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INTRASPECIFIC PLASTICITY DRIVES DIFFERENT DROUGHT-TOLERANCE STRATEGIES AND HELPS TO SHAPE FORESTS PHYTOPHYSIOGNOMIES IN THE BRAZILIAN SAVANNAH

Autora: Maria Lucia Fontineles da Silva Orientadora: Dra. Fernanda S. Farnese Coorientador: Dr. Paulo E. Menezes Silva

Rio Verde – GO Setembro/2024

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BIOGRAFIA

Maria Lucia Fontineles da Silva nasceu em 05 de setembro de 1992 no município de Coelho Neto – MA. Mudou-se para Rio Verde - GO em 2010, aos 18 anos. Em 2011 iniciou sua jornada acadêmica no IF Goiano – Campus Rio Verde, no curso técnico em Contabilidade, o qual concluiu com êxito em julho de 2012. Em fevereiro de 2013 ingressou no curso de Licenciatura em Ciências Biológicas, o qual trancou em 2014, por um período de dois anos para servir em uma missão religiosa. Ao retornar, em 2016, iniciou sua trajetória na pesquisa científica por meio do programa de iniciação científica, sob a orientação dos professores Fernanda Farnese e Paulo Eduardo, que tiveram grande influência em sua vida acadêmica. Após a conclusão da graduação planejou ingressar no Mestrado, mas o plano foi adiado em função da pandemia de Covid-19. Ingressou no Mestrado em 2022, onde foi selecionada para Bolsa de Formação da FAPEG, e em 2024 conseguiu um incentivo para um intercâmbio curto, também pela FAPEG, o qual foi feito na "Universität Ulm", em Ulm na Alemanha. Fora da vida acadêmica, Maria Lucia é apaixonada por livros, música, sua gatinha "Maya" e futebol.

ÍNDICE

AGRADECIMENTOS	i
BIOGRAFIA	vi
ÍNDICE	vii
ÍNDICE DE FIGURAS E TABELAS	viii
LISTA DE SIGLAS E ABREVIATURAS RESUMO	ix x
ABSTRACT	xi
Introduction	1
Material and methods	4
Study areas and species evaluated	4
Environmental variables	5
Leaf water potential	5
Gas exchange	5
Plant water leaks	5
Xylem vulnerability to embolism and hydraulic safety margin	6
Pressure-volume curves	7
Stem density and capacitance	8
Water transport in the plant	8
Biomass investment	9
Data analysis Results	9 9
Environmental variables	9
Tissue hydration and water loss	9
Water storage	11
Water transport safety	12
Carbon acquisition and investment in growth	14
Multivariate Analysis Discussion	15 17
Despite facing a more severe environmental drought, plants in the dry forest maintained similar water potential compared to plants in the Gallery Forest	! 17
Balance between water loss and release: plants in the Gallery Forest lose more water, b not have greater capacitance	ut do 18
Different microclimates result in different drought response strategies	19
Conclusions	21
References	22

ÍNDICE DE FIGURAS E TABELAS

Figure 1 – Diagram showing sampling areas: (A) Gallery Forest and (B) Dry Forest. .. 4 **Figure 2** – Midday Water potential (Ψ_{w-md}) in co-occurring species in Cerrado fragments **Figure 3** – Water loss parameters in co-occurring species in Cerrado fragments (Gallery Forest (blue) and Dry Forest (brown)) collected during the dry season. The following were evaluated: A – Stomatal conductance (g_s) ; B - transpiration rate (E); C – residual leaf transpiration (g_{leaf}) ; D – residual bark transpiration (g_{bark}) ; and E – total leaf area Figure 4 – Water transport safety parameters in co-occurring species in two fragments of the Cerrado (Gallery Forest (blue) and Dry Forest (brown)). A – Xylem vulnerability to embolism; B – Loss of rehydration capacity (PLRC); C – Loss of xylem conductivity of the stem (PLC_{stem}); and D – Hydraulic safety margin (HSM), collected during the dry Figure 5 – Water transport efficiency parameters in co-occurring species in Cerrado fragments (Gallery Forest (blue) and Dry Forest (brown)). A - Leaf hydraulic Figure 6 – Carbon acquisition and carbon investment parameters in co-occurring species in Cerrado fragments (Gallery Forest (blue) and Dry Forest (brown)). A - Net carbon assimilation (A); B – Internal/external carbon concentration (C_i/C_a); C – Carboxylation efficiency (A/C_i) ; D – Water use efficiency (A/E); E – Specific leaf area (SLA); F – Figure 7 – Multivariate analysis (PCA analysis). Two-dimensional PCA biplots showing associations between plants in Gallery (blue) and Dry Forest (brown) and physiological

Sigla	Significado		
Α	Net carbon assimilation rate		
A/Ci	Carboxylation efficiency		
A/E	Water use efficiency		
AH	Air Humidity		
AT	Average temperature		
BGR	Branch growth rate		
С	Leaf capacitance		
Ci	Internal carbon concentration		
Ci/Ca	Internal and external carbon concentration ratio		
C _{stem}	Stem capacitance		
C_{TLP}	Capacitance at turgor loss point		
$D_{ m wood}$	Wood density		
Ε	Transpiration rate		
3	Elastic modulus		
$g_{ m bark}$	Bark minimum conductance to water vapour		
$g_{ m leaf}$	Leaf minimum conductance to water vapour		
$g_{\rm s}$	Stomatal conductance		
HSM	Hydraulic safety margin		
K _{leaf}	Leaf hydraulic conductivity		
K _{max}	Maximum hydraulic conductivity		
K _{stem}	Hydraulic conductivity of the stem		
PLC	Percent loss of conductivity		
P_{12}	Water potential associated to 12% PLC		
P ₅₀	Water potential associated to 50% PLC		
P ₈₈	Water potential associated to 88% PLC		
PCA	Principal component analysis		
PLRC	Percent loss of rehydration capacity		
RWC _{stem}	Relative water content of the stem		
RWC _{TLP}	Relative water content at turgor loss point		
SLA	Specific leaf area		
SM	Soil moisture		
SWC _{Leaf}	Saturated water content of the leaf		
TLA	Total leaf area		
VPD	Vapor pressure deficit		
VWC _{stem}	Volumetric water content of the stem		
Ψ_{\min}	Minimal water potential		
Ψ_{TLP}	Turgor loss point		
$\Psi_{w\text{-md}}$	Midday water potential		
По	Osmotic potential		

RESUMO

SILVA, MARIA LUCIA FONTINELES DA. Instituto Federal Goiano – Campus Rio Verde, setembro de 2024. **Intraspecific plasticity drives different drought-tolerance strategies and helps to shape forests phytophysiognomies in the Brazilian savannah.** Orientadora: Fernanda dos Santos Farnese. Coorientador: Paulo Eduardo de Menezes Silva. Programa de Pós-Graduação em Biodiversidade e Conservação.

