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Interannual Variation in Gas Exchange and Leaf Anatomy in *Cenostigma pyramidale* Is Exacerbated through El Niño and La Niña Climate Events

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Abstract: This study sheds light on the remarkable physiological adaptations that the *Cenostigma pyramidale* makes, particularly during periods of extreme water scarcity, and their remarkable ability to rebound when a new rainy season arrives. *C. pyramidale* employs a survival strategy to mitigate the adverse effects of water shortage and then endures challenging environmental conditions and sustaining vital functions. Previously, this species was classified as deciduous since it retained at least 40% of its leaves to sustain basal gas exchange rates. The discrepancy in classification arises from differences in study methodologies, with this research being conducted in the field under natural conditions. This study demonstrates a negative correlation between rainfall and specific leaf area (SLA), highlighting that plants with smaller SLA are more drought-tolerant. Changes in leaf anatomy, including an increase in palisade parenchyma and reduction in spongy tissue, serve as adaptive strategies to enhance photosynthesis under water stress conditions. Hydraulic conductance plays a crucial role in plant adaptation to water scarcity. An intricate interplay between leaf anatomy and hydraulic conductance is observed, with adjustments in xylem characteristics influencing leaf gas exchange. The phenotypic plasticity is high in *C. pyramidale*, demonstrating the species' ability to adapt to changing environmental conditions. In summary, this study illuminates the multifaceted strategies employed by plants to cope with water scarcity, from leaf shedding to anatomical and physiological adaptations, highlighting the resilience of native species in arid environments. These findings offer valuable insights into plant responses to environmental stress and their ability to thrive in challenging conditions.

Keywords: gas exchange; native species; plant anatomy; phenotypic plasticity; global climatic change



Citation: Pompelli, M.F.; Jarma-Orozco, A.; Jaraba-Navas, J.d.D.; Pineda-Rodriguez, Y.Y.; Rodríguez-Páez, L.A. Interannual Variation in Gas Exchange and Leaf Anatomy in *Cenostigma pyramidale* Is Exacerbated through El Niño and La Niña Climate Events. *Forests* **2024**, *15*, 346. <https://doi.org/10.3390/f15020346>

Received: 9 December 2023

Revised: 10 January 2024

Accepted: 25 January 2024

Published: 10 February 2024



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1. Introduction

Industrial emissions of greenhouse gases contribute to global warming. As the Earth's temperature continues to rise, we witness shifts in climate patterns, including heightened temperature extremes and significant changes in both the timing and geographic distribution of rainfall, ultimately leading to prolonged periods of drought. Projections indicate a growing occurrence of temporary spikes in temperature surpassing the typical physiological limits and more frequent, intense drought periods in the future [1]. The levels of climate-related risk frequently escalate in tandem with rising temperatures, and these risks are occasionally intertwined with various facets of climate change. Today, we are experiencing a pivotal example of the simultaneous occurrence of a substantial reduction in rainfall, along with isolated episodes of torrential rainfall in specific regions [2,3]. This confluence of events can have profound implications for the broader climate landscape, exacerbating vulnerabilities and challenges associated with changing weather patterns and their associated impacts. With global climate change, it becomes increasingly imperative to gain deeper insights into the alterations in both plant physiological and morphological

characteristics. This knowledge is not only pivotal for the conservation of dry tropical forests but also for addressing the broader environmental concerns we face today [4]. In this context, El Niño is a climate phenomenon characterized by the periodic warming of ocean waters in the central and eastern tropical Pacific, leading to significant weather disruptions worldwide. As our planet's temperatures persist in their upward trajectory, the repercussions are becoming ever more conspicuous and all-encompassing [5,6]. With the exacerbation of global climate changes, phenomena like El Niño and La Niña may become more frequent and affect larger geographic areas [7]. Climate scenarios suggest that these global climate changes will disproportionately harm arid and semiarid regions, resulting in prolonged dry periods and posing significant risks to biodiversity [5]. The significant increase in CO₂ emissions poses a grave threat to food and human security, amplifying the risk of severe, pervasive, and irreversible impacts on both ecosystems and people. This underscores the urgent need to address the challenges of global climate change, which can disrupt the delicate balance of our planet's well-being [4].

The interplay between drought conditions and intense solar radiation poses a substantial challenge to the efficiency of net photosynthesis (P_N) and the potential risk of leaf overheating, particularly when decreased transpiration restricts the leaf's ability to cool itself due to a scarcity of water [8,9]. The drought stress is intricate, involving a spectrum of changes in their morphology, physiology, as well as primary and secondary metabolic pathways [10]. In response to drought stress, plants activate intricate defense mechanisms to shield themselves against oxidative stress, which encompasses the loss of turgor, osmotic stress, and the closure of stomata to curtail water loss. Water stress also hampers photosynthesis, causing alterations in chlorophyll concentrations and causing damage to the photosynthetic apparatus [11]. Additionally, a common occurrence is the reduction in enzyme activity within the Calvin Cycle [12–14]. In tropical environments where water stress is prevalent, plants undergo significant adaptations. Their struggle for survival manifests through several pivotal adjustments in their photosynthetic processes. An initial indicator of stress is the disruption of stomatal regulation over leaf gas exchange, resulting in a diminished efficiency in carbon dioxide uptake and inhibition of photosynthesis [11,15–17]. The constraint on P_N due to water stress can imperil the plant, especially under conditions of excessive irradiation. Failure to safely dissipate this excess energy can result in the over-reduction of reaction centers and heightened production of reactive oxygen species (ROS) within the chloroplasts, ultimately causing harm to photosystem (PS)II [18]. Consequently, the damage to photosynthetic membranes, crucial for the conversion of light energy into chemical energy, becomes an unfortunate outcome of the plant's struggle for survival [19].

The correlation between rising temperatures and the risks linked to climate change emphasizes the pressing need for a comprehensive approach to tackle this issue. There is a consensus in the scientific community that plant species thriving in arid and semiarid environments have evolved specific adaptations to endure periods of water scarcity [20,21]. When faced with acute water shortages, regardless of whether they are exacerbated by increasing atmospheric temperatures or not, these plants often employ survival strategies. One such tactic involves shedding leaves as a means to reduce water loss to the atmosphere, enabling them to conserve precious moisture resources [22]. In general, gas exchange is intricately governed by a spectrum of factors, encompassing both external environmental conditions and internal physiological aspects within the plant [23]. During episodes of water stress, a typical response involves reduced water transport from the roots to the leaves, which consequently prompts a reduction in stomatal opening for CO₂ uptake [15,24–27]. Given that CO₂ serves as the primary substrate for photosynthesis, this diminished uptake often translates into a concurrent decrease in photosynthetic rates. Nevertheless, it's important to note that other contributing factors may exist, some of which could exert an equal or even greater influence on the regulation of photosynthesis rates. A simple rise in stomatal CO₂ absorption doesn't automatically lead to an increase in gas exchange. This is due to the fact that CO₂ must traverse several physical barriers before it can reach the RuBisCo carboxylation site [28]. Nevertheless, various other factors can influence

photosynthesis. In addition to physiological and biochemical responses, these plants have developed mechanisms to adapt to water stress through alterations in the anatomical structure of their leaves and roots, as well as modifications in specific characteristics [29,30]. Leaf architecture plays a crucial role in facilitating CO₂ exchange within the mesophyll, making the study of plant leaf anatomy and its xylem vessels particularly intriguing. As the plant responds to decreased osmotic potential, it tends to curtail its water flux, impacting all metabolic processes, not limited to photosynthesis alone [27].

As sessile organisms, plants face a wide range of abiotic stresses, with water stress being a significant condition affecting their growth, development, and productivity, particularly in arid and semiarid regions [27]. Caatinga has a very high plant diversity and rate of endemism but is also a region that is quite degraded because of the unsustainable use of its natural resources; human occupation is followed by abandonment and subsequent natural regeneration of secondary forests [31]. *Cenostigma pyramidale* is considered one of the most frequent plant species in the Caatinga [32]. In this scenario, physiological, biochemical, and morphological attributes play an important role in abiotic and biotic responses to environmental conditions [32]. Moreover, plant sensitivity to adverse environmental conditions is majorly dependent on the severity of the stress as well as plant species, genotype, and developmental stage. Plant tolerance to periodic water deficit is expected to be of increasing importance as climate change intensifies inter- and intra-annual rainfall extremes [33–35]. The responses of native plants to extreme climatic events, such as rising temperatures coupled with reduced rainfall, remain poorly understood [36], making their survival in one of the harshest environments truly remarkable [37]. Substantial efforts have been made to better comprehend the drought tolerance strategies of the trees in Caatinga [12,22,31,37–40]. In this study, we evaluated the phenotypic plasticity in the physiological and anatomical characteristics of individuals of the *Cenostigma pyramidale*, a Fabaceae species. We hypothesize that *C. pyramidale* displays increased resilience when subjected to recurring water shortages. In this sense, this work can contribute to the understanding of the plant physiology of a symbolic species of the Brazilian Caatinga since the analyses were carried out over two years, encompassing a very dry year and another year with rainfall distributed according to the historical average and standard for those evaluated months.

2. Materials and Methods

2.1. Plant Species, Site Description, and Experimental Design

Cenostigma pyramidale (Tul.) Gagnon & G.P. Lewis (Fabaceae) is a Caatinga's symbol that predominates in all landscapes of the ecosystem. This tree is semideciduous and relevant as a pioneer species during the ecosystem succession. *C. pyramidale*, popularly known as “Catingueira,” is a resilient tree thriving in the Caatinga, a challenging semiarid environment. Recognizable by its distinctive thorny branches, this deciduous species acts as vital in the ecological rejuvenation of the region. Its adaptability and cultural significance make it a key emblem of the Caatinga landscape. In this study, we evaluate the effects of climatic changes on the morphophysiological characteristics of this species over two distinct years. For this purpose, we selected ten adult trees (approximately 25 years of age) in the reproductive phase ranging from 2.5 to 4.0 m in height. All the plants were identified by a taxonomist and deposited in a plant collection at the Agronomic Institute of Pernambuco Herbarium (registered by IPA-88.494).

The Caatinga, a Brazilian semiarid forest covering an area of 862,818 km², constitutes approximately 10.1% of the country's landmass [41] (Figure 1). Despite being one of the most biodiverse dry forests globally [42], it remains one of the least studied and protected ecosystems within Brazil [31]. Within the Caatinga, the annual rainy season typically extends for 4 to 6 months, marked by sporadic and meager rainfall patterns (Figure 2) with precipitation ranges around 250 and 700 mm per year, concentrated in 4 months, a few years with precipitation more than 1000 mm [43]. These conditions result in high evaporation rates and limited water-holding capacity within the soil. Consequently, Caatinga trees must

continually adapt to environmental challenges, evolving diverse survival tactics to vie for the scarce water supply [37].

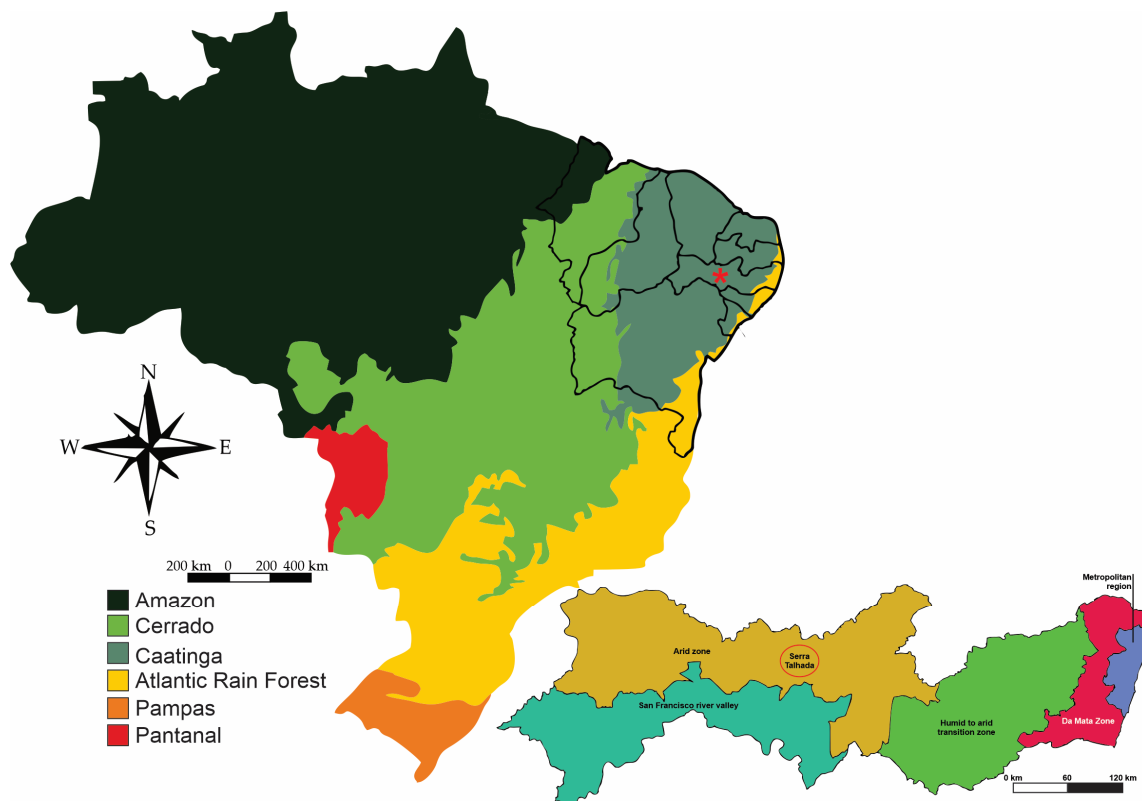


Figure 1. Brazilian ecosystems highlight the Brazilian Northeast, where the Caatinga ecosystem is predominant. The asterisk (*) denotes the Pernambuco state, which is represented in the base of the figure to show Serra Talhada city, where the experiments were conducted.

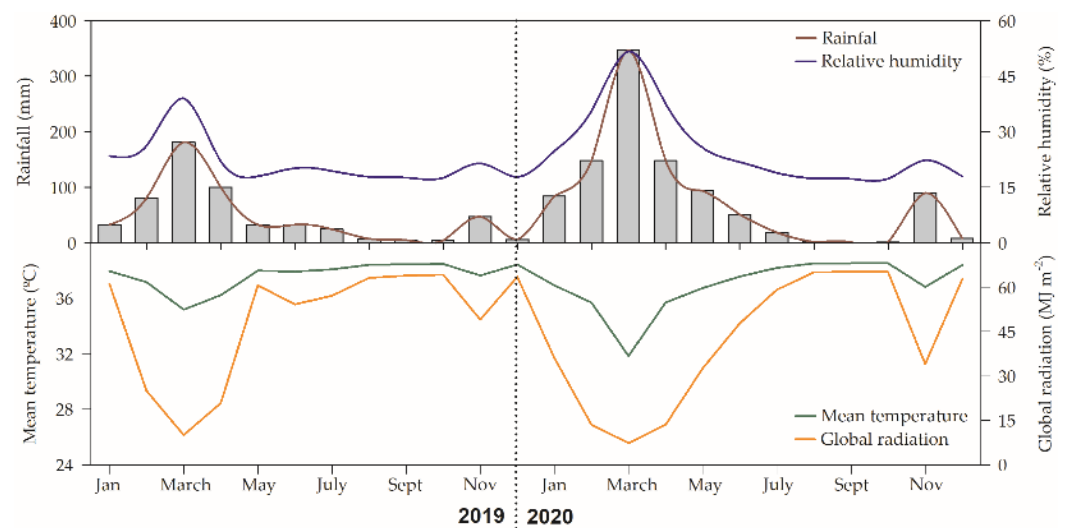


Figure 2. Rainfall (columns), relative humidity (blue line), mean temperature (green line), and global radiation (yellow line) were measured along the experiment in a restructuring Brazilian Atlantic Forest fragment. Source: INMET [43], free access.

