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How does the leaf heat sensitivity relate to the species' geographical distribution range in the Brazilian savanna?

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Abstract Global warming poses a significant impact on plant species in the Cerrado, the largest savanna in the world. However, there is still a gap in understanding how species distribution patterns are associated with their thermal sensitivity. One approach to address this is quantifying species´ specific responses through leaf traits related to heat stress. Therefore, we determined the temperature that caused a 50% reduction (T_{50}) in the light-acclimated quantum efficiency of PSII (F_v'/F_m') and the thermal safety margin (TSM) (T_{50}—maximum leaf temperature), together with Leaf Area (LA) and Leaf Mass Area (LMA) in 12 tree species from two climatic contrasting regions within the Cerrado. We compared the traits between widespread species (co-occurring in both sites) and species restricted to each region, and we explored the relationships between T_{50} and TSM with LA and LMA. As a result, we found that T_{50} and TSM values were similar across species, regardless of study region or species distribution range. Additionally, we observed that study species had lower TSM, which suggests that these species might be likely to approach high-temperature thresholds. Furthermore, the study species exhibited general relationships between LA and LMA with T_{50}, indicating that leaf traits mainly determine the thermal properties of Cerrado tree species.

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1 Introduction

Compelling evidence underscores the impact of global climate change on tropical vegetation (Uribe et al. 2023), making it increasingly apparent that species are approaching critical temperature limits (Doughty et al., 2023; Kunert et al. 2022). Of particular concern is the Brazilian Cerrado, the world's largest and most diverse savanna (Forzza et al. 2012), which has already experienced significant challenges over the last six decades, with a maximum temperature rise of 4 °C (Hofmann et al. 2021).The changes in temperature regime may lead to important implications for the biodiversity and ecosystem functioning of this vegetation.

Studies on the distribution patterns of Cerrado vegetation (Castro 1994; Ratter et al., 2003; Amaral et al. 2017; Françoso et al. 2019) have converged into three main biodiversity supercenters: Northeast, Central Plateau, and Southeast (Vieira et al. 2022). These areas are characterized by a high number of restricted endemic species and share similar floristic compositions between them (Castro et al. 1999; Vieira et al. 2022). The plant communities among these centers are shaped by correlations between flora and morphoclimatic (Castro et al., 1994; Françoso et al. 2019), with temperature being one of the key factors (Neves et al. 2015; Costa-Coutinho et al. 2021). For instance, on the northeast border of the Cerrado, the daily absolute maximum temperatures can reach up to 39 ºC, while on the southeast border, the daily absolute minimum temperatures can drop to 5 ºC (INMET, Instituto Nacional de Meteorolologia—https://bdmep.inmet.gov.br/), leading to different species compositions in each border (Françoso et al. 2019). Although evidence suggests that certain species at the border of the Cerrado are already close to their leaf photosynthetic upper-temperature thresholds (Araújo et al. 2021), little is known about the temperature sensitivity related to species distribution within Cerrado across these different biodiversity supercenters.

The heat tolerance of photosystem II (PSII) photochemistry can provide useful information about plants' heat sensitivity (Xia et al. 2018), shedding light on the physiological mechanisms driving some of the plant's responses in the face of environmental changes (Calosi et al. 2008; Lancaster & Humphreys 2020). PSII photochemistry, one of the most heat-sensitive components of the photosynthetic apparatus, drives the light-dependent reactions that convert absorbed energy into CO_2 fixation (Coast et al. 2022; Xiao et al. 2019). High temperature can impact PSII photochemistry by causing enzymes in chloroplast thylakoid membranes to disassociate and denature (Wahid et al. 2007; Zhu et al. 2018), reducing photosynthesis performance. The effect of temperature on PSII efficiency can be quantified by the ratio between leaf temperature and light-acclimated quantum efficiency of PSII ($F_v´/F_m´$) (Baker 2008). Higher $F_v´/F_m´$ ratios indicate an enhanced capacity of PSII reaction centers to capture excitation energy, reflecting the system's ability to maintain photochemical performance under stress conditions (Borlongan et al. 2017). Additionally, light-adapted quantum yields could provide an alternative method for assessing PSII heat tolerance, particularly for *in situ* measurements under high light and temperature conditions (Perez et al. 2021).