A disponibilidade hídrica desempenha um papel central no crescimento e sobrevivência das plantas e, portanto, é um fator determinante na distribuição das espécies pelo globo. A vulnerabilidade e a dependência das plantas da disponibilidade hídrica envolvem uma série de fatores que atuam em conjunto e podem ser divididos em três grupos principais: i) redução das perdas de água para a atmosfera; ii) capacidade de continuar absorvendo e transportando água durante a seca; e iii) presença de reservatórios internos de água. É provável que a influência da disponibilidade hídrica seja ainda mais preponderante em ambientes mais secos e com alta sazonalidade, como é o caso do Cerrado brasileiro, a maior savana dos Neotrópicos e uma das mais ricas em biodiversidade do mundo, onde a precipitação durante a estação seca pode ser próxima de zero e a disponibilidade hídrica é variável dependendo de onde o fragmento de Cerrado está localizado. Portanto, no presente estudo, analisamos características funcionais que impactam diretamente a vulnerabilidade das plantas à restrição hídrica, com foco em estratégias para manutenção do estado hídrico e tolerância do xilema à seca em espécies que ocorrem simultaneamente em Mata de Galeria e Mata Seca no Cerrado. Nossos dados mostraram que as espécies da Mata Seca foram associadas a características que indicam tolerância à seca, como menor P_{50} (potencial hídrico no qual 50% dos vasos do xilema estão embolizados), ponto de perda de turgor (Ψ_{TLP}) e potencial osmótico (Π_0), enquanto as mesmas espécies, quando localizadas na Mata de Galeria, apresentaram maior reservatório de água e maior transpiração residual. Além disso, em ambas as áreas as espécies operaram em uma ampla margem de segurança hidráulica (HSM), indicando alta resiliência de algumas espécies do Cerrado mesmo com a intensificação das mudanças climáticas. Os resultados obtidos nos permitem observar uma grande plasticidade intraespecífica das espécies que coocorrem na Mata de Galeria e na Mata Seca e apontam para estratégias distintas para lidar com a seca no Cerrado.

Palavras-chave: Vulnerabilidade ao embolismo, crescimento, g_{leaf}, Cerrado.

ABSTRACT

SILVA, MARIA LUCIA FONTINELES DA. Instituto Federal Goiano – Campus Rio Verde, September 2024. Intraspecific plasticity drives different drought-tolerance strategies and helps to shape forests phytophysiognomies in the Brazilian savannah. Supervisor: Fernanda dos Santos Farnese. Co-supervisor: Paulo Eduardo de Menezes Silva. Programa de Pós-Graduação em Biodiversidade e Conservação.

Water availability plays a central role in plant growth and survival and is therefore a determining factor in the distribution of species across the globe. The vulnerability and therefore the dependence of plants on water availability involves a series of factors that act together and can be divided into three main groups: i) reduction of water losses to the atmosphere; *ii*) the ability to continue absorbing and transporting water during drought; and *iii*) the presence of internal water reservoirs. It is likely that the influence of water availability is even more preponderant in drier environments with high seasonality, as is the case with the Brazilian Cerrado, the largest savanna in the Neotropics and one of the richest in biodiversity in the world, where precipitation during the dry season can be close to zero and the water availability is variable depending on the location of the Cerrado fragment. Therefore, in the present study, we analyzed functional traits that directly impact plant vulnerability to water restriction, focusing on strategies for maintaining water status and xylem tolerance to drought in species that occur simultaneously in Gallery Forest and Dry Forest in the Cerrado. Our data showed that the species from the Dry Forest were associated with characteristics that indicate drought tolerance, such as lower P_{50} (Water potential associated to 50% PLC), turgor loss point (Ψ_{TLP}) and osmotic potential (Π_0), while the same species, when located in the Gallery Forest, showed greater water reservoir and greater residual transpiration. Besides, in both areas the species operated in a broad hydraulic safety margin (HSM), indicating high resilience of some Cerrado species even with the intensification of climate change. The results obtained allow us to observe great intraspecific plasticity in the species that co-occur in the Gallery Forest and Dry Forest and point to distinct strategies for dealing with drought in the Cerrado.

Key-words: Embolism vulnerability, growth, *g*_{leaf}; Cerrado.

Introduction

The Cerrado Domain of central Brazil is the largest savanna in the Neotropics and one of the richest in biodiversity in the world, home to more than 12,600 known plant species (Forzza et al., 2012). It contains considerable vegetation heterogeneity, including many types of grasslands, savanna formations, and forests (Ribeiro & Walter, 2008; Bueno et al., 2017). Bueno et al. (2017) found that ecological variables are key to explaining the species composition in different Cerrado vegetation types. When considering the transition between forest formations and savanna formations, the floristic gradient is controlled mainly by soil fertility (Bueno et al., 2013, 2017). Within forest formations, such as Gallery Forest and Dry Forest, there is great variability in water availability (Ribeiro & Walter, 2008; Bueno et al., 2017). Gallery Forest is a physiognomy associated with watercourses, while Dry Forest occurs on well-drained lands. In addition to the greater availability of water in the soil, in Gallery Forests, the relative humidity is high even in the driest season of the year, because the canopies provide tree cover of 70 to 95%. In Dry Forests, canopy cover can be as low as 35% during the dry season (Ribeiro & Walter, 2008). Such differences might create microgradients within each formation that can lead to contrasting environmental challenges, such as high VPD in the Dry Forest.