As shown in Figure 2, the climate conditions in 2020 were very distinct from 2019 [43]. Consequently, in 2019, we experienced a characteristic dry year, with a tendency to a rainy season from February to April, with a higher rainfall in March (181.2 mm). In 2020, we verified a median rainfall as compared to expected rainfall from this area, with a rainy season

extending from January to May, with the peak rainfall occurring in March 2020 (347.3 mm). Similarly, the dry season spanned from June to December 2020, with a tendency for the month to be less dry in November (89.6 mm) (Figure 2). These patterns were consistent not only in terms of precipitation but also with respect to global radiation and relative humidity. The maximum and minimum levels of global radiation were recorded in September 2020 ($65.2 \text{ MJ m}^{-2} \text{ day}^{-1}$) and March 2020 ($7.4 \text{ MJ m}^{-2} \text{ day}^{-1}$). Air humidity ranged from 17.3% (August 2020) to 51.7% (March 2020), reflecting the variations in moisture content in the atmosphere. Meanwhile, air temperatures fluctuated between 31.8°C (March 2020) and 38.5°C (August 2020), representing the seasonal temperature changes over the year.

The experiments were conducted in a completely randomized design in an open field environment, specifically within a Caatinga natural fragment in Serra Talhada ($7^\circ 58' 57'' \text{ S}$; $38^\circ 18' 16'' \text{ W}$; 418 m a.s.l.), Pernambuco, Brazil (Figure 1). We selected a total of 10 *Cenostigma pyramidale* plants for our investigation. All of them were measured between 3 and 5 m in height, with breast diameter of 160 mm and plant age of at least 20 years. We collected data for the rainy (March) and the dry (August) seasons in both 2019 and 2020. In all experiments, to guarantee that the sampled leaves were developed in the rainy and dry seasons, monthly leaf primordia were marked with non-obstructive adhesive tape so that their leaf development could be observed and guaranteed between one collection and another.

2.2. Leaf Area and Specific Leaf Area

In January 2019, leaves primordia were marked with non-obtrusive adhesive tape in order to monitor the development of the leaves until its complete expansion. With each collection carried out, new leaf primordia were marked with adhesive tape to monitor their development. This procedure is necessary to ensure that the leaf that will be collected later was necessarily expanded during the evaluation period and to guarantee that the leaf that will be collected was not already on the mother plant before the treatments were imposed. Thus, in March and August 2019 and in March and August 2020, completely expanded leaves were collected from the plants after the gas exchange experiments described in topic 2.3 were completed. These leaves were inserted into zip-lock plastic packaging and transported under refrigeration to the laboratory. The leaves were digitalized using a scanner (HP Smart Suite, $1200 \times 1200 \text{ dpi}$; Hewlett-Packard Company, Palo Alto, CA, USA), and the images were processed using Image-Pro[®] Plus software (version 4.5, Media Cybernetics, Silver Spring, MD, USA). Then, five fragments 1 cm in diameter were collected, wrapped in an aluminum foil envelope, and placed in an oven at 70°C for 72 h, when their dry mass was measured on an analytical balance (Sartorius Analytical Balance mod. ENTRIS224-1S, Bradford, MA, USA; accurate to 0.1 mg). The specific leaf area was obtained by the ratio of the dry mass to the leaf area of each leaf fragment, obtained by Equation (1):

$$SLA = \frac{DW}{\pi \times r^2} \quad (1)$$

where DW is the dry weight of the leaf fragments, π is 3.14159, and r is the ray of the circumference, in this case 0.5 cm.

2.3. Predawn and Noon Leaf Water Potential (Ψ_w)

To assess leaf water status, we selected and collected one fully expanded leaf (i.e., from the third node from the apex) per tree. We measured the leaf water potential (Ψ_w) at predawn (5:00 a.m.) and noon (12:00 p.m.) with a Scholander-type pressure chamber [44].

2.4. Gas Exchange

In March and August, for both 2019 and 2020, leaf gas exchange was determined on the 3rd attached fully expanded leaf from the apex, using a portable open-flow infrared gas analyzer (LI-6400XT; LI-COR Inc., Lincoln, NE, USA). The net photosynthesis (P_N , $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$), stomatal conductance (g_s , $\text{mol H}_2\text{O g}^{-1} \text{ s}^{-1}$), transpiration (E ,

mol H₂O g^{−1} s^{−1}), internal-to-ambient CO₂ concentration ratio, leaf temperature (T_{leaf}, °C), and vapor pressure deficit (VPD, kPa) were obtained on 20-year-old plants as described by Pinho-Pessoa et al. [36]. All measurements were conducted from 6 a.m. to 6 p.m. (GMT-3) under a cloudless sky and with the leaf irradiance of saturation of 1200 μmol m^{−2} s^{−1} (as previously tested by light curves versus P_N; [36]), fixed CO₂ concentration in 390 μmol mol^{−1} and airflow of 400 μmol s^{−1} [25]. Diurnal integrated CO₂ assimilation (integrated P_N) was obtained by integrating all measurements of P_N measured throughout the day, as previously described in Mendes et al. [22]. With gas exchange parameters, we made a correlation between P_N and g_s, P_N and E, and P_N and internal CO₂ concentration (C_i). WUE_i was obtained by Equation (2).

$$WUE_i = \frac{P_N (\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1})}{g_s (\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1})} \quad (2)$$

Also, VPD was correlated with P_N, g_s, and E.

2.5. Leaf Anatomy

Leaf fragments 5 cm² of the 3rd attached fully expanded leaf from the apex (the same used in the previous topic) were sampled at the same time as described above. In each plant, two leaf fragments were collected, promptly immersed in FAA_{50%} for 48 h, and then stored in 70% (v/v) ethanol until analysis. Leaf samples were dehydrated in an ethylic series and embedded in plastic resin (HistoResin Leica Microsystems Nussloch, Heidelberg, Germany, part number 7592). Following this, all samples were processed as described in detail in Mendes et al. [40]. For each sample, ten images were captured by a digital camera (Mikrosysteme Vertrieb GmbH, model ICC50 HD; Wetzlar, Germany) interfaced with a computer. To estimate the potential hydraulic conductivity (K_p), the principles of the Hagen–Poiseuille equation were implemented using Equation (1).

$$Kp = \left(\frac{\pi p_w}{128 \eta} \right) \times VD \times D_h^4 \quad (3)$$

where K_p is the potential specific stem conductivity, h is the viscosity of water at 20 °C (1.002 × 10^{−3} Pa), p_w is the density of water at 20 °C (998.2 kg m^{−3}), VD is the vessel density, and D_h is the hydraulically weighted vessel diameter (in m). Since the vessels were not exactly circular, the diameter of each vessel was calculated as the mean of the minimum and maximum diameters. The average D_h was calculated as well using the methodology described in Sterck et al. [45]. As recommended by Scholz et al. [46], we measured at least 50 vessels per photomicrograph, resulting in 500 vessels (10 repetitions) per treatment.

2.6. Phenotypic Plasticity

The phenotypic plasticity ranges from 0 (any plasticity) to 1 (full plasticity) was calculated as the difference between the average maximum and minimum measurements for each sample divided by the maximum value [47] for all physiological and anatomical features.

2.7. Experimental Design and Statistical Analyses

The experiments were conducted in a completely randomized block design and ten replicates. All the data were analyzed by Two-way ANOVA, and means were compared using an SNK test (*p* < 0.05) by Statistic version 14.0 (StatSoft, Tulsa, OK, USA). The principal component analysis was estimated after a multivariate analysis for all analyzed features in Minitab 18.1 (Minitab, Inc., Chicago, IL, USA). Heat maps were used to compare the mean of each treatment, using the control (March, the rainiest month) as a reference. After the log₂ transformation, the false color method was used, including a color scale.

3. Results

3.1. Leaf Area (LA) and Specific Leaf Area (SLA)

Tables 1 and 2 show that the specific leaf area (SLA) of *C. pyramidale* varies widely with the levels of rainfall received during its development, with a positive interaction for both year and seasonality (Table 1). Furthermore, we also show that the leaf area increased in the same proportion as rainfall increases, with leaves 40% and 67% larger in the rainy months (March, both in 2019 and 2020, respectively) compared to the driest months (August). The SLA ranges from $11.37 \text{ cm}^2 \text{ g}^{-1}$ to $15.07 \text{ cm}^2 \text{ g}^{-1}$, while leaf area ranges from 1.59 cm^2 to 2.43 cm^2 (Table 2).

Table 1. Summary of ANOVA for specific leaf area (SLA). Data were determined in two consecutive years (2019 and 2020) and two different months (March and August) in accordance with rainfall gradient. Degrees of freedom residuals (DF), sum of squares (SS), mean squares (MS), F value (F), and *p* value (*p*).

Source of Variation	DF	SS	MS	F	<i>p</i>
Year	1	28.415	28.415	219.490	<0.0001
Month	1	13.831	13.831	106.835	<0.0001
Year × Month	1	6.030	6.030	46.575	<0.0001
Residual	20	2.589	0.129		
Total	23	50.865	2.212		

Table 2. Leaf area and specific leaf area (SLA) were determined in two consecutive years (2019 and 2020) and two different months (March and August) in accordance with rainfall gradient, as the ANOVA table showed in Table 1. Each value denotes means ($\pm$ SD). The values followed by different small case letters denote significant differences between seasons in the same year, and the means followed by uppercase letters denote significant differences between years in the same season. ($p \leq 0.001$).

Year/Month	LA (cm^2)	SLA (SE) ($\text{cm}^2 \text{ g}^{-1}$)
March 2019	2.435 ± 0.014 Ba	15.068 ± 0.127 Aa
August 2019	1.741 ± 0.029 Ab	14.552 ± 0.056 Ab
March 2020	2.656 ± 0.021 Aa	13.894 ± 0.234 Ba
August 2020	1.588 ± 0.043 Bb	11.373 ± 0.110 Bb

Knowing that SLA varies widely seasonally, we expect to find more photosynthetic tissues in thicker leaves, that is, in leaves with lower SLA (in the dry season). Therefore, presenting gas exchange data per unit of leaf area would not be the best option. So, in this study, we will present gas exchange data on a gram basis of leaf tissue and not by metric area.

3.2. Water Potential

The predawn Ψ_w measurements from 2019 revealed significant plant water stress, with readings of -5.6 MPa and -4.2 MPa in March and August, respectively (Figure 3). In 2020, these values saw a notable improvement, with predawn Ψ_w readings being 2.6 and 1.4 times higher for the same months in 2019. Interestingly, while predawn Ψ_w values exhibited this substantial shift between the two years, the midday Ψ_w values remained relatively consistent, showing less variability in both 2019 and 2020 (Figure 3).

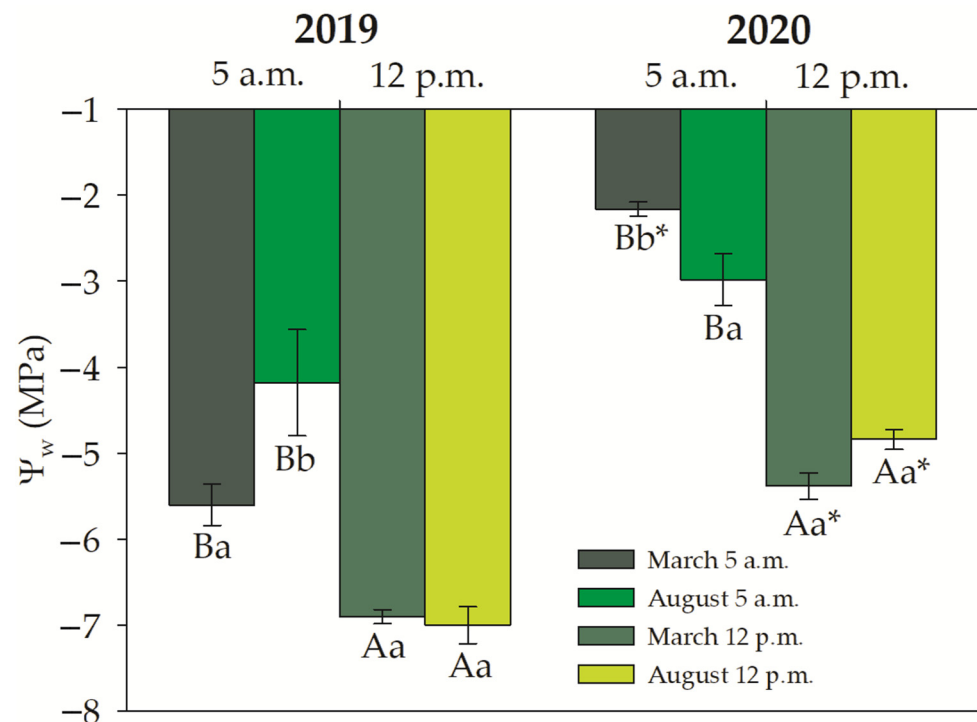


Figure 3. Water potential measured in *Cenostigma pyramidale* grown in field conditions in the driest year (2019) and a normally rain year (2020) in both seasonal conditions (rainy, March and dry, August). The measurements were made at predawn (5 a.m.) or at midday (12 p.m.). Means followed by small case letters denote statistical significance between seasons at the same time (5 a.m. or 12 p.m.), means followed by uppercase letters denote statistical significance between time and the same season (rainy and dry months) and the same year, and asterisks (*) denotes statistical difference between years in the same months and time. All values denote media $\pm$ SD. $n = 10$.

3.3. Gas Exchanges

In both 2019 and 2020, all gas exchange parameters fluctuated throughout the day. Net photosynthesis (P_N), stomatal conductance (g_s), and transpiration (E) start the day with higher values, and these were reduced throughout the day. In 2019, this pattern was very soft for P_N , while for g_s and E , the daily variation is not statistically different (Figure 4). From another perspective, in 2020, for both the rainy (March) and the dry (August) seasons the P_N (at 6 a.m.) is measured at $213.8 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ (Figure 4C) and $122.2 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ (Figure 4D) and fall down to $44.2 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ (-79.3% ; Figure 4C) and $40.6 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ (-66.8% ; Figure 4D) at 6 p.m. Moreover, when the comparisons are made between seasons for both years, we show that the P_N registered at 10 a.m. during the rainy season was 10.2-fold higher in 2020 than those values recorded in 2019. During the dry season, the P_N at 10 a.m. 2020 was 6-fold higher in 2020 than those values recorded in 2019.

The daily fluctuations of g_s and E were similar to P_N . For g_s , the values ranged from $151.5 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ (2019 March, 6 a.m.) to $90 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ (2019 March, 6 p.m.). Measurements taken in August 2019, March 2020 and August 2020 show that g_s ranged respectively from $95.6 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ to $59.0 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ (-38.3%), from $2069.3 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ to $300.7 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ (-85.5%), and from $854.3 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ to $213.8 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ (-75.0%). For the same seasons, E ranged from $2.8 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ to $2.2 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ (-23%), from $1.5 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ to $0.6 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ (-58.1%), from $45.2 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ to $7.1 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ (-84.2%), and from $20.9 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ to $7.4 \text{ mmol H}_2\text{O g}^{-1} \text{ s}^{-1}$ (-64.8%). At 10 a.m., during March and August 2020, it measured 7- and 6.4-fold higher g_s

than in 2019, while E registered 26.6- and 22.0-fold higher in 2020 when compared to the 2019 values (Figure 4).

