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Tree Physiology

de Sousa Oliveira, Tony César; Veenendaal, Elmar; Domingues, Tomas Ferreira

https://doi.org/10.1093/treephys/tpae163

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Tree Physiology, 2025, **45**, tpae163
https://doi.org/10.1093/treephys/tpae163
Advance access publication date 13 December 2024
Research paper

The thermal optimum of photosynthetic parameters is regulated by leaf nutrients in neotropical savannas

Tony César de Sousa Oliveira[1,2,3,4,*], Elmar Veenendaal[1] and Tomas Ferreira Domingues[2,*]

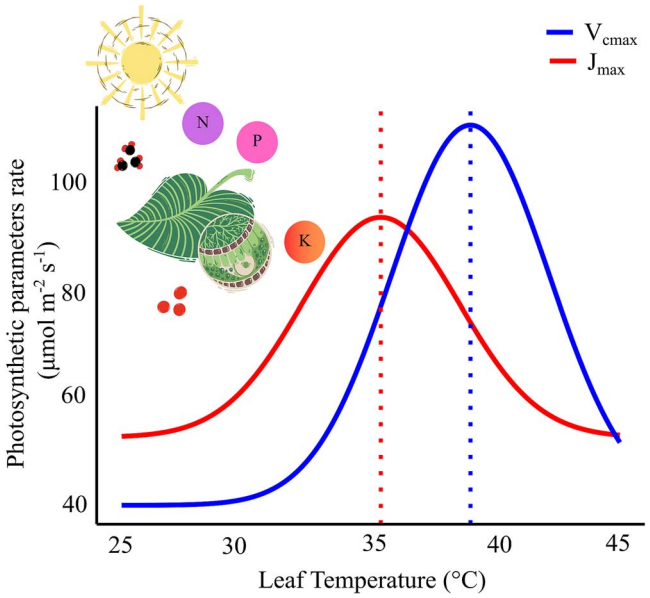
[1]Plant Ecology and Nature Conservation Group, Wageningen University (WU), Droevendaalsesteeg 36708PB, Wageningen, The Netherlands
[2]Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes, 3900, Monte Alegre, Ribeirão Preto, SP 14040-901, Brazil
[3]Institute of Biogeosciences, Forschungszentrum Jülich, Wilhelm-Johnen Strasse, Jülich, 52428, Germany
[4]Faculty of Communication and Environment, Hochschule Rhein-Waal, Südstr. 8 Kamp-lintfort, 47475, Germany

*Corresponding authors (tonycsoliveira@hotmail.com.br; tomas@ffclrp.usp.br)

Handling Editor: Kristine Crous

Global warming significantly threatens species in the Cerrado, the world's largest savannah. Therefore, understanding how plants respond to temperature change, particularly in relation to leaf-level photosynthetic capacity, is crucial to understanding the future of Cerrado vegetation. Here, we determined the optimum temperature of the maximum rate of RuBP-carboxylation and maximum electron transport rate (T_{OptV} and T_{OptJ}, respectively) of 12 tree species in two opposite borders (northeastern and southeastern) of the Cerrado with distinct temperature regimes. We focused on four widespread species found in both sites, four restricted to the northeast, and four to the southeast. We compared T_{OptV} and T_{OptJ} between regions and between widespread species (co-occurring in both sites) and species restricted to each ecoregion. Additionally, we also explored the relationship between T_{OptV} and T_{OptJ} with leaf nitrogen (N), phosphorus (P) and potassium (K). As a result, we found that T_{OptV} and T_{OptJ} values were similar across species, regardless of the study region or species distribution range. The similarity of T_{Opt} values among species suggests that photosynthetic performance is optimized to current temperatures. Additionally, we also observed that the T_{OptV} and T_{OptJ} were similar to the local maximum ambient temperatures. Therefore, if these species do not have enough plasticity, the increasing temperature predicted for this region may reduce their photosynthetic performance. Finally, the studied species exhibited general relationships between the T_{OptV} and T_{OptJ} and foliar key nutrients, particularly with P, suggesting the nutrient availability has an important role in the thermal acclimation of leaves. These findings offer valuable insights into physiological and ecological mechanisms in photosynthesis performance present in the Cerrado species.

Graphical Abstract



Keywords: acclimation, Cerrado, temperature rise, phosphorus, photosynthesis regulation.

Received: July 19, 2024. **Accepted:** December 10, 2024
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Introduction

The largest savanna in the world, the Brazilian Cerrado, is one of the most significant biodiversity global hotspots (Myers et al. 2000), due to its more than 7000 species of vascular plants, of which ~4208 are endemic (Forzza et al. 2012, Colli et al. 2020). However, this unique biome has experienced a considerable change in its climate regime over the last six decades, with an increase in the average maximum temperature of 4 °C (Hofmann et al. 2021). The changes in temperature may have already pushed species living on the borders of Cerrado to their high-temperature thresholds (Araújo et al. 2021, da Silva and Rossatto 2022). This is of particular concern as these border areas serve as transition zones between distinct biomes and are highly sensitive to environmental changes (Castro et al. 1999, Vieira et al. 2022). Therefore, understanding the temperature sensitivity of species in the border regions of the Cerrado can provide valuable insights into this biome's adaptability to ongoing climate change.

Increasing temperatures directly impact photosynthesis, one of the key processes determining individual plant fitness. Net photosynthesis (A_{net}) increases with leaf temperature up to a thermal optimum (T_{OptA}) when it reaches its highest value but rapidly decreases when leaf temperatures rise above that optimum (Lin et al. 2012). Variations in T_{OptA} result from the sensitivity of different photosynthetic biochemistry processes on A_{net} (Wittmann et al. 2022). The two key parameters of the biochemical FvCB model for C_3 photosynthesis (Farquhar et al. 1980)—the maximum carboxylation rate (V_{cmax}) and the maximum rate of electron transport (J_{max})—are considerably sensitive to temperature (Medlyn et al. 2002). This sensitivity arises mainly from the enzymatic and diffusional thermodynamic principles that govern this process (Bernacchi et al. 2009). Past studies have shown variations in the optimum temperature of V_{cmax} and J_{max} (T_{OptV} and T_{OptJ}, respectively) with climate. For example, species tend to increase both T_{OptV} and T_{OptJ} when growing in hotter environments to facilitate carbon assimilation in hot/warm environments (Kumarathunge et al. 2019, Crous et al. 2022). These shifts reflect the photosynthetic machinery's capacity to acclimate (Lin et al. 2012), which may represent plants' functional or ecological strategies for climate adaptation (Atkin et al. 2006). Therefore, understanding the temperature response through these parameters is crucial for elucidating the mechanisms underlying photosynthetic acclimation and adaptation to temperature.

Additionally, it is widely accepted that leaf nutrient concentrations regulate photosynthesis (Butler et al. 2019, Peng et al. 2021), particularly nitrogen (N) and phosphorus (P). This is due to the large amount of leaf N invested in the ribulose 1–5-bisphosphate oxygenase/carboxylase (Rubisco) protein and chlorophyll synthesis, and leaf P role on the ATP and NADPH production, membrane stability and electron transport rates (Walker et al. 2014, Peng et al. 2021). For Cerrado vegetation, leaf P is crucial for regulating photosynthesis, either as a primary limitation or co-limited with leaf N (Gvozdevaite et al. 2018), as well as in other tropical savannas (Domingues et al. 2010, Bloomfield et al. 2014). Additionally, leaf potassium (K) has also been shown to positively affect Cerrado species (Lloyd et al. 2015). Leaf K is particularly important in plant osmotic processes in drought-prone environments (Sardans and Peñuelas 2015), directly affecting the membrane functioning and stomatal conductance (Tränkner et al. 2018). However, very few studies have focused on understanding how leaf nutrients affect the acclimation of the components of photosynthesis' dependence on temperature (Slot and Winter 2017*a*). Controlled experiments have shown that leaf nutrient concentration is related to the adjustment of the photosynthetic capacity under high-temperature conditions (Hochmal et al. 2015, Boaretto et al. 2020). Therefore, understanding how leaf nutrient concentration regulates temperature-dependent acclimation of plant photosynthesis *in situ* may provide crucial insights into Cerrado species adaptation to climate change.