Two widely reported metrics can be used to quantify PSII heat sensitivity. One metric is the T_{50}, which represents the temperature that causes a 50% decrease in PSII efficiency (Perez and Feeley 2020), which is associated with the critical temperature at which irreversible damage to photochemistry occurs (Münchinger et al. 2023). The second metric is the thermal safety margin (TSM), calculated by the difference between T_{50} and the maximum leaf temperature (Araújo et al. 2021), a proxy of plant vulnerability, indicating how closely species operate near their thermal limits under natural conditions (Kitudom et al. 2022). Previous studies have demonstrated significant relationships between T_{50} and TSM to species with large-scale gradients. Specifically, more heat-tolerant species (higher T_{50} and TSM) tend to have widespread distributions, while heat-sensitive species are often restricted to environments with well-defined climatic conditions (Feeley et al. 2020). However, previous studies carried out in Cerrado have also indicated that the relationships between heat tolerance and geographic distribution range might be controversial. For instance, Araújo et al. (2021) found that T_{50} and TSM decline for widely distributed species across different Cerrado phytophysiognomies as air temperatures increase. This pattern might be associated with plant decidedness strategies, which allow plants to reduce thermal stress and maintain physiological function (Kullberg & Feeley 2024). Functional traits associated with the leaf economic spectrum, such as leaf decidedness and structure, have proved to be good predictors for heat tolerance (Zhang et al. 2024). Along the leaf economic spectrum, higher leaf construction investment enhances heat tolerance, while larger leaves with slower heat exchange may increase vulnerability to thermal stress (Sastry & Barua 2017). Thus, while some species might be sensitive to further temperature increases (Araújo et al. 2021), understanding the leaf ecological strategies associated with heat tolerance can also provide important information about the ability of Cerrado species to cope with higher temperatures.

Here, we measured the temperature that caused a 50% decrease in F_v'/F_m'(T_{50}) and the TSM together with leaf area (LA) and leaf mass per area (LMA) in 12 tree species from two opposite centers (northeast and southeast) within the Brazilian Cerrado contrasting in their climate regimes. Our survey focused on tree species that co-occur and are restricted to two opposite sides of the Cerrado. Two questions guided our study: 1) Does T_{50} and TSM differ between widespread and restricted species? 2) How are ecological strategies, including deciduousness and morphological leaf traits (LA and LMA), related to T_{50} and

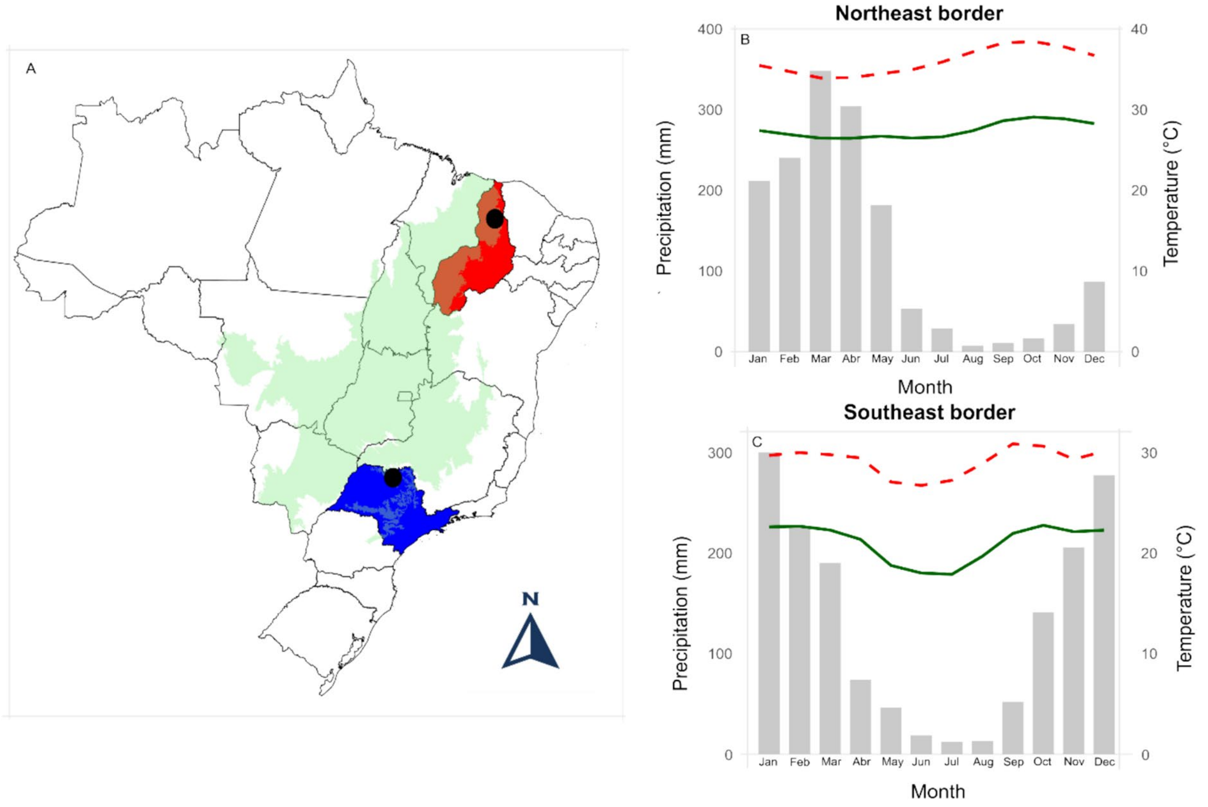

Fig. 1 Sampling sites and climatic conditions (de Sousa Oliveira et al. 2024). Box A is a Brazil map showing the locations of our two study sites in the Cerrado (highlighted in light green). The two study sites are indicated in different colors: the red northeastern border region and the blue southeastern border region. In boxes A and B, the average accumulated precipitation per month (grey bars), mean monthly temperature (green line), and maximum absolute temperature (dashed red line) are displayed for the northeastern and southeastern border regions. Precipitation and temperature data were obtained from the Instituto Nacional de Meteorologia (INMET-Instituto Nacional de Meteorologia – https://bdmep.inmet.gov.br/)

