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Case Report

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Water relations may account for the premature death of the species *Tachigali vulgaris* L.F. Gomes da Silva & H.C. Lima

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Abstract

Tachigali vulgaris is a fast-growing pioneer tree species with a short lifespan, yet the causes behind its premature death remain unclear. Over the past decade, the Brazilian Cerrado has faced recurrent droughts, intensifying die-off events of this species. This study aimed to investigate physiological traits related to water relations to identify potential factors contributing to its decline. During the dry season, *T. vulgaris* maintained high leaf hydraulic conductivity $7.10 \text{ mmol m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$, similar to that observed in the rainy season $8.02 \text{ mmol m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$, due to a consistent transpiration rate. However, this persistence led to a significant drop in water potential in both leaves -2.31 MPa and stems -2.10 MPa , approaching the osmotic potential at incipient plasmolysis -2.36 MPa , suggesting an imminent risk of internal water stress. Despite this, cells did not collapse thanks to the high elasticity of their walls, volumetric elastic modulus of 3.01 MPa , allowing the maintenance of positive turgor pressure and a high relative water content

79.95% at plasmolysis. The species also showed remarkable thermotolerance: the maximum quantum yield of Photosystem II (F_v/F_m) remained high up to 36.97°C, with critical thresholds reached only below 8.69°C or above 65.26°C. Dark respiration followed a similar pattern, peaking at 36.66°C and decreasing by 50% at temperatures below 18.52°C or above 54.79°C. Nonetheless, persistent transpiration during drought, combined with high hydraulic conductivity, may increase the likelihood of xylem cavitation and hydraulic failure. While *T. vulgaris* displays strong heat tolerance, these traits alone may not be enough to withstand the increasing frequency and severity of droughts. Further research is needed to determine whether its high hydraulic conductivity plays a central role in its vulnerability and premature mortality.

Keywords: bulk elasticity modulus, hydraulic conductivity, osmotic potential, relative water content, water potential.

Introduction

Drought poses a significant challenge to plant growth, particularly in dry tropical biomes, where its impacts are exacerbated by specific environmental conditions. It is one of the main stress factors limiting plant development by disrupting water uptake and inducing physiological, biochemical, and molecular changes that compromise photosynthesis, growth, and productivity (Ferreira et al., 2015; De Sousa Leite et al., 2022). The increasing frequency and intensity of drought heighten the risk of plant mortality, especially in dry tropical biomes like the Brazilian Cerrado (Eziz et al., 2017; Liao et al., 2018). The Cerrado is predominantly composed of deciduous species, a high evapotranspiration potential, and low, irregular rainfall patterns (Santos et al., 2014), often resulting in water deficits (Sampaio, 1995; De Farias et al., 2016; Choat et al., 2018).

The state of Mato Grosso, located in the Central-West region of Brazil, is currently experiencing climate warming, which intensifies drought periods, particularly in biomes such as the Cerrado. The drought conditions in 2019, which worsened in 2020, led to a prolonged dry spell that significantly affected local ecosystems. Such extreme drought events increase physiological stress in trees, compromise hydraulic functioning, and ultimately contribute to widespread tree mortality, thereby altering the structure, composition, and functioning of forest ecosystems (Gitlin et al., 2006; van Mantgem and Stephenson, 2007; Allen et al., 2010; Dietrich and Kahmen, 2019; Barros et al., 2020).

T. vulgaris, a species native to the Cerrado, often faces drought periods that lead to significant mortality. This species is particularly vulnerable to premature death, which may be closely related to its water relations. Its behavior, especially in natural habitats where water availability fluctuates considerably, could be a key factor in its early mortality. Reduced water availability has various adverse effects on plants, including limiting growth and development, and potentially causing death through mechanisms such as water stress, increased temperature, xylem embolism, reduced stomatal conductance, and altered photosynthesis (Breshears et al., 2009; Zargar et al., 2017; Zhang et al., 2017; Prestes et al., 2024). Drought can also result in a decrease in photosynthetic pigments due to their rapid degradation, which damages the antenna complexes of photosystems, reducing light-harvesting efficiency and overall photosynthetic capacity (Ashraf and Harris, 2013).

Tachigali vulgaris is a fast-growing pioneer species used by rural communities in the Midwest and Northeast of Brazil for construction, as well as for producing firewood and charcoal (Franke, 1999). Endemic to Brazil, it is found in the Northeast, Midwest, and Northern regions, occurring in the phytogeographical zones of the Caatinga, Cerrado, and Amazon (De Oliveira Ramos et al., 2021). The behavior of *T. vulgaris*, particularly in regions with fluctuating water availability, may help explain its vulnerability. This species plays a crucial role in areas like the Chapada dos Guimarães National Park, where it dominates large portions of the landscape. During the dry season, *T. vulgaris* sheds its leaves and undergoes visible changes, often appearing open areas due to extensive mortality. This phenomenon is particularly concerning given the semi-arid climate of the region.

