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Gas exchange and phenotypic plasticity in three tree species in preserved and anthropized areas in a Tropical Dry Forest

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ABSTRACT

Caatinga, the Brazilian tropical dry forest and source of endemic species, suffers anthropic disturbances that are responsible for affecting plants and their functional traits. This study aimed to evaluate the plasticity of woody species' leaf traits due to abiotic conditions of preserved and anthropized areas in Caatinga. The study took place in Vale do Riacho São José, in the municipality of Caetés, Pernambuco, Brazil. The selected species were *Mimosa tenuiflora*, *M. arenosa,* and *Senna* sp., all belonging to the Fabaceae family. We measured gas exchange, water content, specific leaf area, and phenotypic plasticity index of all selected species in both areas. Considering all species, stomatal conductance was higher in preserved areas, but photosynthesis was higher only for *Senna* sp. which also showed lower water use efficiency among all species. Furthermore, *Senna* sp. presented the highest relative water content in preserved areas and showed no differences in specific leaf areas between preserved and anthropized areas. The plasticity index showed that *Senna* sp. was the most plastic species, mainly adjusting water content and gas exchange parameters according to the area. The less plastic species was *M. arenosa*. A principal component analysis showed a group formation due to anthropization, for all species. However, *Senna* sp. showed the largest distance among species. All analyzed species respond to environmental conditions of preserved and anthropized areas, but this pattern cannot be related to the characteristics of the botanical family due to species-specific leaf traits' variations.

Keywords: Anthropization, functional traits, Caatinga, plant ecophysiology, photosynthesis, water use.

Introduction

Tropical Forests (TDF) comprise over 40% of the world's tropical forests, with areas in South America, Central America, Southeast Asia, India, Australia, the Caribbean, and two parallel belts in Africa (Miles et al., 2006). In recent decades, TDFs have been increasingly exploited, leading to anthropogenic activity becoming one of the main causes of biodiversity loss in these ecosystems (Isaza, Bernal & Howard, 2013).

The Caatinga is an exclusively Brazilian TDF. The population living in this ecosystem depends on the natural resources provided by the forest, exerting significant anthropogenic pressure that has been causing damage to the functioning of the ecosystem (Aquino et al., 2018).

Anthropogenic actions in the Caatinga are mostly related to agricultural and livestock activities but also involve deforestation for construction and uncontrolled exploitation of resources such as logging (Aragão et al., 2014). Over the years, TDFs have been exploited in an unsustainable manner, accelerating the degradation process (Silva et al., 2019). Unsustainable management of natural resources, mainly plants, generates significant impacts on the ecophysiological characteristics of plant species populations, affecting important processes such as photosynthesis, water balance, and ultimately productivity (Andrade et al., 2015). Such disturbances are responsible for modifications in the distribution of organisms and the diversity of biological communities. Additionally, they act as important environmental filters in TDFs, selecting those species that can cope with the effects of anthropogenic disturbances in the abiotic environment (Rito et al., 2016).

Plants, as essentially sessile organisms, have had to develop mechanisms of acclimation to environmental variation through adjustments of their functional attributes, such as photosynthetic rates, to maintain their biological processes functioning (Oguchi, Hikosaka & Hirose, 2003).

The conditions of a particular environment can be considered as selective agents that indicate which individuals present specific responses in key functional attributes necessary to establish and survive in the community (Violle et al., 2007). This ability of functional adjustment is known as phenotypic plasticity. Thus, plant organisms that present more plastic ecophysiological responses, both in morpho-anatomical and physiological attributes, may acquire a competitive advantage over other species in the community, thus maintaining their performance, even in anthropized environments (Koehn et al., 2010; Falcão et al., 2015). Therefore, understanding how anthropization modulates the values of functional attributes is essential for the development of conservation and recovery policies for degraded areas.

Thus, the study aimed to evaluate the photosynthetic capacity and phenotypic plasticity in three tree species in preserved and anthropized areas in a Caatinga site. Our central hypothesis is that plants in the preserved area have higher gas exchange values, but plants that show lower photosynthesis values have greater phenotypic plasticity, highlighting the fundamental trade-off between resource acquisition and utilization.