Here, we determined the T_{OptV} and T_{OptJ} together with leaf N, P and K concentrations in tree species from two opposite biodiversity supercenters (northeast and southeast, Castro 1994) within the Brazilian Cerrado. Our survey analyzed species that co-occur and are restricted to both regions, aiming to answer the following questions: (i) Are there significant differences between T_{OptV} and T_{OptJ} between species in the northeast and southeast Cerrado borders? (ii) How do T_{OptV} and T_{OptJ} differ between widespread and region-restricted species? (iii) Is foliar nutrient concentration related to T_{OptV} and T_{OptJ}? Our first hypothesis is that the T_{OptV} and T_{OptJ} differ among borders, being higher at the warmer region, consistent with the acclimation of the photosynthesis to prevailing ambient temperatures (Kattge et al. 2017). Second, we predict that widespread species will show higher values of T_{OptV} and T_{OptJ}, which explains their ability to adapt to the especially variable climatic conditions of the Cerrado. Our third hypothesis is that N, P and K positively affect T_{OptV} and T_{OptJ}, consistent with the role of leaf nutrients in regulating V_{cmax} and J_{max} in savanna areas (Gvozdevaite et al. 2018), with P as the main explanatory variable (Domingues et al. 2010).

Materials and methods

Study sites

The study was conducted in two sites on opposite latitudinal extremes of the Cerrado with contrasting climate regimes: the northeastern and southeastern borders (Figure 1). In the northeast border, the study was carried out in a transition area between the Cerrado and the Caatinga (a seasonally dry forest in Brazil) at the Parque Nacional de Sete Cidades, Piauí, Brazil (04°02′08″ S and 41°40′45″ W). The region's climate is classified as tropical with a dry winter (Aw) (Alvares et al. 2013), characterized by annual precipitation of 1400 mm, mean monthly temperatures ranging from 25.7 °C to 29.1 °C, and daily temperatures peaking at 38 °C during the hottest months (September to November) (INMET-Instituto Nacional de Meteorologia: doi:bdmep.inmet.gov.br/). In the southeastern border, the study was conducted in a transitional area between the Cerrado and the Brazilian Atlantic rainforest at the buffer zone of the Parque Estadual Furnas do Bom Jesus, São Paulo, Brazil (20°14′49″ S and 47°21′02.7″ W). The climate of that region is classified as humid subtropical (Cw) (Alvares et al. 2013), featuring annual precipitation of 1300 mm and average monthly temperatures ranging from 18.2 °C to 23.2 °C, and maximum temperature typically reaches 35 °C during the warmest months (June to August) (INMET).

Data collection

The ecophysiological data in each region were collected during the rainy season. In the southeast, measurements were

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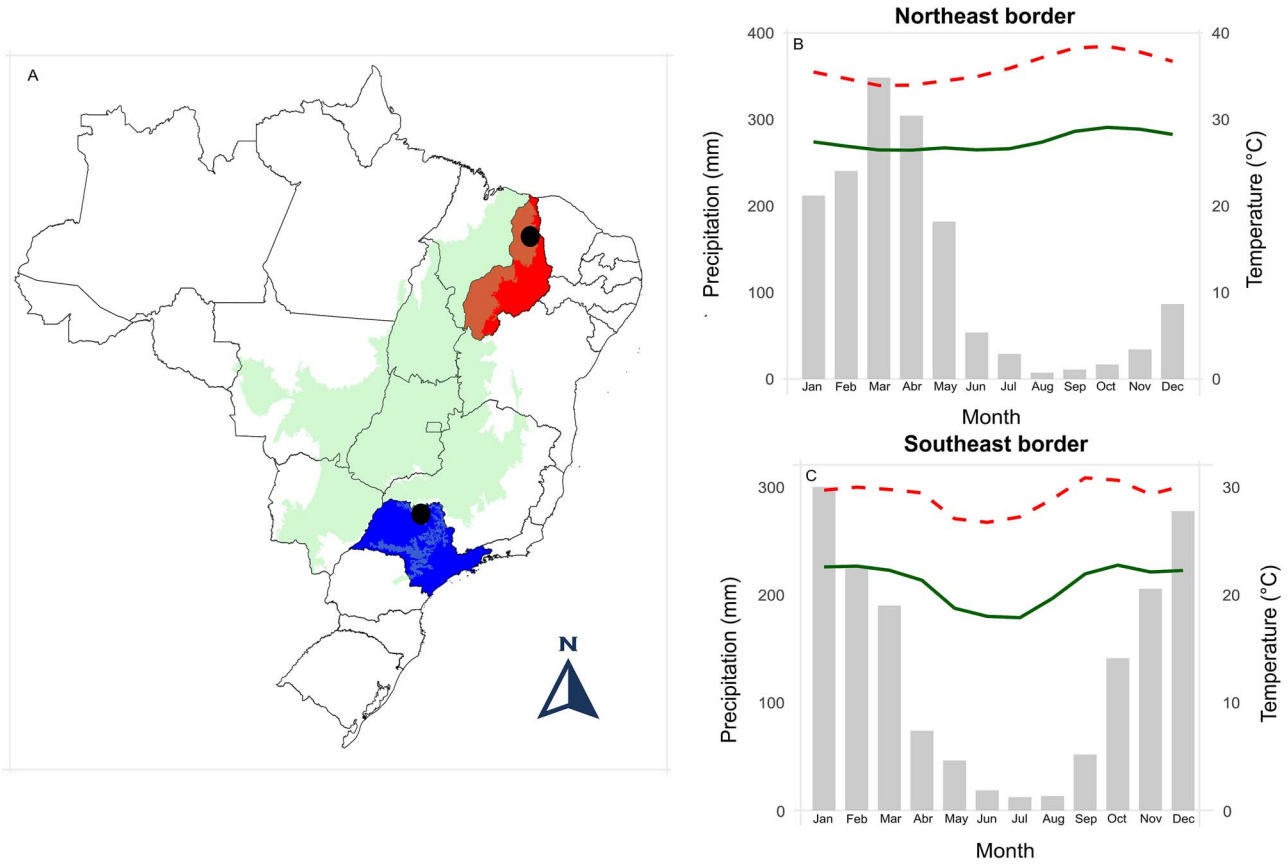


Figure 1. Sampling sites and climatic conditions: Brazil map showing the locations of our two study sites in the Cerrado biome. The two study sites are indicated in different colors(A): the red northeast border region in Piauí state, Brazil, and the blue southeast border region in São Paulo state, Brazil, with their respective precipitation per month (shown as gray bars), mean monthly temperature (indicated by the green line) and daily maximum absolute temperature per month (represented by the dashed red line) (B, C). Precipitation and temperature data were obtained from the Instituto Nacional de Meteorologia (INMET) from 1997 to 2022 (Instituto Nacional de Meteorologia—https://bdmep.inmet.gov.br/).

