous studies reported the occurrence of La Niña in northeastern Brazil in 1998–1999 (Andreoli and Kayano, 2006; Kayano et al., 2011), with a predominance of strong La Nina in 1999 (Kayano and Capistrano, 2014). These findings are consistent with the results found in the present study for changes in rainfall. In the 2002–2003 biennium, all the municipalities studied except Recife were marked by the occurrence of drought caused by El Niño, and resulting in economic losses (Marengo et al., 2013; Rossato et al., 2017).

The years 2004–2005 were marked by above average rainfall (Figure 6), of the climatological normal of the municipalities, except Triunfo. This decrease in rainfall was caused by microclimatic effects with the topography of the site bringing rain to neighboring municipalities and blocking air masses at high altitudes. This phenomenon was also reported by El Alaoui El Fels et al. (2020) in places at an altitude higher than 1,000 m above sea level (asl). The main reasons are the geographical position of the study site together with the role of ENSO in decreasing and/or increasing rainfall, and being influenced by AITG and other micro and large-scale phenomena (Marengo and Espinoza, 2016; Lyra et al., 2017; Zanin and Satyamurty, 2020; Fonsêca et al., 2020).

The rains that occurred in the 2014–2015 biennium showed significant decreases, mainly in 2015, due to a super El Niño (Marengo et al., 2018; Correia Filho et al., 2019; NOAA/CPC, 2020). Highlight for the municipality of Garanhuns with high rainfall recorded in 2014 under the influence of the ENSO-neutral phase (NOAA/CPC, 2020). In the years 2012 to 2017, the entire NEB was affected by a prolonged extreme drought (Marengo et al., 2017), caused by anomalies in the Pacific (Silva et al., 2019), leading to damage to natural, economic and social resources (Costa et al., 2020). Such damage caused by ENSO, when it comes to drought, give rise to changes in the SST of the Pacific and Atlantic oceans and thus influence the productivity and carbon balance of vegetation in NEB (Pereira et al., 2020).

465   For NEB, in the five-year period 2011–2016 observations of extreme drought were reported

466   by Brito et al. (2018) and by Cunha et al. (2019), with critical periods from 2012 to 2017,

467   respectively. Indeed, 2012 is one of the years of greatest drought and impact for the Brazilian

468   semi-arid region (Paredes-Trejo and Barbosa, 2017; Marengo et al., 2017; Rossato et al.,

469   2017). The existence of contrasting changes in rainfall patterns in the region is a typical

470   feature of the climate in Brazil with the presence of ENSO (Grimm, 2011).

471   The decreases in rainy periods and rainfall over the years in the NEB region could put

472   the semi-arid areas of these locations at serious risk of desertification (Costa et al., 2020).

473   The damage caused by drought in Brazil between 1995 and 2014 was particularly

474   catastrophic in the NEB region, where 48% of the events occurred, and the State of

475   Pernambuco was the third most affected by natural disasters, which account for 16.2% of

476   damage caused throughout the region (Souza et al., 2021). However, the rains that occurred

477   in the 2017–2018 biennium were marked by a moderate ENSO phase (La Niña) -

478   (NOAA/CPC, 2020) which increased the rains (mainly in 2017) except for certain

479   municipalities, e.g., Ouricuri, Cabrobó and Petrolândia, these being municipalities that are

480   farthest from the coast (see Figure 6), which weakens the advances of air masses.

481

482   **4. Conclusion**

483   In this study we used multivariate statistical analysis to determine the meteorological

484   seasonality between the different regions of the State of Pernambuco, north-east Brazil. This

485   analysis is important for the population as it makes it possible to improve the productivity of

486   economic activities, especially crop production and livestock rearing. It should be noted that

487   atmospheric pressure, air temperature, evaporation and wind speed are positively associated

488   with the locations of Ouricuri, Petrolândia and Cabrobó. However, rain and relative humidity

489   were associated with a negative component, related to Recife, Garanhuns, Arcoverde and

490   Triunfo. It is worth mentioning that the physiographic factors and the main meteorological

491   systems are responsible for the associations identified in our study, which in turn can cause

492   extreme weather events and social vulnerability. The municipality of Triunfo stands out

493   because of physiographic factors that together with the occurrence of ENSO contribute to the

494   lowest rainfall records compared with surrounding municipalities that presented anomalies

495 in the rains. The ENSO phases directly influence the variability of rainfall in both
496 homogeneous groups identified in the study.

497   In general, the study is promising and still provides support for agricultural and
498 livestock planning, not only for the municipalities investigated but for the entire territory of
499 the State of Pernambuco. Future research with climatic data should be carried out to include
500 other regions of Brazil, and longer data series, to support public policies and the management
501 of municipalities regarding the mitigation of the impacts of future climate scenarios and
502 conditions.

503

513

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894

1 **CHAPTER 4**

2

3 Using remote sensing to quantify the joint effects of climate and land-use changes on the

4 Caatinga biome

5

6 **Abstract**

7 Caatinga biome, located in the Brazilian semi-arid region, is the most populous semi-arid

8 region in the world, causing intensification in land degradation and loss of biodiversity over

9 time. The main objective of this paper is to determine and analyze the changes in land cover

10 and use, over time, on the biophysical parameters in the Caatinga biome in the semi-arid

11 region of Brazil using remote sensing. Landsat-8 images were used, along with the Surface

12 Energy Balance Algorithm for Land (SEBAL) in the Google Earth Engine platform, from

13 2013 to 2019, through spatiotemporal modeling of vegetation indices, i.e., leaf area index

14 (LAI) and vegetation cover (V_C). Moreover, land surface temperature (LST) and actual

15 evapotranspiration (ET_a) in Petrolina, the semi-arid region of Brazil, was used. The principal

16 component analysis was used to select descriptive variables and multiple regression analysis

17 to predict ET_a. The results indicated significant effects of land use and land cover changes

18 on energy balances over time. In 2013, 70.2% of the study area was composed of Caatinga,

19 while the lowest percentages were identified in 2015 (67.8%) and 2017 (68.7%). Rainfall

20 records in 2013 ranged from 270 to 480 mm, with values higher than 410 mm in 46.5% of

21 the study area, concentrated in the northern part of the municipality. On the other hand, in

22 2017 the lowest annual rainfall values (from 200 to 340 mm) occurred. Low vegetation cover

23 rate was observed by LAI and V_C values, with a range of 0 to 25% vegetation cover in 52.3%

24 of the area, which exposes the effects of the dry season on vegetation. The highest LST was

25 mainly found in urban areas and/or exposed soil. In 2013, 40.5% of the region's area had

26 LST between 48.0 and 52.0 ℃, raising ET_a rates (~4.7 mm day^{-1}). Our model has shown

27 good outcomes in terms of accuracy and concordance (coefficient of determination = 0.98,

28 root mean square error = 0.498, and Lin's concordance correlation coefficient = 0.907). The

29 significant increase in agricultural areas has resulted in the progressive reduction of the

30 Caatinga biome. Therefore, mitigation and sustainable planning is vital to decrease the

31 impacts of anthropic actions.

32

35

1. Introduction

The Caatinga biome occupies a large portion of the Brazilian semi-arid region. It has a high ecological diversity of plant species, and it is considered the largest in the world under semi-arid conditions [1,2]. It occupies an area of 900,000 km^2, which corresponds to approximately 70% of the northeast region of Brazil (NEB). However, only 7.5% of this habitat is protected by law [3–5]. The municipality of Petrolina, PE, Brazil, is located in the semi-arid region of the Caatinga biome. It is within the hydrographic basin of the São Francisco river, which favors the development of irrigated agriculture in the region, mainly fruit-growing (e.g., grapes and mangoes) [6–8], and it leads to positive socioeconomic implications, but also increases conflicts regarding water use [2,9].

Caatinga is located in the world's most populated dry area, with more than 53 million inhabitants and a population density close to 34 inhabitants per km^2. This biome has been affected by environmental degradation and loss of biodiversity over the last decades, mainly by the intensification of agriculture (e.g., rainfed and irrigated crops cultivation), urban expansion, and the advance of pasture areas replacing the natural vegetation [10–12]. Expanding agricultural activities has led to the deforestation of native areas, soil disturbance, changes in the hydrological cycle, and higher carbon emissions [13–15]. Together with climate changes, such as reduced rainfall and intensified drought events, this makes the Caatinga biome and the Brazilian ecosystem the most threatened and susceptible to desertification. Furthermore, these changes have been increasingly compromising natural resources and environmental sustainability [16–19] due to the changes in surface properties and biophysical variables, such as vegetation cover (V_C), land surface temperature (LST), and evapotranspiration (ET) [20–22]. ET is one of the main response parameters of vegetated areas as a function of local water conditions, and it is also an important component of the hydrological cycle [23,24].

Therefore, monitoring physical–water indicators of environmental change conditions, such as the loss of biodiversity of biomes and land use and occupation, is vital in managing

scarce water resources. Furthermore, these indicators may be helpful in the planning of agricultural activities, as well as in the management of dry areas and the sustainable use and management of natural resources [17,25–30].

In this scenario, remote sensing has been used as a tool that presents fast and low operational costs, being efficient in calculating the biophysical parameters used in the energy, water, and vegetation balances (e.g., [31–33]). In recent years, remote sensing has also been considered a good alternative for replacing expensive and difficult-to-obtain equipment used in in situ studies [34]. Furthermore, the modeling used in these balances is performed with the help of algorithms, which are essential techniques in the extraction of information from satellite images on a regional and global scale [27,28,33,35]. It may have its efficiency improved by the use of open-source cloud programming languages, e.g., Google Earth Engine (GEE). In GEE, the user can effectively implement algorithms and process large data volumes [36].

In this context, there are several surface energy balance models, such as Mapping EvapoTranspiration at high Resolution with Internalized Calibration (METRIC), Surface Energy Balance System (SEBS), Simple Algorithm for Evapotranspiration Retrieving (SAFER), Atmosphere–Land Exchange Inverse (Alexi), and the Energy Balance Algorithm for Land (SEBAL), based on remote sensing data. The approach is substantiated on biophysical parameters, such as LST, albedo, Normalized Difference Vegetation Index (NDVI), and emissivity, that are crucial for estimating ET [16,37–42]. The SEBAL algorithm has been widely and successfully applied to various world ecosystems, including semi-arid conditions in Brazil [43–46]. Moreover, this method seeks to eliminate the propagation of errors in the partitioning of the energy balance and the need for atmospheric correction in the estimate of surface temperature. These interactions allow the generation of the sensible heat flux corrected for atmospheric stability and instability conditions [47–51]. NDVI is one of the most widely used indices in the literature for vegetation cover analysis, environmental degradation, and vegetation primary production resilience, and it also helps in monitoring agricultural crops, forest ecosystems, and drought assessments [52–54]. With applications in several countries, Bastiaanssen et al. [49] have obtained highly accurate results using the SEBAL algorithm on different vegetated surfaces with forests, agricultural crops (irrigated and rainfed), and even extreme landscapes, such as desert areas. Previous studies have shown

94 that the SEBAL can be used in Petrolina, PE, Brazil, for the algorithm has already been
95 calibrated and validated for the region in various ecosystems with good agreement between
96 orbital images and field measurements [44,55–58].

97   Based on the above, the main objective of this paper is to determine and analyze the
98 changes in land cover, land use, and occupation on biophysical parameters in the Caatinga
99 biome in the semi-arid region of Brazil. In the present study, the changes were assessed from
100 2013 to 2019 using Landsat imagery, and biophysical parameters (net radiation, energy
101 balance, LAI, V_C, ET_a, and LST) were estimated by utilizing remote sensing. Additionally,
102 the SEBAL model was applied to determine the surface energy balance in different
103 vegetation environments. After applying the model, the dataset provided by SEBAL allowed
104 us to determine the turbulent fluxes and actual evapotranspiration (ET_a) of the different land
105 use and land cover (LULC) types. Thus, through the SEBAL products, the spatiotemporal
106 variation patterns of ET_a in agricultural and forestry areas were evaluated.

107

108 **2. Materials and Methods**

109 *2.1. Study Area*

110   The study was carried out in the municipality of Petrolina, located in the State of
111 Pernambuco, Brazil. The region comprises the domain of the Caatinga biome and it belongs
112 to the semi-arid region of the sub-mean of the São Francisco Valley. The town is considered
113 the largest fruit-growing center of the Brazilian semi-arid region due to the easy access to the
114 São Francisco river, which supplies the irrigated perimeters. The municipality comprises a
115 territorial area of 4561.870 km^2 (Figure 1), with an estimated population of 349,145
116 inhabitants [38].

117
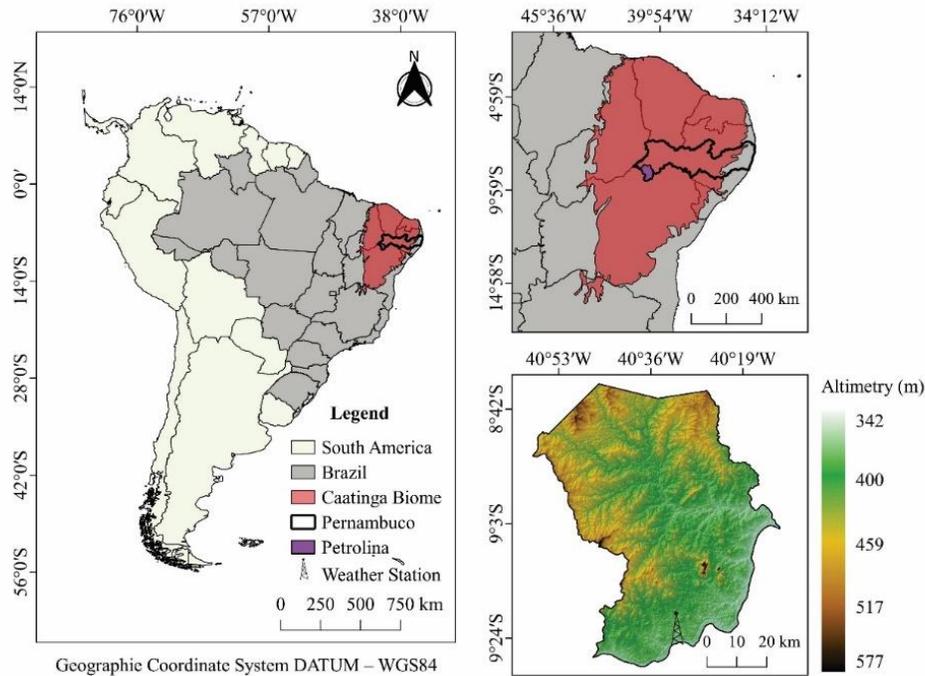
Figure 1. Spatial location of the study area, municipality of Petrolina, Pernambuco, Northeast Brazil.

A characteristic of the Caatinga biome is the presence of different floristic mosaics, consisting of an area of tree and shrub vegetation, which presents its distribution conditioned to climatic and environmental variations, especially rainfall intensity and frequency [59], as well as geological configurations and soil properties [5]. The vegetation of this biome presents deciduous species adapted to water deficit conditions and with expressive biomass production in rainy seasons, resulting from the local climatic conditions [40,60]. The canopy cover of the species of the Caatinga biome presents discontinuous characteristics, making possible the soil exposure in dry periods, presence of herbaceous stratum, cactus species, and shrubs [23,60]. It is worth noting that this region presents an expressive modification of the native landscape (Caatinga) in areas of irrigated agricultural cultivation.

According to the Köppen–Geiger climate classification, the region's climate is of the BSh type, characterized as semi-arid tropical, with an average air temperature of 26.4 ℃, average relative humidity of 62%, and annual rainfall of 520 mm [61,62]. Rainfall pattern is irregular throughout the year, resulting from its geographical location and the Intertropical Convergence Zone (ITCZ) influence, with rainfall predominating from February to May

137 [10,63,64]. The predominant soils in the municipality are Typic Quartzipsamment, Ultisol
138 Plinthic, Arenosol, and Haplic Acrisol [65–67].

139

140 *2.2. Satellite Images and Weather Datasets*

141   Annual records of average air temperature (ºC), global radiation (MJ m^{-2}), relative
142 humidity (%), atmospheric pressure (kPa), wind speed (m s^{-1}), and rainfall (mm) were
143 obtained from the database of the National Institute of Meteorology [68] (Figure 2). The
144 average air temperature (T_a) ranged between 24.1 and 30.7 ºC, in which 2015 and 2019 were
145 the warmest years studied ($T_a > 28$ ºC). Overall, November, December, January, February,
146 and March presented T_a values above 28 ºC (Figure 2).

147
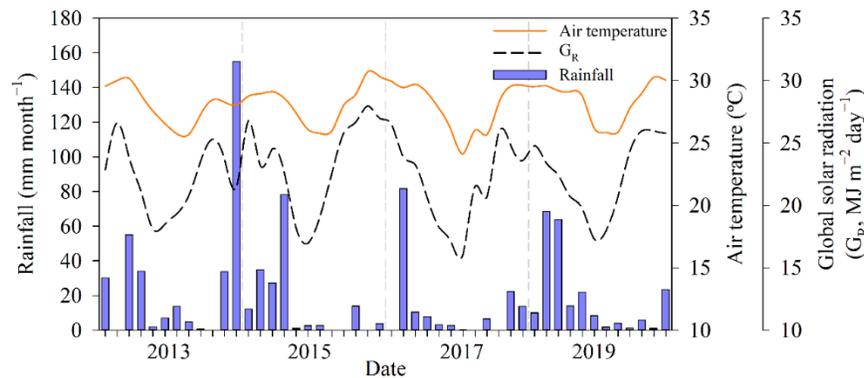
148

149 **Figure 2.** Monthly meteorological variations (rainfall, average air temperature, and global
150 solar radiation) of the municipality of Petrolina, Brazil, from 2013 to 2019.

151

152   The years 2013 (334.4 mm) and 2019 (221.6 mm) showed the highest rainfall rates.
153 Most of the rainfall recorded for Petrolina was concentrated from December to March (Figure
154 2). Such climatic conditions concerning the municipality were also reported in the literature
155 (e.g., [2,69]).

156   Rainfall data corresponding to the 30 days prior to the four imaging dates studied
157 used were obtained from the Climate Hazards Group InfraRed Precipitation with Station
158 (CHIRPS). CHIRPS are new precipitation products covering the coordinates 50º S–50º N
159 and 180º E–180º W, with 0.05º (± 5.3 km) spatial resolution and daily to seasonal, temporal
160 resolutions, available worldwide since 1981 [70]. CHIRPS data were extracted from the

Google Earth Engine platform (https://earthengine.google.com/, accessed on 20 August 2021) using JavaScript programming language. Then, they were exported in spreadsheet format (*.xls), using the dataset since 1981 from the collection ee.ImageCollection ("UCSB-CHG/CHIRPS/DAILY").

We used Operational Land Imager (OLI) Collection 1 Level 1 bands 2 (0.450–0.51 µm), 3 (0.53–0.59 µm), and 4 (0.64–0.67 µm) in the visible spectrum, 5 (0.85–0.88 µm) in the near-infrared, and 6 (1.57–1.65 µm) and 7 (2.11–2.29 µm) in the shortwave infrared, all with a spatial resolution of 30 m, as well as band 10 from the Thermal Infrared Sensor (TIRS) with a 100 m spatial resolution. Besides this, we used four Landsat-8 OLI/TIRS images, path 217 and row 66, corresponding to the years 2013, 2015, 2017, and 2019 (for the dates and times of the satellite overpass, see Table 1). The choice criteria adopted were the absence of clouds (<10%) and the images corresponding to the transition period between the dry and rainy seasons in the region under study, from the years of 2013 to 2019. This period presented severe and extreme drought events in the northeast [23,71]. All the images were obtained from the United States Geological Survey (USGS) platform (https://earthexplorer.usgs.gov/, accessed on 10 August 2021) and processed through the Land Surface Reflectance Code (LaSRC).

Table 1. Date of the Landsat-8 satellite pass, followed by the Julian day (JD), Earth–Sun distance (dr, astronomical units—AU), local time of the equator pass (h, hour; min, minutes), zenith angle (θ, °), solar elevation angle (E, °), and sun azimuth angle (φ, °) for the municipality of Petrolina, Pernambuco, Brazil.

Acquisition Date	JD	dr	Local Time	θ	E	φ
5 October 2013	278	0.99	9 h 49 min a.m.	0.90	65.12	82.93
12 November 2015	316	0.99	9 h 48 min a.m.	0.90	64.85	113.46
16 October 2017	289	0.99	9 h 48 min a.m.	0.91	65.81	92.82
7 November 2019	311	0.99	9 h 48 min a.m.	0.90	65.41	110.36

Note: zenith angle (θ) = sin(E). Source: USGS/NASA [72].

185 *2.3. Vegetation Indices*

186   The Normalized Difference Vegetation Index (NDVI) was calculated to represent the

187 amount and quality of vegetation present on the surface, characterized as an indicator of wet

188 conditions, calculated using Equation (1).

189

$$\text{NDVI} = \frac{\rho_{\text{NIR}} - \rho_{\text{Red}}}{\rho_{\text{NIR}} + \rho_{\text{Red}}} \tag{1}$$

190

191 where ρ_{NIR} and ρ_{Red} are the reflectances measured in the near-infrared and red bands (i.e.,

192 Landsat-8 multispectral bands 5 and 4 of the OLI sensor), respectively, they range from -1

193 to $+1$. Values close to 1 on a positive scale correspond to high photosynthetic activity, and

194 when negative, generally correspond to water bodies.

195

196   Based on the NDVI, we calculated the vegetation cover (V_C) of the study area

197 (Equation (2)), according to Gao et al. [54].

198

$$V_C = \frac{\text{NDVI} - \text{NDVI}_S}{\text{NDVI}_V - \text{NDVI}_S} \cdot 100 \tag{2}$$

199

200 where V_C is the vegetation cover, NDVI_S is the minimum NDVI value from bare soil pixels

201 obtained in the study area, and NDVI_V is the maximum NDVI value found in vegetated areas,

202 i.e., from fully vegetated pixels. The NDVI_S and NDVI_V used to calculate V_C were obtained

203 from the domain of each NDVI image percentile map obtained from the NDVI histograms.

204

205   Soil-Adjusted Vegetation Index (SAVI) was calculated to observe the vegetation

206 cover of the area (Equation (3)).

207

$$\text{SAVI} = \frac{(1 + L) \cdot (\rho_{\text{NIR}} - \rho_{\text{Red}})}{(L + \rho_{\text{NIR}} + \rho_{\text{Red}})} \tag{3}$$

208

209 where L is the adjustment factor to the soil, which varies between 0 and 1. The value 0 does

210 not reach change, and resembles the NDVI. In areas with low-density vegetation, the value

211 1 is assigned; for intermediate-density vegetation areas, the value of 0.5; and for areas with

212 high-density vegetation, the value 0.25 is assigned [73]. The adjustment factor of 0.5 was

213 adopted due to the study region indicating an intermediate vegetation coverage in most of the

214 year, with predominant vegetation of the Caatinga biome, in the Brazilian semi-arid region

215 [74–76].

216

217   To evaluate changes in vegetation biomass, the leaf area index (LAI, m^2 m^{-2}) was

218 determined (Equation (4)), a fundamental biophysical variable for monitoring studies of

219 agricultural land and vegetation moisture conditions [50].

220

$$\mathrm{LAI} = \frac{-\ln\left(\frac{0.69 - \mathrm{SAVI}}{0.59}\right)}{0.91} \tag{4}$$

221

222 *2.4. Methodology for Estimating Evapotranspiration Using Satellite Images*

223   Evapotranspiration was estimated using the Energy Balance Algorithm for Land

224 (SEBAL). For this, routine meteorological data and spectral bands from the Landsat-8

225 satellite were used. The SEBAL algorithm was implemented using JavaScript code through

226 the Google Earth Engine (GEE) platform. The data were exported in spreadsheet format

227 (*.xls). SEBAL uses mathematical modeling and operations to calculate the surface energy

228 balance components and determine evapotranspiration. Thus, energy balance components are

229 computed pixel-by-pixel, as described in Figure 3. Here, we show that the algorithm has a

230 good performance and high accuracy, as well as being calibrated and validated with

231 simultaneous field and Landsat satellite measurements [47–49,55,58,60,77,78].

232
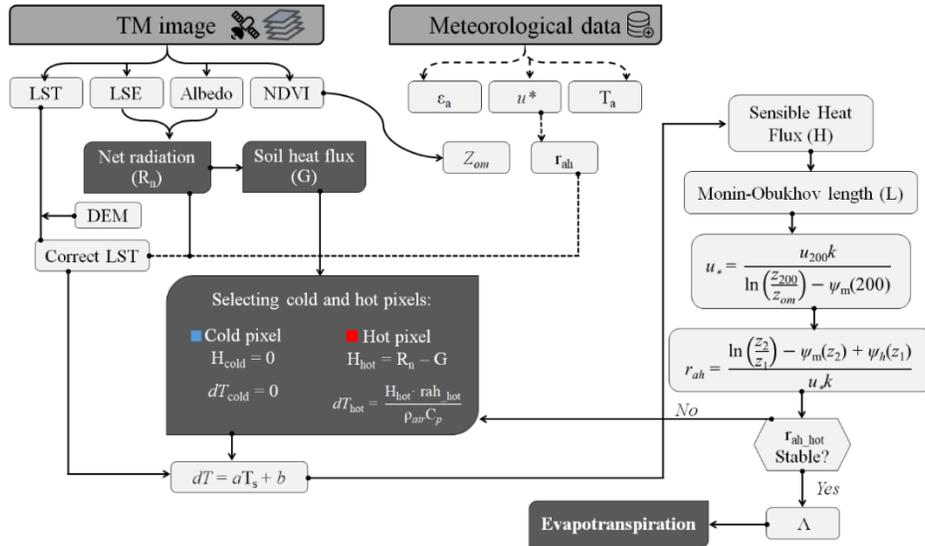
233

234 **Figure 3.** Flowchart of the SEBAL model for estimating evapotranspiration. Note: LST and

235 LSE are the land surface temperature and land surface emissivity, respectively, NDVI is the

236 Normalized Difference Vegetation Index, ε_a is the atmospheric emissivity, u^* is the friction

237 velocity, T_a is the air temperature, R_n is the net radiation, G is the soil heat flux, z_{om} is the

238 momentum roughness length, z_1 and z_2 are the two heights between the surface of the anchor

239 pixels, r_{ah} is the near-surface aerodynamic resistance to heat transport, DEM is the digital

240 elevation model, dT is the near-surface air temperature gradient, a and b are the calibration

241 coefficients, LST or T_s is the land surface temperature, ρ_{air} is the air density, C_p is the specific

242 heat of air, H is the sensible heat flux, ψ_m and ψ_h are the stability correction factors for

243 momentum and sensible heat, respectively, k is the von Karman constant, u_{200} is the wind

244 speed at the height of 200 m, and Λ is the evaporative fraction. These pre- and processing

245 steps were performed inside Google Earth Engine (GEE) cloud platform. The acronyms and

246 symbols used in this study are summarized in the Abbreviations section.

247

248 *2.4.1. Surface Albedo Adjustment*

249 The surface albedo (α_{sup}) corresponds to a measure of the reflectivity of the Earth's

250 surface, for each pixel, with atmospheric correction obtained according to Equation (5)

251 [50,79].

252

$$\alpha_{sup} = \frac{\alpha_{toa} - \alpha_{path}}{\tau_{sw}^2} \tag{5}$$

253

254 where α_{toa} is the albedo at the top of the atmosphere, that is, before atmospheric correction,

255 α_{path} is the atmospheric reflectance (set to 0.03, as used by Silva et al. [79]), and τ_{sw} is the

256 atmospheric transmissivity for clear sky conditions, according to Equation (6) [50,79]:

257

$$\tau_{sw} = 0.35 + 0.627 \cdot \exp\left[\frac{-0.00146 \cdot P_a}{K_t \cdot \cos(\theta)} - 0.075\left(\frac{W}{\cos(\theta)}\right)^{0.4}\right] \quad (6)$$

258

259 where P_a is the atmospheric pressure (kPa), with dataset available freely in

260 https://portal.inmet.gov.br/ (accessed on 10 August 2021), K_t is the turbidity coefficient of

261 the atmosphere ($K_t = 1.0$, for a clear sky day), according to Allen et al. [47] and Silva et al.

262 [79], θ is the solar zenith angle, and W is the precipitable water (mm), estimated from

263 Equation (7) [80].

264

$$W = 0.14 \cdot e_a \cdot P_a + 2.1 \quad (7)$$

265

266 where e_a is the actual atmospheric water vapor pressure (kPa), estimated from Equation (8).

267

$$e_a = \frac{HR \cdot e_s}{100} \quad (8)$$

268

269 where HR is the instantaneous relative humidity (%), and e_s is the water vapor saturation

270 pressure (kPa), estimated from Equation (9).

271

$$e_s = 0.6108 \cdot \exp\left(\frac{17.27 \cdot T_0}{237.3 + T_0}\right) \quad (9)$$

272

273 where T_0 is the instantaneous air temperature (ºC) at the moment of the satellite pass.

274

275 For obtaining α_{toa}, a linear combination of the spectral reflectance of the six reflective

276 OLI bands was performed according to Equation (10) [79]:

277

$$\alpha_{toa} = 0.300\ r_2 + 0.277\ r_3 + 0.233\ r_4 + 0.143\ r_5 + 0.036\ r_6 + 0.001\ r_7 \quad (10)$$

278

279   where r_2, r_3, r_4, r_5, r_6, and r_7 are the surface spectral reflectances for bands 2, 3, 4, 5, 6, and 7

280   of the Landsat-8 OLI, respectively.

281

282   We use Equation (11) to obtain each of the spectral reflectances.

283

$$r_b = \left(\frac{Add_b + Mult_b \cdot DN}{\cos(\theta) \cdot dr} \right) \quad\quad (11)$$

284

285   where the terms Add_b and $Mult_b$ belong to the radiometric rescaling group, specifically

286   reflectance_add_band (equal to -0.1) and reflectance_mult_band (equal to 0.00002),

287   respectively, presented in the metadata of each OLI—Landsat-8 image, DN is the digital

288   number value corresponding to the pixel, θ is the solar zenith angle at the data acquisition

289   time, and dr is the Earth–Sun distance in astronomical units.

290

291   *2.5. Determination of Surface-energy Partitioning*

292   Based on the surface energy balance components, the evaporative fraction was

293   determined. Initially, the surface radiation balance or net radiation—R_n was calculated, which

294   is distributed by the energy partitioning in front of the sensible heat fluxes—H, latent—LE,

295   and soil heat flux—G [47–50,60,77,78]. By performing this process, a linear relationship

296   between the surface and air temperature gradient was considered to exist. From this

297   relationship and the internal calibration process for extreme conditions such as temperature

298   and humidity, it was established the need for obtaining the knowledge of the so-called

299   "anchor pixels", i.e., hot and cold pixels, which are indicative of zero and maximum

300   evapotranspiration, respectively [47,48,60] (Figure 3).

301   The land surface temperature (LST) in K (Kelvin) was obtained using the spectral

302   radiance in band 10 of the TIRS sensor and the emissivity in the nearest band—ε_{nb} by the

303   modified Planck's Law [81], as described in Equation (12).

304

$$LST = \frac{K_2}{\ln\left(\frac{\varepsilon_{nb} \cdot K_1}{L_{10}} + 1\right)} \qquad (12)$$

305

306　where K_1 and K_2 are radiation constants specific for the Landsat-8 TIRS band 10, equaling

307　774.89 W m^{-2} sr^{-1} μm^{-1} and 1321.08 K, respectively, provided by NASA/USGS; and L_{10} is

308　the radiance at the wavelength received by the sensors (band 10, the thermal band).

309

310　　　　The ε_{nb} was calculated based on the LAI for each pixel according to Equation (13)

311　[41].

312

$$\varepsilon_{nb} = 0.97 + 0.0033 \cdot LAI \qquad (13)$$

313

314　　　　Initially, the temperature variation and aerodynamic resistance to heat transport in all

315　pixels of the study area (Petrolina, Pernambuco) were determined. The atmosphere was

316　initially assumed to be in a neutral stability condition. For this study, the hot pixel was

317　considered in the exposed soil plots (i.e., no vegetation cover and/or little vegetation and low

318　moisture content), assuming LE equal to zero. The cold pixel was considered in grape orchard

319　plots irrigated by micro-sprinklers, when H can be considered zero [47,48,60,77,78,82] (see

320　Figure 3). Since turbulent effects affect atmospheric conditions and air resistance, the

321　Monin–Obukhov similarity theory was applied and considered in the computation of H in all

322　pixels of the study area. It is worth noting that the Monin–Obukhov length was used for

323　corrections to the initial stable condition of the atmosphere [47–49,77,78].

324

325　*2.5.1. Calculation of Energy Fluxes (H and LE) and Evaporative Fraction*

326　　　　The sensible heat flux (H) in SEBAL is calculated using an iterative procedure from

327　the aerodynamic function (Equation (14)) [47–49,77,78].

328

$$H = \rho_{air} \cdot C_p \cdot \frac{(a + b \cdot LST)}{r_{ah}} \qquad (14)$$

329

330 where ρ_{air} is the moist air density (kg m^{-3}), C$_p$ is the air specific heat at constant pressure
331 (1004 J kg^{-1} K^{-1}), *a* and *b* are calibration constants of the temperature difference between
332 two heights (i.e., between the roughness length for heat transfer and the reference height,
333 usually 0.1 and 2.0 m above the displacement plane), and r$_{ah}$ is the near-surface aerodynamic
334 resistance to heat transport (s m^{-1}). Fundamentally, the coefficients *a* and *b* are determined
335 through an internal calibration for each satellite image by interactive processes. We consider
336 extreme pixels of wet/cold and dry/hot spots. They were selected to develop a linear
337 relationship between the aerodynamic temperature of the surface and the air temperature
338 difference, and the LST.

340   By knowing the components of the surface energy balance, such as the net radiation
341 (R_n, W m^{-2}), sensible heat flux (*H*, W m^{-2}), and soil heat flux (*G*, W m^{-2}), the latent heat flux
342 (*LE*, W m^{-2}) was determined, both corresponding to the time of the satellite pass over the
343 study area, according to Equation (15).

$$LE = R_n - H - G \qquad\qquad (15)$$

346   Subsequently, we determined the evaporative fraction (Λ) according to Equation (16).

$$\Lambda = \left(\frac{LE}{R_n - G}\right) \qquad\qquad (16)$$

349 *2.6. Estimate of ET$_a$ Using SEBAL Method*

350   Finally, as a SEBAL product, we determine the actual evapotranspiration (ET$_a$, mm
351 day^{-1}) [83] based on Equation (17) below, for each satellite image used. In this study, the
352 implemented SEBAL model had already been extensively validated and calibrated under
353 forests and agricultural land conditions [55,60,84].

$$\text{ET}_a = \left(\frac{\Lambda \cdot R_{n24} \cdot 86{,}400}{\lambda}\right) \qquad\qquad (17)$$

356   where R_{n24} is the daily net radiation (W m^{-2}), 86,400 is a constant for daily timescale
357   conversion (i.e., converts from seconds to days), and λ is the latent heat of vaporization of
358   water (J kg^{-1}). Then, the latent heat of vaporization allows the ET$_a$ expression in mm day^{-1}.
359   Hence, accurate estimation of R_{n24} (Equation (18)) was determined according to Bastiaanssen
360   et al. [49], and Lee and Kim [85]:

361

$$R_{n24} = \Lambda \cdot \left[(1 - \alpha_{sup}) \cdot R_n - a \cdot \tau_{sw} \right] \tag{18}$$

362

363   where a is a regression coefficient of the relationship between net longwave radiation and
364   atmospheric transmissivity on a daily scale, to which we assigned the value 143, as proposed
365   by Teixeira et al. [60]. The acronyms and symbols used in this study are summarized in the
366   Abbreviations section.

367

368   *2.7. Land Use and Land Cover Dynamics*

369   In the present study, we sought to evaluate the impacts of changes in land use and
370   land cover (LULC) under the biophysical variables in the municipality of Petrolina. Thus,
371   we performed the extraction of descriptive statistical parameters (i.e., minimum, maximum,
372   mean, median, and standard deviation) for the variables LAI, V$_C$, ET$_a$, *LE*, *H*, LST,
373   emissivity, and R_n in each class of LULC, from the maps available on the MapBiomas Brazil
374   platform [86]. This collection is highly reliable and it includes annual land use and land cover
375   (LULC) data for the period 1985–2019 and it prioritizes the following classes: (1) arboreal
376   Caatinga, (2) shrub Caatinga, (3) herbaceous Caatinga, (4) pasture, (5) agriculture, (6) mosaic
377   of agriculture and pasture, (7) urban area, and (8) water bodies with a spatial resolution of 30
378   meters [27,87].

379   The MapBiomas classification is a hierarchical system combining land use and land
380   cover. This classification is based on a pixel-by-pixel classification of Landsat images, where
381   we use the machine learning algorithm random forest. Thus, the LULC classes for 2013,
382   2015, 2017, and 2019 were converted from raster files to vector files. We use the
383   "polygonise" tool, which transforms classes into polygons with the help of QGIS 3.16
384   software [88]. After the new datasets were converted, the vector files were used to extract
385   the statistical parameters by using the "zonal statistics" tool of the QGIS 3.16 software [88].

386   This procedure provided a basis with greater data amplitude and greater coverage of the
387   region's surface under study, making it possible to compare the different land use and land
388   cover types. In addition, as a result of this process, four maps were generated, indicating the
389   land use and land cover changes.
390
391   *2.8. Statistical Analyses*

392   In this study, we applied a principal component analysis (PCA) on the biophysical
393   variables—e.g., LAI, V_C, ET_a, *LE*, *H*, LST, albedo, emissivity, and R_n—for 2013, 2015,
394   2017, and 2019. Principal component analysis was performed to reduce the large dataset and
395   convert the data series into sets of uncorrelated linear values without losing relevant
396   information [35,64]. PCA consists of computing the eigenvalues and eigenvectors of the
397   covariance matrix. Moreover, in the generation of PCA, diverse components are created, and
398   the first component is the most important, as it explains the highest percentage of the data
399   variance, while the later components created in the analysis represent a lower variation of the
400   data. Thus, the data were standardized, subtracting the minimum values from each value and
401   dividing by their interval in order to obtain the maximum amount of information extracted.
402   Only eigenvalues greater than 1.0 were taken into account, for they present expressive
403   information from the newly created dataset [89]. The generated loadings indicate the relative
404   importance of a given raw variable from the data sample in the principal component (PC)
405   [64]. Moreover, 400 random points were generated to compose the data of our regression
406   model. One hundred random points were generated across the study area (for variables LST,
407   *H*, and ET_a using SEBAL) for each assessment date [2] through the QGIS (e.g., using the
408   "random points inside polygon" and "point sampling" functions [88]).

409   Subsequently, we built a multiple linear regression model to determine ET_a
410   (predictand) in a simplified way. The selected variables were LST and *H* (predictors) due to
411   their strong correlation over the years with land use and land cover classes (results obtained
412   using PCA). This type of regression model assumes that there is a linear relationship between
413   the response variable *y* and the predictor variables (e.g., x_1, x_2, …, x_n); it may be described as
414   follows: $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + ... + \beta_n x_n + \varepsilon_{rr}$, wherein β_0 is the constant value, β_1, ..., β_n are
415   regression coefficients, and ε_{rr} is the random error. The threshold for predictor variable
416   inclusion was $p < 0.05$.

417

2.8.1. Goodness of Fit

The model performance analysis was based on the root mean square error (RMSE, the values close to zero reduce error and increase accuracy), the mean absolute error (MAE), percent bias (PBIAS), Nash–Sutcliffe efficiency coefficient (NSE), Lin's concordance correlation coefficient (LCCC), Willmott's index of agreement (*d*), which ranges from 0 to 1 (i.e., indicates no agreement at all and perfect agreement, respectively) [90–93], and coefficient of determination (R^2, i.e., indicates the model's accuracy in the prediction of response for a dataset) above 0.90. These metrics allowed us to evaluate the models' quality and enabled the extraction of relevant information in terms of applicability. Therefore, the lower the PBIAS and RMSE values, the better the model prediction performance. Furthermore, NSE is a reliable criterion for evaluating the model's predictive ability. We also used LCCC to measure precision and accuracy between predicted and measured values. Moreover, it indicates the degree of agreement between two methods by measuring the variation of their linear relationship from the 45-degree line through the origin. Thus, good models have LCCC equal or close to 1 [91–93]. Additionally, we applied analysis of variance (ANOVA) and the *F*-test ($p < 0.05$, Fisher's *F*-test) to investigate the statistical significance between ET_a values measured by the SEBAL algorithm and predicted by the model proposed in this study. All statistical analyses were performed using the R software [94].

3. Results and Discussion

3.1. Comparisons of Land Use and Land Cover (LULC)

Based on the classification via the MapBiomas platform and on the Landsat-8 satellite, the thematic maps of land use and land cover for the years 2013, 2015, 2017, and 2019 were highlighted, with the main classes represented in Figure 4.
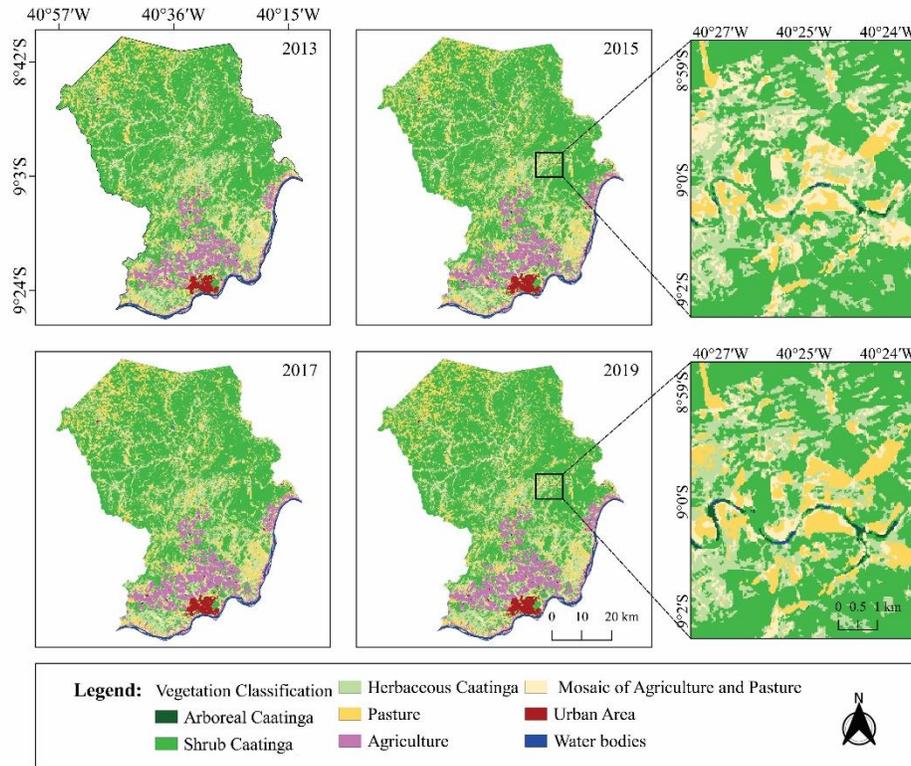
Figure 4. Thematic classification of cover and land use and occupation from MapBiomas between the years 2013 and 2019 for Petrolina, Pernambuco, Brazil.

The advances in exploration of agricultural areas for the municipality of Petrolina occurred mainly in areas nearby the São Francisco river, with a predominance of irrigated fruit farming. Moreover, the irrigated perimeters "Senador Nilo Coelho" and "Bebedouro" in these areas are located there, which, in the 1970s with the construction of the Sobradinho dam, boosted the exploitation and change in land use, impacting the Caatinga [37,95].

In 2013, 70.20% of the area (320,265.44 ha) of Petrolina was composed of Caatinga, being 51.60% shrub, 18.48% herbaceous, and the other 0.12% arboreal (see Figure 4 and Table 2).

Table 2. Annual quantification of land use and land cover conditions from 2013 to 2019 for the semi-arid region of Petrolina, Pernambuco, Brazil.

Classes	Annual Quantification of Land Use/Land Cover Types (ha year^{-1})

	2013	2015	2017	2019
Arboreal Caatinga	540.96	356.43	467.77	878.15
Shrub Caatinga	235,450.18	233,919.88	234,688.22	238,445.74
Herbaceous Caatinga	84,274.3	74,985.47	78,138.28	78,797.94
Pasture	53,346.49	55,356.09	60,156.62	60,176.26
Agriculture	31,919.62	34,209.91	35,678.87	36,718.13
Mosaic of Agriculture and Pasture	39,420.48	45,494.96	34,884.41	29,371.88
Urban area	4855.57	5496.18	5829.13	5825.78
Water bodies	6375.49	6364.17	6339.79	5969.21
Total	456,183.09	456,183.09	456,183.09	456,183.09

Source: Adapted from MapBiomas Brazil.

The lowest percentages of areas occupied by Caatinga vegetation were observed in 2015 (67.8%) and 2017 (68.7%), respectively. Compared to 2013, there was an average reduction of 2%, equivalent to 9123.65 ha of native forest (Caatinga), while in 2019, the reduction was only 0.45% (Table 2). It is important to emphasize that the reduction in Caatinga refers to herbaceous native vegetation. Such phenomena are related to the increase in areas of agriculture, pasture, and urban infrastructure, along with the occurrence of lower rainfall rates recorded between 2015 and 2017. However, between 2013 and 2019, an increase of 0.07 and 0.66% was observed in the native trees and shrubs vegetation areas, respectively (Figure 4 and Table 2). Furthermore, the expansion of arboreal vegetation areas occurred close to water bodies; on the other hand, the expansion of shrub vegetation occurred to replace areas previously occupied by agricultural activities (3234.56 ha), mainly pasture or in the ecological succession of areas of herbaceous vegetation (3679.17 ha) (Supplementary Table S1 and Figure S1). Silva et al. [96] studied the spatial–temporal evolution of agricultural activity in the Brazilian semi-arid region from 1998 to 2018, seeking to investigate the resilience of the Caatinga biome during the dry season. The authors mention that the expansion of the Caatinga biome occurred mainly with the reduction of agricultural activity, which reinforces the results obtained in the present study.

In 2013, the areas occupied with pasture represented 11.7%, agriculture 7.0%, and the mosaic of agriculture and pasture 8.64%, while areas with urban infrastructure and water bodies presented an occupation of 1.06 and 1.40%, respectively (Figure 4 and Table 2). From 2013 to 2019, there was an increase in areas with agricultural activity in the region, while a decrease in native herbaceous vegetation (Caatinga) was observed, which caused the conversion of 10,972.34 ha of native herbaceous vegetation to areas of agricultural activity (see Supplementary Table S1 and Figure S1). The types of LULC indicated the different intensities of human activities in the area. Several authors have reported the occurrence of severe drought events in NEB in the period between 2012 to 2016, in addition to the intensification of anthropic activities in the study region [10,23,27,71,97,98]. Those factors are responsible for significant changes in the phytosociology and floristic composition of the biome [10,23,27,71,97,98].

Drought is costly to Brazil, for it causes strong impacts on agriculture and cattle ranching. For example, the 2012–2013 drought resulted in economic losses of USD 1.5 billion for more than ten important crops in the region and USD 1.6 billion in cattle mortality [99]. Furthermore, Marengo et al. [10] emphasize that among adverse natural climate phenomena, drought is the factor that most affects society, as it impacts large territorial extensions of NEB, with intensified and increasingly long-lasting events over the years.

The agricultural and cattle ranching activity were significant in 2015, 2017, and 2019 with 29.6, 28.7, and 27.7%, respectively. Among the agricultural activities, the class of pastures (in this study, there is no detailed distinction between irrigated and non-irrigated pasture areas) was responsible for the largest occupied area, with values of 55,356 ha in 2015; 60,156 ha in 2017, and 60,176 ha in 2019 (see Table 2). The expansion of pasture areas resulted from the growing demand for food and for animal production, which favored changes in land use and occupation and, consequently, it increased the deforestation rate of the Caatinga biome [19]. Fleischer et al. [100] reported that the constant changes in land use and land cover might cause a significant impact on the flux and carbon stock since they are responsible for changing the sink capacity or carbon source of the ecosystem.

The agriculture class in 2015, 2017, and 2019 showed territorial occupation of 34,209, 35,678, and 36,718 ha, respectively, with an average increase of 0.80% (3616 ha) compared to 2013 (Table 2). This growth was favored by the development of irrigated agriculture in

508   the region, due to the proximity of the São Francisco river's channel, maximizing mainly
509   fruit farming, e.g., grape and mango [6,7]. Most of the times, irrigated fields are inserted in
510   areas previously occupied by Caatinga, which results in changes in the physical, chemical,
511   and biological soil properties [6,65]. In addition, changes in greenhouse gas (GHG) emission
512   fluxes resulting from anthropogenic modifications on native vegetation are also reported in
513   the literature [19,100].
514

3.2. Rainfall Variability in Land Cover Classes

516   Analyzing the spatiotemporal rainfall dynamics in the region over the 30 days
517   preceding the passage of the Landsat-8 satellite on the four assessment dates (5 October 2013,
518   12 November 2015, 16 October 2017, and 7 November 2019) allowed us to observe the
519   variation in rainfall distribution and volume, whose average accumulated values were 5.63,
520   1.7, 0.59, and 10.4 mm, for the respective dates. Despite the low rainfall volume observed in
521   the region, some areas showed a tendency for higher rainfall occurrence, which may be
522   conditioned to the native vegetation and orographic effects of the region (Figure 5).
523

524
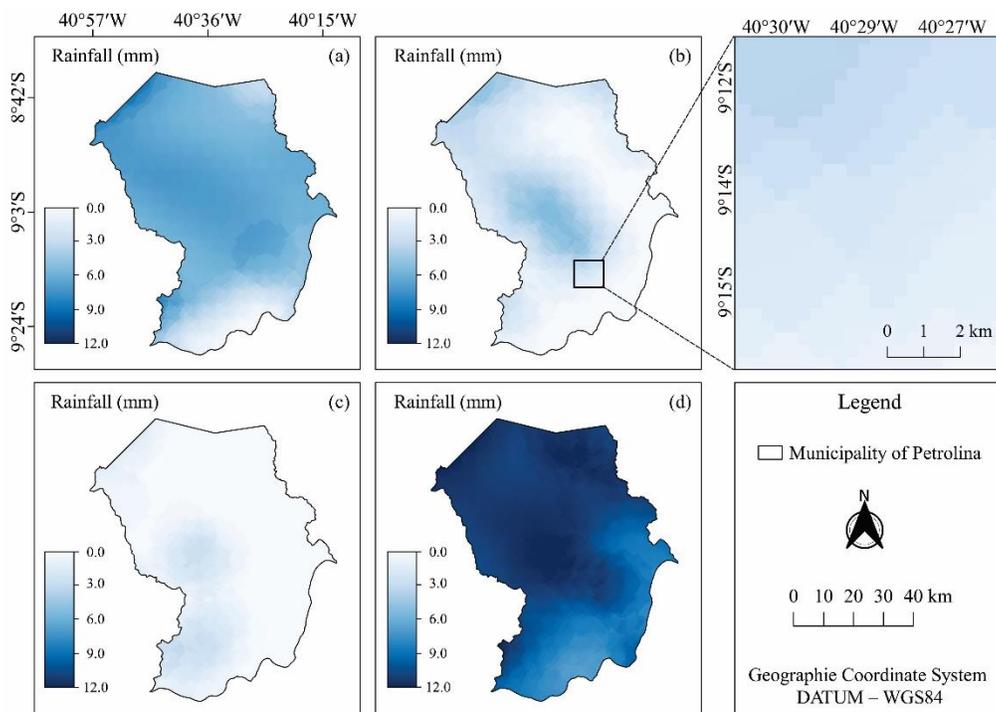
Figure 5. Spatiotemporal rainfall distribution (mm) for the CHIRPS satellite product in the municipality of Petrolina, Pernambuco, Brazil, in the 30-day period before the imaging dates 5 October 2013 (**a**), 12 November 2015 (**b**), 16 October 2017 (**c**), and 7 November 2019 (**d**).

Variations in rainfall distributions and volumes may have caused changes in vegetation cover, surface temperature, and evapotranspiration of the land portions observed in this study. Predominant vegetation of the Caatinga biome is quickly responsive to rainfall regimes, reducing foliage in the dry period (through deciduousness) and gaining biomass by the arrival of a new rainy period, which is considered a condition of defense and physiological adaptation of these highly efficient plants [101,102].