Water availability plays a central role in plant growth and survival and is therefore a determining factor in the distribution of species across the globe (Trueba *et al.*, 2017; Garcia *et al.*, 2022). Oliveira *et al.* (2019), for example, demonstrated that embolism resistance drives the distribution of Amazonian plants, in such a way that plants located in areas with lower precipitation typically have a more drought-tolerant xylem (lower P_{50}). Plants with high P_{50} , on the other hand, tend to occur closer to water bodies or in areas with high precipitation (Oliveira *et al.*, 2019). It is likely that the influence of water bodies is even more preponderant in drier environments with high seasonality, as is the case of the Brazilian Cerrado, where precipitation during the dry season can be close to zero (Campos & Chaves, 2020). Despite this, a study analyzing the distribution of 3,072 Cerrado tree species over 1,165 sites demonstrated that approximately 70% of the species that occur in Dry Forest also occur in Gallery Forest (Bueno *et al.*, 2017). The co-occurrence of Cerrado species in phytophysiognomies with distinct environmental characteristics indicates high intraspecific plasticity (Albert *et al.*, 2010) but the hydraulic traits involved in the acclimatization of these plants are still poorly understood. The vulnerability and, therefore, the dependence of plants on water availability involves a series of factors that act together and can be divided into three main groups: *i*) reduction of water losses to the atmosphere; *ii*) the ability to continue absorbing and transporting water during drought; and *iii*) the presence of internal water reservoirs. Typically, the first response of plants to drought is a reduction in stomatal aperture, and the consequent decrease in transpiration, which helps maintain cellular water potential (Vieira *et al.*, 2017; Alves *et al.*, 2020). However, even after complete stomatal closure, plants continue to lose water to the atmosphere, to a greater or lesser extent, through residual transpiration from leaves (g_{leaf}) (Duursma *et al.*, 2019; Machado *et al.*, 2021; Slot *et al.*, 2021) and bark (g_{bark}) (Loram-Lorenço *et al.*, 2022). Thus, both g_{leaf} and g_{bark} represent a continuous loss of water that can substantially affect the survival of species exposed to water deficit (Duursma *et al.*, 2019b; Loram-Lourenço *et al.*, 2022).

The loss of water to the atmosphere, associated with reduced soil moisture, increases tension in the xylem vessels, which can cause cavitation and, subsequently, embolism. The embolized vessel loses its ability to transport water (Vilagrosa *et al.*, 2012). Depending on the proportion of embolized vessels, the plant may undergo hydraulic failure, which is commonly identified as the main determinant of tree mortality around the world (Hartmann *et al.*, 2018; Hammond *et al.*, 2019). The vulnerability of species to embolism depends on the characteristics of the xylem and some studies have already shown that this trait can be adjusted in plants exposed to water deficit (López *et al.*, 2016a). The P_{50} is the most widely used trait to assess xylem vulnerability and represents the water potential (Ψ_w) at which 50% of the xylem vessels are embolized (Hammond *et al.*, 2019). Plants with lower P_{50} are able to maintain water transport in the face of greater dehydration and are therefore more tolerant to water restriction (Oliveira *et al.*, 2019).

The third determining factor in the dynamics of plant dehydration is the storage and release of water from internal reservoirs (Martinez-Vilalta *et al.*, 2019). Capacitance is a key trait that reflects the potential ability to release water in response to variations in the water status of different plant organs, thus buffering changes in water potential (Meinzer *et al.*, 2003; Salomón *et al.*, 2017). Capacitance showed a strong correlation with water balances in large wood (Carrasco *et al.*, 2015) and herbaceous species (Pereira *et al.*, 2024). The amount of water stored in different tissues is also important to prevent turgor loss, which can lead to loss of membrane function (rupture and cell death) and impairment of central physiological processes, such as photosynthesis (McDowell *et al.*, 2022). Thus, it is likely that capacitance also influences the distribution of plant species along different water gradients.

Although important for plant survival during drought conditions, investment in hydraulic safety (lower P_{50} , g_{leaf} , and g_{bark}) may imply higher costs to plants in terms of carbon investment. Some studies have already shown that more drought-tolerant xylem often results in higher construction costs, *i.e.* higher structural investment in fibers and lignified tissues (B. Eller et al., 2018; Franklin et al., 2023). The reduction in water loss through the cuticle, in turn, appears to be influenced by the length of the carbon chains of the fatty acids. It has been observed that the cuticle of the water-saver plant *Phoenix* dactylifera has a higher proportion of long-chain fatty acids than the cuticle of the waterspender Citrullus colocynthis (Bueno et al., 2019). These components were also associated with higher LMA. In Arabidopsis thaliana the shift in the cuticular wax profile toward the very-long-chain fatty acids delayed the onset of wilting in plants experiencing water deficit (Lü et al., 2012). Similarly, investments in thicker and denser outer bark resulted in significant reductions in gbark of ten Cerrado species (Loram-Lourenço et al., 2022). Therefore, both decreases in g_{leaf} and g_{bark} are strategies that also imply a higher production cost, demonstrating that drought tolerance demands high carbohydrate investment and low carbohydrate availability can limit plasticity. Thus, the existence of a trade-off between drought survival and growth has been widely accepted (Pérez-Ramos et al., 2013; Iida et al., 2023; Ziegler et al., 2024). Although it is an attractive hypothesis, however, it is necessary to consider that lower growth rates would affect the ability to change traits in response to drought.

In the present study, we analyzed functional traits that directly impact plant vulnerability to water restriction, focusing on strategies for maintaining water status and xylem tolerance to drought in species that occur simultaneously in Gallery Forest and Dry Forest in the Cerrado. The main objective of this work was to evaluate how water availability in different phytophysiognomies modulates intraspecific changes in hydraulic traits associated with water loss and storage, and vulnerability to xylem dysfunction, which, in turn, modulates the phytophysiognomies, as it allows the existence of the same species in environments with contrasting climate conditions and resources (*i.e.* water) availability. The following hypotheses were tested: *i*) To allow for successful colonization of environments with contrasting climate and resource availability, high intraspecific plasticity in hydraulic traits (e.g. water leaks, water storage, and vulnerability to embolism) would be observed in Cerrado species cooccurring in different

phytophysiognomies; and *ii*) within species, plants in the Dry Forest will show lower growth rates, when compared to those inhabiting the Gallery Forest, which would help to sustain the high plasticity costs associated with drought-tolerance strategies.