carried out in March 2022, when a monthly precipitation of 136.2 mm was recorded, along with a mean temperature of 23.2 °C and a maximum temperature of 28.1 °C (INMET). In the northeast, the data were collected in April 2023, during which the recorded average precipitation was 173.7 mm, the mean temperature 26.1 °C and the maximum temperature 31.6 °C (INMET). We focused on four widespread species (co-occurring in both sites), another four species geographically restricted to the northeast border and another four species restricted to the southeast border (12 species in total, Table 1). The selection of species considered their relative frequency. For widespread species, we considered the relative frequency of species within the Cerrado and selected only those with a frequency >50% (Françoso et al. 2016), which were present in both study areas. For restricted species, we consider their frequency within the Cerrado's three biodiversity supercenters: Northeast, Central Plateau and Southeast (Castro 1994). For this, we used the frequency association index proposed by Françoso et al. (2019), which organized the Cerrado vegetation in seven biogeographic districts: Central (CE), Central-west (CW), North-east (NE), North-west (NW), South (S), South-east (SE) and South-west (SW). The following districts correspond to Castro's biodiversity supercenters (Castro 1994): NE (N and NE Districts), CE (CW, NW and SW) and SE (S and SE Districts). The frequency of the species studied within the Cerrado and within each biodiversity supercenter can be found in Table S1, available as Supplementary data at *Tree Physiology* Online.

Gas exchange and chlorophyll fluorescence measurements

For each species, we selected three individuals to carry out the ecophysiological measurement. From each individual, one fully sunlit branch (as close as possible to the top of the canopy) was cut and was re-cut underwater immediately (~30 cm) to maintain xylem water flow and prevent stomatal closure. Subsequently, we left the branch in direct sunlight, and one mature leaf was selected for ecophysiological determination. We placed the leaf into a gas exchange chamber and allowed it to acclimate for ~20 min. Leaf gas exchange and chlorophyll fluorescence were measured simultaneously using LI-COR LI-6800 portable photosynthesis systems (Li-Cor Inc., Lincoln, NE, USA) between 7 a.m. and 4 p.m. (Brazil time). Conditions within the leaf chamber were configured as follows: ambient CO_2 concentration (C_a) 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}). Then, we set the leaf temperature to 25 °C whenever possible before initiating the measurements of the temperature response curves. Subsequently, we gradually increased the temperature to 45 °C (when possible)

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Table 1. List of plant species studied per region, their respective botanical families and the species distribution range.

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

at a 3 °C interval approximately every 5 min. Among all curves, the stomatal conductance mean ranged from 0.02 to 0.45 μmol m^{-2} s^{-1}. At each temperature, values of all gas exchange parameters, such as light-saturated photosynthetic rate (A_{sat}), stomata conductance (g_s), leaf temperature (T) and intercellular CO_2 concentration (C_i) were recorded. Additionally, the light-saturating electron transport rate (J, determined by fluorescence) was also recorded using chlorophyll fluorescence measurements.

Estimating temperature response of V_{cmax} and J_{max}

A curve fitting routine based on minimizations of the sums of squared residuals was developed in the 'R' environment (version 4.2.3 R Development Core Team 2020) to derive the parameters that describe the temperature dependence of V_{cmax} and J_{max} based on the peaked Arrhenius function, Eq. (1).

$$K_T = \mathrm{K}_{25} * \exp\left[\frac{E_a * (T_k - 298.15)}{298.15 * R * T_k}\right] * \left[\frac{1 + \exp\left(\frac{298.15 * \Delta_S - H_d}{298.15 * R}\right)}{1 + \exp\left(\frac{T_k * \Delta_S - H_d}{T_k * R}\right)}\right] \quad (1)$$

where K_T is the process rate (J_{max} or V_{cmax}; μmol m^{-2} s^{-1}) at a given temperature (T_k), K_{25} (μmol m^{-2} s^{-1}) is this process rate at 25 °C, E_a (kJ mol^{-1}) is the activation energy that describes the exponential increase in enzyme activity with the increase in temperature, Δ_S (J mol^{-1} K^{-1}) is the entropy term that characterizes the changes in reaction rate caused by substrate concentration (Johnson, Eyring and Williams 1942), H_d (kJ mol^{-1}) is the deactivation energy that describes the decline in enzyme activity at higher temperatures and R is the universal gas constant, equal to 8.314 J mol^{-1} K^{-1}.

We estimated the temperature-scaled apparent maximum carboxylation capacity ($V'_{cmax\text{-}\rho}$) as described by de Sousa Oliveira et al. (2023):

$$V'_{cmax-\rho} = \frac{A_{sat}}{\left(\frac{C_i - \Gamma^*}{C_i + K_m} - 0.015 * \rho\right)} \quad (2)$$

where A_{sat} is the light-saturated net photosynthetic rate at ambient CO_2 concentrations (C_a = 400 p.p.m.), C_i is the intercellular CO_2 concentration, Γ^* is the CO_2 compensation point in the absence of mitochondrial respiration and K_m is the Michaelis–Menten constant for carboxylation and oxygenation. The K_m and Γ^* values were calculated according to the equations listed in De Kauwe et al. (2016), based on the values taken from Bernacchi et al. (2001). The value 0.015 is an assumed ratio between mitochondrial respiration rate in the light (R_{day}) and $V'_{cmax\text{-}\rho}$ at the reference temperature of 25 °C (R_{day}:$V'_{cmax\text{-}\rho}$ ratio) (Collatz et al. 1991, De Kauwe et al. 2016), and ρ is the temperature-scaling factor of the R_{day}:$V'_{cmax\text{-}\rho}$ ratio calculated by the ratio between the temperature dependency of R_{day} [Eq. (3)] and the temperature dependency of V_{cmax} [Eq. (1)] (de Sousa Oliveira et al. 2023).

The relationship between R_{day} and leaf temperature was defined based on the standard Arrhenius function:

$$R_{day_T} = e\,\frac{E_{aR} * (T_k - 298.15)}{298.15 * R * T_k} \quad (3)$$

where R_{dayT} is the R_{day} rate at a given temperature (T_k) and E_{aR} is the activation energy for R_{day}. We therefore fixed E_{aR} to 207 kJ mol^{-1} as done by de Sousa Oliveira et al. (2023) to avoid overeparameterization of the model.

To describe the J_{max}, we used the electron transport rate (J) at saturating light (J'_{max} at 2000 μmol m^{-2} s^{-1}).

$$J'_{max} = \Phi_{PSII} * \alpha * 0.5 * 2000 \quad (4)$$

where Φ_{PSII} is the photochemical efficiency of photosystem II computed from steady-state fluorescence (F') and maximal fluorescence (F_m') during a light-saturating pulse (Genty et al. 1989), α is the total leaf absorptance, the factor 0.5 describes the expected distribution of light between the two photosystems II and I, and 2000 is the photosynthetic photon flux density (μmol m^{-2} s^{-1}).