3.3. Vegetation Cover Indices of the Municipality

Figure 6 shows the percent vegetation cover (V_C) in Petrolina. The first three imaging dates in the study showed that, on average, 52.26% of the territorial area of the region had 0 to 25% vegetation cover (Figure 6a–c), revealing the direct effects of low rainfall volumes resulting from the dry season on native vegetation.
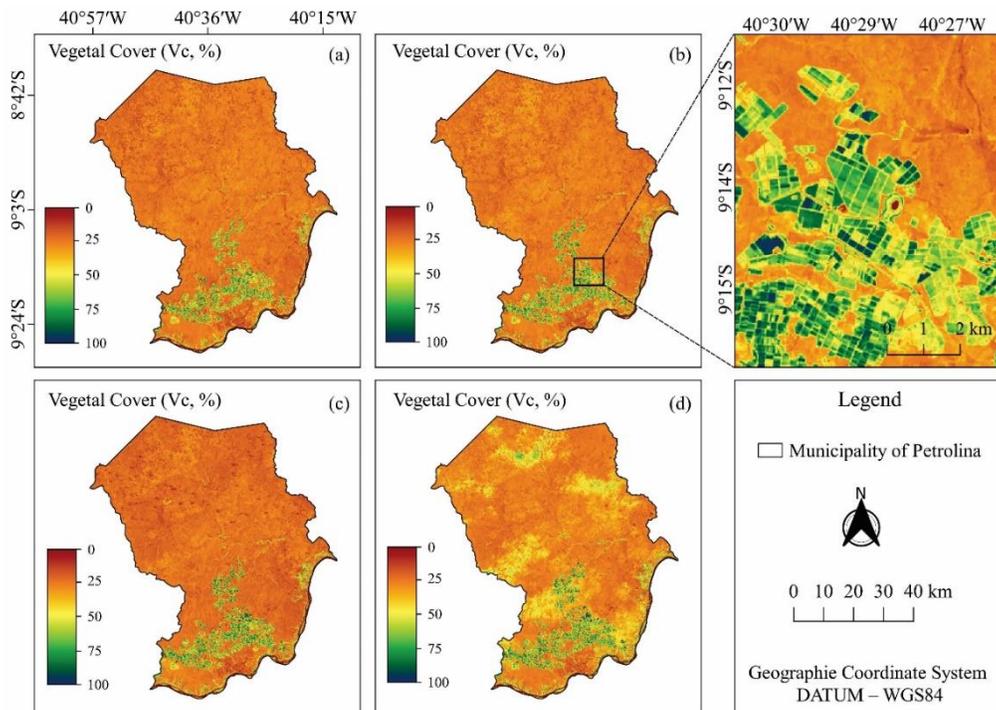
Figure 6. Condition of the different types of vegetation cover in the Caatinga agroecosystem in the municipality of Petrolina, Pernambuco, Brazil, on the imaging dates 5 October 2013 (**a**), 12 November 2015 (**b**), 16 October 2017 (**c**) and 7 November 2019 (**d**).

Under these conditions, variations in NDVI values are strongly linked to biomass production [101]. In studies carried out in the Caatinga, Cunha et al. [22], Leivas et al. [21], and Leivas et al. [103] reported that monitoring large-scale variations of water indicators and vegetation status is of crucial importance to minimize the adverse effects of climate and land use changes on mixed agroecosystems. Moreover, it can help in planning and decision-making processes for rational use of natural resources to mitigate the effects and duration of large-scale drought events.

The results reported here contribute to understanding water limitations and vegetation behavior. Due to the proximity of the São Francisco river, which supplies the irrigation systems, the areas of higher vegetation cover are found in the irrigated agriculture sites in the southern part of the municipality and the few remaining fragments of arboreal Caatinga, reaching average values of $58.71 \pm 22.18\%$ and $59.78 \pm 18.94\%$, respectively, throughout the period under study (Figure 6). However, it can be observed that in areas dominated by pasture, herbaceous, and shrub Caatinga, the mean values of V_C for the dates studied are lower ($22.84 \pm 6.70\%$, $27.17 \pm 5.45\%$, and $24.56 \pm 4.74\%$, respectively) (see also Figure 4). The advanced stage of pasture degradation and the intense grazing activity in natural areas of Caatinga also impact the vegetation density and, hence, its spatiotemporal dynamics and related surface variables such as NDVI, LST, albedo, and emissivity [2,71,104].

Santos et al. [102] emphasize that the arboreal vegetation is less susceptible to climatic variations than shrub and herbaceous vegetation, leading to less drastic reductions in V_C throughout the dry season. This characteristic is intrinsically linked to the adaptive capacity of species, favoring them to withstand the stressful effects of abiotic factors [105].

It is essential to highlight that on 7 November 2019, there was an average increase of 46.81% of areas with V_C higher than 50% in the northern part of the municipality (Figure 6d), which indicates a response of vegetation to the behavior of rainfall in this period, since this was the fraction of the polygon with the highest rainfall index during the 30 days prior to this evaluation date (Figures 5 and 6). The interrelationship of vegetation with

574 meteorological variables plays a crucial role in the ability to slow the advance of aridity, loss
575 of soil quality, and ecological diversity. In areas with consolidated vegetation, soil exposure
576 to solar radiation becomes lower, causing the maintenance of soil moisture and consequently
577 favoring the water availability in the environment for species. The intensification of anthropic
578 activities can directly cause damage to native vegetation, such as soil and vegetation
579 degradation; however, these changes can also influence climatic conditions and cause severe
580 damage to ecosystem services.

581   During the studied dates, the LAI varied between 0.00 and 3.3 m^2 m^{-2} (Figure 7).
582 However, in 97% of the region under study, the LAI values were lower than 0.825 m^2 m^{-2},
583 for in periods with low water availability, the Caatinga usually presents low LAI [106]. The
584 low LAI values can be justified not only by drought events but also by the characteristics of
585 the soils, which, in general, are shallow and have low water storage capacity. In addition, it
586 is worth noting that factors such as deforestation and intensive grazing activity in areas of
587 native vegetation, as well as a high degree of degradation of pasture areas, historically, are
588 common in this region, causing an imbalance of natural ecosystems [107,108].

589

590
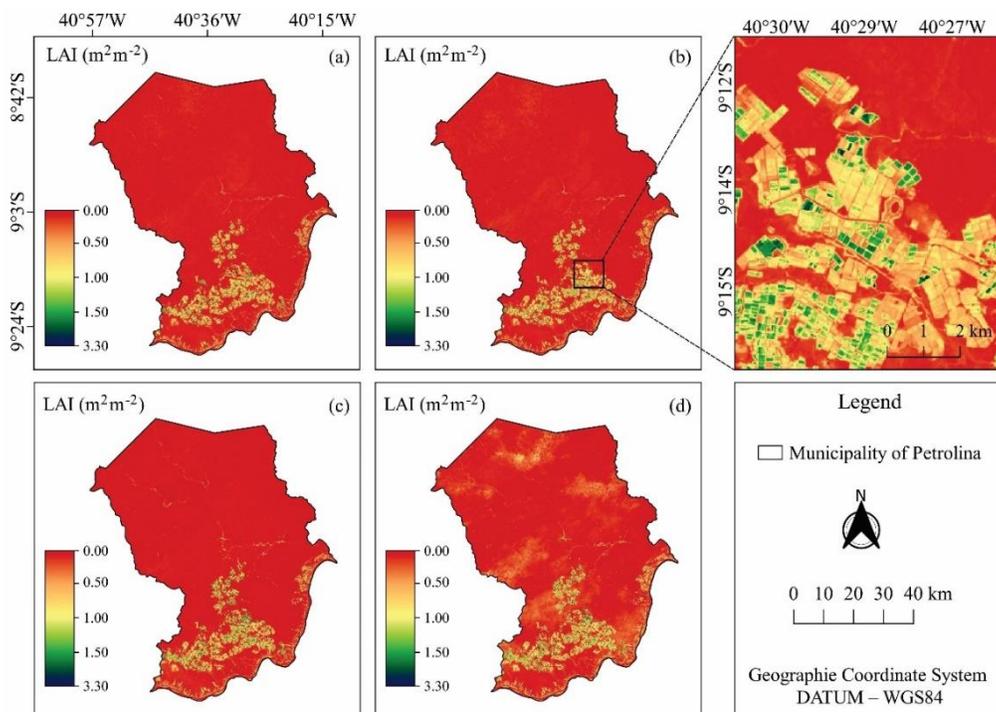
Figure 7. Spatiotemporal distribution of leaf area index (LAI, $m^2\ m^{-2}$) in the municipality of Petrolina, Pernambuco, Brazil, on the imaging dates 5 October 2013 (**a**), 12 November 2015 (**b**), 16 October 2017 (**c**), and 7 November 2019 (**d**).

The highest heterogeneity in LAI values was seen on 7 November 2019 (0.24 ± 0.22 $m^2\ m^{-2}$) (Figure 7d), increasing from the greater variability in the spatial distribution of rainfall accumulation in the previous days. On the other hand, during the dates studied here, the highest mean LAI values stood out only in areas of arboreal Caatinga ($0.58 \pm 0.45\ m^2$ m^{-2}) and agriculture ($0.75 \pm 0.49\ m^2\ m^{-2}$), with the maximum values being associated with irrigated agricultural areas, more specifically orchards, with increased biomass production. However, in areas of pasture, urban infrastructure, and areas of arboreal and herbaceous Caatinga, the LAI values were close to or equal to zero, making its variation more homogeneous, that is, closer to the daily mean, with standard deviation (SD) ranging between 0.05 and 0.10 $m^2\ m^{-2}$ within the land cover classes (Figure 7).

3.4. Land Surface Temperature (LST) in the Studied Classes

In the present study, the minimum LST values were seen in areas of water bodies, while the maximum LST values were seen in areas of exposed soils, located at points of pasture and degraded Caatinga, urban infrastructure (asphalt, concrete, and gravel surfaces), and agricultural areas undergoing soil preparation for cultivation (Figure 8). This result is expected in bare soil locations under intense anthropic activity due to the transformation of land use/land cover classes into non-evaporating surfaces. This makes the place's temperature higher and reduces water availability in the soil, which causes serious problems in agricultural crops. The computed LST map is shown in Figure 8.
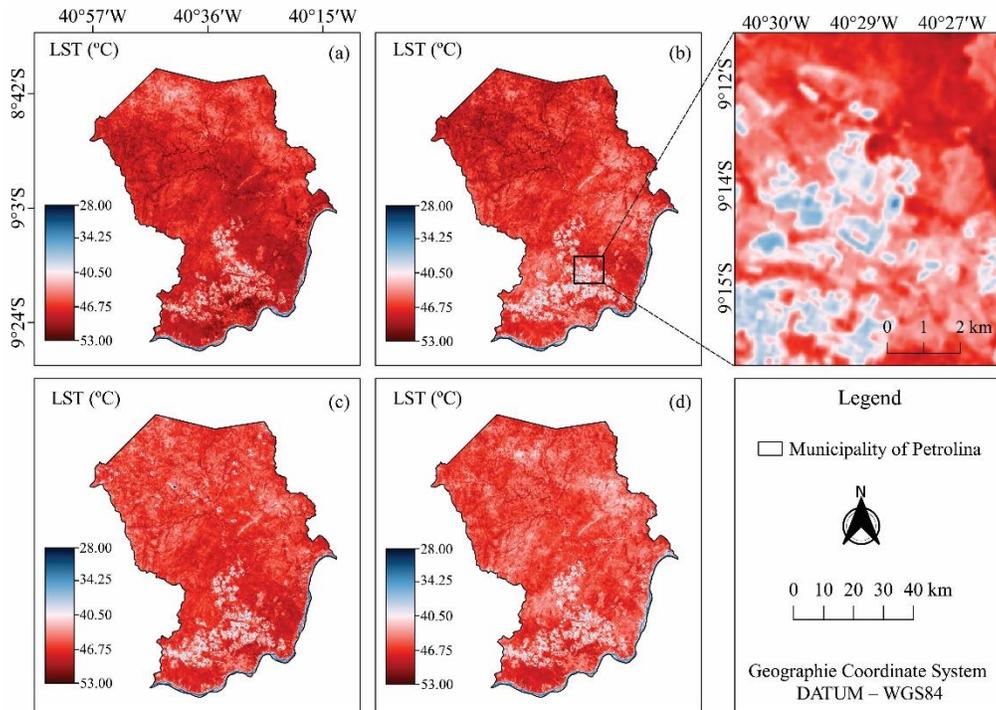
Figure 8. Spatiotemporal distribution of the land surface temperature—LST (ºC) in the municipality of Petrolina, Pernambuco, Brazil, on the imaging dates 5 October 2013 (**a**), 12 November 2015 (**b**), 16 October 2017 (**c**) and 7 November 2019 (**d**).

Due to the replacement of primary vegetation with pastures, agricultural crops, and urban occupation, changes in land use can substantially affect the heat and mass exchange in the soil–plant–atmosphere system, propitiating the retention of a higher amount of heat by the Earth's surface [2,52]. Land abandonment and excessive mechanical disturbance of the soil may also alter the heat exchange with the environment and cause lower thermal and radiant energy lag; thus, the land conversion had increased LST in the area of the non-evaporating surfaces.

It can be observed that the average LST values for the dates studied were higher in the areas dominated by pasture (47.69 ± 1.47 ºC), herbaceous Caatinga (47.28 ± 1.27 ºC), and shrub Caatinga (46.07 ± 1.44 ºC), even higher than those observed in areas with urban infrastructure (45.80 ± 1.52 ºC) (Figure 8). According to Zhao et al. [109,110], sites with different land cover types may have an LST increase gradient along the urban to rural profile. The high LST in the pasture, herbaceous, and shrub Caatinga areas is related to the lower percentage of ground covering by vegetation (see Figure 6), which results in drier exposed

151

635   soil, with higher albedos and lower evaporative cooling flux rates, a factor that increases

636   LST. Another related factor contributing to the high LST of pastures is that grasses have

637   shallower roots. Therefore, they can only access the water available in the superficial soil

638   layers, which depletes faster than in deeper layers [2]. Vegetation canopy can retain rainwater

639   and decrease groundwater recharge by altering evaporative flux and raising the land surface

640   temperature.

641   On the other hand, it is observed, in general, that in areas dominated by arboreal

642   Caatinga and agriculture, the average LST values are lower (38.99 ± 2.48 ℃ and $43.11 \pm$

643   2.30 ℃, respectively) (Figure 8). The highest vegetation cover and the highest soil humidity

644   in the areas dominated by these classes favor LST reduction. However, they present the

645   greatest spatial variations of LST among all land use and land cover classes, according to the

646   standard deviation values ($\pm$SD). The main advantage of using LST data from satellite images

647   is the total surface coverage. In this way, each time series of pixels of the LST map can be

648   considered a "virtual weather station" [111].

649

650   *3.5. Variations of the Actual Evapotranspiration (ET$_a$) of Land Use Classes*

651   Rainfall regime directly influenced ET$_a$, so that on 16 October 2017 (Figure 9c), the

652   date with the lowest rainfall accumulation in the previous days, the lowest ET$_a$ rates were

653   found, with an average value of 2.02 mm day^{-1}. On the other hand, on 7 November 2019

654   (Figure 9d), the period with the highest rainfall accumulation, average ET$_a$ rates were 2.62

655   mm day^{-1} (Figure 9). According to Teixeira et al. [20], high evapotranspiration values in

656   Caatinga areas occur right after rains. Therefore, the previous rainfall raises soil water

657   availability and keeps native species with turgid structures and greener canopy.

658
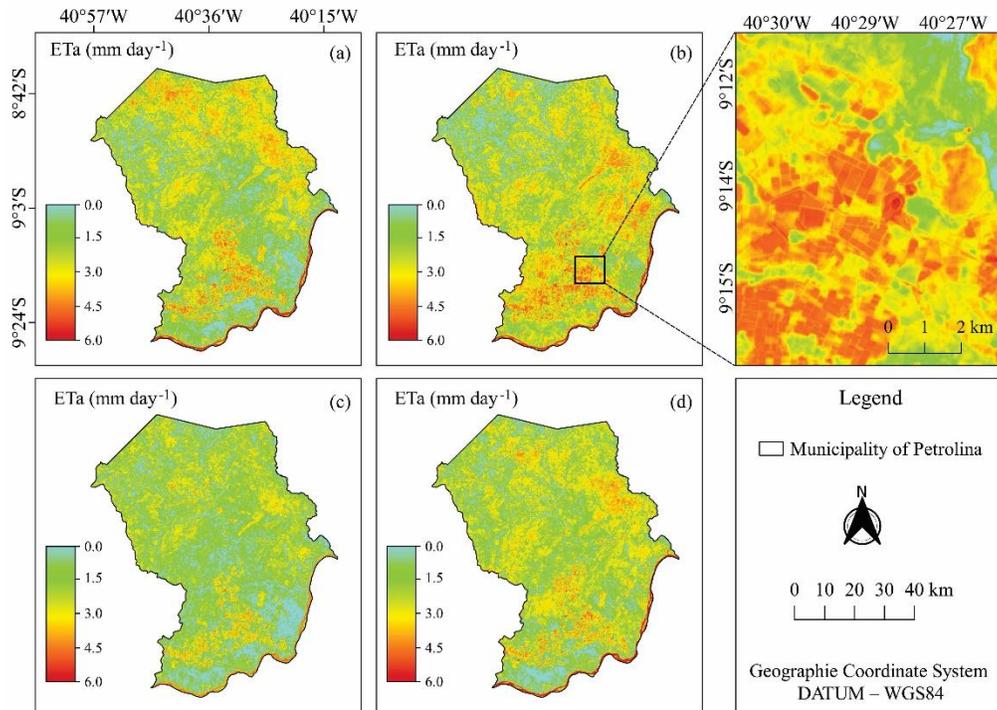
Figure 9. Spatiotemporal distribution of actual evapotranspiration (ET$_a$, mm day^{-1}), calculated with Surface Energy Balance Algorithm for Land (SEBAL), in the municipality of Petrolina, Pernambuco, Brazil, on the imaging dates 5 October 2013 (**a**), 12 November 2015 (**b**), 16 October 2017 (**c**), and 7 November 2019 (**d**).

The ET$_a$ estimated by the SEBAL model showed variation both within and between land use and land cover classes. The lowest ET$_a$ observations in all the evaluated dates were observed in the areas occupied by pasture and mosaic of agriculture and pasture classes, with average values of 0.70 ± 0.73 mm day^{-1} and 1.01 ± 0.96 mm day^{-1}, respectively (Figure 9). These areas have dryland cultivation practices, which causes the lower water availability to affect the evapotranspiration rates; moreover, the heterogeneity of the areas causes sudden variations in ET$_a$.

On the other hand, due to the effect of the increase in air temperature and atmospheric demand verified throughout the dry season in Petrolina, combined with the presence of preserved riparian forests along stretches of water bodies and continuous irrigation in crops, higher mean ET$_a$ values were observed in the arboreal Caatinga (4.73 ± 0.49 mm day^{-1}) and agriculture (3.07 ± 1.23 mm day^{-1}) classes. For presenting areas with irrigated and dry cultivation, the average values of this class become more variable. When there is a greater

153

678 contribution of moisture added to more dense vegetation, there is a favoring of the local
679 microclimate in the region [112,113], a phenomenon reported in areas of arboreal vegetation.

680 　　　　The shrub and herbaceous Caatinga classes showed greater heterogeneity indicated
681 by the largest standard deviations (2.42 ± 0.76 mm day^{-1}) and (1.46 ± 0.71 mm day^{-1}),
682 respectively, relative to the arboreal Caatinga class (Figure 9). Folhes et al. [114] reported
683 that the evapotranspiration values (<2.0 mm day^{-1}) during the dry season for species of
684 herbaceous–shrubby Caatinga. In dry periods, the Caatinga vegetation uses the available
685 energy as sensible heat flux (H), limiting transpiration and photosynthesis, thus reducing
686 evapotranspiration values [20]. However, arboreal vegetation is able to compensate the high
687 vapor pressure deficit in the air, even in dry periods, when compared to shrub and herbaceous
688 vegetation, due to the deep root system keeping up with the water stored in the soil
689 [69,115,116].

690 　　　　The arboreal and shrub species play a fundamental eco-hydrological role, maintaining
691 soil humidity and structuring its porosity, guaranteeing the maintenance of infiltration
692 capacity and favoring the survival of species [115].

693

694 *3.6. Statistical Relations Between the Variables Studied and Land Use*

695 　　　　In this study, we performed a PCA of the environmental variables in relation to land
696 use and land cover classes. Therefore, the first two components with eigenvalues greater than
697 1.0 were extracted separately for the years 2013, 2015, 2017, and 2019 (Figure 10). In 2013,
698 the two principal components explained 94.77% of the total variation, with 70.39% in the
699 principal component 1 (PC1) and 24.38% in the principal component 2 (PC2). On the other
700 hand, in 2015, 2017, and 2019, when added together, PC1 and PC2 represented 94.01, 92.34,
701 and 94.56% of the total variation, respectively (Figure 10). In addition, it can be seen that the
702 LULC class, with the least influence on components 1 and 2 in all years, is shrub Caatinga,
703 with average eigenvalues (0.31 and 0.37, respectively). In addition, the classes with the
704 greatest influence on PC1 with positive and negative eigenvalues are water bodies (2.69),
705 agriculture (−2.35), arboreal Caatinga (−1.92), pasture (0.34), mosaic (0.16), and urban area
706 (0.35). In PC2, the classes of LULC were water bodies (−4.36), mosaic (2.10), agriculture
707 (−1.0), and arboreal Caatinga (−3.40) (Figure 10).

708
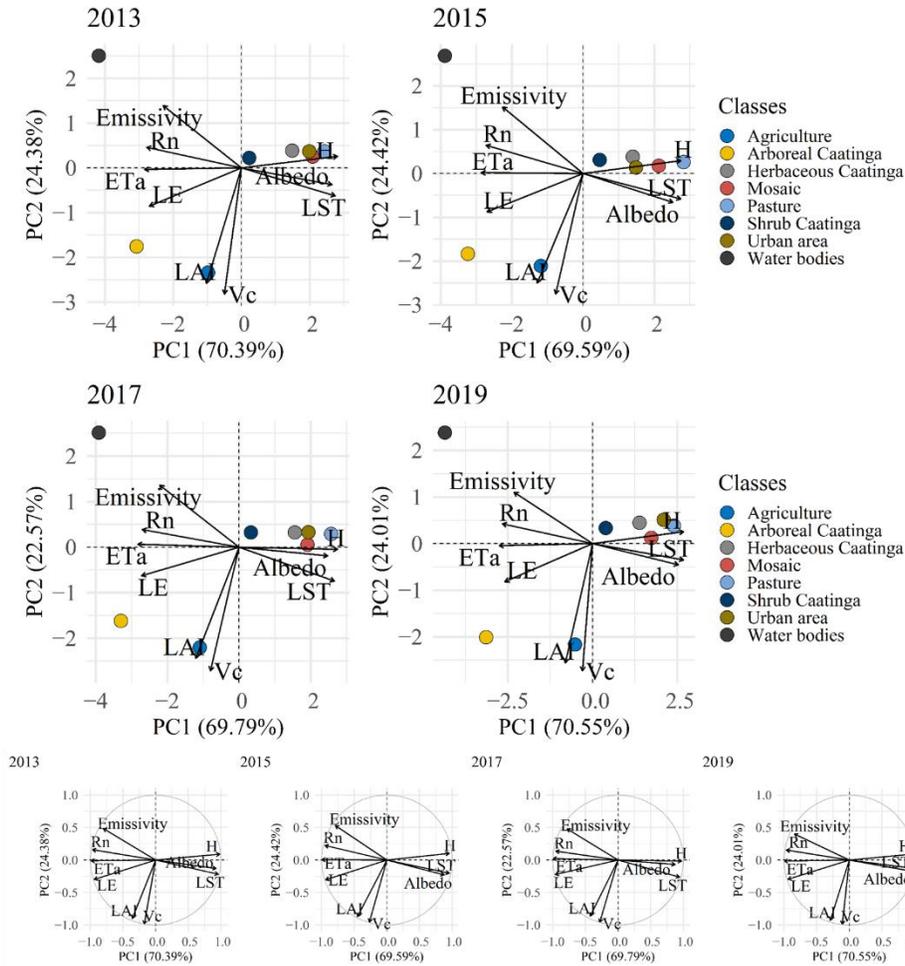
Figure 10. Scores obtained by principal component analysis (PCA) of environmental variables and land use and land cover. PC1 and PC2 are the first and second dimensions of PCA data, respectively. The four inserted panels below the PCA scores plots refer to the loadings plots of the first two principal components from 2013 to 2019.

Through PCA, we observed that the ordering of variables in each principal component (PC) of the axes was influenced by the degree of vegetation cover and surface water status of the LULC classes (Figure 10). Thus, PC1 contributed more to the variability of the response of variables related to energy balance. Therefore, in PC2, the land use and land cover classes (i.e., pasture, mosaic, urban area, and herbaceous Caatinga) influenced the variables R_n, LE, ET_a, and emissivity with higher mean loadings (−0.95, −0.94, −0.99, and −0.80, respectively). On the other hand, they showed a high correlation with the variables H, LST, and albedo. For these LULC classes, this may be related to the presence of bare soil

723   and thin vegetation covers that affect the regional microclimate and soil–plant–atmosphere

724   system fluxes, resulting in higher albedos, lower rates of evaporative cooling fluxes, and

725   highest LST [2,104].

726   On the other hand, PC2 contributed more to the variability of the responses of the

727   variables regarding the canopy interactions (LAI and V_C) due to the strong negative

728   correlation with cultivated land (i.e., agriculture class) (Figure 10). In all years, there was a

729   predominance for *LE* and LAI in areas with arboreal Caatinga and agriculture, with

730   agriculture presenting the highest V_C. Caatinga presents a strong relationship with LAI in

731   rainy periods due to the greater availability of water in the soil [117]. In the present study,

732   the samples were taken in the period with low rainfall, so the LAI was not expressive

733   compared to agricultural areas, which use irrigation and therefore increase the LAI. Thus, the

734   emissivity in the Caatinga vegetation is lower, for the emissivity of the soil is generally lower

735   than that of the leaves [2].

736   The results of the analysis of variance (ANOVA) and multiple regression analysis of

737   the established model are presented in Table 3. For the combination of two-variable models,

738   the two best pre-established parameters based on the PCA results were the variables LST and

739   *H*, used to build the regression model. In particular, these two variables are of great relevance

740   in transferring energy to the atmosphere. The ANOVA results also showed that the model

741   values are significant. Due to the observations, a joint analysis of the coefficient of

742   determination obtained ($R^2 = 0.98$) can be performed, emphasizing the *P*-value obtained from

743   our regression model, which was less than 0.001, thus indicating greater model accuracy and

744   reliability (Table 3). Notably, it can be seen that the model's *F*-value was 16,692.84, being

745   greater than the critical value of $F_{0.05} = 3.018$, which confirms the significance of the

746   proposed model. In addition, the variables used provided a high R^2 and LCCC, being essential

747   for the model's accuracy. Furthermore, the results showed that the multiple linear regression

748   model to determine ET_a achieved a coefficient of determination of 0.98, RMSE of 0.498,

749   MAE of 0.413, and *d* equal to 0.9620. It also resulted in PBIAS, NSE, and LCCC values

750   averaged between −13.32%, 0.826, and 0.907, respectively (Table 3). From the statistical

751   analysis, this model is described as $ET_a = 6.89 − 0.0527LST − 0.0120H$. Based on the RMSE,

752   LCCC, and *d* of this application, the use of the ET_a model, besides presenting a strong

753 correlation between the variables H and LST, as seen in Figure 10, expresses a biophysical
754 model with enough efficiency and high agreement to determine ET_a.

755

756 **Table 3.** Analysis of variance (ANOVA) and regression coefficients results for the suggested
757 model.

Source of Variation	df	SS	MS	*F*-Value	*p*-Value
Regression	2	464.41	232.21	16,692.84	<0.0001
LST	1	335.29	335.29	24,103.8	<0.0001
H	1	129.12	129.12	9281.9	<0.0001
Error	397	5.52	0.01		
Total	399	469.93			

Regression statistics					
Predictors in model	**Regression coefficients**				
	β_0	β_1	β_2	R^2	
LST, *H*	6.89	−0.0527	−0.0120	0.98	

Statistical metrics					
Model	RMSE	MAE	PBIAS (%)	NSE	LCCC	*d*
	0.498	0.413	−13.32	0.826	0.907	0.9620

758 df: degrees of freedom, SS: sum of squares, MS: mean square, LST: land surface temperature,
759 *H*: sensible heat flux, β_0: intercept, β_1 and β_2: estimated coefficient for the factor x, R^2:
760 coefficient of determination, RMSE: root mean square error, MAE: mean absolute error,
761 PBIAS: percent bias, NSE: Nash–Sutcliffe efficiency coefficient, LCCC: Lin's concordance
762 correlation coefficient, and *d*: Willmott's index of agreement. Based on *F*-test, at a
763 probability of 0.05 ($p < 0.05$), significance of equation parameters for each response variable
764 was determined.

765

766 The high d (0.9620) values for ET_a indicated that there was a good agreement between
767 simulated and measured ET_a. In general, the ET_a model showed excellent agreement (LCCC
768 > 0.9), high performance, and low RMSE (0.498) (Table 3). The PBIAS and MAE values for
769 ET_a were between −13.32% and 0.413, confirming the close agreement. Consequently, this
770 result describes the ability to simplify and accurately predict ET_a in deficit environments.

Applications of regression model analysis with environmental variables are common in the literature in dry forests [117–119]. However, these implementations of variables in previous studies may be challenging to acquire for specific locations, requiring more simplified models. Our results also indicate the relationship between H and the LST of ecosystems to determine ET_a, an important variable in the energy balances of environments worldwide.

4. Conclusions

In this study, we point out a significant tendency to increase the agricultural areas, which results in the progressive decrease of the Brazilian Caatinga biome. The vegetation cover is directly influenced by the soil–water regime; years of higher rainfall result in a lower percentage of suppression of the native forest in the municipality of Petrolina, Pernambuco (Brazil). The areas with pasture class presented hotspots due to degradative processes and higher surface temperatures, influenced by the sensible heat flux. A gradual increase in LST is observed in the municipality and it may cause future risks to forest areas.

The SEBAL algorithm used in a semi-arid environment is a helpful tool to determine the energy and mass fluxes in different ecosystems. Notably, the Caatinga biome has particularities in biophysical parameters, according to the land cover and soil exposure on intra and inter-annual scales. The heterogeneity of the surface of the municipality of Petrolina, as a function of land use and land cover patterns, alters the energy exchange with the atmosphere. Our results also suggest a simplified and validated model for ET_a determination in a semi-arid environment. The regression model could accurately predict the spatial distribution of ET_a, with high R^2 and LCCC and low RMSE value.

Thus, it is possible to suggest that the implementation of agricultural activities in the Petrolina should be carried out in a planned and sustainable way in order to mitigate the impacts that anthropic action causes on the Caatinga, especially with the increased vulnerability of this biome to the desertification process. However, further research is needed to investigate the spatial variations of the types of crops covering the soil in the municipality, as well as the dynamics of fires and their impacts on the diversity of the Caatinga biome. Field surveys and the use of unmanned aerial systems (UAS) could provide more detailed information at an intermediate and fine scale.

158

840

841   **Conflicts of Interest:** The authors declare no conflicts of interest.

842

843   **Abbreviations**

844   Summary of all the symbols and acronyms used in this paper.

Item	Description
a and b	Are the calibration coefficients
C_p	Specific heat of air
d	Willmott's index of agreement
DEM	Digital elevation model
dT	Near-surface air temperature gradient
e_a	Actual atmospheric water vapor pressure
e_s	Water vapor saturation pressure
ET_a	Actual evapotranspiration
G	Soil heat flux
GEE	Google Earth Engine
H	Sensible heat flux
HR	Instantaneous relative humidity
k	von Karman constant
LAI	Leaf area index
LCCC	Lin's concordance correlation coefficient
LE	Latent heat flux
LSE	Land surface emissivity
LST	Land surface temperature

LULC	Land use and land cover
MAE	Mean absolute error
NDVI	Normalized Difference Vegetation Index
NSE	Nash-Sutcliffe efficiency coefficient
PBIAS	Percent bias
PCA	Principal component analysis
r_{ah}	Near-surface aerodynamic resistance to heat transport
RMSE	Root mean square error
R_n	Net radiation
R_{n24}	Daily net radiation
R^2	Coefficient of determination
SAVI	Soil-Adjusted Vegetation Index
T_0	Instantaneous air temperature
T_a	Air temperature
$u*$	Friction velocity
u_{200}	Wind speed at the height of 200 m
V_C	Vegetation cover
W	Precipitable water
z_1 and z_2	Are the two heights between the surface of the anchor pixels
z_{om}	Momentum roughness length
α_{sup}	Surface albedo
ε_a	Atmospheric emissivity
Λ	Evaporative fraction
λ	Latent heat of vaporization of water
ρ_{air}	Air density
ψ_m and ψ_h	Stability correction factors for momentum and sensible heat, respectively

845

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1279

CHAPTER 5

Genotypic differences relative photochemical activity, inorganic and organic solutes and yield performance in clones of the forage cactus under semi-arid environment

Abstract

Plants with the crassulacean acid metabolism commonly present good adaptation to arid and semi-arid environments, but it highly depends on the type of species. In this study, chlorophyll fluorescence, the concentration of inorganic and organic solutes and the productive performance were evaluated along with their relationships in different clones of the genera *Opuntia* and *Nopalea*. The experiment was conducted from 2016 to 2018. Four clones of genus *Opuntia* were evaluated: 'Orelha de Elefante Mexicana' (OEM), 'Orelha de Elefante Africana' (OEA), V19 and F8; and two clones of genus *Nopalea*: 'IPA Sertânia' and 'Miúda'. The experiment was arranged in a randomised block design, with six treatments and three replications. The following parameters were measured when harvesting: initial, maximum and variable fluorescence; the quantum yield of PSII (Fv/Fm); light-induction curves of the photochemical parameters (ΔF/Fm', qP, NPQ and ETR); the chlorophyll and carotenoid content; carbohydrates; the sodium (Na^+) and potassium (K^+) content; morphometry; and dry matter accumulation. The values for the effective quantum yield of PSII (ΔF/Fm') and the alterations in photochemical quenching were higher in the OEM clone ($P < 0.05$). There was a difference between clones for non-photochemical quenching, with the F8 clone having the highest values. The Fv/Fm was 0.87 for the OEM. 'IPA Sertânia' obtained the greatest Chl *a/b*, and the highest values for carbohydrate concentration were found in the OEA clone. The OEM clone showed the greatest accumulation of K^+, in addition to a higher cladode area index and greater dry matter accumulation. The results of this study show the high physiological tolerance of the forage cactus to a semi-arid environment, which varies according to the clone.

Keywords: *Opuntia*, *Nopalea*, Chlorophyll, Carbohydrates, Agronomic characteristics.

1 Introduction

The changes occurring in terrestrial systems for decades have promoted changes in climate that offer a challenge to the agricultural sector for food production. These variations in climate can cause the extinction and/or compromise the survival of species from different ecosystems (Aragón-Gastélum et al., 2014). Abiotic factors, e.g. drought, salinity, solar radiation and extreme temperature, limit the growth of various crops and cause physiological damage by overpowering photosynthetic capacity (Al-Turki et al., 2014; Lima et al., 2018).

As such, a key factor in food security is the choice of species that have a high capacity for adaptation to extreme climates and for survival in places where other species find difficulty (Cabrera et al., 2016). In arid and semi-arid environments, particularly in the semi-arid region of Brazil, the forage cactus (*Opuntia* spp. and *Nopalea* spp.) is used to produce cladodes for animal feed in areas of high temperature and low water regime (Lina and Eloisa, 2018; Rocchetti et al., 2018), where, despite these climate conditions, the forage cactus retains the nutritional constituents and productive capacity that are important for the herds (Meza-Herrera et al., 2019; Jardim et al., 2021).

In general, plant response to environmental stress can be identified by measuring changes in chemistry and production. Among the parameters of photochemical efficiency, chlorophyll-*a* fluorescence, the maximum quantum yield of photosystem II (Fv/Fm) and electron transport (ETR) are considered particularly robust and extremely reliable tools (Bussotti et al., 2020; Ojeda-Pérez et al., 2017; Oliveira et al., 2020). Cacti show high concentrations of chlorophyll and photoprotective pigments, contributing to their development (Bussotti et al., 2020; Cabrera et al., 2016) and maximising their photosynthetic activity (Drezner, 2020; Ojeda-Pérez et al., 2017). However, despite this marked efficiency, excessive light can cause damage to the photosystem (He et al., 2019; Oliveira et al., 2020).

Plants with the crassulacean acid metabolism (CAM), e.g. cacti, usually have an excellent response to high thermal amplitudes, but this is highly dependent on the type of species and the growth environment, which may have different effects on the photosystem (Ojeda-Pérez et al., 2017; Walker et al., 2011; Nobel et al., 1986; Chetti and Nobel, 1988; Nobel and De la Barrera, 2003). Al-Turki et al. (2014) state that *Euphorbia fractiflexa*, despite being a CAM species; shows a reduction in the maximum quantum yield of the

177

61 photosystem II (Fv/Fm) in areas of high temperature, as a result of stomatal closure, which
62 helps in the photoprotection of the photosystem II (PSII) by dissipating energy.

63   In clones of *Opuntia*, this tolerance is more marked than in other CAM species
64 (Ojeda-Pérez et al., 2017). In addition to elevated tolerance to abiotic stresses, cacti also
65 presents a high water-use efficiency—which is estimated by the amount of CO_2 fixed
66 compared to the volume of transpired water. It is estimated to be about three and six times
67 higher than C4 and C3 plants, respectively (Silva-Ortega et al., 2008; Borland et al., 2009;
68 Borland et al., 2015; Cushman et al., 2015). This characteristic present in CAM plants is
69 favourable for their survival, and for its higher dry matter yield under adverse conditions
70 compared to other species, mainly presented in arid and semi-arid regions (Borland et al.,
71 2009; Cushman et al., 2015). However, it is not clear which biochemical or productive
72 parameters are most relevant when evaluating the photochemical efficiency of forage cacti
73 in agricultural areas of semi-arid environments.

74   This study tested the hypothesis that maintaining the photochemical efficiency of
75 forage cactus clones under semi-arid stressful conditions could favour the yield performance.
76 Thus, parameters of chlorophyll fluorescence, concentration of inorganic and organic solutes
77 and productive performance were evaluated together with their relationships in different
78 fully-grown clones of genera *Opuntia* and *Nopalea* in a semi-arid environment.

79

80 **2 Material and methods**
81 *2.1 Study area and species under evaluation*
82   The experiment was conducted from 2016 to 2018 at the Serra Talhada Academic
83 Unit of the Federal Rural University of Pernambuco, located in the municipality of Serra
84 Talhada, Pernambuco, Brazil (7º59' S, 38º15' W at 431 m a.s.l.). According to the Köppen
85 climate classification, the region has a semi-arid climate, type BSwh' (dry and hot with a
86 rainy season in the summer) (Alvares et al., 2013). The average rainfall is 642.1 mm year^{-1},
87 with an average air temperature of 24.8 ℃, relative humidity of 62.5% and atmospheric
88 demand greater than 1,800 mm year^{-1} (Silva et al., 2015). During the experimental period,
89 the environmental conditions were monitored by an automatic weather station of the National
90 Institute of Meteorology, located 45 m away from the experimental field (Figure 1). The

91   reference evapotranspiration (ETo) was calculated as per Penman-Monteith (Allen et al.,
92   1998).

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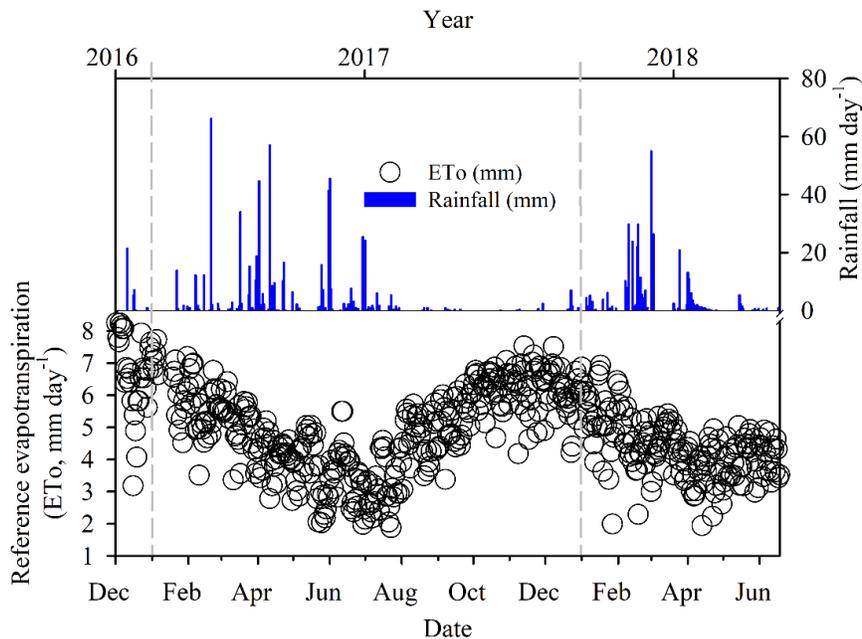
Figure 1. Weather conditions in the municipality of Serra Talhada, Pernambuco, during the
experimental period from 2016 to 2018.

96

97   The soil of the experimental area, of flat relief, was classified as a typic eutrophic
98   Haplic Cambisol, with the following physical and chemical attributes measured at a depth of
99   0.0–0.20 m: $pH_{(water)}$ = 5.95, electrical conductivity of the soil saturation extract = 0.32 dS
100   m^{-1}, $P_{(Mehlich-1)}$ = 168.96 mg dm^{-3}, K^+ = 13.8 $cmol_c$ dm^{-3}, Na^+ = 1.09 $cmol_c$ dm^{-3}; Ca^{2+} = 3.45
101   $cmol_c$ dm^{-3}, Mg^{2+} = 1.90 $cmol_c$ dm^{-3}, H+Al = 0.6 $cmol_c$ dm^{-3}, sum of bases = 20.25 $cmol_c$
102   dm^{-3}, cation exchange capacity = 20.85 $cmol_c$ dm^{-3}, base saturation = 97.15%; organic matter
103   = 7.93 g kg^{-1}, organic carbon = 4.6 g kg^{-1}; bulk density of 1.45 g cm^{-3}, sand = 828.6 g kg^{-1},
104   silt = 148.25 g kg^{-1}, and clay = 23.15 g kg^{-1}. Before planting, the soil was prepared
105   mechanically (ploughing and harrowing) and a total of 32.7 kg ha^{-1} NPK chemical fertiliser
106   was applied (Jardim et al., 2020).
107   The forage cactus clones were planted in December 2016, inserting the basal cladodes
108   up to 50% in the soil, in single rows, at a spacing of 1.2 × 0.2 m, equal to a density of 41,667
109   plants ha^{-1}. Four clones of genus *Opuntia* were used: 'Orelha de Elefante Mexicana' (OEM)

179

110 (*O. stricta* (Haw.) Haw.), 'Orelha de Elefante Africana' (OEA) (*O. undulata* Griffiths), V19

111 (*O. larreyi* F.A.C. Weber ex Coult.) and F8 (*O. atropes* Rose), and two clones of genus

112 *Nopalea*: 'IPA Sertânia' (IPA) (*N. cochenillifera* (L.) Salm-Dyck) and 'Miúda' (MIU) (*N.*

113 *cochenillifera* (L.) Salm-Dyck), all tolerant to the cochineal insect [*Dactylopius opuntiae*

114 (Cockerell, 1896)]. The experiment was arranged in a randomised block design, with six

115 treatments and three replications, where the treatments corresponded to the forage cactus

116 clones. Each plot comprised three rows of 15 plants of each clone, giving a total of 45 plants

117 per plot, distributed over an area of 3.60×3.0 m (10.8 m^2).

118   Irrigation was carried out three times a week using a drip system with a uniformity

119 coefficient of 93% and a flow rate of 1.25 L h^{-1} (working pressure: 100 kPa). The micro

120 drippers were spaced 0.4 m apart, providing water replacement based on 120% of the crop

121 evapotranspiration (ETc) using the crop coefficient (Kc = 0.52) of the forage cactus (Queiroz

122 et al., 2016). The irrigation water had an electrical conductivity of 1.62 dS m^{-1}, and was

123 classified as C3, i.e. of high salinity (Richards, 1954), pH = 6.84, Na$^+$ = 168.66 mg L^{-1} and

124 K$^+$ = 28.17 mg L^{-1}. The control of spontaneous plants and the cropping treatments included

125 manual weeding.

126

127 *2.2 Measurement of chlorophyll fluorescence and accessory pigments*

128 *2.2.1 Chlorophyll fluorescence*

129   Chlorophyll *a* (Chl *a*) fluorescence was measured 516 days after planting, between

130 09:00 and 12:00 h, using a portable pulse-modulated fluorometer (Mini-PAM II, Heinz Walz,

131 Effeltrich, Germany), in intermediate cladodes after a period of 50 min pre-adaptation to the

132 dark with the aid of support clips placed around the cladode. After the period of dark

133 adaptation, they were exposed to one flash at a photosynthetic photon flux density of 1600

134 μmol m^{-2} s^{-1}, giving the PSII parameters of initial (Fo), maximum (Fm) and variable

135 fluorescence (Fv), and maximum quantum yield (Fv/Fm).

136   For the rapid light-response curve, the cladodes were also adapted to the dark for a

137 period of 50 min and to photosynthetic photon flux densities (PPFD) of 0, 25, 45, 65, 90,

138 125, 190, 285, 420, 630, 820, 1150, 1500 μmol photons m^{-2} s^{-1} at intervals of 20 s between

139 each PPFD, thereby obtaining the following parameters: the effective quantum yield of

140   photosystem II (ΔF/Fm'), the photochemical quenching coefficient (qP), non-photochemical

141   quenching coefficient (NPQ), and the relative electron transport rate (ETR).

142

143   *2.2.2 Chlorophyll and carotenoid content*

144   Fresh cladodes harvested in the field were then identified and taken to the laboratory.

145   Two cross sections of approximately 2.0 cm thick each were performed in the centre of the

146   cladode. Samples were weighed on electronic balance for the chlorophyll analysis, as

147   described in more detail later. This also allowed the identification and the distribution of

148   epidermis structural tissues, i.e. upper epidermis—adaxial, lower epidermis—abaxial, and

149   also parenchymal cells (e.g. chlorenchyma and hydrenchyma in all-cell); which are

150   abundantly present on cladodes (in the inner part and including the cuticle layer) of cacti and

151   leaves of succulent plants, according to Scalisi et al. (2016) and Griffiths and Males (2017).

152   The chlorophyll (Chl) was extracted from a 0.2 g fresh weight (FW), removed from the

153   cladode, in contact with 5 mL 80% (v/v) acetone. The threaded test tubes were taken to a

154   refrigerated environment from 48 to 72 h, after that the levels of chlorophyll and carotenoids

155   (g kg^{-1}) were measured at absorbances of from 470 to 664 nm, and calculated using the

156   equations: Chlorophyll *a* (Chl *a*) = [(12.21 · A_{663}) − (2.81 · A_{646})]; Chlorophyll *b* (Chl *b*) =

157   [(20.13 · A_{646}) − (5.03 · A_{663})]; total Chlorophyll (total Chl) = [(Chl *a*) + (Chl *b*)] and

158   Carotenoids (Car_{x+c}) = [((1000 · A_{470}) − (3.27 · Chl *a*)) − (104 · Chl *b*)]/229 (Lichtenthaler

159   and Wellburn, 1983).

160

161   *2.3 Measurement of carbohydrates*

162   In order to determine the total soluble carbohydrates, samples of 0.375 g of fresh

163   weight (FW) were collected from the central part of the cladodes (procedures for cross

164   section and tissue identification of fresh cladodes are described in detail according to the

165   section 2.2.2). The samples were then macerated in liquid nitrogen and homogenised with

166   1.5 mL of a 0.1 M potassium phosphate buffer solution (pH 7.0). The homogenate was then

167   centrifuged (Hettich, Mikro 220 R, DJB Labcare Ltd., Newport Pagnell, UK) at 12000 *g* for

168   15 minutes at 4 ºC; the supernatant was then collected. The total soluble carbohydrates were

169   determined by the phenol-sulphuric acid method (Dubois et al., 1956), using D-(+)-glucose

170 (Sigma-Aldrich) as the standard. Absorbance readings were taken at 490 nm, and the results

171 expressed in µmol g^{-1} FW.

172

173 *2.4 Levels of Sodium (Na$^+$) and potassium (K$^+$)*

174 The contents of Na$^+$ and K$^+$ were measured by flame photometry, as described by

175 Rodrigues et al. (2013). After oven-drying to determine the dry weight (DW), the cladode

176 tissue was ground in a Wiley knife-mill to obtain the flour, samples (20 mg) of which were

177 then submitted to extraction by incubating in test tubes with threaded caps containing 15 mL

178 ultra-pure water, and boiling in a water bath at 100 ℃ for 1 h. The extracts were filtered and

179 used for reading the Na$^+$ and K$^+$ in a flame photometer (Micronal, B462, São Paulo, Brazil).

180 The Na$^+$ and K$^+$ contents were estimated based on an NaCl and KCl standard curve

181 respectively (0 to 1000 µM), with the results expressed in µmol g^{-1} DW.

182

183 *2.5 Morphometry and dry matter accumulation*

184 At the end of the clone cycle, morphometric variables of the cladodes (length, width

185 and perimeter) were measured with the aid of a tape (Jardim et al., 2020). These

186 measurements were used to calculate the cladode area index (CAI, m^2 m^{-2}) (Pinheiro et al.,

187 2015; Silva et al., 2014). The fresh weight of the plants (FW) was obtained using an electronic

188 balance. The complete working experimental plot was weighed, and the yield expressed in

189 kg plant^{-1}. The material was then placed in a forced air circulation oven at 55 ℃ to constant

190 weight to determine the dry matter (DM) of the forage cactus clones, expressed in kg DM

191 plant^{-1}.

192

193 *2.6 Statistical analysis*

194 The Shapiro-Wilk test for normality and Bartlett's test of homogeneity were applied

195 to the data and later to the analysis of variance (ANOVA). To determine possible differences

196 among the photochemical parameters (i.e., ΔF/Fm', qP, NPQ and ETR) of the clones

197 responding to photosynthetic photon flux densities, a ANOVA ($P < 0.05$) test was used. The

198 data were expressed by the mean and standard deviation for each treatment ($n = 3$). When

199 differences were detected by ANOVA, the mean values were compared by the Scott-Knott

200 test at a level of 0.05 probability ($P < 0.05$). The principal component analysis (PCA) was

201 carried out to detect the associations and correlations between the measured variables, and to
202 identify the most important factors in the productive performance of the six clones. Once the
203 data set was standardised to eliminate the influence of dimensions, and the principal
204 components were selected based on those with eigenvalues (λ) greater than 1.0 (Kaiser,
205 1960). All the analyses were carried out with the aid of the R software (R Core Team, 2020).
206

207 **3 Results**

208 *3.1 Measurement of the parameters of chlorophyll fluorescence*

209   Values for the effective quantum yield of photosystem II ($\Delta F/Fm'$) were higher at the
210 beginning of the analysis. All the clones have also been shown a decrease of $\Delta F/Fm'$ as the
211 photosynthetic photon flux density (PPFD) increased. At 1600 PPFD, the F8 clone displayed
212 less quantum efficiency ($P < 0.05$), approximately 43% of the mean $\Delta F/Fm'$ of the other
213 clones (Figure 2A). As shown in Figure 2A, clearly the greatest changes in $\Delta F/Fm'$ were
214 noticeable at 200 PPFD.
215
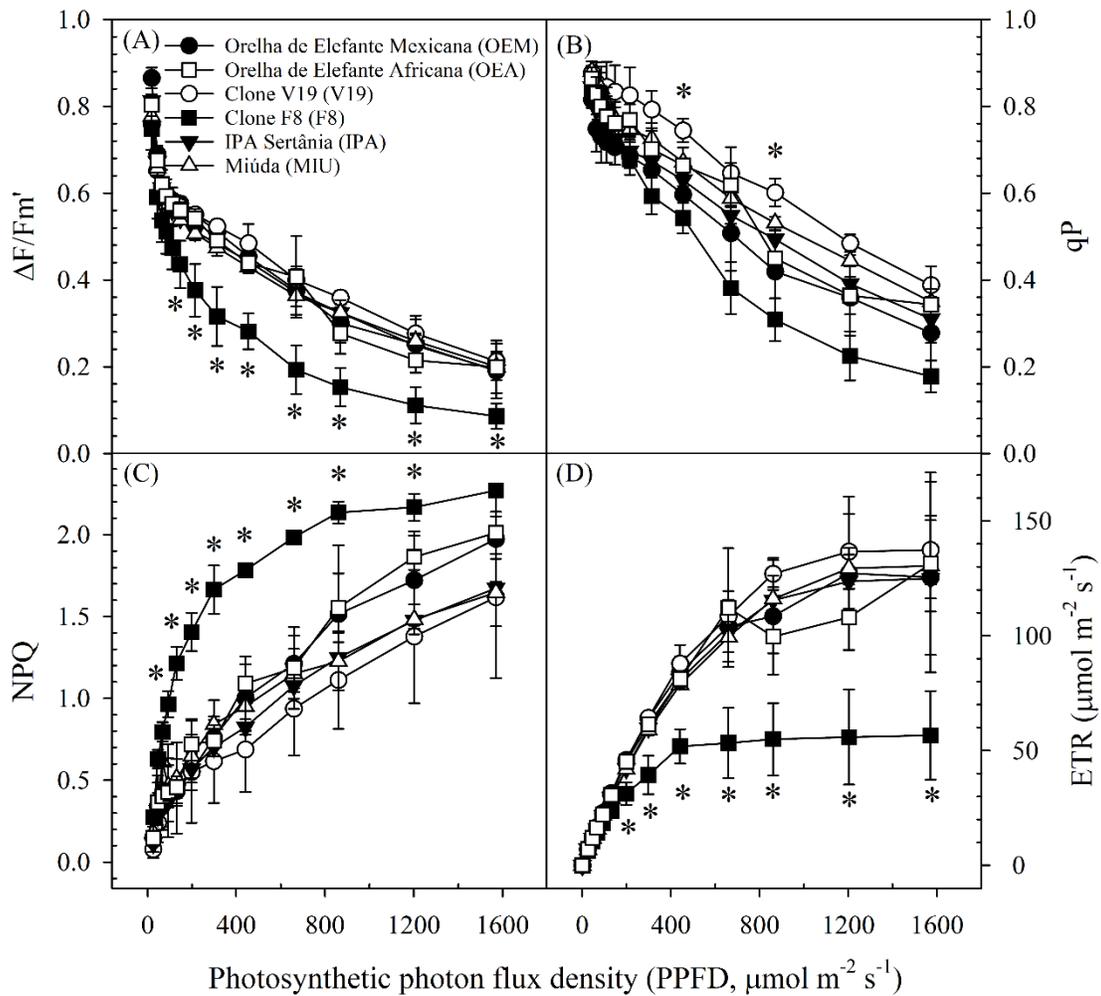
Figure 2. Induction curve of photochemical parameters in response to photosynthetic photon flux density (PPFD) in forage cactus clones irrigated with saline water in the semi-arid region of Brazil. (A) effective quantum yield of photosystem II ($\Delta F/Fm'$), (B) photochemical quenching (qP), (C) non-photochemical quenching (NPQ), and (D) relative electron transport rate (ETR, $\mu mol\ m^{-2}\ s^{-1}$) subjected to maximum light fluorescence. Data are presented as mean $\pm$ standard deviation ($n = 3$). (*) Asterisks indicate significant differences among cacti at each value of PPFD ($P < 0.05$; ANOVA test). Data obtained between 09:00 and 12:00 h from different cladodes under steady state conditions, i.e. constant light intensity.