TSM? Specifically, we hypothesized that: H1. Widespread species in Cerrado will be more heat sensitive than restricted species (Araújo et al. 2021); H2. Both restricted and widespread species studied from the northeastern border—the hottest region— are less heat sensitive (higher T_{50} and TMS) than those from the southeastern border (O'sullivan et al. 2017). H3. We also predicted that higher values T_{50} and TSM would be related to higher LMA and lower LA.

2 Material and methods

2.1 Study areas and species selection

The study was carried out in two sites on opposite border extremes of the Cerrado: the northeastern and southeastern border (Fig. 1). On the northeastern border, the study was conducted in the Sete Cidades National Park, Piauí state, Brazil (04º 02′ 08'' S and 41º 40′ 45'' W). The park is situated in a transitional zone between the Cerrado and Caatinga, the Brazilian seasonally dry forest. The climate in the region is classified as Aw (tropical climate with a dry winter) (Stape et al. 2014), with total annual precipitation of 1400 mm and mean monthly temperature varies from 25.7 ºC to 29.1 ºC, with the maximum temperatures reaching 39 °C in the hottest months (INMET). On the southeast margin, the study was carried out at the buffer zone of the Furnas do Bom Jesus State Park, in São Paulo state, Brazil (20° 14′ 49" S and 47° 21′ 02.7" W), in a transition area between Cerrado and Atlantic Forest. The climate in this area is classified as Cwa (humid subtropical climate) (Stape et al. 2014), with annual precipitation of 1300 mm and a monthly average temperature ranging from 18.2 °C to 23.2 °C, with a maximum temperature reaching 35 °C during the warmest months (INMET).

2.2 Species sampling

In each site, we studied four widespread species (found in both areas), four species restricted to the northeast border, and another four species restricted to the southeast border (12 species in total, Table 1). The species selection was based on their frequency. For widespread species, we chose those with a frequency above 50% within the Cerrado (Françoso et al. 2016), which occurred in both study areas. The restricted species were chosen based on their frequency within the three Cerrado biodiversity supercenters: Northeast (NE), Central Plateau (CE), and Southeast (SE). his selection was guided by indicator species data from Françoso et al. (2019), who organized Cerrado vegetation into seven biogeographic districts: Central (CE), Central-West (CW), Northeast (NE), Northwest (NW), South (S), Southeast (SE), and Southwest (SW). These districts correspond to Castro's biodiversity centers as follows: NE (N and NE), CE (CW, NW, and SW), and SE (S and SE). Table S1 provides a detailed overview of the

Table 1 List of plant species studied per region, their respective botanical families, deciduousness and their distribution range. *Note*: SD = semi-deciduous species, DC = deciduous species, and EV = evergreen species

Species	Family	Deciduousness	Distribution
Annona coriacea Mart	Annonaceae	SD	Widespread
Qualea grandiflora Mart	Vochyseacea	SD	Widespread
Hymenaea stigonocarpa Mart. ex Hayne	Fabaceae	SD	Widespread
Xylopia aromatica (Lam.) Mart	Annonaceae	SD	Widespread
Caryocar coriaceum Wittm	Caryocaraceae	EV	Northeast restricted
Stryphnodendron coriaceum Benth	Fabaceae	SD	Northeast restricted
Vatairea macrocarpa (Benth.) Ducke	Fabaceae	SD	Northeast restricted
Oxandra sessiliflora R.E.Fr	Malvaceae	DE	Northeast restricted
Ormosia arborea (Vell.) Harms	Fabaceae	DE	Southeast restricted
Ouratea spectabilis (Mart.) Engl	Ochnaceae	SD	Southeast restricted
Stryphnodendron adstringens (Mart.) Coville	Fabaceae	DE	Southeast restricted
Vochysia tucanorum Mart	Vochyseacea	DE	Southeast restricted

frequency of restricted species among the biodiversity centers.

2.3 Data collection

Since most study species were deciduous or semi-deciduous (Table 1), the study was conducted during the rainy season in each region. Data collection in the southeastern region was conducted in March 2022, when monthly precipitation measured was 136.2 mm, the mean temperature was 23.2 °C, and the maximum temperature was 28.1 °C (INMET). In the northeastern region, measurements were taken in April 2023, during which the average precipitation was recorded at 173.7 mm, mean temperature of 26.1 °C and a maximum temperature of 31.6 °C (INMET). For each species, we sampled three adult individuals to carry out the study. For each tree, one fully sunlit branch (about 1.3 m long) as close to the top of the canopy as possible) was cut and immediately placed in water. Subsequently, we made a second cut underwater, approximately 30 cm from the original cut, to re-establish water flow. Finally, we left the branch in direct sunlight for further measurements, which were made within one hour of the first cut. From each branch, one mature leaf (not senescent), healthy, and fully expanded leaf with no mechanical damage was used for integrated chlorophyll fluorescence and gas exchange determinations.