Material and methods

Study areas and species evaluated

The study was conducted in two Cerrado fragments with distinct phytophysiognomies, both located in the city of Rio Verde - GO, approximately 1.0 km apart from each other. One of the fragments contains a water body, to which a Gallery Forest is associated; whereas the second area has a vegetation formation typical of Dry Forest. Five species found in both studied areas were selected: *Chrysophyllum marginatum* (Sapotaceae), *Lithraea molleoides* (Anacardiaceae), *Rhamnidium elaeocarpum* (Rhamnaceae), *Tocoyena formosa* (Rubiaceae) and *Bauhinia forficata* (Fabaceae). The species were selected according to their availability, in an adequate number of replicates (n = 5), in the two Cerrado fragments.



Figure 1 – Diagram showing sampling areas: (A) Gallery Forest and (B) Dry Forest.

Environmental variables

To characterize the areas under study, data on air humidity, temperature, and soil moisture were collected on two non-simultaneous days, at 9 points close to the sampled trees, totaling 18 sampling points (**Table 1**). Air humidity and temperature were obtained using digital thermo-hygrometers (EXBOM FEPRO-MUT60OS), with measurements being taken simultaneously in both areas. Soil moisture was determined with a soil moisture sensor (HydroSense II), at 9 a.m. and 1 p.m. Sampling was conducted during the dry season of the Cerrado. The only exception was the xylem vulnerability curve to embolism, which was conducted during the rainy season to avoid artifacts in the technique. The analyses performed are described below.

Leaf water potential

To evaluate the water status of the plants during peak transpiration, the midday water potential (Ψ_{w-md}) of a sun-exposed leaf was measured using a pressure chamber. Before each measurement, the sampled leaves were equilibrated for at least 5 min inside ziplock bags with damp paper towels (Rodriguez-Dominguez *et al.*, 2022).

Gas exchange

Leaf gas exchange was measured using an open-flow infrared gas exchange analyzer system equipped with a leaf chamber fluorometer (LI-6800; Li-Cor). Stomatal conductance (g_s), and the transpiration rate (E) were determined on attached, fully expanded leaves. Environmental conditions in the leaf chamber consisted of a photosynthetic photon flux density of 1000 µmol m⁻² s⁻¹, a vapor pressure deficit of 1.0– 1.5 kPa, an air temperature of 25 °C, and an ambient CO₂ concentration of 400 µmol mol⁻¹ air. Net carbon assimilation rate (A, µmol CO₂·m⁻²·s⁻¹) and internal carbon concentration (Ci, µmol·m⁻²·s⁻¹) were also obtained.

Plant water leaks

Bark and leaf minimum conductance to water vapour (g_{bark} and g_{leaf} respectively) were determined gravimetrically from the consecutive weight loss of desiccating organs (Sack *et al.*, 2003; Wolfe, 2020; Machado *et al.*, 2021). Before analysis, the branches

were recut underwater and allowed to rehydrate overnight in the dark to ensure water saturation of stem and leaf tissues. For g_{bark} , a leafless segment (i.e. 5 cm in length) was removed from the branch base whereas for g_{leaf} , we sampled a sun-exposed, fully expanded leaf of the same branch. Melting paraffin wax was used to seal the wounds of cut stems and petioles of leaves. Stems and leaves were dried in a growth chamber at controlled temperature (25°C) under dark conditions (to induce stomatal closure) and weighed at regular intervals (30 – 45 min). The temperature and relative humidity inside the chamber were measured at 20-minute intervals with a digital thermal hygrometer to check for variation during measurements. Bark and leaf minimum transpiration was estimated as the slope of water loss versus time, normalized by the stem section area or the total leaf surface area and divided by the average mole fraction vapor pressure deficit (VPD).

Xylem vulnerability to embolism and hydraulic safety margin

The leaf vulnerability to embolism was determined using the optical vulnerability technique (Brodribb et al., 2016). During the rainy season, branches approximately 1 m long were collected from 3-4 individuals of each species in the late afternoon (18:00 h), in the two areas analyzed. Each branch was placed in a recipient with water, covered with a moist plastic bag, and moved to the laboratory. The branches were kept in rehydration overnight. The next day, plants were placed on a bench and a leaf from each branch was introduced into the optical apparatus. The leaf remained attached to the plant throughout the analysis period. During the dry-down period, xylem water potential was measured in leaves previously covered with aluminum foil and plastic bag (e.g. 30 minutes before measurements), using a Scholander pressure chamber every 1-3h. Water potential was interpolated for each time point using the slope and intercept of the linear equation following the optical vulnerability method in OPEN-SOURCEOV (OSOV; http://www. opensourceov.org) (Brodribb et al., 2016). Images from time-lapse stacks were imported into ImageJ and analyses were conducted using the OSOV software package. Vulnerability curves were generated by using the *fitPLC* function (Duursma & Choat, 2017; Suissa & Friedman, 2021) in *R* v.4.0.2 (R Core Team, 2018, Preprint). Xylem vulnerability was evaluated and compared using the Ψ w, resulting in 12% (P_{12}), 50% (P_{50}), and 88% (P_{88}) xylem embolism. These values were extracted directly from the data for each vulnerability curve.

The hydraulic safety margin was calculated based on the difference between P_{50} and Ψ_{min} . Since water potential was collected at midday (during the peak of the transpiration), and during the driest month of the year, the Ψ_{w-md} was considered as Ψ_{min} (i.e. the lowest water potential during the season) (B. Eller *et al.*, 2018), as follow:

$HSM = P_{50} - \Psi_{min}$

The native hydraulic conductivity of the stem segments (K_{stem}) was determined with a flow system, following the proposed by Markesteijn *et al.* (2011). Sun-exposed branches were collected in the field, kept in a container with water, and transported to the laboratory. In the laboratory, the branches were dipped into the perfusion solution (distilled and degassed water at 10 mM KCl) and the ends of the stem were cut off. The end portions of the stem were connected to a hydraulic flow apparatus (Sperry *et al.*, 1988). The mass of solution flowing per unit of time through the stem was constantly monitored using volumetric pipettes. This value, together with the applied pressure and the length of the stem segment was used to obtain the hydraulic conductance of the stem (*K*h). The sapwood area was estimated in a cross-section at the distal end of the segment and subtracted from the heartwood area, assuming that the entire sapwood area was functional. The specific conductivity of the sapwood of the stem (K_{stem}) was calculated by dividing *K*h by the sapwood area.