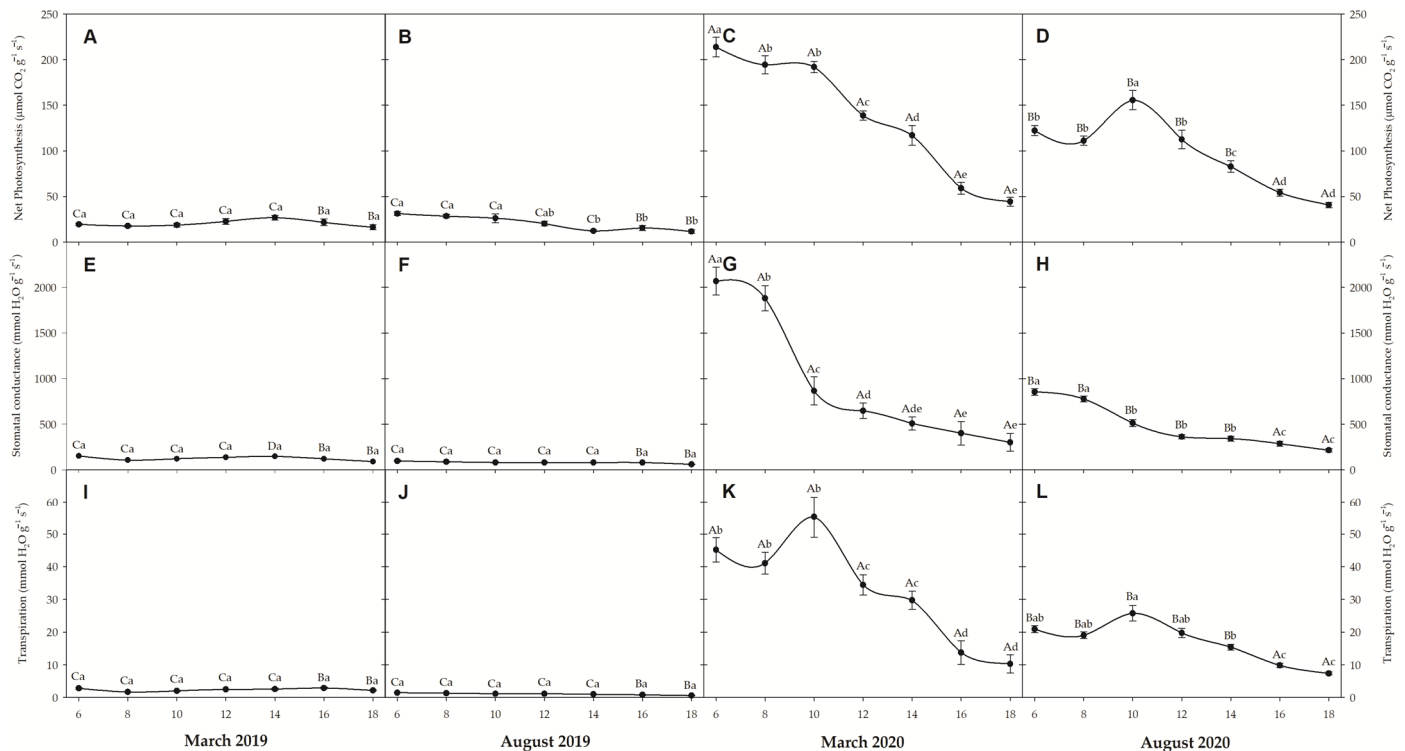


Figure 4. Net photosynthesis (A–D), stomatal conductance (E–H), and transpiration (I–L) were measured in March 2019 (A,E,I), August 2019 (B,F,J), March 2020 (C,G,K), and August 2020 (D,H,L) in *Cenostigma pyramidale* grown in field conditions in the driest year (2019) and a normal rain year (2020) in both seasonal condition (rainy, March and dry, August). Means followed by small case letters denote statistical significance between months, regardless of year, and means followed by uppercase letters denote statistical significance between years in the same month. All values denote media $\pm$ SD. n = 10.

As described above, the comparisons of net photosynthesis are time-dependent. Thus, when comparing the daily integrated P_N values between seasons and years (Figure 5), the differences are still more evident because those values were 6.6-fold higher in March 2020 as compared to March 2019 or 4.9-fold in August 2020 when compared to August 2019 (Figure 5). Between seasons, within the same year, we verified a significant effect only in 2020, when the daily integrated P_N values were 37.1% larger in March than in August.

The correlations (Supplementary data file) of both g_s and E could be modulated P_N since correlations between P_N and g_s or P_N and E were, respectively, 0.860 and 0.908 (both $p < 0.00001$). Therefore, to confirm that g_s is not the preponderant factor mediating photosynthesis, we show in Figure 6A,B a regression between P_N and g_s and P_N and E . The way of interpretation was season-dependent to contribute to correlations. In this case, we verify that all regressions between P_N and E (Figure 6B) return higher regression coefficients than regressions between P_N and g_s (Figure 6A). As regression coefficients are high, we perform a regression between P_N and C_i to infer the instantaneous ribulose 1,5-diphosphate carboxylase/oxygenase carboxylation efficiency. The analysis of this variable shows us that in the rainy months, the P_N/C_i regression curve tended to be more responsive than in the dry months, although none of the curves were significant. However, when C_i is analyzed in an integrated manner with the other variables (multivariate analysis, Figure 10), C_i was highly responsive to photosynthesis and responsible for the separation of variables that led to the distinction of the August 2020 cluster (Details, see Figure 10). All this data confirms that in *C. pyramidale*, the P_N is limited by stomatal conductance. This idea is confirmed by

analysis of the Ci:Ca ratio throughout the day for all seasons (Figure 7A–D). We verify that all records from 2019 return a Ci:Ca ratio lower than 0.5 (dotted line in Figure 7A–D). In 2020, all values of the Ci:Ca ratio were higher than 0.5, with the exception of the record at noon in March 2020, during an effect that in plant physiology is called midday depression.

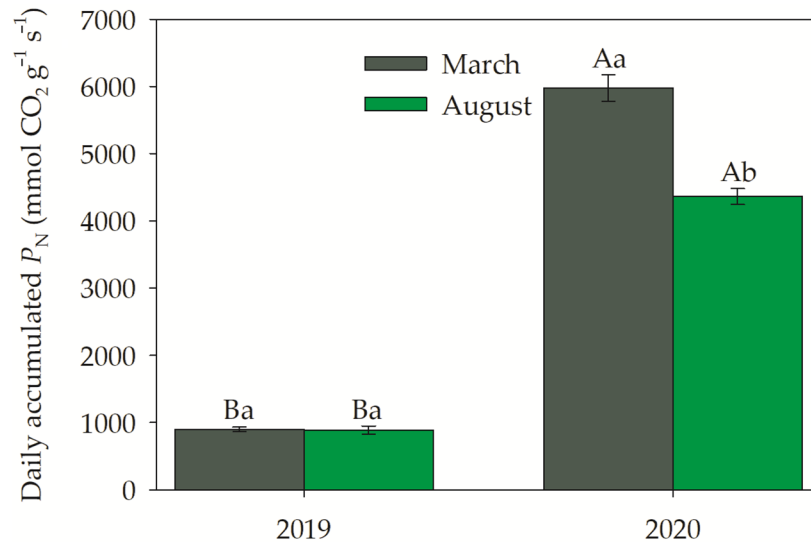


Figure 5. Daily integrated CO₂ assimilation (integrated P_N) measured in *Cenostigma pyramidale* grown in field conditions in the driest year (2019) and a normally rain year (2020) in both seasonal conditions (rainy, March, and dry, August). Means followed by small case letters denote statistical significance between months, regardless of year, and means followed by uppercase letters denote statistical significance between years in the same month. All values denote media $\pm$ SD. $n = 10$.

The intrinsic water use efficiency (WUEi; Figure 7E–H) fluctuates throughout the day, as do other gas exchange parameters. However, in the rainy season, the WUEi increased throughout the day, while in the dry season, the value measured at 6 p.m. was higher than that measured at 6 a.m. Regardless of season or evaluation time, the WUEi was higher in all analyses since this feature is dependent on net photosynthesis and stomatal conductance. This statement is confirmed by a negative correlation between rainfall and WUEi ($r = -0.224$) and a positive correlation between P_N and WUEi ($r = 0.215$).

Along the day, the leaf temperature (Figure 7I–L) returns values dependent on air temperature and transpiration rate. As a consequence, T_{leaf} shows a negative correlation between $\Psi_{w(\text{md})}$ ($r = -0.505$), P_N ($r = -0.692$), daily P_N ($r = -0.748$), g_s ($r = -0.669$), and E ($r = -0.744$). These patterns confirm that leaf transpiration decreases leaf temperature and improves net photosynthesis.

The vapor pressure deficit (VPD; Figure 8) also reflects the effect of air temperature with lower values in the early morning and late afternoon and higher values registered between 10 a.m. and 12 p.m. Commonly, VPD has an influence on the P_N , g_s , and E , because it is atmospheric water potential that governs VPD, and by analogy, P_N , g_s , and E are shown with a correlation between VPD and P_N ($r = -0.624$), g_s ($r = -0.632$), and E ($r = 0.678$). However, when correlations were made with these parameters (Figure 9), only E returned a weakly significative correlation of coefficients (Figure 9C).

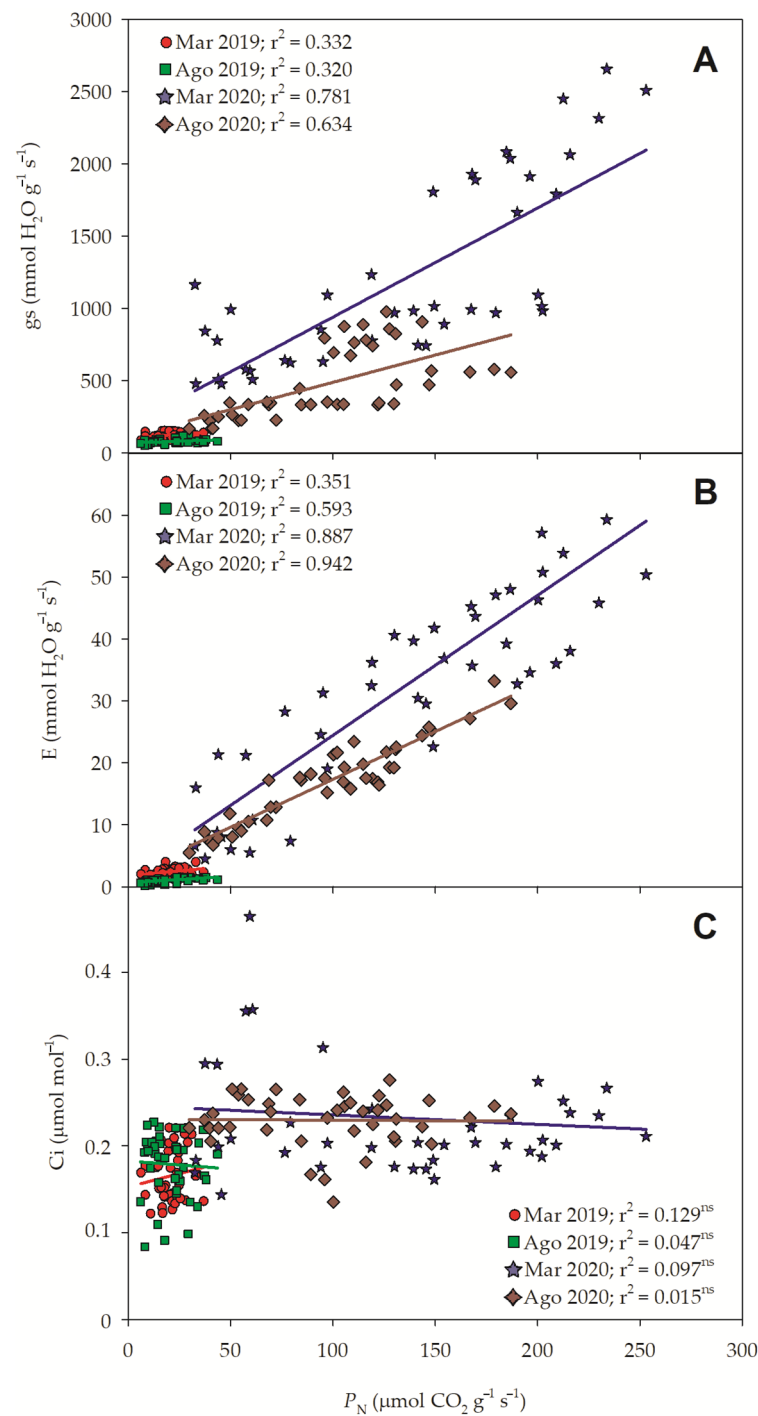


Figure 6. Relationship between net photosynthesis (P_N), and stomatal conductance (g_s) (A), transpiration (E) (B), and internal carbon concentration (C_i) (C) measured in March 2019 (red symbols), August 2019 (green symbols), March 2020 (blue symbols) and August 2020 (brown symbols) in *Cenostigma pyramidale* grown in field conditions. Each point denotes one plant. Regression coefficients were shown. $n = 10$.

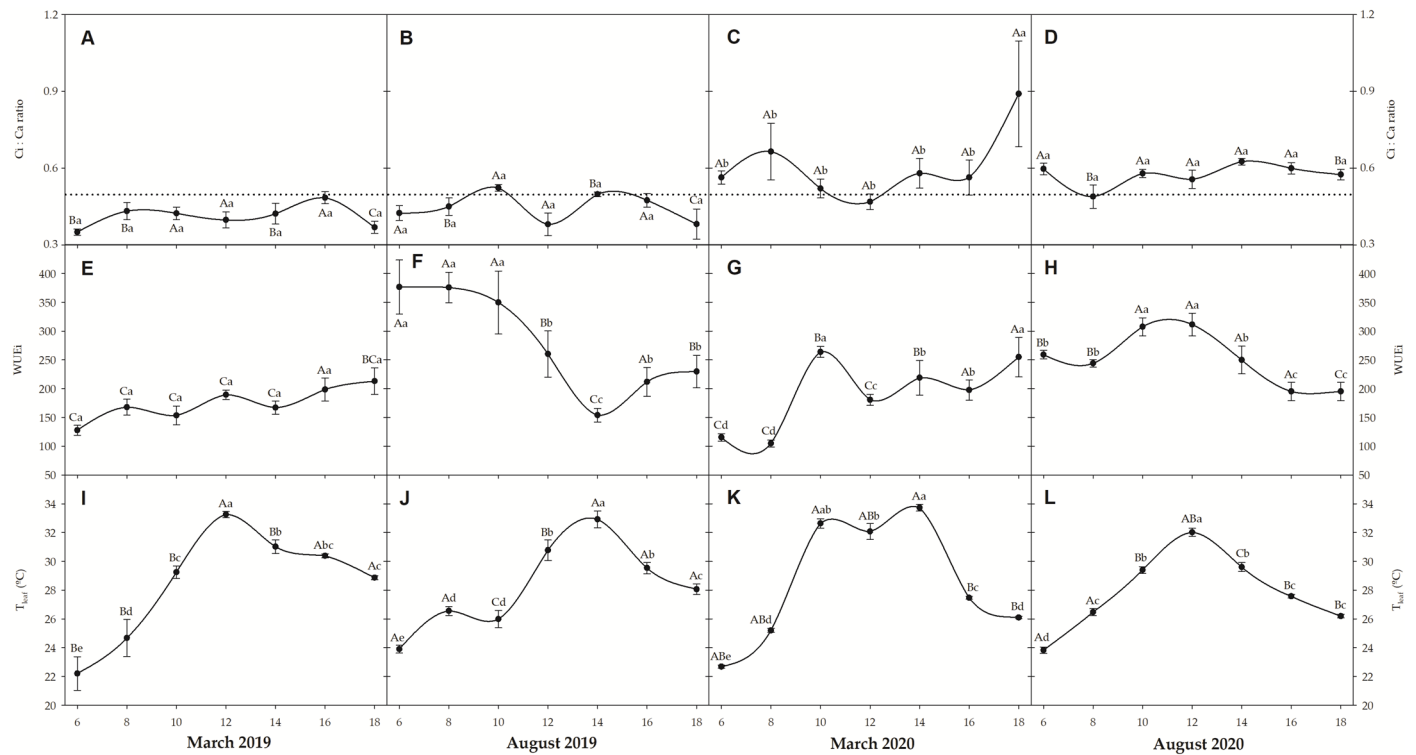


Figure 7. Internal-to-ambient CO₂ concentration (Ci:Ca ratio; (A–D)), intrinsic water use efficiency (WUEi; (E–H)), and leaf temperature (T_{leaf}; (I–L)) measured in March 2019 (A,E,I), August 2019 (B,F,J), March 2020 (C,G,K), and August 2020 (D,H,L) in *Cenostigma pyramidale* grown in field conditions in the driest year (2019) and a normal rain year (2020) in both seasonal condition (rainy, March and dry, August). Means followed by small case letters denote statistical significance between months, regardless of year, and means followed by uppercase letters denote statistical significance between years in the same month. All values denote media ± SD.