The trend for the changes in photochemical quenching (qP) (Figure 2B) were similar to the results for $\Delta F/Fm'$, with lower magnitudes at the higher PPFD, and differences between clones ($P < 0.05$). However, these variations were more marked from 600 $\mu mol\ m^{-2}\ s^{-1}$,

demonstrating the stress suffered by the clones with the increase in light density. The 'Orelha de Elefante Mexicana', 'Orelha de Elefante Africana', V19, 'IPA Sertânia' and 'Miúda' clones showed the greatest activity at the reaction centre, with F8 being 53% lower than the other clones, but displaying no significant difference ($P > 0.05$).

There was a significant difference between clones for non-photochemical quenching (NPQ) (Figure 2C) from the application of 100 µmol m^{-2} s^{-1} PPFD. Clone F8 had the highest NPQ values, indicating excessive heat dissipation in photosystem II due to the abiotic stress of the environment. Despite being a clone of genus *Opuntia*, F8 shows inferior performance to the other clones of the same genus ($P < 0.05$). The 'Orelha de Elefante Mexicana' and 'Orelha de Elefante Africana' clones showed similar NPQ values ($P > 0.05$), presumably, for they both have the same nuclear genome, as well as they are species included in the same genus i.e. *Opuntia*.

The relative electron transport rate (ETR) was different between clones from a PPFD of 200 µmol m^{-2} s^{-1} (Figure 2D). Above 400 µmol m^{-2} s^{-1}, a significant difference was only found in clone F8 ($P < 0.05$), which at 1600 µmol m^{-2} s^{-1} reached a 44% reduction in ETR compared to the other clones ($P < 0.05$).

There was no effect from genus on the darkness-dependent parameters for initial fluorescence (Fo) ($P < 0.05$). However, for maximum fluorescence (Fm) and variable fluorescence (Fv), the F8 and V19 clones were less efficient, around 24% and 30% respectively in relation to the other clones (Table 1). Values for the maximum quantum yield of photosystem II (Fv/Fm) were higher in the 'Orelha de Elefante Mexicana' clone ($P < 0.05$), at 0.87. On the other hand, clones V19, F8 and 'Miúda' showed 12% less efficiency than the 'Orelha de Elefante Mexicana' clone (Table 1).

Table 1. The photochemical parameters of initial (Fo), maximum (Fm) and variable (Fv) fluorescence, and maximum quantum yield of photosystem II (Fv/Fm) in forage cactus clones in a semi-arid environment.

Clones	Fo	Fm	Fv	Fv/Fm
'Orelha de Elefante Mexicana'	293.33a	2180.67a	1887.33a	0.87a
'Orelha de Elefante Africana'	368.00a	1866.33a	1498.33a	0.80b
V19	336.67a	1396.33b	1059.67b	0.76c

F8	410.00a	1661.00b	1251.00b	0.75c
'IPA Sertânia'	391.67a	2093.00a	1701.33a	0.81b
'Miúda'	428.00a	1909.00a	1481.00a	0.78c

Mean values followed by the same letters in a column do not differ statistically by Scott-Knott, at a level of 0.05 ($P < 0.05$).

255

256   *3.2 Chlorophyll and carotenoid content of the cladodes*

257   The photosynthetic and photoprotective pigments of the clones showed differences in

258   relation to the genera of the cacti (Table 2). The concentrations of chlorophyll *a* (Chl *a*),

259   chlorophyll *b* (Chl *b*) and total chlorophyll (total Chl) were higher in the 'Orelha de Elefante

260   Mexicana' and V19 clones. The Chl *a/b* ratio also displayed differences between clones

261   (Table 2). The 'IPA Sertânia' clone had the highest Chl *a/b* ratio ($P < 0.05$), 32% greater than

262   the 'Orelha de Elefante Africana' and F8, and 51% greater than the 'Orelha de Elefante

263   Mexicana', V19 and 'Miúda'. There was no significant difference in the carotenoid

264   concentration (Car_{x+c}) of the clones.

265

266   **Table 2.** Chlorophyll content (Chl *a*, Chl *b* and total Chl), the Chl *a/b* ratio and carotenoid

267   content (Car_{x+c}) (g kg^{-1}) in forage cactus clones in a semi-arid environment.

Clones	Chl *a*	Chl *b*	Total Chl	Chl *a/b*	Car_{x+c}
'Orelha de Elefante Mexicana'	0.0563a	0.0177a	0.0740a	3.3063c	0.0237a
'Orelha de Elefante Africana'	0.0399b	0.0104b	0.0503b	3.8501b	0.0191a
V19	0.0498a	0.0216a	0.0715a	2.3092c	0.0183a
F8	0.0381b	0.0086b	0.0467b	4.1647b	0.0188a
'IPA Sertânia'	0.0422b	0.0073b	0.0495b	5.8642a	0.0186a
'Miúda'	0.0384b	0.0132b	0.0516b	2.9759c	0.0178a

268   Mean values followed by the same letters in a column do not differ statistically by Scott-

269   Knott, at a level of 0.05 ($P < 0.05$).

270

271   *3.3 Carbohydrate content*

272   There was a significant difference in carbohydrate concentration between clones, with

273   the highest values found in the 'Orelha de Elefante Africana' clone (Figure 3), on average,

274　59% greater than in the 'Orelha de Elefante Mexicana' and F8 clones with the lowest

275　concentration of carbohydrates.

276
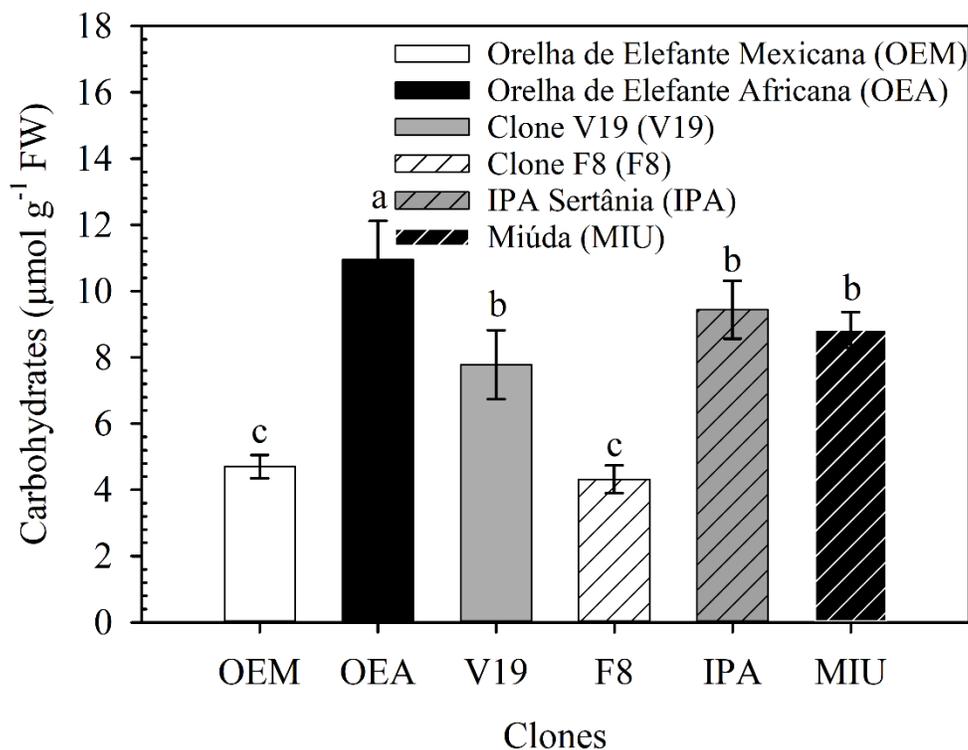
277　**Figure 3.** Total soluble carbohydrates in the cladodes of forage cactus clones irrigated with

278　saline water in the semi-arid region of Brazil. Data are presented as mean $\pm$ standard

279　deviation ($n = 3$). Mean values followed by the same letter do not differ statistically by Scott-

280　Knott test at a level of 0.05 ($P < 0.05$).

281

282　*3.4. Na$^+$ and K$^+$ concentration*

283　　The clones, regardless of genus, showed no difference ($P > 0.05$) in the sodium (Na$^+$)

284　content of the cladode tissue (Figure 4A). Whereas the concentrations of potassium (K$^+$)

285　displayed high values and a significant difference ($P < 0.05$) (Figure 4B). The 'Orelha de

286　Elefante Mexicana' clone had the greatest accumulation of K$^+$, being on average 66% higher

287　than the V19, F8, 'IPA Sertânia' and 'Miúda' clones. The lowest concentrations of K$^+$ were

288　seen in the 'Orelha de Elefante Africana' clone ($P < 0.05$), of 432.09 μmol g^{-1} DW, 62%

289　lower than in the 'Orelha de Elefante Mexicana'. Due to the significant variations in Na$^+$ and

290   K^+ content, the K^+/Na^+ ratio in the cladodes was much higher in the 'Orelha de Elefante

291   Mexicana' in relation to the other clones ($P < 0.05$) (Figure 4C). On average, Na^+ and K^+

292   levels in the 'Orelha de Elefante Mexicana' forage cactus were 39% higher than in the other

293   clones.

294
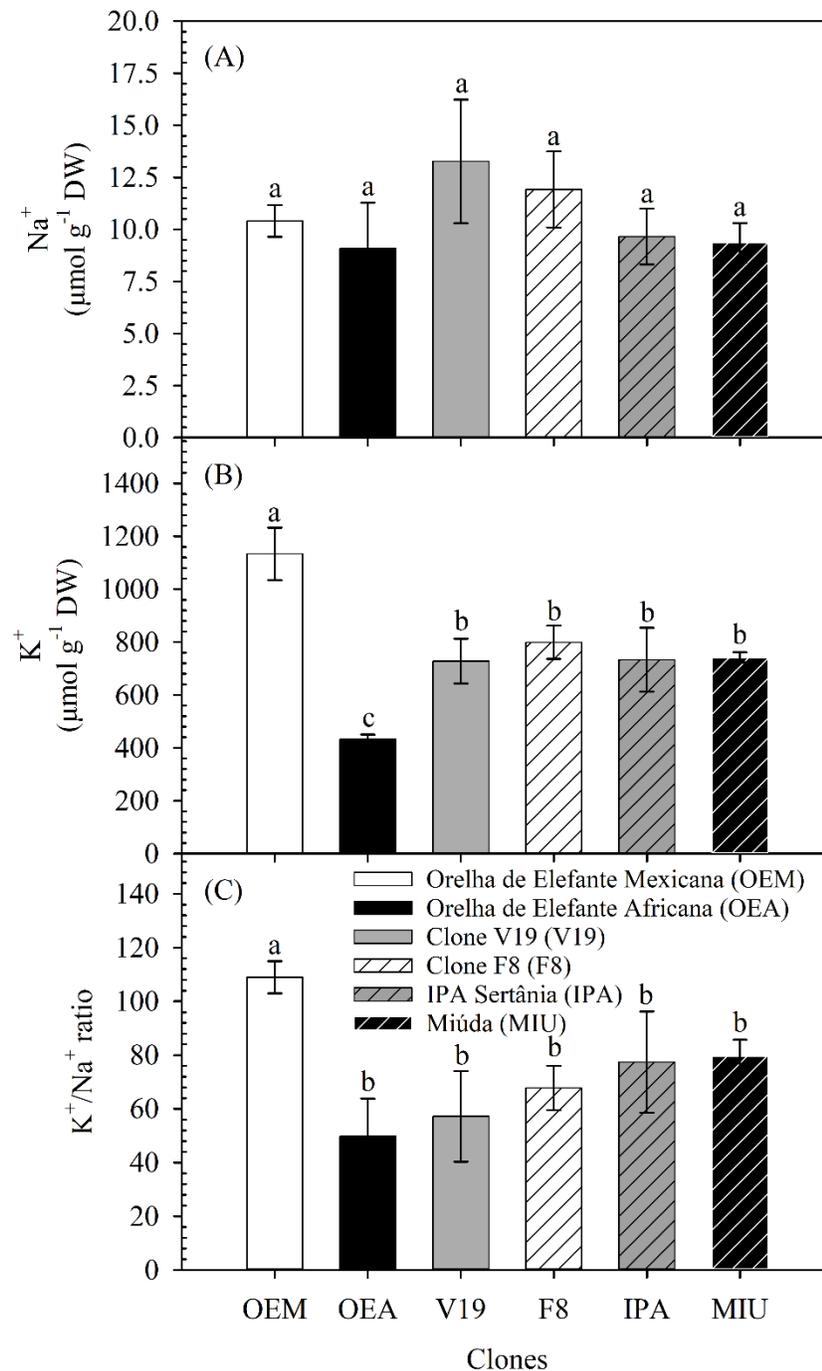
295 **Figure 4.** Na^+ and K^+ content, and the K^+/Na^+ ratio (A, B and C, respectively) in the cladodes
296 of forage cactus clones irrigated with saline water in the semi-arid region of Brazil. Data are
297 presented as mean ± standard deviation ($n = 3$). Mean values followed by the same letter do
298 not differ statistically by Scott-Knott test at a level of 0.05 ($P < 0.05$).

299

300 *3.5 Morphometry and dry matter accumulation*

301   The morphometric and yield characteristics of the six clones are shown in Table 3.
302 There was a significant difference for both the cladode area index (CAI) and cladode yield
303 between the cacti ($P < 0.05$). The 'Orelha de Elefante Mexicana' and 'Orelha de Elefante
304 Africana' clones had the greatest CAI, achieving 90% more than the F8 and 'IPA Sertânia'
305 clones. For dry matter accumulation, the 'Orelha de Elefante Mexicana' was 34% more
306 productive than V19, 'IPA Sertânia' or 'Miúda', with a yield that was 54% greater than the
307 F8 and 'Orelha de Elefante Africana' clones.

308

309 **Table 3.** Morphometry and dry matter production in forage cactus clones.

Clones	CAI ($m^2\ m^{-2}$)	Yield (kg DM plant^{-1})
'Orelha de Elefante Mexicana'	0.9163a	0.5530a
'Orelha de Elefante Africana'	1.0759a	0.2830c
V19	0.3163b	0.3794b
F8	0.1062c	0.2241c
'IPA Sertânia'	0.0996c	0.3415b
'Miúda'	0.3037b	0.3777b

310 Mean values followed by the same letters in a column do not differ statistically by Scott-
311 Knott, at a level of 0.05 ($P < 0.05$).

312

313 *3.6 Association between variables with principal component analysis*

314   In Figure 5, the principal component analysis between the variables under analysis
315 showed that two principal components (PC) were enough to explain 70% of the total variation
316 of the data. PC1 explained 43%, showing a negative correlation between dry matter (DM)
317 production and initial fluorescence (Fo), and a positive correlation with the maximum
318 quantum yield of photosystem II (Fv/Fm), effective quantum yield of photosystem II

319   (ΔF/Fm'), relative electron transport rate (ETR), chlorophyll content (Chl *a*, Chl *b*, and total

320   Chl), carotenoids (Car_{x+c}), K^+ content, and the K^+/Na^+ ratio (Figure 5A). The positive weights

321   of this component had a greater association with the 'Orelha de Elefante Mexicana' and were

322   inversely related to F8 (Figure 5B), indicating that, respectively, these variables explain the

323   best and worst productive performance of these clones. PC2 explained 27% of the total

324   variation in data, with a negative correlation with Chl *a/b*, Fv and Fm, and a positive

325   correlation with the Na^+ content and photochemical quenching (qP). V19 showed a positive

326   association with the Na^+ content and qP, and a negative association with Chl *a/b*, Fv and Fm

327   (Figure 5A and B).

328
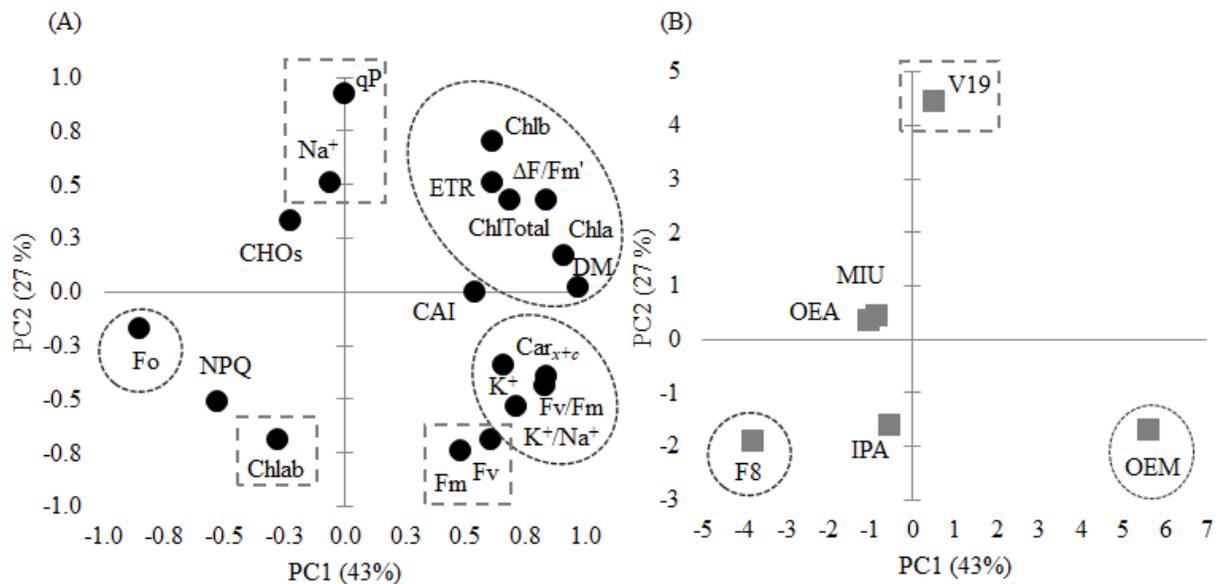
329   **Figure 5.** Principal component analysis (PCA) between the photochemical parameters initial

330   (Fo), maximum (Fm) and variable (Fv) fluorescence; the maximum quantum yield of

331   photosystem II (Fv/Fm); effective quantum yield of photosystem II (ΔF/Fm'); photochemical

332   quenching (qP); non-photochemical quenching (NPQ); relative electron transport rate (ETR,

333   μmol m^{-2} s^{-1}); chlorophyll content (Chl *a*, Chl *b* and total Chl) and the Chl *a/b* ratio;

334   carotenoids (Car_{x+c}); total soluble carbohydrate content (CHOs); Na^+ and K^+ content, and the

335   K^+/Na^+ ratio; cladode area index (CAI); and dry matter (DM) production in forage cactus

336   clones grown in a semi-arid environment. Note: PC - principal component; circles and

337   rectangles show parameter groupings. The (A) panel shows the loadings for each factor, and

338   the (B) panel shows the distribution of forage cactus clones scores in the PCA in the

339   ordination. See section 2.1 for abbreviations of clone's names.

340

341   **4 Discussion**

342   Stressful environmental factors, e.g. drought, excessive solar radiation and

343   temperature, are responsible for changes in energy transfer in different species. As an

344   alternative to the harmful effects, the mechanisms of photoacclimation, whether

345   morphological or physiological, are activated so that there is no damage to the photosynthetic

346   system of species, especially to photosystem II (PSII) (He et al., 2019). The greatest changes

347   in $\Delta F/Fm'$, with sharper reductions as seen in the present results, confirm that tensions from

348   environmental factors express as stress in the plants, thereby dissipating more energy

349   (Makonya et al., 2019). The value of qP shows the portion of photosynthetic electrons

350   transferred after the pigment in the antenna of the reaction centre absorbs radiated light,

351   reflecting the opening of the photosystem II reaction centre. This dissipated energy shows

352   the ability of the plant to release more electrons from the PSII quinone receptor, resulting in

353   greater ATP and NADPH consumption. Generally, losses that occur in the photochemical

354   activity of the species are correlated with a reduction in stomatal conductance, restricting the

355   flow of CO_2 in the cells. In cactaceous species, e.g. *Opuntia streptacantha*, Ojeda-Pérez et

356   al. (2017) report up to 50% impairment of photochemical parameters and a reduction in the

357   consumption of malic acid when the plants are exposed to extreme temperatures (4 ºC and

358   40 ºC). The inhibition of $\Delta F/Fm'$ and qP (see Figure 2) support degradation of the

359   chlorophylls, promoting abnormality in photosynthetic capacity (Zhang and Liu, 2018).

360   The high fluorescence values for non-photochemical quenching (NPQ) reflect the

361   photoprotective action of the plants, which increases continuously during exposure to high

362   light density, favouring oxidative protection over the singlet oxygen generated in the

363   chlorophyll. In hostile environments, an increase in NPQ is an alternative for energy

364   dissipation linked to the xanthophyll cycle; although cacti show excellent adaptation to these

365   ecosystems, especially genus *Opuntia* to the large thermal amplitudes of day and night, they

366   compromise energy efficiency and CO_2 fixation (Ojeda-Pérez et al., 2017), as seen in the

367   present results (Figure 2C). In PSII, NPQ limits the excessive transport of electrons in the

368   region of photosystem I (PSI) via linear electron flow.

369   Despite their photochemical efficiency being compromised, cacti are able to maintain

370   photosynthetic activity. Cacti have specialised anatomical and physiological structures (e.g.

371   storage tissues, fast-growing roots, controlled transpiration and nocturnal CO_2 uptake), which

372   are crucial for survival and longevity in environments unfavourable to maintaining the water

373   status (Lina and Eloisa, 2018). Such photochemical changes in cacti of the genera under study

374   and among other species in environments under environmental stress have also been reported

375   in the literature. Water and temperature restrictions inhibit CO_2 uptake, closing the stomata

376   and reducing the thickness of the leaf structures (Aragón-Gastélum et al., 2014; Ojeda-Pérez

377   et al., 2017).

378   In succulent species of families Cactaceae and Agavaceae, low levels of ETR and

379   high levels of NPQ have been reported as factors of species plasticity in arid and semi-arid

380   environments that contribute to a tolerance of adverse factors, despite a reduction in

381   photosynthetic performance. ETR is involved in the transport of electrons to PSII, and NPQ

382   is involved in dissipating stressful levels of energy (Aragón-Gastélum et al., 2020, 2014).

383   For Aragón-Gastélum et al. (2014), the high temperatures also resulted in significant costly

384   changes in the electron transport rate in cacti.

385   Parameters of chlorophyll fluorescence, i.e. Fo, Fm, Fv and Fv/Fm, are commonly

386   used as indicators of plant sensitivity. For example, under normal conditions, Fv/Fm ranges

387   between 0.80 and 0.83 (Maxwell and Johnson, 2000); values of less than 0.80 indicate the

388   presence of stress to the plant (Aragón-Gastélum et al., 2014). Interestingly, two *Opuntia*

389   clones (V19 and F8) and one *Nopalea* clone ('Miúda') were the most affected. These

390   photochemical changes between the species *Nopalea cochenillifera* (Adams et al., 1989) and

391   *Opuntia basilaris* were investigated by Adams et al. (1987), who found significant changes

392   in solar-energy dissipation, corroborating the present results. However, these changes can be

393   found in species with another type of metabolism, i.e. in genotypes of *Cicer arietinum* (L.),

394   type C3, as reported by Makonya et al. (2019).

395   Despite being considered plants adapted to stressful conditions, changes in

396   photoinhibition can be seen in CAM (crassulacean acid metabolism) plants (see Table 1), as

397   well as in optional CAM species (i.e. C4/CAM metabolism), which, despite showing

398   metabolic plasticity, present reductions in photochemical yield when submitted to water

399   restrictions and high light intensity. These not-so-marked losses are caused by

photoprotective pigments, i.e. anthocyanins, which help to protect the photosynthetic apparatus (Li et al., 2015). Working with *Opuntia streptacantha*, Ojeda-Pérez et al. (2017) reported Fo and Fv/Fm similar to the present study; however, from the 10th day of exposure to temperatures of 40 ºC, the value for Fo was greater than 400, indicating a decline in photosynthetic efficiency.

Cactus cladodes are rich in photosynthetic and photoprotective pigments, such as chlorophylls and carotenoids, respectively, but also pigments such as betaxanthin and betalains. These phenolic compounds contribute to the antioxidant capacity of the plants and the production of protective enzymes (Kharrat et al., 2018). In cacti, due to the high presence of chlorophylls in the region of the chloroplast, the production and regeneration of NADPH remains efficient, even when subjected to high temperatures, favouring the photosynthetic capacity and protecting from oxidative damage (Hara et al., 1997). Antioxidant functions in the cactus can vary between *Opuntia* and *Nopalea* and within each species (Alves et al., 2017).

Chl *a*, Chl *b*, total Chl and the Chl *a/b* ratio varied between clones; this did not occur with the carotenoids (Table 2). These results are similar to those reported by Falcão et al. (2013), in which the 'Orelha de Elefante Mexicana' displayed higher levels of Chl *a* than did clone F8, while there was no difference in Chl *b* or the carotenoids ($P > 0.05$). Furthermore, according to those authors, the levels of photosynthetic pigments in the cladodes may vary according to the time of year. In *Nopalea cochenillifera* submitted to treatments with doses of chromium, Adki et al. (2013) noted that, compared to the control treatment, the total chlorophyll content was maintained in the plant tissue. Analysing seven clones of *Nopalea* and *Opuntia*, Alves et al. (2017) found differences in the photoprotective pigments and antioxidant capacity; however, during periods of greater water availability, clone V19 displayed lower concentrations of antioxidant compounds.

The Chl *a/b* ratio is positively related to the ability of the plants to intercept light (Chen et al., 2019), with the marked green of the cladodes being the particular result of Chl *a* (Cabrera et al., 2016), which is mainly responsible for the photochemical reaction, even when the cladodes are undergoing post-harvest processing. The concentrations of Chl *a*, Chl *b* and total Chl are high, and degradation occurs gradually throughout the storage process due to enzyme activity (Guevara et al., 2003). It is worth noting that the chlorophyll content of

both the vegetative and reproductive structures is reduced during the ripening process (Walker et al., 2011). Cayupán et al. (2011) reported changes in the colour of the pulp and peel of the plant material, mainly due to changes in the Chl *a*, Chl *b* and total Chl content, and the levels of pigments such as betalains, with the Chl *b* concentration being generally more marked, which is different to the present study employing cladodes.

In clones of *Opuntia*, the high concentration of Chl *a* and total Chl promote an improvement in PEPC (phosphoenolpyruvate carboxylase) activity, helping to fix CO_2 and favouring the production of soluble sugars, which are not used exclusively for biomass production, but to maintain the metabolic requirements of the plants (Falcão et al., 2013). In this type of plant, because it uses CAM, the PEPC enzyme plays a key role in photosynthetic metabolism, at high concentrations catalysing oxaloacetate and producing metabolic energy (Walker et al., 2011). Above all, this metabolic energy is more efficient when the cladodes are able to intercept photosynthetically active radiation, aiding in the production of a substrate for photosynthesis; an efficiency that can be compromised even in sunny environments due to the overlap between cladodes and to the plant architecture resulting in photoinhibition (Drezner, 2020).

Carbohydrates are constituents found in most foods. In cacti the main carbohydrates are sugars i.e. glucose and fruits (De Santiago et al., 2018). Clones of genus *Nopalea* have higher concentrations of carbohydrates than do clones of genus *Opuntia*. However, in the present study, some clones showed a high concentration of carbohydrates (Figure 3). Carbohydrates in significant concentrations can be found in cactus species (Krümpel et al., 2020), where they act as precursors of secondary metabolites (Falcão et al., 2013). *Nopalea* clones have higher levels of non-fibrous carbohydrates, which is important for lamb diets, aiding food intake, energy gain and digestive processes in the rumen (Cardoso et al., 2019). Diaz-Vela et al. (2013) reported high levels of carbohydrates and antioxidant agent in *Opuntia* clones.

Plant species tend to accumulate low-molecular-weight carbohydrates in order to survive under hostile conditions. These compounds play a fundamental role in reducing osmotic potential, helping to maintain the water status of the cells and reducing the production of reactive oxygen species (Ahanger and Agarwal, 2017). Due to the photochemical efficiency of the *Opuntia* clones (e.g., 'Orelha de Elefante Mexicana', IPA-

194

462   20 and F8), enzyme capacity and the regeneration of Rubisco (Ribulose-1,5-bisphosphate
463   carboxylase/oxygenase) are factors that favour the synthesis of secondary compounds and
464   the production of carbohydrates; these are more marked in the 'Orelha de Elefante Mexicana'
465   among the three clones mentioned above, and aid resistance to abiotic agents (Falcão et al.,
466   2013).

467   Among the essential nutrients, potassium has a crucial regulatory function in the
468   metabolic process of plants, as an aid to the water absorption capacity and in controlling
469   stomatal opening and closing, promoting defence mechanisms against stress (Chakraborty et
470   al., 2016). Despite not being considered an essential nutrient for most plants, Na^+ at low
471   concentrations has an osmotic function in the vacuole, since in agricultural areas with low
472   K^+ availability, cation exchange occurs due to the affinity of the substrate during molecular
473   synthesis (White, 2013). Among the minerals present in the forage cactus, K^+ is considered
474   to have the highest concentration (Dick et al., 2020; Galizzi et al., 2004). At high levels in
475   the plant, it helps in the firmness of its constituent parts, aiding in the formation of protein
476   compounds and favouring photosynthesis (Galizzi et al., 2004). Dick et al. (2020) also found
477   high concentrations of K^+ compared to Na^+ in cladodes of *Opuntia*, with levels of K^+ four
478   times higher than those of Na^+, characterising it as the most abundant mineral in the forage
479   cactus. These higher concentrations of K^+ and negligible levels of Na^+ were also highlighted
480   by Méndez et al. (2015) in *Opuntia* clones (*O. dillenii* and *O. ficus-indica*). The present
481   results corroborate earlier studies, and emphasise the affinity of forage cactus clones to the
482   mineral K^+ (Figure 4).

483   The differences seen in Na^+ and K^+ content between clones showed that the 'Orelha
484   de Elefante Mexicana' had the highest K^+/Na^+ ratio (Figure 4C). These results demonstrate
485   its greater capacity for reducing Na^+ accumulation in the cladodes as well as its greater
486   efficiency in K^+ uptake, which could be attenuate the toxic effects of Na^+ excess in the tissue
487   favouring cell ionic homeostasis. From the higher K^+ amount relative to Na^+ content
488   presented in the tissues in all clones here evaluated (see Figure 4B and A, respectively)
489   resulting in an elevated K^+/Na^+ ratio, the results suggest a relatively higher selectivity for K^+
490   over Na^+ in this genotype. The K^+ content in the plant cell cytosol is estimated to be relatively
491   higher than the Na^+ content, leading to an elevated K^+/Na^+ ratio, which is necessary to the
492   cell physiological functions (Wang et al., 2020).

493   Environment disturbances that affect the K^+/Na^+ ratio may change the cell ionic
494   balance and affect several biochemical and physiological processes key to plant growth and
495   yield. The results found in this study, showed that clones presented elevated K^+ uptake along
496   with an adequate allocation of this ion in the cladodes. And it is a characteristic that
497   contributes to resistance to water deficit under semi-arid areas. It is also an important
498   physiological characteristic even for the xerophytes succulents species, in which the increase
499   in Na^+ content relative to K^+ also may change cell ionic homeostasis (Wang et al., 2004;
500   Tang et al., 2015; Pan et al., 2016; Cui et al., 2019; Wang et al., 2020). This feature affords
501   the clone greater adaptability. It is evident that there is a high concentration of K^+ in the
502   tissues of the forage cactus (Figure 4B) influenced by the availability of the nutrient in the
503   soil and by the time of year, favouring the production of proteins when assimilated (Krümpel
504   et al., 2020).

505   In the present study, despite the low electrical conductivity of the soil saturation
506   extract, the cumulative effect of the salts found in the irrigation water may promote an
507   increase in the Na^+ of the soil-plant system. In a clone of *Nopalea cochenillifera*, the
508   highlighted presence of sodium in the soil caused changes in the morphometric
509   characteristics and a reduction in plant yield, especially in young cladodes, indicating a lower
510   tolerance to excess salt compared to others clones in this study (Freire et al., 2018).
511   Interestingly, *Opuntia* clones are less sensitive when grown in environments that have a
512   higher concentration of salts in the soil (Bañuelos et al., 2012).

513   Results indicate that supply of salts found in the plant tissue together with the
514   environmental conditions caused intrinsic changes in the morphology and yield of the cacti
515   (Table 3). Plant morphology undergoes changes when faced with exposure to established
516   conditions; the cactus is characteristic for its tortuous canopy structure, which results in
517   changes in light interception in order to overcome the conditions of stress and guarantee
518   survival (Adli et al., 2019; Pinheiro et al., 2015). It is reported in the literature that the 'Orelha
519   de Elefante Mexicana' has significant forage yield as well as being morphologically superior,
520   since the position of the cladodes makes the plant more efficient in using photoassimilates,
521   promoting more advantageous performance (Silva et al., 2015). Adli et al. (2019) found that
522   in clones of *Opuntia ficus-indica* under arid and semi-arid conditions, the environment has a
523   strong effect on the morphometric variables of the cacti, e.g. the width and length of the

cladodes, influencing the cladode area index. Silva et al. (2014) reported different CAI values to the present results in clones of *Opuntia* and *Nopalea*, but a similar mean biomass yield (Silva et al., 2015).

The cladode area index (CAI) is a yield indicator obtained from ratio between the cladode area and the cultivated area by each plant, and it represents a morphometric feature commonly used as yield indicator to forage cactus (Dubeux Jr. et al., 2006; Silva et al., 2014; Pinheiro et al., 2015). In this study both forage cactus clones 'Orelha de Elefante Mexicana' and 'Orelha de Elefante Africana' presented similar elevated CAI, but 'Orelha de Elefante Africana' showed yield relatively lower to dry matter. This apparent discrepancy observed may be justified, at least in part, by the differences between the number and size of cladode, which are intrinsic characteristic of each clone and/or species (Han and Felker, 1997; Dubeux Jr. et al., 2006). In fact, the clone 'Orelha de Elefante Africana' presented a lower number of cladode, but its cladode had relatively bigger size when compared to 'Orelha de Elefante Mexicana'. Thus, its yield did not present a direct relation with the CAI and this index can not be used as the main yield marker for this clone.

Additionally, it was found that this performance is closely associated with the maximum quantum yield of photosystem II (Fv/Fm), the effective quantum yield of photosystem II (ΔF/Fm'), the relative electron transport rate (ETR), the chlorophyll content (Chl *a*, Chl *b*, and total Chl), carotenoids (Car_{x+c}), K^+ content, and the K^+/Na^+ ratio of the clone that affords it greater dry matter accumulation (Figure 5).

5 Conclusion

The present study shows clear evidence that the stress of the environmental conditions had a greater impact on the F8, V19 and 'Miúda' clones, reducing electron use efficiency in carbon fixation, causing damage to PSII, and high energy dissipation. The low chlorophyll and carbohydrate content is involved in the poor photochemical performance of the plants. In addition, the 'Orelha de Elefante Mexicana' was superior in several photochemical parameters, osmotic adjustment, CAI and biomass yield. The unprecedented evidence provided by this study reports the high physiological tolerance of forage cactus species, as an aid in dealing with the potential effects of semi-arid environments and selecting the economically most important species of cactus for agricultural production systems. Further

555 studies are therefore essential to clarify the underlying photochemical mechanisms of the
556 forage cactus in different environments and at different points on the canopy, whether under
557 abiotic stress or not.
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823

CHAPTER 6

3   To what extent are turbulent flux, the energy budget and water relations in the field

4   compromised in *Nopalea cochenillifera* during the wet and dry seasons?

5

6   **Abstract**

7   The *in-situ* quantification of turbulent flux and evapotranspiration (ET) is necessary to

8   monitor crop performance in stressful environments. However, little is known about the

9   seasonal variability of these surface fluxes in cacti, where understanding is still in the early

10   stages. In the present study, we investigate the interannual and seasonal behaviour of

11   components of the surface energy balance (SEB), environmental conditions,

12   morphophysiological parameters and water relations in a crop of *Nopalea cochenillifera* in

13   the semi-arid region of Brazil. Data were collected from a micrometeorological tower

14   between 2015 and 2017. The ET, and flux partitioning into net radiation (R_n), latent heat flux

15   (LE), sensible heat flux (H), and soil heat flux (G) were obtained by means of the SEB, using

16   the Bowen ratio. The performance of the cactus and its response to environmental factors

17   were evaluated using growth rates, phenophases, biomass yield, water relations, the

18   Normalised Difference Vegetation Index (NDVI) and the Evaporative Stress Index (ESI).

19   Generally, R_n was significantly higher during the wet season, being on average 14% higher

20   than during the dry season and transitions. LE was not significant between the wet season

21   (2.87 MJ m^{-2} day^{-1}) or the dry season (2.41 MJ m^{-2} day^{-1}); during the wet-dry transition

22   season, LE is reduced by 25% due to the cactus. During the dry-wet transition season in

23   particular, H was 13% higher than during the other seasons. We observed a large decline in

24   G (203%) during the wet season. At the same time, there was no difference in ET during the

25   wet or dry seasons, however, there was a 40% reduction during the dry-wet transition. The

26   wet seasons and wet-dry transition showed the lowest ESI values (a mean of 0.41 and 0.56,

27   respectively). The mean NDVI was 0.23, cladode water content > 89%, and biomass 12.47

28   Mg ha^{-1}. These findings indicate high rates of growth, high biomass and a high cladode water

29   content, and explain the response of the cactus regarding energy partitioning and ET.

30

31   **Keywords:** Energy redistribution; Semi-arid; Microclimate conditions; Cactus

32

1. Introduction

The cactus, *Nopalea cochenillifera* (L.) Salm-Dyck, is an important plant used in animal diets in semi-arid environments, particularly in the driest areas of north-eastern Brazil and around the world. This species of family Cactaceae is known worldwide for its tolerance to abiotic stress, and is able to survive in places with low annual rainfall (250–450 mm) (Jardim et al., 2021a; Kumar et al., 2022; Winter and Smith, 2022). Plants that exhibit crassulacean acid metabolism (CAM) are more resistant, and have greater water use efficiency (WUE) compared to plants with a C3 or C4 photosynthetic pathway, which are normally less tolerant to high heat and severe drought (Hartzell et al., 2021; Ho et al., 2019; Nobel, 1991; Scalisi et al., 2016). *N. cochenillifera* is composed of vegetative structures called cladodes—modified succulent stems, which offer the animals a high concentration of non-fibrous carbohydrates (~54.3%) and high total nutrient digestibility, in such a way that they are considered a great source of energy. In addition, they are rich in water (~900 g kg^{-1} dry matter) and minerals (especially, Ca^{2+}, K^+ and P). On the other hand, cladodes have low levels of dry-matter, crude protein (~5.4%), neutral detergent fibre (~24.8%), and acid detergent fibre (Dubeux Jr. et al., 2021; Pessoa et al., 2020; Rocha Filho et al., 2021).

Due to their high productive performance, several studies have been carried out with cacti (*Opuntia* spp. and *Nopalea* spp.) in a semi-arid environment, adopting management practices or evaluating the water deficit on the growth and productivity of the crop (e.g., Araújo Júnior et al., 2021; Campos et al., 2021; Jardim et al., 2021a; Kumar et al., 2022; Scalisi et al., 2016). However, few studies have been developed to evaluate the plant-environment interaction using the energy balance method, some with *Opuntia* spp. (Consoli et al., 2013; Gibbs and Patten, 1970) and some with other species and ecosystems that include Cactaceae (Flanagan and Flanagan, 2018; Guevara-Escobar et al., 2021; Lewis et al., 1977). Consoli et al. (2013), under a semi-arid climate in Sicily (Italy), evaluated ecophysiological variables and energy balance in an irrigated crop of *O. ficus-indica*, where they reported the importance of applying a method that detected changes in plant transpiration on a daily scale under wet and dry conditions. Pierini et al. (2014) reported that the heat flux is high in vegetation that includes species of cactus (*O. spinisior* and *O. engelmannii*) in Tucson in the Sonoran Desert (Arizona).

In terrestrial ecosystems, energy and water exchange plays a fundamental role in hydrological control, climate phenomena and species survival. To quantify the land-atmosphere fluxes, and understand this partition, the surface energy balance (SEB) predicts variations in turbulent fluxes and evapotranspiration (ET) from interaction of the soil-vegetation-atmosphere system (Alves et al., 2022; Anderson and Vivoni, 2016; Kuiyue Zhang et al., 2022). In addition to being considered a fairly robust and valid method under semi-arid conditions, it can be applied to different vegetated surfaces (e.g., areas of forest and agricultural crops), and areas with small footprints (i.e., different fetch-to-height ratios) (Awada et al., 2021; Guevara-Escobar et al., 2021; Hicks et al., 2020). Among the methods used to determine turbulent flux, the Bowen ratio indirectly quantifies the latent heat flux (LE) using net radiation (R_n), soil heat flux (G) and the air temperature and humidity gradients (Bowen, 1926; Hu et al., 2014). In addition to being a low-cost method compared to the eddy covariance and weighing lysimeter methods, the Bowen ratio method uses simple sensors, and is preferred in ET studies in agricultural ecosystems (Hicks et al., 2020; Pokhariyal and Patel, 2021; Pozníková et al., 2018).

On a global scale, part of the water from ecosystems is returned to the atmosphere by the ET (Chen et al., 2022). Basically, two processes are involved in ET: evaporation—the phenomenon concerning the change in the liquid phase from water to vapour; and transpiration—the process of transferring water via the plant structures (e.g., stomata) to the atmosphere in the form of water vapour. The sum of these two physical phenomena, i.e., evapotranspiration, consumes more than half of the solar energy, with approximately 60% of the precipitation being transferred to the atmosphere by the LE (Allen et al., 1998; Awada et al., 2021; Cheng et al., 2021; Cheng et al., 2022).

ET is perhaps one of the most studied variables in arid and semi-arid environments, helping to explain the response of the vegetation to water availability. However, in dry landscapes, the available energy is high, and when the ET decreases due to water availability, there is an increase in the sensible heat flux (H) (Anderson and Vivoni, 2016; Awada et al., 2021; Chen et al., 2022; Cheng et al., 2022). Within this context, these factors can trigger conditions of stress for some plant species, and when added to the excessive heat flux and high energy may become more hostile.

In the field, hydrological conditions (i.e., wet and dry seasons) can cause changes in the energy fluxes and ET on different scales. In addition, the vegetation can modify the release of energy in response to its growth and phenology (Awada et al., 2021; Hermance et al., 2015; Lewis et al., 1977). In this respect, using such information as vegetation indices (e.g., cladode area index, and Normalised Difference Vegetation Index) and growth indices (e.g., growth rate and phenophases) can be fundamental in understanding plant feedback to growing conditions.

Finally, although there are studies on monitoring mass and energy fluxes in dry forests and grasslands in a semi-arid environment (Alves et al., 2022; Marques et al., 2020; Shao et al., 2017; Silva et al., 2017; Yue et al., 2019), as far as we know, there are no studies that report information on growth stages, ecophysiology or surface energy balance in *N. cochenillifera*. Therefore, our hypothesis is that (i) even under adverse stress conditions, the performance of the cactus for energy flux and evapotranspiration remains good; and (ii) its growth, water relations, and water and nutrient use efficiency are maintained throughout each season. Furthermore, we believe that our results will provide new insights into CAM plants and their exchange of energy with the ecosystem. The aim of this study is to evaluate the interannual and seasonal behaviour of components of the surface energy balance (SEB), environmental conditions, morphophysiological parameters and water relations, during the wet and dry seasons in a crop of *N. cochenillifera* in the semi-arid region of Brazil. To achieve this aim, we quantified the heat fluxes, partitioned the net radiation, and determined growth rates, plant phenophases and cladode succulence.

2. Materials and methods

2.1. Location and information of the experimental area

The experiment was conducted in a study area located in the district of Mirandiba, in the state of Pernambuco, Brazil (8º3.73' S, 38º43.69' W, altitude 490 m) under the conditions of a water deficit (Figure 1). According to the Köppen classification, the climate in the region is classified as semi-arid, type BSh (i.e., dry and hot with a rainy season in the summer) (Alvares et al., 2013; Beck et al., 2018). Rainfall predominates from January to June, with an annual average of 431.8 mm, average air temperature of 25.2ºC, relative humidity of 64.6%, and a high atmospheric demand that can reach 1,600 mm year^{-1}. The environment is

124 characterised by high luminosity, irregular spatiotemporal distribution of the rainfall, and the

125 occurrence of periodic droughts.

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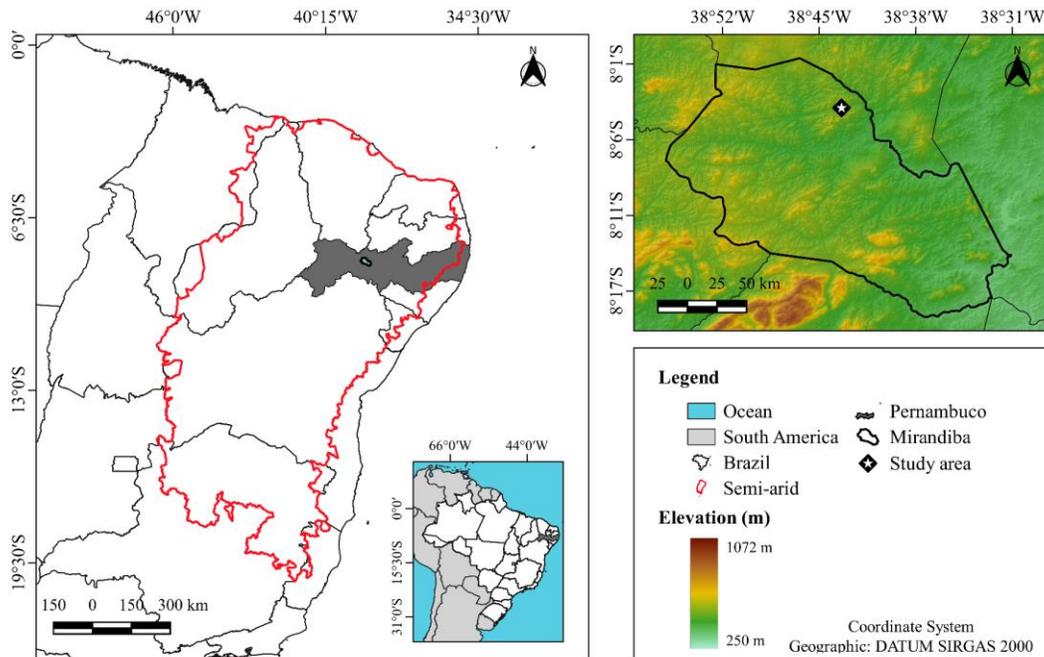
127

128 Figure 1. Geographic location of the study area in the district of Mirandiba, Pernambuco,

129 Brazil.

130

131   Based on the beginning and end of the rainfall regime, we considered four seasons

132 (wet, wet-dry transition, dry, and dry-wet transition) for each year under study from 2015 to

133 2017. If the sum of rainfall values in the 30 days preceding or following the day under

134 analysis is less than 20 mm, and there have been less than five rainy days, it is considered a

135 dry season. However, if in the same time interval, rainfall values greater than 20 mm are

136 recorded on five or more days, the season is considered wet. A transition season is determined

137 when none of these criteria apply. If this happens after a dry season, it is said to be a dry-wet

138 transition season, and when it occurs after a wet season, it is considered a wet-dry transition

139 season (Leite-Filho et al., 2019; Salack et al., 2016). For example, using this approach the

140 wet season included 21 February 2015 to 23 July 2015, 7 January 2016 to 1 February 2016,

211

141 and 21 February 2017 to 1 July 2017; the wet-dry transition included 24 July 2015 to 21

142 August 2015, and 2 February 2016 to 26 July 2016; the dry season included 22 August 2015

143 to 7 December 2015, and 27 July 2016 to 17 November 2016; and the dry-wet transition, 8

144 December 2015 to 6 January 2016, and 18 November 2016 to 20 February 2017.

145 The soil in the experimental area was classified as a Chromic Luvisol (Soil Survey

146 Staff, 2014), comprising 54% sand, 21% silt and 25% clay. Soil samples were collected at

147 depths of 0–0.20 m, with a bulk density of 1.45 g cm^{-3} (measured by the cutting-ring

148 sampling method), soil organic carbon content of 10.1 g kg^{-1}, field capacity of 0.26 cm^3 cm^{-3},

149 soil pH of 6.1 (measured at a soil to water ratio of 1:2.5 using an ion pH meter), and terrain

150 slope between 3% to 5%.

151 The experiment was conducted from April 2015 to April 2017 over a total area of 1.8

152 ha, using the cactus, *Nopalea cochenillifera* (L.) Salm-Dyck, a species tolerant to

153 *Dactylopius opuntiae* Cockerell (Hemiptera: Dactylopiidae). The crop was planted in

154 January 2015. After the initial soil preparation (i.e., ploughing, harrowing and furrowing),

155 the cladodes were planted, leaving 50% of their height in the soil. The plants were arranged

156 in single crop rows with the cladodes aligned bilaterally (i.e., parallel to each other), at a

157 spacing of 2.0 × 0.50 m (10,000 plants ha^{-1}). Cropping treatments (i.e., hand weeding, and

158 the application of herbicide and insecticide) were carried out whenever necessary to avoid

159 competition with spontaneous plants and promote full growth of the crop. The cactus was

160 grown under rainfed conditions throughout the evaluation cycle.

161

162 *2.2. Measuring the meteorological variables*

163 A 3-metre micrometeorological tower was installed in the centre of the experimental

164 area. Net radiation (R_n) data were measured using a closed-cell thermopile sensor (NR-Lite,

165 Kipp & Zonen, Delft, Netherlands), in addition to two net radiometers (SP-230, Apogee

166 Instruments, Logan, Utah, USA). The two radiometer sensors were installed 2.8 m above the

167 canopy, one to quantify the incident radiation and the other for radiation reflected by the

168 canopy (i.e., with the sensors facing up and down). The soil heat flux (G) was measured at a

169 depth of 0.05 m from the surface using a heat flux plate (HFT3, REBS, Hukseflux, Delft,

170 Netherlands) buried close to the crop row. Air temperature (T_a) and relative humidity (RH)

171 were determined using two aspiration psychrometers—creating a vertical profile 0.5 and 1.5

172   m above the surface of the soil. Wind speed and direction were measured using a Wind Sentry

173   model 03002 anemometer (R. M. Young Company, Traverse City, Michigan, USA). Rainfall

174   data were quantified using an automatic rain gauge (CS700-L, Hydrological Services Rain

175   Gauge, Liverpool, Australia) installed 3 m above the canopy, and the photosynthetically

176   active radiation (PAR) was measured using a quantum sensor (LI -190SB, LI-COR, Inc.,

177   Lincoln, Nebraska, USA). In addition, due to the size of the area and the location and height

178   of the meteorological instruments, a suitable search to height ratio (100:1) was determined

179   as per a methodology proposed by Heilman et al. (1989).

180   The data were collected every 60 seconds by data logger (CR10X, Campbell

181   Scientific Inc., North Logan, Utah, USA) with a storage interval of 10 minutes.

182   Measurements were collected continuously both day and night. However, the flux data used

183   in applying the Bowen ratio-energy balance (BREB) method were considered on a daytime

184   scale only. This is because at night, when the temperature/humidity gradients are small,

185   erroneous flux data may be quantified. Each dataset is referred to in terms of local time

186   (GMT-3).