To assess the heat sensitivity of the efficiency of PSII, we evaluated the temperature response of the maximum light-adapted efficiency of PSII (F_v'/F_m') using chlorophyll fluorescence measurements. The curves were performed using a LI-COR LI-6800 portable photosynthesis system equipped with a Multiphase Flash Fluorometer (Li-Cor Inc., Lincoln, NE, USA). The chamber settings for fluorescent determinations were configured as follows: chamber CO_2 concentration (Ca) at 400 µmol mol^{-1}, the red target was set to 8000 µmol m^{-2} s^{-1}, the output rate was maintained at 100 Hz, and we utilized a multiphase flash, particularly suitable for full-sun plants, and with saturating incident photosynthetic photon flux density (2000 µmol m^{-2} s^{-1}) (LI-COR Biogeosciences 2017). The duration of the saturating pulse was set to 1 s, and the intensity of the measuring light was approximately 25 µmol m^{-2} s^{-1}. After 30 min of leaf acclimation, we started the temperature response curve. Whenever possible, leaf temperature was set at 25 °C and raised to 45 °C (when possible) at a rate of 3 °C. *F'* was constantly monitored, with *F_m'* taken 3 min after each temperature by applying a saturating pulse (8000 µmol m^{-2} s^{-1}, for 1 s). These parameters were used to calculate F_v'/F_m'. Additionally, at each leaf temperature, we also recorded the light-saturated assimilation rate (A_{sat}).

2.4 *Determining T_{50} and TSM*

The relationship between F_v'/F_m' and the measured leaf temperature (T_{leaf}) was estimated for each individual using a logistic decay model, specified as $\text{lm}\{[\text{logit}(F_v'/F_m')]\sim T_{leaf}\}$. Subsequently, we used the intercept (θ_b) and slope (θ_c) coefficients of logit ($F_v'/F_m' \sim T_{leaf}$) to model the temperature response of F_v'/F_m' over a predicted temperature range of 25 °C to 60° using R's nls function, following the equation:

$$F'_v/F'_m(T) = \frac{\theta_a}{1 + e^{-(\theta_b + \theta_c * T_{leaf})}} \tag{1}$$

where θ_a is the control value of F_v'/F_m' (≈ 0.8).

Using the θ parameters, we modelled the temperature that caused a 50% decline in F_v'/F_m' (Eq. 2):

$$heattolerance = \frac{log\left(\frac{\theta_a}{x} - \theta_b\right)}{\theta_c} \tag{2}$$

where x represents a 50% reduction in F_v'/F_m' compared to F_v'/F_m' at 25 °C. The measured values of F_v'/F_m', the modeled response of F_v'/F_m' for leaf temperatures varying between 25 °C and 60 °C, along with the T_{50} for each species measured in each region, can be found in Figure S1.

Additionally, we estimated the maximum leaf temperature (T_{max}) (Cunningham and Read, 2023)

$$A_{sat}(T) = \left\{ b * \left(T_{leaf} - T_{min}\right) * \left[1 - e^{c*\left(T_{leaf} - T_{max}\right)}\right] \right\}^2 \tag{3}$$

where $A_{sat}(T)$ is the assimilation rate at a given temperature (T_{leaf}), T_{min} and T_{max} are the theoretical low and high-temperature compensation point temperature, and b and c are species-specific constants.

Finally, we calculated the TSM of each leaf as the difference between the individual´s heat tolerance (T_{50}) and estimated maximum leaf temperature (T_{max}) following Araújo et al., (2021).

The parameters in Eqs. 2 and 3 were estimated by fitting the non-linear least squares (nls) function in R's base stats package (Core Team 2020).

2.5 Leaf structure determination

Leaves, or all leaflets if compound, were collected immediately after measurement and were scanned, and their leaf area (LA, cm^2) was calculated using ImageJ software. The leaves were then placed in an oven at 70 °C and dried for 48 h to determine their dry mass (g). The leaf mass per area (LMA; $g\ m^{-2}$) was calculated as the dry mass ratio to leaf area (Perez-Harguindeguy et al. 2013).

2.6 Data analysis

To assess the degree of variation in heat sensitivity parameters among species, we calculated the minimum, maximum, average, and standard errors for T_{50}, TSM, LA, and LMA. To test our first and second hypotheses and investigate the general differences in measured traits between restricted and widespread species, we performed a two-way ANOVA to assess the effects of distribution (widespread vs. restricted) and region (Northeast vs. Southeast) on T_{50}, TSM, LA, and LMA with species as random factor, followed by post-hoc comparisons to identify pairwise differences between groups. Data normality and homogeneity of variance were checked using Shapiro–Wilk and Levene tests, respectively. The same analysis was performed to compare restricted and widespread species on the northeastern border with those on the southeastern border and to examine differences between widespread and restricted species within regions. To address our third hypothesis, we employed linear regression analyses to assess the relationship between LMA and LA with T_{50} and TSM. Normal distribution of the regression residuals was formally tested using the Shapiro–Wilk test. Additionally, we tested the differences in T_{50} and TSM among species of different leaf deciduousness using linear mixed models with species units as random effects. All analyses were performed within the R environment (Core Team 2020).