Model fitting

The graphical summary of the curve fitting routine is presented in Figure S1, available as Supplementary data at *Tree Physiology* Online. The central aspect of our strategy was to use gas-exchange and chlorophyll fluorescence data to generate estimations of the peaked Arrhenius model parameters, considering the interconnections between equations dependent on these parameters. First, we set the key parameters of the peak temperature response Arrhenius-type curve of V'_{cmax} and J'_{max} following Eq. (1). Secondly, using the Arrhenius temperature-response parameters, we modeled the values of $V_{cmax\text{-}Arrh}$ and $J_{max\text{-}Arrh}$ in relation to leaf temperature according to Eq. (1). Third, we set the temperature-dependent scaling factor (ρ) in Eq. (2) by dividing

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the temperature responses of V_{cmax} Eq. (1) by the temperature responses of R_{day} Eq. (3). Subsequently, we computed values of the temperature-scaled apparent maximum carboxylation capacity ($V'_{cmax\text{-}\rho}$) using Eq. (2). Furthermore, based on the FvCB model, we back-calculated the assimilation rate (A_w) as the minimum value between the assimilation limited by V_{cmax}, assumed as $V_{cmax\text{-}Arrh}$ (A_c), and the assimilation limited by J_{max}, assumed as $J_{max\text{-}Arrh}$ (A_j). The function error to be minimized was computed by the sum of the squared differences of three terms: (i) between the measured and modeled assimilation rates (A_{sat} and A_w), (ii) between $V_{cmax\text{-}Arrh}$ and $V'_{cmax\text{-}\rho}$ and (iii) between $J_{max\text{-}Arrh}$ and J'_{max}. Finally, three function minimization algorithms were used to derive the temperature dependence parameters to ensure the best parameter estimations (R packages OptimX, DEoptim and GenSA) (Ardia et al. 2011, Mullen et al. 2011, Xiang et al. 2013).

The peaked Arrhenius function temperature dependence parameters of $V'_{cmax\text{-}\rho}$ and J'_{max} derived from the best-optimized solution were then applied to the optimum temperature (T_{OptV} and T_{OptjJ}, consecutively) (Medlyn et al. 2002).

$$T_{Opt} = \frac{H_d}{\Delta_S - R * \ln\left(\frac{E_a}{H_d - E_a}\right)} \quad (5)$$

Leaf traits and chemistry determination

After conducting gas exchange measurements, the fresh leaves were scanned, and the leaf area (LA, cm^2) was calculated using the software ImageJ. After that, the leaves were placed in an oven set at 70 °C and dried for 48 h before determining the dry mass (g). The ratio between leaf dry mass and its LA (LMA; g m^{-2}) was then calculated. The dried leaf samples were used to determine leaf N, P and K contents (mg g^{-1}), respectively, by Kjeldahl (Bradstreet 1965), nitric-perchloric acid digestion (Grimshaw 1987) and flame atomic emission spectroscopy (Walinga et al. 1989) at Ribersolo-Agricultural Analysis Laboratory, Ribeirão Preto, Brazil. The leaf N, P and K concentrations were then divided by LMA to be expressed in area-based (g m^{-2}). We acknowledge that both area- and mass-based expressions of nutrient variation provide valuable insights into leaf photosynthetic capacity (Lloyd et al. 2013, Niinemets et al. 2014), with both representations considered complementary for evaluating plant function (Westoby et al. 2013). However, in this study, we opted for the area-based approach, as photosynthetic traits and nutrient variations related to the structure and function of the photosynthetic machinery are better represented by this metric (Lloyd et al. 2013), while mass-based correction is more appropriate for assessing carbon economy, whole-plant function or growth and the defensive or structural roles of nutrients (Xu et al. 2023). The relationships between T_{OptV} and T_{OptJ} (°C) with N_{mass}, P_{mass}, and K_{mass} (mg g^{-2}) are, however, provided for consultation in Figure S2.

Statistical analyses

First, to assess the degree of variation of the traits among species, we calculated the maximum, minimum, average and standard deviation of the temperature response of T_{OptV} and T_{OptJ} and leaf nutrient concentrations (Table 2). To answer our first and second questions and account for general differences in T_{OptV} and T_{OptJ} between the study regions and species distribution, we conducted one-way analyses of variance (ANOVA) followed by post hoc Tukey's HSD test with species as a random factor. Data normality and homogeneity of variance were checked using Shapiro–Wilk and Levene tests, respectively. The same analysis was performed to test the difference in foliar nutrients between regions. Additionally, for the widespread species found in both sites, we performed individual ANOVAs to investigate the variability in the study traits at the species level. To address our third question, we employed linear regression models to assess the relationship between leaf nutrient concentrations and T_{OptV} and T_{OptJ}. Beforehand, the normal distribution of regression residuals was formally tested using the Shapiro–Wilk test. Additionally, we extended our analysis to multiple linear regressions to understand the additive effect of these nutrients and their interaction with these parameters. The regression analyses were performed at the species level throughout the entire dataset and between each study region. To ensure robustness, we applied a correlation threshold to exclude highly correlated variable pairs (correlation >0.5) and enhance the interpretability of results. For those, the model selection was carried out using the lower Akaike information criterion (AIC) and the highest R-squared (r^2) (Tang et al. 2019), ensuring the most suitable subset models were chosen. All analyses were performed in the R environment (R Core Team, 2020).

Results

We explore below the findings presented in Table 2, which summarizes T_{OptV}, T_{OptJ}, N_{area}, P_{area} and K_{area} for each species within each study area. The Arrhenius temperature dependence parameters of $V'_{cmax\text{-}\rho}$ and J'_{max}, g_s and leaf-to-air VPD information are provided in Table S2, available as Supplementary data at *Tree Physiology* Online. The LMA and leaf nutrients on a mass basis are provided in Table S3, available as Supplementary data at *Tree Physiology* Online.

Optimum temperature

Among all species (Table 2), the T_{OptV} mean was 39.0 ± 0.6 °C (mean ± standard error), ranging from 34.8 ± 1.0 °C to 43.1 ± 0.8 °C, and the T_{OptJ} mean was 35.4 ± 0.3 °C, ranging from 32.7 ± 1.3 °C to 38.2 ± 0.1 °C. Regarding our first question, there was no significant difference in T_{OptV} between regions (Figure 2a, p-value = 0.17). Similarly, T_{OptJ} values were observed to be quite uniform between regions (Figure 2b, p-value = 0.17). Considering all the study species in the northeast border (widespread and restricted), a mean T_{OptV} of 38.4 ± 0.8 °C and T_{OptJ} of 35.0 ± 0.5 °C, while on the southeast border, the mean T_{OptV} was 39.7 ± 0.6 °C and T_{OptJ} of 35.8 ± 0.4 °C.

Concerning our second question, no differences were observed among species distribution ranges (p-value = 0.56 and 0.74, for T_{OptV} and T_{OptJ}, respectively). Overall, widespread species had a mean T_{OptV} of 39.4 ± 0.9 °C and a mean T_{OptJ} of 35.5 ± 0.6 °C, while among all restricted species (from northeast and southeast) had a mean T_{OptV} of 38.7 ± 0.5 °C and a mean T_{OptJ} of 35.3 ± 0.3 °C (Figure 2c and d). In the northeast border, restricted species had a mean T_{OptV} of 38.3 ± 3.0 °C and a mean T_{OptJ} of 35.5 ± 1.9 °C, while widespread species had a mean T_{OptV} of 38.4 ± 4.7 °C and T_{OptJ} of 34.6 ± 2.7 °C. In the southeast border, restricted species had a mean T_{OptV} of 39.1 ± 2.3 °C

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Table 2. Species mean T_{OptV} (°C) and T_{OptJ} (°C) and nitrogen (N), phosphorus (P) and potassium (K) area-based foliar concentrations (g m^{-2}) with standard deviation (SD) across study borders in Cerrado, according to the distribution range groups.