187

188   *2.3. Surface energy balance method*

189   We used the surface energy balance (SEB) method, which is based on the law of

190   conservation of energy (Equation 1).

191

192        $R_n - G = LE + H$ (1)

193

194   where R_n is the net radiation (W m^{-2}), G is the soil heat flux (W m^{-2}), LE is the latent heat

195   flux (W m^{-2}), and H is the sensible heat flux (W m^{-2}).

196

197   The turbulent flux components, i.e., sensible heat and latent heat fluxes were

198   determined based on the Bowen ratio (β) (Equation 2). The Bowen ratio method is widely

199   used to partition energy flux components in relation to the total available energy ($R_n - G$).

200   We can therefore estimate this ratio by quantifying the temperature gradient and vapour

201   pressure above the canopy (Bowen, 1926). In the present study, we did not assume similarity

202   of equality between the turbulent transfer coefficients of the sensible heat (K_h) or of the water

203   vapour (K_w) (Gavilán and Berengena, 2007). Therefore, latent heat flux (*LE*) and sensible

204   heat flux (*H*) were estimated by combining the available energy balance and Bowen ratio

205   (Equations 3 and 4, respectively).

206

207
$$\beta = \frac{H}{LE} = \left(\frac{P_a \times c_p}{\lambda \times \varepsilon} \times \frac{\Delta T}{\Delta e} \times \frac{K_h}{K_w} \right) \qquad (2)$$

208
$$LE = \frac{R_n - G}{1 + \beta} \qquad (3)$$

209
$$H = \frac{\beta}{1 + \beta} \times (R_n - G) \qquad (4)$$

210

211   where β is the Bowen ratio (dimensionless), P_a is the atmospheric pressure (kPa), c_p is the

212   specific heat capacity of the air (1004.67 J kg^{-1} ºC^{-1}), λ is the latent heat of vaporisation

213   (2.454 MJ kg^{-1} at 20ºC), ε is the ratio of the molecular weights of the air and water vapour

214   (0.622), ΔT is the difference in air temperature between the two heights (ºC), Δe is the

215   difference in vapour pressure between the two heights (kPa), K_h is the eddy diffusivity for

216   heat (m^2 s^{-1}), and K_w is the eddy diffusivity for water vapour (m^2 s^{-1}). Quality control was

217   carried out on the calculated *LE* as per Perez et al. (1999).

218

219   Furthermore, in the present study, to calculate the energy balance closure, we ignored

220   the energy from metabolic activities and heat storage in the plant tissue and in the canopy, as

221   well as horizontal advection. This condition can be applied when the surface is uniform,

222   keeping in mind that the vertical gradient that comprises the meteorological elements is far

223   greater than the horizontal gradient. As such, these terms are ignored in building Equation 1

224   (Hu et al., 2014; Pokhariyal and Patel, 2021).

225

226   *2.3.1 Data selection criteria for the energy balance method*

227   In the present study, for the acceptance and/or rejection criteria of the data collected

228   by the Bowen ratio-energy balance (BREB) method, we used the approach proposed by Perez

229   et al. (1999), which parameterises the criteria for using variables to compile the method

230   (Table 1); this is because the Bowen ratio depends on measuring the temperature and vapour

231   pressure gradients. That said, the presence of abnormal data occurs when the available-

232 energy heat flux $(R_n - G)$ is very small. In this way, faults may occur in applying the energy

233 balance by the Bowen ratio (β) and later trigger several errors, e.g., when (1) the sensor

234 resolution is inadequate to solve the gradient in ΔT and Δe; (2) stable atmospheric conditions,

235 e.g., at dawn and dusk, return β values close to -1, resulting in evapotranspiration tending to

236 infinity, which is inconsistent; and (3) the conditions change abruptly, causing measurement

237 errors (Table 2) (Hu et al., 2014; Ortega-Farias et al., 1996; Perez et al., 1999; Unland et al.,

238 1996).

239

240 Table 1. Consistency criteria for data generated by the Bowen ratio method under non-
241 advective conditions.

Available energy[†]	Vapour pressure gradient	Bowen ratio	Heat flux
$R_n - G > 0$	$\Delta e > 0$	$\beta > -1$	$LE > 0$ and $H \leq 0$ for $-1 < \beta \leq 0$ or $H > 0$ for $\beta > 0$
	$\Delta e < 0$	$\beta < -1$	$LE < 0$ and $H > 0$
$R_n - G < 0$	$\Delta e > 0$	$\beta > -1$	$LE > 0$ and $H < 0$
	$\Delta e < 0$	$\beta < -1$	$LE < 0$ and $H \geq 0$ for $-1 < \beta \leq 0$ or $H < 0$ for $\beta > 0$

242 † data considered satisfactory as described by Perez et al. (1999).

243 R_n is the net radiation, G is the soil heat flux, Δe is the difference in vapour pressure between

244 the two measurement heights, β is the Bowen ratio, LE is the latent heat flux, and H is the

245 sensible heat flux.

246

247 Table 2. Summary of error types when faults occur using the Bowen ratio-energy balance
248 method.

Type of error	Applied conditions
A	$R_n - G > 0$, $\Delta e > 0$ and $\beta < -1 + |\varepsilon|$
B	$R_n - G > 0$, $\Delta e < 0$ and $\beta > -1 - |\varepsilon|$
C	$R_n - G < 0$, $\Delta e > 0$ and $\beta > -1 - |\varepsilon|$
D	$R_n - G < 0$, $\Delta e < 0$ and $\beta < -1 + |\varepsilon|$

| $\overline{E}$ | Referring to a rapid change in temperature and vapour pressure. |

249 β is the Bowen ratio, and ε is the error interval that defines the threshold for excluding values

250 of the Bowen ratio close to −1 (Perez et al., 1999).

251

252 *2.4. Resource use efficiency*

253 *2.4.1. Water efficiency*

254 The actual evapotranspiration component (ET, mm day^{-1}) was calculated as described

255 in Equation 5 (Mulovhedzi et al., 2020). To help understand the aboveground dry biomass

256 yield in relation to the volume of water consumed, we calculated the water use efficiency

257 (WUE, kg m^{-3}) of the crop (Equation 6) (Kai Zhang et al., 2022).

258

259
$$\text{ET} = 86{,}400 \times \frac{LE}{\lambda \times \rho_w} \tag{5}$$

260
$$\text{WUE} = \frac{Y}{\text{ET}} \tag{6}$$

261

262 where 86,400 is the time unit conversion factor (i.e., converting from seconds to days), *LE* is

263 the latent heat flux measured over 24 h (W m^{-2}), ρ_w is the density of water (kg m^{-3}), *Y* is the

264 dry matter yield (kg ha^{-1}), and ET is the total amount of seasonal evapotranspiration (m^3

265 ha^{-1}).

266

267 *2.4.2. Radiation use efficiency*

268 The radiation use efficiency (RUE) of the cactus was calculated to describe the light-

269 absorption dynamics of the crop (Equation 7). To achieve this, we used the ratio between the

270 total aboveground dry weight of the plant and the radiation intercepted throughout the

271 growing season (Raza et al., 2019).

272

273
$$\text{RUE} = \frac{Y}{I_0 \times f\text{PAR}} \tag{7}$$

274

275   where RUE is the radiation use efficiency (g MJ^{-1}), I_0 is the amount of daily incident

276   photosynthetically active radiation (PAR) above the canopy (MJ m^{-2}), and fPAR is the

277   fraction of intercepted photosynthetically active radiation.

278

279   The intercepted photosynthetically active radiation was estimated monthly using the

280   AccuPAR LP-80 ceptometer (Decagon Devices, Logan, Utah, USA), manually calibrated

281   prior to taking the readings. To maintain consistent measurement conditions and avoid the

282   influence of the angle of the sun's rays, readings were taken under clear skies between 11:00

283   and 13:00, recording the incident radiation above and below the canopy. Three simultaneous

284   readings were taken below the canopy (with the sensor rod positioned parallel and

285   perpendicular to the crop rows) and one above, on four similar plants in the experimental

286   area. We then calculated fPAR using Equation 8, and the light extinction coefficient (k) based

287   on the Beer–Lambert law (Equation 9). As the cactus has cladodes instead of leaves, we

288   calculated k considering the cladode area index (CAI).

289

290       $$f\text{PAR} = \left(1 - \frac{I_t}{I_0}\right) \tag{8}$$

291       $$f\text{PAR} = 1 - e^{(-k \times \text{CAI})} \tag{9}$$

292

293   where I_t is the PAR measured at the bottom of the canopy, and CAI is the cladode area index,

294   determined according to Pinheiro et al. (2014).

295

296   *2.4.3. Nutrient use efficiency*

297   After cutting (aboveground biomass), the cladodes were weighed on an electronic

298   scale to quantify the fresh biomass (g FM $plant^{-1}$) and then dried in a forced air circulation

299   oven at 55ºC to constant weight, i.e., dry matter per plant (g DM $plant^{-1}$). The dried cladode

300   samples were then ground using a Model 4 Wiley mill (Thomas Scientific) with a 1 mm

301   sieve. The mineral-element concentration in the plant tissue was then determined:

302   phosphorus (P, mg kg^{-1}) using the vanadate-molybdate method with readings by UV-visible

303   spectrophotometry at 430 nm (Du Toit et al., 2018); potassium (K^+, mg kg^{-1}) and sodium

304   (Na^+, mg kg^{-1}) by flame photometry (Rodrigues et al., 2013); and Calcium (Ca^{2+}, mg kg^{-1})

305 and magnesium (Mg^{2+}, mg kg^{-1}) by atomic absorption spectrophotometry (Loupassaki et al.,

306 2007). Finally, nutrient use efficiency (NUE, mg m^{-3}) was calculated as per Equation 10.

307

308
$$NUE = \frac{Y \times Nu}{ET}$$
(10)

309

310 where Nu is the concentration of the nutrient in the analysed sample of plant tissue (mg kg^{-1}).

311 To improve understanding of nutrient uptake by the plants, we adapted Equation 10 (Zhang

312 et al., 2020), making it a function of crop evapotranspiration. This adaptation affords more

313 clarity in explaining the nutrient uptake capacity of the plant from the soil solution, together

314 with the water consumption lost through evapotranspiration.

315

316 *2.5. Analysing growth, phenology, cutting time and yield*

317   Morphometric data were collected monthly and samples of plant biomass were taken

318 at 60-day intervals. Four plants were measured for each analysis in each evaluation period.

319 Height was evaluated considering the vertical distance from the ground to the apex of the

320 canopy, and width, considering the average of two measurements from the edge of the

321 canopy. The length (CL, cm), width (CW, cm) and perimeter (CP, cm) of the cladodes were

322 measured, and the number of cladodes (NC, units) determined by counting the cladodes in

323 order of appearance on the plant (i.e., first-order, second-order, third-order, and so on). The

324 total number of cladodes was determined summing the cladodes by order.

325   The cladode area (CA) was determined from the morphometric data as per the

326 equation proposed by Silva et al. (2014) (Equation 11). We then quantified the cladode area

327 index (CAI) using the equation proposed by Pinheiro et al. (2014) (Equation 12). In addition,

328 from the dry mass yield and cladode measurements, we calculated the morphophysiological

329 indices and phenology using a sigmoidal model with three parameters (Equation 13) and

330 accumulated degree-days (Equation 14) (Arnold, 1959; Jardim et al., 2021c).

331

332
$$CA = 1.6691 \times \left(\frac{1 - e^{(-0.0243 \times CP)}}{-0.0243} \right)$$
(11)

333
$$CAI = \left[\sum_{n}^{i=1} (CA) \bigg/ \frac{10{,}000}{(S1 \times S2)} \right] \qquad (12)$$

334
$$y = \frac{a}{1 + e^{\left(-\frac{x-x0}{b} \right)}} \qquad (13)$$

335
$$ADD = \sum_{j=1}^{n} \left[\frac{(T_{max} + T_{min})}{2} - Tb \right] \qquad (14)$$

336

337 where i is the observation number, n is the total number of observations, 10,000 is the

338 conversion factor from cm² to m², and S1 × S2 is the spacing between the rows and plants

339 (1.0 × 0.2 m), respectively.

340

341   The following parameters were used in the morphophysiological and phenological

342 analysis: y is the response variable (e.g., cladode dry matter, cladode area index, and the

343 number of cladodes); a is the maximum value for the growth rate (i.e., the distance between

344 the two asymptotes); x is the accumulated degree-days; $x0$ is the number of degree-days

345 necessary for the plant to express 50% of the maximum growth rate (i.e., the inflection point

346 of the curve); and b is the number of degree-days necessary to the start of growth; ADD is

347 the accumulated degree-days (°Cday); j is the daily time step; n is the total number of days;

348 T_{max} is the daily maximum air temperature (°C); T_{min} is the daily minimum air temperature

349 (°C); Tb is the lower base temperature (°C). Tb is the minimum temperature at which cactus

350 cladodes grow (22°C). If the daily average temperature drops below 22°C, the ADD becomes

351 negative. Negative ADD values were set to zero.

352   The growth indices were then quantified: absolute growth rate (AGR, Mg ha^{-1}

353 °Cday^{-1}); relative growth rate (RGR, Mg Mg^{-1} °Cday^{-1}); net assimilation rate (NAR, Mg ha^{-1}

354 °Cday^{-1}); specific cladode area (SCA, Mg^{-1} °Cday^{-1}); and cladode emission rate (CER, units

355 °Cday^{-1}) based on earlier studies (Jardim et al., 2021c). The cladode emission rate is a very

356 important variable in phenological analysis, as it is used to obtain the phenological phases of

357 the crop (Amorim et al., 2017; Jardim et al., 2021c). We determined the cutting time as when

358 the absolute growth rate reached 25% of the maximum peak (Jardim et al., 2021c).

359

360   *2.6. Measuring the plant water status*

361   The cladode water content (CWC, %) was calculated from the fresh matter weight

362   (FM) and dry matter weight (DM) of the samples (Equation 15) and from the cladode

363   succulence (CS, g cm^{-2}) (Equation 16) (Corrado et al., 2020; Ho et al., 2019).

364

365        $$CWC = \left(\frac{FM - DM}{FM}\right) \times 100 \qquad\qquad (15)$$

366        $$CS = \left(\frac{FM - DM}{CA}\right) \qquad\qquad (16)$$

367

368   *2.7. Indicators of water and environmental stress*

369   In this study, we examined the Normalised Difference Vegetation Index (NDVI) and

370   the Evaporative Stress Index (ESI) for seasonal and interannual variations. The association

371   between the NDVI and ESI allows the health status of plants to be understood in response to

372   the intensity of hydrological drought (Anghileri et al., 2022; Wolf et al., 2016). The NDVI

373   was derived using images from the Landsat-8 Operational Land Imager (OLI) and Landsat-

374   7 Enhanced Thematic Mapper (ETM+), available on the United States Geological Survey

375   (USGS) website at 30 m resolution for the red (0.64–0.67 μm) and near-infrared (0.85–0.88

376   μm) bands (Jardim et al., 2022; Prăvălie et al., 2022). Landsat images acquired from April

377   2015 to April 2017 were then processed using the Google Earth Engine (GEE) platform.

378   With the GEE Application Programming Interface (API) we implemented code written in

379   JavaScript to quantify the NDVI (Jardim et al., 2022). In addition, a pixel-quality attribute

380   mask was applied to the images to mask clouds, cloud shadow and water using the CFMask

381   algorithm, with the values expressed as surface reflectance (Foga et al., 2017; Hurni et al.,

382   2019). The NDVI can take dimensionless values ranging from −1 to +1, being positive when

383   the crops show photosynthetic activity, and generally referring to bodies of water when

384   negative. On the other hand, low positive NDVI values are characteristic of stressed

385   vegetation or vegetation with a small leaf area.

386   Although the ESI can be quantified via remote sensing, we used field data to quantify

387   it as per Equation 17 (Anderson et al., 2007). The ESI generally ranges from 0 to 1, and is

388   linked to the evaporative demand of both the surface and the atmosphere. When the ESI is

389   close to 1, it indicates water stress in the ecosystem; when it approaches 0, it indicates the

390 absence of water stress (Wolf et al., 2016; Yue et al., 2019). In addition, the reference

391 evapotranspiration (ET_0) was estimated using the FAO-56 Penman-Monteith method, and

392 then multiplied by the crop coefficient (K_c) to obtain the potential crop evapotranspiration

393 (PET_c) (Allen et al., 1998).

394

395 $$ESI = 1 - \frac{ET}{PET_c} \tag{17}$$

396

397 *2.8. Soil moisture*

398 We considered the soil water balance method proposed by Thornthwaite–Mather to

399 determine the available water fraction (AWF) over time (Bielski et al., 2018; Lyra et al.,

400 2016; Pardo et al., 2020; Thornthwaite and Mather, 1955). This fraction expresses the total

401 available water that a crop can extract without undergoing water stress (Bielski et al., 2018;

402 Pardo et al., 2020). Daily soil and micrometeorological data from the tower located in the

403 experimental area were used. The available water capacity of the soil and a respective root-

404 system depth of 75 cm and 60 mm were considered as per Aparecido et al. (2021) and

405 Almagbile et al. (2019).

406

407 *2.9. Statistical analysis*

408 In the first step, we applied nonlinear sigmoid functions for the morphophysiological

409 indices and cutting time, adopting the significance of the F-test ($P < 0.05$) and the coefficient

410 of determination ($R^2 > 0.85$) as the criterion for choosing the model. Data on the NDVI, ET_0,

411 ESI, available water fraction and rainfall were submitted to descriptive statistics and

412 expressed as the mean and standard deviation. In the next step, the time-scale data of the

413 energy balance components (R_n, *LE*, *H*, and *G*), ET, and VPD for the four seasons under

414 study (i.e., wet season, dry season, wet-dry transition and dry-wet transition) were submitted

415 to one-way analysis of variance (ANOVA) by F-test ($P < 0.05$). The mean values were

416 compared by Tukey's HSD (honestly significant difference) test for multiple comparisons

417 ($P < 0.05$). Data on the cladode water content and environmental conditions were evaluated

418 using boxplots showing the median, interquartile range and 1.5 times the interquartile range.

419   Finally, the interrelationships between the plant parameters and environmental
420   conditions were tested using principal component analysis (PCA). We applied PCA to the
421   mean value of the environmental variables (R_n, *LE*, *H*, *G*, VPD, ESI, NDVI and ET_0) and
422   plants variables (ET, NUE, WUE, AGR, RGR, NAR, SCA, CWC, CS, RUE and yield). The
423   response variables were standardised using the z-transform (mean = 0, standard deviation =
424   1), subtracting from the mean value and then dividing by the standard deviation. This is due
425   to the different magnitudes and units of the variables under study, and makes them directly
426   comparable. Significant principal components were selected according to the Kaiser
427   criterion, considering only eigenvalues greater than 1.0 (Jardim et al., 2021a, 2022; M. V. da
428   Silva et al., 2021). The analysis was carried out using the R software (R Core Team, 2022).
429

430   **3. Results**

431   *3.1. Surface energy budget*

432   Figure 2 shows daytime values for the hourly variation in the energy balance fluxes
433   during the experimental period, with the components evaluated during the wet and dry
434   seasons and their transitions (i.e., wet-dry and dry-wet seasons). During the wet season, the
435   lowest daily values for net radiation (R_n) were seen in 2015 (Figure 2a), and the maximum
436   in 2016 (Figure 2e), with mean values of 172.21 and 247.92 W m^{-2}, respectively. Among the
437   energy fluxes, most of the R_n came from the sensible heat flux (*H*), with the exception of
438   2015, which showed a mean value of 95.49 W m^{-2}. In 2017, the highest value was seen for
439   *H* (143.58 W m^{-2}), whereas 2015 and 2016 saw the lowest and highest values for latent heat
440   flux (*LE*), respectively, with a mean value of 47.62 and 145.38 W m^{-2}. During the wet season,
441   the soil heat flux (*G*) was greater in 2017, showing a mean value of 32.13 W m^{-2}, with a
442   gradual increase throughout the day and maximum values around noon (11:00 to 14:00 local
443   time). On the other hand, we found lower values for *G* during 2016, with a mean of 23.33 W
444   m^{-2}. As shown in Figures 2b and 2f (wet-dry transition), R_n was 12% lower than during the
445   wet season. There was a considerable variation in *LE* between 2015 and 2016, with mean
446   values of 80.88 and 51.32 W m^{-2}, respectively. This seasonal pattern was responsible for
447   smaller turbulent fluxes; furthermore, there was an increase in *G* (34%) compared to the
448   previous season.
449
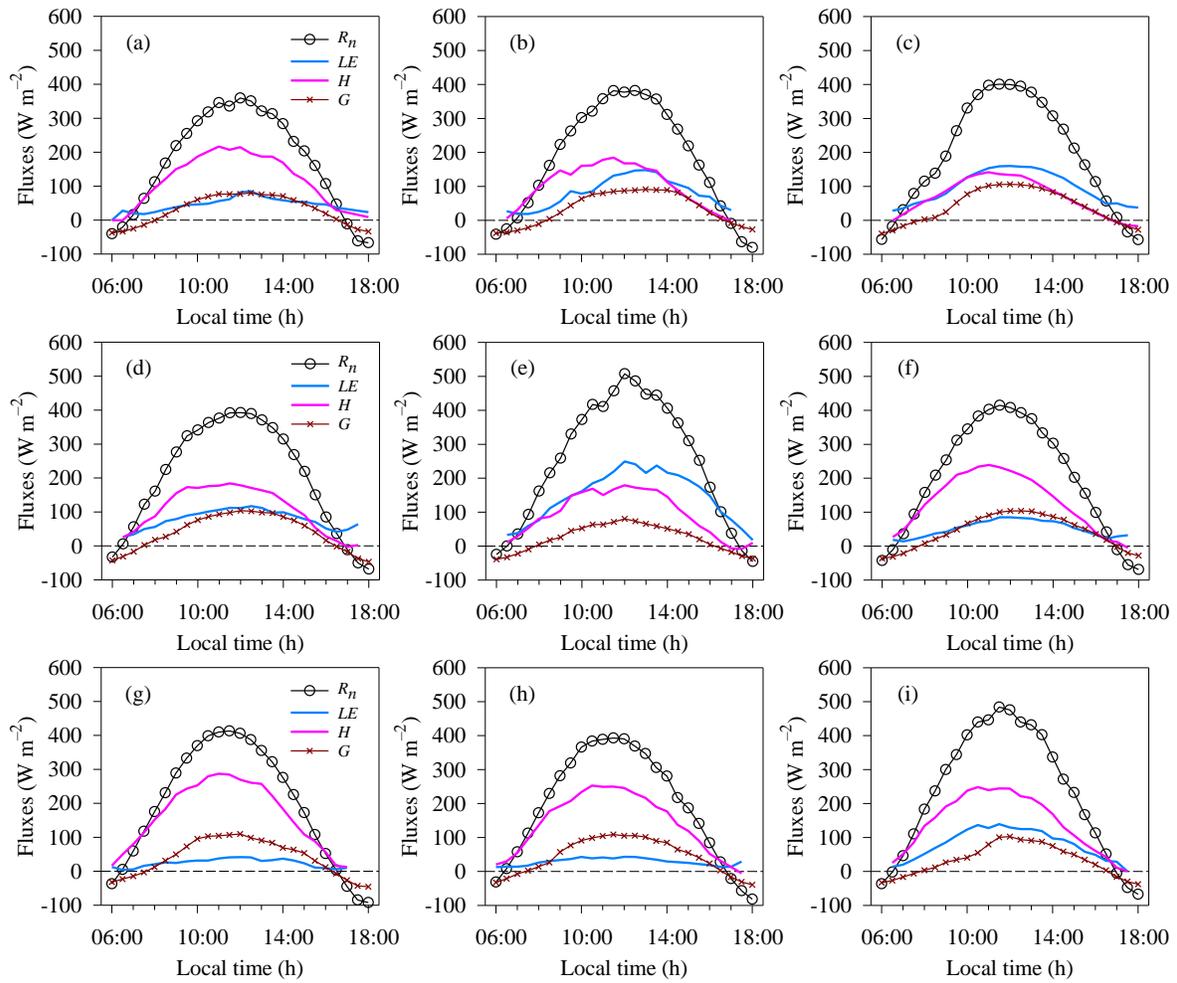
Figure 2. Hourly daytime mean energy flux over the area of cactus for different periods: wet season (a, e, and i), wet-dry transition (b and f), dry season (c and g), and dry-wet transition (d and h). Here Rn is the net radiation, LE is the latent heat flux, H is the sensible heat flux, and G is the soil heat flux, all calculated in W m^{-2}. Note: panels (a), (b) and (c) show the seasons for 2015; (d), (e), (f) and (g) for 2016; and (h) and (i) for 2017.

The values for R_n obtained throughout the day during the dry season in 2015 and 2016 (Figure 2c and 2g) were very similar, with mean values of 191.83 and 194.02 W m^{-2}, respectively. These results for the energy budget are similar to the wet-dry transition season, and different to those seen during the wet season. Specifically, G showed a significant increase (42%) compared to the wet season. For the turbulent fluxes, LE was 41% greater than H during the dry season in 2015. On the other hand, H showed contrasting behaviour in

463   2016 due to atmospheric conditions, being 141% higher than in 2015. Even so, the total

464   turbulent flux was similar for the two years mentioned above, with a mean value of 176 .87

465   W m^{-2}. In general, the turbulent fluxes exhibited opposite trends over time, and was the

466   component with the greatest contribution to the energy budget. Figures 2d and 2h show the

467   daily fluxes during the dry-wet transition season for 2016 and 2017. The result for R_n in 2016

468   was 3.79% higher than in 2017, and comparing the two transition seasons, the value for R_n

469   during the dry-wet transition season is higher than during the wet-dry transition (4%). There

470   was a large temporal variation in G during the study period. During the dry-wet transition

471   season especially, G was approximately 18% higher than during the other seasons. Despite

472   making a significant contribution to the energy balance, our results for H were approximately

473   2% (wet season), 6% (wet-dry transition) and 7% (dry season) higher during the dry-wet

474   transition season. Furthermore, for the same season, which includes a dry phase, there was a

475   reduction in LE (26%) compared to the other seasons. Based on this, it is clear that most of

476   the available net surface energy contributed to the sensible heat flux.

477   On a temporal scale, changes can clearly be seen in the energy budget throughout

478   each year (Figure 3). The mean values for global solar radiation (R_g) decrease significantly

479   from May to July, being 22% lower in relation to the other years (Figure 3a). We also saw a

480   greater range in December 2015 (median 24.38 MJ m^{-2} day^{-1}, interquartile range 18.47 to

481   25.92) and January 2016 (median 21 MJ m^{-2} day^{-1}, interquartile range 13.72 to 22.33). In

482   2015, 2016 and 2017 the mean values for R_g were 20.45, 20.27, and 20.84 MJ m^{-2} day^{-1},

483   respectively, despite an intermonthly variation (median 20.96 MJ m^{-2} day^{-1}, interquartile

484   range 17.75 to 23.73). Figure 3b shows the variation in R_n throughout the experiment. In

485   April 2015, January and February 2016, and from March to April 2017, the values for R_n

486   were higher, with a mean of 8.82 MJ m^{-2} day^{-1}. However, the mean R_n for the three years

487   was 6.52 MJ m^{-2} day^{-1} (median 6.15, interquartile range 5.27 to 7.21), with a reduction of

488   26% compared to the months with the higher values shown above. As a result of cloudiness,

489   R_n had the lowest values in June, with a mean of 4.51 MJ m^{-2} day^{-1}.

490

491
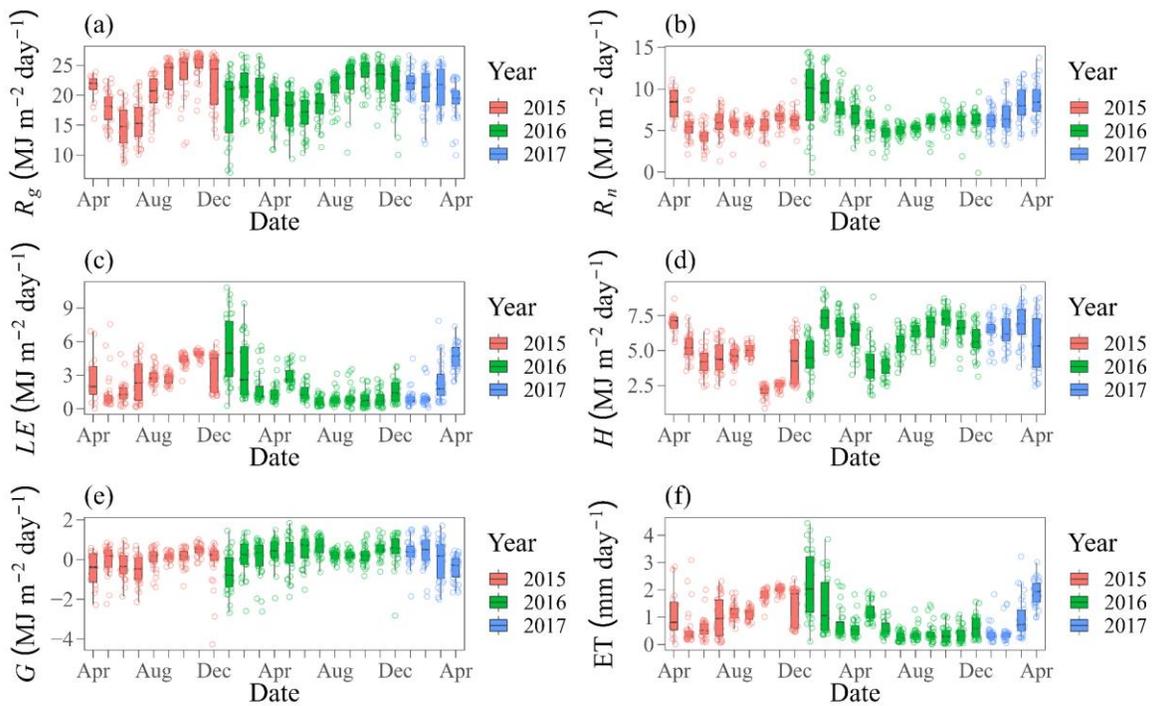
Figure 3. Time series for the energy budget in an area of cactus from 2015 to 2017. R_g is the global solar radiation (a), R_n is the net radiation (b), LE is the latent heat flux (c), H is the sensible heat flux (d), G is the soil heat flux (e), and ET is the evapotranspiration (f). The boxplots show the median; horizontal bars represent the 25th, 50th, and 75th percentiles; whiskers (lower and upper) represent the 1.5× interquartile ranges. Corresponding data are represented by circles.

Figures 3c and 3d show the turbulent fluxes in the energy balance, with a mean value for LE of 2.32 MJ m^{-2} day^{-1}, and maximum and minimum values of 5.41 and 0.70 MJ m^{-2} day^{-1}, respectively, in January (median 4.97 MJ m^{-2} day^{-1}, interquartile range 2.88 to 7.83) and July (median 0.56 MJ m^{-2} day^{-1}, interquartile range 0.31 to 0.98), both in 2016. After the occurrence of high LE values from January to April 2016, there was a significant value (2.92 MJ m^{-2} day^{-1}) in May 2016 due to the rainfall events (Figure 5i). Obvious inversion of the turbulent fluxes can be seen from the values for LE in relation to H (Figures 3c and 3d). Although the values for LE are relatively high, energy consumption is synchronous with that of H. During 2015–2017, H showed a mean value of 5.39 MJ m^{-2} day^{-1}. Interestingly, the minimum values of H, with a mean of 2.11 MJ m^{-2} day^{-1} (median 2.21 MJ m^{-2} day^{-1}, interquartile range 1.93 to 2.35) and maximum values, with a mean of 7.21 MJ m^{-2} day^{-1}

225

510 (median 7.24 MJ m^{-2} day^{-1}, interquartile range 6.80 to 7.86) occurred in October 2015 and

511 2016, respectively, and due to the influence of the rainfall, resulted in a difference of 71%.

512 Furthermore, H gradually increased in value from July to September 2015 and July to

513 October 2016, with mean values during this period of 4.70 and 6.37 MJ m^{-2} day^{-1},

514 respectively.

515 Figures 3e and 3f show the behaviour of G and of the evapotranspiration (ET). For G,

516 the values were more negative during 2015 (April to July, and December) as well as in

517 January 2016, and April 2017. As shown, the minimum values (median –0.77 MJ m^{-2} day^{-1},

518 interquartile range -1.37 to 0.10) and maximum values (median 0.71 MJ m^{-2} day^{-1},

519 interquartile range 0.36 to 1.07) ranged, on average, from -0.65 to 0.67 MJ m^{-2} day^{-1},

520 respectively. We found high values for ET when G and H were low. Despite the interannual

521 variability, the range of values for ET agree with the turbulent heat fluxes, ranging from 0.29

522 to 2.22 mm day^{-1} (median 0.23 MJ m^{-2} day^{-1}, interquartile range 0.13 to 0.40; and median

523 2.03 MJ m^{-2} day^{-1}, interquartile range 1.18 to 3.21, respectively), with a mean of 0.95 mm

524 day^{-1} during the period under study.

525 In Figure 4 and Table 3, we present a detailed seasonal boxplot analysis of the energy

526 budget, heat exchange capacity and water vapour in the cactus during the four seasons (wet,

527 wet-dry, dry, and dry-wet), together with the energy partition ratios. For R_n, the values were

528 significantly higher during the wet season (Tukey's HSD test, $P < 0.05$; median 6.61 MJ m^{-2}

529 day^{-1}, interquartile range 4.99 to 9.37), being on average 14% higher than during the other

530 seasons (Figure 4a). Despite showing similar mean values for R_n, during the dry season, the

531 energy was 7% lower than during the dry-wet transition season. For LE (Figure 4b), there

532 was no significant difference ($P > 0.05$) between the wet and dry seasons, with mean values

533 of 2.87 and 2.41 MJ m^{-2} day^{-1}, respectively. On the other hand, there was a 25% reduction

534 ($P < 0.05$) in LE with the arrival of the wet-dry transition season. Notably, the lowest and

535 highest values for LE and H were seen during the dry-wet transition season, 1.57 and 5.89

536 MJ m^{-2} day^{-1}, respectively. These effects were even greater for H (Figure 4c), with

537 significantly higher values ($P < 0.05$) during the dry-wet transition season (median = 6.16

538 MJ m^{-2} day^{-1}, interquartile range 5.20 to 6.84). In general, during the dry-wet transition

539 season, H was 13% greater than during the other seasons, showing that in the cactus under a

540 semi-arid environment most of the R_n is destined for this process (Figure 4c). Verifying the

energy partitions (Table 3), the H/R_n ratio was generally responsible for the highest power consumption (58%). The LE/R_n ratio varied between 17% and 30%, with a total mean value of 24% over all the seasons. In addition, the G/R_n ratio reached an average of 17%, with the smallest partition (13%) during the wet season (Table 3).
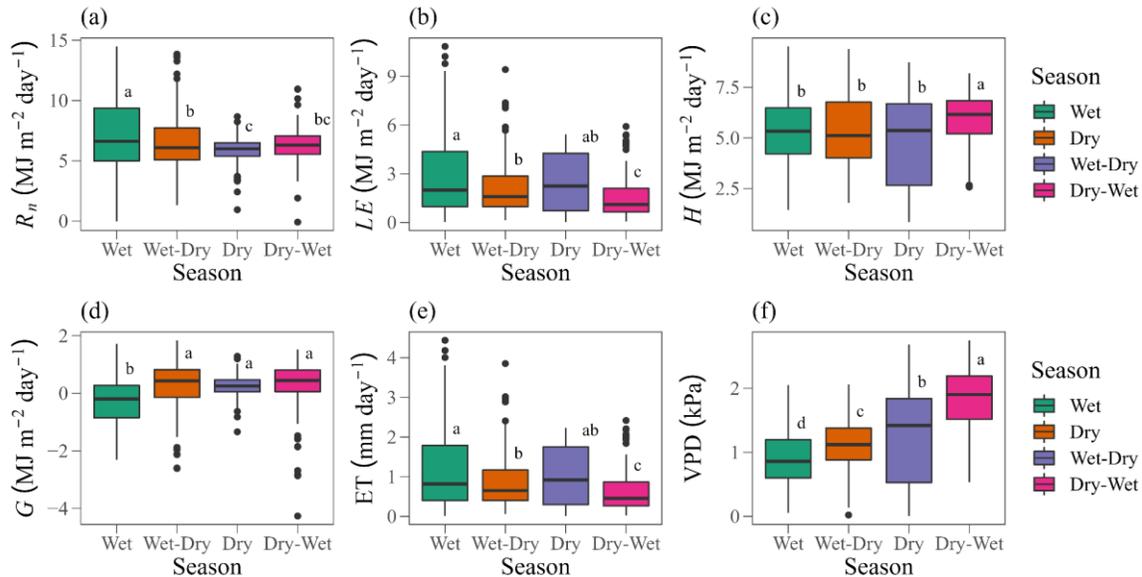
Figure 4. Boxplot of seasonal variations in energy and water exchange in an area of cactus. R_n is the net radiation (a), LE is the latent heat flux (b), H is the sensible heat flux (c), G is the soil heat flux (d), ET is the evapotranspiration (e), and VPD is the vapour pressure deficit (f). The boxplots show the median; horizontal bars represent the 25th, 50th, and 75th percentiles; whiskers (lower and upper) represent the 1.5× interquartile ranges; dots represent outliers. Significance was calculated using one-way analysis of variance (ANOVA) with Tukey's honestly significant difference (HSD) post hoc test. Different letters above each box indicate significant differences ($P < 0.05$).

Table 3. Energy budget component partitioning during the wet, wet-dry, dry, and dry-wet seasons in an area of cactus.

Season	Partition ratio (%)		
	LE/R_n	H/R_n	G/R_n
Wet	30	57	13
Wet-dry	23	58	19

Dry	26	55	19
Dry-wet	17	64	19
Mean ratio	24	58	17

R_n is the net radiation; LE is the latent heat flux; H is the sensible heat flux; G is the soil heat flux.

558

559   The lowest values for G (Figure 4d) were seen during the wet season (−0.28 to 0.28
560   MJ m^{-2} day^{-1}), with a marked reduction of 203% in relation to the other seasons. The sharp
561   decrease in G and the G/R_n ratio during the wet season (Table 3) is clearly due to the high
562   volumes of rainfall and soil moisture (Figure 5) during this period. Similar to the behaviour
563   of LE, there was no significant difference in ET values during the wet or dry seasons (Figure
564   4e). This confirms the hypothesis that ET is maintained during the dry season and decreases
565   during the dry-wet transition season (median 0.46 MJ m^{-2} day^{-1}, interquartile range 0.26 to
566   0.86). We saw reductions of 40.31% and 26.68% during the dry-wet transition when
567   comparing the wet and dry seasons and the wet-dry transition season, respectively ($P < 0.05$).

568   There was a clear significant seasonal variation in the vapour pressure deficit (VPD)
569   (Figure 4f), with a mean of 1.82 kPa during the dry-wet transition season, being 45% and
570   97% higher during the dry season (median 1.42 kPa, interquartile range 0.53 to 1.84) and wet
571   season (median 0.86 kPa, interquartile range 0.60 to 1.20), respectively. Furthermore, there
572   was a significant difference ($P < 0.05$) when comparing the VPD of the transition seasons,
573   where the VPD of the wet-dry season was 38% lower than that of dry-wet season (median
574   1.12 and 1.90 kPa, interquartile ranges 0.88 to 1.38 and 1.52 to 2.19, respectively).

575

576   *3.2. NDVI signatures, environmental data and the impact of drought*

577   We selected a time series for the Normalised Difference Vegetation Index (NDVI),
578   reference evapotranspiration (ET$_0$), Evaporative Stress Index (ESI), available water fraction
579   (AWF) and rainfall during the experimental period (Figure 5). There was no NDVI saturation
580   during any of the cactus growing seasons (Figures 5a and 5b). The highest NDVI values were
581   seen during the wet season, with a mean of 0.23. Every year, the mean value of the wet-dry,
582   dry, and dry-wet seasons (transitions) were, respectively, 9%, 26%, and 39% lower than
583   during the wet season. In addition, it should be noted that the NDVI decreased more

significantly (17%) during the change from the dry season to the dry-wet transition season (Figure 5b). Despite oscillations in the NDVI trajectory in the area, the final periods of the cycle show greater consistency, with a rise in the index. Variations in the NDVI are influenced by the canopy cover, cladode morphometry (see Figure 6) and environmental conditions (Figure 5c and 5e). As shown in Figure 5c and 5d, the mean values for ET_0 ranged from 4.26 ($\pm$0.83) to 7.85 ($\pm$0.63) mm day^{-1} (mean $\pm$ standard deviation), both variations occurring in 2015. Variations, both intermonthly and throughout the year, can also be seen in the ET_0, with lower values between May and July, mainly due to the lower incidence of solar radiation and the lower air temperature (Figure 5c). During the present study, the ET_0 was, on average, 6.24 mm day^{-1}, with emphasis on the dry season (6.87 mm day^{-1}) and the dry-wet transition season (6.78 mm day^{-1}). On the other hand, we found lower values during the wet and wet-dry seasons, of 5.79 and 5.33 mm day^{-1}, respectively. Although high ET_0 values can be found for approximately 48% of the experimental period, the values remained below 6.24 mm day^{-1}.
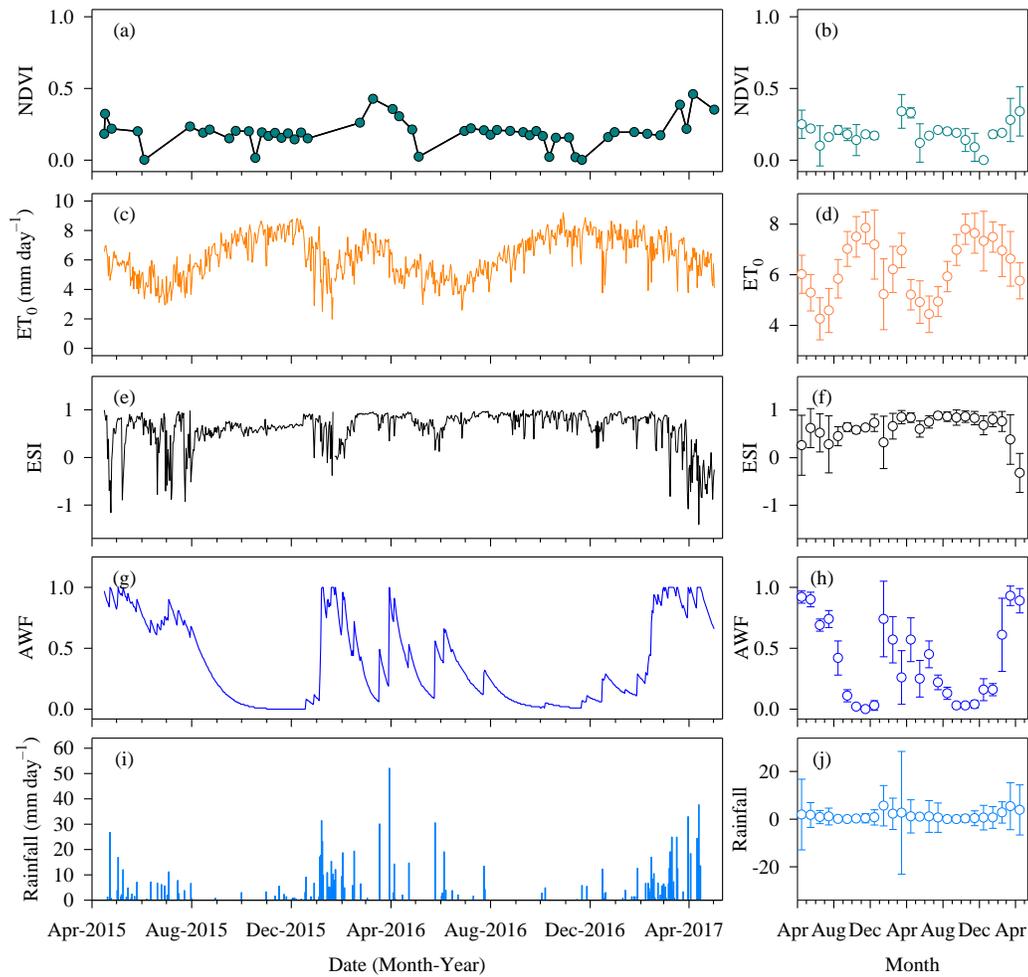
Figure 5. Temporal evolution of the Normalised Difference Vegetation Index [NDVI] (a), reference evapotranspiration [ET_0] (c), Evaporative Stress Index [ESI] (e), available water fraction [AWF] (g), and rainfall (i) for an area cultivated with cactus. The five panels (b), (d), (f), (h), and (j) show monthly results over each year for NDVI, ET_0, ESI, AWF and rainfall during the experimental period, respectively. Data with error bars represent the mean ± SD (standard deviation).

The monthly mean ESI ranged from −0.32 to 0.88 (Figure 5f). We saw negative ESI values (Figure 5e and 5f) due to the concentrated rainfall events, favouring greater soil moisture (Figure 5g and 5i). The wet season and the wet-dry transition season had the lowest ESI values, with a mean of 0.41 and 0.56, respectively. On the other hand, 2016 saw an exception in the behaviour of the ESI during the wet-dry transition season, with mean values

612 greater than 0.7. During the dry season, the index was 35% higher than during the other
613 seasons, reaching 78% compared to the wet season. This clearly confirms that the most
614 stressful conditions occur during the dry season, which in turn has a high atmospheric
615 demand. The variations in AWF largely occurred together with those of the above-mentioned
616 variables (Figure 5g); in addition, the greatest mean value (0.77) was seen during the wet
617 season. The monthly variation in AWF in the soil ranged from 0.002 to 0.931, and notably,
618 these variations showed more critical values during the dry season, with a mean of 0.12 and
619 0.09 during 2015 and 2016, respectively. However, even with a water scarcity during the
620 wet-dry and dry-wet transition seasons, the AWF was 0.48 and 0.31, respectively, being
621 289% greater compared to the dry season. Although the four seasons under study differ when
622 compared to each other, there was a similar trend in their behaviour for the same season in
623 each of the different years (Figure 5h).

624 We found a clear variation in rainfall events during the experimental period (Figure
625 5i and 5j). The values for 2015, 2016 and 2017 were 183.31 ($\pm$17.53), 477.13 ($\pm$49.19) and
626 382.78 ($\pm$61.71) mm year^{-1}, respectively, a total of 1043.22 mm (347.74 $\pm$ 150.01 mm
627 year^{-1}). In 2016, the period with the greatest accumulation of rain, more than 50% of the rain
628 was concentrated from January to February (wet season). In addition, it should be noted that
629 in March of the same year the rainfall events were less homogenous, resulting in higher
630 values for the standard deviation. In general, the months from August to November show an
631 extreme water deficit, with the monthly rainfall varying from 0 to 11.44 mm (Figure 5j).

632

633 *3.3. Growth parameters, phenological characteristics, and cutting time*

634 The curves of the morphophysiological parameters, phenophases, and cutting time of
635 the cactus are shown in Figure 6. Analysing the absolute growth rate (AGR), we found that
636 the cactus used more than 53% of the thermal time to reach the maximum AGR (0.0041 Mg
637 ha^{-1} ºCday^{-1}) at 2500 ºCday. Based on the AGR, the ideal cutting time of the plants was at
638 3760 ºCday, although the species was harvested at 4700 ºCday (Figure 6a). Notably, the
639 relative growth rate (RGR) was higher during the initial growth period, and gradually
640 decreased until it reached minimum values. The maximum RGR value of the cactus was
641 0.0021 Mg Mg^{-1} ºCday^{-1}. Again, both growth rates (i.e., AGR and RGR) showed a
642 significant fall in biomass accumulation upon reaching the cutting time. When analysing the

643 net assimilation rate (NAR), our results showed a mean NAR of 17.76 Mg ha^{-1} ºCday^{-1}, with

644 a variation of 1.60 to 40.22 Mg ha^{-1} ºCday^{-1}. Although the NAR was higher at 2500 ºCday,

645 there was a 50% reduction in the photosynthetic capacity of the cactus by the end of the cycle

646 (4700 ºCday) compared to the initial growth period (Figure 6b).

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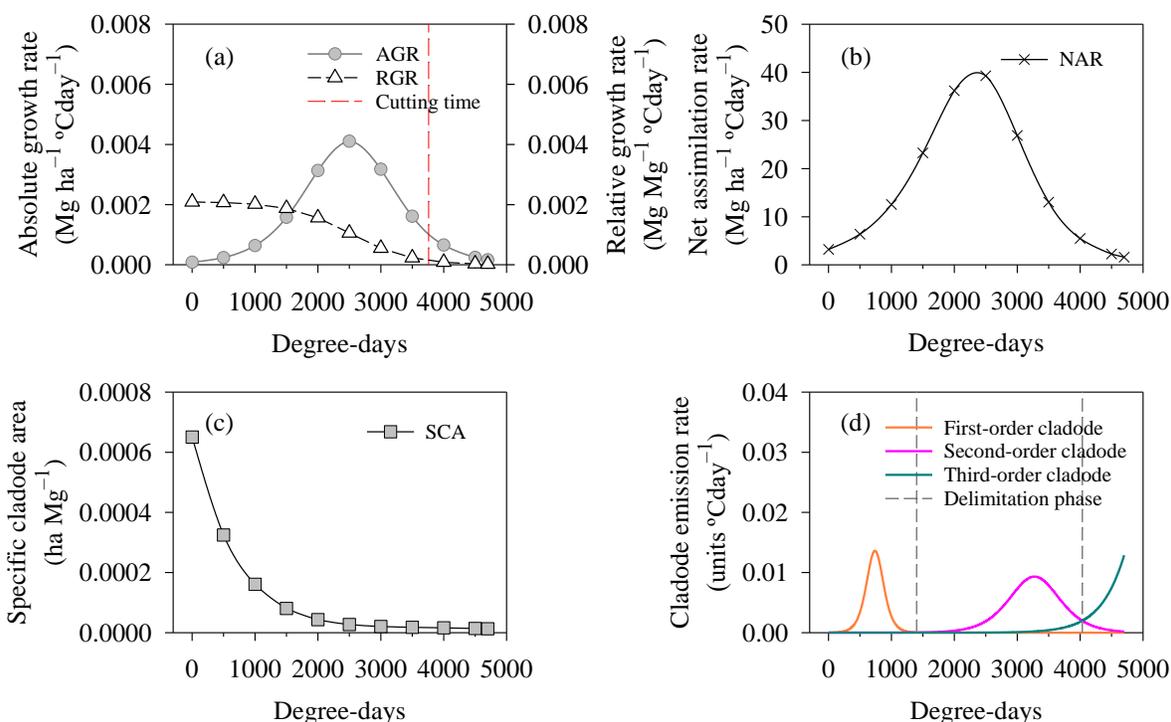
648
649 Figure 6. Absolute growth rate—AGR and relative growth rate—RGR (a), net assimilation

650 rate—NAR (b), specific cladode area—SCA (c), and cladode emission rate (d) in *N.*

651 *cochenillifera* (L.) Salm-Dyck under a semi-arid environment.

652

653 Figures 6c and 6d show the performance of the specific cladode area (SCA) and

654 cladode emission rate. The SCA values were higher at the start, and decreased significantly

655 over time, as was also seen with the RGR. The maximum SCA reached by the cactus was

656 0.00065 ha Mg^{-1}; furthermore, when the plants reached the thermal sum of 1500 ºCday, there

657 was a mean reduction of 0.00002 ha Mg^{-1} in SCA over time. Our results show that the cactus

658 had three cladode phenophases (Figure 6d). The first-order cladodes reached the highest

659 emission rate during these phenophases, with a mean of 0.0136 units ºCday. There was a

660 reduction of 32% and 5% in phenophases two and three, respectively, relative to the first

661   phenophase. Interestingly, we also found a prolongation of phenophase two, with an

662   accumulated thermal time of 2632 ºCday, while the first phenophase (1402 accumulated

663   ºCday) and third phenophase (666 ºCday, with the lowest cumulative value) were shorter.

664   We did not completely analyse the third phenophase, as the experiment had already been

665   harvested before the phenophase ended.

666

667   *3.4. Water relations, Bowen ratio, biophysical efficiency, and yield*

668   We found significant variation in the water relations of the cladodes throughout the

669   experimental period (Figure 7). The cladode water content (CWC) had a mean value of

670   89.03%, varying from 77% to 95%, with interquartile ranges of 76% to 78% and 94% to

671   95%, respectively (Figure 7a). We also found a more-expressive gradual loss of cladode

672   turgidity between samples four and six, and later, rehydration of the cladodes. Samples five

673   and six included October to December 2016, with low rainfall and low soil moisture (see

674   Figure 5). Although the lower water availability caused significant dehydration, the cladodes

675   rehydrated at the end of the cycle, with an increase of 20% in the CWC. From the second

676   sample onwards, the plants showed a similar variation in cladode succulence to that of the

677   CWC (Figure 7b). On the other hand, due to the high turgidity and smaller cladode area,

678   succulence was generally greater in the first sample (3.16 g cm^{-2}). The mean value for

679   cladode succulence was 0.92 g cm^{-2}, ranging from 0.07 to 4.66 g cm^{-2}. The magnitude of the

680   changes in water relations, whether increasing or decreasing, paralleled the levels of water

681   availability and cladode development.