Material and Methods

Study area

The study was conducted in areas of Caatinga vegetation in the Riacho São José Valley, located in the municipality of Caetés, Pernambuco. This area has a medium-fertility soil of the Planosol type (Bernardo et al., 2014), with an annual temperature ranging between 25°C and 30°C, and average precipitation of less than 800 mm.

The location is characterized by a rainy season occurring between late March and July, and a dry season occurring between August and February (Chaves et al, 2022). The risk of drought is higher than 60%. The temperature and precipitation data were obtained from the Agritempo database (https://www.agritempo.gov.br). Two areas with different levels of disturbance were selected, one anthropized (08°46’33,614” S, 36°43’6.321” W) and one preserved (08°46’26.004” S, 36°43’5.520” W). The areas are 263 meters apart from each other. In each area, a plot of 20 m x 20 m was delimited with the aid of demarcation stakes.

The anthropized plot underwent clear-cutting for the subsequent planting of forage cacti. After years of cultivation, the area was abandoned, and fenced, and is currently in the process of natural regeneration for less than five years. The preserved plot has no history of clear-cutting or significant anthropogenic activity in the last 40 years.

Three adult tree species *Mimosa tenuiflora* (Willd.) Poir., *M. arenosa* (Willd.) Poir. and *Senna* sp., all belonging to the Fabaceae family, with at least five adult and healthy individuals each, with a diameter at breast height higher than 10 cm, occurring in both plots, were selected. Species from the same family were selected to avoid the responses found to be influenced by the phylogenetic history of the species.

All analyses were performed at the beginning of the rainy season, in March. Interestingly, in this year, the water balance data indicated an excess of soil moisture since January, which was observed in the field. Therefore, we selected the month of March for the analyses and collections because the vegetation already exhibited the expected growth typical of the rainy season. The plants were collected, pressed into exsiccates, and taken for identification in the herbaria (Herbário IPA - Dárdano de Andrade Lima of the Instituto Agronômico de Pernambuco and Herbário UFP - Geraldo Mariz of the Universidade Federal de Pernambuco), and compared with other records made in the region.

Air temperature, air humidity, and vapor pressure deficit (VPD) were measured (Figure 1). The soil water balance in the first four months of the year was calculated using the Thornthwaite & Mather (1955) methodology. Temperature and air humidity were measured with a digital thermo-hygrometer (Termo-Higro SH 122, J Prolab. São José dos Pinhais, BR). The VPD was calculated using the formula: VPD = es-ea, where es is saturated vapor pressure, and ea is the pressure deficit in the environment (Campbell & Norman, 1998).

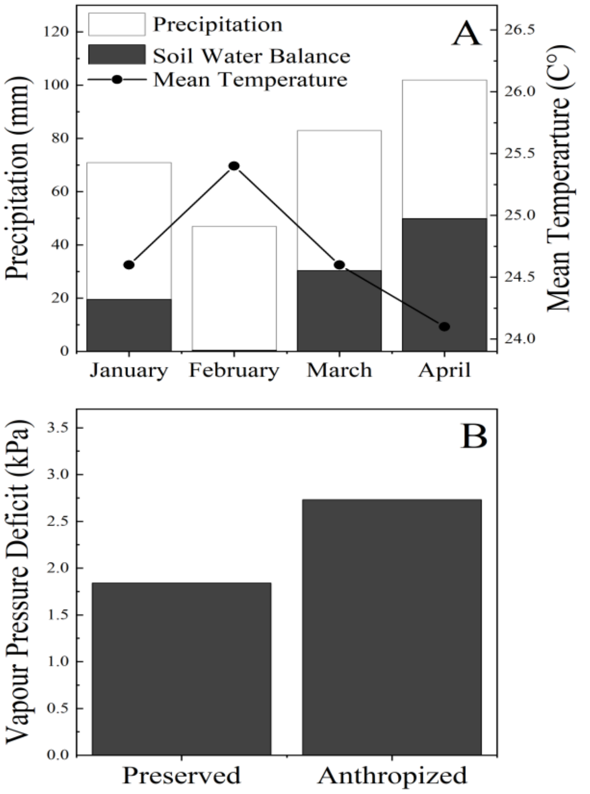

Figure 1. A. Total precipitation, soil water balance, and average air temperature. from January to April 2022; B. Vapor Pressure Deficit of preserved and anthropized areas of a Caatinga region in the municipality of Caetés, Brazil. Font: Cavalcanti et al. (2023).