Understanding the physiological responses of trees to water stress and drought-induced mortality is crucial for improving our ability to predict their decline. While numerous studies have aimed to identify the causes and critical moments of tree mortality, accurately predicting when it will occur remains a challenge (Hartmann et al., 2018). Research has often focused on mechanisms such as leaf hydraulic conductance (Kleaf) and carbon starvation, both of which play significant roles in tree mortality (Scoffoni et al., 2011; McDowell et al., 2008; Adams et al., 2017).

Extreme heat waves can disrupt various critical tree functions (Barriopedro et al. 2011). In leaves, photosynthesis decreases, oxidative stress increases leaves drop, and the growth rate of remaining leaves slows. When heat waves are combined with water stress,

the detrimental effects are amplified, potentially leading to tree mortality. However, some species exhibit exceptional resilience to heat stress by adapting their metabolism to mitigate the impact on photosynthesis and by reducing respiration in the absence of light (Teskey et al., 2015).

In this study, variables related to water relations could help identify potential factors contributing to the mortality of *T. vulgaris*. Among these variables, leaf water potential at the turgor loss point (Ψ_{π}^{100} , in MPa) is a key indicator for assessing plant water stress and identifying factors contributing to mortality (Niinemets, 2001; Brodribb and Holbrook, 2003; Lenz et al., 2006; Bartlett et al., 2012). Essential information can also be derived from the pressure-volume curve, such as relative water content (RWC), volumetric elastic modulus, and osmotic potential, which are critical for understanding the water relations of plants under drought stress, as well as their ability to tolerate water deficits and maintain physiological functions during water scarcity (Turner, 1988; Bartlett et al., 2012; Scoffoni et al., 2014; Browne et al., 2023; Nadal et al., 2023; Castillo-Argaez et al., 2024). These parameters provide insights into key physiological thresholds, including osmotic potential at incipient plasmolysis ($\Psi\pi^0$) and symplastic relative water content at incipient plasmolysis (RWC_s^0), which are essential indicators of cell turgor maintenance and plant dehydration tolerance, especially under drought conditions (John et al., 2017; Sack et al., 2018; Trueba et al., 2019). Additionally, the temperature at which the maximum quantum efficiency of photosystem II (F_v/F_m) and dark respiration (R_d) are reduced to a critical point helps assess a plant's ability to preserve PSII integrity and basal metabolism, respectively, under extreme temperatures (Figueroa et al., 2003; Lípová et al., 2010; Zhang et al., 2012).

Moreover, we analyzed thermal traits as factors influencing drought resistance and premature mortality in *T. vulgaris*, based on their response to water status, as these traits play a crucial role in regulating leaf temperature, protecting the photosynthetic apparatus, and maintaining metabolic stability under heat and water stress conditions (da Costa et al., 2010; Docherty et al., 2023). By measuring thermal traits associated with hydraulic conductivity, leaf respirations and R_d thermotolerance, the objective of this study was to evaluate variables related to water relations to identify potential factors responsible for the mortality of this species.

Materials and methods

Study sites

The study was conducted in the Chapada dos Guimarães National Park, a fully protected conservation unit located in the south-central mesoregion of Mato Grosso, a state in Brazil, at geographical coordinates 15°25' S and 50°51' W, with an altitude of 800 meters above sea level. This park (Figure 1) is situated 80 km from Cuiabá and 6 km from the town of Chapada dos Guimarães, in the central-western region of Brazil. The area is characterized by a tropical seasonal climate, with a marked dry season from May to September and a rainy season from October to April, and it plays a key role in the preservation of the Cerrado biome and the ecological processes that support biodiversity (ICMBio, 2009). In the case of this study, the plant materials of *Tachigali vulgaris* L.F. Gomes da Silva & H.C. Lima collected were deposited and registered in the UFMT Herbarium under the registration number UFMT 48916.

The climate of this region, according to the Köppen classification, is divided into two categories: Aw for the Cuiabá Depression and Cwa for the Chapada. These categories reflect a tropical highland climate typical of the plateau, characterized by two distinct seasons. The soils are generally deep, sandy, loamy, or even clayey (IPEM, 2002). The native vegetation consists of a mix of savanna formations, ranging from wooded savannas to gallery forests and open savannas (BRASIL, 1982).