		T_{OptV} (°C)		T_{OptJ} (°C)		N_{area} (g m^{-2})		P_{area} (g m^{-2})		K_{area} (g m^{-2})	
Region	Spp	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Northeast border	Widespread species										
	A. coriacea	39.9	5.2	35.9	4.3	1.94	0.8	0.06	0.0	0.53	0.2
	H. stigonocarpa	34.8	1.7	34.5	1.6	1.62	0.3	0.05	0.0	0.76	0.3
	Q.gradiflora	39.4	2.9	32.6	2.2	2.28	0.4	0.08	0.0	0.51	0.2
	X. aromatica	39.7	7.4	35.2	2.5	2.59	0.5	0.13	0.0	0.78	0.1
	Restricted species										
	C.coriaceum	37.8	4.4	36.4	3.2	2.01	0.9	0.09	0.0	0.79	0.3
	O.sessiliflora	36.3	2.7	33.9	1.8	1.38	0.4	0.07	0.0	0.67	0.2
	S. coriaceum	40.5	3.0	36.5	1.0	1.94	0.2	0.10	0.0	0.67	0.2
	V. macrocarpa	38.6	0.8	35.4	0.0	2.16	0.7	0.10	0.0	1.11	0.6
Southeast border	Widespread species										
	A. coriacea	36.0	2.4	34.8	2.9	1.80	0.5	0.08	0.0	0.78	0.1
	H.stigonocarpa	39.7	2.9	36.2	1.5	2.54	0.2	0.10	0.0	0.63	0.3
	Q.grandiflora	43.1	1.4	38.2	0.2	2.93	0.8	0.14	0.0	0.96	0.2
	X. aromatica	42.6	2.0	36.7	3.9	2.69	0.3	0.14	0.0	0.77	0.2
	Restricted species										
	O. arborea	36.6	0.9	33.7	1.2	2.21	0.3	0.07	0.0	0.51	0.2
	O. spectabilis	39.5	2.4	35.6	0.8	2.25	0.2	0.11	0.0	0.69	0.2
	S. adstringens	38.3	0.4	34.9	2.1	2.00	0.2	0.09	0.0	0.66	0.4
	V. tucanorum	41.8	1.4	36.1	0.3	2.07	0.6	0.10	0.0	0.81	0.3

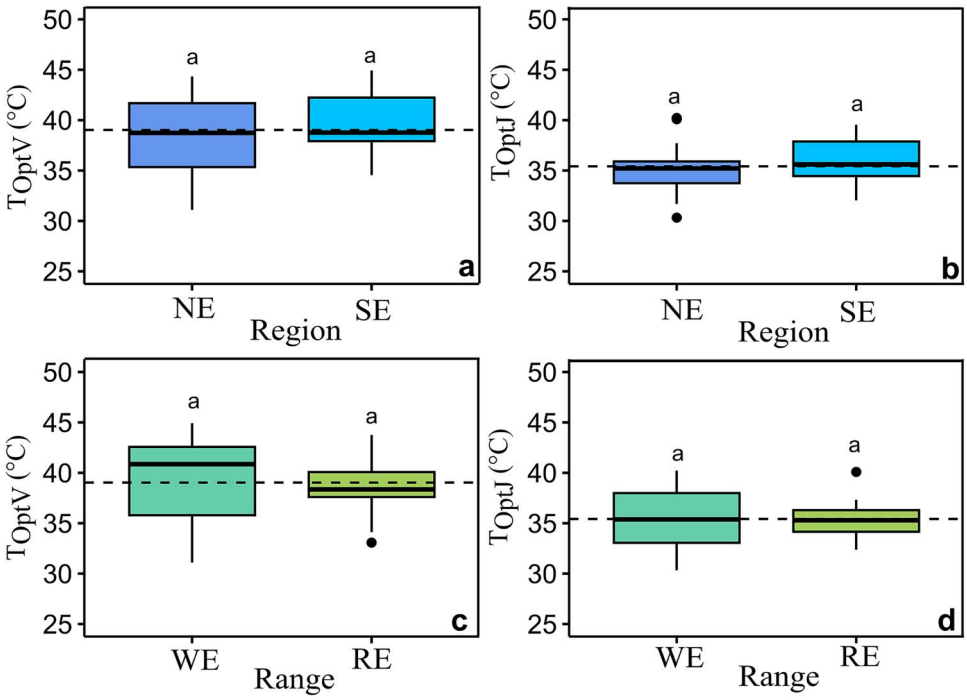


Figure 2. Boxplots display the difference in T_{OptV} and T_{OptJ} between study regions in (a) and (b) (northeast border—NE and southeast border—SE), and between species distribution groups in (c) and (d) (widespread—WE and restricted—RE species). The dashed line represents the overall average of T_{OptV} and T_{OptJ} for the dataset as a whole. Different letters indicate a statistically significant difference (p-value <0.05). Note: the box boundaries represent the 25th and 75th percentiles, with the median indicated by a solid line. The whiskers extend to the 10th and 90th percentiles, and outliers are shown as dots.

and a mean T_{OptJ} of 35.1 ± 1.5 °C, and widespread species had a mean T_{OptV} of 40.3 ± 3.5 °C and a mean T_{OptJ} of 36.5 ± 2.5 °C. However, no significant differences were observed in T_{OptV} and T_{OptJ} between restricted species for the northeast and southeast border nor for widespread species from each region (see Table S4 available as Supplementary data at *Tree Physiology* Online). For those widespread species, no significant differences were observed in T_{OptV} and T_{OptJ} values, except for *Qualea grandiflora*, which has shown a higher mean T_{OptJ} in the Southeast border (p-value = 0.01).

Leaf nutrients

The average of key leaf nutrients among all species were as follows: N_{area} was 2.15 ± 0.10 g m^{-2}, P_{area} was 0.09 ± 0.01 g m^{-2} and K_{area} was 0.73 ± 0.04 g m^{-2}. When comparing regions, mean N_{area} (0.99 ± 0.11 g m^{-2}) and P_{area}

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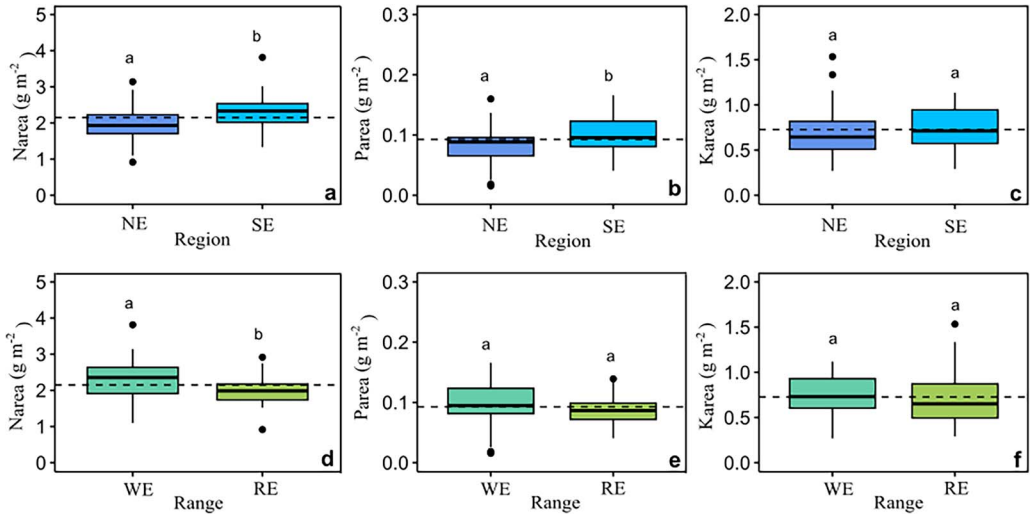


Figure 3. Difference in nitrogen (N), phosphorus (P) and potassium (K) area-based foliar concentrations (g m^{-2}) between study regions (northeast border—NE and southeast border—SE) in boxplots a, b and c respectively, and between species distribution groups in (c) and (d) (widespread—WE and restricted—RE species) in boxplots d, e and f respectively. The dashed line represents the average of the foliar nutrient level for the whole dataset. Different letters indicate a statistically significant difference (p-value <0.05). The box boundaries represent the first and third quartiles, with the median shown by a solid line. The whiskers extend to the minimum and maximum values, while outliers are displayed as individual dots.