Relative water content

To evaluate the hydration of plant tissues, the analysis of relative water content (RWC) was performed on 3 leaves per individual per species in each plot. Leaf samples were collected in the early morning, at the time of highest water potential, and immediately weighed on an analytical balance to obtain the fresh weight. The samples were then placed in flasks containing water for rehydration for 24h, at which point they were weighed again to obtain the turgid weight. After that, the samples were taken to a forced ventilation oven for 72h and weighed to obtain the dry weight. RWC was calculated by the formula: RWC = {[(FW - DW) / (TW - DW)] x 100} %, following the methodology of Barrs & Wheaterley (1962), where FW is the fresh weight, TW the turgid weight, and DW the dry weight.

Photosynthetic capacity

Gas exchanges were performed using an Infrared Gas Analyzer (LCi, ADC Bioscientific, Hoddeston, UK) on three fully expanded and undamaged leaves per individual, on a sunny morning between 8:00 am and 10:00 am. The gas analyzer was calibrated with the incident solar radiation at the time of measurement. Net CO_2 assimilation rate (A), stomatal conductance (g_s), leaf transpiration (E). The intrinsic water use efficiency (iWUE) was obtained by dividing A by g_s. Specific leaf area (SLA) was obtained by collecting the leaves used in gas exchange, scanning them on a table scanner to obtain leaf area, and drying them in a forced ventilation oven to obtain dry weight. SLA was obtained by dividing leaf area by dry weight (cm^{-2}.g).

Data analysis

All data were tested for normality and homogeneity, showing that they were all parametric. A t-test was performed for each species to compare the values of relative water content, gas exchange, and specific leaf area, with the type of plot (preserved or anthropized) as the independent variable.

The phenotypic plasticity of leaf functional traits, and the mean plasticity of each species, were calculated according to Valladares et al. (2007). To verify if the functional leaf traits analyzed were sufficient to differentiate plant responses based on anthropization, we conducted a Principal Component Analysis (PCA).

The overall phenotypic plasticity of each species was obtained by averaging the plasticity values of the measured functional traits. All analyses were performed using the open-access software BioEstat 5.0.

Results and Discussion

During the data analysis period, the average temperature ranged from 24.2ºC to 25.4ºC between January to April, with precipitation of 47 mm to 100 mm during the same period (Figure 1A). In turn, the soil water balance varied from 0 to 24.9 mm (Figure 1A). Water stress conditions can affect leaf functional traits, mainly those related to gas exchange and water potential (Violle et al., 2007). Thus, the soil water balance indicates that the analyzed attributes and parameters were not altered due to water deficit, since the collections were made in March, which had a surplus of about 30 mm.

The RWC is a good indicator of water quantity in plants, which did not show a significant difference in *M. arenosa* between preserved and anthropized areas (Figure 2A). In turn, *M. tenuiflora* showed different RWC in the studied areas, with values >40% in the anthropized area and >30% in the preserved area.