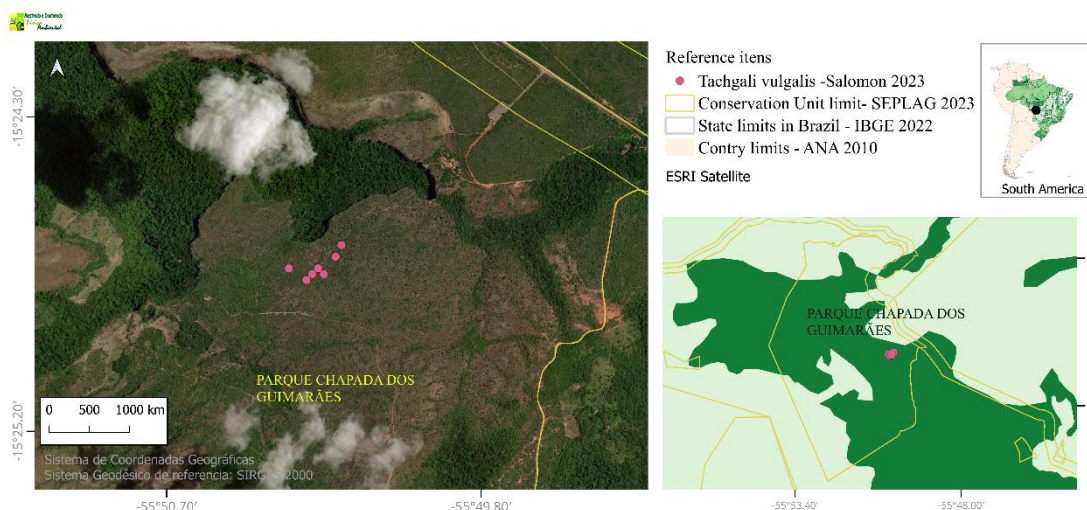


Figure 1. Location of the study site in Chapada dos Guimarães National Park, Brazil. The map was generated in QGIS v.3.14 using background maps from the Instituto Brasileiro de Geografia e Estatística's database (IBGE, 2021). (<https://www.ibge.gov.br/>)

Leaf thermotolerance

The evaluation of leaf thermotolerance was performed using two analysis variables: the F_v/F_m ratio and dark respiration (Rd).

The F_v/F_m ratio is an indicator of the maximum quantum efficiency of Photosystem II (PSII). Plant leaves under normal, non-stressed conditions typically show F_v/F_m values around 0.83 (Murchie and Lawson, 2013). Therefore, the F_v/F_m ratio was used to assess the photochemical stability of Photosystem II (PSII), with a decrease in this ratio indicating inactivation damage to PSII (Ghouil et al., 2003). There is some consensus in the scientific community that plant leaves under mild stress may exhibit values around $0.75 \leq F_v/F_m \leq 0.82$, recovering after the stress; plants under moderate stress show values of $0.60 \leq F_v/F_m \leq 0.74$, with potential recovery only if the stress factor is removed, and plants under severe stress have F_v/F_m values < 0.6 , with the damage being almost irreversible (Backer, 2008; Maxwell and Johnson, 2000).

The variable Rd is directly related to the plant's metabolic capacity to generate energy and carbon skeletons to ensure the maintenance and growth of cells, tissues, and organs. It also plays a critical role in balancing energy production and consumption, especially under stress conditions such as drought (Penning de Vries, 1975).

Both processes (photosynthesis and respiration) depend on the stability of the organelle membranes where they occur (chloroplasts and mitochondria), and this stability is influenced by temperature (Wahid et al., 2007).

The collection of plant material for analysis followed the same protocol defined for obtaining material for the PV curve. The only difference was that for determining the F_v/F_m ratio and Rd, before the overnight rehydration of the tissues, seven leaves were selected and covered with aluminum foil to adapt them to the dark. Seven leaves were used because there were seven thermal treatments.

Measurements of each variable (F_v/F_m ratio and Rd) were conducted on different days. In both cases, a portable photosynthesis measurement system, LI-6400XT (LI-COR Biosciences, Lincoln, NE, USA), was used. In this equipment, a fluorometer model 6400-40 (LI-COR Biosciences, Lincoln, NE, USA) was used as the measurement chamber for the F_v/F_m ratio, and a chamber with a light source model 6400-02B (LI-COR Biosciences, Lincoln, NE, USA) was used for Rd measurement.

Measurement, were conducted in a room with interference light (cool lights were covered with green cellophane paper) to minimize the effect of light on these variables.

For F_v/F_m ratio measurements, the equipment was set to a block temperature of 28°C, relative humidity around 60%, and atmospheric CO_2 concentration at 400 $\mu\text{mol mol}^{-1}$. For R_d measurements, the equipment was set up in the same way as for F_v/F_m ratio measurements. In this case, the measurement chamber light was kept off to maintain the dark condition.

The thermal treatments evaluated included temperatures of 30, 35, 40, 45, 50, 55, and 60°C. After rehydration, the first batch, consisting of one dark-adapted leaf from each specimen in the study, was placed in a preheated oven at 30°C for 30 minutes. After this period, the leaves were transferred to room temperature for the measurement of the F_v/F_m ratio and R_d , depending on the designated measurement day. This procedure was repeated for the remaining leaves and thermal treatments.

The adjustment curves for F_v/F_m and R_d as a function of temperature were modeled using a second-order polynomial (Eq. 3).

$$F_v/F_m \text{ or } R_d = a + bT + cT^2 \quad \text{Eq. 3}$$

Where: F_v/F_m = maximum quantum yield (dimensionless), R_d = dark respiration ($\text{mmol m}^{-2} \text{s}^{-1}$), a , b , and c = adjustment constants, T = temperature (°C).

Leaf hydraulic conductance

The measurement of leaf hydraulic conductance (K_{leaf}) was obtained according to Ohm's law applied to hydraulic flow (Brodribb and Holbrook, 2003a). These measurements were conducted during two seasonal periods: the rainy season and the dry season.

