



# Deciduous trees could benefit more from the rise in [CO<sub>2</sub>] than evergreens in the Brazilian Cerrado

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## Abstract

The Cerrado, a Neotropical savanna, is the second largest vegetation domain in Brazilian territory and presents a gradient of physiognomies. Among the savanna formations, the cerrado *stricto sensu* stands out. The responses of woody species of the cerrado related to increased CO<sub>2</sub> concentration ([CO<sub>2</sub>]), as predicted by global climate change, may differ among distinct leaf persistence groups. Elevated [CO<sub>2</sub>] could enhance the resprouting capacity of woody species, which might intensify encroachment in grasslands, such as the cerrado *stricto sensu*. We investigated the influence of elevated [CO<sub>2</sub>] (eCO<sub>2</sub>) on vegetative growth, root non-structural carbohydrates (NSC), and biomass allocation pattern among roots, stems, and leaves in two deciduous and three evergreen cerrado woody species. We carried out the experiment in open-top chambers with five young individuals of cerrado woody species under ambient [CO<sub>2</sub>] (aCO<sub>2</sub>) and eCO<sub>2</sub> of 430 and 700 ppm, respectively. Measurements occurred in young plants with 294, 379, and 466 days old, i.e., after 104, 189, and 276 days of eCO<sub>2</sub> exposition. While the species under aCO<sub>2</sub> decreased the NSC in roots on the 189th day, the plants under eCO<sub>2</sub> did not show a decrease over time. The deciduous species under eCO<sub>2</sub> showed higher RGR at the beginning of the experiment (104 days) than the evergreens species under eCO<sub>2</sub>. Also, the eCO<sub>2</sub> promoted fast leaf development in four out of five studied species (except *Anadenanthera peregrina*). The characteristics analyzed among the species could demonstrate that the deciduous grown under eCO<sub>2</sub> presented higher relative growth rate and root/stem ratio than the species with evergreen habit.

**Keywords** Climate change · Leaf deciduousness · Vegetative morphometry · Relative growth rate

## Introduction

Human activities have increased CO<sub>2</sub> concentration [CO<sub>2</sub>] in the atmosphere, intensifying global climate change (IPCC 2019). Rising [CO<sub>2</sub>] and atmospheric warming would change species distribution and abundance (Siqueira and Peterson 2003; Van der Putten et al. 2010; Bellard et al. 2012; Peterson et al. 2019; Pecl et al. 2017; Nunez

et al. 2019), and regional variations in productivity patterns (Nowak et al. 2004; Newingham et al. 2013). In C<sub>3</sub> woody species, it is expected that one of the main effects of increase in [CO<sub>2</sub>] occurs close to the light compensation point of photosynthesis, making plants more efficient at low light intensity (Ainsworth and Long 2005). Increases are expected in the light-driven photochemical reactions in C<sub>3</sub> species growing under elevated (eCO<sub>2</sub>), when photosynthesis is limited by the amount of active Rubisco (Li et al. 2009). In addition, in C<sub>3</sub> species growing under eCO<sub>2</sub> an increase in water use efficiency, decreased transpiration, and stomatal conductance is expected (Ainsworth and Rogers 2007). Under appropriate water and nutrient availability in the soil, the increase in [CO<sub>2</sub>] promotes the growth of woody species (Ainsworth and Long 2005; Souza et al. 2016). In a general context, woody species growing under eCO<sub>2</sub> would show increased root growth, a higher concentration of non-structural carbohydrates in the roots, and improved ability to resprout after disturbances (Hoffman et al. 2000; Kgope

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et al. 2010; Manea and Leishman 2019) than plants growing under ambient  $[\text{CO}_2]$  ( $a\text{CO}_2$ ). Therefore, it is essential to investigate the effects caused by climate change, mainly the increase in  $[\text{CO}_2]$ , on the resprouting potential of cerrado woody species.

Resprout capacity is an essential functional trait determining plant responses and vegetation dynamics after disturbances, such as fire, which shape most savannas (Clarke et al. 2016). The capacity to resprout after the fire is related to the accumulation of carbohydrates and nutrient reserves that need recharging between burn events (Hoffman et al. 2000; Franco et al. 2014). In response to the disturbance, plants can die because they do not have the capacity or resources to replace the foliage through protected meristems, or they can resprout using underground reserves in the roots, such as the non-structural carbohydrates and nitrogen (Clarke et al. 2013). The atmospheric  $[\text{CO}_2]$  is known to have high effects on plant carbohydrate status (Korner and Miglietta 1994; Bassirirad et al. 1996; Read and Morgan 1996; Cruz et al. 1997). Furthermore, the increased  $[\text{CO}_2]$  in the atmosphere would change plant resource allocation patterns and resprouting capacity (Clarke et al. 2016; Manea and Leishman 2019). Kgpoe et al. (2010) in a study with two *Acacia* species found an increased C allocation to non-structural carbohydrates storage along a  $[\text{CO}_2]$  gradient. In addition, the resprouting ability and root non-structural carbohydrates of a tropical savanna tree, *Kielmeyera coriacea* Mart & Zucc., were significantly greater under  $e\text{CO}_2$  and nutrient enrichment (Hoffmann et al. 2000). Manea and Leishman (2019) analyzed the effect of increasing  $[\text{CO}_2]$  on the resprout capacity of 16 woody and grass species from temperate regions. Woody and grass species grown under  $e\text{CO}_2$  showed an increase in biomass production. However, only woody species showed a higher accumulation of non-structural carbohydrates in roots under  $e\text{CO}_2$ , and increased root biomass (Manea and Leishman 2019), indicating improved resprout capacity.