(0.08 ± 0.01 g m^{-2}) were significantly lower on the northeast border and higher on the southeast border with mean N_{area} of 2.31 ± 0.10 g m^{-2} and mean P_{area} of 0.10 ± 0.01 g m^{-2} (Figure 3a and b). Unlike N_{area} and P_{area}, leaf K_{area} showed no significant differences between regions.

Considering the species distribution range, widespread species had N_{area} mean of 2.30 ± 0.13 g m^{-2}, P_{area} mean of 0.09 ± 0.4 g m^{-2} and K_{area} mean of 0.72 ± 0.2 g m^{-2}, while restricted species had N_{area} mean of 2.00 ± 0.08 g m^{-2}, P_{area} mean of 0.89 ± 0.3 g m^{-2} and K_{area} mean of 0.73 ± 0.3 g m^{-2}. However, only N_{area} has differed significantly between widespread and restricted species (Figure 3d). In addition, there was no significant difference in leaf nutrient concentration between the species restricted to the northeast and those restricted to the southeast (p-value = 0.13 for N_{area}, p-value = 0.79 for P_{area} and p-value = 0.29 for K_{area}). For widespread species, only P_{area} showed higher levels in the southeast (0.11 ± 0.04 g m^{-2}) compared with the northeast (0.09 ± 0.04 g m^{-2}) with p-values of 0.13 for N_{area}, 0.04 for P_{area} and 0.14 for K_{area}. Considering individual widespread species, *Q. grandiflora* showed higher P_{area} (p-value = 0.04) and K_{area} (p-value = 0.05) and *H. stigonocarpa* exhibited higher N_{area} (p-value = 0.01) in the southeast area.

Relationships between T_{OptV} and T_{OptJ} with leaf nutrient

Concerning our third question, we observed positive relationships between leaf nutrients and T_{OptV} and T_{OptJ} (Figure 4). Considering all the data, T_{OptV} was significantly related to N_{area} and P_{area} but not to K_{area}. Meanwhile, T_{OptJ} had a significant relationship with all nutrients. Overall, considering all datasets, P_{area} was found to be the best explanatory variable for both T_{OptV} and T_{OptJ} evidenced by the lowest AIC and highest r^2 (Table 3). Multiple regression models did not perform better than simple regression when more than one nutrient was included (see Table S5 available as Supplementary data at *Tree Physiology* Online).

In the southeast border, T_{OptV} was positively correlated with N_{area} and P_{area}, but not with K_{area} and T_{OptJ} was related to N_{area}, P_{area} and K_{area} (Table 3). Among these, P_{area} was identified as the best explanatory variable for both T_{OptV} and T_{OptJ} (Table 3). In contrast, no significant relationships between foliar nutrients and T_{OptV} or T_{OptJ} were observed in the northeast border. Additionally, when considering species distribution range, our results indicated that T_{OptV} had a significant positive relationship with N_{area} and P_{area} in widespread species, and with P_{area} in restricted species. For both widespread and restricted species, P_{area} was the best explanatory variable (lowest AIC value). Finally, for T_{OptJ}, a significant relationship with P_{area} was found only for restricted species, while no significant correlations between leaf nutrients and T_{OptJ} were observed in widespread species.

Discussion

Given the projected temperature increase in specific regions of Cerrado (Hofmann et al. 2021), it is crucial to assess the acclimation components of photosynthesis in Cerrado's species. In this study, we examined how the optimal temperature of photosynthetic biochemical parameters varies between two borders of Cerrado and among species' distribution ranges. We also investigated how key leaf nutrients are related to T_{OptV} and T_{OptJ}. Here, we discuss three main findings: first, no differences in T_{OptV} and T_{OptJ} were observed among species, regardless of the study region, or between restricted and widespread species. Second, among the species, the values of T_{OptV} and T_{OpJ} were similar and/or close to the maximum air temperatures in the study areas. Finally, we observed a strong relationship between the thermal optimum of photosynthetic parameteres and leaf nutrient concentration, with P_{area} as the best explanatory variable for T_{OptV} and T_{OptJ}.

Consistent temperature optima of photosynthetic capacity across borders and distribution ranges

The T_{OptV} and T_{OptJ} values found in our study fall within the typical range reported in other studies on tropical species, from 33–41 °C for T_{OptV} to 30–38 °C for T_{OpJ} (Medlyn et al. 2002, Slot and Winter 2017a, b, Kumarathunge et al. 2019,

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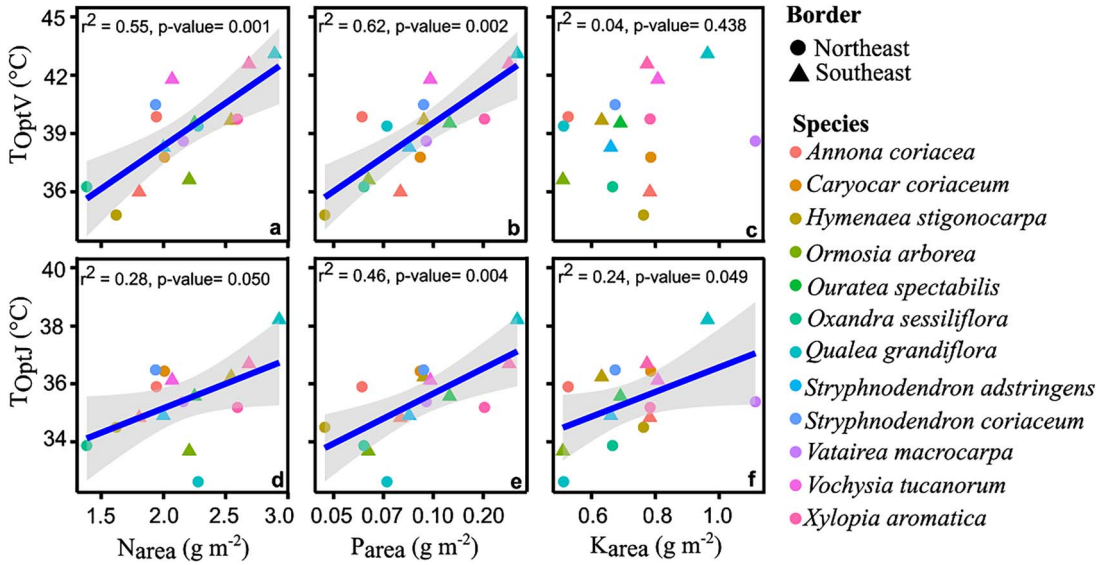


Figure 4. Relationships between the T_{OptV} and T_{OptJ} (°C) with N_{area}, P_{area} and K_{area} (g m^{-2}). The *p*-values and r^2 values are shown for each relationship. Data points represent species means, with different colors representing different species and distinct shapes indicating the two study areas. The relationships between T_{OptV} and T_{OptJ} with N_{area} are shown in panels a and d, with P_{area} in panels b and e, and with K_{area} in panels c and f. Note: the 16 points represent four restricted species in the northeast, four restricted species in the southeast, four widely distributed species in the northeast and four widely distributed species in the southeast.