The day before the measurements, two adjacent, healthy, fully expanded leaves exposed to sunlight were selected from each specimen for the procedures. One leaf was covered with an aluminum foil bag and then a zip-lock plastic bag to promote stomatal closure and prevent transpiration, allowing the water potential of this leaf (Ψ_{leaf}) to equal the water potential of the xylem in the branch (Ψ_{stem}). The other leaf was left in the same condition.

On the morning of the following day, the Ψ_{stem} of the covered leaf was measured, and the transpiration rate (E) and its corresponding Ψ_{leaf} for the adjacent leaf were

determined. The measurements of E were conducted using a portable photosynthesis measurement system, model LI-6400XT (LI-COR Biosciences, Lincoln, NE, USA), adjusted for the environmental conditions at that time (light, temperature, relative humidity, and atmospheric CO_2 concentration) for that seasonal period. The determinations of Ψ_{leaf} and Ψ_{stem} of the plants was performed using a homemade pressure chamber (with a manometer limited to 50 kgf cm^{-2} and a resolution of 0.2 kgf cm^{-2}), following the method of Scholander et al. (1965). The data obtained for Ψ_{leaf} and Ψ_{stem} was converted to MPa by multiplying by 0.0980665 (considering gravity as 9.80665 m s^{-2}). From the measurements of Ψ_{stem} , Ψ_{leaf} , and E , the values of K_{leaf} were obtained according to Eq. 1 (Brodribb and Holbrook, 2003).

$$K_{leaf} = \frac{E}{\Psi_{stem} - \Psi_{leaf}} \quad \text{Eq. 1}$$

Where: K_{leaf} = leaf hydraulic conductance ($\text{mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$), E = transpiration rate ($\text{mmol m}^{-2} \text{ s}^{-1}$), Ψ_{leaf} = leaf water potential (MPa), Ψ_{stem} = xylem water potential of the stems (MPa).

Pressure–volume (P-V) curves traits

In the field, for each plant of the evaluated species, a branch approximately 1.0 m long, containing several leaves, was cut using pruning shears. The branches were properly labeled and placed in a plastic bag with a bundle of moist paper to maintain a saturated atmosphere, and then immediately transferred to a cooler containing ice to prevent water loss from the plant tissue. They were then transported to the laboratory.

In the laboratory, the basal part of these branches was placed in a container with water (a plastic tray) to be recut underwater to avoid embolism, removing approximately 25 cm. The branch was then transferred to another container with water (a PET bottle), keeping its base submerged and covering the aerial part with black plastic. In the laboratory conditions with air conditioning (24°C), all containers with the branches and leaves of the plants were maintained until the next morning to allow for complete rehydration of the leaves (rehydration period of 4 to 8 hours).

The procedure for performing the PV curve was carried out according to the protocol described by Tyree and Hammel (1972), which involves the gradual dehydration of leaf samples to generate a pressure-volume relationship, allowing the determination of

key parameters such as the osmotic potential at full turgor, the turgor loss point, and the bulk modulus of elasticity. This method is widely used to evaluate plant water status and drought tolerance across species. However, to obtain the maximum number of data pairs on the curve, the waiting time between measurements was minimized. The procedure began with the removal of a leaf from the branch and its weighing. Immediately after weighing, the leaf water potential (Ψ_w) was determined. After determining the water potential, the next weighing was done as soon as the leaf was removed from the pressure chamber, and this procedure was repeated until the equipment's measurement capacity limit was reached (50 kgf cm^{-2}). Instead of the volume of water removed from the leaf tissue, the PV curve was constructed using the relationship between the inverse of the leaf water potential and its corresponding water saturation deficit (Equation 1), which is the complement of the relative water content (Equation 2).

$$WSD = \frac{W_{sat} - W_f}{W_{sat} - W_d} \times 100 = 100 - RWC \quad \text{Eq. 1}$$

$$RWC = \frac{W_f - W_d}{W_{sat} - W_d} \times 100 \quad \text{Eq. 2}$$

Where: WSD = water saturation deficit (%), W_{sat} = saturated fresh mass(g), W_f = current fresh mass (g), W_d = dry mass (g), RWC = relative water content (%).

From the PV curve of each leaf from each specimen, the following data were obtained: osmotic potential at full turgor (Ψ_{π}^{100}), osmotic potential at incipient plasmolysis (Ψ_{π}^0) and cell wall volumetric elasticity modulus (ϵ).

Statistical analysis

All quantitative response variables were previously evaluated to ensure they fit Dixon's requirements to eliminate outliers at $\alpha = 5\%$ (Sokal and Rohlf, 1998). The selected values were then used to generate a mean value with respective nonparametric confidence interval (95%) using the bootstrap method with 1000 resamplings with replacement. A polynomial regression analysis was employed to fit F_v/F_m and R_d as a function of temperature. All the statistical analyses were done with the R (R Core Team, 2019).

Results

Leaf thermotolerance

The Fv/Fm and Rd curves as a function of temperature for *T. vulgaris* were polynomial (Figure 2), differing from the commonly observed pattern of an exponential curve with very well-defined thresholds, which indicates a greater range of tolerance in these plants.