Maximum K (K_{max}) was measured similarly to native hydraulic conductivity (K_{stem}) but after removing any embolism from the segments by flushing them with the same perfusion solution at a pressure of 0.15 MPa for 30 min. PLC was calculated as:

$$PLC = \frac{(K_{max} - K_{stem})}{K_{max}} x \ 100$$

Pressure-volume curves

Leaves were collected in the predawn, scanned for leaf area measurements, recut underwater, and allowed to rehydrate for at least 6 h until water potential was higher than -0.1 MPa. Leaf fresh weight and water potential were measured over time during slow bench dehydration. After measurements, the leaves were placed in an oven at 70 °C for approximately 72 hours and used to obtain dry mass. The relative water content was calculated and plotted against the inverse of leaf water potential (Scholander *et al.*, 1965; Tyree & Hammel, 1972). Using data from the pressure-volume curves, the elastic modulus (ϵ), leaf capacitance (*C*), turgor loss point (Ψ_{TLP}), and osmotic potential (Π_0) were estimated.

Stem density and capacitance

The same stem fragments were used to determine wood density, relative water content, volumetric water content, and capacitance. Wood density (D_{wood}) was calculated as dry mass divided by volume and expressed in g cm⁻³ (Loram-Lourenço *et al.*, 2020). The stem relative water content (RWC_{stem}) was determined according to the following formula:

$$RWC_{stem} (\%) = \left(\frac{M_f - M_d}{M_s - M_d}\right) \times 100$$

Where M_f is the sample fresh mass, M_d is the sample dry mass, and M_s is the sample saturated mass (Ziemińska *et al.*, 2020).

To calculate the stem volumetric water content (VWC_{stem}) indicates the total water volume per sample volume and was calculated as follows:

$$VWC_{stem} = \frac{(M_f - M_d) \times p^{-1}}{V}$$

where ρ is water density, assumed to be equal to 1 g cm⁻³.

To determine the stem capacitance (C_{stem}), the cumulative water released (CWR) was measured in the predawn (CWR_{pd}) and at midday (CWR_{md}), as proposed by Meinzer *et al.* (2003) and adapted by Ziemińska *et al.* (2020):

$$CWR = \frac{(M_s - M_f)}{V}$$

The C_{stem} was then calculated as follows:

$$C_{\rm stem} = \frac{\rm CWR_{md} - \rm CWR_{pd}}{\Psi_{pd} - \Psi_{md}}$$

Water transport in the plant

Leaf hydraulic conductivity (K_{leaf}) was determined as the ratio between leaf transpiration rate (*E*) and the difference between xylem Ψ_{w} and $\Psi_{\text{w-md}}$ (Brodribb & Holbrook, 2003), according to the formula:

$$K_{leaf} = \frac{E}{(\Psi_{w-xylem} - \Psi_{w-md})}$$

E and Ψ_{w-md} were obtained as previously described. Leaves located close to those used for the other measurements were used to determine Ψ_{w_xylem} . For this measurement, leaves were covered with aluminum foil, at least, for 1 hour before analysis.

Biomass investment

To determine the investment in biomass, the specific leaf area (SLA – ratio of leaf area and leaf dry mass)(Crawley, 2009), and branch growth rate were calculated. To determine the branch growth rate (BGR), two branches from five individuals per species were selected and measured every 15 days during one month of the dry season. The values of BGR (cm² day⁻¹) represent the average growth over the period (Loram-Lourenço *et al.*, 2022).

Data analysis

The data obtained were submitted to the t-test ($p \le 0.05$) to determine the difference between the two areas. Principal component analysis (PCA) was used to explore the variation of the evaluated characteristics, to better understand the physiological behavior of the species between the sampled areas. Statistical analyses were performed using the statistical program R v4.2.0 (R Core Team, 2018).

Results

Environmental variables

The microclimate of the two studied areas was markedly different, as shown in Table 1. The Dry Forest region had a considerably higher temperature and lower relative humidity, culminating in a higher VPD, in addition to lower soil moisture compared to the Gallery Forest.

Table 1 – Environmental variables in two Cerrado phytophysiognomies during the dry season. The data presented in the table show the average of eighteen measurements during the dry season. AT – average temperature; AH – air humidity; VPD – Vapor pressure deficit; and SM – soil moisture. The presence of an asterisk represents a statistical difference by the t-test (***, $P \le 0.01$).

Area	AT (°C)	AH (%)	VPD (kPa)	SM (%)
Gallery Forest	28.33	49.72	1.94	19.21
Dry Forest	31.93	39.71	2.86	8.67

Tissue hydration and water loss

The midday water potential (Ψ_{w-md}) did not differ between areas (**Fig. 2**). Furthermore, there was no difference in the main traits involved with the overall plant water loss (**Fig. 3**): stomatal conductance (g_s) , transpiration rate (*E*), total leaf area (TLA) and bark minimum conductance to water vapour (g_{bark}) . The only exception was the leaf minimum conductance to water vapor (g_{leaf}) , which was significantly lower on plants growing in the Dry Forest (Fig. 3C)



Figure 2 – Midday water potential (Ψ_{w-md}) in co-occurring species in Cerrado fragments (gallery forest (blue) and dry forest (brown)) collected during the dry season.



Figure 3 – Water loss parameters in co-occurring species in Cerrado fragments (Gallery Forest (blue) and Dry Forest (brown)) collected during the dry season. The following were evaluated: A – Stomatal conductance (g_s); B - transpiration rate (E); C – residual leaf transpiration (g_{leaf}); D – residual bark transpiration (g_{bark}); and E – total leaf area (TLA). (t-test, *** P \leq 0.01).

Water storage

The main components of water storage evaluated here, as well as pressurevolume curve parameters, did not show any significant difference between the areas (**Table 2**). However, the leaf-saturated water content (SWC_{Leaf}), stem volumetric water content (VWC_{stem}), and stem relative water content (RWC_{stem}) were higher in the Gallery Forest. Moreover, the osmotic potential at full turgor (Π_o) and turgor loss point (Ψ_{TLP}) were more negative in the Dry Forest.