3 Results

Across all study species (Table 2), the temperatures that caused a 50% decrease in F_v'/F_m' function (T_{50}) had a mean of 49.4 ± 0.4 °C, ranging from 51.3 ± 2.1 °C in *Xylopia aromatica* to 51.3 ± 2.1 °C in *Caryocar coriaceum,* a restricted species from the northeast part of the Cerrado, showed the lowest T_{50} (46.7 ± 2.0 °C). The thermal safety margin (TSM) had an overall mean of 1.2 ± 0.6 °C, ranging from – 3.0 ± 5.8 °C in *Stryphnodendron adstringens* to 3.9 ± 1.7 °C in *Ouratea spectabilis*.

Table 2 Mean per species of the temperature that caused a 50% decrease in F_v'/F_m'(T_{50}) and the thermal safety margin (TSM), leaf area (LA) and leaf mass per area (LMA). SE represents standard errors (± 1)

Species	T_{50} (°C)		TSM (°C)		LA (cm^2)		LMA ($g\ m^{-2}$)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Annona coriacea	49.4	1.3	2.4	1.3	89.1	4.1	150.1	10.8
Hymenaea stigonocarpa	48.7	2.8	2.5	3.9	91.2	1.0	161.6	9.5
Qualea grandiflora	50.4	1.3	– 0.3	1.5	57.2	2.5	197.1	18.3
Xylopia aromatica	51.2	2.1	3.4	3.1	26.3	3.9	165.3	5.4
Caryocar coriaceum	47.6	1.6	0.3	1.4	86.0	3.8	166.4	14.6
Vatairea macrocarpa	49.9	0.9	2.4	2.1	29.1	1.3	120.7	26.7
Oxandra sessiliflora	49.2	0.8	2.3	1.3	100.3	1.1	126.7	4.8
Stryphnodendron coriaceum	47.4	0.7	1.1	0.8	74.8	2.9	157.2	6.5
Ormosia arborea	50.7	1.0	3.9	1.7	60.9	0.7	163.2	0.8
Ouratea spectabilis	49.7	1.9	1.6	1.6	32.8	2.0	168.5	10.2
Stryphnodendron adstringens	48.3	2.8	-3.0	5.8	93.9	2.0	124.1	11.8
Vochysia tucanorum	50.8	2.4	-1.5	2.9	32.0	2.8	164.5	4.3

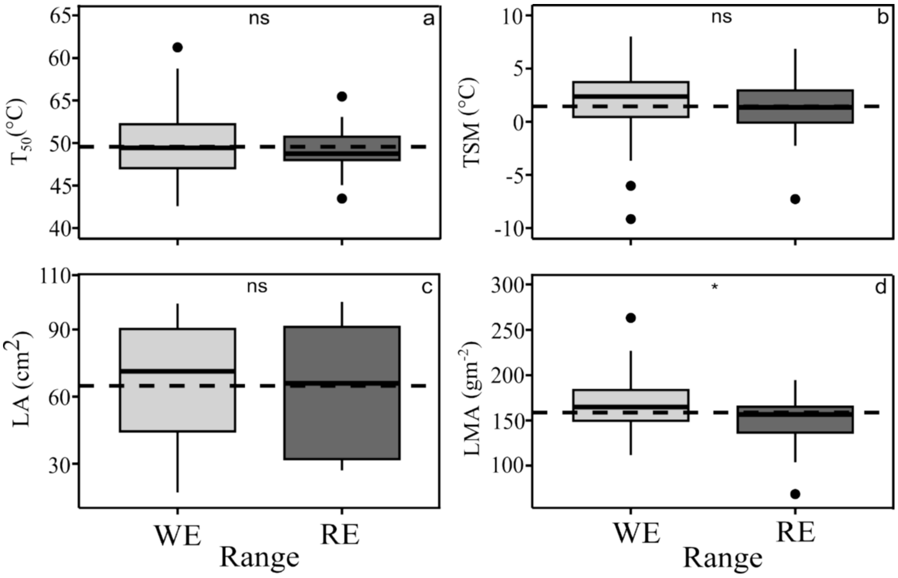

Fig. 2 Boxplots showing the leaf heat sensitivity metrics, (T_{50}) (a) and TSM (b), and leaf traits, (LA) (c) and LMA (d) between widespread (WE) and restricted (RE) species. The dashed line represents the overall average of the metrics. Significance level: $^{**}P < 0.05$; ns $P > 0.05$

Table 3 The mean values that resulted in a 50% reduction in F_v'/F_m' (T_{50}), thermal safety margin (TSM), leaf area (LA), and leaf mass per area (LMA), with their respective standard errors (±1) in restricted and widely distributed species studied in the northeast and southeast borders. Letters indicate the results of post hoc tests