The leaves of *T. vulgaris* were adapted to high temperatures, with the maximum Fv/Fm value of 0.947 obtained at a temperature of 36.97°C and the maximum Rd value of 1.36 obtained at a temperature of 36.66°C.

The loss of integrity of the photosynthetic apparatus, considered based on the critical Fv/Fm value of 0.6 for a severe stress condition, occurred at temperatures equal to or lower than 8.69°C or equal to or higher than 65.26°C. For Fv/Fm, this assessment makes more sense than considering the loss of 50% of the maximum Fv/Fm value as the threshold, because in the latter case, the loss of the integrity of photosystem II is far exceeded. For example, for *T. vulgaris*, 50% of maximum Fv/Fm is equal to 0.474 and would occur when the temperature was equal to or less than 3.93°C or equal to or greater than 70.02°C.

The inability to adequately meet the energy demand for the respiratory process, with a loss of 50% of maximum Rd, occurred at temperatures equal to or lower than 18.52°C or equal to or higher than 54.79°C.

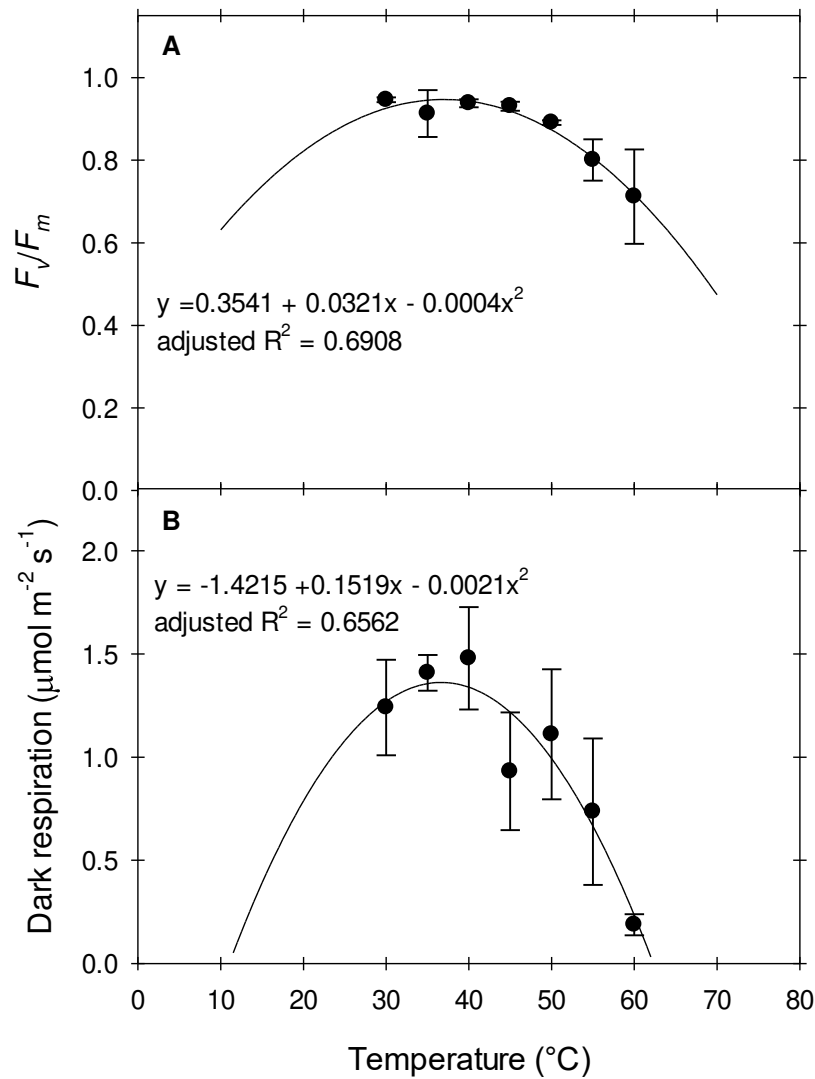


Figure 2. Temperature response curves for the evaluation of the integrity of Photosystem II (A) and supply of energy by dark respiration (B) in *Tachigali vulgaris*.

Seasonal change in leaf hydraulic conductance between the rainy and dry seasons

Tachigali vulgaris presented no significant difference in K_{leaf} between rainy and dry season periods. This trend was due to the maintenance of E in the dry season similar to the rainy season, leading to an equivalent decrease in both Ψ_{leaf} and Ψ_{stem} during dry season (Table 1).

Table 1. Seasonal variations in leaf hydraulic conductance (K_{leaf}), leaf water potential (Ψ_{leaf}), stem water potential (Ψ_{stem}), and transpiration rate (E) in *Tachigali vulgaris*.

Period	Statistics	Variables			
		K_{leaf} (mmol m ⁻² s ⁻¹ MPa ⁻¹)	Ψ_{leaf} (MPa)	Ψ_{stem} (MPa)	E (mmol m ⁻² s ⁻¹)
Rainy season	$\bar{X}$	8.02	-1.46	-1.27	1.98
	<i>L.L.</i>	5.36	-1.68	-1.66	1.44
	<i>U.L.</i>	10.46	-1.21	-0.80	2.62
Dry season	$\bar{X}$	7.10	-2.31	-2.10	1.48
	<i>L.L.</i>	4.52	-2.48	-2.19	1.12
	<i>U.L.</i>	9.90	-2.14	-2.01	1.90

Note: $\bar{X}$ is the mean value, *U.L.* is the upper limit, and *L.L.* is the lower limit.