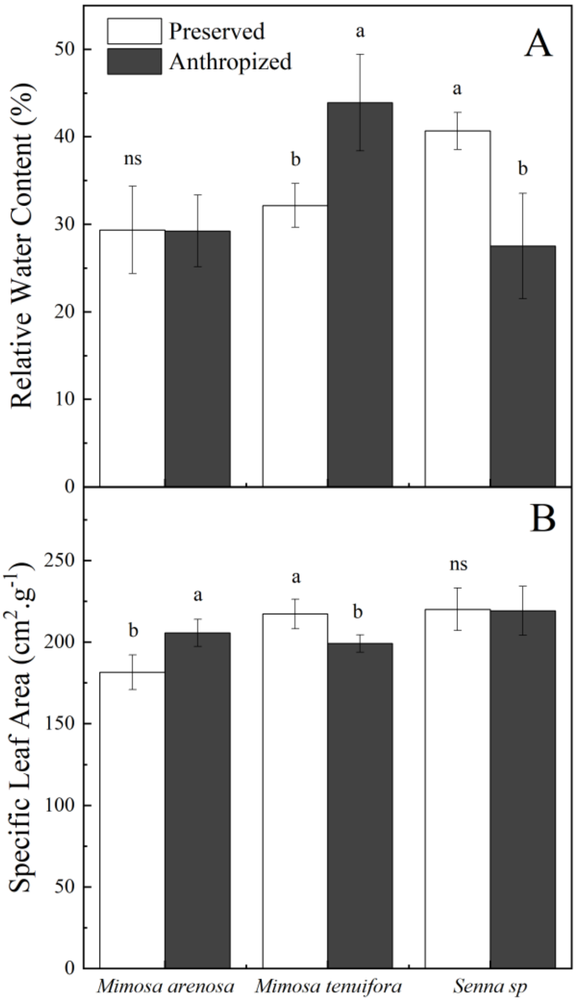

Figure 2. A. Relative water content; B. specific leaf area of three woody species from the Caatinga region in the municipality of Caetés, Brazil, in preserved and anthropized areas. Columns with the same letters, within the same species, did not differ from each other by the Student Newman-Keul's test (5%), n = 3, ns = not significant. Font: Cavalcanti et al. (2023).

Despite observing distinct response patterns among the three species, net assimilation of CO_2 (Figure 3A) only differed between areas in *Senna* sp., with lower values in the anthropized area than in the preserved area. Although both *Mimosa* species showed lower stomatal conductance in the anthropized area, their CO_2 assimilation remained constant, possibly due to the high iWUE presented by these species when found in the anthropized area (Figure 3C).

Considering the leaf, iWUE is related to several factors that control important physiological processes, such as VPD and water availability in the soil (Hatfield & Dold, 2019). Indeed, *M. arenosa* showed a similar RWC between areas, and *M. tenuiflora* showed a higher RWC in the anthropized area. These RWC values possibly directly influenced the iWUE values in these species, favoring CO_2 assimilation even under higher VPD conditions. Jin et al. (2017) state that RWC is one of the main physiological factors that limit photosynthesis in plants, and it is possible to observe that the three species show gas exchange responses associated with VPD and RWC conditions between the study areas.

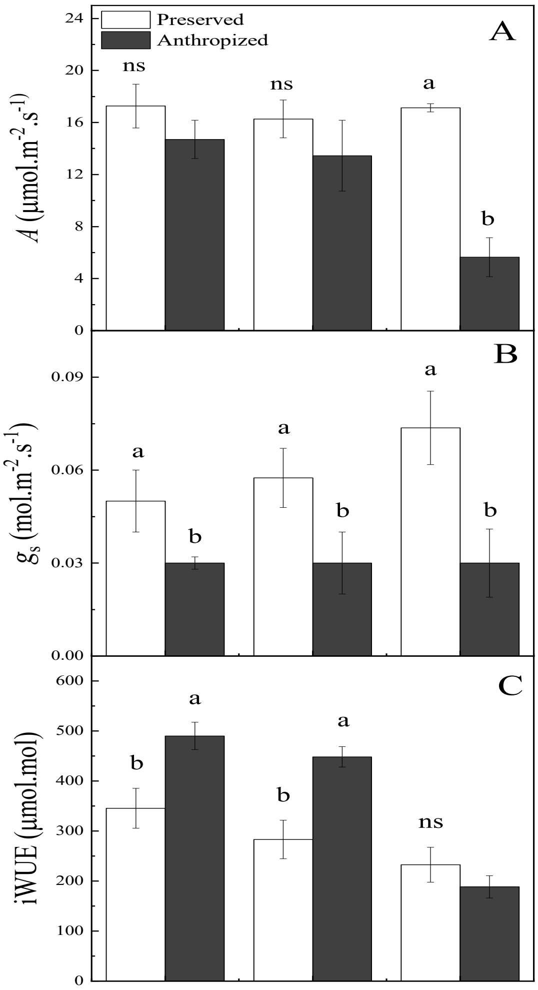

Figure 3. A. Net CO_2 assimilation; B. stomatal conductance; C. intrinsic water use efficiency of three woody species from Caatinga in the municipality of Caetés, Brazil, in preserved and anthropized areas. Font: Cavalcanti et al. (2023).