Distribution	Region	T_{50} (°C)			TSM (°C)			LA (cm^2)			LMA (g m^{-2})		
		Mean	SE	Post-hoc	Mean	SE	Post-hoc	Mean	SE	Post-hoc	Mean	SE	Post-hoc
Widespread	Northeast	49.4	1.1	a	-0.1	0.9	a	70.2	7.7	a	154.2	6.3	a
	Southeast	50.7	1.5	a	2.4	2.2	a	61.7	8.7	a	183.0	10.5	ab
Restricted	Northeast	48.3	0.7	a	2.0	0.6	a	72.6	8.1	a	143.0	8.9	c
	Southeast	49.9	1.1	a	0.2	1.7	a	54.9	7.7	a	155.2	6.4	a

3.1 PSII thermal sensitivity among species distribution range

Regarding our first question, all restricted species (including those from both the northeast and southeast) had a mean T_{50} of 49.2 ± 0.8 °C and a mean TSM of 1.2 ± 0.9 °C, while the widespread species had a mean T_{50} of 49.4 ± 0.7 °C and a mean TSM of 0.6 ± 0.9 °C. However, contrary to our first hypothesis, no significant difference was observed in T_{50} and TSM between widespread species and those restricted (Fig. 2a, b). Comparing between regions, restricted species from the northeastern border had a mean T_{50} of 48.3 ± 0.7 °C and TSM of 2.0 ± 0.6 °C, while those restricted from the southeastern area had a mean T_{50} of 49.9 ± 1.1 °C and TSM of 0.2 ± 1.7 °C. However, no significant difference was observed between them (Table 3). Similar uniformity was observed by comparing widespread species measured in both areas (Table 3), where at the northeastern border we found a mean T_{50} of 49.4 ± 1.1 °C and TSM of − 0.1 ± 0.9 °C, and mean T_{50} of 50.7 ± 1.5 °C and TSM of 2.4 ± 2.2 °C for those studied at the southeastern border (Table 3). Considering the variation within each of the regions studied, no significant differences in heat sensitivity metrics were observed (Table 3). Restricted species exhibited similar mean T_{50} (48.3 ± 0.7 °C) and TSM (2.0 ± 0.6 °C) values to widespread species (T_{50} of 49.4 ± 1.1 °C and a TSM of − 0.1 ± 0.9 °C) in the northeastern border. Likewise, restricted species in the southeastern border showed a mean T_{50} of 49.9 ± 1.1 °C and a mean TSM of 0.2 ± 1.7 °C, compared to the widespread species (T_{50} of 50.7 ± 1.5 °C and a TSM of 4.4 ± 2.2 °C).

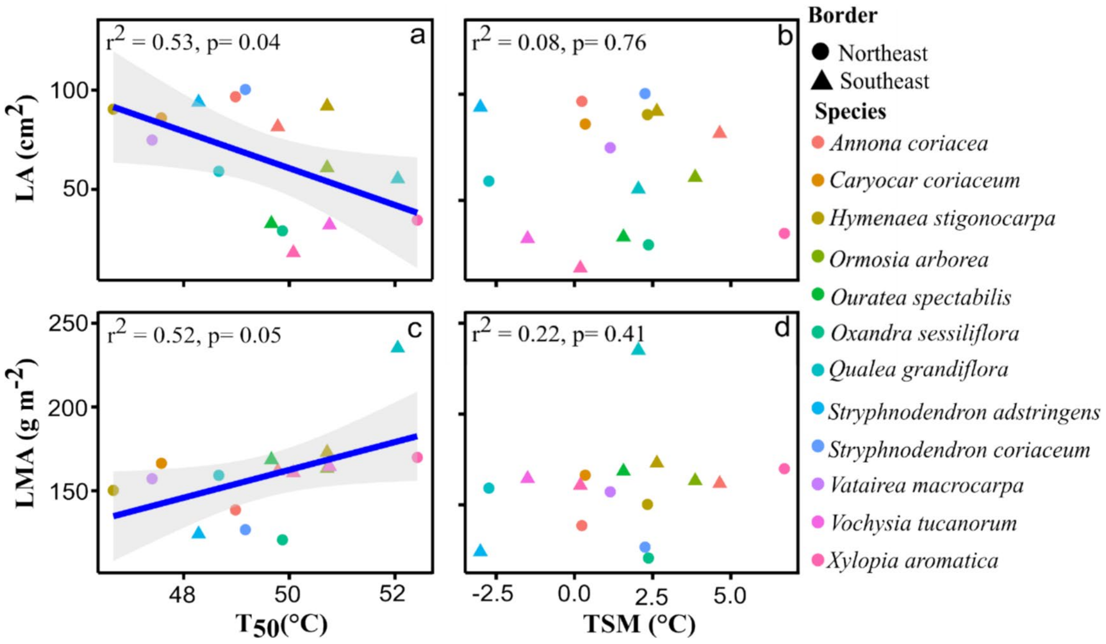

Fig. 3 Relationship between the temperature causing a 50% decline in F_v'/F_m' (T_{50}) (a and c) and thermal safety margin (TSM) (b and d) with leaf area (LA) (a and b) and leaf mass per area (LMA) (c and d)