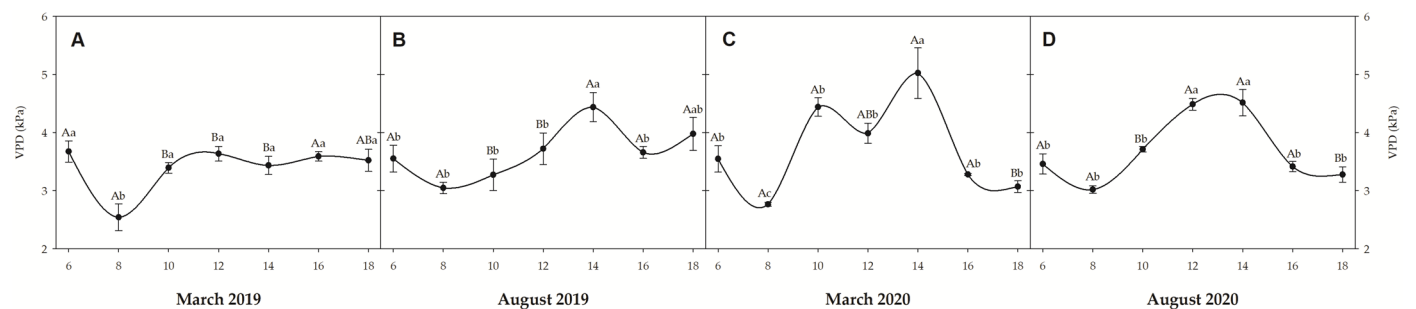


Figure 8. Vapor pressure deficit (VPD) measured in March 2019 (A), August 2019 (B), March 2020 (C), and August 2020 (D) in *Cenostigma pyramidale* grown in field conditions in the driest year (2019) and a normal rain year (2020) in both seasonal condition (rainy, March and dry, August). Means followed by small case letters denote statistical significance between months, regardless of year, and means followed by uppercase letters denote statistical significance between years in the same month. All values denote media ± SD.

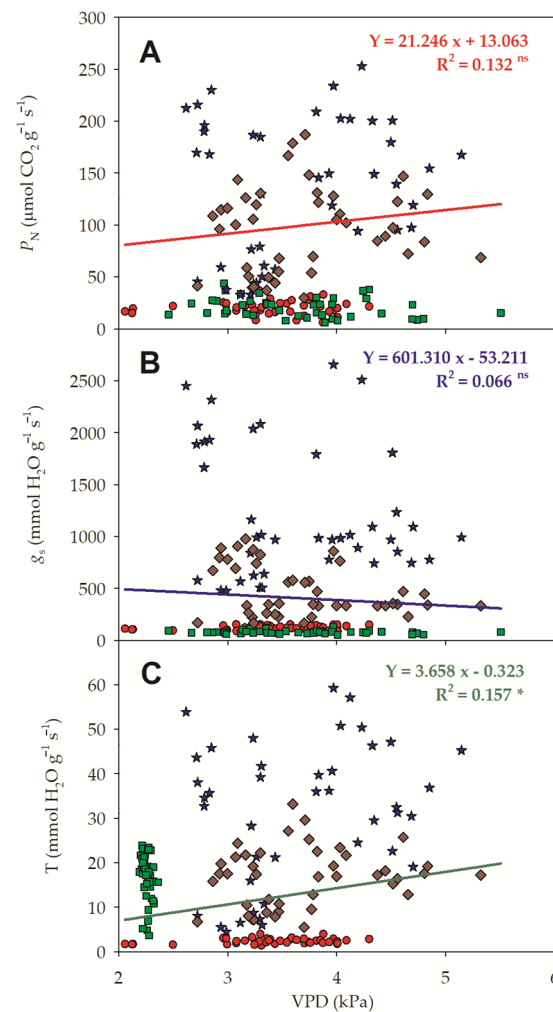


Figure 9. The relationship between vapor pressure deficit (VPD) and net photosynthesis (P_N ; (A)), stomatal conductance (g_s ; (B)), and transpiration (E ; (C)) measured in March 2019 (red symbols), August 2019 (green symbols), March 2020 (blue symbols) and August 2020 (brown symbols) in *Cenostigma pyramidale* grown in field conditions. Each point denotes one plant. Equation and regression coefficients are shown. ns = non-significant; * significant to $p \leq 0.05$. $n = 10$.

3.4. Plant Anatomy

C. pyramidale leaflets consist of uniseriate epidermises, with anticlinal outer cell walls covered by a thin cuticle (Figure 10), and unicellular tectorial trichomes, stomata occurring on the abaxial epidermal surface, with glandular trichomes on the abaxial surface. The mesophyll is dorsiventral, consisting of 1–2 layers of palisade parenchyma (PP) and 3–4 layers of spongy parenchyma (SP). Vascular bundles (VB) are collateral and associated with pericyclic fibers (Figure 9B). The secretory structures are located in the spongy parenchyma with fibers of the pericycle.

The midrib is biconvex, and its epidermis is uniseriate with a thin cuticle, also containing a few tectorial trichomes.

In this paper, we show that the leaf thickness varies seasonally. In 2019, there were no significant differences in mesophyll thickness. However, in 2020, the leaves sampled during the dry season were, on average, 25% thicker than the leaves sampled in the rainy season plants (Table 3). An impressive part of this increase is due to the greater thickness of the PP, which was 71% greater than during the dry season. Adaxial epidermis thickness (ADAE) (19.9%) and abaxial epidermis thickness (ABAE) (27.9%) contributed little to this thickness, while SP contributed negatively (−18.1%) to the increase in the mesophyll thickness (Table 3).

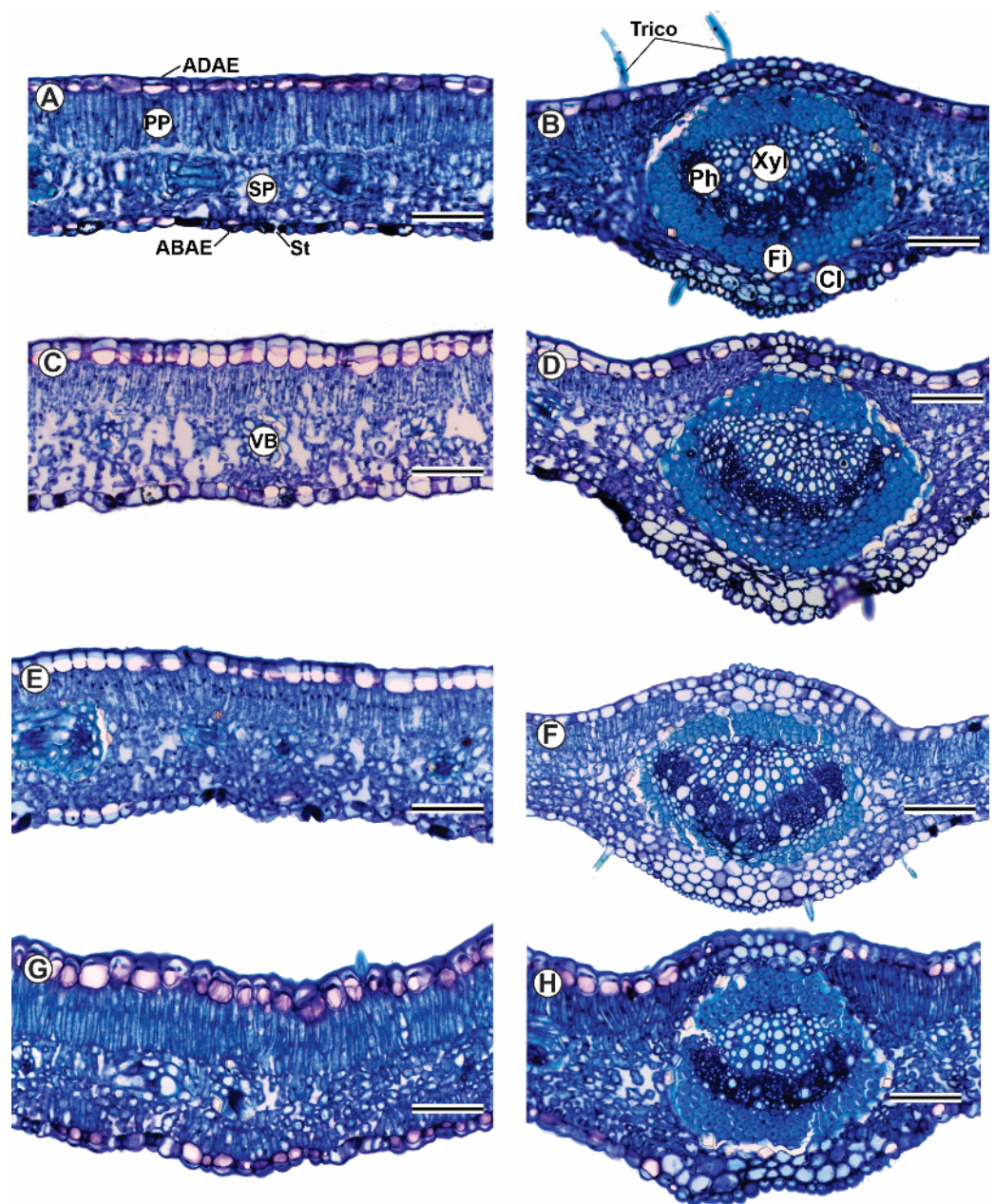


Figure 10. Cross section of *Cenostigma pyramidale* leaves grown in field conditions in March 2019 (A,B), August 2019 (C,D), March 2020 (E,F), and August 2020 (G,H) in field conditions. In (B,D,F,H), the midrib is shown in cross-section. ADAE, Adaxial epidermis surface thickness; ABAE, Abaxial epidermis surface thickness; PP, palisade mesophyll thickness; SP, spongy mesophyll thickness; St, stomata; Xyl, xylem; Ph, Phloem; Cl, Collenchyma; Fi, Fibers; Trico, tectorial foliar trichomes; VB, vascular bundles. Scales = 100 μ m.

In comparison to the values presented in March 2019, the values presented in August 2019 increased by 10.9%, 16.5%, 2.2%, 12.1%, 2.6%, and 14.9%, respectively, in total leaf thickness (TLT), ADAE, ABAE, PP, midrib thickness (MT), midrib length (ML), and midrib area (MA). In another way, the TLT, spongy mesophyll thickness (SP), midrib xylem thickness (MXT), midrib xylem area (MXA), vessel area (VA), number of vessels (NV), and potential specific stem conductivity (Kp), respectively decreased in August 2019 in 3.5%, 26.2%, 9%, 4.2%, 11.2%, 4.1%, and 10.8%. In plants evaluated in 2020, the following features were increased in August with respect to March: TLT (24.9%), ADAE (19.7%), ABAE (27.9%), and PP (70.8%). Other features included SP (15.3%), MT (15.6%), ML

(17.3%), MA (39%), MXT (29.3%), MXA (41.4%), VA (43.6%), NV (17.1%), and Kp (47%) were decreased in plants evaluated in August 2020 in comparison to plants evaluated in March 2020 (Tables 3 and 4). Thus, regarding water stress th, the following features were negatively correlated: TT ($r = -0.496$), ABAE ($r = -0.589$), and PP ($r = -0.429$), while the following features were positively correlated with rainfall, MA ($r = 0.748$), MXT ($r = 0.629$), MXA ($r = 0.835$), VA ($r = 0.786$), NV ($r = 0.507$), and Kp ($r = 0.535$). Similarly, Kp shows a positive correlation with ML ($r = 0.397$), MA ($r = 0.554$), MXT ($r = 0.527$), MXA ($r = 0.497$), VA ($r = 0.621$) and negative with NV ($r = -0.475$) (Supplementary data file). Based on these correlations, we can infer that the development of more vessel elements is strongly correlated with a smaller caliber for new vessels, as demonstrated by the strong negative correlation between these two factors ($r = -0.691$) (Supplementary data file). Thus, while it may be a semiarid and arid native plant, *C. pyramidale* presents an efficient system for controlling the size of the conducting vessels to provide control for the development of more vessels, but with a smaller caliber, which facilitates the hydraulic conductance from soil to leaves even in times of scarce rainfall.

Table 3. Total leaf thickness, adaxial epidermis thickness, abaxial epidermis thickness, palisade mesophyll thickness, and spongy mesophyll thickness measured in *Cenostigma pyramidale* grown in field conditions in the driest year (2019) and a normal rain year (2020) in both seasonal conditions (rainy, March and dry, August). Means followed by small case letters denote statistical significance between months, regardless of year, and means followed by uppercase letters denote statistical significance between years in the same month. All values denote media $\pm$ SD. n = 10.

Parameters	2019		2020	
	March	August	March	August
Total leaf thickness (TLT; μm)	146.6 $\pm$ 3.3 Aa	141.4 $\pm$ 3.1 Ba	126.1 $\pm$ 3.2 Bb	157.5 $\pm$ 3.5 Aa
Adaxial epidermis thickness (ADAE; μm)	21.5 $\pm$ 0.5 Ab	23.8 $\pm$ 1.1 Aa	20.6 $\pm$ 0.6 Ab	24.7 $\pm$ 0.8 Aa
Abaxial epidermis thickness (ABAE; μm)	13.2 $\pm$ 0.3 Ab	15.4 $\pm$ 0.6 Ba	14.0 $\pm$ 0.4 Ab	17.9 $\pm$ 0.5 Aa
Palisade mesophyll thickness (PP; μm)	57.0 $\pm$ 2.6 Aa	58.2 $\pm$ 3.0 Ba	44.8 $\pm$ 2.1 Bb	76.4 $\pm$ 2.5 Aa
Spongy mesophyll thickness (SP; μm)	58.5 $\pm$ 1.5 Aa	43.2 $\pm$ 2.0 Ab	50.8 $\pm$ 1.5 Ba	43.0 $\pm$ 1.7 Ab

Table 4. Midrib thickness, midrib length, midrib area, midrib xylem thickness, midrib xylem area, vessel area, number of vessels, and potential specific stem conductivity measured in *Cenostigma pyramidale* grown in field conditions in the driest year (2019) and a normal rain year (2020) in both seasonal conditions (rainy, March and dry, August). Means followed by small case letters denote statistical significance between months, regardless of year, and means followed by uppercase letters denote statistical significance between years in the same month. All values denote media $\pm$ SD. n = 10.

Parameters	2019		2020	
	March	August	March	August
Midrib thickness (MT; μm)	297.6 $\pm$ 8.6 Ba	333.7 $\pm$ 23.7Aa	340.2 $\pm$ 16.8 Aa	287.1 $\pm$ 7.6Ab
Midrib length (ML; μm)	332.5 $\pm$ 20.9 Ba	341.3 $\pm$ 24.5 Aa	402.1 $\pm$ 19.0 Aa	332.6 $\pm$ 16.0 Ab
Midrib area (MA; μm^2)	70,285.0 $\pm$ 2947.4 Bb	80,763.9 $\pm$ 4436.7 Ba	152,425.5 $\pm$ 7897.2 Aa	93,033.1 $\pm$ 4956.5 Ab
Midrib xylem thickness (MXT; μm)	45.0 $\pm$ 2.3 Ba	40.9 $\pm$ 3.4 Ba	64.4 $\pm$ 1.9 Aa	45.5 $\pm$ 1.7 Ab
Midrib xylem area (MXA; μm^2)	8353.8 $\pm$ 621.3 Ba	8001.4 $\pm$ 496.6 Bb	17,095.0 $\pm$ 1142.2 Aa	10,012.0 $\pm$ 978.7 Ab
Vessel area (VA; μm^2)	36.9 $\pm$ 1.6 Ba	32.8 $\pm$ 3.0 Ba	65.7 $\pm$ 3.4 Aa	37.1 $\pm$ 1.5 Ab
Number of vessels (NV)	36.3 $\pm$ 2.3 Ba	34.8 $\pm$ 3.1Ba	54.6 $\pm$ 1.7 Aa	45.1 $\pm$ 3.5 Ab
Potential specific stem conductivity (Kp; $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$)	316.3 $\pm$ 60.1 Ba	282.2 $\pm$ 34.6 Ba	923.3 $\pm$ 84.1 Aa	489.2 $\pm$ 84.8 Ab

3.5. Principal Component Analysis

The principal component analysis (Figure 11) shows that the PC1 + PC2 axis makes up 93.60% of the possible variations. This analysis is divided into two points: those features that are responsive to net photosynthesis and those that are responsible for water deficit. On the right side of Figure 11 we have two different quarters: one directly responsible for a cluster of net photosynthesis and other features; characteristics that can subdivide both sides in features found to be responsive as August 2020 and other features that are

responsive to rainfall and clustered as March 2020. On the left side of the PCA, we show positive responsiveness to leaf thickness (total leaf thickness and both epidermises) and clustered as in August 2019. On the downside, we describe SLA, SP, and MT, with all characteristics presenting negative correlations to P_N (Supplementary data file), which are clustered as of March 2019. Also, the PCA shows that $\Psi_{w(pd)}$ (21.8%), E (26.8%), g_s (26.7%), T_{leaf} (25.4%), VPD (27%), MA (26.4%), MXT (23.7%), MXA (25.8%), VA (24.7%), and NV (26.9%) contributes to increasing P_N while TLT (17.7%), $ADAE$ (17.8%), $ABAE$ (4.2%), and MT (18.5%) contribute to a decreasing P_N (Supplementary Table S1). Also, the PCA analysis describes that there are ten features positively correlated with rainfall: ML (39.5%), SP (39.4%), SLA (37.3%), MXT (19.3%), MT (15.1%), VA (13.5%), MXA (9.7%), Kp (8.4%), T_{leaf} (8.3%), and VPD (8.3%). Another 11 features are described as negatively influenced by rainfall: $ABAE$ (40.3%), $\Psi_{w(md)}$ (26.2%), TLT (26%), $ADAE$ (23%), $\Psi_{w(pd)}$ (19.9%), P_N (16.8%), daily P_N (13.1%), g_s (7.3%), E (4.7%), MA (1.5%), and NV (0.3%) (Supplementary Table S1).