The SLA is an indicator of biomass allocation and plant growth (Cheng et al., 2016). Furthermore, this leaf trait is directly related to environmental disturbance, varying positively according to the intensity of the disturbance (Prado Junior et al., 2015).

The species *M. arenosa* showed lower SLA in the preserved area (150 $cm^2.g^{-1}$) than in the anthropized area (200 $cm^2.g^{-1}$), while *M. tenuiflora* showed the opposite behavior, with higher SLA in the preserved area (220 $cm^2.g^{-1}$) and lower in the anthropized area (200 $cm^2.g^{-1}$) (Figure 2B).

Senna sp. did not show a significant difference in SLA between the studied areas. SLA is one of the main indicators of biomass distribution in plants. Consequently, it is related to photosynthesis and the plant's ability to capture and use water resources (Cheng et al., 2016; Pérez-Harguindeguy et al., 2016). Thus, it is crucial to observe the variation in SLA between areas in conjunction with the other measured functional traits.

In general, plants located in disturbed areas have a higher specific leaf area, higher leaf turnover, and higher photosynthetic rates (Dwyer et al., 2014; Prado Junior et al., 2015). Indeed, this behavior can be observed in *M. arenosa*. The higher specific leaf area in this species in the disturbed area leads to greater water loss to the atmosphere. However, this seems to be a strategy to maintain its high photosynthetic rates even under high VPD.

The efficient stomatal control and water use of this species allow it to maintain a similar water-use efficiency to plants found in the preserved area (Figure 3B). Thus, this species can cope well with the most severe conditions in the disturbed area. Fagundes, Mazzochini & Ganade (2023) point out that biomass production was higher in restored communities with species that had high specific leaf areas, which makes this species an important factor in degraded area restoration programs.

The VPD was lower in the preserved area when compared to the anthropized area (Figure 1B). VPD refers to atmospheric evaporative demand. Thus, in situations of high VPD values, plants tend to close their stomata to reduce water loss through transpiration (Grossiord et al., 2020). The results show that stomatal conductance (g_s) was lower in the anthropized area than in the preserved area for the three species analyzed in this study (Figure 3B).

Mimosa tenuiflora showed higher SLA in the preserved area (Figure 2B). It is important to note that this species had a high RWC in the anthropized area, which favored the production of smaller leaves with greater biomass. Despite having similar gas exchange rates to *M. arenosa*, several studies suggest that leaf area is controlled by factors other than VPD, such as N availability, temperature, light intensity, air shade tolerance, and soil moisture (Fender et al., 2011; Li et al., 2015).

Senna sp. showed similar SLA values between the areas (Figure 2B). The RWC of this species was lower in the anthropized area, which led to very low photosynthetic rates (Figures 2A and 3A) since water availability is the main limiting factor for photosynthesis (Caferri & Bassi, 2022). This species invests the fixed carbon in maintaining its leaf area to capture more light. In this sense, water use efficiency would be essential to avoid excessive water loss through transpiration, since *Senna* sp. can maintain a similar water use efficiency between the areas.

Studies indicate that productivity may be influenced more by iWUE than by water use rates, a concept that has already been addressed in investigations on agriculture but may have important ecological implications (Basso & Ritchie, 2018; Velasco-Muñoz, 2018). In a scenario of climate change, for example, an increased demand for water is expected due to reduced precipitation and rising average air temperatures, which will elevate the evaporative demand of the soil. Thus, plants with high iWUE can allocate more biomass with less water usage, which can be a competitive success factor (Hatfield & Dold, 2019).

The principal component analysis shows a clear spatial separation between species, both within the same area and between anthropized and preserved areas (Figure 4).