3.2 Role of leaf ecological strategies

The average LMA among all species was 153.2 ± 5.5 g m^{-2}, ranging from 120.7 ± 26.7 g m^{-2} to 235.1 ± 14.52 g m^{-2}. All restricted species exhibited significantly lower mean LMA (148.9 ± 5.5 g m^{-2}) compared to widespread species (Fig. 2d), which had higher mean values (168.5 ± 6.7 g m^{-2}) (Fig. 2d). LA values varied between 26.28 ± 3.9 cm^2 and 100.3 ± 1.1 cm^2, with a mean value of 64.8 ± 4.0 cm^2 across all species. However, no significant difference in LA was found between widespread (65.9 ± 5.7 cm^2) and restricted species (63.7 ± 5.8 cm^2) (Fig. 2c). Both LMA and LA were significantly correlated with T_{50}. Species with higher T_{50} values exhibited lower LA (Fig. 3a) and higher LMA (Fig. 3a). In contrast, TSM showed no significant correlation with LA (Fig. 3b) and LMA (Fig. 3d). Finally, species deciduousness did not affect their T_{50} or TSM. However, these relationships were only significant when considering all species together. When analyzed separately, no significant correlations were found for widely distributed or restricted species (Fig. S2). Finally, species deciduousness did not affect their T_{50} or TSM, with p-values of 0.58 and 0.69, respectively.

4 Discussion

In our study, we examined the heat sensitivity to the leaf temperature range in Cerrado species and how it relates to the geographical distribution and leaf traits. Here, we highlight two main findings: Firstly, no significant differences in (T_{50}) and TSM were found among species, regardless of their distribution range. Secondly, species characterized by greater investment in the structural components of leaves tended to be less heat-sensitive. We discuss these two main findings, as well as their implications for this vegetation in the face of climate change.

Overall, not many studies of this nature have been carried out on Cerrado species. However, the mean of temperatures that caused a 50% decrease in F_v´/F_m´ (T_{50}) function observed in our study (~ 1.2 °C), were found to be quite similar to temperatures that caused a 50% decrease in maximum quantum yield (F_v/F_m) in species at the Cerrado-Amazon border

(T_{50} at ~ 48.5 °C; Araújo et al. 2021). Similarly, the mean T_{50} of $F_v´/F_m´$ in our study for species studied at the Cerrado-Atlantic Forest border (~ 50 °C) was found to be quite similar to the T_{50} of F_v/F_m reported by Da Silva and Rossatto (2022) (~ 49 °C), which also studied tree species from the same vegetation border.

Experimental approaches to determine T_{50} are highly variable. In general, most studies have assessed the PSII efficiency using F_v/F_m temperature response (Perez et al. 2021). Here, however, we used an alternative approach by analyzing the instantaneous temperature response of $F_v´/F_m´$ through single-point leaf chlorophyll fluorescence measurements in situ. This approach is particularly relevant since reductions in PSII efficiency under light conditions are typically associated with a decrease in the proportion of open PSII reaction centres and a reduced capacity of these centres to effectively capture light energy effectively, indicated by $F_v´/F_m´$ values (Genty, Briantais, and Baker 1989). Additionally, light-adapted quantum yields may be a better approach to assess PSII function under natural conditions (Perez et al. 2021), since F_v/F_m is a reliable proxy for PSII heat tolerance only under low light and minimal photorespiration (Baker 2008). Nonetheless, $F_v´/F_m´$ has been increasingly applied in studies investigating physiological acclimation to temperature stress (Baker et al. 2007; Ogweno et al. 2009; Agrawal and Jajoo 2021; Oivukkamäki et al. 2023). Although $F_v´/F_m´$ is not a commonly used method to estimate PSII heat sensitivity, the T_{50} values of $F_v´/F_m´$ observed in our study (~ 49.2 °C) fall within T_{50} of F_v/F_m previously reported for temperate tree species (~ 48.7 °C; Münchinger et al. 2023, ~ 50.0 °C, Kunert et al., 2022), tropical tree species (~ 49.6 °C; Perez and Feeley 2020, ~ 49.5 °C, Slot et al. 2019, ~ 51 °C; Tiwari et al. 2020, Kullberg et al. 2024), and as previously reported, Cerrado species (Araújo et al. 2021; da Silva & Rossatto 2022).

The mean TSM observed in our study (~ 1.2 °C), was found to be similar to those reported by Araújo et al. 2021 (~ 1.6 °C) in Cerrado, but lower than the TSM reported in Amazon tree species (~ 11.0 °C; Kullberg et al. 2024). This observation adds to the evidence that plants' heat sensitivity tends to decrease from the cool/wet to the hot/dry regions (Kitudom et al. 2022). Adding to this, a lower TSM was observed in our study, and some species, such as *S. astringent*, *V. tucanorum* and *Q. grandiflora,* exhibited negative TSM (Table 2). This might indicate that their predicted temperatures increase, plants can exceed their tolerance thresholds, disrupting photosynthetic processes and leading to their performance (Sastry & Barua 2017). Further temperature increases may cause cellular damage, decrease chlorophyll concentration, and impair enzyme activity (Zhu et al. 2018), impacting the plant's performance (Cook et al. 2021). This result, therefore, adds to the growing evidence that some Cerrado species may face greater risks from intensifying heat stress events caused by global warming (Araújo et al. 2021).