Traits derived from pressure-volume (P-V) curves

T. vulgaris presented values of Ψ_{π}^{100} similar to immature leaves of broadleaved tree species, Ψ_{π}^0 similar to many deciduous and also some sclerophyllous evergreen species, and RWC^0 like those observed for drought-tolerant tree species. However, it showed elastic cells (low value of ε), that are typically found in xeromorphic plants (Table 2).

Table 2. Variables obtained from pressure-volume curves for *Tachigali vulgaris*: relative water content at incipient plasmolysis (RWC^0), leaf osmotic potential at full turgor (Ψ_{π}^{100}), osmotic potential at incipient plasmolysis (Ψ_{π}^0) and volumetric modulus of elasticity (ε).

Statistics	Variables			
	RWC^0 (%)	Ψ_{π}^{100} (MPa)	Ψ_{π}^0 (MPa)	ε (MPa)
$\bar{X}$	79.95	-0.98	-2.36	3.01
<i>U.L.</i>	85.09	-0.89	-1.59	4.65
<i>L.L.</i>	73.73	-1.07	-3.34	1.65

Note: $\bar{X}$ is the mean value, $U.L.$ is the upper limit, and $L.L.$ is the lower limit.

Discussion

Temperature Response of Photosynthesis and Dark Respiration

It is plausible that an upper limit exists for the thermal tolerance of photosynthetic and respiratory metabolism in tropical plants. This hypothesis is supported by previous studies that highlight the role of heat shock proteins produced in chloroplasts and mitochondria in plant responses to high temperatures (O'Sullivan et al., 2017; Kim et al., 2012; Downs and Heckathorn, 1998). These studies also explored the relationship between thermal tolerance and variations in photosynthesis rates under extreme temperatures (Wahid et al., 2007; Barua et al., 2008).

In *T. vulgaris*, PSII demonstrates a high resilience to extreme temperatures, with an optimal operating temperature of 36.97°C ($F_v/F_m = 0.947$). Sastry et al. (2017) reported temperatures of 44.5°C and 48.1°C at which the maximum quantum efficiency of photosystem II (F_v/F_m) dropped by 50% (T_{50}) in less and more thermally tolerant tropical species, respectively. Similarly, Slot et al. (2021) conducted a comprehensive analysis involving 147 tropical forest species, finding an average T_{50} of 49.9°C, although substantial interspecific variation was observed. These results emphasize the relevance of T_{50} as a critical physiological trait for assessing species' vulnerability to high temperatures and predicting their responses to global warming. Furthermore, other studies (Zhang et al., 2012; Sastry and Barua, 2017) have identified 55.23°C as the approximate threshold for irreversible damage to F_v/F_m , indicating a point beyond which photosystem II suffers permanent thermal injury, and recovery is unlikely. However, our data suggests that for *T. vulgaris*, this reduction only occurs under extreme conditions, with temperatures reaching 70°C or dropping to 3.93°C, as indicated by the second-degree polynomial in Fig. 3. This suggests superior thermal tolerance compared to many other species related to *T. vulgaris*' photosystem integrity. Previous studies have shown that PSII efficiency is strongly influenced by temperature, with significant declines when leaves are exposed to heat stress or extreme cold (Neri et al., 2024). Moreover, some plant species develop rapid PSII adjustments under high temperatures, optimizing their tolerance to thermal stress (Havaux & Tardy, 1996). These findings support our results, suggesting that *T. vulgaris*

demonstrates remarkable thermal resilience, standing out for its superior PSII stability under extreme temperature conditions.

On the other hand, *T. vulgaris* presented temperature effects on Rd similar to numerous species, with its maximum value ($Rd = 1.36 \mu\text{mol m}^{-2} \text{s}^{-1}$) reached at a temperature of 36.67°C and a reduction of 50% of this value when the temperature drops to 18.52°C or rises to 54.79°C . According to many researchers (Bilger et al., 1984; Cunningham and Read, 2006; Zhang et al., 2012), 55.23°C is a common temperature at which a reduction in 50% of Rd occurs, indicating irreversible damage in the process of generating metabolic energy.

Leaf Hydraulic Conductance

During the dry season, *Tachigali vulgaris* maintained a leaf hydraulic conductance (K_{leaf}) similar to that recorded during the rainy season. This stability can be attributed to comparable transpiration rates in both seasons, this being a typical behavior of an isohydric plants. In this particular case, it appears that maintaining high transpiration rates during the dry season was not sufficient to cause any hydraulic injury to the plants. However, this may be just an instantaneous condition, i.e., with the increase in water deficit and maintaining high transpiration rates, there will come a time when the hydraulic system will collapse, when the capacity to replenish evaporated water cannot be supplied by the flow in the conducting system. This can be observed by the fact that maintaining high transpiration rates during the dry season led to a reduction in the water potential in the stem and leaf. When these water potentials reach their critical values, cavitation and consequent embolism will be inevitable. This means that this particular species does not have good control in terms of water economy through stomatal control of water loss by transpiration.