682
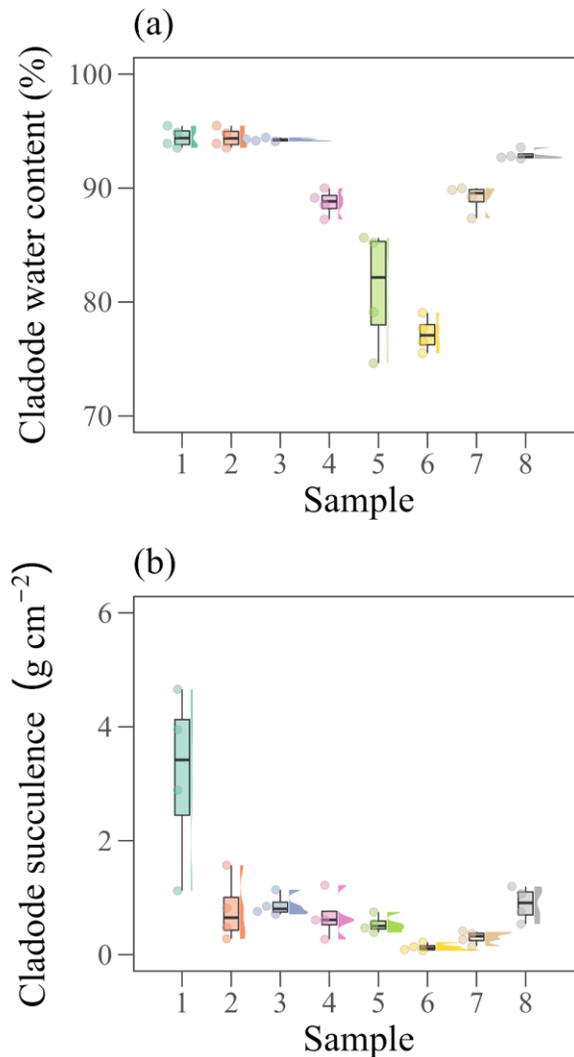
Figure 7. Cladode water content (a) and cladode succulence (b) in *N. cochenillifera* (L.) Salm-Dyck over time (2015 to 2017) under a semi-arid environment. The boxplots show the median; horizontal bars represent the 25th, 50th, and 75th percentiles; whiskers (lower and upper) represent the 1.5× interquartile ranges.

Table 4 shows our results for the efficiency of the biophysical parameters, the Bowen ratio and biomass yield in the cactus at the end of the experimental period. The high radiation use efficiency (RUE) of the cactus can clearly be seen, with a mean value of 3.95 g MJ^{-1}, which favoured the process of photosynthesis, and consequently, significant biomass conversion, with a mean of 12.47 Mg ha^{-1} dry matter. In addition, a value of 1.75 kg m^{-3} was found for water use efficiency (WUE). Considering the information provided by the surface

695   energy distribution between the turbulent fluxes, our results point to a mean Bowen ratio (β)

696   of 3.53 (Table 4).

697

698   Table 4. Summary of the efficiency of the biophysical parameters, Bowen ratio and yield in

699   the cactus at the end of the experimental period.

Variable	Mean value	Standard deviation
β (dimensionless)	3.53	±2.45
Yield (Mg ha^{-1})	12.47	±2.20
RUE (g MJ^{-1})	3.95	±0.70
WUE (kg m^{-3})	1.75	±0.31
NUE$_{[Calcium]}$ (mg m^{-3})	29.03	±1.14
NUE$_{[Magnesium]}$ (mg m^{-3})	12.44	±2.25
NUE$_{[Phosphorus]}$ (mg m^{-3})	62.13	±11.71
NUE$_{[Potassium]}$ (mg m^{-3})	50.88	±5.50
NUE$_{[Sodium]}$ (mg m^{-3})	0.22	±0.02

RUE is the radiation use efficiency; β is the annual Bowen ratio based on annual energy budgets; WUE is the water use efficiency; NUE is the nutrient use efficiency; Yield is the yield of aboveground dry biomass.

700

701   According to our results, the cactus showed greater efficiency in the use of

702   phosphorus and potassium, with mean values of 62.13 and 50.88 mg m^{-3}, respectively (Table

703   4). Calcium use efficiency was 133% higher than that of magnesium. Clearly, the cactus is

704   highly efficient in using the above nutrients, while sodium use efficiency was low (0.22 mg

705   m^{-3}), which indicates greater selectivity of the absorption channels for K$^+$ in relation to Na$^+$.

706

707   *3.5. Interrelationships between environmental variables and plant responses*

708   The interrelationship between the environmental variables and the plant variables can

709   be explained using principal component analysis (PCA) (Figure 8). Our results show that the

710   first two principal components were responsible for 86.82% of the total variance, with a

711   strong relationship between the environmental and plant variables during the growing

712   seasons. Despite presenting an eigenvalue greater than 1, the third principal component was

713   not shown due to the lack of any information relevant to the present study. On the other hand,

714   with eigenvalues also greater than 1, the first principal component (PC1) contributed with

715   50.03%, while the second principal component (PC2) contributed with 36.79% of the total

716   variance. The PCA revealed the clear separation of the growing seasons along the two

717   dimensions of the principal component (Figure 8a). The wet and dry seasons, and the wet-

718   dry transition season presented the greatest contribution to PC1, with scores of −2.46, 0.60

719   and 1.21, respectively. For PC2, the two transition seasons contributed the most, with scores

720   of −2.32 (dry-wet) and 1.63 (wet-dry). In addition to the higher PC1 scores, there is an

721   obvious difference between the groups of environmental and plant variables.

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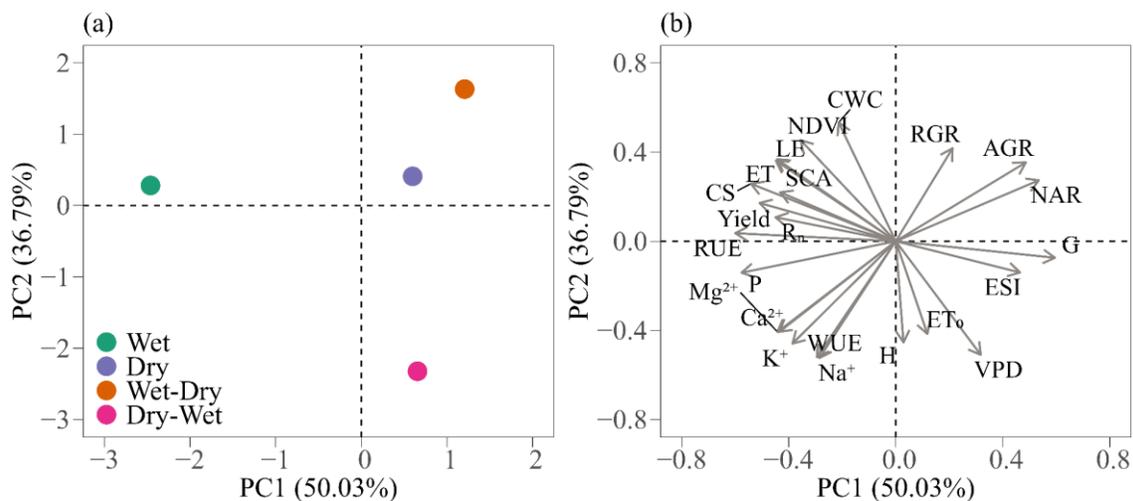
723

724   Figure 8. Principal component analysis (PCA) ordered biplot of environmental and plant

725   factors. Score plot (a) and loading plot (b) of the first two principal components (PC) during

726   the wet and dry seasons and transition periods. P (phosphorus), Mg^{2+} (magnesium), Ca^{2+}

727   (calcium), K^+ (potassium), and Na^+ (sodium) refer to the efficiency of use of each nutrient.

728   The following abbreviations are used: net radiation (R_n), latent heat flux (LE), sensible heat

729   flux (H), soil heat flux (G), evapotranspiration (ET), vapour pressure deficit (VPD),

730   Evaporative Stress Index (ESI), Normalised Difference Vegetation Index (NDVI), water use

731   efficiency (WUE), reference evapotranspiration (ET_0), absolute growth rate (AGR), relative

732   growth rate (RGR), net assimilation rate (NAR), specific cladode area (SCA), cladode water

733   content (CWC), cladode succulence (CS), radiation use efficiency (RUE), and biomass yield

734   (Yield).

735

The variables G, NAR, AGR, ESI, VPD, RGR, ET_0 and H are positively correlated with PC1, with loadings varying from 0.59 to 0.03 (Figure 8b). On the other hand, the remaining variables (i.e., CWC, Na^+, WUE, NDVI, K^+, SCA, Ca^{2+}, Mg^{2+}, LE, ET, R_n, Yield, CS, P, and RUE) showed a negative correlation with PC1, with loadings ranging from -0.21 to -0.60. The dry season and wet-dry transition showed the highest correlation (most-positive) with G (0.59), NAR (0.53), AGR (0.49) and RGR (0.21); the first three with the greatest PC1 loadings. The results clearly show that for the above-mentioned seasons, the cactus shows lower nutrient and water use efficiency (i.e., most-negative PC scores). In particular, the group of variables showing a high correlation with the atmospheric conditions (i.e., H, ET_0, VPD and ESI) did so during the dry-wet transition season. In addition, the wet season showed a positive correlation with the largest grouping of biophysical and plant variables (Figure 8b).

All the variables grouped together during the wet season (e.g., CWC, NDVI, LE, ET, CS, SCA, Yield, R_n and RUE) had the highest (most-positive) contribution to the total explained variance for PC2 (36.79%). The variables with the highest loading during the wet season were CWC (0.53) and NDVI (0.45). In addition, during the wet season, the cactus shows greater biomass yield, LE and ET than during the other seasons under study. Finally, the correlation between the variables and the wet season shows that the cactus has a greater SCA, CS and RUE, which explains the greater NDVI and biomass yield loadings.

4. Discussion

4.1. Mean daytime patterns, seasonal variations in the energy fluxes, and evapotranspiration

In semi-arid areas with a vegetated surface, the energy balance undergoes changes in the soil-atmosphere system (Chen et al., 2022). The hourly energy partition showed the most-sensitive variations, with changes in the fluxes during the morning and afternoon (Figure 2). On the other hand, on a daily scale, the behaviour was similar, but of different magnitudes over the years, as well as during the wet to dry and transition seasons (Figure 3). These more marked variations in turbulent flux and soil heat flux were also seen by Shao et al. (2017), and require greater attention when there is excessive heating of the environment, since this can compromise photosynthetic efficiency. Evaporation and transpiration can reduce the heat stored in the soil and in the plant, however, the cactus being a CAM plant, transpiration is

767 almost zero during the day (Hartzell et al., 2021; Nobel, 1991; Winter and Smith, 2022),
768 resulting in a smaller contribution to the *LE*.

769 Latent heat flux and sensible heat flux are the main variables in net energy
770 consumption, with *H* prominent in the energy budget of a surface cultivated with cactus. In
771 some cases, *LE* is less significant, an indication of environmental water limitations. Most of
772 the time, daytime fluxes show a downward concave shape, with minimum values occurring
773 at dawn and dusk (Awada et al., 2021; Nassar et al., 2021). It is possible that the proximity
774 of turbulent fluxes in the morning (before 10:00) during some wet and dry seasons may have
775 been due to the increased atmospheric demand and soil moisture that favour
776 evapotranspiration. CAM plants have the ability to cool the soil overnight (Cao et al., 2019),
777 and although their metabolism is generally nocturnal, we believe that this thermal reduction
778 lasted until the early hours of the morning (Guevara-Escobar et al., 2021). In this case,
779 evaporation from the soil may have resulted in greater change in the turbulent fluxes (Kuiyue
780 Zhang et al., 2022). Unlike forest species, cacti do not store intercepted water in the canopy,
781 but in the parenchymatic tissue. Such plants are able to carry out hydraulic redistribution of
782 the water in the soil, making it available in the surface layers. In this way, the evaporated
783 water may come mostly from the soil (Montesinos-Navarro et al., 2019; Novoa et al., 2021).

784 Based on the above analyses, we found similarities in the R_n curves (Figure 2).
785 However, it is clear that R_n was significantly higher during the wet season due to the greater
786 absorption of thermal and radiant energy by the humid atmosphere (Figure 4), contributing
787 to the *LE* (Alves et al., 2022; Silva et al., 2017). Using the surface energy balance with the
788 cactus *O. ficus-indica* (L.) Mill., Consoli et al. (2013) also found a higher R_n (~13 MJ m^{-2}
789 day^{-1}) in a semi-arid environment. The turbulent fluxes and soil heat flux showed marked
790 variations on an hourly scale and during the seasons under study (Figures 2 and 3). *G* was
791 clearly more expressive during the afternoon, mainly due to the accumulation of energy
792 throughout the morning, and with the greater soil moisture and radiation, there is an increase
793 in the thermal conductivity of the soil (Chen et al., 2022). In addition, the lower values for *G*
794 may be associated with the biophysical and growth parameters of the plants (Wang et al.,
795 2020). To substantiate this further, the cactus showed a high growth rate and high NDVI even
796 when there was a reduction in soil moisture, resulting in reduced radiation input due to the
797 greater soil cover. Although the cactus does not present a denser, more-uniform canopy, the

798 cladodes remain on the plant throughout the cycle, which may cause variations in energy
799 exchange due to the spaces between them. With greater results than those reported in the
800 present study, Flanagan and Flanagan (2018) found a mean value of 2 MJ m^{-2} day^{-1} for G in
801 an area of saguaro cactus (*Carnegiea gigantea*). Furthermore, the authors point out that the
802 greatest net energy dissipation was via surface heating and the sensible heat flux. Under semi-
803 arid conditions and vegetation consisting of the cacti *O. spinisior* and *O. engelmannii*, Pierini
804 et al. (2014) also found higher values for the sensible heat flux compared to the latent heat
805 flux.

806   Indeed, meteorological conditions have a strong relationship with the variables of the
807 surface energy balance (Figure 3 and Table 3). We saw a similar strong consistency in global
808 solar radiation (R_g), with seasonal trends consistent with the climate in the region (Lima et
809 al., 2019; T. G. F. da Silva et al., 2021). Areas of low latitude and dry climate in particular
810 have a lower *LE* and greater *H* (Jung et al., 2019). This is because the incidence of solar
811 radiation is high, and due to the low water availability, the latent heat flux is lower resulting
812 in limitations on evapotranspiration. The energy balance partition patterns were consistent
813 with the other environmental variables. For example, when the sensible heat energy was low,
814 the cactus increased evapotranspiration, behaving as an important energy sink (Figure 3).
815 Other studies point to variations in turbulent fluxes in areas of Cactaceae, and the effects of
816 changes in the energy balance due to water availability (e.g., Consoli et al., 2013; Flanagan
817 and Flanagan, 2018; Gibbs and Patten, 1970; Lewis et al., 1977).

818   The vapour pressure deficit (VPD) is closely related to ET (Dhungel et al., 2021).
819 Even under deficit conditions, more specifically during the dry season, the cactus maintained
820 ET on a significant scale. Interestingly, even during extremely critical periods (e.g., during
821 the dry season and dry-wet transition), the cactus can keep water lost to the atmosphere well
822 below that seen in species with C3 and C4 metabolism. For these plants, maintaining
823 transpiration during critical periods has important benefits, such as the removal of excessive
824 heat from the cladodes and the maintenance of net photosynthesis (Gibbs and Patten, 1970).
825 This supports our hypothesis that the cactus manages to maintain satisfactory ET. Under
826 rainfed conditions, as in the present study, the mean was 0.95 mm day^{-1} during the
827 experimental period, with a value of 1.18 mm day^{-1} during the wet season, 0.99 mm day^{-1}
828 during the dry season, 0.88 mm day^{-1} during the wet-dry transition, and 0.65 mm day^{-1}

829 during the dry-wet transition (Figure 4). In contrast, studies by Consoli et al. (2013),
830 Goldstein et al. (1991), and Lima et al. (2018), evaluating species of cactus (*Opuntia* spp.)
831 under irrigated conditions, found values for ET greater than 2 mm day^{-1}. Under rainfed
832 conditions, Han and Felker (1997) found a mean daily value of 1.44 mm in *O. ellisiana*.
833 While in a semi-arid ecosystem with cactus (*O. engelmannii*) and shrubs, Anderson and
834 Vivoni (2016) found approximate ET values ranging from 0 to 3.5 mm day^{-1}.
835
836 *4.2. Variations in the NDVI, seasonal environmental changes and soil moisture*
837   Vegetation and terrestrial ecosystems have intrinsic characteristics regarding
838 environmental conditions, and consequently different spectral responses. To evaluate plant
839 behaviour, the Normalised Difference Vegetation Index (NDVI) is a very promising method,
840 and widely used in arid and semi-arid ecosystems. This is because information in the near-
841 infrared spectrum has a direct relationship with the photosynthetic rate of the vegetation, and
842 helps in estimating biomass accumulation (Hermance et al., 2015). For the cactus, we found
843 an NDVI with a mean value of 0.19 throughout the experimental period (Figure 5). In
844 addition, there are reports of a low NDVI and low vegetation indices in areas of cacti (Ouko
845 et al., 2020). Similarly, M. V. da Silva et al. (2021) found vegetation indices ranging from
846 0.1 to 0.5 in areas cultivated with *O. stricta* and *N. cochenillifera* in the Agreste region of
847 Pernambuco, Brazil. The quick response of the NDVI for cacti, even under low water
848 availability, may be related to the roots that remain in the surface layers of the soil absorbing
849 rainwater and water vapour from the air (Ouko et al., 2020), thereby maintaining both growth
850 and photosynthesis, even if at a reduced rate. Furthermore, if the high atmospheric demand
851 is combined with water availability in the soil, plant evapotranspiration will be high.
852 Variations in atmospheric demand are generally caused by water availability and the time of
853 year. With a mean of 6.24 mm day^{-1} (Figure 5c), the results for reference evapotranspiration
854 (ET$_0$) were consistent with the environmental conditions and the rainfall events that occurred.
855 The ET$_0$ in semi-arid regions of Brazil is high due to the high incidence of radiation and low
856 rainfall volumes, and can vary on average from 6 mm day^{-1} in areas of cactus to more than
857 8 mm day^{-1} in a seasonally dry forest (Caatinga) (Jardim et al., 2021b; Marques et al., 2020).
858   In the case of environments with high atmospheric demand and low soil moisture, the
859 Evaporative Stress Index (ESI) can identify problems in plant performance (Anderson et al.,

860 2007). Although the ESI presented values close to one during the present study, with this
861 value classified as a stressor for the crop (Anderson et al., 2007), the cactus maintained its
862 active development. The resistance to hostile climate and environmental factors is overcome
863 due to the anatomical and morphophysiological characteristics of the plant (Gibbs and Patten,
864 1970; Han and Felker, 1997; Jardim et al., 2021a; Lima et al., 2018). On the other hand, when
865 the periods of drought are more severe and prolonged, the yield, growth, and biochemical
866 and physiological parameters of the cactus may be impaired (Jardim et al., 2021a; Scalisi et
867 al., 2016; Ventura-Aguilar et al., 2017). In addition, characteristics of the root system,
868 parenchymal tissue and stomatal control allow the cactus to take advantage of the soil
869 moisture and show good performance even when water availability is low (Scalisi et al.,
870 2016). The mean value of the rainfall was 347.74 mm year^{-1}, within the values for plant
871 survival (Campos et al., 2021; Kumar et al., 2022).
872

873 *4.3. Allometry, phenological phase, and cutting time*

874   One characteristic of plants is to present differing adaptations, phenotypic plasticity
875 and behaviour in terms of growth rate. Earlier studies (e.g., Amorim et al., 2017; Araújo
876 Júnior et al., 2021; Jardim et al., 2021c; Souza et al., 2022) also reported similarities in the
877 growth curves of the cactus; however, compared to genus *Opuntia*, genus *Nopalea* does not
878 show very high rates of growth. When evaluating growth rates (i.e., absolute growth rate—
879 AGR and relative growth rate—RGR) in *N. cochenillifera* under rainfed conditions in a semi-
880 arid environment, Araújo Júnior et al. (2021) found a lower AGR (< 0.004 Mg ha^{-1} °Cday^{-1})
881 and higher RGR (> 0.002 Mg Mg^{-1} °Cday^{-1}) compared to our results (Figure 6). The AGR
882 helps explain the ratio of dry matter accumulation in the crop, while the RGR shows the
883 relative increase in dry matter per unit of time (Jardim et al., 2021c). Generally, a reduction
884 in both of the above rates can clearly be seen throughout the cycle. This is because, as plants
885 grow, they consume photoassimilates, causing a natural reduction in these rates (Amorim et
886 al., 2017; Araújo Júnior et al., 2021; Jardim et al., 2021c; Souza et al., 2022). The ideal
887 cutting time favours a more promising crop, with better use of photoassimilates and better
888 biomass accumulation (Jardim et al., 2021c). Other studies point out that the cactus shows
889 variations in harvest time depending on the agronomic management and/or environmental

890 conditions (Amorim et al., 2017; Araújo Júnior et al., 2021; Jardim et al., 2021c; Souza et
891 al., 2022).

892   Our results showed high values for the cactus in terms of photosynthetic capacity, a
893 ratio predicted by the net assimilation rate (NAR). From our findings, the crop presented
894 significant net photosynthesis, with little influence from self-shading of the cladodes due to
895 the smaller specific cladode area (SCA), favouring a high NAR (Figures 6b and 6c). For
896 Scalisi et al. (2016), morphometric variables such as cladode area help us understand the
897 growth behaviour of plants. The number of cladodes is also a fundamental variable for
898 understanding the phenology of the cactus. In the present study, the cactus presented up to
899 the third phase, i.e., the successive emission of third-order cladodes (Figure 6d). This agrees
900 with other studies on cactus subjected to a semi-arid environment (Araújo Júnior et al., 2021;
901 Jardim et al., 2021c). These findings also confirm the hypothesis that plants continue to
902 develop, increasing their growth rate under different environmental conditions. On the other
903 hand, it is possible that, despite the plants having reached the third phase, the phases were
904 prolonged due to the low water availability.

905

906 *4.4. Water relations and biophysical parameters of cladodes*
907   Anatomically, the cactus has the capacity to store water in various structures, such as
908 parenchyma and hydrenchyma cells (Jardim et al., 2021a; Scalisi et al., 2016). Our results
909 showed that both the cladode water content and cladode succulence presented significant
910 variations (Figure 7). During dry periods, samples five and six showed greater water loss;
911 plants from sample six in particular lost more water due to the long period of drought (Scalisi
912 et al., 2016). In addition, when plants lose water to the environment, they reduce their cladode
913 area, resulting in a loss of cell turgor and succulence (Figure 7b) (Montesinos-Navarro et al.,
914 2019; Nobel, 1991; Scalisi et al., 2016). Even with a significant loss of cladode water content,
915 succulent plants are able to store water more efficiently than plants with a C3 or C4
916 photosynthetic pathway, favouring species survival and the metabolic pathways (Nobel,
917 1991; Ventura-Aguilar et al., 2017). While the cladodes are still young and have a smaller
918 area than mature cladodes, cladode succulence may be greater, since the area is reduced and
919 the water content is high, as seen in the first batch of samples (Figure 7b). These results
920 corroborate those of Scalisi et al. (2016), who found variations of approximately 45% to 85%

242

921 in cladode water content. When the number of cladodes increases, their water content may
922 decrease due to competition for water by the cladodes. Other studies point to variations of
923 60% to 95% in the cladode water content, influenced by soil moisture (Bilderback et al.,
924 2021; Melero-Meraz et al., 2022). Such variations in turgor may occur due to the drought
925 tolerance of the plant, since the cactus is able to maintain turgor pressure for months
926 (Goldstein et al., 1991; Nobel, 1991).

927 When plants are highly efficient in using biophysical resources, the probability of
928 achieving better yields is high (Jardim et al., 2021b). The results shown here generally
929 underline the high efficiency of the cactus in using radiation, water and nutrients (see Table
930 3). One of the factors to help in radiation use efficiency (RUE) is the canopy architecture,
931 which favours the interception of photosynthetically active radiation (PAR) and the capture
932 of CO_2, to be later converted into biomass (Cortazar et al., 1985; Flanagan and Flanagan,
933 2018; Nobel, 1991). The relationship between RUE, water use efficiency (WUE), and
934 nutrient use efficiency (NUE) is true, since the plants showed high dry biomass yield. The
935 study by Han and Felker (1997) reports the high WUE of *O. ellisiana* (1 kg of dry matter per
936 162 kg of water), however such results are still in the early stages for *N. cochenillifera* under
937 rainfed conditions. Our findings of 1.75 kg m^{-3} are higher than those reported by Mbava et
938 al. (2020) for C3 and C4 species, e.g., wheat (1.18 kg m^{-3}), sorghum (1.48 kg m^{-3}), maize
939 (1.47 kg m^{-3}) and cotton (0.22 kg m^{-3}).

940 As seen in earlier studies with the cactus (Du Toit et al., 2018; Nedjimi, 2021; Saraiva
941 et al., 2021), we found that the plants showed greater efficiency and accumulation for such
942 nutrients as P, K$^+$, Ca^{2+}, Mg^{2+} and Na$^+$ (Table 4), in order of use efficiency. Nedjimi (2021)
943 and Saraiva et al. (2021), respectively evaluating *Opuntia* and *Nopalea,* also found greater
944 concentrations of P and K$^+$ in the cladodes. They concluded that cacti have higher
945 concentrations of the above nutrients, favouring the nutritional value for human/animal
946 consumption. In addition, the high concentration of such nutrients as K$^+$ can help improve
947 performance against abiotic factors, such as environmental changes, salinity and heat (Jardim
948 et al., 2021a). The high Bowen ratio was due to the greater heat flux (Table 4), conditions
949 characteristic of a deficient climate (Alves et al., 2022), and which can be damaging to crops.
950 High values can also be seen for the *H*/*LE* ratio in an arid ecosystem of cactus (Flanagan and
951 Flanagan, 2018). The Bowen ratio can change depending on the meteorological variables,

952 soil conditions and vegetation, in which case, adapted plants tend to suffer less. Despite the
953 semi-arid conditions to which the plants were exposed, the cactus showed a high yield of dry
954 biomass (mean of 12.47 Mg ha^{-1}). In this respect, our data are superior to those found by
955 Jardim et al. (2021a, 2021b), where the cactus was harvested at a younger age in a semi-arid
956 environment.
957

958 *4.5. Principal component analysis (PCA)*

959   For the purposes of this study, we applied PCA to the variables that were most
960 influenced by the wet and dry seasons and their transitions (Figure 8). The analysis allowed
961 a reduction in the data set, transforming the data into a series of interrelated variables without
962 losing the principal characteristics of the data. Several variables were correlated with the
963 growing seasons, and the first two principal components (PC) explained 86.82% of the total
964 variance, which was distributed over the 23 variables of the PC1 and PC2 coordinates. The
965 formed groups are clearly correlated based on water availability and the environmental
966 conditions. This is because, in addition to the microclimate caused by the rainfall, according
967 to Campos et al. (2021), the cactus responds to different levels of soil water availability.
968 Jardim et al. (2021a) used the PCA method to understand which environmental and plant
969 variables have greater interaction with different cactus genotypes (*Opuntia* spp. and *Nopalea*
970 spp.) irrigated with saline water in the semi-arid region of Brazil. Furthermore, according to
971 the authors, this type of analysis helps in understanding how plants behave in the face of
972 environmental stressors.

973   Previous studies showed the grouping of cladode and plant variables (Jardim et al.,
974 2021a; Kumar et al., 2022), where correlated variables of the same sign explain, for example,
975 the greater yield of the plants. It is interesting to see water use efficiency grouped with
976 nutrient use efficiency, since these variables were inversely related to the growth rates, which
977 explains their lesser accumulation during the wet-dry transition and dry season. Recently,
978 several studies have identified variations in the energy budget during wet and dry seasons
979 (Alves et al., 2022; Chen et al., 2022; Dhungel et al., 2021; Jardim et al., 2022). Plant
980 evapotranspiration may be limited by the available energy, water and evaporative demand;
981 thus, as the plants increased evapotranspiration, the heat stress index and evaporative demand
982 were reduced. The information presented here implies a clear effect from the wet and dry

983 seasons on energy balance, turbulent fluxes, and plant responses, due to grouping of the
984 variables and the contribution of each component.

985

986 **5. Conclusions**

987 In this study, we used data from a micrometeorological tower, remote sensing, and
988 morphometric and water variables of cactus plants during the wet to dry seasons of 2015–
989 2017. We analysed the seasonal and interannual variation in the components of the surface
990 energy balance, and performance of the cactus in a semi-arid environment. Our results lead
991 to the following conclusions: the energy budget showed seasonality, with the latent heat flux
992 (LE) and sensible heat flux (H) compromised more strongly during the dry-wet transition
993 season, 1.57 and 5.89 MJ m^{-2} day^{-1}, respectively. The values for the H/R_n ratio on a seasonal
994 scale were always higher than those of the LE/R_n ratio during each of the four seasons. In
995 general, during the wet and dry seasons, cactus vegetation maintains high evapotranspiration
996 (1.08 mm day^{-1}). The dry season showed the lowest net radiation (5.89 MJ m^{-2} day^{-1}). The
997 soil heat flux (G) was strongly dependent on the rainfall and the end of the wet season; there
998 is no difference in soil heat transfer over the seasons. The seasonal fluctuations in the NDVI
999 and growth rates confirm the influence of the wet and dry seasons, however, the cactus plants
1000 maintained their growth even during the most critical periods. When there is moisture in the
1001 soil and a low vapour pressure deficit, more energy is consumed for LE, resulting in greater
1002 evapotranspiration; while there is a water restriction, more energy is attributed to G and H,
1003 also increasing the Bowen ratio and Evaporative Stress Index. We found that energy
1004 distribution is greater, and preferably converted into sensible heat. The study also
1005 demonstrated how principal component analysis can help and be effectively used to
1006 understand the way plants respond to environmental factors, and which variables of the
1007 energy balance are correlated with plant growth.

1008 Our results can be a particularly valuable baseline for studies on cacti in semi-arid
1009 ecosystems, where we believe this to be a pioneering study, with application of the surface
1010 energy balance and flux partitioning to *Nopalea cochenillifera* (L.) Salm-Dyck. Finally, these
1011 findings may also be useful for decision makers in environmental management, the
1012 rehabilitation of degraded lands, and climate change, targeting CAM plants as an alternative
1013 way of reducing heat fluxes, and for their tolerance to low water availability. In future studies,

1014 it would be interesting to quantify CO_2 fluxes in the soil and in the environment in wetlands

1015 and drylands cultivated with cactus.

1016

1017 **Acknowledgments**

1024

1025 **References**

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1382

CHAPTER 7

2

3   Quantifying the energy budget, water use efficiency and photochemistry of two of the most

4   cultivated cactus species in the world

5

6   **Abstract**

7   Linking knowledge of energy fluxes and evapotranspiration (ET) in cacti is useful for

8   understanding plant growth. However, there is little quantitative understanding of the latent

9   (LE) and sensible (H) heat fluxes in drylands of cactus. We therefore investigated the

10   feedback from plants of *Nopalea* and *Opuntia* on an interannual and seasonal scale, of the

11   surface energy balance (SEB) components, morphophysiological parameters, biomass, water

12   relations and photochemical relationships during the wet and dry seasons of 2018–2021 in

13   the semi-arid region of Brazil. To analyse the data, four periods were selected (dry season,

14   wet season, and dry-wet and wet-dry transitions). Our results showed that the *LE* (105.26 W

15   m^{-2}) of *Opuntia* was 77.02% greater than that of *Nopalea*. In all seasons, *H* was the SEB

16   component with the highest energy consumption in the two cacti, with *LE* the second most

17   affected. Under *Nopalea*, the soil heat flux increased at the surface (111.65%) during the wet

18   and dry seasons (a mean of 1.61 MJ m^{-2} day^{-1}). The mean ET of *Nopalea* and *Opuntia* was

19   1.71 and 1.96 mm day^{-1}, respectively. The H/R_n ratio showed decreasing behaviour from the

20   dry to the wet season, with a reduction of 36.90% in *Nopalea* and 14.04% in *Opuntia*. The

21   NDVI ranged from 0.19 to 0.67 (*Nopalea*), and 0.17 to 0.70 for *Opuntia,* similar to the

22   Chlorophyll Index, which maintained the seasonality of the NDVI. Overall, we found spatial

23   patterns for the Photochemical Reflectance Index of -0.01 to 0.14 for *Nopalea* and *Opuntia*.

24   Under the same conditions, *Opuntia* showed a higher growth rate and net assimilation rate.

25   The mean cladode water content was 86.01% in *Nopalea* and 88.91% in *Opuntia*. Biomass

26   and water use efficiency were greater in *Opuntia* (56.01 Mg ha^{-1} and 7.54 kg m^{-3},

27   respectively). We also found that these comparisons indicate greater sensitivity in *Nopalea*,

28   and more-significant quantification of the SEB in *Opuntia*.

29

31

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. Around 41% of the earth's surface is covered by drylands and 30% covered by pasture, an ecosystem that is of great importance for global energy exchange in 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., 2021a; 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., 2021a; 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 and Camarena-Rangel, 2019; Scalisi et al.,

259

63   2016; Tenorio-Escandón et al., 2022). According to Nobel and De La Barrera (2003), cacti

64   (*Nopalea* and *Opuntia*) can survive in regions with a high thermal amplitude (-6ºC to 65ºC)

65   and high vapour pressure deficit (VPD), although the excess light and heat can cause

66   problems in dissipating photochemical energy (Adams et al., 1989; Jardim et al., 2021a). Part

67   of the downward global solar radiation interacts with the plant canopy and with the soil,

68   promoting changes in the energy balance and evapotranspiration (Alves et al., 2022; Chen et

69   al., 2022; Dhungel et al., 2021). One way of understanding the response of plants to imposed

70   environmental conditions is by quantifying turbulent fluxes, growth and photochemical

71   parameters.

72   So far, there have been few studies quantifying turbulent fluxes by means of the

73   surface energy balance (SEB) in ecosystems with cacti (Flanagan and Flanagan, 2018;

74   Guevara-Escobar et al., 2021; Lewis et al., 1977) - only some with *Opuntia* (Consoli et al.,

75   2013a, 2013b; Unland et al., 1996) and none with *Nopalea*. The SEB is a promising method

76   for quantifying energy exchanges originating from the net radiation (R_n) and partitioned into

77   elements for heating the water, air and soil (Campos et al., 2019; Chen et al., 2022; Irmak

78   and Kukal, 2022). In addition to being a fairly robust method, it can be applied in various

79   ecosystems, from arid to humid (Jung et al., 2019; Unland et al., 1996; Yue et al., 2018). For

80   example, Consoli et al. (2013a) observed changes in the latent heat flux (*LE*) and sensible

81   heat flux (*H*) in irrigated *O. ficus-indica* in relation to the time of year and the physiological

82   state of the plants, in a cultivated area in western Sicily in the semi-arid region of Italy.

83   Furthermore, according to the authors, during the growth period of the cactus, SEB

84   evapotranspiration was fairly accurate when compared with microlysimeters. In terms of

85   water and energy fluxes, Pierini et al. (2014) reported higher values for *H* compared to *LE* in

86   an ecosystem with *O. spinisior* and *O. engelmannii* in the Sonoran Desert. Consoli et al.

87   (2013b) also used the SEB to determine evapotranspiration, where they found a high WUE

88   in plants of *O. ficus-indica* under the Mediterranean climate of Italy.

89   In agricultural ecosystems, the interaction between the biogeochemical cycle and the

90   vegetation is fundamental for understanding energy partitioning and the way changes occur

91   in the distribution of turbulent fluxes (i.e., *LE* and *H*) and the soil heat flux (*G*) on the surface

92   (Alves et al., 2022; Bezerra et al., 2022; Chen et al., 2022; Dhungel et al., 2021). These

93   elements, together with climate and environmental factors, can cause changes in

94   evapotranspiration (ET) during the plant growing season. Overall, ET is a variable of great

95   importance in the hydrologic cycle, comprising the physical processes of evaporation and

96   transpiration that transfer a mass of water and energy to the atmosphere (Chen et al., 2022;

97   Irmak and Kukal, 2022). Generally, this variable can be accurately determined by weighing-

98   lysimeter and eddy covariance techniques, despite being high-cost methods of determining

99   flux (Dhungel et al., 2021; Jung et al., 2019; Pokhariyal and Patel, 2021). Here, we highlight

100   the Bowen ratio-energy balance method, which quantifies the energy equivalent of ET, i.e.,

101   the latent heat flux using the R_n, air temperature, humidity and G, employing accurate sensors

102   at a lower cost (Bowen, 1926; Ortega-Farias et al., 1996; Yue et al., 2018). These

103   measurements are valuable for understanding the water status of plants and, consequently,

104   their levels of climate adaptation.

105   Integrating micrometeorological variables, such as vegetation indices (e.g.,

106   Normalised Difference Vegetation Index), physiological responses (e.g., Chlorophyll Index;

107   Photochemical Reflectance Index), and growth rates can help as early indicators of plant

108   response to abiotic stress (Jardim et al., 2021b; Perez-Priego et al., 2015; Sanchez et al.,

109   2022), since these variables can serve as indicators of biomass production, the photosynthetic

110   pigment pool and growth performance. Therefore, our hypothesis is that (i) cactus species

111   can maintain their performance for energy fluxes, ecophysiological fluxes and

112   evapotranspiration fluxes even under conditions of stress. Although the hypothesis tested

113   here may be true, we believe that (ii) *O. stricta* presents better adaptation and, consequently,

114   higher yield, and spectral, photochemical and hydric responses compared to *N.*

115   *cochenillifera*.

116   Based on the above, the aim of this study was to compare the feedback from cactus

117   plants (*Nopalea* and *Opuntia*) on an interannual and seasonal scale, of surface energy balance

118   components, morphophysiological parameters, biomass yield, water relations and

119   photochemical relationships during the wet and dry seasons in a semi-arid environment. To

120   achieve this goal, we quantified the heat fluxes, partitioned the net radiation, and calculated

121   growth rates, plant spectral responses, and cladode succulence. The arguments presented here

122   are based on four years observing surface fluxes, and six years analysing the growth of cacti.

123   This is also the first study to measure energy fluxes in *Nopalea* and *Opuntia*.

124

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 (8º17' S, 36º53' W, at an altitude of 792 m above sea level), in the district of Pesqueira in Pernambuco, Brazil (Figure 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 26ºC, respectively. The soil texture is a sandy loam, comprising 71% sand, 22% silt, and 7% clay at a depth of 0–0.40 m at the site cultivated with *Nopalea cochenillifera* (L.) Salm-Dyck, while the site cultivated with *Opuntia stricta* (Haw.) Haw. was of loamy sand (74% sand, 24% silt, and 3% clay), also at a depth of 0–0.40 m. Table 1 shows the physical and chemical data of the soil from the experimental sites.
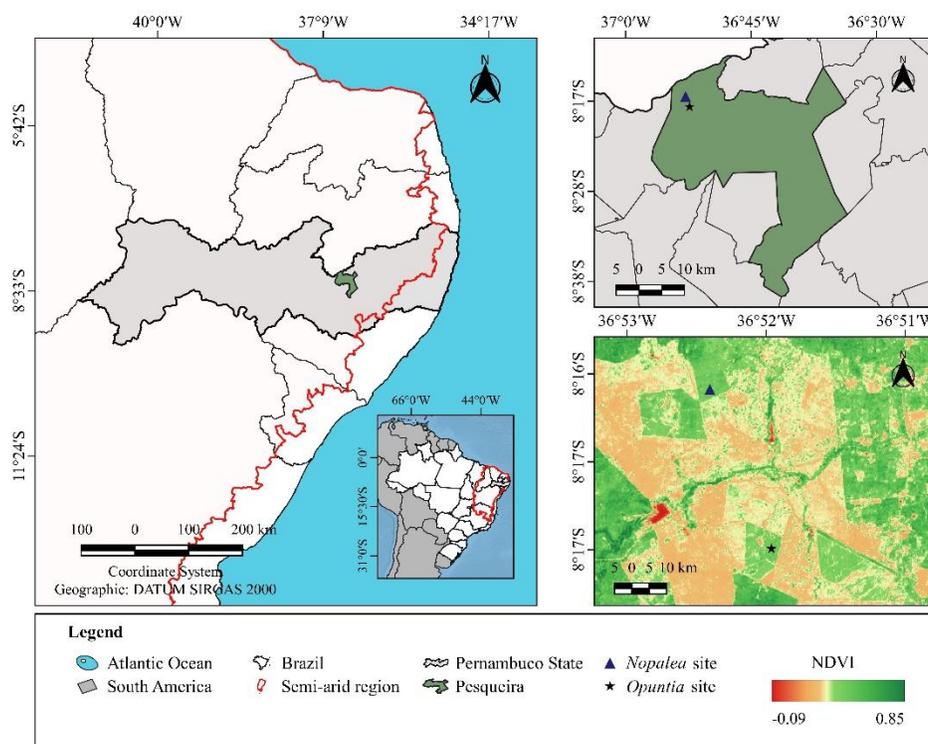
Figure 1. Geographic location of the two study sites cultivated with *Nopalea* and *Opuntia* in the district of Pesqueira, Pernambuco, Brazil.

142   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$_2$O at a ratio of 1:2.5 v/v; CEC is the cation exchange capacity.

143

144   The experiment was conducted from January 2015 to December 2021 with the cacti
145 *Nopalea cochenillifera* (hereafter called *Nopalea*) and *Opuntia stricta* (hereafter called
146 *Opuntia*), both species resistant to the carmine mealybug [*Dactylopius opuntiae* (Cockerell);
147 Hemiptera: Dactylopiidae]. The soil was initially prepared by ploughing, harrowing and
148 furrowing. The cladodes were then planted in January 2015, inserting 50% of their height
149 into the soil. The two experimental sites comprised a planted area of approximately 27 ha of
150 *Nopalea* and 36 ha of *Opuntia* (Figure 1). The linear distance between the sites was 2.4 km.
151 All the plants were arranged in single rows, at a spacing of 1.5×0.2 m. For every nine rows

152 of cactus (i.e., plant rows with no bare areas) there was an uncultivated area of 3 m (i.e., areas

153 of bare soil), this was repeated until reaching a total density of 27,273 plants ha^{-1} (Figure 2).

154 The cropping treatments included manual weeding, with herbicide and insecticide applied as

155 necessary to avoid competition with weeds and promote full growth of the crop. Throughout

156 the experimental period, the cacti were grown under rainfed conditions. All field

157 management practices were the same at both sites.

158
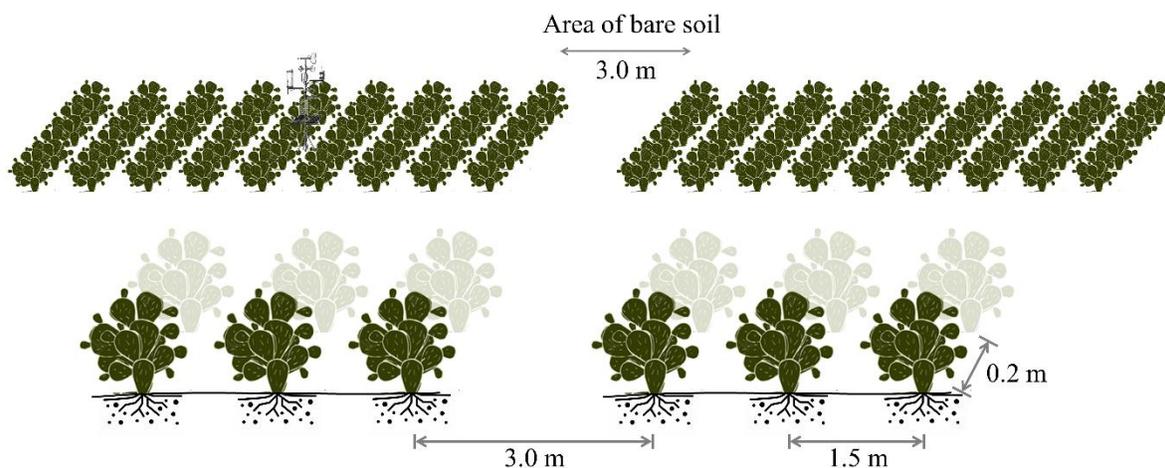
159

160 Figure 2. Schematic diagram showing the planting patterns for *Nopalea* and *Opuntia*.

161 Distances between rows and plants (1.5 × 0.2 m) are indicated. There was a distance of 3.0

162 m between nine rows of cacti.

163

164   In this study, to investigate the effects of rainfall availability on the vegetation, we

165 evaluated the hydrological periods in four seasons (wet, wet-dry transition, dry, and dry-wet

166 transition) from 2018 to 2021 (Table 2), based on the start and end of the rainfall (Leite-Filho

167 et al., 2019; Salack et al., 2016).

168

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

170 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.

171

2.2. Measurements and instrumentation

172

173   Meteorological measurements were obtained from January 2018 to December 2021,

174   from two towers, 3 m in height, installed in the centre of each experimental area, above the

175   cactus canopy. Each tower comprised the same type of sensors for measuring flux. To

176   measure the net radiation (R_n), closed-cell thermopile-type sensors were used (NR-Lite, Kipp

177   & Zonen, Delft, Netherlands). The two radiometric balance sensors were installed 2.8 m

178   above the canopy. The soil heat flux (G) was quantified using heat flux plates (HFT3, REBS,

179   Hukseflux, Delft, Netherlands) buried close to the rows of cactus at a depth of 0.05 m. Air

180   temperature and relative humidity were determined with the aid of two thermo-hygrometers

181   (HMP155A, Campbell Scientific, Logan, Utah, USA), creating a vertical profile of 0.5 and

182   1.5 m above the surface of the plant canopy. Rainfall data were quantified using an automatic

183   rain gauge (AeroCone, Rain Collect, Hayward, CA, USA), installed 3 m above the canopy.

184   In this study, a fetch to height ratio of more than 100:1 was obtained, an acceptable value

185   when measuring the Bowen ratio (Heilman et al., 1989). The dataset was recorded every 60

186   seconds (CR1000, Campbell Scientific Inc., Logan, Utah, USA), with a storage interval of

187   10 minutes. Measurements were collected continuously throughout the day and night.

188

2.3. Calculation of the surface energy balance and parameters

189

190   In this study we used the simplified version of the surface energy balance method.

191   This method is based primarily on the principle of conservation of energy (Equation 1).

192   According to Bowen (1926), the Bowen ratio (β) (Equation 2) can be calculated using the

193   sensible heat flux (H) to latent heat flux (LE) ratio. This ratio is closely linked to the vertical

194   gradients of air temperature and humidity; we therefore assume similarity of equality

195   between the turbulent transfer coefficients of sensible heat and water vapour suggested by

196   Gavilán and Berengena (2007). LE and H were estimated by combining the available energy

197   from the energy balance and the Bowen ratio (Equations 3 and 4). The flux data used in

198   applying the Bowen ratio-energy balance (BREB) method were considered on a daytime

199   scale, from sunrise to sunset only. This is because during the night and before sunrise, when

200   the temperature/humidity gradients are small, they can cause the quantification of erroneous

201 data and inconsistent fluxes (e.g., with β generally close to -1 or tending to infinity). Each

202 dataset is referred to in local time (i.e., GMT-3).

203

204 $$R_n - G = LE + H \tag{1}$$

205 $$\beta = \frac{H}{LE} = \left(\frac{P_a \cdot c_p}{\lambda \cdot \varepsilon} \cdot \frac{\Delta T}{\Delta e} \cdot \frac{K_h}{K_w} \right) \tag{2}$$

206 $$LE = \frac{R_n - G}{1 + \beta} \tag{3}$$

207 $$H = \frac{\beta}{1 + \beta} \cdot (R_n - G) \tag{4}$$

208

209 where R_n is the net radiation (W m^{-2}); G is the soil heat flux (W m^{-2}); LE is the latent heat

210 flux (W m^{-2}); H is the sensible heat flux (W m^{-2}); β is the Bowen ratio (dimensionless); P_a

211 is the atmospheric pressure (kPa); c_p is the specific heat capacity of air (1004.67 J kg^{-1} °C^{-1});

212 λ is the latent heat of vaporisation (2.454 MJ kg^{-1} at 20°C); ε is the ratio of the molecular

213 weights of the air and water vapour (0.622); ΔT is the air temperature difference between two

214 heights (°C); Δe is the vapour pressure difference between two heights (kPa); K_h is the eddy

215 diffusivity of heat (m^2 s^{-1}); K_w is the eddy diffusivity of water vapour (m^2 s^{-1}).

216

217   The energy from metabolic activities, heat storage in the plant tissue and canopy, and

218 horizontal advection, were considered insignificant. As such, these energy components were

219 not included in our energy balance algorithm (Equation 1) (Hu et al., 2014; Pokhariyal and

220 Patel, 2021). After determining LE (W m^{-2}), we converted this variable into

221 evapotranspiration (ET), dividing the LE by the latent heat of vaporisation of water in J kg^{-1}.

222 In this way, the hourly values of ET are integrated, giving the daily values in mm day^{-1}

223 (Mulovhedzi et al., 2020).

224

225 *2.4. Criteria for selecting data for the energy balance method*

226   For the acceptance and/or rejection criteria of the data collected by the BREB method,

227 we used the approach proposed by Perez et al. (1999), which parameterises the criteria for

228 using variables in composing the method. This is because the Bowen ratio depends on

229 measuring temperature and vapour pressure gradients. That said, abnormal data is seen when

230   the available-energy heat flux is very small ($R_n − G$), or negative ($R_n − G < 0$). In this way,

231   errors can occur in applying the energy balance using the Bowen ratio (β), later triggering

232   physical inconsistency in the data. Here, we summarise some of the information that results

233   in errors in the results of the Bowen ratio method: (1) when the sensor resolution is inadequate

234   to resolve the gradient in ΔT and Δe; (2) stable atmospheric conditions, e.g., at dawn and

235   dusk, cause β values close to -1, resulting in evapotranspiration tending to infinity, which is

236   clearly inconsistent; and (3) when conditions change abruptly, they induce measurement

237   errors (Hu et al., 2014; Ortega-Farias et al., 1996; Perez et al., 1999; Unland et al., 1996).

238

239   *2.5. Yield measurements*

240   Biomass yield was determined annually, considering the weight of four randomly

241   chosen representative plants from each site. The biomass above the basal cladode (a

242   vegetative structure planted directly in the soil) was fully harvested and weighed on an

243   electronic balance to quantify the fresh matter (g FM plant^{-1}), and then dried in a forced air

244   circulation oven at 55ºC to constant weight. We determined the dry matter weight per plant

245   (g DM plant^{-1}), and the annual increase in productivity of the cacti (Mg ha^{-1}) was then

246   estimated, considering a final density of 27,273 plants ha^{-1}.

247

248   *2.6. Allometry and measurements of plant growth*

249   Every three months we collected morphometric and biomass data of the plants.

250   During the evaluations, four plants from each site were measured to comprise the

251   morphometric data, and another four plants were collected to analysis the biomass over time.

252   For each plant, we quantified morphometric variables of the cladodes and of the plant. The

253   length, width and perimeter of the cladodes were measured, and the number of cladodes

254   determined by order of appearance on the plant (i.e., first order, second order, third order and

255   so on); the total number of cladodes was then determined. To measure plant height, we

256   considered the vertical distance from the ground to the apex of the canopy; plant width was

257   measured as two widths of the top of the canopy. The collected samples were then used to

258   quantify the morphophysiological indices of the cacti. Using the morphometric data, the

259   cladode area—CA (Equation 5) and cladode area index—CAI (Equation 6) were determined

260   (Pinheiro et al., 2014; Silva et al., 2014). In addition, from the dry matter yield and cladode

261   parameters, we calculated the morphophysiological indices of the cacti using a three-
262   parameter sigmoid model (Equation 7) (Jardim et al., 2021b).

263

264
$$
CA = \begin{cases} 1.6691 \cdot \left[\dfrac{1 - e^{(-0.0243 \cdot CP)}}{-0.0243} \right] & \text{for } \textit{Nopalea} \\[4mm] 0.7086 \cdot \left[\dfrac{1 - e^{(-0.000045765 \cdot CL \cdot CW)}}{0.000045765} \right] & \text{for } \textit{Opuntia} \end{cases}
$$
(5)

265
$$
CAI = \left[\sum_{n}^{i=1} (CA) \Big/ \dfrac{10,000}{(S1 \cdot S2)} \right]
$$
(6)

266
$$
y = \dfrac{a}{1 + e^{\left(-\frac{x-x0}{b}\right)}}
$$
(7)

267

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

277

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

287

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 55ºC to constant weight. We calculated the cladode water content (%) from the fresh matter (FM) and dry matter (DM) weight of the samples (Equation 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 (Equation 9) (Corrado et al., 2020; Ho et al., 2019).

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

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

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

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

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.,

316   10, 20, and 60 m) available from the United States Geological Survey (USGS,
317   https://www.usgs.gov/). Here, we use reflectances of 800 and 670 nm for the NDVI, 531 and
318   570 nm for the PRI, and 750 and 705 nm for the CI (Gitelson and Merzlyak, 1994; Perez-
319   Priego et al., 2015; Sanchez et al., 2022). The images were acquired from 16 January 2018
320   to 31 December 2021 under <10% cloud cover. All the image processing and calculations
321   were carried out using the Google Earth Engine (GEE) platform. In addition, we applied a
322   pixel quality attribute mask to the images, masking clouds, cloud shadow and water, using
323   the CFMask algorithm (Foga et al., 2017; Hurni et al., 2019).