Table 2 – Water storage parameters in co-occurring species in Cerrado fragments (Gallery Forest and Dry Forest) collected during the dry season. The following were evaluated: Saturated water content in leaves (SWC_{Leaf}); Elastic modulus (\mathcal{E}); Relative water content at the turgor loss point (RWC_{TLP}); Osmotic potential (Π_o); Turgor loss point (Ψ_{TLP}); Capacitance at full turgor (C); Capacitance at the turgor loss point (C_{TLP}); Stem density (D_{stem}); Volumetric water content of the stem (VWC_{stem}); Relative water content of the stem (RWC_{stem}); and Stem capacitance (C_{stem}) (t-test, ** P \leq 0.05; *** P \leq 0.01).

Traits -	Gallery Forest	Dry Forest	
	Mean SE	Mean SE	p
SWC _{Leaf} (g)	1.471 ± 0.039	1.365 ± 0.038	** 0.04
E (MPa)	13.550 ± 0.981	13.348 ± 1.239	0.78
RWC_{TLP} (%)	86.34 ± 1.007	$83.41 \hspace{0.2cm} \pm \hspace{0.2cm} 1.454$	0.10
П _о (-MPa)	$1.58 \ \pm \ 0.043$	$1.73 \hspace{0.2cm} \pm \hspace{0.2cm} 0.041$	*** 0.01
Ψ_{TLP} (-MPa)	$2.01 \hspace{.1in} \pm \hspace{.1in} 0.047$	$2.17 \hspace{0.2cm} \pm \hspace{0.2cm} 0.035$	*** 0.01
C (MPa ⁻¹)	$0.065 \ \pm \ 0.005$	$0.071 \hspace{0.2cm} \pm \hspace{0.2cm} 0.005$	0.50
C_{TLP} (MPa ⁻¹)	$0.187 \hspace{0.2cm} \pm \hspace{0.2cm} 0.018$	$0.228 \hspace{0.2cm} \pm \hspace{0.2cm} 0.022$	0.14
D_{stem} (g cm ⁻³)	$0.469 \ \pm \ 0.016$	$0.498 \hspace{0.2cm} \pm \hspace{0.2cm} 0.017$	0.22
VWC _{stem} (g cm ⁻³)	$0.622 \ \pm \ 0.012$	$0.553 \ \pm \ 0.021$	** 0.02
RWC _{stem} (%)	$89.67 \ \pm \ 0.792$	83.91 ± 1.943	** 0.02
C_{stem} (kg cm ⁻³ MPa ⁻¹)	$62.94 \hspace{0.2cm} \pm \hspace{0.2cm} 9.106$	$68.89 \hspace{0.2cm} \pm \hspace{0.2cm} 10.02$	0.95

Water transport safety

The differences in the microclimate of each phytophysiognomy influenced the vulnerability to embolism, with more resistant xylem (lower P_{12} and P_{50}) being observed on plants growing in the dry forest (**Fig. 4A**). However, for P_{88} , which is considered the hydraulic failure point for most angiosperms, significant differences between areas were not observed. Regarding the PLRC, no differences were observed (**Fig. 4B**). The stem of the species proved to be remarkably safe, with low PLC_{stem} being observed in both areas (**Fig. 4C**). Both phytophysiognomies had wide hydraulic safety margins (HSM) (**Fig. 4D**).

There was no difference in water transport capacity between plants growing in the Gallery and Dry Forest (**Fig. 5**). In fact, both K_{leaf} and K_{stem} remained unchanged between areas, probably as a consequence of the wide HSM, the absence of difference in *E*, and the low PLC_{stem}.



Figure 4 – Water transport safety parameters in co-occurring species in two fragments of the Cerrado (Gallery Forest (blue) and Dry Forest (brown)). A – Xylem vulnerability to embolism; B – Loss of rehydration capacity (PLRC); C – Loss of xylem conductivity of the stem (PLC_{stem}); and D – Hydraulic safety margin (HSM), collected during the dry season (t-test, ** $P \le 0.05$; *** $P \le 0.01$).



Figure 5 – Water transport efficiency parameters in co-occurring species in Cerrado fragments (Gallery Forest (blue) and Dry Forest (brown)). A – Leaf hydraulic conductivity (K_{leaf}); B – Stem hydraulic conductivity (K_{stem}).

Carbon acquisition and investment in growth

Photosynthetic rate (*A*), carboxylation efficiency (*A*/*Ci*) and water use efficiency (*A*/*E*) were higher in Dry Forest, as shown in Figure 6. Specific leaf area (SLA) and *Ci*/*Ca* ratio, in turn, were higher in Gallery Forest. No differences were observed in branch growth rate (BGR).



Figure 6 – Carbon acquisition and carbon investment parameters in co-occurring species in Cerrado fragments (Gallery Forest (blue) and Dry Forest (brown)). A – Net carbon assimilation (*A*); B – Internal/external carbon concentration (C_i/C_a); C – Carboxylation efficiency (A/C_i); D – Water use efficiency (A/E); E – Specific leaf area (SLA); F – Branch growth rate (BGR) (t-test, ** P ≤ 0.05; *** P ≤ 0.01).

Multivariate Analysis

The first two components of the principal component analysis (PCA) explained 47.28% of the data variation (PC1 = 26.23% e PC2 = 21.05%, **Fig. 7**), showing a clear separation between the two areas. Gallery Forest plants were positively correlated with variables related mainly to water accumulation (Ψ_w , SWC, RWC_{stem}, SM, RWC_{TLP}, *K*_{Leaf}) and a high *g*_{Leaf}; while Dry Forest plants were correlated with *A*, *D*_{stem}, VPD and BGR.

Furthermore, the negative correlation between with P_{50} , Ψ_{TLP} , Π_0 and g_{Leaf} also indicates that Dry Forest plants presented drought tolerance traits.



Figure 7 – Multivariate analysis (PCA analysis). Two-dimensional PCA biplots showing associations between plants in the Gallery (blue) and Dry Forest (brown) and physiological traits.