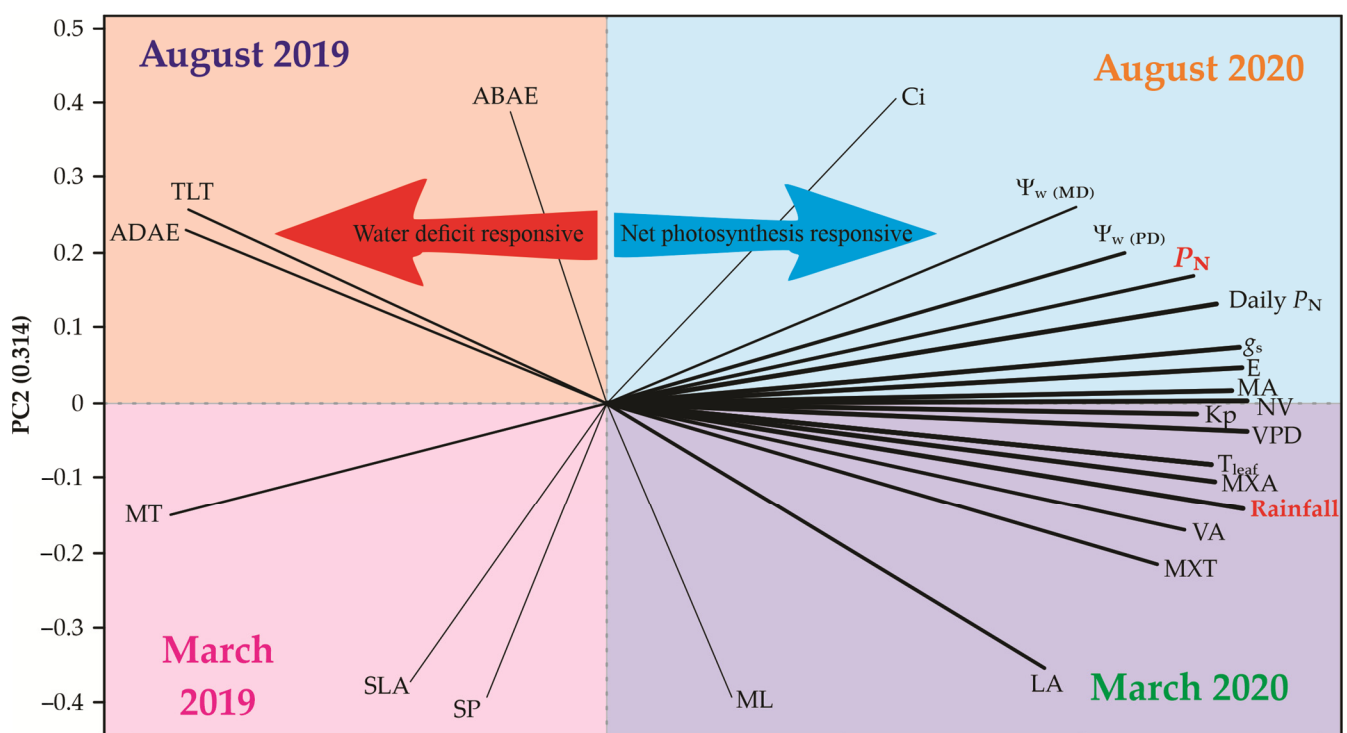


Figure 11. Principal component analysis showing the net photosynthesis (P_N) and its correlated features. On the right side are presented all features responsive to P_N , while on the left side, all features responsive to water deficit. Each feature is demonstrated with its vector and its strength via different line thicknesses. C_i , substomatal CO_2 concentration; $\Psi_{w(md)}$, water potential measured at midday; $\Psi_{w(pd)}$, water potential measured at predawn; g_s , stomatal conductance; E , transpiration; MA , midrib area; NV , number of vessels; Kp , potential specific stem conductivity; VPD , vapor pressure deficit; T_{leaf} , leaf temperature; MXA , midrib xylem area; VA , vessel area; MXT , midrib xylem thickness; LA , leaf area; ML , midrib length; SP , spongy mesophyll thickness; SLA , specific leaf area; MT , midrib thickness; $ADAE$, adaxial epidermis surface thickness; TLT , total leaf thickness; $ABAE$, abaxial epidermis surface thickness.

3.6. Heatmap

The heatmap was constructed with a rainfall gradient instead of by applied treatments (Figure 12). So, all increases or decreases are due to changes in rainfall. Thus, we verify that $\Psi_{w(pd)}$ decreased in March 2019 and August 2019, 61.5% and 48.3%, respectively, causing a decrease in P_N of 90.2% and 86.5%, respectively. Transpiration and stomatal conductance also decreased during the same months, 96.3%, 98% (to E), 85.8%, and 90.8%

(to g_s), respectively. Plants evaluated in August 2020 show an increase in TLT (24.9%), ADAE (19.7%), ABAE (27.9%), and PP (70.8%), while SP shows a decrease of 30.6%. All vessels or midrib features were decreased by water deficit in comparison to the value presented in March 2020. The decreases were 15.6% (MT), 17.3% (ML), 39% (MA), 29.3% (MXT), 41.4% (MXA), 43.6% (VA), and 17.4% (VN). These decreases negatively affected Kp in 47%.

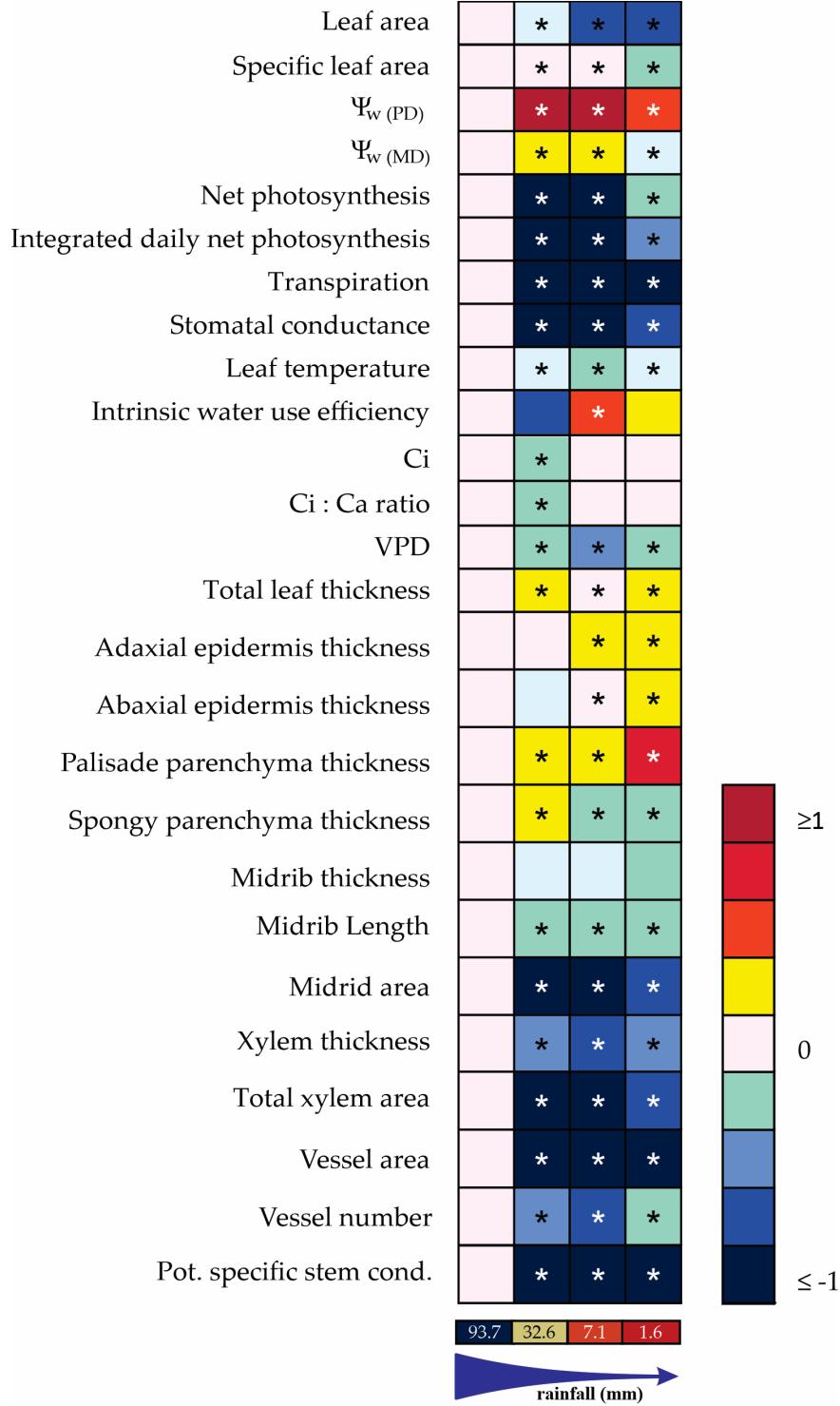


Figure 12. Heatmap showing the degree of modulation in leaf characteristics of *Cenostigma pyramidale* evaluated as rainfall gradient. The sequence of reading is March 2020, March 2019, August 2019, and August 2020. The color code is followed by scale, and rainfall is scaled too. Asterisks (*) denote significant at $p < 0.05$.

3.7. Phenotypic Plasticity

Phenotypic plasticity denotes the degree of modulation of the physiological and anatomical features when exposed to a specific environment situation. Table 5 shows us that physiological plasticity ranged from 0.077 ($\Psi_{w(md)}$) to 0.995 (g_s).

Table 5. The plasticity index of physiological and anatomical features in the leaves of *Cenostigma pyramidale* plants grows in a natural environment of semiarid Brazilian Caatinga in 2019/March to 2020/August in accordance with historical rainfall. Means followed by smallcase letters denote statistical differences between samples in the same feature (Newman–Keuls test $p \leq 0.001$), and uppercase letters denote statistical differences between features (Bonferroni’s test at $p \leq 0.001$).

Physiological Features	March 2019	Aug 2019	March 2020	Aug 2020	Mean Value
$\Psi_{w(pd)}$	0.300	0.975	0.333	0.905	0.628
$\Psi_{w(md)}$	0.077	0.250	0.200	0.156	0.171
Net photosynthesis	0.831	0.862	0.871	0.841	0.851
Daily Net Photosynthesis	0.221	0.390	0.194	0.171	0.244
Stomatal conductance	0.437	0.592	0.962	0.830	0.705
Transpiration	0.637	0.847	0.947	0.834	0.816
Internal CO ₂ concentration	0.449	0.632	0.793	0.510	0.596
Internal to ambient [CO ₂]	0.449	0.632	0.793	0.510	0.596
Leaf temperature	0.445	0.328	0.351	0.293	0.354
Intrinsic water use efficiency	0.633	0.786	0.783	0.683	0.721
Vapor pressure deficit	0.521	0.553	0.634	0.489	0.549
Mean Value	0.455 ± 0.208 a	0.622 ± 0.233 a	0.624 ± 0.298 a	0.565 ± 0.275 a	0.567 ± 0.223 A
Anatomical features					
Leaf area	0.085	0.237	0.123	0.337	0.195
Specific leaf area	0.055	0.025	0.101	0.059	0.060
Total leaf thickness	0.248	0.329	0.384	0.294	0.314
Adaxial epidermis thickness	0.298	0.553	0.410	0.459	0.430
Abaxial epidermis thickness	0.316	0.420	0.450	0.414	0.400
Palissade parenchyma thickness	0.509	0.623	0.512	0.411	0.514
Spongy parenchyma thickness	0.412	0.605	0.395	0.422	0.458
Midrib thickness	0.333	0.620	0.582	0.299	0.459
Midrib length	0.548	0.594	0.499	0.531	0.543
Midrib area	0.540	0.666	0.506	0.540	0.563
Midrib xylem thickness	0.507	0.664	0.350	0.456	0.494
Midrib xylem area	0.694	0.663	0.633	0.771	0.690
Vessel area	0.517	0.652	0.624	0.440	0.558
Number of vessel elements	0.632	0.712	0.408	0.632	0.596
Pot. specific stem conductivity	0.867	0.852	0.679	0.900	0.825
Mean Value	0.437 ± 0.220 a	0.548 ± 0.211 a	0.444 ± 0.167 a	0.464 ± 0.201 a	0.473 ± 0.187 B

However, the high amplitude of the standard deviation provokes a non-significant mean value for other factors, but the plasticity index of March 2020 was 37.1% higher than those media presented in March 2019. An analogous situation occurred in anatomical plasticity, where the plasticity index ranged from 0.025 (SLA) to 0.900 (Kp). As a result, the amplitude of standard deviation does not provide a statistical difference between anatomical plasticity. Moreover, the mean value of the physiological plasticity was 0.567 ± 0.223 , while an anatomical plasticity of 0.473 ± 0.187 shows a higher physiological plasticity (~20%) than anatomical plasticity ($p \leq 0.01$).

Some physiological features present a strong ability to modulate when comparing the dry season with the rainy season, regardless of the year of evaluation. In this sense, the most plastic features are $\Psi_{w(pd)}$, $\Psi_{w(md)}$, Ci, Ci:Ca ratio, and T_{leaf} . Anatomical features also showed a degree of plasticity but to a lesser extent. As mentioned above, the anatomical variables also modulate, and the most plastic is leaf area, ADAE, SP, MT, MXT, VA, NV, and Kp.

4. Discussion

Our findings highlight the pronounced seasonality of rainfall and drought in the Brazilian Caatinga environment [1]. *C. pyramidale* showed a semideciduous pattern since it maintains at least 40% of the leaves on the plant, even during the dry season. This concept disagrees with Santos et al. [2], who classify this species as deciduous. The different patterns described for the same species probably arise from the methodology applied in the study. While Santos et al. [2] studied potted plants under artificial conditions, this study was conducted in the field with the plants in natural conditions. The discrepancy in this concept also is exacerbated by Santos et al. [2], which suspended 100% of the total irrigation of *C. pyramidale* seedlings for 5 days, but the plants still make photosynthesis, strict evidence of the presence of leaves since in this plants extremely drought stressed Water deficit could reduce leaf growth and, in turn, leaf area, because leaf area expansion depends on leaf turgor, temperature, and assimilating the supply for growth, which can be affected by drought as observed in this study and several other species [22,48–50]. In general, SLA is the main component of leaf water content. Leaf tissue density decreases as leaf water content increases and is influenced by precipitation [32]. This statement is aligned with our results, which show a higher SLA in the driest year in comparison to the rainiest. The negative correlation between rainfall and SLA ($r = -0.231$) confirms our Table 2 data. Similar results were previously reported by Falcão et al. [51] in a study with this same species. The SLA of *C. pyramidale* was higher as the rain occurrence in both evaluated years in distinct forms were presented before [36], where SLA just increased in the rainy year and presented a similar pattern in the driest year. This finding supports our initial hypothesis that *C. pyramidale* displays increased resilience when subjected to recurring water shortages, given its status as a native species and its robust adaptation to the fluctuating environmental conditions throughout the seasons. This enduring nature was previously reported by Pagotto et al. [52] when this species was studied in the same biome as this study. These results lead us to argue that the increased SLA during the dry year may be indicative of compromised leaf biomass due to extremely low water potentials, which directly affects the turgor pressure required for cell elongation to make it more difficult. It is worth noting that SLA is influenced not only by leaf area but also by leaf density and thickness [53,54]. These adaptive strategies permit the plant to conserve water, preventing significant drops in P_N and increases in transpiration. Following the restoration of normal water availability in 2020, all plant physiological parameters rebounded strongly. The reduced g_s in 2019 registered in the dry season were primarily due to a typical feed-forward response, where stomata closed in response to VPD, confirmed by a strongly significant correlation between VPD and E ($r = 0.678$) and g_s ($r = 0.632$). Comparing 2020 with 2019, it's apparent that in 2019, the stomata tended to stay less open during the dry season, resulting in reduced daily photosynthesis. These findings suggest that in *C. pyramidale*, net photosynthesis is more constrained by stomatal conductance than by other parameters, as was previously reported [36].