Studies have shown that plants adjust their K_{leaf} in response to water availability and physiological demands. Brodribb and Holbrook (2003b) observed that seasonal variations in K_{leaf} are common in species from arid environments, enabling them to maintain efficient water transport under water stress. A reduction in K_{leaf} due to water stress is well-documented (Brodribb and Holbrook, 2006; Johnson et al., 2009) and is often attributed to dehydration-induced mechanisms such as xylem cavitation, implosion of conducting elements (Cochard et al., 2004), and changes in turgor pressure (Brodribb and Holbrook, 2003a).

Xylem embolism in leaves, a critical factor contributing to reductions in K_{leaf} , becomes inevitable under water deficit conditions. Woodruff et al. (2007) and Johnson et al. (2009) documented this phenomenon, predicting decreases and limited recovery of K_{leaf} in *T. vulgaris* even during the rainy season. Similarly, Meinzer et al. (2004) observed seasonal variations in K_{leaf} in this tropical species, corroborated by *in situ* measurements of stem transpiration and differences in water potential between covered and exposed leaves.

Tyree and Cochard (1996) and Klein et al. (2018) suggested that embolism reduces hydraulic conductivity in the vascular system but has a limited role in drought tolerance, as only extremely negative water potentials are capable of causing significant damage or tree mortality.

In addition, previous studies have demonstrated that leaf hydraulic conductance (K_{leaf}) increases with temperature (Tyree et al., 2005; Scoffoni et al., 2008; Voicu et al., 2008). Despite this, the water potential of leaves and stems significantly decreased during the dry season for leaves and for stems during both the rainy and dry seasons. Furthermore, the leaf water potential in the dry season was statistically comparable to the osmotic potential at the point of plasmolysis, highlighting a high risk of internal water stress.

Numerous studies have demonstrated that xylem cavitation in stems is a common response to water stress (Canny, 2001; Cochard, 2002; Bucci et al., 2003). As leaves experience dehydration, xylem cavitation becomes inevitable. Water potential relaxation studies further support the significant loss of K_{leaf} at potentials below -2 MPa (Brodribb and Holbrook, 2003). Salleo et al. (2002), reported that fluctuations in stem and leaf hydraulics in deciduous species are a key factor linking vascular function and leaf senescence, particularly in the absence of photoperiodic or frost signals. Reduced hydraulic conductivity plays a central role in the leaf abscission process during water stress (Sperry et al., 2002). Thus, in this study, the high K_{leaf} observed may be a primary factor contributing to the premature mortality of *T. vulgaris*.

Pressure-Volume (P-V) Curve Traits

ψ_{π}^{100} reflects the solute concentration in plant cells, with more negative values indicating higher solute accumulation. This can result from osmotic adjustment, a widespread drought response mechanism in many forest species that helps maintain

turgor under water stress. *T. vulgaris* exhibits a relatively high Ψ_{π}^{100} , a characteristic often observed in broadleaved tree species with immature or expanding foliage (Myers et al., 1987). This suggests that *T. vulgaris* may not significantly utilize osmotic adjustment as a physiological mechanism for drought tolerance.

However, it is interesting to note that *T. vulgaris* has a Ψ_{π}^0 value comparable to that found in some evergreen plants (Kunert et al., 2020), despite being a deciduous species that sheds its leaves during the driest season. Ψ_{π}^0 is a crucial physiological parameter in a plant's response to water stress and has been used for decades to evaluate drought tolerance, as it reflects the osmotic potential at which cells begin to lose turgor. This threshold is essential for understanding a plant's capacity to maintain cellular function under declining water availability and is widely recognized as a reliable indicator of drought resistance across species and ecosystems (Bartlett et al., 2012). Several species lose their turgor at Ψ_{π}^0 between -1.00 and -4.08 MPa (Lenz et al., 2006). A lower Ψ_{π}^0 is linked to a species' ability to survive and persist in environments with pronounced seasonal moisture stress, as it broadens the range of leaf water potential at which the leaf remains turgid and functional, allowing the plant to better manage drought periods and maintain essential physiological processes even under conditions of low water availability (Bartlett et al., 2012). There is evidence that the association between Ψ_{π}^0 and the environment occurs in evergreen plants but not in deciduous ones (Kunert et al., 2020). Evergreen plants require a lower Ψ_{π}^0 because their leaves endure longer periods of stress, whereas deciduous plants do not. In this case, the leaves of *T. vulgaris*, when losing water during the dry season due to the maintenance of high transpiration rates, increase the concentration of solutes inside the cells. This may be one of the factors that determines lower Ψ_{π}^0 values in these plants. It will be shown later that e potentially also can contribute to this.