Discussion

In the present study, we evaluated functional traits of co-occurring species in Cerrado fragments with distinct microclimatic characteristics. The ability to grow and survive in such contrasting conditions, especially considering the strong variation in water availability between areas, relies on the great plasticity of traits involved in water loss, storage, and embolism tolerance. The PCA data showed that the occurrence of different phytophysiognomies makes the species physiologically distinct, allowing clear differentiation between the two groups. In general, species growing in the Dry Forest were associated with characteristics that indicate higher drought tolerance, such as P_{50} , Ψ_{TLP} , and wood density, while the same species, when located in the Gallery Forest, were directly correlated with higher water storage capacity and residual transpiration. The understanding of intraspecific diversity in the Cerrado environment provides more mechanistic insight into its ability to buffer ecosystem changes and provide resiliency under future droughts.

Despite facing a more severe environmental drought, plants in the dry forest maintained similar water potential compared to plants in the Gallery Forest

Although the Cerrado fragments were located close to each other and exposed to the same levels of annual precipitation (INMET, 2024), the microclimatic conditions were markedly different between the areas (**Table 1**). One of the main factors that influences the microclimate of a region is soil moisture (Greiser *et al.*, 2024), which is greater in Gallery Forests due to their proximity to a water body. Soils with high water availability favor seedlings establishment and support greater tree growth, which tend to have greater canopy coverage (D'Odorico *et al.*, 2007). Zhang *et al.* (2013) correlated the coverage and height of the forest canopy with the reduction in temperature and increase in humidity, mainly due to the greater capacity to filter solar radiation, which also contributes to greater retention of soil and air moisture (Wang *et al.*, 2018).

Environmental conditions in the dry forest, such as higher temperature and lower relative humidity, which thus leads to high VPD, can significantly increase plant transpiration (Zhao *et al.*, 2022). This factor, associated with lower soil moisture, often results in dehydration of plant tissues (Alves *et al.*, 2020). Despite this, however, the species growing in the Dry Forest did not differ from the species in the Gallery Forest in relation to Ψ_{w-md} (Challis *et al.*, 2022) (**Fig. 2**). The ability to maintain tissue hydration is probably a determining factor for the distribution of the same species along the water availability gradient that exists between the forest physiognomies of the Cerrado and indicates high plasticity of mechanisms involved in the response to drought (Challis *et al.*, 2022). In order to clarify these mechanisms, we analyzed differences between the areas regarding the processes of water loss, storage, and embolism tolerance, as well as the process of carbon acquisition and growth.

Balance between water loss and release: plants in the Gallery Forest lose more water, but do not have greater capacitance

Decreased transpiration, either through stomatal closure or leaf shedding, is a typical plant response to water restriction (Brodribb & Holbrook, 2003). Plants growing in the Dry Forest, however, did not show more pronounced reductions in g_s , E_s , or in total leaf area compared to species in the Gallery Forest (Fig. 3A-B, E), contrary to what was expected based on the Ψ_{w-md} values. The g_{leaf} , on the other hand, was lower in Dry Forest (Fig. 3C), which contributes to the maintenance of the plant's water status. Residual transpiration has been recognized as a significant factor affecting tissue water potential and drought survival rates (Duursma et al., 2019; Machado et al., 2021; Challis et al., 2022). Lower g_{leaf} values also helped plants to equilibrate with the wettest soil layer in the rooting zone overnight. In fact, since the stomata are dark adapted during the measurements, gleaf will continue during the night and, in some species, this night transpiration can reach up to 30% of daytime transpiration (Caird et al., 2007). Changes in g_{leaf} reflect anatomical and/or structural modifications and have already been observed in other species subjected to conditions of low water availability (Duursma et al., 2019). Considering the long duration of the dry season in the Cerrado $(4 \sim 6 \text{ months})$, this acclimatization may be essential for the survival of species in different phytophysiognomies, while at the same time does not impact photosynthesis to the same extent as drops in g_s and in leaf area. On the other hand, the g_{bark} remained unchanged between sampling areas (Fig. 3D). Unlike leaves, the bark is a less plastic structure, and variations in g_{bark} appear to be genetically determined (Ávila-Lovera & Winter, 2024).

The Ψ_{TLP} was lower in the Dry Forest, probably due to the decrease in osmotic potential (Π_0) (Huo *et al.*, 2021) (**Table 2**), and it is an important trait for assessing physiological tolerance to drought. More negative values of Ψ_{TLP} indicate that the cell can remain turgid and maintain its functioning even at lower values of Ψ_w (Bartlett *et al.*, 2012). In agreement with our findings, Zhu *et al.* (2018) correlated Ψ_{TLP} with an environmental Aridity Index (AI), showing that species from environments with higher

19

AI had lower Ψ_{TLP} values. It is important to note, however, that Ψ_{TLP} is a proxy for stomatal closure and, therefore, lower values indicate the ability to tolerate dehydration rather than avoid it and may result in delayed stomatal closure, with greater water loss to the atmosphere.

The lower water content observed in the leaves and stems of the Dry Forest is, mainly, due to the lower soil moisture. Despite this, the capacitance of the stem and leaf did not differ between the areas (**Table 2**). The capacitance determines the extent to which the internal water pool buffers the xylem water potential during drought (Pereira *et al.*, 2024). Thus, although plants in the Gallery Forest accumulated more water in their tissues, this did not reflect a greater capacity to release water during the dry season. Other studies found a weak correlation between the saturated water content and capacitance (Nadal *et al.*, 2018; Pereira *et al.*, 2024). For instance, Ziemińska *et al.* (2020) observed that lumen volumetric water content is a better predictor of stem capacitance than just the total VWC. It is possible, therefore, that plants in the Dry Forest were able to adjust other traits that allowed them to maintain the same capacitance as plants in the Gallery Forest, even with lower water accumulation in their tissues, thus suggesting better management of available water resources.

Different microclimates result in different drought response strategies

The high plasticity of xylem tolerance to embolism of the analyzed species was one of the main traits that contributed to the separation of the groups in the PCA (**Fig. 7**), with the plants growing in dry forest showing greater resistance to embolism (lower P_{50}) (**Fig. 4A**) in response to lower soil and air humidity. This result is particularly interesting when we consider that many plasticity studies indicate a low rate of variation in P_{50} (Johnson *et al.*, 2018; Skelton *et al.*, 2019). Nevertheless, xylem plasticity has already been observed in species from the Amazon (Garcia *et al.*, 2022) and temperate forest (Fuchs *et al.*, 2021), in which plants located in environments with lower water availability had more tolerant xylems. In the present study, this plasticity played a preponderant role in the occurrence of the species in both areas because, by delaying embolism, it allowed the continuity of water transport in plants in the Dry Forest, contributing to the maintenance of water potential; and made reductions in Ψ_{TLP} possible without increasing the occurrence of cavitation events (Sorek *et al.*, 2022). Although P_{12} and P_{50} values were not quantified in the stem, PLC data (**Fig. 4C**) demonstrate the absence of embolism in this organ in both areas. Based on these data, it is not possible to verify whether the plasticity observed in the leaf extends to the stem, although it is feasible that this had happened since the plants maintained K_{stem} (Fig. 5B) and a low PLC in the microclimatic conditions of the Dry Forest.