Wright et al. [55] describe that *C. pyramidale* has more stable water use efficiency, which represents a background contribution to the evapotranspiration pattern over shorter timescales. Then, transpiration shifts were not detected, and responses were more buffered to VPD. In accordance with these authors, given this hydraulic response and because the phenological timing of this species is cued by rainfall, *C. pyramidale* is likely more vulnerable to acute drought. In situations of water scarcity, the carbon equilibrium within plant systems is disrupted as a protective measure [56]. Consequently, a delicate balancing act unfolds for plants when they confront stress-inducing circumstances, primarily hinging on their ability to strike a balance between sustaining photosynthetic processes and preserving growth. Notably, our findings align with prior research documenting seasonal fluctuations in photosynthesis among Caatinga species and others [36,51,57,58]. For instance, a study with *Croton blanchetianus* reported P_N ranging from 15–20 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ during the rainy season to less than 5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the dry season [22,40]. Similarly, Pinho-Pessoa et al. [36] identified variations in the P_N , with values ranging from 13.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$

during the rainy season to $6.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in *C. pyramidale* under water-stressed conditions.

Similar results were described in other Caatinga species, such as *Spondias tuberosa* [20], *Cenostigma pyramidale* [36], *Croton blanchetianus* [22], *Jatropha curcas* [15], and *Cynophalla flexuosa* [59]. According to Pinho-Pessoa et al. [36], *Cenostigma pyramidale* displays lower values of P_N mediated by stomatal closure. This statement becomes clearer with the analysis of Figure 6, which shows that E is more responsive for P_N than g_s . The decrease in the Ci:Ca ratio indicates that constraints of g_s are dominant under drought conditions, as further evidenced in the evaluations from the driest year. During this period, the *C. pyramidale* leaves displayed reduced Ci:Ca ratios coupled with diminished P_N , implying limitations in carbon assimilation in a direct way. The confluence of drought conditions with an excess of incident radiation can result in a reduction in radiation use efficiency. Additionally, under such circumstances, there is an increased risk of leaf overheating, particularly when transpirational leaf cooling is compromised as a consequence of water deficits [8,9,60]. Thus, we can argue that transpiration must modulate gas exchange more intensely than stomatal conductance. This is particularly evident during the dry months when high temperatures and stomatal closure prevail in the region [22,31,36,39,40]. Furthermore, it must be considered that CO_2 , when captured by the stomata, must follow a very complex path until it reaches the rubisco carboxylation site, a route called mesophilic conductance [61–63]. Furthermore, Rubisco and other enzymes of the Calvin-Benson Cycle must also be activated to receive this carbon, process it into triose phosphates, and send it to the sink organs [64,65]. High Ci:Ca ratio in the rainy seasons at the expense of the dry seasons may serve as a complement to our hypothesis that transpiration and stomatal conductance are mainly responsible for governing gas exchange in the dry months of the year. High Ci:Ca ratios also lead to a slower flow of CO_2 through the mesophyll (mesophilic conductance) and/or enzymatic restrictions in the Calvin Cycle. This is a critical point to be considered in future studies.

According to Falcão et al. [57], *C. pyramidale* can keep its photosynthetic rates even with low leaf water potential. This finding contradicts our results because a distinct reduction of net photosynthesis was found in the dry year compared to a year with a normal rainy season. However, net photosynthesis does not show a constant or fixed net value; instead, it ranges across the measurement of time. So, to give an accurate comparison, these values must be acquired at the same time or integrated in a full day. In this study, we verify that in March 2020, the net photosynthesis was increased in 11.1-, 11.1-, 10.2-, 6.1-, 4.4-, 2.7-, and 2.7-fold higher than the same times evaluated in 2019. For this reason, we preferred to present the data as integrated daily values, which were 6.6- and 4.9-fold higher in 2020 in comparison to 2019, respectively, in both the rainy and dry seasons. The transpiration rate, as part of the gas exchange, increased in March 2020 between 4.7- to 26.6-fold in comparison to evaluations conducted at the same times as in 2019, a range that was lower or higher than those presented only a singular evaluation (17-fold) by Falcão et al. [51]. Falcão et al. [51] also describe that WUE_i was higher in the driest year (63%) in comparison to the rainy year, a fact that contradicts our results, which, with the exception of those values registered at 8 a.m., all other values were 1- to 1.7-fold higher in the rainy year in comparison to the driest year. A reduction in transpiration via stomatal closure prevents excessive water loss in cases of low water availability and protects the hydraulic architecture of the plant, even under conditions of low leaf water potential [66,67]. Wright et al. [55] describe that *C. pyramidale* appears to be operating near maximum hydraulic conductivity. The highest values of P_N and g_s from the first hours of the day agree with Dombroski et al. [37]. Also, according to Roach et al. [68], drought conditions promote heat stress at the plant level. This is primarily due to the decrease in E , which, in turn, leads to a reduction in transpiration cooling, as demonstrated by a negative correlation between rain and T_{leaf} ($r = -0.902$) and T_{leaf} and E ($r = -0.744$) (Supplementary data file). Higher VPD conditions were observed to coincide with a significant increase in transpiration rates ($r = 0.678$) and transpiration reduce T_{leaf} ($r = -0.744$). Smaller leaves come with distinct advantages, including large convection

coefficients and reduced resistance to heat transfer across leaf boundary layers [69]. This structural adjustment serves as a response to fine-tune leaf temperature in the face of drought stress. This hypothesis is corroborated by a positive correlation between leaf area and transpiration ($r = 0.443$), T_{leaf} ($r = 0.637$), and VPD ($r = 0.474$) or negative with WUEi ($r = -0.436$) maximizing the water use efficiency with less water loss to achieve the same leaf cooling.

Many scholars have shown that trees can increase their WUE when exposed to a water deficit [20,70,71]. In this study, we show a reduction in P_N due to low $\Psi_{w(\text{pd})}$ ($r = 0.788$) as well $\Psi_{w(\text{md})}$ ($r = 0.851$) or g_s ($r = 0.860$). This phenomenon is notably evident through a strong correlation between rainfall and water potential (Ψ_w), with intermediate coefficients observed both in predawn ($r = 0.518$) and midday ($r = 0.528$), aligning with the findings of several other studies during the dry season in the Caatinga ecosystem, like *Caesalpinia pyramidale* [37], *Cenostigma pyramidale* [36], *Spondias tuberosa* [20]. These findings underscore the remarkable resilience of these plants, demonstrating their capacity to endure and recover swiftly under severe water scarcity conditions. This underscores the remarkable adaptability of this particular species within arid environments. The very negative values of osmotic potential, reaching -7.7 MPa in plants evaluated at midday in August 2019, are consistent with other studies carried out with *C. pyramidale*, one on plants in a system similar to this one [36] and another with an artificial system in potted plants [72]. Only plant species that are fully adapted to semiarid conditions can withstand very negative pressures [36]. To do so, the walls of the plant vessels must be highly lignified in a way that avoids collapse or cavitation [69,73]. Under water stress, the volume of water in the soil is not enough, so the water potential of the absorbing root cells can extract it from the soil and raise this water to the conductive vessels, which reduces water uptake from the soil [74] as well as its transmission to the leaves, a process that is called hydraulic conductivity (Kp) [75–77]. An extracted relationship between water deficiency and tree physiology is based on hydraulic failure when the transpiration rate is higher than the root uptake, creating high tension in xylem vessels and leading to embolism and loss of conductivity of the tree transport system [78,79]. This perception was also verified in our study when we correlated the rainfall with Kp ($r = 0.535$), Kp with P_N ($r = 0.389$), g_s ($r = 0.364$), E ($r = 0.444$), T_{leaf} ($r = 0.507$), and VPD ($r = 0.386$) (Supplementary data file).

Plants are extraordinary organisms that have developed an adaptation modifying their Kp, which essentially governs the flow of water through the plant's vascular system [80]. In response to limited water availability, plants finely tune their Kp to uphold a favorable water balance [74,81,82]. Through this regulation of water flow, plants can efficiently distribute it, ensuring that vital processes like photosynthesis and nutrient uptake continue to function even during arid spells. Also, the Kp shows a significative correlation between rainfall ($r = 0.635$), leaf area ($r = 0.320$), $\Psi_{w(\text{pd})}$ ($r = 0.333$), P_N ($r = 0.389$), E ($r = 0.444$), g_s ($r = 0.364$), VPD ($r = 0.386$), and T_{leaf} ($r = 0.507$). These results show an intimate relationship between evaporative demand (VPD), with transpiration and stomatal conductance in support of the current transpiration, assisted by the osmotic potential of the leaves, facts that translate into adjustments in hydraulic conductivity, which resulted in values 1.25- and 1.57-fold higher in the rainy season in comparison to the driest season. If we compare the average Kp of the rainy year and the dry year, the rainy year showed a 2.4-fold higher Kp compared to the dry year. These data are corroborated by a recent study that showed how hydraulic force is formed in *Jatropha curcas* plants evaluated over a period of 2 years in an arid climate under irrigation with saline water [27]. Studies with *Cyprus* species [83] have shown that plants acclimatized in a given environment have a water memory to the point of regulating their Kp according to the need and the time of exposure to stressful conditions. In that study, the authors showed that in the first year, little significant effect of the moderate drought treatment on hydraulic conductivity was demonstrated; however, there were significant effects in the second year of the study. The same results were shown in *Pinus sylvestris* and *Quercus pubescens* [41]. However, the reduction in the lumen vessel area emerges as a crucial strategy for countering and evading stresses [45,66,82]. Furthermore, other

pivotal factors exert their influence on altering resistances within the xylem, consequently leading to variations in hydraulic conductance. These factors encompass the characteristics of secondary wall thickening, perforation plates, vessel dimensions, and density [84]. In a study conducted by Xu et al. [84], the intricate relationship between anatomical traits of vessels and water transport within *J. curcas* xylem was meticulously analyzed. Their findings underscored that despite xylem vessels offering a low-resistance conduit for water transport, even subtle changes in the inner diameter of the vessels had a significant impact on overall resistance. Recently, Pompelli et al. [85] showed by different methodologies that hydraulic conductance measured in the sugarcane stalk showed a fine-tuning with g_s as a determining coefficient higher than 0.86 to non-irrigated plants and 0.94 with those that are irrigated. Typically, the atmosphere presents a negative water potential, often as low as -100 MPa. Consequently, leaves are forced to release water into the atmosphere through the process of transpiration [40]. However, in order to prevent dehydration and potential harm, when faced with water scarcity, the leaf takes a defensive stance by closing its stomata, effectively minimizing or nearly halting transpiration, including the latent heat fluxes. Consequently, leaves with closed stomata, which are not actively transpiring, experience a rise in T_{leaf} . This increase in leaf temperature is inversely related to photosynthesis, often leading to reduced photosynthetic activity, as shown in this study, where these features showed a negative correlation ($r = -0.692$) between them. On the other hand, plants inhabiting arid and xerophytic habitats tend to exhibit characteristics that promote the formation of smaller, thicker leaves [22,36,40,86,87]. Larger leaves tend to possess reduced convection coefficients and exhibit greater resistance to heat transfer through the boundary layers of the leaves in comparison to their smaller counterparts [69]. Consequently, these plants may undergo adjustments in leaf size as an adaptive strategy to optimize their T_{leaf} . As emphasized by Glover [88], trichomes are prominent in saving water. Specifically, the non-glandular trichomes, such as those described herein *C. pyramidale*.

Oliveira and Almeida [89] demonstrated that leaves of *C. pyramidale*, which developed in the dry season, were more tender and sclerophyllous than leaves collected in the rainy season. In this study, we describe that in the rainy year, the less rainfall caused an increase in TLT, ADAE, ABAE, and PP, respectively in 24.9%, 19.7%, 27.9%, and 70.8% aligned with Taratima et al. [90] and Taratima et al. [91] which described that anatomical adaptations also do occur under drought stress with an increase in the cuticle, epidermis, and leaf thickness prevent water loss. An increase of 70.8% in PP could be related to an increase in the photosynthetic cells and then a higher number of chloroplasts, as well as a decrease in the thickness of spongy tissue, which facilitates CO_2 reaching chloroplasts in the PP. These anatomical alterations could be an adaptation strategy to facilitate the photosynthesis process under stress conditions [92,93]. In fact, in this study, we described a negative correlation ($r = -0.391$) between the palisade and the spongy parenchyma (Supplementary data file). In accordance with Vogelmann et al. [94], the arrangement of a palisade mesophyll composed of a single cell layer arrangement may be directly associated with the channeling of the light path within the leaf.

In accordance with Evert [54], a greater palisade parenchyma should be able to compensate for the reduction in leaf area, thus contributing to the increase in the total leaf thickness as a response to drought stress. As previously reported in the literature [54], xeric leaves displayed a notable increase in xylem thickness and total xylem area when contrasted with their counterparts in the forest. This adaptation appears to be a compensatory response aimed at accommodating the augmented transpiration rates associated with an elevated water supply. In this sense, it is probable that during the dry season, leaves exhibited a decreased xylem thickness in comparison to the wet season, aligning with findings from other investigations [95]. These observations strongly suggest that, in these plant species, the hydraulic transport system is predominantly modulated by the availability of water.

Notably, all the attributes associated with the midrib displayed a positive correlation with net photosynthesis in our study. This finding suggests that alterations in vein xylem

characteristics may play a pivotal role in regulating hydraulic mechanisms for gas exchange, particularly when adapting to water scarcity. It implies that the species under investigation adapt their midrib features, including the reduction in vessel area and vessel density, as a strategy to enhance their tolerance to reduced water availability during the dry season. These shifts in vein xylem conductivities can significantly influence leaf gas exchange and its responsiveness to changing environmental conditions. This assertion is substantiated by previously published correlation analyses between leaf hydraulic conductance and leaf anatomy [96], which describe the connection between leaf hydraulic conductance and leaf anatomy across six ecologically diverse species under both high and low irradiance levels. Their findings established that anatomical modifications statistically accounted for 40% of the observed variation in leaf hydraulic conductance across species. In line with these previous studies, our results highlighted substantial variations in midrib traits, particularly in the total midrib area, total xylem area, and vessel area. This aligns with findings from other investigations [96,97], further emphasizing the significance of these adaptations in leaf hydraulic regulation.

The ability of plants to alter their characteristics in response to changing environmental conditions is termed phenotypic plasticity, and it appears as morphological and/or physiological changes [98,99]. Clearly, the variations in functional attributes depend on the plant species, the choice of the attributes to be analyzed, and the environment to which the plants are subjected [51]. Higher plasticity index was previously reported in *C. pyramidale* [51,57]. However, these authors do not conduct any phenotypic plasticity analysis to confirm their hypothesis. For clarity, phenotypic plasticity is an index ranging from 0 to 1 estimated using the maximum and minimum value for each analyzed feature estimation [47,100]. Contrary to this, in our study, the phenotypic plasticity was computed for many features in several combinations of conditions. In accordance with Ribeiro et al. [32] and Gratani [98], higher standard deviations in the leaves of trees growing in some xerophytic environments could be related to the phenotypic plasticity of this species. Our results corroborate these presented data and add that due to a higher variance for data, any statistical difference was able to be distinguished in anatomical features, although physiological plasticity was higher than anatomical plasticity.