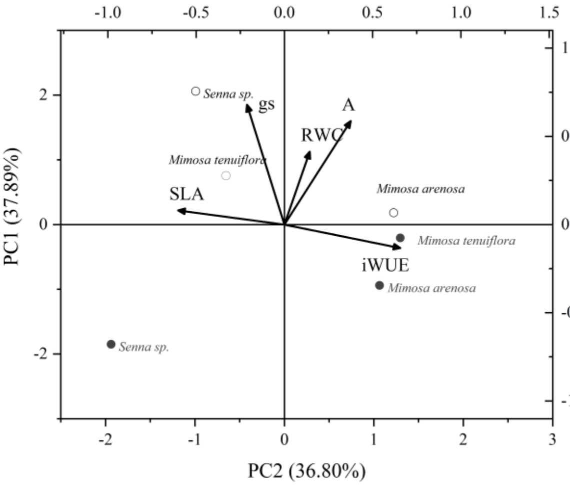

Figure 4. Principal component analysis of leaf functional traits of three woody species from a Caatinga area in the municipality of Caetés, Brazil, in preserved (open circles) and anthropized areas (black circles). Font: Cavalcanti et al. (2023)

The measured attributes explain 74.69% of the spatial distribution of the species, with SLA (-0.60) and iWUE (0.65) being the main ones responsible for the separation of species between preserved and anthropized areas. In other words, the environmental conditions of the studied areas directly influenced how plants used water and invested in carbon. This response pattern can be confirmed by analyzing the phenotypic plasticity of species (Table 1). SLA was more plastic in *M.*

arenosa (0.41), while the most plastic in *M. tenuiflora* was iWUE (0.50). In *Senna* sp., the most plastic attribute was CO_2 assimilation (0.73), followed by g_s (0.63).

Table 1. Coefficient of variation of leaf functional traits of three woody species from Caatinga in the municipality of Caetés, Brazil, between preserved and anthropized areas. SLA = specific leaf area; RWC = relative water content; A = net CO_2 assimilation; g_s = stomatal conductance; iWUE = intrinsic water use efficiency; Mean = mean plasticity of the species (trait value per number of traits). Font: Cavalcanti et al. (2023).

Species	**Functional traits**					
	SLA	**RWC**	**A**	g_s	**iWUE**	**Mean**
Mimosa arenosa	0.41	0.26	0.21	0.40	0.32	0.32
Mimosa tenuiflora	0.14	0.38	0.38	0.46	0.50	0.37
Senna sp.	0.16	0.51	0.73	0.63	0.37	0.48

Phenotypic plasticity refers to the plant's ability to adjust its functional traits according to changes in the environment, and these conditions influence evolutionary and adaptive processes (Nicotra et al., 2010). Furthermore, phenotypic plasticity allows us to understand the processes involved in species responses and how they will respond to scenarios caused by environmental changes (Parmesan, 2006; Van Kleunen & Fischer, 2007; Lande, 2009; Matesanz, Gianoli & Valladares, 2010).

The data shows that the total plasticity of each species differs among them, with the most plastic species being *Senna* sp. (0.48). The attributes of this species can adjust more strongly to the conditions of preserved and anthropized areas than *M. arenosa* and *M. tenuiflora* (0.32 and 0.37, respectively). Having high plasticity in functional attributes, especially those related to water and carbon capture, such as gs and A, is a competitive advantage against the scenarios of anthropization and desertification in the Caatinga (Sultan, 2000).

In general, in dry forests, where the main environmental filter is water availability (Lebrija-Trejos et al., 2010), functional traits related to water uptake and use will be most affected, and are expected to show the greatest plasticity responses, such as SLA, iWUE, and g_s, as observed in the analyzed species (Table 1).

Although the studied species are from the Fabaceae family and are found in the same plot (anthropized or preserved), the responses of their leaf functional traits were differentiated because they do not depend solely on external factors such as RWC and VPD, but also on internal factors of the plant organism (Boyer, Kertesz & Bruno, 2009; Duan et al., 2022). Bradshaw (1965) stated that plasticity can differ even among closely related species and that these differences are difficult to explain unless we consider that the plasticity of a functional trait is subject to the specific genetic control of each species.

Conclusion

This study showed the difference in the variation of leaf functional traits in response to changes in the environment of three Fabaceae species located in preserved and anthropized areas. The most plastic functional traits were specific leaf area, intrinsic water use efficiency, and stomatal conductance. Thus, we can observe that the ability to capture and use water to assimilate CO_2 is a key factor for the success of plants in anthropized environments. Among the analyzed species, *Senna* sp. showed greater phenotypic plasticity than *M. arenosa* and *M. tenuiflora*. This greater capacity to adjust its functional traits to environmental conditions is essential for maintaining its population in an environment like the Caatinga, one of the most threatened forests by increasing anthropization and climate change.

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