Table 3. Summary of the best linear mixed-effects models testing relationships of the T_{OptV} and area-based foliar nutrient concentrations, such as nitrogen (N_{area}), phosphorus (P_{area}) and potassium (K_{area}). Akaike information criterion values (AIC) are comparable vertically, *t* value assesses significance, r^2 measures the goodness of fit and *p*-values indicate significance. The best predictor models are highlighted in bold.

	$T_{OptV} \sim N_{area}$				$T_{OptJ} \sim N_{area}$			
	t	r^2	*p*-values	AIC	*t*	r^2	*p*-values	AIC
All data	1.05	0.55	0.001	64.84	2.14	0.28	0.050	55.73
Northeast	2.33	0.47	0.058	33.35	0.19	0.01	0.859	35.19
Southeast	2.82	0.57	0.030	36.53	3.09	0.62	0.021	25.11
Restricted	1.01	0.14	0.357	36.49	0.76	0.08	0.475	28.27
Widespread	**4.99**	**0.81**	**0.002**	**31.28***	1.18	0.34	0.126	32.39
	$T_{OptV} \sim P_{area}$				$T_{OptJ} \sim P_{area}$			
	t	r^2	*p*-values	AIC	*t*	r^2	*p*-values	AIC
All data	**4.88**	**0.62**	**0.002**	**62.00***	**3.44**	**0.46**	**0.004**	**50.47***
Northeast	2.00	0.40	0.092	34.40	0.93	0.13	0.386	31.15
Southeast	**4.58**	**0.78**	**0.004**	**31.27***	**5.35**	**0.83**	**0.002**	**18.72***
Restricted	**3.04**	**0.61**	**0.023**	**30.29***	**3.61**	**0.66**	**0.011**	**19.76***
Widespread	3.37	0.65	0.015	35.93	2.07	0.42	0.841	31.47
	$T_{OptV} \sim K_{area}$				$T_{OptJ} \sim K_{area}$			
	t	r^2	*p*-values	AIC	*t*	r^2	*p*-values	AIC
All data	0.79	0.04	0.438	77.19	2.15	0.24	0.049	55.72
Northeast	−0.47	0.22	0.655	38.21	0.79	0.09	0.455	31.43
Southeast	2.15	0.43	0.752	38.72	3.49	0.67	0.013	23.87
Restricted	0.73	0.08	0.491	37.05	1.12	0.17	0.305	27.48
Widespread	0.47	0.03	0.652	44.12	1.89	0.37	0.107	32.02

Hernández, Winter and Slot 2020, Wang et al. 2020, Dusenge et al. 2021). Following the evidence available in the literature, it would be expected that T_{OtpV} and T_{OptJ} would be higher in species from the northeast border, the warmest region (Kositsup et al. 2009, Atkin et al. 2015, O'Sullivan et al. 2017, Kumarathunge et al. 2019). However, no differences in T_{OptV} and T_{OptJ} were observed between regions. Similar uniformity in T_{OtpV} and T_{OptJ} among species growing at different temperatures in tropical biomes has already been reported by other surveys (Zaka et al. 2016, Slot and Winter 2017b, Dusenge et al. 2021, Kullberg et al. 2023). The small range of T_{Opt} values observed in our study may be due to local adaptation or acclimation to site conditions (Zhu et al. 2018). Plants from tropical regions, which are regularly exposed to heatwaves, have been shown to operate close to upper-temperature limits of the photosynthetic apparatus (Huang et al. 2019). In this case, plants must fine-tune their photosynthetic efficiency (Dos Anjos et al. 2015) to ensure optimum

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performance within regional air temperatures (Benomar et al. 2016).

While recent studies have suggested that species with higher thermal tolerances are likely to have higher geographic ranges (Reich et al. 2015, Aspinwal et al. 2019, Feeley et al. 2020, Perez et al. 2021), our study did not find systematic differences in T_{OtpV} and T_{OptJ} between restricted and widespread species. Few studies have demonstrated narrow photosynthetic tolerances between restricted and widespread plant species (Baskauf and Eickmeier 1994, Dusenge et al. 2021, Kullberg, Slot and Feeley 2023). Although, biochemical parameters related to leaf photosynthesis may not fully explain plant acclimation (Hernández, Winter and Slot 2020, Fang et al. 2022, Niinemets 2023). While species from different habitats may show similar leaf-level assimilation rates, they can differ in traits related to biomass allocation (Wright et al. 2004), supporting their wider geographic range. Indeed, in our study, widespread species tend to have higher LMA (see Table S4 and Figure S3, available as Supplementary data at *Tree Physiology* Online) and N_{area} (Figure 3).

The mean daily maximum temperature at the warmest months in the northeast border (39 °C) is similar to or marginally above the mean T_{OptV} (38.4 ± 0.8 °C) and at least 4 °C above T_{OptJ} (35.0 ± 0.5 °C) for the study species in the region. Similarly, the mean daily maximum temperature at the warmest months (35 °C) in the southeast region is similar to T_{OptJ} (35.0 ± 0.4 °C) and 4 °C below the T_{OptV} (39.7 ± 0.6 °C). The V_{cmax} and J_{max} typically increase with rising leaf temperature until an optimum point (T_{Opt}), beyond which the rates decrease, heading to the high-temperature carbon-compensation point (Bernacchi et al. 2009). Therefore, with the ongoing rise in maximum temperatures in various regions of the Cerrado (Hofmann et al. 2021), if these species are not plastic enough, it would likely lead to reduced photosynthetic efficiency and consequently impact plant performance, which can have substantial implications for the species composition of this unique biome (Wahid et al. 2007). Here, we have shown for the first time the sensibility of the biochemical parameters of photosynthesis for Cerrado tree species. Although our study investigated a limited number of species, it adds to the growing evidence that Cerrado species might be approaching their temperature threshold (Araújo et al. 2021, da Silva and Rossatto 2022). However, further surveys studying the plasticity of Cerrado species in relation to growth temperatures are needed to better predict aspects of the acclimation and adaptation of the temperature dependence of photosynthesis in this biome.

Additionally, it is important to consider thermoregulatory traits, such as stomatal properties, which can decouple leaf and air temperatures (Kullberg, et al. 2023). Even though we only used curves with mean g_s higher than 0.02 mol m^{-2} s^{-1} (see Table S2 available as Supplementary data at *Tree Physiology* Online), as a premise for a good model fit (De Kauwe et al. 2016, de Sousa Oliveira et al. 2023), low g_s is a limiting factor for the temperature response of net photosynthesis (Mott and Peak 2010, Slot et al. 2024). Additionally, the OPM-ρ disregards the influence of g_m over $V'_{cmax\text{-}\rho}$ (de Sousa Oliveira et al. 2023), assuming it to be large enough to cause C_i to be similar to chloroplastic CO_2 concentration (C_c) (De Kauwe et al. 2016). However, g_m varies with leaf temperature due to enzymatic dynamics and CO_2 diffusion (Von Caemmerer and Evans 2014). Another important aspect to consider is the temperature dependence of Γ^* and Michaelis–Menten constant (Sargent et al. 2024), since the stoichiometry of CO_2 release by Rubisco oxygenation is influenced by how these parameters respond to temperature (Bernacchi et al. 2001). In this study, we assumed Γ^* and K_m to be constant among the different species (de Sousa Oliveira et al. 2023), following the common practice of applying a single function to adjust this parameter to a given leaf temperature (Bernacchi et al. 2001; Duursma 2015). However, different assumptions regarding Γ^* can alter the relationship between temperature and the R_{day}:V_{cmax} ratio (De Kauwe et al. 2016). Therefore, a better understanding of different processes that together determine the temperature response of photosynthesis is needed to better comprehend the parametrization of the components of the adaptation and acclimation of photosynthesis.