324

325   *2.9. Data analysis*

326   We used the cladode area index and dry matter data to determine the growth rates of
327   the plants using nonlinear sigmoid models. The models were evaluated and chosen based on
328   significance ($P < 0.05$; using the F-test), and a coefficient of determination greater than 0.85.
329   To test the difference between the energy balance components, i.e., R_n, LE, H, and G, as well
330   as ET, and VPD during the four seasons under study (i.e., wet season, dry season, wet-dry
331   and dry-wet transitions) in the two species of cactus, we used Student's t-test and set a
332   significance of $P < 0.01$. We also included box and whisker plots, showing the median,
333   interquartile range and 1.5 times the interquartile range for the data related to cladode water
334   content, succulence, energy balance, ET and VPD. To examine the interrelationships
335   between the plant parameters and environmental conditions, principal component analysis
336   (PCA) was applied. This type of analysis is used to reduce variables or a large dataset using
337   orthogonal transformation, generating linearly uncorrelated variables (Lamichhane et al.,
338   2021). In this way, we constructed a PCA of twenty variables (R_n, LE, H, G, LE/R_n, H/R_n,
339   G/R_n, VPD, NDVI, PRI, CI, ET, DMY, WUE, CWC, CS, AGR, RGR, NAR and SCA). In
340   addition, it should be noted that before carrying out the analysis, each response variable was
341   standardised using the z-transform, with zero mean and unit standard deviation. Finally, the
342   significant principal components were selected based on the Kaiser criterion, considering
343   only eigenvalues greater than 1.0 (Jardim et al., 2021a; Kaiser, 1960; Lamichhane et al.,
344   2021). The data were processed and analysed using the R software (R Core Team, 2022).

345

270

3. Results

3.1. Daytime variation in the energy fluxes

Figure 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* (Figure 3a–d) and *Opuntia* (Figure 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}, 77.02% 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 to 12:30 local time (Figure 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 to 12:30 (Figure 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} (Figure 3e), 2.03% higher than in *Nopalea*, which occurred during the dry-wet transition season (Figure 3b). In both of the cactus crops, the soil heat flux (*G*) was greater during the dry season (Figure 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.
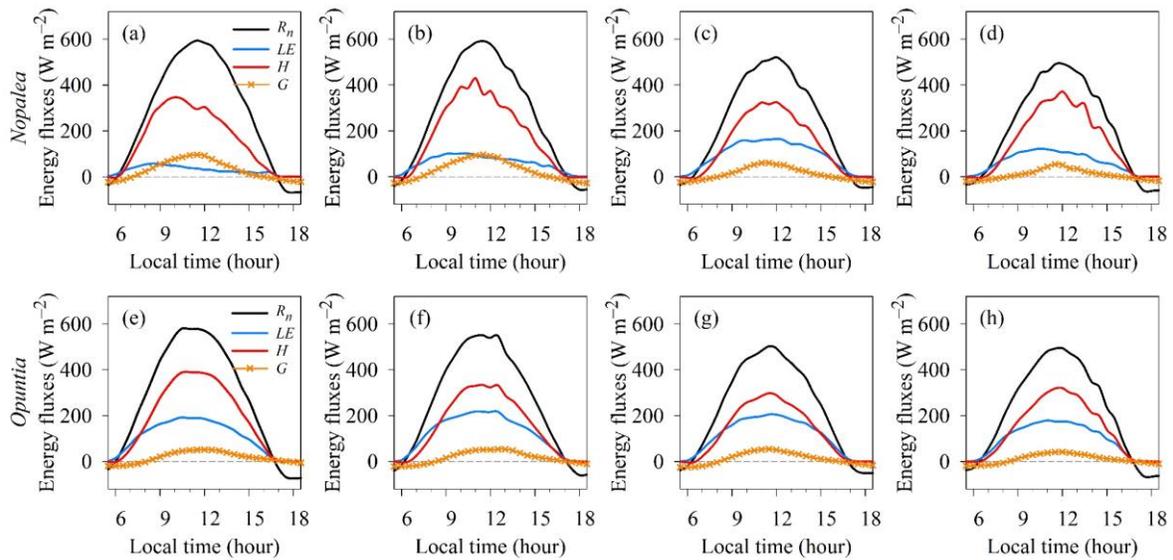
Figure 3. Mean daytime evolution of the surface energy balance components (net radiation—R_n, latent heat flux—LE, sensible heat flux—H, and soil heat flux—G) between the two experimental sites, with *Nopalea* (a–d) and *Opuntia* (e–h). The measurements were taken during the dry season (a and e), dry-wet transition season (b and f), wet season (c and g), and wet-dry transition season (d and h), from 2018 to 2021.

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 Figure 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 to 14.07) and *Opuntia* (interquartile range 11.85 to 13.76), respectively. At both sites, the lowest and highest values of R_n occurred in June and October, respectively (Figure 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* (Figure 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 to 3.77), while LE for *Opuntia* was 79.72% 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

390   *LE* during periods of greater deficiency. For example, whereas *Nopalea* experienced a

391   significant reduction in *LE* when the vapour pressure deficit (VPD) was high (~1.22 kPa),

392   *Opuntia* maintained a stabilised *LE*, with less significant reductions. With the exception of

393   November 2020, *Nopalea* had the lowest value for *LE* from September to November (0.69

394   MJ m^{-2} day^{-1}), while during the same period the value for *Opuntia* was higher (5.37 MJ m^{-2}

395   day^{-1}). As a result, *H* had a mean value of 8.84 MJ m^{-2} day^{-1} (interquartile range 6.36 to 10.86)

396   in *Nopalea*, with a mean of 7.04 MJ m^{-2} day^{-1} (interquartile range 6.01 to 7.53) in *Opuntia*

397   throughout the period (Figure 4c). In both cacti, the range of results for *H* was broader, and

398   the results higher, between September and December.

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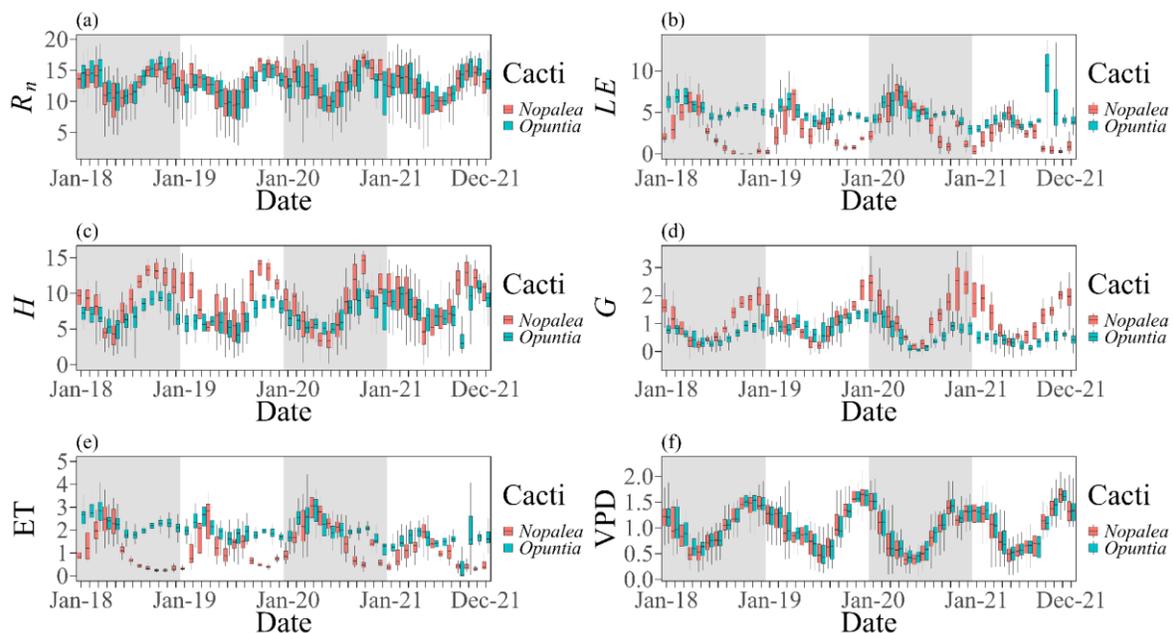
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401   Figure 4. Temporal variation in energy flux (i.e., net radiation—R_n (a), latent heat flux—*LE*

402   (b), sensible heat flux—*H* (c), and soil heat flux—*G* (d), expressed in MJ m^{-2} day^{-1}) and water

403   (i.e., evapotranspiration—ET (e) and vapour pressure deficit—VPD (f), expressed in mm

404   day^{-1} and kPa, respectively) in two species of cactus from 2018 to 2021. The boxplots denote

405   the median, 25th, 50th, and 75th percentiles, the whiskers indicate 1.5 times the interquartile

406   range. The shaded areas represent year boundaries.

407

408   Corresponding to the turbulent fluxes from the vegetated surfaces, Figure 4d shows

409   the variations in *G* for the cacti. Notably, we found higher values for *G* in *Nopalea*, ranging

410 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

411 differing patterns between surfaces, with *Nopalea* 81.85% greater than *Opuntia*. The highest

412 values, and the most-pronounced variation in *G* occurred from October to February: 1.78 MJ

413 m^{-2} day^{-1} in *Nopalea* and 0.86 MJ m^{-2} day^{-1} in *Opuntia*. In addition, on average, when

414 compared to the other months under analysis, a reduction can be seen for *G* between April

415 and August, of 66.10% in *Nopalea* and, to a lesser extent in *Opuntia* (48.04%) (Figure 4d),

416 the results being consistent with the location and time of year. The results for

417 evapotranspiration (ET) also showed significant variations over the years at sites with

418 *Nopalea* and *Opuntia* (Figure 4e). Both cacti kept the ET synchronous with the VPD (Figure

419 4f) and turbulent fluxes (i.e., *LE* and *H*). Under these conditions, the ET ranged from 0.43 to

420 2.30 mm day^{-1} in *Nopalea* (mean 1.71 mm day^{-1}, interquartile range 0.61 to 1.53), and 1.65

421 to 2.46 mm day^{-1} in *Opuntia* (mean 1.96 mm day^{-1}, interquartile range 1.71 to 2.13). Although

422 the VPD at both sites is similar, we found a strange variation in ET for *Nopalea* in relation

423 to *Opuntia*, with a mean reduction of 40.06% when comparing water lost to the atmosphere.

424 Similarly, during the last four months of each year (2018-2021), the decline in ET in *Nopalea*,

425 in relation to the overall mean ET, was more marked (53.42%), in contrast to *Opuntia*

426 (7.33%). The sharpest decline in ET occurred predominantly in October and December in

427 *Nopalea* and *Opuntia*, respectively.

428   Figure 5 shows the energy balance components, ET and VPD, during the dry season,

429 dry-wet transition, wet season, and wet-dry transition. Only during the wet-dry transition

430 season was there any highly significant difference in R_n between the two species of cactus (*P*

431 < 0.001) (Figure 5a). We also found the mean value of R_n to be 3.05% higher for *Opuntia*

432 during the wet-dry transition (median 11.33 MJ m^{-2} day^{-1}, interquartile range 9.47 to 13.20)

433 compared to *Nopalea* for the same period. The *LE* was significantly higher in *Opuntia* during

434 the dry season (513.39%), with an interquartile range of 4.30 to 5.51 MJ m^{-2} day^{-1} (Figure

435 5b). During each of the seasons under evaluation, there was a significant difference in *LE*, *H*,

436 *G*, ET and VPD between the cacti. The lowest values for *LE* in *Nopalea* were during the dry

437 season (0.85 MJ m^{-2} day^{-1}), whereas for *Opuntia* it was during the wet-dry transition season

438 (4.22 MJ m^{-2} day^{-1}). Our results further show that, on average, during the wet season, the

439 difference in *LE* between *Opuntia* and *Nopalea* was relatively low (0.55 MJ m^{-2} day^{-1}).

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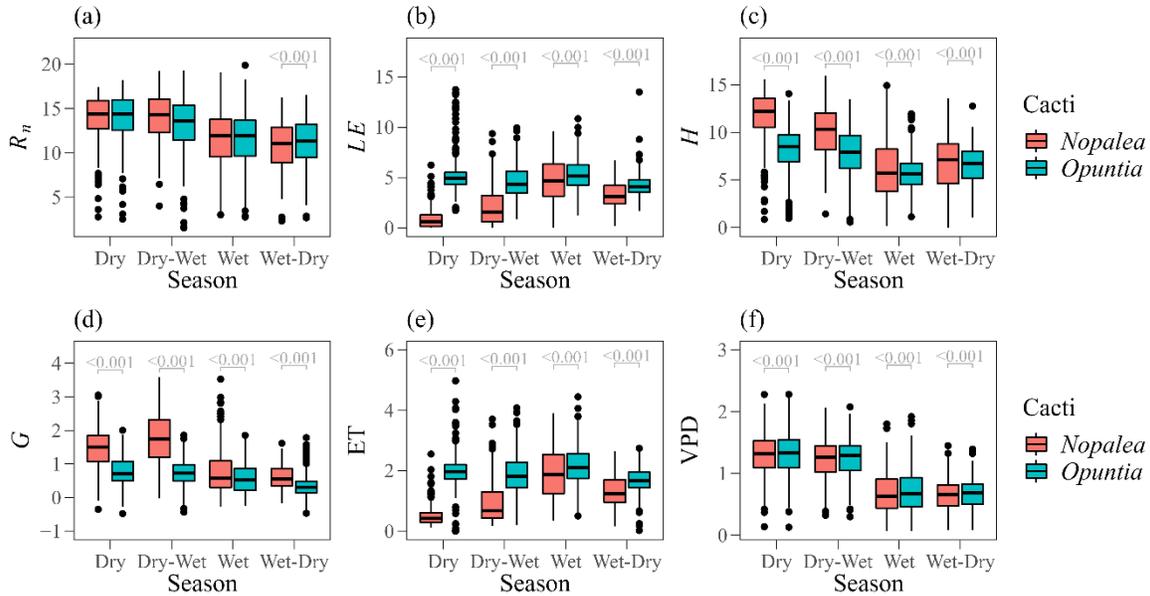
Figure 5. Boxplot showing energy flux components and water exchange in two species of cactus (*Nopalea cochenillifera* and *Opuntia stricta*) during the wet and dry seasons, and the dry-wet and wet-dry transition seasons. The *P* value was calculated using Student's t-test ($P < 0.01$). R_n is the net 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.

During the dry season and the dry-wet transition, *H* was higher and more significant in *Nopalea*, respectively 44.75% and 29.10% higher than in *Opuntia* for the same seasons (Figure 5c). This resulted in similar behaviour between the surfaces for the other fluxes, with *G* in *Nopalea* 139.03% higher than *Opuntia* during the dry-wet transition season, followed by 85.84% higher during the dry season ($P < 0.001$, Figure 5d). Although the sites generally have similar weather conditions, there were also differences between the surfaces for ET and VPD (Figure 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}.

461   *3.3. Changes in energy partitioning for surfaces with cacti*

462   Figure 6 shows the seasonal changes in energy partitioning during the four seasons

463   for both cacti. Despite the similarity of energy inputs previously shown by R_n (Figure 5a),

464   interaction with the two vegetated surfaces significantly alters energy partitioning (Figure 6).

465   The H/R_n ratio in the area of *Nopalea* was the highest in each season (a mean of 0.69), 22.32%

466   higher than the mean H/R_n ratio in *Opuntia*. Although the mean value of H/R_n is lower in

467   *Opuntia* (18.25%), it is obvious that H was the main consumer of R_n in both areas of cacti,

468   heating the air. We observed decreasing behaviour in H/R_n from the dry to the wet season,

469   with a partition ratio 36.90% lower in *Nopalea* and 14.04% in *Opuntia*. During the same

470   seasons, i.e., wet and dry, the LE/R_n ratio was highly variable in *Nopalea*, and at both sites

471   LE was inversely proportional to the seasonal variations in H. The G/R_n ratio was equal to

472   0.10 and 0.12 in *Nopalea* during the dry and dry-wet transition seasons, however, during the

473   dry season and dry-wet transition, *Opuntia* was, respectively, 40% and 50% lower.

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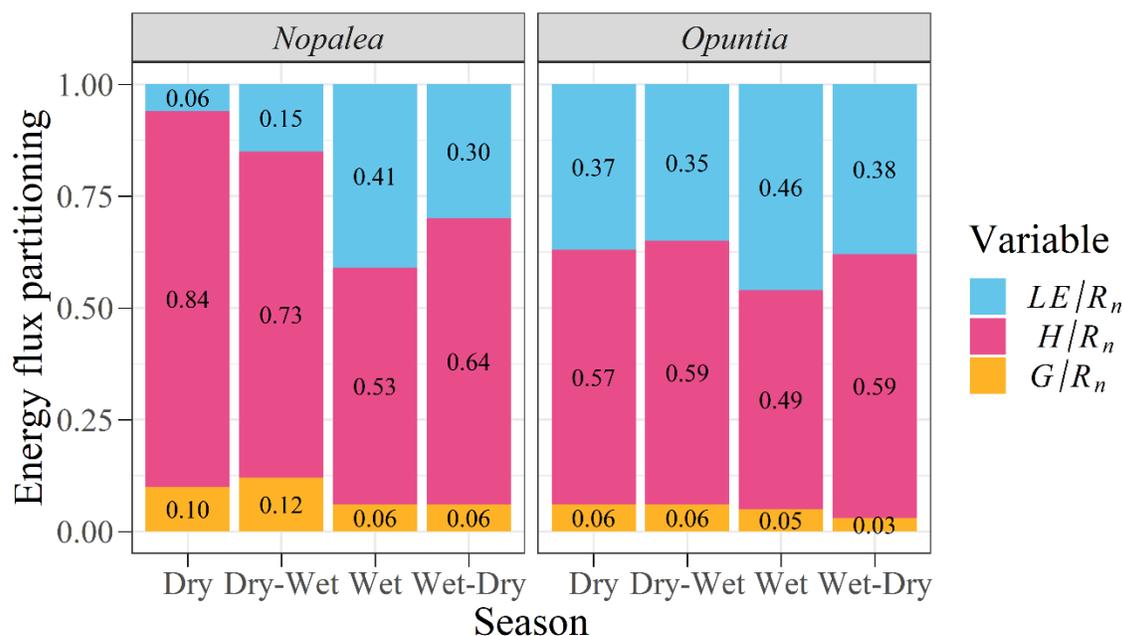
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476   Figure 6. Surface energy partitioning in two agroecosystems with cacti (*Nopalea*

477   *cochenillifera* and *Opuntia stricta*).

478

479 *3.4. Changes in the vegetation, photochemical and pigment indices*

480   Variations in the Normalised Difference Vegetation Index (NDVI), Photochemical

481 Reflectance Index (PRI), Chlorophyll Index (CI) and rainfall for the sites cultivated with

482 *Nopalea* and *Opuntia* are shown in Figure 7. The results show that the NDVI for *Nopalea*

483 ranged from 0.19 to 0.67 (mean ± standard deviation: 0.36 ± 0.13), only slightly different to

484 *Opuntia*, with values between 0.17 and 0.70 (a mean of 0.37 ± 0.11) (Figure 7a). Furthermore,

485 we found that during the wet season the results for the NDVI were higher in both species.

486 This was also true for the CI (Figure 7c). The best results for NDVI and CI were clearly

487 between April and May, with a mean of 0.52 and 0.33, respectively, for *Nopalea*, whereas,

488 for *Opuntia,* during the months in question, the respective values were 5.34% and 5.60%

489 lower. We also found that between April and May the PRI showed a lower photochemical

490 response, with a mean of 0.02 for both cacti (Figure 7b).

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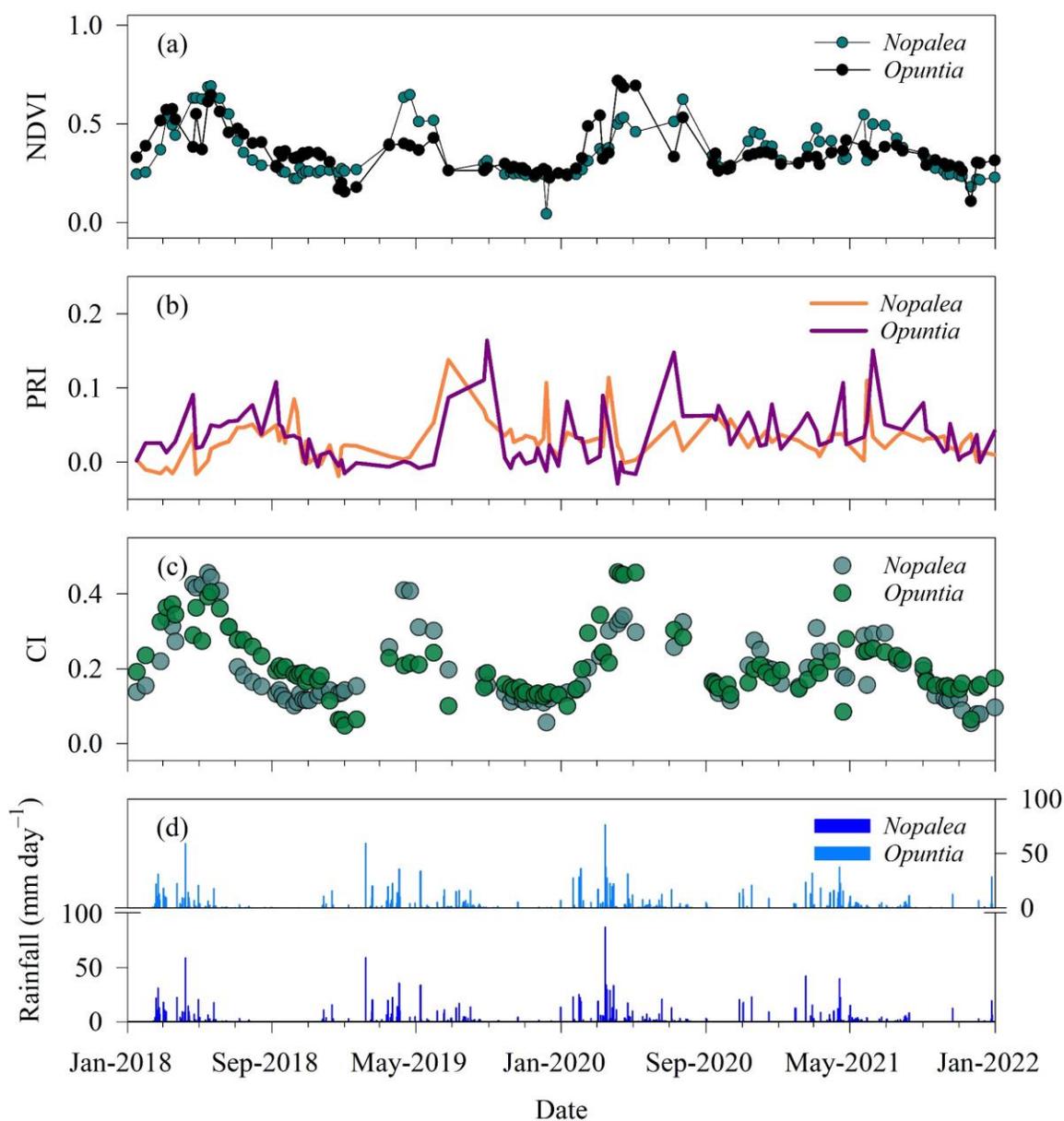
Figure 7. Normalised Difference Vegetation Index—NDVI (a), Photochemical Reflectance Index—PRI (b), Chlorophyll Index—CI (c), and rainfall (d) in two areas of cactus (*Nopalea cochenillifera* and *Opuntia stricta*), from January 2018 to December 2021.

The photosynthetic responses of the plants under environmental 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 when water availability was low (Figure 7d). In particular, when the

278

501   NDVI and CI were drastically reduced by the plants, the values of the PRI were higher. These

502   clear changes in the vegetation indices relative to the photosynthetic indices help clarify the

503   photochemical efficiency and pigment pools of the plants. In addition, when the PRI showed

504   no sudden variations relative to the NDVI or CI (November 2018 to May 2019 and November

505   2020 to May 2021), the cacti presented a reduced photosynthetic response despite a lack of

506   stress conditions. The temporal pattern of the rainfall was very similar at both sites: *Nopalea*

507   (mean 454.50 mm year^{-1}, total 1818.0 mm) and *Opuntia* (mean 472.48 mm year^{-1}, total

508   1889.90 mm), with 2020 the wettest year (Figure 7d). It is important to note that a brief 3.95%

509   greater difference in water availability in the area of *Opuntia* may have been one of the causes

510   of the changes in the PRI, CI and NDVI at the end of the experiment in 2021.

511

512   *3.5. Rates of plant growth, morphology, and physiology*

513   Figure 8 shows the seasonal variation in absolute growth rate (AGR), relative growth

514   rate (RGR), net assimilation rate (NAR), and specific cladode area (SCA) for the two species

515   under study. We measured morphometric variables in both cacti from 2015 to 2021 to assess

516   plant growth performance. During this period, one cycle of *Nopalea* and two cycles of

517   *Opuntia* were evaluated. For the latter, the first cycle was harvested on 12 December 2018

518   (day of year [DOY] 1428), and the second cycle on 31 December 2021 (DOY 1115). The

519   *Nopalea* was harvested on the same date, but 2543 days after planting. The absolute growth

520   rate curves for *Nopalea* in the first cycle (Figure 8a), and *Opuntia* in the second cycle (Figure

521   8c), were very similar, however, the performance of the AGR in *Opuntia* averaged 0.10 Mg

522   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}

523   ^{1}) in *Nopalea*. When examining the AGR in *Opuntia* in more detail during the first cycle, we

524   found far higher values compared to *Nopalea* (379.61%). Similarly, the AGR in *Opuntia*

525   during the first cycle was 11.25% higher compared to the second cycle.

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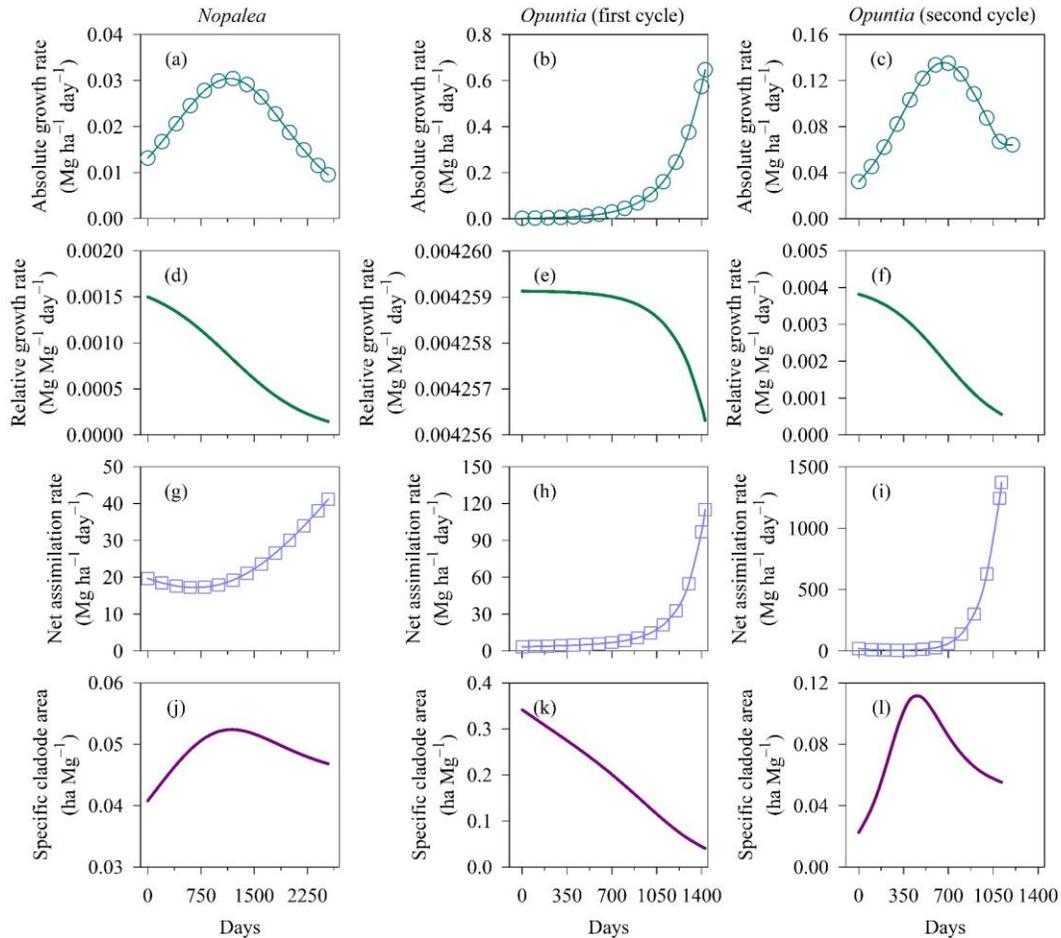
Figure 8. Seasonal changes in absolute growth rate (a–c), relative growth rate (d–f), net assimilation rate (g–i), and specific cladode area (j–l) in two species of cactus (*Nopalea cochenillifera* and *Opuntia stricta*) measured over a period of seven years (2015 to 2021).

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} (Figure 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) (Figure 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 (Figure 8h–i);

280

542   whereas for *Nopalea*, the mean value for NAR was 23.57 Mg ha^{-1} day^{-1} (Figure 8g). Our

543   results for NAR therefore show that species *Nopalea*, despite a high NAR throughout the

544   cycle, did not show greater photosynthetic capacity than *Opuntia*.

545   To further explore the contributions of environmental factors to the variation in plant

546   growth rates, we analysed the behaviour of the SCA (Figure 8j–l). During the first cycle,

547   *Opuntia* exhibited a mean SCA of 0.19 ha Mg^{-1}, ranging from 0.04 to 0.34 ha Mg^{-1}. These

548   results afforded a percentage superiority for the SCA in *Opuntia*; when compared to *Nopalea*

549   and to *Opuntia* in the second cycle the values were, respectively, 292.53% and 154.92%

550   higher. Despite the high values of the SCA in *Opuntia* during the first cycle, there was a

551   strong, almost linear reduction over time (Figure 8k). During the single cycle of *Nopalea* and

552   the second cycle of *Opuntia*, there was a peak in the SCA (humped curve) following the start

553   of evaluations; results observed around DOY 1175 and 450, respectively.

554

555   *3.6. Water relations, increase in annual biomass yield, and water use efficiency*

556   Figure 9 shows the cladode water content and cladode succulence for the two species

557   of cactus. There was a significant difference in the cladode water content during the sampling

558   periods (Figure 9a). We found more-pronounced dehydration in samples 4, 8, 10 and 13, with

559   a mean of 81.09% and 82.30% for *Nopalea* and *Opuntia*, respectively. In addition, the

560   cladode water content ranged from 73.24% to 93.69%, with a mean of 86.01% in *Nopalea*,

561   and, in contrast, a mean of 88.91% in *Opuntia*, reaching values between 79.43% and 95.71%.

562   Our results show a similar albeit not significant trend for cladode succulence in *Nopalea* and

563   *Opuntia* (Figure 9b). The minimum and maximum values obtained in both species ranged

564   from 0.22 to 0.84 g cm^{-2} in *Nopalea* and 0.11 to 0.70 g cm^{-2} in *Opuntia*. In fact, regardless of

565   the sampling period, cladode succulence in *Nopalea* was on average 40.03% greater than in

566   *Opuntia*. Although both have succulent cladodes, the high value for cladode succulence in

567   *Nopalea* was probably due to the smaller cladode area promoting greater succulence.

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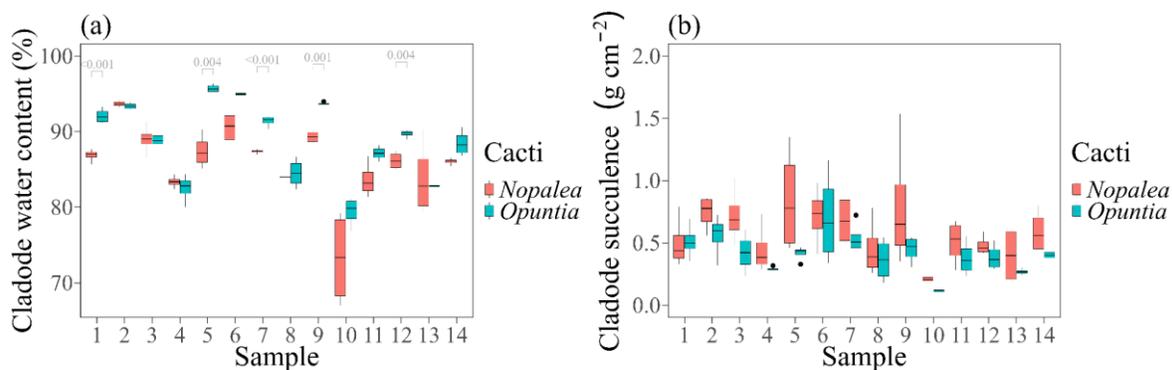
Figure 9. Variation in cladode water content (a) and cladode succulence (b) in two species of cactus (*Nopalea cochenillifera* and *Opuntia stricta*) from 2018 to 2021 in a semi-arid environment. The boxplots denote the median, 25th, 50th, and 75th percentiles, the whiskers indicate 1.5 times the interquartile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

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 78.02%. 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 99.43% 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).

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.

592

3.7. Associations between variables

594   To examine patterns or trends in the sampled data, we applied principal component
595 analysis (PCA) for the two species of cactus (Figure 10). We used the first two principal
596 components (PC1 and PC2) to explain the total variance of the data. This criterion was
597 chosen, as the principal components present eigenvalues greater than 1 (Kaiser, 1960). Figure
598 10a shows the scores of PC1 (71.41%) and PC2 (20.30%) for *Nopalea*, responsible for
599 explaining 91.71% of the total accumulated variation. There was a clear difference between
600 the wet season (with respective PC1 and PC2 scores of 1.76 and -1.46), the dry season (with
601 respective PC1 and PC2 scores of -1.75 and 0.03), the wet-dry transition (with respective
602 PC1 and PC2 scores of 0.86 and 2.22) and the wet-dry transition (with PC1 and PC2 scores
603 of -0.87 and -0.79), in relation to the plant and environmental variables. In fact, in PC1, the
604 plant growth variables, such as SCA, AGR, RGR and WUE presented higher negative
605 loadings (-0.56, -0.56, -0.59 and -0.61, respectively) during the dry season and dry-wet
606 transition (Figure 10b–c). This may indicate that the species has less growth during wetter
607 periods. In contrast, the variables NAR, NDVI and CI showed positive grouping during the
608 wet season (Figure 10b), with strong positive loadings in PC1, and values of 0.52, 0.62 and
609 0.62, respectively (Figure 10c). Furthermore, ET, *LE* and the *LE*/R_n ratio presented loadings
610 greater than 0.6 during the same season in the above PC. We found high loadings, ranging
611 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
612 availability and in PC1. For *Nopalea*, the most significant variables in PC2 were CWC (-
613 0.62) and PRI (0.60) (Figure 10d).

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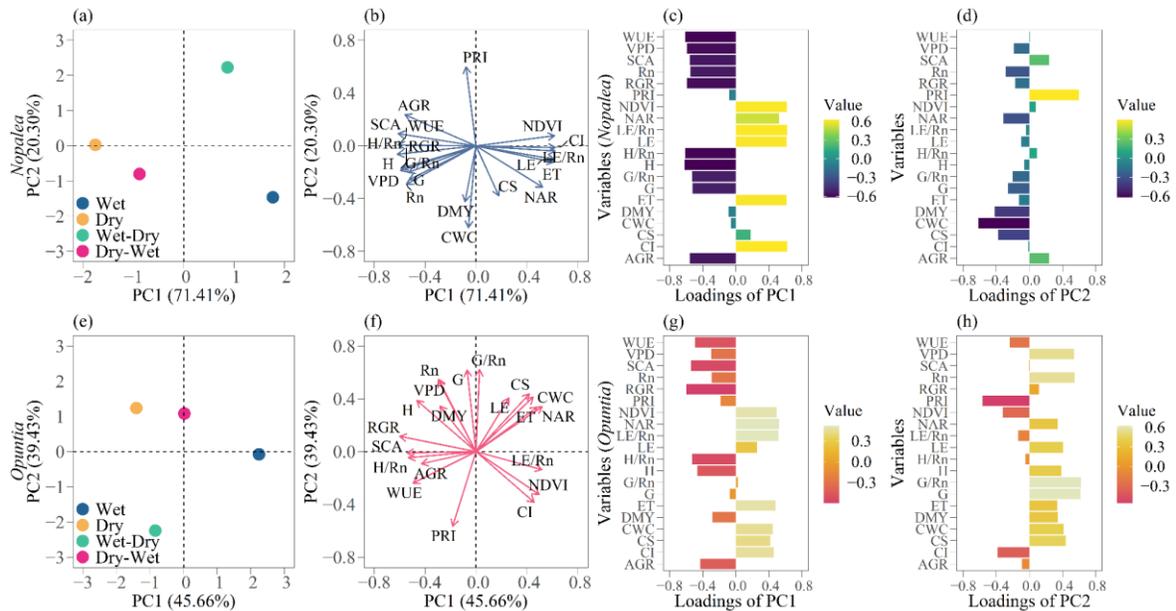
Figure 10. Key dimensions of the multivariate space of the cactus species (*Nopalea* and *Opuntia*) associated with the seasons, and environmental and plant variables. Biplots with scores from the principal component analysis—PCA (a and e), and loadings of the first two principal components (b and f). 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).

The PCA results for *Opuntia* are shown in Figure 10e–h, where the first two components contributed with 85.09% of the total variance. PC1 separated the wet season from the other seasons, thereby contributing with 45.66% of the total variance. On the other hand, PC2 explained 39.43%, and was represented by the dry season and dry-wet transition (Figure 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 (Figure 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 (Figure 10f). During the dry season and dry-wet transition, both more strongly inserted in PC2 (scores

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636 of 1.23 and 1.08, respectively), the most positively significant variables were G/R_n, G, R_n and

637 VPD, with respective loadings of 0.62, 0.62, 0.55 and 0.54. Here, we found that both *Nopalea*

638 and *Opuntia* showed similar groupings during the wet season, but with different loadings and

639 contributions.

640

641 **4. Discussion**

642 *4.1. Energy balance and partitioning*

643   The analyses presented here show that vegetation type can easily promote changes in

644 the surface energy fluxes (i.e., turbulent, radiation and ground heat), on a daily and seasonal

645 scale. We found that species of family Cactaceae, i.e., *Nopalea cochenillifera* and *Opuntia*

646 *stricta*, afford marked changes in the turbulent energy fluxes and available energy, even

647 under similar environmental conditions (Figures 3 and 4). In the present study, on an hourly

648 daytime scale, R_n and H were the most prominent variables for the two surfaces (Figure 3).

649 Over the year, these variations may even be similar (Rahman et al., 2019), but generally

650 undergo changes in magnitude and value over the course of each season due to energy

651 availability and the response of the vegetation (Bezerra et al., 2022; Rahman et al., 2019;

652 Souza et al., 2021). In addition, this type of behaviour is well supported by research in semi-

653 arid environments (Souza et al., 2021), being due to deficiencies and low water availability.

654 The sensible heat flux and net radiation gradually increase between 09:00 and 15:00, with

655 considerably higher peaks at noon in response to the greater absorption of surface energy

656 (Bezerra et al., 2022).

657   During the dry season, the combined effect of a high R_n and high H, together with a

658 low *LE* are conditions that can lead to a water deficit (Rahman et al., 2019). This is because

659 during the dry season, R_n is mainly converted into sensible heat flux (Kuiyue Zhang et al.,

660 2022). *G* also showed behaviour typically linked to the seasons and to humidity (e.g., rainfall

661 and VPD), considering that the thermal conditions of the soil are greater during the day due

662 to insolation, and can vary with the water availability, VPD, and physical characteristics of

663 the soil. Loss of energy contained in the soil surface can also occur due to the rainfall, which

664 partially helps to absorb this energy (Yang et al., 2022). In general, all hourly flux

665 components of the energy balance showed parabolic behaviour, synchronous with changes

666 in the R_n (Figure 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 (Figure 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 Kuiyue 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 (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 atmospheric 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 (Figure 4). This confirms the hypothesis of adaptability to hostile environments for *Opuntia* as opposed to *Nopalea*. 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 (-6ºC to 65ºC) (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., 2021a).

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 (Figure 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) (Figure 6). The LE partitioning fluxes in *Nopalea* were

287

729   far lower, and this may indicate greater sensitivity to a lack of rain and, consequently, lower
730   water availability in the soil. Together with a high VPD and high H, plants can trigger
731   physiological controls that reduce stomatal conductance in the leaves and canopy, lowering
732   the LE and LE/R_n ratio (Yue et al., 2019). This is clearly noticeable in the daily ET, with a
733   mean of 1.71 mm day^{-1} in *Nopalea*, and 1.16 mm day^{-1} in *Opuntia*, reinforcing the findings
734   of Han and Felker (1997) with *O. ellisiana* under rainfed conditions (1.44 mm day^{-1}). When
735   irrigated, other species of genus *Opuntia* presented an ET greater than 2 mm day^{-1} (Consoli
736   et al., 2013a; Goldstein et al., 1991; Lima et al., 2018).

737

738   *4.2. Temporal responses to rain of the NDVI, PRI and CI in the cactus canopy*

739   We evaluated spectral indices of the cactus vegetation in response to the
740   environmental conditions in order to understand the yield performance and health of the
741   plants, using the NDVI and CI, and, by means of the PRI, their photosynthetic characteristics.
742   In general, the results showed, similar behaviour for the NDVI, ranging from 0.17 to 0.70 for
743   the cacti, with *Opuntia* being slightly higher (Figure 7). Silva et al. (2021) documented
744   spectral responses of the vegetation of between 0.1 and 0.5 in areas of *N. cochenillifera* and
745   *O. stricta*, in the Agreste region of Pernambuco, Brazil. These findings confirm the high
746   levels of chlorophyll, as well as the photochemical efficiency of the plants, and are consistent
747   with the results of Hartfield et al. (2022) and Jardim et al. (2021a). In addition, the NDVI can
748   help in understanding biomass performance and can also be an indicator of stress in the crops
749   (Gerhards et al., 2019). Because of this, we strengthened our investigational analysis of plant
750   stress, applying further indices related to the relevant photosynthetic pigments (e.g.,
751   chlorophylls and carotenoids) and the PRI. For Panigada et al. (2014), the PRI has a marked
752   ability for identifying water stress in the aerial part of plants. This is because the PRI is linked
753   to photosynthetic processes, and its sensitivity in identifying xanthophyll pigments reflects
754   photochemical stress in the plants due to increased heat dissipation (Norton et al., 2022;
755   Panigada et al., 2014). As such, the plants, by means of the xanthophyll cycle, increase their
756   spectral emissions and energy dissipation so as not to cause oxidative damage (Gamon et al.,
757   1997). Despite varying results for the PRI, the consistent responses, and its importance,
758   studies reporting its application in the cactus are scarce.

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

770

771   *4.3. Plant dynamics and growth rate*

772   Environmental conditions are important factors in the adaptive process of plants, and
773   can cause changes in the morphological and physiological characteristics of both species. As
774   the species are highly adaptable to conditions of stress, the cactus presents physiological
775   plasticity and a slow relative growth rate—RGR (Luo and Nobel, 1993; Martínez-Berdeja
776   and Valverde, 2008). In the present work, we found marked characteristics for the growth
777   rates of both species under study. As previously described by Jardim et al. (2021b) and
778   Araújo Júnior et al. (2021), both *Nopalea* and *Opuntia* generally showed a high growth rate,
779   but with different patterns of development (Figure 8). Various studies have shown this type
780   of behaviour in *Opuntia* [e.g., Araújo Júnior et al. (2021), Jardim et al. (2021b), Scalisi et al.
781   (2016), and Silva et al. (2014)], where the higher AGR and RGR, are probably related to the
782   high use of photoassimilates and to leaf expansion, represented by the NAR and SCA. In
783   *Nopalea*, the low values of the net assimilation rate and specific cladode area may serve as
784   an indication that photosynthesis is limiting plant growth. Another possible explanation is
785   that high resistance to desiccation and water stress in *Opuntia* compared to other species,
786   favours its development (Tapia et al., 2019). In addition, we do not rule out the benefits of
787   the extra 71.90 mm of rain in the area cultivated with *Opuntia*, which may have favoured
788   performance. For example, Han and Felker (1997) reported improvements in the
789   development and yield of the cacti after rainfall, with an increase in the photosynthetic area

790 (analogous to the cladode area index). For Hassan et al. (2020), such factors as light, soil
791 characteristics, temperature and the dry weight of the basal cladodes are essential for growth
792 in the cactus. This finding confirms our second hypothesis that *Opuntia* enjoys better
793 performance and successful growth parameters.

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

809   The superior performance of the NAR may be related to a better use of the luminous
810 energy by *Opuntia*. This tactic is related to the rapid growth of the species, where two cycles
811 of *Opuntia* were superior in development to that of the single cycle of *Nopalea* (all evaluated
812 during the same chronological period). The high SCA of the *Opuntia* cactus in both cycles
813 may be a way of the plants better allocating photoassimilates, thereby expressing more-
814 significant growth rates. It is possible that self-shading caused greater problems in the growth
815 rates of *Nopalea* (Jardim et al., 2021b). For Izaguirre-Mayoral and Marys (1996), among
816 species with a CAM pathway, *N. cochenillifera* is not tolerant to shading, and this can cause
817 problems in absorbing CO_2. This characteristic was also seen in *O. ficus-indica* (Luo and
818 Nobel, 1993), but in this study we found a lower performance in *Nopalea*. Plants with
819 significant tolerance to stress have low relative growth rates and short stature (Luo and Nobel,
820 1993). For example, species of *Nopalea* are morphologically taller, while those of *Opuntia*

821 have smaller individuals (Nobel and Zutta, 2008); this may be a strong key indication of
822 tolerance in the present study.
823
824 *4.4. Plant water relations and biomass production*

825   A significant water content was found in the cladodes of both species, especially
826 *Opuntia*, with a mean value of 88.91% ($\pm$ 5.07%). This particular trait was not so expressive
827 as to cause any significant difference in cladode succulence (Figure 9b), probably due to the
828 functional anatomical characteristics of CAM plants, which are able to store large volumes
829 of water in their cells (Borland et al., 2011; Hassan et al., 2020; Nobel, 1991; Nobel et al.,
830 1992; Winter and Smith, 2022). Furthermore, high succulence may be a key feature for
831 maximising biomass production when plants are under a water restriction, helping to
832 maximise the night-time absorption of CO_2 (Borland et al., 2011). This response may explain
833 the expressiveness of the plants of *Opuntia* in relation to those of *Nopalea*. Observations
834 concerning the high cladode water content were also reported by Scalisi et al. (2016) (45%
835 to 85%) and Melero-Meraz et al. (2022) (60% to 95%). One important explanation for the
836 variation in cladode water content is related to the availability of water in the soil (Melero-
837 Meraz et al., 2022; Scalisi et al., 2016), given that our plants did not undergo long months of
838 drought (see Figure 7d).
839   Consistent with earlier literature (Consoli et al., 2013b; Han and Felker, 1997; Lima
840 et al., 2018; Snyman, 2013), the cactus plants showed high WUE, with *Opuntia* higher (7.54
841 kg m^{-3}) compared to *Nopalea* (0.08 kg m^{-3}) throughout the experiment (Table 3). During the
842 dry season, WUE increased in both species, being greater than 8 kg m^{-3} in *Opuntia* and greater
843 than 0.1 kg m^{-3} in *Nopalea*. Generally, CAM plants have an exceptionally high WUE, around
844 three and six times higher than C4 and C3 plants, respectively (Jardim et al., 2021a; Snyman,
845 2013; Winter and Smith, 2022). In addition, genus *Opuntia* is known for its greater tolerance
846 than other CAM species, which are ideal for arid regions due to their enhanced conversion
847 of water into biomass (Han and Felker, 1997; Ojeda-Pérez et al., 2017). Such characteristics
848 as high WUE and aboveground biomass yield were noticeable in our study. Actually, these
849 results are not enough to report that *Nopalea* plants are more sensitive, but they demonstrate
850 the superiority of *Opuntia* in this environment. A respective WUE of 7.66 and 7.87 kg m^{-3}
851 for *O. robusta* and *O. ficus-indica* were found by Snyman (2013) in Bloemfontein, in the

852 semi-arid region of South Africa. Although the results for WUE found by Snyman (2013) in
853 species of *Opuntia* are similar to those of the present study, the aboveground dry biomass
854 yield was lower, even with the plants receiving 521.75 mm of annual rainfall. Under optimal
855 conditions, dry matter production in C3, C4 and CAM species would be similar; on the other
856 hand, under the deficient conditions of arid and semi-arid climates, CAM plants present
857 greater biomass production (Snyman, 2013).

858

859 *4.5. Explanatory power of the different combinations of variables*

860   We used principal component analysis (PCA) to aid joint interpretation of the intrinsic
861 information of the data. Figure 10 shows distinct associations between the environmental
862 variables and variables of *Opuntia* and *Nopalea* during the dry season, dry-wet transition
863 season, wet season and wet-dry transition season. This type of PCA presentation using biplots
864 is very useful in a structure that includes large data matrices (Figure 10). For the first two
865 principal components, the plants of *Nopalea* and *Opuntia* retain high total variance for the
866 data, with 91.71% and 85.09%, respectively. During the wet season, variables such as WUE,
867 AGR and RGR are less expressive, showing that both cacti have less growth and reduce their
868 WUE. On the other hand, even with the poorly expressed variables mentioned above, the
869 plants showed no signs of stress, since the PRI was low (i.e., low loading in PC1), and NDVI
870 and CI were high (i.e., high loadings in PC1). This is because the vectors are in the same
871 direction, showing the strong correlation of the variables with each other, albeit conflicting
872 with the season. The cacti show satisfactory growth responses with the increased water
873 availability (Campos et al., 2021; Lima et al., 2018; Scalisi et al., 2016), however, their
874 growth may vary as shown here. In fact, there were improvements in the photosynthetic
875 efficiency of the plants, since the NAR, NDVI and CI were high. As they are CAM plants,
876 the available rainfall improves the microclimate conditions, resulting in an increase in CO_2
877 efflux (Campos et al., 2021; Nobel, 1991; Winter and Smith, 2022). Due to the high NAR
878 and low PRI, the high water content of the cladodes shown in our results may have favoured
879 cell turgor and improved photosynthetic activity (Winter and Smith, 2022).

880   Spatial projection of the first principal component highlighted for the variables
881 (vectors) energy balance and VPD, show that both environments, whether cultivated with
882 *Nopalea* or *Opuntia*, presented better-correlated R_n, H, G, VPD, H/R_n and G/R_n, and grouped

883   the most deficient seasons (i.e., dry season and dry-wet transition). According to Alves et al.
884   (2022), this is due to greater energy availability in the environment, which causes abundant
885   air and soil heating. As expected, the other variables of the energy balance (LE and LE/R_n)
886   and ET remained more correlated with the wet seasons due to the increase in water
887   availability in the system. Changes in energy availability and turbulent fluxes over the course
888   of each season have also been reported by various studies (Alves et al., 2022; Chen et al.,
889   2022; Dhungel et al., 2021; Jardim et al., 2022). Therefore, during seasons of greater water
890   availability, the variables better explain the health of the vegetation, chlorophyll,
891   photosynthetic performance and exchange of water vapour to the atmosphere, while the
892   growth variables have a greater correlation with the thermal conditions and the lower
893   availability of water.

894

895   **5. Conclusions**

896   Our analyses provide the first observational evidence of turbulent fluxes and surface
897   energy partitioning in two simultaneous cultivations of *Nopalea* and *Opuntia* cacti in a semi-
898   arid environment. In this study, we show interactive processes of energy and water vapour
899   exchange between the plants and the environment during the wet and dry seasons. The results
900   for the succulent species studied here, underline that, despite the CAM, their behaviour
901   during heat exchange and evapotranspiration differs over the course of each season. Further
902   analysis revealed that the latent (LE) and sensible (H) heat fluxes have marked seasonality,
903   with the low LE in *Nopalea* occurring during the dry season (0.85 MJ m^{-2} day^{-1}), while for
904   *Opuntia*, during the wet-dry transition season (4.22 MJ m^{-2} day^{-1}). During each season, the
905   LE and evapotranspiration (ET) were higher in *Opuntia*. In general, *Nopalea* provides greater
906   H and soil heat flux (G), even under humid conditions. In both cacti, H showed the highest
907   consumption of net radiation (R_n), with *Nopalea* having the highest H/R_n ratio and the lowest
908   LE/R_n ratio (mean 0.23) during each season. Furthermore, the vegetation showed different
909   responses for the spectral, photochemical, chlorophyll and water use efficiency indices,
910   which explains the better yield of *Opuntia* and the greater sensitivity of *Nopalea*. Similarly,
911   the growth rates and biomass of the cacti were different, with *Opuntia* obtaining the greatest
912   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.