In theory, low Ψ_{π}^0 can result from three mechanisms: the accumulation of osmotically active solutes (leading to lower Ψ_{π}^{100} values), an increase in the fraction of apoplastic water (a_f), or greater cell wall elasticity (lower ε). However, conflicting findings on whether a_f and ε increase or decrease have led Bartlett et al. (2012) to investigate the physiological factors that govern Ψ_{π}^0 variation within and between species in response to environmental water availability, aiming to clarify how osmotic adjustment and cell wall properties contribute to drought tolerance and to understand the ecological implications of these traits in diverse plant communities. To do that, they performed a meta-analysis of a new global database, and related P-V parameters to aridity within and

across biomes. They conclude that Ψ_{π}^0 and Ψ_{π}^{100} are reliable indicators of species' drought tolerance across biomes, unlike other P-V parameters. Their findings suggest that Ψ_{π}^0 is primarily influenced by Ψ_{π}^{100} , with ε playing a minimal direct role. The relationship between Ψ_{π}^0 and Ψ_{π}^{100} is strong across all Ψ_{π}^{100} values and any ε level, with Ψ_{π}^0 decreasing as Ψ_{π}^{100} becomes more negative. However, this decline is more rapid at low ε . In contrast, Ψ_{π}^0 is not equally sensitive to ε ; while a reduction in ε can theoretically lower Ψ_{π}^0 , this effect is limited to a narrow range of low ε values and depends on Ψ_{π}^{100} .

The mean relative water content (RWC⁰) of 79.95% reflects the water retention capacity of *T. vulgaris* tissues at the point de perte de turgescence. Previous studies indicate that higher water content during drought periods is often correlated with better drought resistance (Morgan, 1984). Values of RWC⁰ below 75% is associated with physiological damages like severe inhibition of ATP, RuBP and protein production (Lawlor and Cornic, 2002). In general, it is considered that high RWC⁰ is typically associated with drought-tolerant plants that possess a strong water storage capacity in their tissues, providing a significant advantage in drought-prone environments. However, the explanations for why high levels of RWC⁰ occur in drought tolerant plants are theoretically associated with cell wall rigidity (high ε), as increased stiffness may limit cell volume reduction during dehydration, thereby maintaining turgor pressure and allowing physiological functions to continue under water deficit conditions (Bartlett et al., 2012). One of these explanations would be that rigid walls provide the structural support necessary to withstand the high turgidity condition associated with an osmotic adjustment in which very negative values of Ψ_{π}^{100} and Ψ_{π}^0 are observed. Another explanation is that in cells with rigid walls (higher ε) and less negative Ψ_{π}^0 , a small change in cell volume due to water loss are immediately perceived, triggering physiological responses such as the reduction of stomatal conductance to reduce or stop water loss through transpiration. It is interesting that Bartlett et al. (2012) concluded that both explanations could not be evidenced in their work, because: (a) cell wall can withstand experimental pressures many times higher than their turgor pressure before rupture, and (b) Ψ_{π}^0 is very insensitive to ε at high values of ε , and early stomatal closure can be developed independently of Ψ_{π}^0 and at leaf water potential higher than Ψ_{π}^0 .

T. vulgaris appears to have a wider range between Ψ_{π}^{100} and Ψ_{π}^0 in its leaves compared to other species. Likewise, the species has low ε values, which characterizes it as having flexible cell walls. As mentioned before, *T. vulgaris* presented Ψ_{π}^{100} higher than

what expected for wood tropical plants, so it appears to rely more on elastic adjustment, characterized by flexible cell walls (low ε) allowing volume changes during dehydration without loss of turgor, rather than on osmotic adjustment, to cope with cell solute concentration and lower Ψ_{π}^0 . This result challenges the claims made by Bartlett et al. (2012), who suggested that ε has no significant effect on Ψ_{π}^0 and that low ε values in deciduous malacophily may merely reflect minimal cell wall investment in short-lived leaves.

However, a fundamental aspect raised by Bartlett et al. (2012) makes it evident that P-V curve analysis can provide how the leaf behaves under a particular environmental condition. In other words, tolerant leaves can occur in plants that, as a whole, present serious problems of susceptibility to stress and vice-versa, susceptible leaves can occur in resistant plants. This highlights that leaf traits measured in isolation do not always reflect the integrated response of the entire organism to water stress, reinforcing the need for a multi-level approach when assessing drought tolerance.

Conclusions

The results of this study suggest that the high leaf hydraulic conductivity in *T. vulgaris* may significantly contribute to its premature mortality. Although the species can maintain hydraulic conductivity during dry periods, this characteristic increases its susceptibility to internal water stress. This heightened vulnerability could potentially lead to hydraulic failure caused by xylem cavitation and embolism, thereby amplifying the risk of mortality. Further research is needed to investigate the interplay between hydraulic properties and environmental factors, such as recurrent droughts, to better understand the mechanisms driving die-off events in *T. vulgaris* within the Brazilian Cerrado. Additionally, if future climatic conditions surpass the adaptive capacity of this species, implementing assisted dispersal strategies will be crucial to ensure its survival, maintain its distribution, and preserve its ecological role in Cerrado ecosystems.

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Conflict of interest

None declare

Ethics declarations

Not applicable

Consent to participate

Not applicable

Consent to publish

Not applicable.

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