Foliar nutrient constraints on optimum temperature of photosynthetic capacity

Leaf nutrient concentrations have been identified as an important factor for regulating the photosynthetic capacity of tropical plant communities (Butler et al. 2019, Peng et al. 2021). The average values of the leaf P, N and K concentrations (area-based) found in this study concur with those reported in previous studies carried out with Cerrado vegetation (Lloyd et al. 2015, Gvozdevaite et al. 2018). Between regions, leaf N_{area} and P_{area} means were lower in species in the northeast border than those from the southern region. Although soil characterization was not within the scope of this study, differences in soil fertility might reflect foliar nutrient concentrations (Lloyd et al. 2015, Miatto et al. 2016, Miatto and Batalha 2016). For instance, soil total phosphorus values are lower in the Parque Nacional Sete Cidades (156 mg kg^{-1}) reported by Brunello et al. (2024) than in the Parque Estadual Furnas do Bom Jesus (605 mg kg^{-1}) reported by Tralli (2015). Soil fertility is also likely to explain the differences in some key nutrients within some widespread species growing at different sites. In addition, widespread species showed higher N_{area}. This may be associated with the carbon and nitrogen allocation strategy (Dong et al. 2022), which maximizes efficient resource capture (higher LMA, Table S4 and Figure S3, available as Supplementary data at *Tree Physiology* Online), revealing competition in different habitats (Poorter et al. 2009).

By testing the relationship between T_{OptV} and T_{OptJ} and some key leaf nutrients, contrasting relationships were observed (Figure 4). Overall, P_{area} was the main explanatory variable for both T_{OptV} and T_{OptJ}. The influence of leaf P in regulating photosynthetic capacity has been reported in previous studies carried out in savanna areas (Domingues et al. 2010, Bloomfield et al. 2014). Even more so in the Cerrado region (Gvozdevaite et al. 2018), where P levels in the soil are remarkably low (Resende et al. 2011). Several factors might be associated with this, such as the role of P in ATP synthesis (Vance, Uhde-Stone and Allan 2003), ATP/ADP ratio (Rychter and Rao 2005) and the Rubisco activase (Carstensen et al. 2018, Singh et al. 2019) affecting the V_{cmax} peak. Additionally, P plays a significant role in neutralizing reactive oxygen species (ROS) and reducing the impact of heat on disruptions in Photosystem II function (Krieger-Liszkay et al. 2008, Walker et al. 2014), which might improve the J_{max} peak. Our findings contribute to the growing evidence that leaf P plays a critical role in regulating plant performance

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in Cerrado vegetation (Lloyd et al. 2015, Gvozdevaite et al. 2018).

Additionally, N_{area} was the primary nutrient related to T_{OptV} in widespread species. Indeed, leaf N_{area} was higher in those species, indicating a more substantial investment of leaf nitrogen in Rubisco, which is pivotal in carbon fixation (Evans and Clarke 2018). Finally, K_{area} significantly correlated with T_{OptJ} (Figure 4f), but not with T_{OptV} (Figure 4c). Some studies have shown that plants from warm biomes tend to direct resources to maximize energy production and prioritize the transport of electrons (Ahluwalia et al. 2021). Indeed, several studies conducted in the Cerrado have indicated an overall lack of a significant relationship between K_{area} and V_{cmax} (Lloyd et al. 2015, Gvozdevaite et al. 2018), which is attributed to the strategies used for allocating K to membrane stability (Chadwick et al. 1999, Wang et al. 2013).

Study implications

Although the role of leaf nutrient concentration in regulating the photosynthesis response to temperature still needs a better understanding, our data represent, for the first time, strong evidence of the involvement of nutrients in regulating the temperature response of photosynthesis in tropical savanna vegetation. Our findings have important implications for modeling tropical vegetation in the face of ongoing climate change, as the structure and function of different types of vegetation in these regions vary based on factors such as climate, soil and canopy nutrients (Lloyd et al. 2015, Veenendaal et al. 2018). Therefore, it is critical to expand this approach to various ecosystems and gain a comprehensive understanding of how different leaf nutrients are connected to photosynthetic responses in relation to temperature increase. Further, it is crucial to recognize that many other factors influence the temperature-dependent performance of photosynthesis, including other physiological processes, biochemistry, morphology and anatomy (Way and Yamori 2014, O'Sullivan et al. 2017, Zhu et al. 2018). Understanding these intricate relationships is pivotal for advancing our comprehension of ecological dynamics and ensuring a practical understanding of the future of global vegetation.

Conclusion

Contrary to our initial expectation, our data have demonstrated a remarkable similarity in T_{OptV} and T_{OpJ} values among the studied Cerrado species, regardless of their geographic distributions. Additionally, we found that T_{OptV} and T_{OpJ} are close to the maximum temperatures experienced in the Cerrado. This might imply that, with the projected temperature increases in the Cerrado over the coming decades, these species can experience higher-temperature biochemical thresholds. Additionally, higher leaf optimum temperatures are associated with larger investments of nutrients, adding an additional cost to plant acclimation to increasing temperatures. This result aligns with current theories implemented in global vegetation models.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Acknowledgments

The authors want to thank the University of São Paulo (USP) and Wageningen University (WU) for their financial and logistical support during the fieldwork. Additionally, they would like to thank the São Paulo Research Foundation—FAPESP for their contributions. They are also grateful to the Coordination for the Improvement of Higher Education Personnel (CAPES) and WU for providing the T.C.S.O. Ph.D. scholarships. T.F.D. acknowledges the financial support from the Brazilian National Council for Scientific and Technological Development (CNPq) grants 312589/2022-0 (Bolsa de produtividade em Pesquisa).

Authors' contributions

T.C.S.O., T.F.D. and E.V. designed the study; T.C.S.O. collected the data; T.C.S.O. performed the data analysis; T.C.S.O., T.F.D. and E.V. interpreted the analysis and results; T.C.S.O. wrote the first draft; T.F.D. and E.V. contributed to writing.

Conflict of interest

The authors have no conflicts to declare.

Funding

This study was supported by Wageningen University and Research (WUR) to T.C.S.O. (project number 5160957987) and the São Paulo Research Foundation (FAPESP) (grant 2015/50488-5). T.F.D. acknowledges the financial support from the Brazilian National Council for Scientific and Technological Development (CNPq) grant 312589/2022-0 (Bolsa de produtividade em Pesquisa).

Data availability

The final data and the curve fitting routine code used in the manuscript are available via doi: github.com/tonydoliveira/Cerrado-TOptV-TOptJ.

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Tree Physiology, 2025, 45, tpae163
https://doi.org/10.1093/treephys/tpae163
Research paper