Acknowledgments

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1305

CHAPTER 8

Sink or carbon source? How the *Opuntia* cactus interacts in the use of carbon, nutrients and radiation in a semi-arid environment

Abstract

Anthropogenic disturbances directly influence environmental processes and increase the concentration of carbon (C) in the atmosphere. Here, we compare the differences in the seasonality of the balance of carbon, energy, and radiation, as well as seek to identify the interrelationships between these environmental variables and their impact on the growth of *Opuntia* cactus. Data were acquired from an eddy covariance flux tower over a cactus crop (2019–2021) in the Brazilian semi-arid region. In addition, we use plant growth rates, nutrient stocks, carbon and water use efficiency (WUE), and radiation (RUE). We show that the closure of the surface energy balance was 71%, although there are minimal fluxes of available energy lost (29%) by unquantified processes. At all seasons, the highest net ecosystem CO_2 exchange (NEE) rate was between 11:00–13:00 (-16.36 μmol m^{-2} s^{-1}). During the wet-dry transition season, there was the lowest daily gross primary productivity (GPP) (9.96 μmol m^{-2} s^{-1}) and net radiation—R_n (217.97 W m^{-2}). Ecosystem respiration was more expressive during the wet season (3.73 μmol m^{-2} s^{-1}), and maximum diurnal value of 4.46 μmol m^{-2} s^{-1}. Furthermore, the latent heat flux was higher during the wet season (114.68 W m^{-2}) and lowered in the dry season (9.39 W m^{-2}). The net assimilation rate showed higher values during the dry-wet transition. The dry and wet seasons presented, respectively, higher and lower efficiency in the use of nutrients and WUE. The RUE of the wet season was 81.48% higher than in the dry season. Overall, the cactus is a potential year-round C sink (NEE: $-4,517$ g C m^{-2}; GPP: 2,352 g C m^{-2}). The results help us to understand that most of the R_n energy is used in the sensible heat flux (58% ratio).

Keywords: Eddy covariance; Rainfed cactus; Net ecosystem CO_2 exchange; Carbon budget; CAM plant

1. Introduction

Anthropogenic activities are one of the main contributors to the increase in the concentration of carbon (C) in the atmosphere, and this has been causing damage and threats to the survival of various species worldwide. Terrestrial ecosystems, in general, are responsible for exchanging carbon and energy with the atmosphere, which provides annual sequestration of 3.2 ± 0.6 Pg C, with great spatial and temporal variability between regions of the globe (Del Grosso et al., 2018; Rodda et al., 2021; Yao et al., 2018; Zeng et al., 2020). In agricultural land, since 44% of them are inserted in arid lands (Kumar et al., 2021), soil management, type of cultivation, and species used can alter the carbon dioxide (CO_2) balance of landscapes (Bilderback et al., 2021; Camelo et al., 2021; Wilson et al., 2002; Zeng et al., 2020).

In pastures composed of grasses and legumes with C3 and C4 photosynthetic metabolism, the ability to sequester carbon is similar or greater compared to forest ecosystems (Saliendra et al., 2018). Plants that have crassulacean acid metabolism (CAM) photosynthesis, for example, cacti, have reduced water loss and high efficiency in the use of water and carbon (i.e., more efficient than C3 and C4 photosynthesis plants), helping to survive even in places with high-stress conditions, mainly abiotic (Cortázar and Nobel, 1986; Dubeux Jr. et al., 2006; Jardim et al., 2021a; Nobel and Bobich, 2002; Owen et al., 2016). Although cacti are promising in carbon and water use (Nobel and Bobich, 2002; Scalisi et al., 2016; Snyman, 2006), to our knowledge, this is the first study quantifying carbon-energy fluxes with the eddy covariance technique in exclusive cultivation of cactus (*Opuntia stricta*) in the Brazilian semi-arid region and South America. In the Sonoran Desert region of the United States, studies such as those by Flanagan and Flanagan (2018) and Bilderback et al. (2021) evaluated CO_2 fluxes in ecosystems composed of species of the genus *Opuntia*, demonstrating the deposition of carbon in the soil (Bilderback et al., 2021), and that the photosynthetic activity of the cactus exceeds respiration (Flanagan and Flanagan, 2018).

For many decades, monitoring of environmental conditions has been carried out by flux towers in various biomes and surfaces (Baldocchi et al., 2000; Costa et al., 2022; Cunliffe et al., 2022; McGloin et al., 2018). Among the applied techniques, the eddy covariance method is well established in several parts of the world, measuring latent heat (*LE*) fluxes and the net ecosystem CO_2 exchange (NEE) (Cunliffe et al., 2022; Flores-

62   Rentería et al., 2023). In this method, the *LE* and NEE results are measured by the transport

63   of turbulent fluxes in the boundary layer of the vegetation canopy and atmosphere (Anapalli

64   et al., 2019). In turn, the high-frequency data—generally measured at 10 to 20 Hz by the

65   eddy covariance system such as the *LE*, can be used to determine the evapotranspiration (ET)

66   of the crop, and the NEE carbon flux can be partitioned in gross primary production (GPP)

67   and ecosystem respiration (R_{eco}), aiding in the understanding of crop water and the local

68   carbon budget (Anapalli et al., 2019; Cunliffe et al., 2022; Flores-Rentería et al., 2023;

69   Guevara-Escobar et al., 2021).

70   In places with average annual precipitation of 200–700 mm, as is the case in a semi-

71   arid environment (Kumar et al., 2021), understanding the carbon balance, and the specific

72   responses of the net ecosystem exchange of CO_2, gross primary production and ecosystem

73   respiration at different times of the year help to understand how vegetation behaves as a

74   carbon sink and source. According to Mendes et al. (2020), evaluating the Caatinga biome,

75   a typical dry ecosystem with the presence of cacti, grasses, and tree-shrub species, found

76   NEE results ranging from –169.0 to –145.0 g C m^{-2} year^{-1}, with a strong influence of the

77   GPP in the wet and dry seasons. Flores-Rentería et al. (2023) evaluated xerophilous

78   shrubland in the Chihuahuan Desert of Northeast Mexico, with species of *Opuntia* spp. and

79   other CAM plants (e.g., *Agave asperrima*, *Cylindropuntia leptocaulis*) found annual NEE of

80   –303.5 g C m^{-2}, GPP of 841.3 g C m^{-2}, and cumulative R_{eco} of 537.7 g C m^{-2}. These authors

81   concluded that the ecosystem was a sink during most of the year because the vegetation is

82   adapted to grow and absorb carbon under arid conditions. Notably, information on cactus

83   ecosystems is lacking, with some of these processes of carbon fluxes and stocks being

84   difficult to quantify.

85   Thus, the hypothesis that motivated this research was—do cactus crops have a high

86   CO_2 absorption capacity for long periods, and can they be efficient even in dry seasons?

87   Based on the rationale for this hypothesis, the objectives of this study were (1) to compare

88   the differences in the seasonality of the balance of carbon, energy, and radiation and (2) to

89   identify the interrelationships between fluxes of carbon, energy and radiation, meteorological

90   variables and its impacts on the growth of cactus plants (*Opuntia stricta*) cultivated in a semi-

91   arid environment. The findings and details of the dynamics of CO_2 and energy fluxes during

92   the seasons can inform agricultural management decisions and provide a baseline for future

93   work aimed at carbon sequestration in cactus agroecosystems.

94

95   **2. Materials and methods**

96   *2.1. Study site description*

97   The study was conducted in a crop field located in the municipality of Floresta, State

98   of Pernambuco, Brazil (8º18' S, 38º30' W, and 367 m above mean sea level) (Figure 1a).

99   The climate is characterized by irregular rainfall from December to April, classified as hot

100   semi-arid (BSh), according to Köppen-Geiger (Beck et al., 2018). The annual average

101   rainfall, relative humidity, and air temperature are 489 mm, 61% and 26.1 ℃, respectively,

102   and 2023 mm year^{-1} of reference evapotranspiration. The dominant wind direction is

103   Southeast, with an average annual speed of 1.8 m s^{-1}. The soil has a sandy loam texture (56%

104   sand, 41% silt, and 3% clay) of the Chromic Luvisols type, with a bulk density of 1.33 g cm^{-3},

105   total porosity of 48.05%, pH of 5.35, the electrical conductivity of 0.28 dS m^{-1}, cation

106   exchange capacity of 8.08 cmol$_c$ dm^{-3} and base saturation of 78.60%. All soil samples were

107   collected from the 0–0.40 m depth layer. Soil pH and electrical conductivity were determined

108   in a 1:2.5 soil/distilled water suspension. The average slope at the site is less than 1%.

109
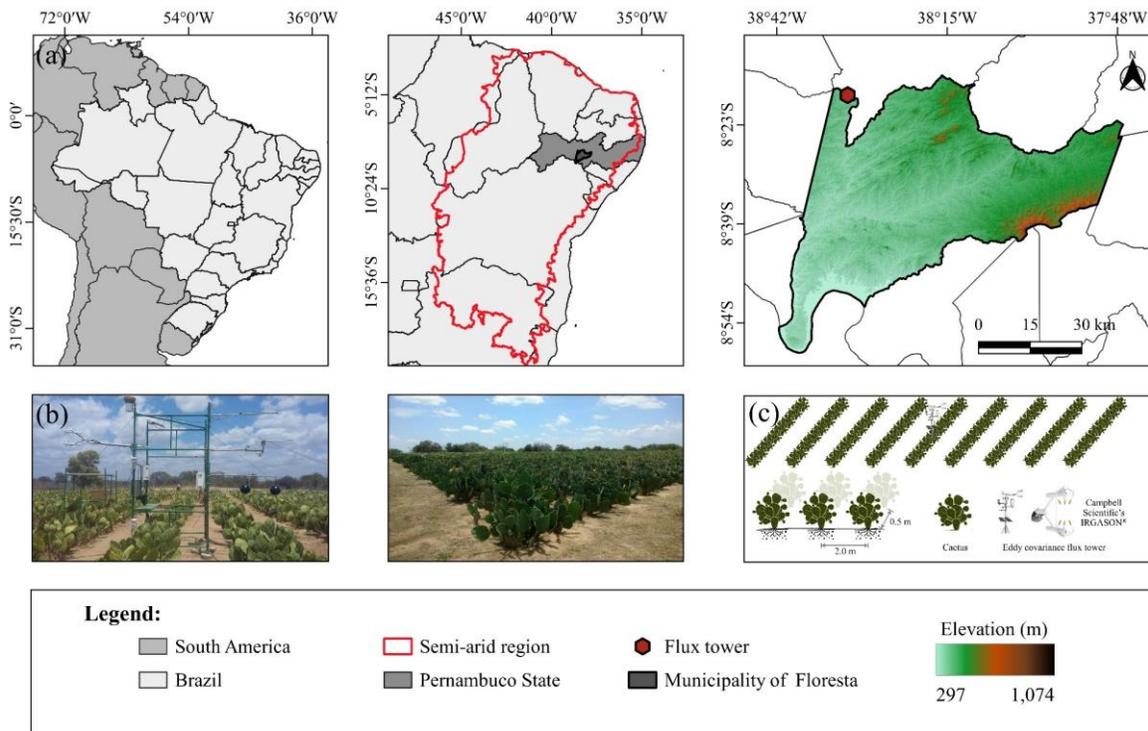
Figure 1. Description and geographical location of the study area (a). Photo of the flux tower with eddy covariance system, cultivation of *Opuntia stricta* cactus (b), and schematic layout of the experimental field (c).

Data were collected between January 2019 and December 2021 at a site cultivated with cactus [*Opuntia stricta* (Haw.) Haw.] (henceforth called *Opuntia*), species resistant to *Dactylopius opuntiae* Cockerell (Hemiptera: Dactylopiidae). In August 2014, cactus planting and conventional soil preparation were carried out, i.e., plowing, harrowing, and furrowing. We used single crop rows spaced 2.0×0.5 m, totaling a plant density of 10,000 plants ha^{-1} (Figure 1b–c). After soil preparation, the cladodes were planted, keeping the lower base inserted at 50% of the soil surface. To maintain ideal growth conditions, cultural treatments (i.e., manual weeding, herbicide, and insecticide application) were carried out when necessary, thus reducing competition with weeds and the presence of phytopathogens. In addition, the cactus plants were grown in rainfed conditions throughout the experimental period, and no fertilization was applied.

126   Based on the climatic conditions, we differentiated the wet and dry seasons from 2019

127   to 2021 into four seasons: wet, dry, transitional dry-wet and wet-dry (Table 1). For example,

128   the wet season is when the accumulated rainfall in five or more consecutive days is at least

129   20 mm, without any dry period exceeding seven days during the following 30 days. If in 30

130   days the accumulated rainfall is less than 20 mm with less than five days of rainfall, the dry

131   season occurs. On the other hand, if none of these criteria are met, the dry-wet or wet-dry

132   transition season occurs, the first being after the dry season and the second after the

133   occurrence of the wet season. This delimitation was to explore the role of seasonal

134   hydrological components as a function of the onset and end of rainfall (Leite-Filho et al.,

135   2019; Salack et al., 2016).

136

137   Table 1. Delimitation of the beginning and end of seasons during the experimental period

138   from January 2019 to December 2021 in *Opuntia* cactus cultivation in the Brazilian semi-

139   arid region.

Season	Start date	End date	Length (days)	Rainfall totals (mm)
Dry-wet transition	1 January 2019	20 January 2019	20	24
Wet season	21 January 2019	6 April 2019	76	834
Wet-dry transition	7 April 2019	8 September 2019	155	166
Dry season	9 September 2019	27 October 2019	49	7
Dry-wet transition	28 October 2019	5 December 2019	39	76
Wet season	6 December 2019	1 June 2020	179	928
Wet-dry transition	2 June 2020	22 July 2020	51	31
Dry season	23 July 2020	4 October 2020	74	17
Dry-wet transition	5 October 2020	19 February 2021	138	146
Wet season	20 February 2021	18 April 2021	58	381
Wet-dry transition	19 April 2021	29 July 2021	102	37
Dry season	30 July 2021	27 October 2021	90	6
Dry-wet transition	28 October 2021	27 November 2021	31	46
Wet season	28 November 2021	31 December 2021	34	58

140

141   *2.2. Measurements of environmental variables*

142   Micrometeorological measurements were performed using a 3 m high tower installed

143   above the cactus canopy near the center of the experimental area. To measure the net radiation

144   (R_n) components, we used closed-cell thermopile-style sensors (NR-Lite, Kipp & Zonen,

145   Delft, Netherlands) in addition to net radiometers (SP-230, Apogee Instruments, Logan,

146   Utah, USA) that measure upward and downward shortwave and longwave radiation. Each

147   radiometer sensor was installed 2.8 m above the canopy to quantify the incident radiation and

148   another one for the radiation reflected by the canopy, i.e., sensors positioned up- and down-

149   looking. Photosynthetically active radiation (PAR) was measured with a quantum sensor (LI-

150   190SB, LI-COR, Inc., Lincoln, Nebraska, USA) mounted at the top and bottom of the

151   canopy. Soil heat flux (G) was measured using a heat flux plate (HFT3, REBS, Hukseflux,

152   Delft, Netherlands) installed at a depth of 0.05 m close to the cactus crop line. Air temperature

153   and relative humidity were measured by two thermo-hygrometers (HMP45C, Campbell

154   Scientific, Logan, Utah, USA), creating a vertical profile 0.5 and 1.5 m above the soil surface.

155   Rainfall was measured using an automatic rain gauge (CS700-L, Hydrological Services Rain

156   Gauge, Liverpool, Australia) positioned 3 m above the canopy. Soil moisture ($m^3\ m^{-3}$) was

157   quantified at a depth of 0.30 m using a time domain reflectometry (TDR) sensor (Campbell

158   Scientific CS616, Logan, UT, USA) buried vertically in the soil next to the eddy covariance

159   tower. Data from the micrometeorological sensors were recorded by a CR3000 data logger

160   (Campbell Scientific Inc., Logan, Utah, USA) every 60 seconds, with a storage interval of

161   10 minutes. Measurements were collected continuously during the daytime and nighttime.

162

163   *2.3. Flux measurements and data processing*

164   Flux measurements with the eddy covariance system were performed using an open-

165   path CO_2/H_2O gas analyzer and a sonic anemometer (IRGASON; Campbell Scientific Inc.,

166   Logan, Utah, USA), with data stored in averages of 30 minutes on a CR3000 data logger

167   (Campbell Scientific Inc., Logan, Utah, USA). The IRGASON is a system that combines an

168   open-path infrared gas analyzer (IRGA) together with a three-dimensional sonic anemometer

169   (Figure 1b–c). The sensor was fixed during the entire experimental period at 2.0 m above

170   ground level, oriented towards the Southeast (135º) in favor of the predominance of the wind,

171   to ensure that the measurements were contained in the appropriate coverage area of the flux

172   system. In this way, the average value of the fetch/height ratio in almost stable conditions

173   was 65:1. For calculations of latent heat flux (LE), sensible heat flux (H), and CO_2 flux, we

174   used EasyFlux PC software (Campbell Scientific Inc.) which performs high frequency (10

175   Hz) raw data corrections, generating averages every 30 minutes. During the post-processing

176   step in EasyFlux all necessary corrections were applied, including outlier removal (Vickers

177   and Mahrt, 1974), bias correction (Rannik and Vesala, 1999), rotation of two-dimensional

178 coordinates (Wilczak et al., 2001), sonic temperature correction (Schotanus et al., 1983), and

179 frequency response (Moore, 1986) and Webb-Pearman-Leuning density corrections (Webb

180 et al., 1980). In addition, flux measurements were classified according to three quality

181 criteria: high, moderate, or low-quality data (Yang et al., 2022). In this step, only high- and

182 moderate-quality flux measurements were used. Finally, after the post-processing step and

183 quality filtering, 94% of the CO_2 flux data were suitable for analysis.

184   We used the online platform developed by the Max Planck Institute for

185 Biogeochemistry in Jena, Germany (http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/) to

186 perform the partitioning of the net ecosystem CO_2 exchange (NEE) (Wutzler et al., 2018).

187 NEE was monitored using the eddy covariance technique and refers to the net exchange of

188 CO_2 between the ecosystem and the atmosphere, basically composed of gross primary

189 productivity (GPP) and ecosystem respiration (R_{eco}), the latter being equivalent to the sum of

190 autotrophic and heterotrophic respiration (Silva et al., 2022). In the present study, we used

191 the meteorological convention, i.e., negative NEE values indicate CO_2 absorption in the

192 ecosystem, while positive values indicate net CO_2 loss to the atmosphere (Silva et al., 2022).

193 With the adjusted *LE* data measured by the eddy covariance system, we converted it to

194 evapotranspiration—ET in millimeters (mm) through the latent heat of water vaporization

195 (2.45 MJ kg^{-1}) (Salazar-Martínez et al., 2022).

196

197 *2.4. Surface energy budget*

198   The estimate of Earth's surface radiation was made through the energy balance

199 between short and longwave radiation described as follows:

200       $SR_n = SR_d - SR_u$ (1)

201       $LR_n = LR_d - LR_u$ (2)

202       $R_n = SR_n + LR_n$ (3)

203 where SR_n is the net shortwave radiation, SR_d is the downward shortwave radiation, SR_u is

204 the upward shortwave radiation (i.e., reflected outgoing shortwave radiation), LR_n is the net

205 longwave radiation, LR_d is the downward longwave radiation, LR_u is the upward longwave

206 radiation, and R_n is the net radiation. All radiation variables were measured in W m^{-2}. Still

207 using ascending and descending shortwave radiation, we calculated the albedo (α) of the

208 cultivated surface with cactus:

209 $$\alpha = \frac{SR_u}{SR_d} \qquad\qquad (4)$$

210

211 *2.5. Energy budget partitioning*

212   In this paper, we use the simplified version of the surface energy balance method

213 (Equation 5). This method is based on the principle of conservation of energy:

214      $R_n = LE + H + G$ (5)

215 where LE is the latent heat flux (W m^{-2}), H is the sensible heat flux (W m^{-2}), and G is the

216 soil heat flux (W m^{-2}).

217

218   All data sets are presented in local time (i.e., 3 h behind Greenwich Mean Time).

219 Furthermore, energy from metabolic activities, heat storage in plant tissue and canopy, and

220 horizontal advection were omitted and considered insignificant (Papale et al., 2006). Thus,

221 these energy components were not included in our energy balance algorithm. The

222 components described in Equation 5 are normally positive during the daytime, with net

223 radiation and soil heat flux positive downwards and latent and sensible heat fluxes positive

224 upwards.

225

226 *2.5.1. Energy balance closure*

227   A common feature when using measurements with eddy covariance is the lack of

228 closure of the surface energy budget. Thus, the sum of latent and sensible heat fluxes ($LE +$

229 H) is commonly smaller than the measured available energy ($R_n - G$), which causes an energy

230 imbalance in the system (Dhungel et al., 2021; Widmoser and Wohlfahrt, 2018). To analyze

231 the energy balance closure (EBC), we fitted an origin-forced linear regression model to the

232 half-hour data, establishing a relationship between the turbulent fluxes as the dependent

233 variable and the available energy as the independent variable (McGloin et al., 2018). This

234 type of linear regression approach provides a stable and robust estimate of energy balance

235 closure, even when available energy is close to zero. Furthermore, we do not use any

236 technique for forcing the closure of the energy balance. Here, the quotient of latent and

237 sensible heat fluxes and available energy expresses the EBC:

238      $$\text{EBC} = \frac{(LE + H)}{(R_n - G)} \qquad\qquad (6)$$

239

2.6. Biomass yield and growth allometry

241   We determined the biomass yield produced each year and season, considering the
242   weight of four representative random plants. The aboveground plant biomass was harvested
243   entirely and weighed on an electronic balance to quantify the fresh matter (g FM plant^{-1}) and
244   subsequently dried in a forced air circulation oven at 55 ºC until reaching a constant weight.
245   Here, we determined the weight of dry matter per plant (g DM plant^{-1}); thus, the productivity
246   of cacti was estimated in grams per square meter per season or year (g m^{-2} season^{-1} and g
247   m^{-2} year^{-1}, respectively). In addition, morphometric data and plant biomass were collected
248   monthly, with five plants being measured to compose the morphometric data and another
249   four plants collected for biomass analysis over time. For each plant, we quantified the cladode
250   and plant morphometric variables. In cladode structures, the length and width were measured,
251   as well as the number of cladodes (units), by counting cladodes in order of appearance in the
252   plant (i.e., first order, second order, third order and so on) and the total number of cladodes,
253   i.e., through the sum of cladodes by order. For plant height measurements, we considered the
254   vertical distance from the ground to the canopy apex, and the plant width was across two
255   widths from the canopy edge. Then, the collected samples were used to quantify the
256   morphophysiological indices of the cacti.

257   In our study, Equations 7 and 8 were used to determine the cladode area—CA and the
258   cladode area index—CAI (Pinheiro et al., 2014; Silva et al., 2014). Furthermore, with data
259   on dry mass yield and cladode parameters, we calculated the morphophysiological indices of
260   *Opuntia* using a sigmoidal model with three parameters (Equation 9) (Jardim et al., 2021b).

261
$$CA = 0.7086 \times \left[\frac{1 - e^{(-0.000045765 \times CL \times CW)}}{0.000045765} \right] \tag{7}$$

262
$$CAI = \left[\sum_{n}^{i=1} (CA) \Bigg/ \frac{10{,}000}{(S1 \times S2)} \right] \tag{8}$$

263
$$y = \frac{a}{1 + e^{\left(-\frac{x-x0}{b}\right)}} \tag{9}$$

264   where CL is the cladode length (cm), CW is the cladode width (cm), i is the observation
265   number, n is the total number of observations, 10,000 is the conversion factor from cm^2 to
266   m^2, and S1 × S2 is the spacing between the rows and plants of each cactus (i.e., 2.0 × 0.5 m),

267   respectively. Here, the parameters for the morphophysiological analysis were: y is the

268   response variable (e.g., cladodes dry matter, cladode area index, and the number of

269   cladodes), a is the maximum value for the rate (i.e., the distance between the two

270   asymptotes), x is the accumulated days, $x0$ is the number of days necessary for the plant to

271   express 50% of the maximum rate (i.e., the inflection point of the curve), and b is the number

272   of days necessary for the start of the rate.

273

274   Next, we quantified the relative growth rate—RGR (g g^{-1} day^{-1}), net assimilation

275   rate—NAR (g m^{-2} day^{-1}), and specific cladode area—SCA (m^2 g^{-1}) (Jardim et al., 2021b;

276   Khapte et al., 2022). The RGR is determined by fitting the increase in dry biomass with the

277   accumulated biomass over time. NAR represents the dry mass produced by cladode area per

278   unit of time, and this variable is commonly used to represent the net photosynthesis rate of

279   plants. The SCA refers to the cladode area useful for photosynthesis (Jardim et al., 2021b).

280   All growth rates were calculated during the experimental period of the plants, from 2015 to

281   2021.

282

283   *2.7. Resource use efficiencies*

284   *2.7.1. Water use efficiency*

285   The water use efficiency (WUE, g m^{-2} mm^{-1}) was calculated by dividing the crop

286   biomass yield and its evapotranspiration (Kai Zhang et al., 2022):

287    $$\text{WUE} = \frac{\text{DMY}}{\text{ET}}\tag{10}$$

288   where DMY is the dry matter yield (g m^{-2}), and ET is the evapotranspiration (mm).

289

290   *2.7.2. Radiation use efficiency and interception photosynthetically active radiation*

291   The radiation use efficiency (RUE, g MJ^{-1}) over the entire experimental period was

292   calculated using the following equation (Raza et al., 2019):

293    $$\text{RUE} = \frac{\text{DMY}}{I_0 \times f\text{IPAR}}\tag{11}$$

294   where I_0 is the amount of daily-incident photosynthetically active radiation (PAR) above the

295   canopy (MJ m^{-2}), and fIPAR is the fraction of PAR intercepted (400–700 nm). Therefore,

296   we can calculate fIPAR using Equations 12 and 13 as follows:

297 $$f\text{IPAR} = \left(1 - \frac{\text{PAR}_b}{I_0}\right)$$ (12)

298 $$f\text{IPAR} = 1 - e^{(-k \times \text{CAI})}$$ (13)

299 where PAR_b is the PAR measured below the plant canopy, and k is the light extinction

300 coefficient based on the Beer-Lambert law.

301

302 *2.7.3. Nutrient stocks and use efficiency*

303   Above-ground dry biomass was ground to powder using a Wiley-type mill (Model 4,

304 Thomas-Wiley Laboratory Mill, Thomas Scientific) with a 1 mm sieve. The nutrients

305 presented here were chosen because they are essential and indispensable for the growth and

306 development of cactus plants. Then, we carried out an analysis of the concentration of

307 mineral elements in the plant tissue of the plants. The micro-Kjeldahl method determined the

308 cladode's total nitrogen content (N, mg kg^{-1}) (Santos et al., 2020). Phosphorus (P, mg kg^{-1})

309 was measured by the vanado-molybdate method with UV-visible spectrophotometry reading

310 at 430 nm (Du Toit et al., 2018). Meanwhile, the potassium (K$^+$, mg kg^{-1}) was determined

311 by a flame photometer (Rodrigues et al., 2013). To determine calcium (Ca^{2+}, mg kg^{-1}) and

312 magnesium (Mg^{2+}, mg kg^{-1}), we used an atomic absorption spectrophotometer (Loupassaki

313 et al., 2007). The dry biomass's carbon content (C, mg kg^{-1}) was determined by the Dumas

314 method via dry combustion (Adamič and Leskovšek, 2021). Finally, the nutrient use

315 efficiency (NUE, mg m^{-2} mm^{-1}) was calculated according to Equation 14. The nutrient stock

316 (g m^{-2}) was obtained by multiplying the dry biomass per square meter by the nutrient

317 concentration.

318 $$\text{NUE} = \frac{\text{DMY} \times Nu}{\text{ET}}$$ (14)

319 where Nu is the concentration of the nutrient in the analyzed sample of plant tissue. Equation

320 14 was adapted (Zhang et al., 2020), making it a function of crop evapotranspiration. This

321 adaptation provides more clarity in understanding the nutrient uptake capacity of the plant

322 from the soil solution, together with the consumption of water lost through

323 evapotranspiration.

324

325 *2.7.4. Carbon stock and efficiency*

326 Using the carbon that was quantified in the plants' dry biomass (without the root

327 biomass), we quantified the carbon use efficiency—CUE ($\mu g\ m^{-2}\ mm^{-1}$). Thus, based on

328 Equation 14, the efficiency in the use of carbon was realized. Furthermore, the carbon stock

329 ($g\ m^{-2}$) was calculated by multiplying the elemental carbon concentration by the dry biomass

330 produced per square meter (Siddiq et al., 2021).

331

332 *2.8. Statistical analysis*

333 In this study, we use the linear regression method to quantify the energy balance

334 closure of the eddy covariance system through the ratio between available energy ($R_n - G$)

335 and turbulent heat fluxes ($LE + H$) during the experimental period. We fitted non-linear

336 regression models (sigmoidal model) for plant growth rates. The components of carbon,

337 energy, and radiation balances during the four seasons (i.e., wet season, dry season, wet-dry

338 and dry-wet transitions) were presented in curves and boxplots over time (i.e., hour, month,

339 year and station). All boxplots include median, whiskers, and 1.5 times the upper and lower

340 interquartile ranges. Subsequently, we applied principal component analysis (PCA) to

341 examine the interrelationships between seasons and environmental and cactus plant

342 parameters. PCA is a type of multivariate analysis that reduces large data sets through

343 orthogonal transformation, generating linearly uncorrelated variables called principal

344 components (Lamichhane et al., 2021). In this way, the new set of data generated by the PCA

345 provides new values, called scores and loadings, and are visualized in biplots in multivariate

346 space. Furthermore, before performing the PCA, all variables were standardized using the z-

347 transformation, with zero mean and unit standard deviation. Finally, the significant principal

348 components were selected according to the Kaiser criterion, considering only eigenvalues

349 greater than 1.0 (Jardim et al., 2021a; Kaiser, 1960; Lamichhane et al., 2021). All data

350 processing and analysis were performed using the R program version 4.1.3 (R Core Team,

351 2022).

352

3. Results

3.1. Energy balance closing overview

Figure 2 shows the relationship between available and turbulent energy fluxes with half-hour data from eddy covariance measurements. The result of the energy balance closure (EBC) during the period from 2019 to 2021 was 0.71 (corresponding to the slope of the estimated line), and the coefficient of determination (R^2) of 0.94 ($P < 0.001$). The closer the EBC result is to 1.0, the better the energy closure response status. In this analysis, we chose to force the intercept to zero, helping to visualize the slope of the regression line in relation to the 1:1 line. The regression and determination coefficients show adequate data fit. Furthermore, the horizontal (i.e., $R_n - G$) and vertical (i.e., $LE + H$) coordinate boxplots show that the fluxes are concentrated at 316.83 W m^{-2} (median 314, interquartile range 150–478 W m^{-2}) and 236.69 W m^{-2} (median 238, interquartile range 133–339 W m^{-2}), respectively, and the rest of the scattered data above the mean are causing a slope of the line for available energy (i.e., indicating greater expressiveness of this flux). Although there is a high EBC value, minimal fluxes of available energy are being lost (29%) by unquantified processes, e.g., heat storage in the canopy. In addition, we did not use a technique to force the EBC, such as for example, the Bowen ratio and the residual technique.
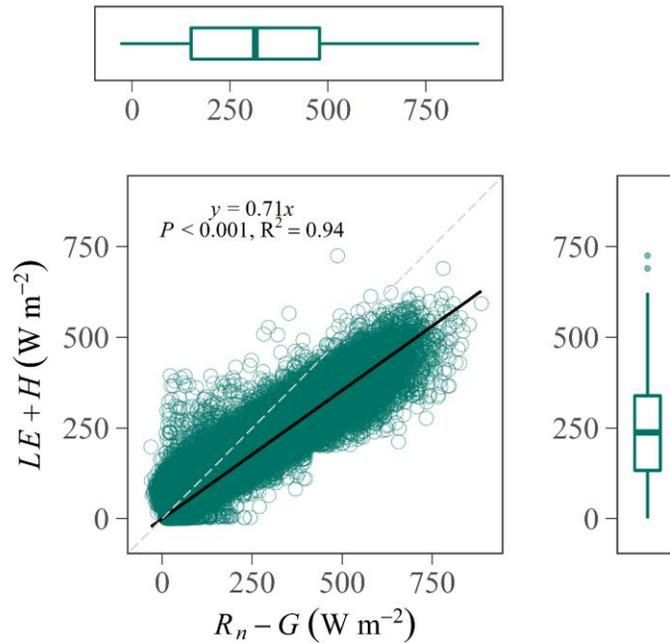
Figure 2. Relationships between available energy ($R_n - G$) and turbulent fluxes ($LE + H$) for half-hour measurements from 2019 to 2021 in cactus cultivation in the Brazilian semi-arid region. The white dashed line is the 1:1 line, and the black line is the fitted line determined by linear regression. The boxes represent the 25th, 50th (median) and 75th percentiles of the data; the whiskers represent the lowest (or highest) datum within the 1.5× interquartile range. Dots above the boxplots indicate outliers.

3.2. Environmental conditions during the experimental period

Our timescale results for environmental conditions are shown in Figure 3. During the study period, the average air temperature was 26.58 ℃, with minimum (July 2020) and maximum (November 2019) values of 23.25 and 29.77 ℃, respectively. On average, the lowest records occurred from June to August (24.09 ℃), being 12.13% lower in relation to the other months (Figure 3a). The results for relative humidity (*RH*) and vapor pressure deficit (VPD) showed consistent trends over the years (Figure 3b–c) with air temperature and rainfall. The *RH* average was 49.57%, with the wettest months from February to May being 16.78% higher than the annual average. The VPD showed a similar variation with air temperature, an average of 1.94 kPa, with the most deficit period from April to July, and 2021 with the lowest average (1.88 kPa). The mean annual rainfall was 820.32 mm, 67.76% above the climatological normal for the municipality (489 mm year^{-1}). The highest rainfall

was in 2020 (964.34 mm), followed by 2019 and 2021 with 924.14 and 572.48 mm, respectively. March 2019 reached the highest accumulated rainfall (343.55 mm), and the lowest (0.6 mm) occurred in September 2019. In addition, the rainiest months had the lowest average wind speed (1.35 m s^{-1}), 20.62% lower than the average (Figure 3d–e). The variation in soil moisture ranged from 0.08 to 0.29 m^3 m^{-3}, and the months from February to May showed the highest results (Figure 3f). Particularly, in March 2019, we observed the highest soil moisture, with 0.29 m^3 m^{-3} (median 0.29, interquartile range 0.25–0.32 m^3 m^{-3}), and in 2021 there was the highest moisture deficit (mean of 0.13 m^3 m^{-3}).
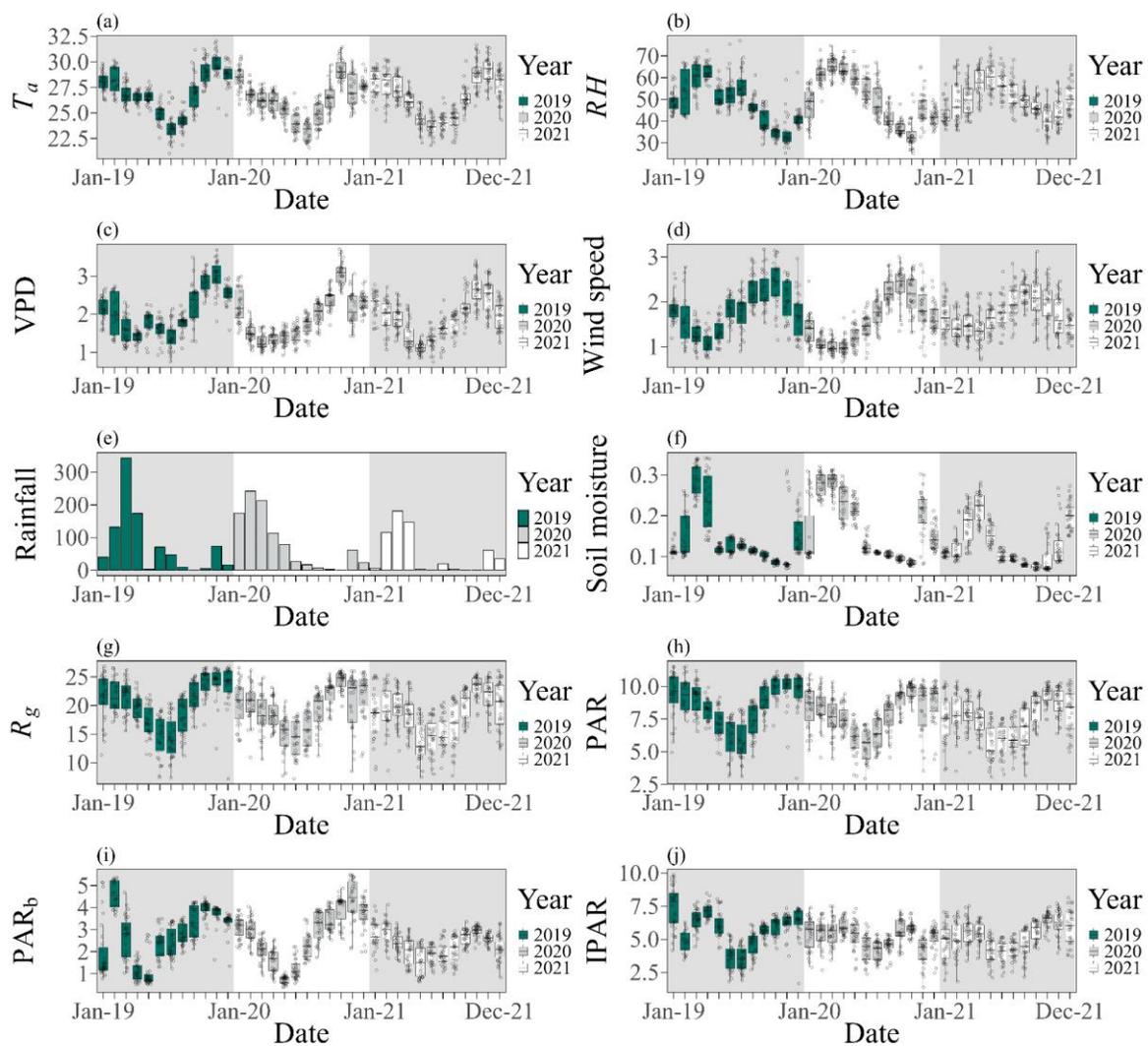
Figure 3. Monthly environmental conditions during the study period (2019–2021) in cactus cultivation in the Brazilian semi-arid region. The plots show the local conditions of (a) air

404   temperature—T_a (ºC), (b) relative air humidity—RH (%), (c) vapor pressure deficit—VPD

405   (kPa), (d) wind speed (m s^{-1}), (e) rainfall (mm), (f) soil moisture (m^3 m^{-3}), (g) global solar

406   radiation—R_g (MJ m^{-2} day^{-1}), (h) photosynthetically active radiation—PAR (MJ m^{-2} day^{-1}),

407   (i) PAR measured below the cactus canopy—PAR$_b$ (MJ m^{-2} day^{-1}), and (j) intercepted

408   photosynthetically active radiation—IPAR (MJ m^{-2} day^{-1}). The shaded areas indicate the

409   boundaries of the years.

410

411   For each year studied, there was a very similar intra-annual cyclic variation in global

412   solar radiation—R_g (Figure 3g). In the middle of each year (i.e., between May and July), we

413   observed the lowest average values of R_g (14.99 MJ m^{-2} day^{-1}), and the highest values

414   occurred between October and December (22.62 MJ m^{-2} day^{-1}). However, the three-year

415   average R_g was 19.31 MJ m^{-2} day^{-1}. During the warmer months and with high R_g,

416   photosynthetically active radiation (PAR) results were more expressive each year (Figure

417   3h). In this study, the lowest PAR value occurred in June 2020, being 5.55 MJ m^{-2} day^{-1}

418   (median 5.69, interquartile range 4.44–6.62 MJ m^{-2} day^{-1}), and the highest in November

419   2019, with 9.94 MJ m^{-2} day^{-1} (median 10.18, interquartile range 9.76–10.57 MJ m^{-2} day^{-1}),

420   while the average value for 2019–2021 was 7.91 MJ m^{-2} day^{-1}. The temporal variation of

421   PAR below the canopy (PAR$_b$) and PAR intercepted by the cactus canopy (IPAR) was due

422   to environmental conditions and canopy density (Figure 3i–j). On average, the months with

423   the lowest PAR$_b$ results annually occur from April to June (1.48 MJ m^{-2} day^{-1}). Interestingly,

424   there was a high dispersion and response in January and February 2019 (average of 3.27 MJ

425   m^{-2} day^{-1}) and September to November 2020 (3.90 MJ m^{-2} day^{-1}) due to two harvests carried

426   out on cactus during these periods (i.e., January 2019 and September 2020), leaving the soil

427   partially uncovered by vegetation. Furthermore, these variations are also visible in the canopy

428   radiation interception response. We observed significant inter-annual and intra-annual IPAR

429   variations, with the years 2019 and 2021 having the highest values, with mean of 5.66 and

430   5.16 MJ m^{-2} day^{-1}, respectively, both averaging 5.91% higher than the 2020 IPAR (Figure

431   3j).

432

3.3. Seasonal and temporal variation in the balance of carbon, energy and radiation

Figure 4 shows the half-hourly averages of carbon, energy, and radiation exchanges in *Opuntia* cactus cultivation during the four seasons (dry season, dry-wet transition, wet season, and wet-dry transition). Diurnal dynamics of carbon exchange exhibited similar patterns of variation across seasons. Clearly, during the night, the net ecosystem CO_2 exchange (NEE) was positive—release, and at dawn, it became more negative, increasing its absorption of CO_2 (Figure 4a). The highest daytime absorption rate of all seasons occurred between 11:00–13:00, averaging -16.36 μmol m^{-2} s^{-1}. At the same time, the dry, wet, and dry-wet transition seasons showed similarity and the highest average (more negative) -17.10 μmol m^{-2} s^{-1}, with 20.70% higher than the wet-dry transition season that had the lowest CO_2 absorption (less negative). Gross primary productivity (GPP) exhibited marked variations across the seasons, and the wet season had a daytime average of 12.94 μmol m^{-2} s^{-1} ranging from 0.02 to 22.16 μmol m^{-2} s^{-1} over 6:00–18:00 (Figure 4b). There was a minimal difference in mean cactus GPP during the dry and wet-dry transition seasons (0.76 μmol m^{-2} s^{-1}), both of which were, on average, 9.27% lower than during the wet season. We observed a lower diurnal GPP of 9.96 μmol m^{-2} s^{-1} during the wet-dry transition season, with both the seasonal trend of GPP and NEE limited by PAR. Consistent with previous results, ecosystem respiration—R_{eco} was more expressive during the wet season (mean of 3.73 μmol m^{-2} s^{-1}), and maximum daytime value of 4.46 μmol m^{-2} s^{-1}. In addition, the dry-wet, wet-dry and dry seasons were respectively 27.13, 34.27, and 58.17% lower than the wet season (Figure 4c). After 15:00 in all seasons, there was a clear decline in the respiration rate in cactus cultivation. On average, the PAR during the dry-wet transition season was higher, with a peak of 1590.4 μmol m^{-2} s^{-1} and a mean value of 915.05 μmol m^{-2} s^{-1}, while between the dry and wet seasons, there was no difference (mean of 838.17 μmol m^{-2} s^{-1}). During the wet-dry transition, we observed the lowest PAR value, a mean of 656.38 μmol m^{-2} s^{-1} (Figure 4d), and a peak around noon.
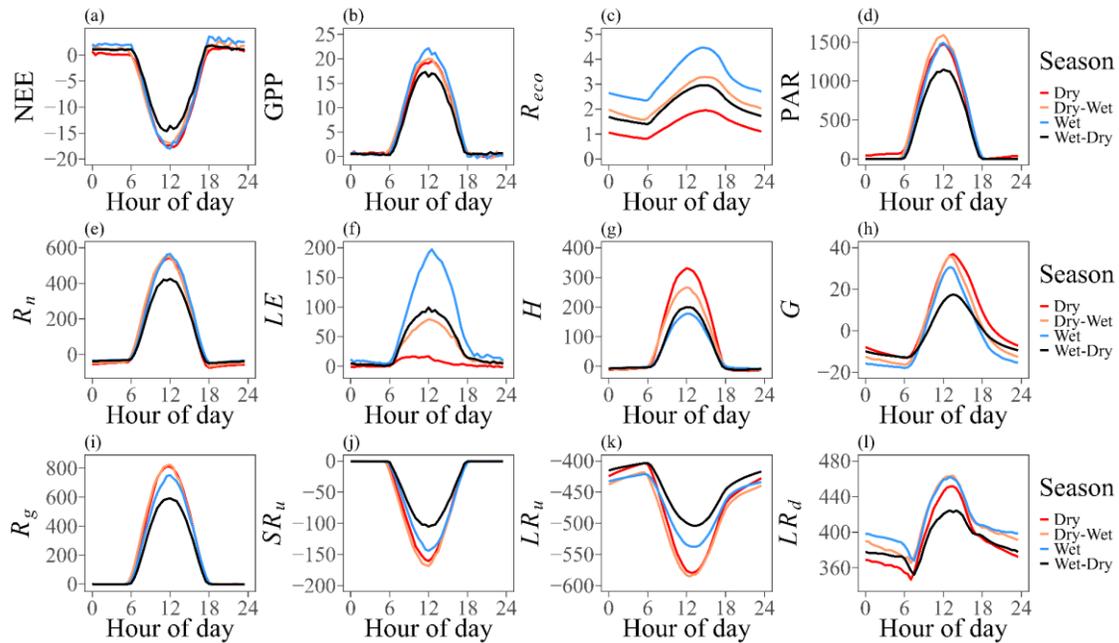
Figure 4. Diurnal cycle of carbon exchange, energy budget, and hourly radiation during dry and wet seasons (i.e., dry season, dry-wet transition, wet season, and wet-dry transition) in cactus cultivation in the Brazilian semi-arid region. (a) Net ecosystem CO_2 exchange—NEE, (b) gross primary productivity—GPP, (c) ecosystem respiration—R_{eco}, (d) photosynthetic active radiation—PAR, are expressed in μmol m^{-2} s^{-1}. (e) Net radiation—R_n, (f) latent heat flux—LE, (g) sensible heat flux—H, (h) soil heat flux—G, (i) global solar radiation—R_g, (j) upward shortwave radiation—SR_u, (k) upward longwave radiation—LR_u, and (l) downward longwave radiation—LR_d, all expressed in W m^{-2}. Negative values in panel (a) indicate carbon uptake while positive values in panels (b) and (c) indicate carbon release by the ecosystem.

Net radiation (R_n) exhibited smaller flux patterns during the wet-dry transition season, with a daytime average of 217.97 W m^{-2} and a peak occurring at noon (Figure 4e). On the other hand, we did not observe the difference between the dry season, dry-wet transition, and wet season, with an average value of 283.11 W m^{-2} and a gradual decline for all stations after solar noon. The latent heat flux (LE) was higher during the wet season (114.68 W m^{-2}) and lowered in the dry season (mean of 9.39 W m^{-2}). In addition, the transition stations (i.e., dry-wet and wet-dry) presented intermediate LE fluxes, with the wet-dry season averaging 60.05 W m^{-2} and the dry-wet transition slightly lower (17.57%) (Figure 4f). The dry and wet

480 seasons had the highest (183.33 W m^{-2}) and lowest (93.82 W m^{-2}) sensible heat flux—H

481 values, respectively. In contrast, H decreased in the dry-wet (19.07%) and wet-dry (43.08%)

482 transitions compared to the dry season. Soil heat flux (G) was highest during dry season >

483 dry-wet transition > wet season > wet-dry transition and peaked between 13:00 and 14:00,

484 ranging from 36.90 to 17.42 W m^{-2} between the dry season and the wet-dry transition season,

485 respectively.

486   In general, the radiation balance was lowest during the wet-dry transition season. For

487 example, global solar radiation (R_g) in the wet-dry transition was on average 21.02% lower

488 than the wet season, 27.98% lower than the dry season, and 29.88% lower than the dry-wet

489 transition (Figure 4i). We also observed the same tendency for shortwave—SR_u and

490 longwave—LR_u radiation for cactus cultivation (Figure 4j–k). However, there was a greater

491 distance after noon from the LR_u during the dry and dry-wet transition seasons than during

492 the wet season. Our results show no difference between the wet season and the dry-wet

493 transition, with an average of 422.99 W m^{-2} for descending longwave radiation (LR_d). As for

494 the dry season, the average was 408.93 W m^{-2} with a peak of 451.47 W m^{-2}, followed by the

495 wet-dry transition (average of 398.03 W m^{-2}), reaching a peak of 424.41 W m^{-2}.

496   Figure 5 shows the cactus agroecosystem response to carbon, energy and radiation

497 exchanges on an annual scale (2019–2021). In 2021, there was an apparent decrease in NEE

498 on a diurnal scale, while 2019 and 2020 were more expressive sinks, with the NEE being

499 14.36 and 28.36% higher, respectively (Figure 5a). The GPP showed the same trend as the

500 NEE, with a peak occurring at noon and a daytime average of 0.22 g C m^{-2} during 2021, 0.23

501 g C m^{-2} (2019), and 0.30 g C m^{-2} (2020). Here, we reveal that the cactus agroecosystem

502 becomes a carbon sink as global solar radiation increases. We observed variation with a mean

503 GPP value of 0.01 to 0.51 g C m^{-2} (Figure 5b). In this study, during 2020, which was

504 particularly wet, R_{eco} was higher than in 2021 and 2019, and the highest values occurred

505 between 13:30 and 16:30 (Figure 5c). Overall, the ecosystem respiration rate in 2020 is

506 approximately 49% higher than in 2021 and 94% higher than in 2019. The carbon budget

507 was also boosted by the increase in PAR, although there were no differences between 2020

508 and 2021 (Figure 5d).

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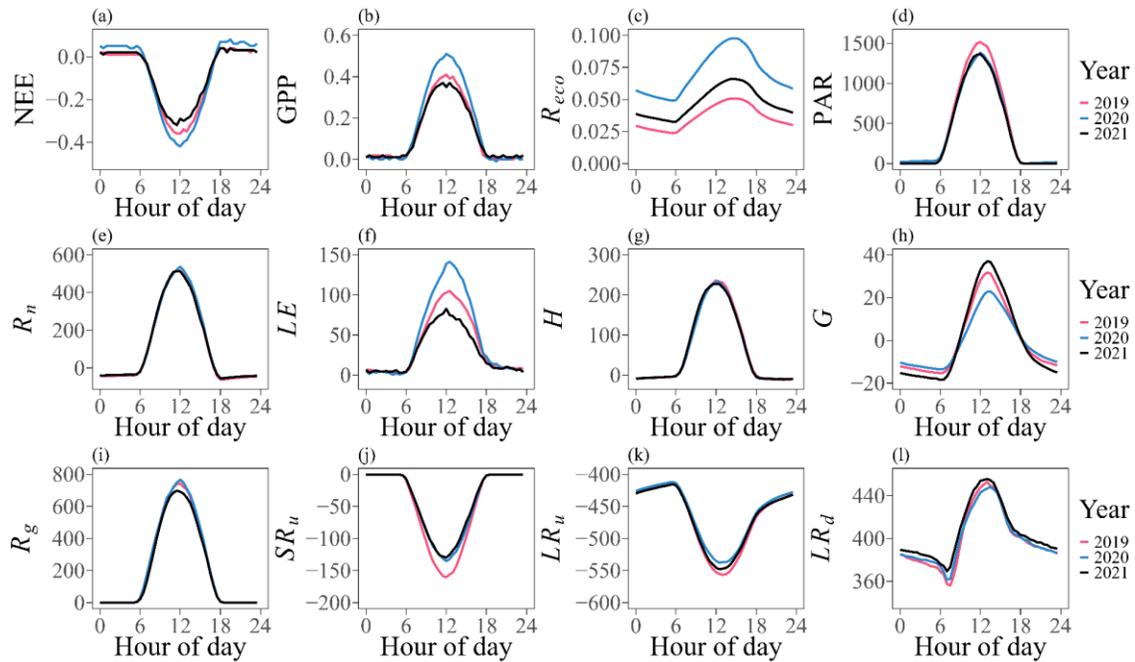
Figure 5. Variation of carbon exchange, energy budget and radiation on an hourly scale during 2019–2021 in cactus cultivation in the Brazilian semi-arid region. (a) Net ecosystem CO_2 exchange—NEE, (b) gross primary productivity—GPP, (c) ecosystem respiration—R_{eco}, are expressed in g C m^{-2}, and (d) photosynthetic active radiation—PAR, is expressed in μmol m^{-2} s^{-1}. (e) Net radiation—R_n, (f) latent heat flux—LE, (g) sensible heat flux—H, (h) soil heat flux—G, (i) global solar radiation—R_g, (j) upward shortwave radiation—SR_u, (k) upward longwave radiation—LR_u, and (l) downward longwave radiation—LR_d, all expressed in W m^{-2}. Negative values in panel (a) indicate carbon uptake while positive values in panels (b) and (c) indicate carbon release by the ecosystem.