5. Conclusions

The data presented in this study leads us to believe that the main effect that led to the extremely low gas exchange in 2019 was the occurrence of the La Niña meteorological phenomenon, which cools the waters of the North Pacific, causing an extreme lack of rain in Northeast Brazil and other areas of the world. The primary action employed by *C. pyramidale* to mitigate desiccation and sustain essential photosynthetic rates involved lowering its foliar water potential. This reduction, aligned with transpiration chances and stomatal closure, serves to curtail excessive water loss during periods of limited water supply, safeguarding the plant's hydraulic structure even when the leaf water potential is low. Also, our dataset shows that *C. pyramidale* responds quickly to changes in the environment, such as variations in annual rainfall, VPD, transpiration, SLA, and leaf area. The lower Ψ_w reduced the plant metabolism and, per analogy, net photosynthesis as a strategy to stress fugue or stress avoidance because the activation energy is lowered more than Ψ_w . Thus, *C. pyramidale* can be considered an important species in the management and reforestation of degraded areas due to its phenotypic plasticity. This adjustment shows that *C. pyramidale* is a good indicator for the regrowth of Caatinga dry forest.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/f15020346/s1>, Supplementary data file; Supplementary Table S1. Principal component analysis autovectors. Supplementary Figure S1. Net photosynthesis (A–D), stomatal conductance (E–H), transpiration (I–L) and intrinsic water use efficiency (M–P) measured in March 2019 (A,E,I,M), August 2019 (B,F,J,N), March 2020 (C,G,K,O), and August 2020 (D,H,L,P) in *Cenostigma pyramidale* grown in field conditions in the driest year (2019) and a normal rain year (2020) in both seasonal condition (rainy, March and dry, August). Means followed by small case letters denote

statistical significance between months, regardless of year, and means followed by uppercase letters denote statistical significance between years in the same month. All values denote media $\pm$ SD. $n = 10$.

Author Contributions: M.F.P. Conceptualization, methodology, software, formal analysis, investigation, writing—original draft preparation, writing—review and editing. A.J.-O. Conceptualization, investigation, writing—original draft preparation, writing—review and editing, funding acquisition. J.d.D.J.-N. Conceptualization, investigation, writing—original draft preparation, writing—review and editing, funding acquisition. Y.Y.P.-R. formal analysis, investigation; L.A.R.-P. Conceptualization, investigation, writing—original draft preparation, writing—review and editing, funding acquisition. All authors have read and agreed to the published version of the manuscript.

Funding: Foundation for Science and Technology of Pernambuco, FACEPE (Grants APQ-0239-2.03/15) for financially supporting this research.

Data Availability Statement: The data statement is evaluable on Supplementary Figure S1.

Conflicts of Interest: The authors declare no conflict of interest.

References

- Haworth, M.; Marino, G.; Brunetti, C.; Killi, D.; De Carlo, A.; Centritto, M. The impact of heat stress and water deficit on the photosynthetic and stomatal physiology of olive (*Olea europaea* L.—A case study of the 2017 heat wave. *Plants* **2017**, *7*, 76. [CrossRef]
- Ramirez, R. Quatro Gráficos Alarmanes que Mostram o Quão Extremo o Clima Está Atualmente. *CNN Brasil*. 2023. Available online: <https://www.cnnbrasil.com.br/internacional/quatro-graficos-alarmanes-que-mostram-o-quao-extremo-o-clima-esta-atualmente/> (accessed on 7 December 2023).
- Planelles, M. Crise Ambiental Avança e Clima Extremo Desafia o Mundo. *El País*. 2021. Available online: <https://brasil.elpais.com/ciencia/2021-08-01/clima-extremo-desafia-o-mundo.html> (accessed on 7 December 2023).
- Schleuning, M.; Fründ, J.; Schweiger, O.; Weld, E.; Albrecht, J.; Albrecht, M.; Beil, M.; Benadi, G.; Blüthgen, N.; Bruehlheide, H.; et al. Ecological networks are more sensitive to plant than to animal extinction under climate change. *Nat. Commun.* **2016**, *7*, 13965. [CrossRef]
- Almar, R.; Boucharel, J.; Graffin, M.; Abessolo, G.O.; Thoumyre, G.; Papa, F.; Ranasinghe, R.; Montano, J.; Bergsma, E.W.J.; Baba, M.W. Influence of El Niño on the variability of global shoreline position. *Nat. Commun.* **2023**, *14*, 3133. [CrossRef]
- McKenna, M.; Karamperidou, C. The impacts of El Niño diversity on northern hemisphere atmospheric blocking. *Geophys. Res. Lett.* **2023**, *50*, e2023GL104284. [CrossRef]
- Glotfelty, T.; Zhang, Y. Impact of future climate policy scenarios on air quality and aerosol-cloud interactions using an advanced version of CESM/CAM5: Part II. Future trend analysis and impacts of projected anthropogenic emissions. *Atmos. Environ.* **2017**, *152*, 531–552. [CrossRef]
- Rizhsky, L.; Liang, H.J.; Mittler, R. The combined effect of drought stress and heat shock on gene expression in tobacco. *Plant Physiol.* **2002**, *130*, 1143–1157. [CrossRef]
- Rizhsky, L.; Liang, H.; Shuman, J.; Shulaev, V.; Davletova, S.; Mittler, R. When defense pathways collide: The response of *Arabidopsis* to a combination of drought and heat stress. *Plant Physiol.* **2004**, *134*, 1683–1696. [CrossRef]
- Sun, S.; Jung, E.; Gaviria, J.; Engelbrecht, B.M.J. Drought survival is positively associated with high turgor loss points in temperate perennial grassland species. *Funct. Ecol.* **2020**, *34*, 788–798. [CrossRef]
- Pompelli, M.F.; Martins, S.C.V.; Antunes, W.C.; Chaves, A.R.M.; DaMatta, F.M. Photosynthesis and photoprotection in coffee leaves is affected by nitrogen and light availabilities in winter conditions. *J. Plant Physiol.* **2010**, *167*, 1052–1060. [CrossRef] [PubMed]
- Pompelli, M.F.; Ferreira, P.P.B.; Chaves, A.R.M.; Figueiredo, R.C.Q.Q.; Martins, A.O.; Jarma-Orozco, A.; Batista-Silva, W.; Endres, L.; Araújo, W.L. Physiological, metabolic, and stomatal adjustments in response to salt stress in *Jatropha curcas*. *Plant Physiol. Biochem.* **2021**, *168*, 116–127. [CrossRef] [PubMed]
- Ronchi, C.P.; DaMatta, F.M.; Batista, K.D.; Moraes, G.A.B.K.; Loureiro, M.E.; Ducatti, C. Growth and photosynthetic down-regulation in *Coffea arabica* in response to restricted root volume. *Funct. Plant Biol.* **2006**, *33*, 1013–1023. [CrossRef]
- Praxedes, S.C.; DaMatta, F.M.; Loureiro, M.E.; Ferrão, M.A.G.; Cordeiro, A.T. Effects of long-term soil drought on photosynthesis and carbohydrate metabolism in mature robusta coffee (*Coffea canephora* Pierre var. kouillou) leaves. *Environ. Exp. Bot.* **2006**, *56*, 263–273. [CrossRef]
- Arcoverde, G.B.; Rodrigues, B.M.; Pompelli, M.F.; Santos, M.G. Water relations and some aspects of leaf metabolism of *Jatropha curcas* young plants under two water deficit levels and recovery. *Braz. J. Plant Physiol.* **2011**, *23*, 123–130. [CrossRef]
- Lawlor, D.W.; Tezara, W. Causes of decreased photosynthetic rate and metabolic capacity in water-deficient leaf cells: A critical evaluation of mechanisms and integration of processes. *Ann. Bot.* **2009**, *103*, 561–579. [CrossRef]
- Pompelli, M.F.; Barata-Luís, R.M.; Vitorino, H.S.; Gonçalves, E.R.; Rolim, E.V.; Santos, M.G.; Almeida-Cortez, J.S.; Endres, L. Photosynthesis, photoprotection and antioxidant activity of purging nut under drought deficit and recovery. *Biomass Bioenergy* **2010**, *34*, 1207–1215. [CrossRef]

18. Smirnov, N. Antioxidant systems and plant response to the environment. In *Environment and Plant Metabolism: Flexibility and Acclimation*; Smirnov, N., Ed.; Bios Scientific: Oxford, UK, 1995; pp. 217–243.
19. Krieger-Liszczay, A.; Fufezan, C.; Trebst, A. Singlet oxygen production in photosystem II and related protection mechanism. *Photosynth. Res.* **2008**, *98*, 551–564. [\[CrossRef\]](#)
20. Antunes, W.C.; Mendes, K.R.; Chaves, A.R.M.; Ometto, J.P.; Jarma-Orozco, A.; Pompelli, M.F. *Spondias tuberosa* trees grown in tropical, wet environments are more susceptible to drought than those grown in arid environments. *Rev. Col. Ciên. Hortic.* **2016**, *10*, 9–27. [\[CrossRef\]](#)
21. Gatti, L.V.; Gloor, M.; Miller, J.B.; Doughty, C.E.; Malhi, Y.; Domingues, L.G.; Basso, L.S.; Martinewski, A.; Correia, C.S.C.; Borges, V.F.; et al. Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature* **2014**, *506*, 76–83. [\[CrossRef\]](#) [\[PubMed\]](#)
22. Mendes, K.R.; Granja, J.A.A.; Ometto, J.P.; Antonino, A.C.D.; Menezes, R.S.C.; Pereira, E.C.; Pompelli, M.F. *Croton blanchetianus* modulates its morphophysiological responses to tolerate drought in a tropical dry forest. *Funct. Plant Biol.* **2017**, *44*, 1039–1051. [\[CrossRef\]](#)
23. Ashraf, M.; Harris, P. Photosynthesis under stressful environments: An overview. *Photosynthetica* **2013**, *51*, 163–190. [\[CrossRef\]](#)
24. Acosta-Motos, J.R.; Ortuño, M.F.; Bernal-Vicente, A.; Diaz-Vivancos, P.; Sanchez-Blanco, M.J.; Hernandez, J.A. Plant responses to salt stress: Adaptive mechanisms. *Agronomy* **2017**, *7*, 18. [\[CrossRef\]](#)
25. Corte-Real, N.; Miranda, P.V.V.C.; Endres, L.; Souza, E.R.; Pompelli, M.F. Tolerance to salinity in *Jatropha curcas* are genotype-dependent. *Braz. J. Dev.* **2019**, *5*, 22169–22199. [\[CrossRef\]](#)
26. Gomes, M.F.C.; Binneck, E.; Ferreira-Neto, J.R.C.; Luz, G.A.; Benko-Iseppon, A.M.; Pompelli, M.F.E.L.; Kido, É.A. Transcriptome analysis uncovers the *Jatropha curcas* L. transportome after NaCl (150 mM) exposure. *Physiol. Plant* **2021**, in press.
27. Cao, H.; Han, Y.; Cheng, Z.; Lv, Q.; Pompelli, M.F.; Pereira, J.D.; Araújo, W.L. Long exposure to salt stress in *Jatropha curcas* leads to stronger damage to the chloroplast ultrastructure and its functionality than the stomatal function. *Forest* **2023**, *14*, 1868. [\[CrossRef\]](#)
28. Fernández-Marín, B.; Guliás, J.; Figueroa, C.M.; Iñiguez, C.; Clemente-Moreno, M.J.; Nunes-Nesi, A.; Fernie, A.R.; Cavieres, L.A.; Bravo, L.A.; García-Plazaola, J.I.; et al. How do vascular plants perform photosynthesis in extreme environments? An integrative ecophysiological and biochemical story. *Plant J.* **2020**, *101*, 979–1000. [\[CrossRef\]](#)
29. Ennajeh, M.; Vadel, A.M.; Cochard, H.; Khemira, H. Comparative impacts of water stress on the leaf anatomy of a drought-resistant and a drought-sensitive olive cultivar. *J. Hortic. Sci. Biotechnol.* **2010**, *85*, 289–294. [\[CrossRef\]](#)
30. Tomás, M.; Medrano, H.; Brugnoli, E.; Escalona, J.M.; Martorell, S.; Pou, A.; Ribas-Carbo, M.; Flexas, J. Variability of mesophyll conductance in grapevine cultivars under water stress conditions in relation to leaf anatomy and water use efficiency. *Aust. J. Grape Wine Res.* **2014**, *20*, 272–280. [\[CrossRef\]](#)
31. Santos, M.G.; Oliveira, M.T.; Figueiredo, K.V.; Falcão, H.M.; Arruda, E.C.P.; Almeida-Cortez, J.S.; Sampaio, E.V.S.B.; Ometto, J.P.H.B.; Menezes, R.S.C.; Oliveira, A.F.M.; et al. Caatinga, the Brazilian dry tropical forest: Can it tolerate climate changes? *Theor. Exp. Plant Physiol.* **2014**, *26*, 83–99. [\[CrossRef\]](#)
32. Ribeiro, I.M.C.; Arruda, E.C.P.; Oliveira, A.F.M.; Almeida, J.S. Physical and chemical defenses of *Cenostigma pyramidale* (Fabaceae): A pioneer species in successional caatinga areas. *Rev. Caatinga* **2021**, *34*, 398–409. [\[CrossRef\]](#)
33. Almazroui, M.; Islanm, M.N.; Saeed, F.; Alkhalaf, A.K.; Dambul, R. Assessing the robustness and uncertainties of projected changes in temperature and precipitation in AR5 Global Climate Models over the Arabian Peninsula. *Atmos. Res.* **2017**, *194*, 202–213. [\[CrossRef\]](#)
34. Angulo-Brown, F.; Sánchez-Salas, N.; Barranco-Jiménez, M.A.; Rosales, M.A. Possible future scenarios for atmospheric concentration of greenhouse gases: A simplified thermodynamic approach. *Renew. Energy* **2009**, *34*, 2344–2352. [\[CrossRef\]](#)
35. O'Neill, B.C.; Oppenheimer, M.; Warren, R.; Hallegatte, S.; Kopp, R.E.; Pörtner, H.O.; Scholes, R.; Birkmann, J.; Foden, W.; Licker, R.; et al. IPCC reasons for concern regarding climate change risks. *Nat. Clim. Chang.* **2017**, *7*, 28–37. [\[CrossRef\]](#)
36. Pinho-Pessoa, A.C.B.; Mendes, K.R.; Jarma-Orozco, A.; Pereira, M.P.S.; Santos, M.A.; Menezes, R.S.C.; Ometto, J.P.; Pereira, E.C.; Pompelli, M.F. Interannual variation in temperature and rainfall can modulate the physiological and photoprotective mechanisms of a native semiarid plant species. *Ind. J. Sci. Technol.* **2018**, *11*, 1–17. [\[CrossRef\]](#)
37. Dombroski, J.L.D.; Praxedes, S.C.; Freitas, R.M.O.; Pontes, F.M. Water relations of Caatinga trees in the dry season. *S. Afr. J. Bot.* **2011**, *77*, 430–434. [\[CrossRef\]](#)
38. Pompelli, M.F.; Mendes, K.R.; Ramos, M.V.; Santos, J.N.B.; Youssef, D.T.A.; Pereira, J.D.; Endres, L.; Jarma-Orozco, A.; Solano-Gomes, R.; Jarma-Arroyo, B.; et al. Mesophyll thickness and sclerophylly among *Calotropis procera* morphotypes reveal water-saved adaptation to environments. *J. Arid Land* **2019**, *11*, 795–810. [\[CrossRef\]](#)
39. Mendes, K.R.; Campos, S.; Mutti, P.R.; Ferreira, R.R.; Ramos, T.M.; Marques, T.V.; Dos Reis, J.S.; Vieira, M.M.L.; Silva, A.C.N.; Marques, A.M.S.; et al. Assessment of SITE for CO₂ and energy fluxes simulations in a seasonally dry tropical forest (Caatinga Ecosystems). *Forests* **2021**, *12*, 86. [\[CrossRef\]](#)
40. Mendes, K.R.; Batista-Silva, W.; Dias-Pereira, J.; Pereira, M.P.S.; Souza, E.V.; Serrão, J.E.; Granja, J.A.A.; Pereira, E.C.; Gallacher, D.J.; Mutti, P.R.; et al. Leaf plasticity across wet and dry seasons in *Croton blanchetianus* (Euphorbiaceae) at a tropical dry forest. *Sci. Rep.* **2022**, *12*, 954. [\[CrossRef\]](#)
41. IBGE. *Biomass e Sistema Costeiro-Carinho do Brasil: Compatível com a Escala 1:250.000 v.45*; Instituto Brasileiro de Geografia e Estatística: Rio de Janeiro, Brazil, 2019; p. 168.
42. Holzman, B.A. *Tropical Forest Biomes*; Greenwood Press: Westport, CT, USA, 2008.