In both the Dry and Gallery Forest, the water potential of the leaves was far from P_{50} , allowing the species to operate at a wide HSM (Fig. 4D), with significantly higher values in the Dry Forest. HSM is closely linked to the mortality of plant species exposed to low water availability (Delzon & Cochard, 2014). Given the increase in temperature and drought events worldwide, plants are likely to experience Ψ_w increasingly close to the lethal threshold of embolism (Brodribb & Cochard, 2009; Choat, 2013), incurring mortality risk for species operating with narrow HSM (Garzón et al., 2018; Yan et al., 2020). However, despite the large HSM, in plants growing in the Gallery Forest, the water potential of the leaves had already reached P_{12} (Fig. 2, 4A), which represents the starting point of the embolism (Guan *et al.*, 2022). P_{12} is an important marker because it has been shown that leaf necrosis (Cardoso et al., 2020) and drought-induced leaf shedding (Walthert et al., 2021) start at low embolism levels. It is therefore likely that Dry Forest leaves have a greater leaf life span, a hypothesis corroborated by their lower SLA (Reich et al., 1991). Leaf lifespan describes the average duration of each leaf constructed and is negatively related with SLA in different species and across biomes (Reich et al., 1998). It is also worth noting that, under different environmental conditions, most species have Ψ_{TLP} greater than P_{12} (Martin-StPaul *et al.*, 2017; Sorek *et al.*, 2022) which suggests that stomatal closure is important to limit drops in Ψ_w to avoid embolism (Sorek *et al.*, 2022). However, for the species evaluated here, this pattern only occurred in Dry Forest. Finally, while the leaves of the species in Gallery Forest had already reached P_{12} , the PLC in the stem remained close to 4% (Fig. 4C). The greater tolerance to embolism in the stem compared to the leaves is a typical response of plants that present hydraulic segmentation (Johnson et al., 2016). Taken together, all these data point to the fact that building a more tolerant xylem and avoiding the occurrence of leaf embolism is a strategy that was only adopted by plants that were exposed to conditions of great water scarcity. For plants growing in the Gallery Forest, where water deprivation is probably a sporadic event, losing the embolized leaves may be a more viable alternative. This is true especially considering the high hydraulic safety of their stems, which could minimize the risks of plant dieback (Walthert et al., 2021).

The contrasting strategies observed between areas may reflect differences in carbohydrate availability. Investing in a more tolerant xylem to ensure water transport

involves a considerable carbon cost (Eller et al., 2017; Franklin et al., 2023). Similarly, other characteristics observed in the leaves of species in the Dry Forest, such as lower g_{leaf} , Ψ_{TLP} and SLA are also associated with increased carbon investment (Lü *et al.*, 2012; Zhu et al., 2018). Despite this, plants in the Dry Forest did not show lower growth rates (Fig. 6G), contradicting the existence of a trade-off between drought survival and growth potential for the species studied. In this sense, it is important to consider that maintaining growth may be necessary for species to acclimatize to the climate variations that occur seasonally in the Cerrado. In addition, although the characters involved in tolerance to water restriction require greater structural investment, conductivity losses, due to the increase in hydraulic safety (e.g. reduction in P_{50}), also imply long-term costs. Therefore, investing in drought tolerance does not necessarily imply greater carbon expenditure in the long term. Still, the magnitude of the plastic response will depend on carbohydrate availability (Huber et al., 2012). The photosynthetic rate, much higher in species in the Dry Forest (Fig. 6A), allowed for the maintenance of growth and investment in drought tolerance mechanisms. Luminosity tends to be markedly different between Gallery and Dry Forests, due to differences in canopy cover (Dodds et al., 1996; Ribeiro & Walter, 2008). The greater light availability, associated with the lower Ψ_{TLP} , allowed the plants in the Dry Forest to produce more carbohydrates, although it is possible that other biochemical factors also contributed to the difference between the areas. The higher SLA in the Gallery Forest (Fig. 6E), on the other hand, maybe an acclimation to deal with low light availability (Ackerly et al., 2002). Thus, both environmental and physiological factors resulted in high photosynthesis in the Dry Forest, which enabled the production of carbohydrates necessary for response strategies to cope with lower water availability.

Conclusions

Intraspecific variation in response to the characteristics of the environment in which they are inserted is not a universal condition among plant species, either due to genetic limitations or the costs associated with plasticity (DeWitt *et al.*, 1998; Schneider, 2022). The results obtained allow us to observe the great intraspecific plasticity of the species that co-occur in the Gallery Forest and Dry Forest and point to distinct strategies for dealing with drought in the Cerrado. In plants growing in the Dry Forest, the data reinforce the existence of positive feedback between photosynthesis and plasticity to drought: the higher carbon assimilation capacity in the Dry Forest made carbohydrates available for the development of leaves that are more tolerant to water restriction; at the

same time, having more tolerant leaves allows these organs to remain viable for longer periods, without completely closing the stomata, favoring the maintenance of photosynthesis. In Gallery Forest, on the other hand, high water availability and low photosynthesis drive the construction of drought-sensitive leaves and point to the existence of hydraulic segmentation, with leaves being shed as the drought becomes more intense. It is therefore possible to see that plant responses to water availability are multidimensional and influenced by the interaction between genetic potential and abiotic factors of an environment. It is also worth noting that regardless of the strategy adopted, in both areas the species operated in a broad HSM, indicating high resilience to drought of some Cerrado species even with the intensification of climate change. This characteristic may result in the homogenization of the Domain, since species that do not have such high plasticity and that are restricted to certain environmental conditions will, probably, not be able to compete with species that co-occur in different phytophysiognomies.

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