Despite the high values of net radiation and sensible heat fluxes, with an average peak of 522.36 and 232.10 W m^{-2}, respectively, our results show no significant changes between 2019–2021 (Figures 5e and 5g). In contrast, the LE began to differ between years after 7:30 and reached a maximum value around noon (12:00–13:00). Indeed, the latent heat flux averaged 82.78 W m^{-2} in 2020 and had lower diurnal responses during 2021 and 2019, averaging 49.57 and 63.52 W m^{-2}, respectively (Figure 5f). We observed substantial variations in the soil heat flux, with 2021 having the highest result, an average of 12.79 W m^{-2}. In all years, the sharpest decline in G occurs after 14:00 (Figure 5h). Throughout the daytime, we observed a slight difference between the peaks of global solar radiation during

327

530   2019–2021, in addition to greater losses (more negative) of short and long radiation by the

531   surface of cacti (Figure 5i–k). Likewise, the LR_d was slightly higher in 2021, averaging

532   419.96 W m^{-2} and diurnal variation from 369.49 to 455.70 W m^{-2}. On the other hand, the

533   LR_d of 2019 and 2020 showed no difference, an average of 412.57 W m^{-2} with its peaks at

534   13:00 (2019) and 13:30 (2020) and a less significant decrease after 16:30 (Figure 5l).

535   Figure 6 shows the monthly scale variability of the carbon balance and

536   photosynthetically active radiation absorbed by growing *Opuntia* during 2019–2021.

537   Throughout all the years, we can observe that in each month, the cactus mainly was a carbon

538   sink on average (Figure 6a). On a monthly scale, the maximum (most negative) mean NEE

539   values were −6.02 g C m^{-2} day^{-1} and −5.83 g C m^{-2} day^{-1} in January and April 2019,

540   respectively. In 2020, the highest NEE values were in September (−5.61 g C m^{-2} day^{-1}) and

541   October (−5.41 g C m^{-2} day^{-1}), and in 2021 it also occurred in September and October, with

542   an average of −4.73 and −4.91 g C m^{-2} day^{-1}, respectively. The *Opuntia* cactus presented

543   GPP ranging from 4.32 to 10.38 g C m^{-2} day^{-1} and an average for the entire period of 6.51 g

544   C m^{-2} day^{-1} (Figure 6b). In addition, R_{eco} presented very similar variations between the years,

545   with higher respiration between March and May, and we also observed more expressive

546   peaks occurring in 2020 (Figure 6c). Contrary to what was seen in 2020, our results show

547   lower R_{eco} in 2019 (mean of 1.73 g C m^{-2} day^{-1}), which coincides with high NEE and PAR

548   values absorbed by the cactus. In 2019, substantial variations were found in the absorbed

549   photosynthetically active radiation (APAR) by the cactus (Figure 6d), with a minimum value

550   (2.46 MJ m^{-2} day^{-1}) and a maximum value (5.55 MJ m^{-2} day^{-1}) in November 2020 and April

551   2019, respectively.

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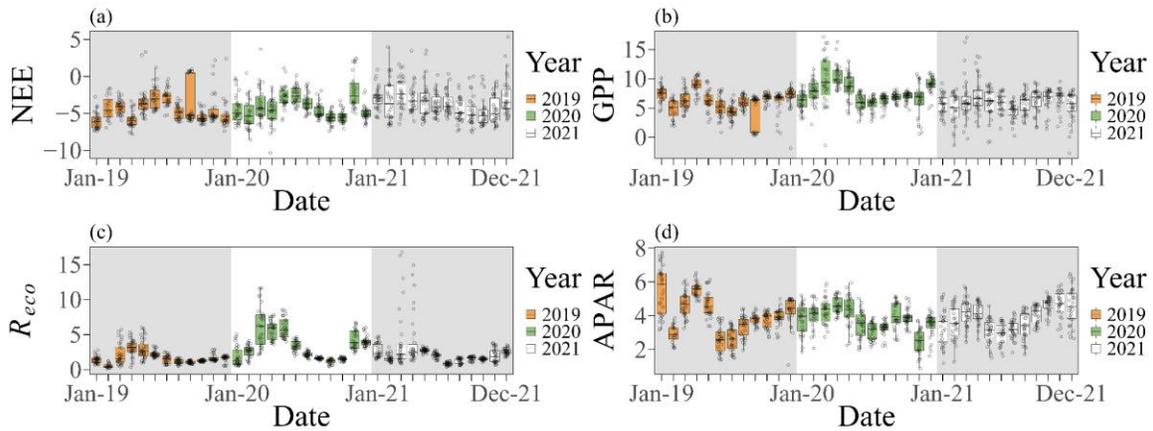
553

554   Figure 6. Monthly variation of carbon balance (i.e., net ecosystem CO_2 exchange—NEE,

555   gross primary productivity—GPP, and ecosystem respiration—R_{eco}) and absorbed

556   photosynthetically active radiation (APAR) in *Opuntia* cactus cultivation during 2019–2021

557   in the Brazilian semi-arid region. The shaded areas indicate the boundaries of the years. Note:

558   NEE, GPP, R_{eco} in g C m^{-2} day^{-1}, and APAR in MJ m^{-2} day^{-1}.

559

560   There were significant variations in the energy balance between months and years in

561   cactus cultivation (Figure 7). The lowest mean value of R_n was found in May–July (9.61 MJ

562   m^{-2} day^{-1}); by contrast, fluxes were higher at the beginning and end of the year (Figure 7a).

563   In 2019, the months with the lowest *LE* results were September–November; in 2020, they

564   were August–October, followed by 2021 with the lowest *LE* responses in June–October.

565   Furthermore, *H* reached its minimum value in March (2.48 MJ m^{-2} day^{-1}) and its maximum

566   value in September (9.05 MJ m^{-2} day^{-1}), both in 2020. Clearly, when the *H* was high, there

567   was a lower energetic contribution to *LE* (Figure 7b–c). For *G*, curiously there was a flux

568   variation very similar to the trend of *H* (Figure 7d). For example, we found higher soil heat

569   fluxes at the beginning and end of the year, and the maximum flux occurred in October 2019,

570   averaging 0.51 MJ m^{-2} day^{-1}. On the other hand, the lowest soil heat flux was observed in

571   February 2020 (mean −0.40 MJ m^{-2} day^{-1}) due to rainfall (see Figure 3e).

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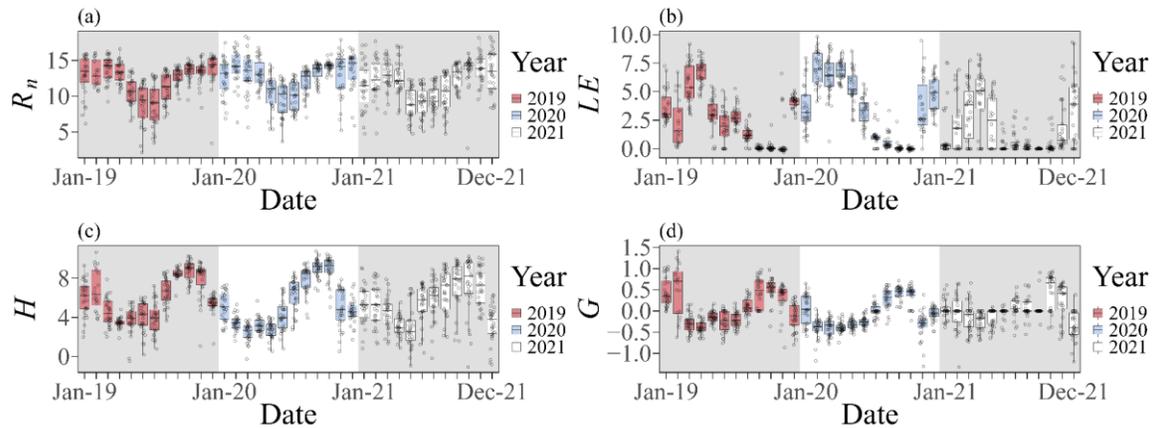
Figure 7. Diurnal variation of (a) net radiation—R_n, (b) latent heat flux—LE, (c) sensible heat flux—H, and (d) soil heat flux—G during the period 2019–2021 in *Opuntia* cactus cultivation in the Brazilian semi-arid region. All the variables were measured in MJ m^{-2} day^{-1}. The shaded areas indicate the boundaries of the years.

On average, the R_g varied between 13.86 and 24.31 MJ m^{-2} day^{-1}, with the minimum and maximum values occurring in May 2021 and October 2020, respectively (Figure 8). Although a similar variation is observed over the years, in 2021 the lowest R_g balance occurred on average (18.44 MJ m^{-2} day^{-1}) (Figure 8a). At the beginning of the year, SR_u is higher (more negative), and at the end, it is more pronounced. The months of June–August had the lowest values of SR_u (mean −2.69 MJ m^{-2} day^{-1}), while October–December was on average 68.73% higher than June–August (Figure 8b). Likewise, LR_u was similar to SR_u, but with different magnitudes, with longwave radiation lost more significantly (Figure 8c). Consequently, after January and February of each year, there was a gradual decrease in the LR_u until mid-year, ranging from −36.87 to −43.15 MJ m^{-2} day^{-1}, and we observed significant variations in the LR_d from 32.16 to 36.49 MJ m^{-2} day^{-1} (Figure 8d).

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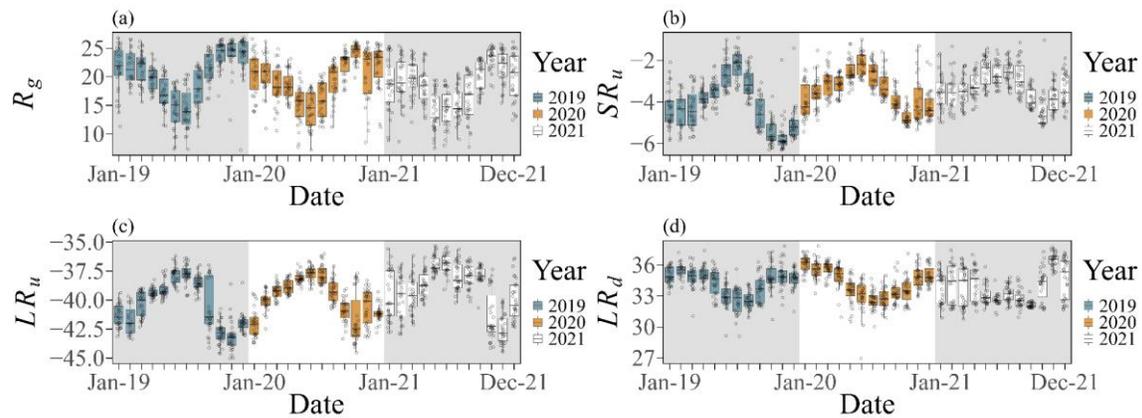
Figure 8. Temporal variation of radiation balance in *Opuntia* cactus cultivation in the Brazilian semi-arid region. (a) R_g is the global solar radiation, (b) SR_u is the upward shortwave radiation, (c) LR_u is the upward longwave radiation, and (d) LR_d is the downward longwave radiation. All the variables were measured in MJ m^{-2} day^{-1}. The shaded areas indicate the boundaries of the years.

3.4. Characteristics of seasonal changes in radiation, energy, carbon and water fluxes

The wet-dry transition season showed the lowest values of the radiation balance components (Table 2). On average, the R_g of the wet-dry transition season was 26.74% lower than all stations (e.g., dry-wet, wet, and dry) that had solar radiation greater than 20 MJ m^{-2} day^{-1}. Consequently, in this same wet-dry transition season, the lowest results of short and long radiation (i.e., SR_u, LR_u, and LR_d) and net radiation for the cactus surface occurred on average. During the dry season, *LE* was lower than in all seasons and caused an excessive increase in *H* (7.9 MJ m^{-2} day^{-1}), followed by 6.4 MJ m^{-2} day^{-1}, referring to the dry-wet transition season. In wet seasons the energy for soil heat flux was more negative, while the results of dry seasons were positive, i.e., higher energy for soil heating. Overall, there was stability in the carbon balance for cactus cultivation. Our results show that the cactus was a carbon sink in all seasons and years, with more expressive values during the dry-wet (−4.3 g C m^{-2} day^{-1}) and dry (−5 g C m^{-2} day^{-1}) seasons. Furthermore, during the wet season, the NEE of the cactus was 23.67% lower than in the dry season. NEE presented very similar results annually, although in 2021 it was 11.56% lower than the annual average (Table 2).

Table 2. Diurnal variation of radiation and energy balance, carbon budget, evapotranspiration (ET) and rainfall for three years of cactus cultivation in the Brazilian semi-arid region. Net ecosystem CO₂ exchange (NEE), gross primary productivity

616 (GPP), and ecosystem respiration (R_{eco}) with negative values indicate carbon input into the ecosystem (absorption), while
617 positive values indicate carbon loss (release).

Season / Year	R_g	SR_u	LR_u	LR_d	R_n	LE	H	G	NEE	GPP	R_{eco}	ET	Rainfall
	MJ m^{-2} day^{-1}								g C m^{-2} day^{-1}			mm	
Dry-wet/2019	23.2	5.1	42.4	34.8	13.2	2.0	7.0	0.2	−5.0	6.6	1.6	48	100
Wet/2019	22.2	4.6	41.2	35.0	13.7	4.4	5.5	0.1	−5.0	6.5	1.6	169	849
Wet-dry/2019	16.7	3.1	38.4	33.4	10.5	2.8	4.2	−0.2	−3.6	5.8	2.1	178	166
Dry/2019	23.1	5.1	42.3	34.6	13.2	0.1	8.2	0.6	−5.2	6.4	1.1	3	7
Dry-wet/2020	22.2	4.3	41.1	34.5	13.6	3.0	6.1	−0.03	−4.1	7.4	3.3	108	85
Wet/2020	18.6	3.3	39.7	35.1	12.7	5.8	3.4	−0.3	−4.1	8.6	4.5	365	913
Wet-dry/2020	14.7	2.4	37.7	32.8	9.6	2.3	4.9	−0.2	−2.8	5.8	2.9	47	31
Dry/2020	20.6	3.6	39.9	33.0	12.6	0.5	8.3	0.3	−5.1	6.5	1.5	14	17
Dry-wet/2021	20.2	3.7	40.6	34.6	12.6	1.2	6.2	0.1	−4.0	6.1	2.1	41	107
Wet/2021	19.5	3.4	39.8	34.6	13.2	3.9	3.9	−0.2	−2.4	6.0	3.6	148	439
Wet-dry/2021	14.8	2.6	37.3	33.0	9.5	1.0	4.4	−0.1	−3.5	5.4	1.9	41	37
Dry/2021	19.8	3.7	39.0	33.0	12.2	0.1	7.1	0.2	−4.7	6.2	1.5	5	6
Season													
Dry-wet	21.9	4.4	41.4	34.6	13.2	2.1	6.4	0.1	−4.3	6.7	2.4	65	97
Wet	20.1	3.7	40.2	34.9	13.2	4.7	4.3	−0.2	−3.8	7.0	3.2	227	733
Wet-dry	15.4	2.7	37.8	33.0	9.9	2.0	4.5	−0.1	−3.3	5.6	2.3	88	78
Dry	21.2	4.1	40.4	33.5	12.7	0.2	7.9	0.4	−5.0	6.4	1.4	7	10
Crop cycle													
1	19.1	3.7	39.8	34.3	12.1	3.4	5.0	−0.04	−4.2	6.8	2.6	819	2075
2	19.5	3.6	39.6	33.8	12.3	1.7	5.8	0.04	−3.9	6.3	2.4	347	680
Year													
2019	21.3	4.5	41.1	34.5	12.7	2.3	6.2	0.2	−4.7	6.3	1.6	398	1122
2020	19.0	3.4	39.6	33.8	12.1	2.9	5.7	−0.04	−4.0	7.1	3.1	534	1045
2021	18.6	3.4	39.2	33.8	11.9	1.6	5.4	0.002	−3.6	5.9	2.3	235	589
Annual mean	19.6	3.7	40.0	34.0	12.2	2.3	5.8	0.05	−4.1	6.4	2.3	388.7	918.5

R_g is the global solar radiation, SR_u is the upward shortwave radiation, LR_u is the upward longwave radiation, LR_d is the downward longwave radiation, R_n is the net radiation, LE is the latent heat flux, H is the sensible heat flux, G is the soil heat flux, NEE is the net ecosystem CO_2 exchange, GPP is the gross primary productivity, R_{eco} is the ecosystem respiration, and ET is the evapotranspiration.

618

619 Our results also show an expressive contribution of GPP during the experimental
620 period (Table 2). GPP during the wet-dry transition season showed the lowest results,
621 averaging 5.6 g C m^{-2} day^{-1}. When examining only the dry season, we observed a lower
622 carbon efflux due to low ecosystem respiration and, consequently, a high NEE response.
623 Also, in this season, there were the lowest average records of evapotranspiration and rainfall
624 (7 mm and 10 mm, respectively), while the season with the greatest influence of rainfall, for
625 example, the wet season (average of 733 mm of rainfall) had a R_{eco} of 136.74% higher than
626 the dry season. On an annual scale, as well as for each crop cycle, the radiation and energy

627 balances were very similar. As for the carbon balance, the first cactus cycle was more
628 expressive, with greater carbon accumulation and high productivity. In addition, the total flux
629 of CO_2 released from the ecosystem between the two cycles showed a difference of 8.23%,
630 with the first cactus cycle being larger. Evapotranspiration (ET) in the first cactus cycle was
631 more expressive (accumulated 819 mm) but decreased by more than half in the second cycle,
632 which reveals the influence of rainfall in this agroecosystem and ET responses.

633

634 *3.5. Flux partitioning*

635 Table 3 shows our results of partitioning the radiation and energy fluxes, as well as
636 the PAR fraction intercepted in cactus cultivation. The SR_u/R_g ratio ranged from 0.16 to 0.22
637 during the seasons and years, with the wet-dry transition season having the lowest response
638 (mean of 0.17). R_n was responsible for 64% and 60% of global radiation during the wet season
639 and wet-dry transition, respectively. Interestingly, the PAR/R_g ratio averaged 0.41 in all
640 seasons and showed slight variation over time. Furthermore, our results show a greater
641 fraction of PAR intercepted (*f*IPAR) during the wet season and wet-dry transition and a
642 greater increase in the LE/R_n ratio during these previously mentioned seasons. The dry and
643 dry-wet transition seasons represented 3% and 19%, respectively, of the LE/R_n, thus
644 configuring the lowest ratios of this partition. Consequently, the highest response of the H/R_n
645 ratio was during the dry season (mean of 0.78), being 107.13%, 38.69%, and 30.27% higher
646 than the wet season and wet-dry and dry-wet transitions, respectively. The partitioning of R_n
647 into *LE* and *H* differed between the wettest and driest seasons and years during the
648 experimental period. There was a smaller contribution to the partition of the *G* in relation to
649 net radiation. The G/R_n ratio during the dry season was the most expressive, with an average
650 of 4%, while the other seasons were equal to or less than 2%. For each evaluated year and
651 cactus cycle, the flux partitions were slightly similar, except for the LE/R_n of the first cycle,
652 which was 122.13% higher than the LE/R_n of the second cycle.

653

654 Table 3. Partitions of radiation, energy and photosynthetic active radiation (PAR) during seasons (dry-wet transition, wet
655 season, wet-dry transition, and dry season) and years (2019–2021) in cactus cultivation in the Brazilian semi-arid region.

Season / Year	SR_u/R_g	R_n/R_g	PAR/R_g	*f*IPAR	LE/R_n	H/R_n	G/R_n
Dry-wet/2019	0.22	0.56	0.42	0.71	0.19	0.66	0.03
Wet/2019	0.20	0.61	0.42	0.66	0.39	0.48	0.02
Wet-dry/2019	0.18	0.60	0.42	0.70	0.36	0.51	0.003

Dry/2019	0.22	0.56	0.42	0.61	0.01	0.79	0.05
Dry-wet/2020	0.19	0.60	0.40	0.55	0.26	0.54	0.01
Wet/2020	0.17	0.67	0.41	0.74	0.52	0.31	0.003
Wet-dry/2020	0.16	0.62	0.39	0.73	0.31	0.63	0.001
Dry/2020	0.17	0.60	0.40	0.61	0.06	0.82	0.03
Dry-wet/2021	0.18	0.59	0.40	0.66	0.11	0.61	0.02
Wet/2021	0.17	0.65	0.41	0.71	0.34	0.35	0.003
Wet-dry/2021	0.18	0.58	0.40	0.71	0.13	0.56	0.004
Dry/2021	0.18	0.56	0.41	0.68	0.02	0.74	0.02
Season							
Dry-wet	0.20	0.58	0.41	0.64	0.19	0.60	0.02
Wet	0.18	0.64	0.41	0.70	0.42	0.38	0.01
Wet-dry	0.17	0.60	0.41	0.71	0.27	0.56	0.003
Dry	0.19	0.57	0.41	0.63	0.03	0.78	0.04
Crop cycle							
1	0.19	0.61	0.41	0.70	0.35	0.51	0.01
2	0.18	0.59	0.40	0.66	0.16	0.58	0.01
Year							
2019	0.20	0.58	0.42	0.67	0.24	0.61	0.03
2020	0.17	0.62	0.40	0.66	0.29	0.57	0.01
2021	0.18	0.59	0.41	0.69	0.15	0.56	0.01
Annual mean	0.19	0.60	0.41	0.67	0.22	0.58	0.02

SR_u is the upward shortwave radiation, R_g is the global solar radiation, R_n is the net radiation, PAR is the photosynthetic active radiation, fIPAR is the fraction of PAR intercepted, LE is the latent heat flux, H is the sensible heat flux, and G is the soil heat flux.

656

3.6. Yield and efficiency responses in the use of biophysical resources

658   The average contribution of biomass, changes in morphophysiological rates, nutrient
659 and carbon stocks, and efficiency in the use of biophysical resources was calculated for each
660 season, cycle and year during the experimental period in *Opuntia* cactus cultivation (Table
661 4). We found higher values of dry biomass during wet seasons (i.e., wet and wet-dry
662 transition) reaching 356–361 g m^{-2}. The cactus clearly increased its CAI during the wet-dry
663 transition season, with an average growth of 1.14 m^2 m^{-2} and average values reaching 0.88
664 to 1.37 m^2 m^{-2}. Although the cactus maintained a high CAI during the dry season, it was
665 13.31% lower in relation to the wet-dry transition. The net assimilation rate (NAR) showed
666 higher values during the dry-wet transition, and 2019 was the most expressive year for net
667 photosynthesis; consequently, the relative growth rate (RGR) was higher during this period.
668 On the other hand, the specific cladode area (SCA) was higher during the wet-dry transition
669 (0.001 m^2 g^{-1}) and dry season (0.001 m^2 g^{-1}), with the dry-wet transition having the lowest

cactus response to SCA (mean 0.0003 m^2 g^{-1}). For the first cycle, the cactus was more productive and slightly similar in terms of cladode and morphophysiological characteristics.

Table 4. Biomass, morphophysiological index and growth rate, stocks and efficiencies of nutrients, water and radiation in cacti cultivation in the Brazilian semi-arid region.

Season / Year	Dry biomass	CAI	NAR	RGR	SCA	Stock N	P	K+	Ca2+	Mg2+	C	NUE N	P	K+	Ca2+	Mg2+	C	WUE	RUE
	g m^{-2}	m^2 m^{-2}	g m^{-2} day^{-1}	g g^{-1} day^{-1}	m^2 g^{-1}	g m^{-2}						mg m^{-2} mm^{-1}					µg m^{-2} mm^{-1}	g m^{-2} mm^{-1}	g MJ^{-1}
Dry-wet/2019	245	0.79	91	0.004	0.0003	2.9	0.8	4.8	12.7	10.2	84	60	18	100	264	211	1738	5.09	0.89
Wet/2019	895	0.37	120	0.006	0.0001	10.6	3.1	17.6	46.3	37.1	306	62	18	104	274	220	1809	5.30	2.24
Wet-dry/2019	978	0.88	11	0.003	0.0003	11.5	3.4	19.2	50.7	40.6	334	65	19	108	285	229	1881	5.51	1.71
Dry/2019	84	1.17	1	0.001	0.0004	1.0	0.3	1.7	4.4	3.5	29	359	105	597	1576	1263	10393	30.43	0.47
Dry-wet/2020	450	0.07	80	0.007	0.0001	5.3	1.6	8.8	23.3	18.7	154	49	14	82	217	174	1428	4.18	1.57
Wet/2020	28	1.17	0.2	0.0001	0.0004	0.3	0.1	0.6	1.5	1.2	10	1	0.3	2	4	3	27	0.08	0.04
Wet-dry/2020	2	1.17	0.03	0.00001	0.0004	0.0	0.0	0.0	0.1	0.1	1	0.4	0.1	1	2	2	13	0.04	0.01
Dry/2020	221	0.42	59	0.007	0.0002	2.6	0.8	4.3	11.5	9.2	76	181	53	300	793	635	5229	15.31	0.83
Dry-wet/2021	200	0.75	9	0.002	0.0006	2.4	0.7	3.9	10.4	8.3	68	58	17	97	256	205	1688	4.94	0.63
Wet/2021	145	1.20	2	0.001	0.0009	1.7	0.5	2.8	7.5	6.0	49	12	3	19	51	41	334	0.98	0.37
Wet-dry/2021	102	1.37	1	0.001	0.0010	1.2	0.4	2.0	5.3	4.2	35	29	9	49	129	104	853	2.50	0.32
Dry/2021	25	1.38	0.2	0.0002	0.0009	0.3	0.1	0.5	1.3	1.0	8	57	17	95	249	200	1645	4.82	0.07
Season																			
Dry-wet	299	0.54	60	0.004	0.0003	3.5	1.0	5.9	15.5	12.4	102	54	16	90	236	189	1558	4.56	1.02
Wet	356	0.91	41	0.002	0.0005	4.2	1.2	7.0	18.4	14.8	122	18	5	31	81	65	535	1.57	0.74
Wet-dry	361	1.14	4	0.001	0.001	4.3	1.2	7.1	18.7	15.0	123	48	14	80	211	169	1392	4.08	1.02
Dry	110	0.99	20	0.002	0.001	1.3	0.4	2.2	5.7	4.6	38	174	51	290	765	613	5046	14.77	0.41
Crop cycle																			
1	2233	0.92	33	0.0020	0.0003	26.3	7.7	43.8	115.7	92.7	763	32	9	53	141	113	931	2.73	0.96
2	1143	0.88	24	0.0029	0.0006	13.5	3.9	22.4	59.2	47.5	391	39	11	65	171	137	1126	3.30	0.61
Year																			
2019	2203	0.80	56	0.003	0.0003	6.5	1.9	10.8	28.5	22.9	752	16	5	27	72	57	1892	5.54	6.17
2020	702	0.71	35	0.003	0.0003	2.1	0.6	3.4	9.1	7.3	240	4	1	6	17	14	449	1.31	2.06
2021	472	1.18	3	0.001	0.001	1.4	0.4	2.3	6.1	4.9	161	6	2	10	26	21	687	2.01	1.36
Annual mean	1126	0.90	31	0.003	0.0005	3.3	1.0	5.5	14.6	11.7	384	8.7	2.6	14.5	38.3	30.7	1010	2.96	3.19

NUE is the nutrient use efficiency (mg m^{-2} mm^{-1}), CAI is the cladode area index (m^2 m^{-2}), NAR is the net assimilation rate (g m^{-2} day^{-1}), RGR is the relative growth rate (g g^{-1} day^{-1}), SCA is the specific cladode area (m^2 g^{-1}), WUE is the water use efficiency (g m^{-2} mm^{-1}), and RUE is the radiation use efficiency (g m^{-2}).

The cactus had higher nutrient and carbon stocks during the wet season and wet-dry transition (Table 4). The dry-wet transition season was generally the third season with the best performance of nutrient and carbon stocks, making it clear that the lowest stock performances occurred in the dry season. Our results highlighted a lower efficiency of nutrients, carbon, and water and radiation use when cacti were exposed to more wet periods, i.e., during the dry-wet, wet-dry, and wet season transitions smaller ones (ranked by decreasing order). In contrast, the dry and wet seasons showed higher and lower efficiency in the use of nutrients and water, respectively. However, the wet season was 81.48% higher than the dry season for radiation use efficiency (RUE) data. Furthermore, the RUE of the

685 dry-wet and wet-dry transition seasons was the same, averaging 1.02 g MJ^{-1}. We found that

686 in cactus plants with high dry biomass and values of nitrogen and carbon stocks, their

687 efficiency in the use of radiation is maximized, and the inverse condition is true as seen in

688 the first (higher) and second (lower) crop cycles.

689

690 *3.7. Principal component analysis*

691   Figure 9 shows the principal component analysis (PCA) of the measured environment

692 and cactus variables to examine their interactions within a multivariate space. For

693 visualization purposes, the biplots generated in the PCA focus on the first two components

694 (Figure 9a–b), although five principal components have presented eigenvalues greater than

695 1.0 when we use the Kaiser criterion (Kaiser, 1960) (Figure 9c). Principal component score

696 plots depict the characteristics of stations and help you understand their dispersion pattern

697 for variables. The variance explained by the first two components was 71.57%, with 38.78%

698 explained by principal component 1 (PC1), while 32.79% was explained by principal

699 component 2 (PC2). In the season score plot (Figure 9a), our results show a clear dispersion

700 between the dry seasons (i.e., dry and dry-wet) presented on the left side of the biplot and

701 wet seasons (i.e., wet and wet-dry) projected on the right side. Here, the loading plots display

702 the relationships between the analyzed variables, with loadings ranging between principal

703 components from −0.70 to 0.71 (Figure 9b–c).

704
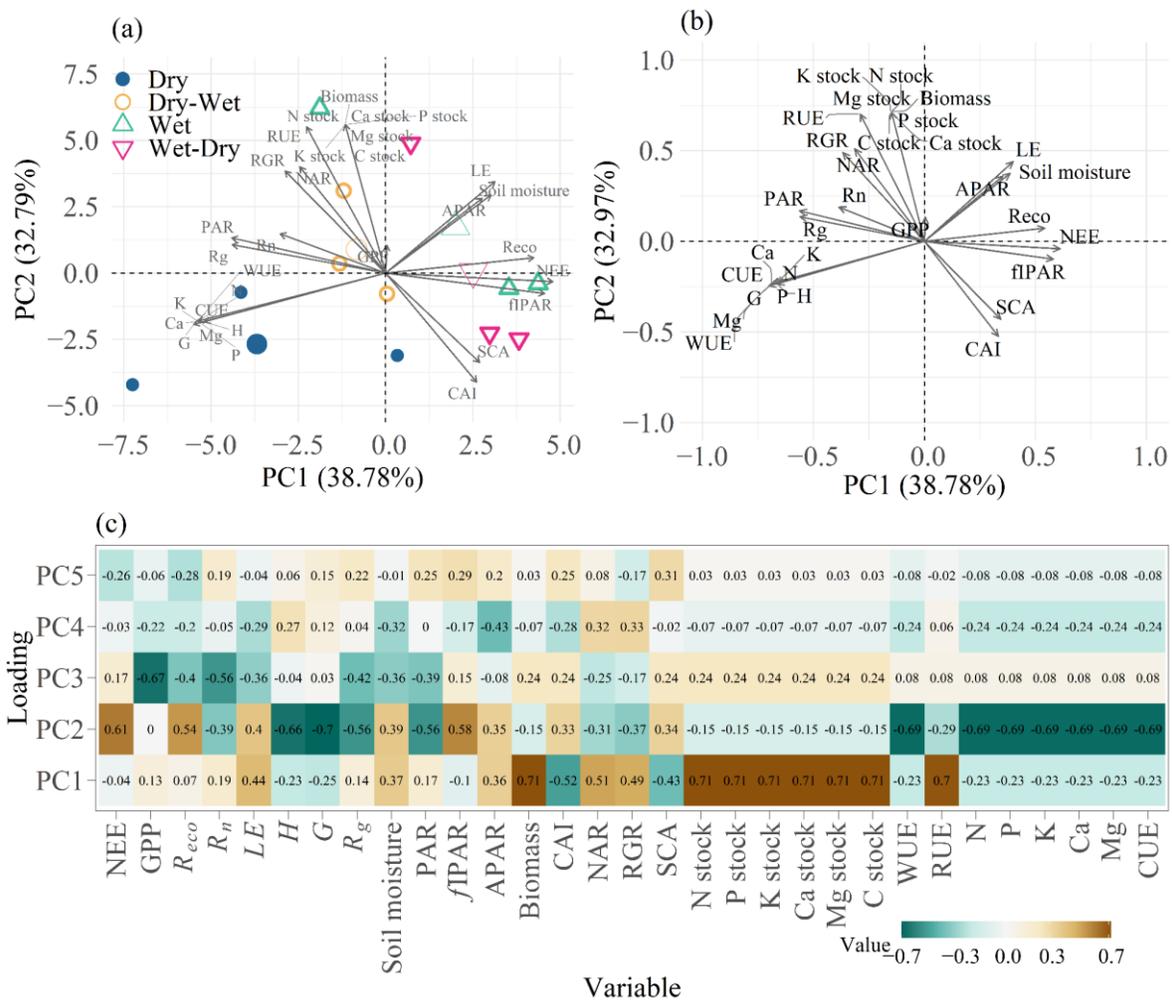
Figure 9. Principal component analysis (PCA) shows the relationship between environmental and cactus plant variables. The panels show (a) season score variation along the first (PC1) and second (PC2) principal components, (b) variable loadings on the first two axes, and (c) component matrix with loading factors for each variable in the first five principal components with an eigenvalue greater than 1.0. For full variable names, see the Material and Methods section. The variables N, P, K, Ca and Mg mentioned represent the efficiency in the use of these nutrients. The symbols denote the four seasons (dry season, dry-wet transition, wet season and wet-dry transition) evaluated.

Figure 9b illustrates the variables that represent the nutrient-use efficiency (e.g., N, P, K, Ca, and Mg), water (WUE), and carbon (CUE) indicate that low loadings are found in PC1 (0.23), and high loadings are found in PC2 (0.69), with a high correlation with the dry season (see Figure 9c). Dry biomass, CAI, NAR, nutrient stocks, and RUE were the main

719   contributors to PC1 (presence of positive and negative loadings greater than 0.5). In contrast,

720   NEE, R_{eco}, H, G, R_g, PAR, fIPAR, WUE, and nutrient and carbon use efficiency mainly

721   contributed to the PC2 (positive and negative charge value $\geq$ 0.5). When presenting highly

722   correlated components, the environmental and plant variables pointed approximately in the

723   same direction. Furthermore, we observed that during the dry season, there was greater

724   expressiveness of the variables G and H (with loadings of −0.7 and −0.66, respectively), with

725   both inserted in CP2. During the dry-wet transition season, the highest negative loadings

726   were grouped between the variables R_n (−0.39), R_g (−0.56), and PAR (−0.56) for PC2, and

727   positively in PC1 at variables RGR, NAR, and RUE with loadings of 0.49, 0.51 and 0.7,

728   respectively (Figure 9b–c). An interesting finding was the similarity between the GPP of all

729   four seasons, explained by the proximity of the vector (variable) to the biplot's central axis.

730   In the wet and wet-dry transition seasons, we observed greater correlations (i.e., narrow

731   angles between vectors) between plant nutrient and carbon stocks, biomass, soil moisture,

732   LE, APAR, R_{eco}, NEE, fIPAR, SCA and CAI. The higher the soil moisture, the higher the

733   LE, APAR and R_{eco} during the wet season. Clearly, when the cactus had a high WUE (loading

734   of −0.69) in the dry season (entered in PC2), the R_{eco} was lower, and consequently the NEE

735   increased. The CAI and SCA variables were more expressive in the wet-dry transition season

736   since, in this same season, when CAI and SCA increased, there was a decrease in NAR and

737   RGR. This is because CAI and SCA have opposite relationships with NAR and RGR

738   promoting proportional positive and negative loadings on principal components.

739

740   **4. Discussion**

741   *4.1. Energy balance closure and overview of site environmental conditions*

742   One way to evaluate the performance of the data collected by the eddy covariance

743   system is through the degree of energy balance closure using linear regression (Baldocchi et

744   al., 2000; Wilson et al., 2002). When the result of the ratio between turbulent fluxes and

745   available energy is equal to 1, the balance closure is perfect. However, several studies report

746   a classic lack of energy balance closure (EBC) on different vegetated surfaces (e.g., dry and

747   humid forests, cacti, and agricultural crops) when using the eddy covariance system (Campos

748   et al., 2019; Eshonkulov et al., 2019; Flanagan and Flanagan, 2018). This study found that

749   cactus vegetation under semi-arid conditions displayed an EBC of 0.71; therefore, sensible

750 and latent heat flux underestimated the available energy by up to 29%. A 29% imbalance in

751 the vegetated surface may be a high value; however, it is not inconsistent (Grachev et al.,

752 2020) and may still be satisfactory (Wilson et al., 2002). Our EBC results are in line with the

753 findings of Campos et al. (2019) in Caatinga (mean of 0.7), in the Brazilian semi-arid region,

754 and lower than those reported by Owen et al. (2016) in *Agave* and *Opuntia* cultivation, in

755 Jalisco, semi-arid region of Mexico, with an average closure of 0.9. For example, San-José

756 et al. (2007) reported an energy imbalance of 0.9 for growing pineapple [*Ananas comosus*

757 (L.) Merr.] in Santa Barbara, Venezuela. Still, according to the cited authors, factors such as

758 short and homogeneous cultivation growing in a flat area and the absence of advection help

759 close the balance.

760   In some cases, incorporating variables such as the energy stored in the canopy and

761 energy from photosynthesis favors the improvement of the closure of the surface energy

762 balance (Eshonkulov et al., 2019; Kutikoff et al., 2019). This adjustment can benefit the

763 accuracy of the method, increasing the slope of the line and leaving the intercept close to

764 zero (Campos et al., 2019; Kutikoff et al., 2019) when it is not forced to such a value. We

765 believe that variations in seasons (dry season, dry-wet transition, wet season, and wet-dry

766 transition), such as periods of greater and lesser rainfall events, may have caused an

767 imbalance in the EBC (Chatterjee et al., 2021). Furthermore, we assume that the architecture

768 of the cactus canopy, which does not completely cover the ground due to the cladodes'

769 position and the two harvests carried out, may have caused changes in the turbulent energy

770 exchange.

771   The effects of weather conditions on *Opuntia* cactus cultivation were explored in this

772 study (Figure 3). Our results indicate high air temperature, high VPD, and low relative

773 humidity over the years. Classically, this type of evidence is common in places with a semi-

774 arid climate due to poor environmental conditions (Flanagan and Flanagan, 2018). Although

775 these conditions can cause problems with some species' performance, cacti develop well in

776 hostile and high-temperature conditions (Nobel and De La Barrera, 2003; Ojeda-Pérez et al.,

777 2017; Zutta et al., 2011). During the months with higher rainfall events, there was a

778 significant decrease in wind speed and VPD due to the thermal cooling of the environment

779 caused by the entry of water into the system, consequently contributing to higher soil

780 moisture. Decreased wind speed may cause instability of turbulent fluxes, and thus, this could

781   be a hypothesis for lower energy balance closure (Flanagan and Flanagan, 2018; Teng et al.,

782   2021). Plants can help cool the environment through transpiration and the soil through

783   evaporation when there is high soil moisture and favorable air temperature. Furthermore,

784   Pimienta-Barrios et al. (2000) stated that decreasing air temperature (< 29 ℃) and increasing

785   soil moisture provide improvements in CO_2 uptake for the *Opuntia ficus-indica* cactus. On

786   the other hand, when temperatures are very low, photosynthesis is inhibited in *Opuntia stricta*

787   (Barker et al., 1998; Ojeda-Pérez et al., 2017).

788   The highest input of R_g in the crop was followed by a high PAR over the months, and

789   the reduction in R_g automatically caused a decrease in PAR (Figure 3 and Figure 4). The

790   photosynthetically active radiation intercepted by the canopy helps to understand the

791   photosynthetic processes of plants, although meteorological conditions and the phenological

792   phase of the species can influence this characteristic (Cortázar and Nobel, 1986; Hartzell et

793   al., 2021; Ma et al., 2021). Cortázar and Nobel (1986) reported that PAR limitations can

794   significantly compromise the performance of *Opuntia ficus-indica*. This is because

795   cloudiness decreases the intensity of PAR and causes a reduction in the photosynthetic

796   efficiency of *Opuntia* (Geller and Nobel, 1987; Pimienta-Barrios et al., 2000). In addition,

797   several species of *Opuntia* cacti may undergo changes in morphology due to the anisotropic

798   characteristics of PAR (Drezner, 2020; Geller and Nobel, 1987). In the present study, periods

799   with high R_g and PAR also presented significant rainfall events, which favored the

800   photosynthetic activity of the cactus and light interception. Even with water restriction, cacti

801   maintain their cells turgid because the cladodes compensate for a prolonged period of low

802   water availability in the environment (Pimienta-Barrios et al., 2000; Scalisi et al., 2016).

803

804   *4.2. Changes in the balance of carbon, energy, and radiation*

805   Our results revealed that the climatic conditions of the wet-dry transition season alter

806   the biophysical factors and result in more abrupt changes in the carbon balance (Figure 4 and

807   Figure 6). Due to the lower PAR magnitude during the wet-dry transition season, carbon

808   uptake by plants was lower, limiting CO_2 sequestration (Nobel and Bobich, 2002). Still,

809   cactus cultivation showed strong potential for carbon sequestration, a crucial component of

810   the carbon cycle in arid environments (Figure 5 and Figure 6). These results lead us to believe

811   that PAR is an important modulating indicator of carbon uptake by cacti. Guevara-Escobar

et al. (2021) also observed positive results for NEE at night, despite the ecosystem being composed of cacti. Our results are slightly similar to those found by Guevara-Escobar et al. (2021), although we found higher magnitudes (NEE greater than -10 μmol m^{-2} s^{-1}) around noon. Furthermore, cacti do not shed their leaves (cladodes) like some forest species, and thus the NEE is maintained higher (more negative) for longer periods (Guevara-Escobar et al., 2021).

The release of carbon from R_{eco} was not as high (Figure 4 and Figure 5), with NEE much higher. This carbon loss may be linked to the growth and maintenance of roots, as well as respiration by organisms in the soil (Bilderback et al., 2021; De León-González et al., 2018; Nobel and Bobich, 2002). On the other hand, we found significant R_{eco} during the wet season (Figure 4), which supports that rainfall stimulates the rate of heterotrophic respiration and can often equal or exceed photosynthesis daily or even seasonally (Del Grosso et al., 2018; Flores-Rentería et al., 2023). The cactus has small caliber roots—called "rain roots" that are fast growing and specialized in water absorption (Camelo et al., 2021; Hassan et al., 2019); we believe that they may have caused greater respiration during the period with higher soil moisture. Snyman (2006) reported that cactus rain roots are short-lived in plants, and their decomposition contributes to microbial activity and increased soil respiration. Studying cacti of the genus *Opuntia*, Dubeux Junior et al. (2013) found that at a density of 20,000 plants per ha, a cactus plant produces 136 g of root biomass, which contributes to the heterotrophic respiration fraction and increases ecosystem respiration. Clearly, on days without rainfall, seasonal daytime carbon uptake exceeds respiration (Del Grosso et al., 2018; Flores-Rentería et al., 2023), and even with low rainfall events (~2 mm), microbial respiration in a semi-arid environment responds quickly (Huxman et al., 2004). GPP may decrease during the dry season (Flores-Rentería et al., 2023); however, in the present study, R_{eco} was more sensitive than GPP at the same time (Figure 4 and Figure 6). The expressive behavior of the cactus sink can be explained because it is a perennial plant, and, together with the CAM pathway and the presence of humidity in the environment, its carbon absorption is maximized during the seasons, whether in dry or wet periods.

Solar radiation makes an important contribution to stimulating photosynthesis for plants, and by carrying out photosynthesis, ecosystems' carbon and water exchange processes are driven (Flanagan and Flanagan, 2018; Nobel, 1980). On the other hand, inadequate water

843   and solar radiation availability can negatively influence plants' photosynthetic efficiency and

844   cause photochemical damage (Han et al., 2020; Jardim et al., 2021a). In this study, energy

845   and radiation balances were affected by environmental conditions and the time of year.

846   According to Gao et al. (2022), the short upward radiation is mainly controlled by the short

847   downward radiation and is influenced by ground cover. Factors such as surface temperatures

848   control the daily and seasonal variations of the long descending and ascending radiation,

849   influenced mainly by air temperature and humidity. Here, we found that lower availability of

850   R_g and R_n influenced the carbon balance and decreased G, SR_u, LR_u and LR_d. Wettest seasons

851   promoted higher LE and lower H, while transition seasons, as expected, presented

852   intermediate fluxes to extremely dry and wet seasons. In the rainy period, LE increases

853   rapidly due to the availability of water and energy, which increases ET and water vapor

854   exchange (J. Ma et al., 2022; Kuiyue Zhang et al., 2022). Although high LE values can be

855   reached in rainy periods, the cactus still uses a substantial part of the net radiation for sensible

856   heat flux (Unland et al., 1996).

857   During the two evaluated cycles, the cactus vegetation showed little variation in the

858   radiation and energy budgets. In the energy balance, the variables most responsive to rainfall,

859   such as latent and soil heat fluxes, showed greater discrepancies (Table 2). In terms of

860   sensible heat flux, despite the expressive cumulative difference in rainfall, the mean

861   difference in sensible heat flux (0.8 MJ m^{-2} day^{-1}) for the two cropping cycles (Table 2) may

862   be due to the greater use of net radiation in H (Unland et al., 1996). Regarding the temporal

863   variability of the carbon balance, we found greater carbon accumulations during the cactus's

864   first cycle because the plants had higher productivity. Even in the first cycle, ET was higher

865   due to higher rainfall (2,075 mm) and higher GPP (6.8 g C m^{-2} day^{-1}). Although biological

866   and abiotic factors may influence plant performance (Jardim et al., 2021a; Roeber et al.,

867   2021), our findings clarify that the *Opuntia* cactus had a high carbon sink capacity throughout

868   the experimental period. This clearly agrees with the capacity for efficient use of water and

869   carbon that CAM plants possess (H. Ma et al., 2022; Pikart et al., 2018).

870

871   *4.3. Flux partitioning and efficiency in the use of biophysical resources in cactus cultivation*

872   In the present study, we show that the components of radiation, energy balances, and

873   PAR can be affected by environmental conditions and plant characteristics (Table 3). This

occurs due to the interaction of the balance components and the surface. We believe that the lower responses of the SR_u/R_g ratio during the wet-dry transition season may be related to the higher CAI and SCA (Table 4) since the short upward radiation is influenced by the land cover (Gao et al., 2022) due to greater absorption of radiation by the canopy (Braghiere et al., 2020). In our cactus plants, no phenological phase changes were observed, with only the vegetative phase nor cladode senescence, which justifies the high similarity of the PAR/R_g ratio results (Baldocchi et al., 1984). In addition, PAR/R_g measurements were always performed at the same depth of the canopy (i.e., at the top of the canopy) since, as one approaches the ground, the PAR/R_g ratio may decrease (Baldocchi et al., 1984). Due to the plants being more developed during the wet season and wet-dry transition, as a result of the higher CAI and SCA, this development was crucial for better intercepted PAR fraction (*f*IPAR) responses. In the same period, the plants had a higher dry biomass yield, which shows the close relationship of *f*IPAR with the photosynthetic activity of plants (Li et al., 2021; Nobel, 1980).

When the environmental deficit is high, plants can decrease the LE/R_n ratio through physiological controls, reducing water loss to the atmosphere (Yue et al., 2019). On the other hand, the LE reduction caused an increase in H, with 78% of the R_n being converted into H during the dry season. According to Campos et al. (2019) and Costa et al. (2022), in the dry forest (Caatinga) in the Brazilian semi-arid region, approximately 70% of R_n was converted into H, and less than 5% was converted into LE during the dry season, and these results are consistent with our study. Similar to dry forests, environments with cacti are marked by high fluxes of sensible heat in relation to latent heat fluxes; this was also observed by Pierini et al. (2014) in a landscape of cacti (*Opuntia spinisior* and *Opuntia engelmannii*) in the semi-arid region of Tucson, Arizona. Despite being influenced by the H, the G/R_n ratio was equal to or less than 4%, and this ratio may change due to rainfall events and radiation incidence in cactus cultivation (Consoli et al., 2013; Flanagan and Flanagan, 2018). Flanagan and Flanagan (2018) found a mean of 2.0 MJ m^{-2} day^{-1} for G, explaining the low flux values of this variable.

Our results indicate a strong relationship between environmental conditions in response to growth, nutrient, and carbon stocks in *Opuntia* cactus plants (Table 4). Despite the expressive adaptability of *Opuntia* cactus, it has a slow relative growth rate (Luo and

905   Nobel, 1993; Martínez-Berdeja and Valverde, 2008). Although slow but not low, the rates

906   that express plant growth and net carbon assimilation have greater relevance in periods with

907   lower humidity. A likely explanation is that because these plants are adapted to conditions

908   with less rainfall, their response is less expressive in high rainfall (Jardim et al., 2021b).

909   Regarding stored nutrients and carbon in the cladodes, cacti have a significant accumulation

910   of calcium, potassium, and magnesium, being important forage foods (Garcia et al., 2021;

911   Mayer and Cushman, 2019). Potassium, for example, helps regulate the osmotic potential of

912   cells, decreasing water loss and consequently increasing WUE and photochemistry (Mostofa

913   et al., 2022). This supports our satisfactory WUE and RUE results, with the RUE being more

914   sensitive to conditions with lower water availability. In addition, cacti can store carbon very

915   similar to forest ecosystems (De León-González et al., 2018), which maximizes their

916   exploitation potential in areas with low resource availability.

917

918   *4.4. Relations between variables and environment*

919   The results presented in Figure 9 highlighted the distinct associations between

920   environmental and plant variables under the four seasons. Clearly, the factor loadings in the

921   PCA revealed the most important variables and their grouping in relation to environmental

922   water availability (Mounir et al., 2020). Although the five principal components were

923   significant, the first two principal components were fundamental for the best visualization of

924   the biplot and explained 71.57% of the data variation. Using PCA, Juhász et al. (2020) and

925   Mounir et al. (2020) reported dispersions between seasons and the analyzed plant variables.

926   There is a correlation between the efficiency of the use of water, nutrients, and carbon during

927   the dry season due to the CAM pathway the plants have. In addition to their high WUE and

928   CUE values, the nutrients boost the osmotic effect of their cells, making the best use even

929   easier of these resources and, therefore, the best use of carbon as well (H. Ma et al., 2022;

930   Nobel and Bobich, 2002). The cladode and plant biomass variables were included in PC1, in

931   agreement with the findings of Jardim et al. (2020) and Jardim et al. (2021a), using cactus

932   species of the genus *Opuntia* and *Nopalea*. A high CAI value in cactus plants is an important

933   indicator of the high biomass yield of the crop (Dubeux Jr. et al., 2006; Jardim et al., 2021a,

934   2020). In the wet seasons, the variables (biplot vectors) R_{eco} and NEE point in the same

935   direction and with parallel vectors (Figure 9); this shows that in the wet period, there was

greater ecosystem respiration (positive) and lower (less negative) NEE. In this way, the cultivation of *Opuntia* cactus proved to be an important atmospheric CO_2 sink during the dry season, with higher (more negative) NEE results, a behavior also observed by Mendes et al. (2020) in dry forests (Caatinga). Bilderback et al. (2021) also reported higher carbon losses in an environment with cacti (e.g., *Opuntia chlorotica* and *Cylindropuntia acanthocarpa*) in the rainy season in the Sonoran Desert of Arizona. In addition, research shows that moisture and radiation conditions can change the behavior of the energy balance and carbon flux in a cactus ecosystem (Camelo et al., 2021; Flanagan and Flanagan, 2018; Guevara-Escobar et al., 2021; Jardim et al., 2022).

5. Conclusions

We analyzed eddy flux covariance data over three years (2019–2021) in a cactus crop, observing the behavior of carbon, energy, and radiation balance. This work shows that on a surface cultivated with the cactus *Opuntia stricta*, the energy balance closure using data from the eddy covariance system reached satisfactory results (71%). We found that the cactus is a potential carbon sink throughout the year, with net ecosystem CO_2 exchange cumulative in three years of $-4,517$ g C m^{-2}; thus, it can be an important alternative for revitalizing degraded areas of the semi-arid region. Regardless of the season and adverse weather conditions, the cactus persisted with net CO_2 sequestration, being an important carbon sink. The cumulative (2019–2021) gross primary production and ecosystem respiration averaged 2352 g C m^{-2} and 846 g C m^{-2}, respectively. In addition, the rainfall, despite having increased the release of CO_2 from the environment, did not transform the semi-arid ecosystem of cacti into a source of carbon. Meteorological conditions act as the main drivers of physiological adjustments and plant growth. Our analyses revealed that the latent and sensible heat fluxes had marked seasonality, with most of the net radiation energy used in the sensible heat flux (58% ratio), with an annual average of 5.8 MJ m^{-2} day^{-1}. We found a substantial amount of nutrients in the cactus biomass and high efficiency in the use of water and nutrients during the dry seasons. Particularly, the findings presented here bring news in studies with CAM plants and can help in the better use of agricultural land or places where agricultural and forest species may have a low capacity to develop and obtain a better balance of terrestrial carbon.

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