Contrary to our expectations in H1 and H2, we observed notable similarities in T_{50} and TSM values among the studied species, regardless of their distribution range (widespread or restricted) or growth region (northeast or southeast). This result contrasts previous studies that reported a relationship between thermal tolerance and plant performance across large-scale spatial and climatic gradients (Feeley et al. 2020; Araújo et al. 2021; Perez et al. 2021). However, the small range of T_{50} and TSM may be due to local adaptation or acclimation to site conditions (Zhu et al. 2018). Although deciduousness did not directly influence T_{50} and TSM values in our data (Table S4), this uniformity could be explained by the fact that most of the studied species are deciduous or semi-deciduous (Table 1). In terms of the leaf economic spectrum (Wright et al., 2004), deciduous leaves generally involve lower structural investment compared to evergreens (Kröber et al., 2015), which may lead to greater heat sensitivity (Zhang et al. 2024). Therefore, the observed uniformity among species likely reflects a clustering of ecological strategies. Moreover, since the deciduous nature of these plants provides an adaptive mechanism to cope with dangerously high temperatures (Araújo et al. 2021), further studies exploring the plasticity of photosynthetic heat tolerance in deciduous species are essential to deepening our understanding of the physiological resilience of Cerrado trees under future climate conditions.

As predicted in our H3, we observed a significant and positive relationship between LMA and T_{50} (Fig. 3c). This finding is consistent with the previous statement for tropical vegetation (Slot & Winter 2017; Sastry & Barua 2017; Sastry, Guha & Barua, 2018; Slot et al. 2021). Leaves with higher LMA recover photosynthetic electron transport more effectively after heat stress (Knight & Ackerly 2003). Additionally, elevated LMA promotes enhanced nitrogen allocation, optimizing nitrogen use (Dong et al. 2022) and potentially increasing electron transport rates (Evans & Clarke 2018). On the other hand, LA was negatively related to T_{50} (Fig. 3a). These results are consistent with established literature (Sastry, Guha & Barua, 2018). Larger leaves have slow heat exchange between the leaves and the ambient air (Baldocchi and Wilson, 2001), which restricts leaf cooling and may impact the photosynthetic apparatus function. These results indicate that their leaf traits might shape the thermal sensitivity of the studied tree species.

Conversely, TSM did not exhibit a significant relationship with either LMA or LA, which is inconsistent with previous findings that reported a positive relationship (Naseef et al. 2024). This lack might be associated with the fact that the study species are near their temperature thresholds (lower TSM). This suggests that the relationship between heat tolerance and leaf economic traits may be context-dependent, varying with plant types or climates (Sastry & Barua 2017). In warmer vegetation, plant species must perform optimally within a narrow temperature range (Togashi et al. 2018). Therefore, they must fine-tune their photosynthetic efficiency to ensure survival within this ecological niche regardless of their functional characteristics (Doughty & Goulden 2009; Drake et al. 2018).

Finally, building on the limited research efforts that have investigated thermal sensitivity in Cerrado species (Araújo et al. 2021; da Silva and Rossatto 2022, 2024), our study contributes valuable insights to this emerging field and underscores important implications for the future of the Cerrado. Given the projected temperature rise for the Cerrado over the next three decades (Hofmann et al. 2021), plants are likely to face more frequent and prolonged heat stress, potentially damaging their photosynthetic machinery and impairing both plant performance and ecosystem function (Bita & Gerats 2013). Therefore, more details on the direct and indirect effects of temperature on leaf-level photosynthetic dynamics (Slot et al. 2024) are still necessary to better understand the acclimation and adaptation of Cerrado species.

5 Conclusion

Our study has provided insights into the thermal tolerance in the Cerrado. Although T_{50} and TSM values were similar across study regions and species distribution ranges, the low TSM values indicate the vulnerability of these species. Additionally, we also observed that T_{50} is related to leaf area (LA) and leaf mass per area (LMA), which suggests that the thermal properties are influenced by leaf traits. This emphasizes the importance of further research on the plasticity of functional, morphological, and physiological leaf traits related to heat and drought disturbances. Such studies are essential for better understanding the components of acclimation and adaptation to temperature responses in Cerrado species.

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Author contributions TCSO: design the study; TCSO, VDO, and LBG: data collection; TCSO: data analysis; TCSO, TFD, BK, and EV: interpreting the analysis and results; TCSO: writing the first draft; TCSO, TFD, EV, BK and VDO: final draft review and editing.

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Data availability The code and data used in the models are available at https://github.com/tonydoliveira/Cerrado-PHS.

Declarations

Conflict of interest The authors have no conflicts to declare.

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