43. INMET. Estações Climáticas, Gráficos. *diário*. 2023. Available online: <https://portal.inmet.gov.br/dadoshistoricos> (accessed on 10 August 2023).
44. Scholander, P.F.; Bradstreet, E.d.; Hemmingsen, E.A.; Hammel, H.T. Sap pressure in vascular plants negative hydrostatic pressure can be measures in plants. *Science* **1965**, *148*, 339–346. [\[CrossRef\]](#)
45. Sterck, F.J.; Zweifel, R.; Sass-Klaassen, U.; Chowdhury, Q. Persisting soil drought reduces leaf specific conductivity in Scots pine (*Pinus sylvestris*) and pubescent oak (*Quercus pubescens*). *Tree Physiol.* **2008**, *28*, 529–536. [\[CrossRef\]](#)
46. Scholz, A.; Klepsch, M.; Karimi, Z.; Jansen, S. How to quantify conduits in wood? *Front. Plant Sci.* **2013**, *4*, 56. [\[CrossRef\]](#)
47. Valladares, F.; Balaguer, L.; Martinez-Ferri, E.; Perez-Corona, E.; Manrique, E. Plasticity, instability and canalization: Is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? *New Phytol.* **2002**, *156*, 457–467. [\[CrossRef\]](#)
48. Reddy, T.; Reddy, V.; Anbumozhi, V. Physiological responses of groundnut (*Arachis hypogea* L.) to drought stress and its amelioration: A critical review. *Plant Growth Regul.* **2003**, *41*, 75–88. [\[CrossRef\]](#)
49. Leigh, A.; Sevanto, S.; Close, J.D.; Nicotra, A.B. The influence of leaf size and shape on leaf thermal dynamics: Does theory hold up under natural conditions? *Plant Cell Environ.* **2016**, *40*, 237–248. [\[CrossRef\]](#)
50. Markesteijn, L.; Poorter, L.; Bongers, F. Light-dependent leaf trait variation in 43 tropical dry forest tree species. *Am. J. Bot.* **2007**, *94*, 515–525. [\[CrossRef\]](#)
51. Falcão, H.M.; Medeiros, C.D.; Silva, B.L.R.; Sampaio, E.V.S.B.; Almeida-Cortez, J.; Santos, M.G. Phenotypic plasticity and ecophysiological strategies in a tropical dry forest chronosequence: A study case with *Poincianella pyramidalis*. *For. Ecol. Manag.* **2015**, *340*, 62–69. [\[CrossRef\]](#)
52. Pagotto, M.A.; Roig, F.A.; Ribeiro, A.S.; Lisi, C.S. Influence of regional rainfall and Atlantic sea surface temperature on tree-ring growth of *Poincianella pyramidalis*, semiarid forest from Brazil. *Dendrochronologia* **2018**, *35*, 14–23. [\[CrossRef\]](#)
53. Onoda, Y.; Wright, I.J.; Evans, J.R.; Hikosaka, K.; Kitajima, K.; Niinemets, Ü.; Poorter, H.; Tosens, T.; Westoby, M. Physiological and structural tradeoffs underlying the leaf economics spectrum. *New Phytol.* **2017**, *214*, 1447–1463. [\[CrossRef\]](#)
54. Evert, R.F. *Esau's Plant Anatomy—Meristems, Cells, and Tissues of Tre Plant Body—Their Structures, Function and Development*, 3rd ed.; John Wiley & Sons, Inc.: Hoboken, NJ, USA, 2013; p. 624.
55. Wright, C.L.; West, J.B.; de Lima, A.L.A.; Souza, E.S.; Medeiros, M.; Wilcox, B.P. Contrasting water use strategies revealed by species-specific transpiration dynamics in the Caatinga dry forest. *Tree Physiol.* **2023**, *in press*. Available online: <https://pubmed.ncbi.nlm.nih.gov/37935389/> (accessed on 1 December 2023). [\[CrossRef\]](#)
56. Warren, C.R.; Adams, M.A. Evergreen trees do not maximize instantaneous photosynthesis. *Trends Plant Sci.* **2004**, *9*, 270–274. [\[CrossRef\]](#)
57. Falcão, H.M.; Medeiros, C.D.; Almeida-Cortez, J.; Santos, M.G. Leaf construction cost is related to water availability in three species of different growth forms in a Brazilian tropical dry forest. *Theor. Exp. Plant Physiol.* **2017**, *29*, 95–108. [\[CrossRef\]](#)
58. Costa Júnior, E.O.; Silva-Oliveira, E.C.; Moura, J.C.M.; Melo, T.H.L. Photochemical quantum efficiency of *Aspidosperma pyrifolium* (Mart) and *Poincianella pyramidalis* (Tul.) L. P. Queiroz in an area of semiarid tropics (Soledade City, Paraíba, Northeast Brazil). *Braz. J. Biol. Sci.* **2014**, *1*, 59–65. [\[CrossRef\]](#)
59. Barros, V.; Froisi, G.; Santos, M.; Ramos, D.G.; Falcao, H.M.; Santos, M.G. Arbuscular mycorrhizal fungi improve photosynthetic energy use efficiency and decrease foliar construction cost under recurrent water deficit in woody evergreen species. *Plant. Physiol. Bioch.* **2018**, *127*, 469–477. [\[CrossRef\]](#)
60. Valladares, F.; Pearcy, R.W. Interactions between water stress, sunshade acclimation, heat tolerance and photoinhibition in the sclerophyll *Heteromeles arbutifolia*. *Plant Cell Environ.* **1997**, *20*, 25–36. [\[CrossRef\]](#)
61. Bernacchi, C.J.; Portis, A.R.; Nakano, H.; von Caemmerer, S.; Long, S.P. Temperature response of mesophyll conductance. Implications for the determination of Rubisco enzyme kinetics and for limitation to photosynthesis in vivo. *Plant Physiol.* **2002**, *130*, 1992–1998. [\[CrossRef\]](#)
62. Asargew, M.F.; Masutomi, Y.; Kobayashi, K.; Aono, M. Water stress changes the relationship between photosynthesis and stomatal conductance. *Sci. Total Environ.* **2024**, *907*, 167886. [\[CrossRef\]](#)
63. Huang, G.; Zeng, Y. Increased stomatal conductance and leaf biochemical capacity, not mesophyll conductance, contributing to the enhanced photosynthesis in *Oryza* plants during domestication. *Planta* **2024**, *259*, 28. [\[CrossRef\]](#)
64. Dunford, S. Translocation in the Phloem. In *Plant Physiology*, 5th ed.; Taiz, L., Zeiger, E., Eds.; Sinauer Associates Inc.: Sunderland, MA, USA, 2010; pp. 271–303.
65. Buchanan, B.B.; Wolosiuk, R.A. Photosynthesis: The carbon reactions. In *Plant Physiology*, 5th ed.; Taiz, L., Zeiger, E., Eds.; Sinauer Associates Inc.: Sunderland, MA, USA, 2010; pp. 199–242.
66. Tyree, M. Dynamic measurements of root hydraulic conductance using a high pressure flowmeter in the laboratory and field. *J. Exp. Bot.* **1995**, *46*, 83–94. [\[CrossRef\]](#)
67. North, G.B.; Brinton, E.K.; Browne, M.G.; Gillman, M.G.; Roddy, A.B.; Kho, T.L.; Wang, E.; Fung, V.A.; Brodersen, C.R. Hydraulic conductance, resistance, and resilience: How leaves of a tropical epiphyte respond to drought. *Am. J. Bot.* **2019**, *106*, 943–957. [\[CrossRef\]](#)
68. Roach, T.; Neuner, G.; Kranner, I.; Buchner, O. Heat acclimation under drought stress induces antioxidant enzyme activity in the alpine plant *Primula minima*. *Antioxidants* **2023**, *12*, 1093. [\[CrossRef\]](#)
69. Woodward, F.I. Do plants really need stomata? *J. Exp. Bot.* **1998**, *49*, 471–480. [\[CrossRef\]](#)

70. Hsie, B.S.; Mendes, K.R.; Antunes, W.C.; Endres, L.; Campos, M.L.O.; Souza, F.C.; Santos, N.D.; Singh, B.; Arruda, E.C.P.; Pompelli, M.F. *Jatropha curcas* L. (Euphorbiaceae) modulates stomatal traits in response to leaf-to-air vapor pressure deficit. *Biomass Bioenergy* **2015**, *81*, 273–281. [\[CrossRef\]](#)
71. Drake, P.L.; Froend, R.H.; Franks, P.J. Smaller, faster stomata: Scaling of stomatal size, rate of response, and stomatal conductance. *J. Exp. Bot.* **2013**, *64*, 495–505. [\[CrossRef\]](#)
72. Santos, M.; Barros, V.; Lima, L.; Frosi, G.; Santos, M.G. Whole plant water status and non-structural carbohydrates under progressive drought in a Caatinga deciduous woody species. *Trees* **2021**, *35*, 1257–1266. [\[CrossRef\]](#)
73. Maherali, H.; DeLucia, E.H. Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. *Tree Physiol.* **2000**, *20*, 859–868. [\[CrossRef\]](#)
74. Tsuda, M.; Tyree, M.T. Plant hydraulic conductance measured by the high pressure flow meter in crop plants. *J. Exp. Bot.* **2000**, *51*, 823–828. [\[CrossRef\]](#)
75. Yuksel, M.; Al-agele, H.A.; Nackley, L.; Higgins, C.W. Hydraulic Conductivity of The Hemp Stems Under Water Stress. *bioRxiv* **2023**. [\[CrossRef\]](#)
76. Oliveira, P.S.; Pereira, L.S.; Silva, D.C.; Souza Júnior, J.O.; Laviola, B.G.; Gomes, F.P. Hydraulic conductivity in stem of young plants of *Jatropha curcas* L. cultivated under irrigated or water deficit conditions. *Ind. Crops Prod.* **2018**, *116*, 15–23. [\[CrossRef\]](#)
77. Krieger, L.; Schymanski, S.J. A new experimental setup to measure hydraulic conductivity of plant segments. *AoB Plants* **2023**, *15*, plad024. [\[CrossRef\]](#)
78. McDowell, N. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytol.* **2008**, *178*, 719–739. [\[CrossRef\]](#)
79. Sevanto, S.; McDowell, N.G.; Dickman, L.T.; Pangle, R.; Pockman, W.T. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant Cell Environ.* **2014**, *37*, 153–161. [\[CrossRef\]](#)
80. Poorter, L.; McDonald, I.; Alarcón, A.; Fichtler, E.; Licona, J.-C.; Peña-Claros, M.; Sterck, F.; Villegas, Z.; Sass-Klaassen, U. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytol.* **2010**, *185*, 481–492. [\[CrossRef\]](#)
81. Dodd, I.C. Abscissic acid and stomatal closure: A hydraulic conductance conundrum? *New Phytol.* **2013**, *197*, 6–8. [\[CrossRef\]](#)
82. Ladjal, M.; Huc, R.; Ducrey, M. Drought effects on hydraulic conductivity and xylem vulnerability to embolism in diverse species and provenances of Mediterranean cedars. *Tree Physiol.* **2005**, *25*, 1109–1117. [\[CrossRef\]](#)
83. Linton, M.J.; Sperry, J.S.; Williams, D.G. Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: Implications for drought tolerance and regulation of transpiration. *Funct. Ecol.* **1998**, *12*, 906–911. [\[CrossRef\]](#)
84. Xu, T.; Zhang, L.; Li, Z. Computational fluid dynamics model and flow resistance characteristics of *Jatropha curcas* L xylem vessel. *Sci. Rep.* **2020**, *10*, 14728. [\[CrossRef\]](#)
85. Pompelli, M.F.; Jarma-Orozco, A.; Rodríguez-Paéz, L.A. Screening of morphophysiological, anatomical, and ultrastructural traits to improve the elite genotype selection in sugarcane (*Saccharum officinarum* L.). *Horticulturae* **2022**, *8*, 1069. [\[CrossRef\]](#)
86. Bhatt, A.; Gallacher, D.; Jarma-Orozco, A.; Fernandes, D.; Pompelli, M.F. Seed provenance selection of wild halophyte seeds improves coastal rehabilitation efficiency. *Estuar Coast. Shelf Sci.* **2022**, *265*, 107657. [\[CrossRef\]](#)
87. Bhatt, A.; Chen, X.; Pompelli, M.F.; Jamal, A.; Mancinelli, R.; Radicetti, E. Characterization of invasiveness, thermotolerance and light requirement of nine invasive species in China. *Plants* **2023**, *12*, 1192. [\[CrossRef\]](#)
88. Glover, B.J. Differentiation in plant epidermal cells. *J. Exp. Bot.* **2000**, *51*, 497–505. [\[CrossRef\]](#)
89. Oliveira, J.A.B.; Almeida, J.S. Do the successional stage and plant architecture influence herbivory by insects in *Cenostigma pyramidale* in a dry tropical forest? *J. Environ. Anal. Progr.* **2021**, *6*, 352–362. [\[CrossRef\]](#)
90. Taratima, W.; Samattha, C.; Maneerattananurongroj, P.; Trunjaruen, A. Physiological and anatomical response of rice (*Oryza sativa* L.) ‘Hom Mali Daeng’ at different salinity stress levels. *Acta Agrobot.* **2023**, *76*, 764. [\[CrossRef\]](#)
91. Taratima, W.; Ritmaha, T.; Jongrungklang, N.; Maneerattananurongroj, P.; Kunpratun, N. Effect of stress on the leaf anatomy of sugarcane cultivars with different drought tolerance (*Saccharum officinarum*, Poaceae). *Rev. Biol. Trop.* **2020**, *68*, 1159–1170. [\[CrossRef\]](#)
92. El-Banna, M.F.; Abdelaal, K.A.A. Response of strawberry plants grown in the hydroponic system to pretreatment with H₂O₂ before exposure to salinity stress. *J. Plant Prod.* **2018**, *9*, 989–1001. [\[CrossRef\]](#)
93. Toscano, S.; Ferrante, A.; Tribulato, A.; Romano, D. Leaf physiological and anatomical responses of *Lantana* and *Ligustrum* species under different water availability. *Plant Physiol. Biochem.* **2018**, *127*, 380–392. [\[CrossRef\]](#)
94. Vogelmann, T.; Nishio, J.; Smith, W.K. Leaves and light capture: Light propagation and gradients of carbon fixation within leaves. *Trends Plant Sci.* **1996**, *1*, 65–70. [\[CrossRef\]](#)
95. Sack, L.; Scoffoni, C. Leaf venation: Structure, function, development, evolution, ecology and applications in the past, present and future. *New Phytol.* **2013**, *198*, 983–1000. [\[CrossRef\]](#)
96. Scoffoni, C.; Chatelet, D.S.; Pasquet-Kok, J.; Rawls, M.; Donoghue, M.J.; Edwards, E.J.; Sack, L. Hydraulic basis for the evolution of photosynthetic productivity. *Nat. Plants* **2016**, *2*, 16072. [\[CrossRef\]](#)
97. Nardini, A.; Pedà, G.; Rocca, N. Trade-offs between leaf hydraulic capacity and drought vulnerability: Morpho-anatomical bases, carbon costs and ecological consequences. *New Phytol.* **2012**, *196*, 788–798. [\[CrossRef\]](#)
98. Gratani, L. Plant phenotypic plasticity in response to environmental factors. *Adv. Bot.* **2014**, *2014*, 208747. [\[CrossRef\]](#)

99. Valladares, F.; Sanchez-Gomez, D.; Zavala, M.A. Quantitative estimation of phenotypic plasticity: Bridging the gap between the evolutionary concept and its ecological applications. *J. Ecol.* **2006**, *94*, 1103–1116. [[CrossRef](#)]
100. Valladares, F.; Arrieta, S.; Aranda, I.; Lorenzo, D.; Sanchez-Gomez, D.; Tena, D.; Suárez, F.; Pardos, J.A. Shade tolerance, photoinhibition sensitivity and phenotypic plasticity of *Ilex aquifolium* in continental Mediterranean sites. *Tree Physiol.* **2005**, *25*, 1041–1052. [[CrossRef](#)]

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