Savanna ecosystems cover about 20% of the terrestrial land surface (Kgope et al. 2010). The Cerrado, a Neotropical savanna, is the second largest vegetation domain in Brazilian territory and presents a gradient of physiognomies, ranging from grasslands to tree forests rich in endemic species (Coutinho 2006; Overbeck et al. 2015; Durigan and Ratter 2016). Among the savanna formations found in this vegetational domain (Batalha 2011), the cerrado *stricto sensu* stands out, being characterized by the abundance of woody species, with different degrees of leaf deciduity and by a herbaceous stratum rich in different growth forms (Eiten 1972). In Cerrado, the influence of climate change on vegetation dynamics is more dramatic because half of the original vegetation area has been converted by anthropic activities (Myers et al. 2000; Klink and Machado 2005; Franco et al. 2014; Lapola et al. 2014; Hughes 2017). The global

climate change in the Cerrado could modify interspecific competition for limited resources (such as water and nutrients), changing the vegetation structure (Melo et al. 2018). Cerrado plant species are expected to lose more than half of their distribution range under the pessimistic scenario (RCP8.5) of climate change and land use (Velazco et al. 2019). Understanding the response of Cerrado vegetation to climate change implies investigating the effect of  $e\text{CO}_2$  on the growth, development, and resprouting of woody species (Souza et al. 2016; Melo et al. 2018; Maia et al. 2019). These responses could be different between species grouped by leaf functional traits (Souza et al. 2009a, b, 2011; Borges and Prado 2018).

Interactions among photosynthesis, photorespiration, and respiration processes would likely define how much carbon is available for plant growth and resprouting after drought or fire events (Franco et al. 2014). Some studies have found that  $\text{CO}_2$  stimulates resprouting following defoliation (Fajer et al. 1991; Pearson and Brooks 1996; Wilsey et al. 1997; Maia et al. 2019). Oliveira et al. (2021), found a positive response to  $e\text{CO}_2$  in plants of *Chrysolaena obovata* (Less.) M. Dematt., a  $\text{C}_3$  species native from cerrado. The plants grown under  $e\text{CO}_2$  showed higher growth, photosynthetic rate, aerial biomass production, underground rhizophore biomass, and consequently higher carbohydrate productivity than plants under  $a\text{CO}_2$ . Souza et al. (2016) found higher biomass production, growth, leaf area ratio, and net photosynthesis in *Hymenaea stigonocarpa* Mart. ex Hayne, *Solanum lycocarpum* A. St.-Hil., and *Tabebuia aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore, growing under  $e\text{CO}_2$ . However, all these studies did not analyze the possible differential responses among species with distinct leaf persistence in cerrado vegetation due to climate change. Species with different leaf persistence could show different responses to  $e\text{CO}_2$  due to distinct ecological strategies. Deciduous woody species showed a more acquisitive strategy, maximizing uptake and use of resources (Ouédraogo et al. 2013; Souza et al. 2020). On the other hand, evergreens show a more conservative strategy to resource use (Ouédraogo et al. 2013; Souza et al. 2020). Thus, rising  $[\text{CO}_2]$  could result in different ecophysiological responses among species with distinct leaf persistence.

The objective of the present study was to evaluate the influence of  $e\text{CO}_2$  on vegetative growth, biomass allocation, and resprouting potential in deciduous and evergreen woody species from Cerrado. We predicted that  $e\text{CO}_2$  would increase plant biomass, vegetative growth, and non-structural carbohydrates in the roots of all species. The higher non-structural carbohydrates allocation to the root system could increase the potential for resprouting of cerrado woody species, which would benefit them mainly after disturbance (Souza et al. 2016; Manea and Leishman 2019). These changes would help the establishment of cerrado

woody species in native areas under the new climatic conditions. We also predicted a higher investment in the aerial growth of deciduous species grown under eCO<sub>2</sub> as these species show faster shoot growth (synchronous leaf production) at the end of the dry season (Damascos et al. 2005; Damascos 2008; Souza et al. 2009a, b) to maximize growth in the next rainy season. However, evergreens could show few changes, as these species have an immediate consumption of the current resource throughout the year (Damascos et al. 2005; Damascos 2008; Souza et al. 2009a, b), being more conservative in the growth.

## Materials and methods

### Study area and open-top chambers

The experiment was carried out in open-top chambers (OTC, Figure S1) located at the Federal University of Viçosa, *campus* Florestal, Minas Gerais, Brazil (19°52′29″ S and 44°25′12″ W). We use OTC built with rectangular modules with side doors facilitating data collection (Silva 2010; Souza et al. 2016). The air intake in the chambers was controlled through an air injection system composed of a centrifugal fan, with a 20 cm diameter propeller and 50 mm diameter perforated PVC tubes. In this system, the air flow from the fan was directed into the chambers through PVC tubes. To enrich the atmosphere of the chambers with CO<sub>2</sub> during the experiment, CO<sub>2</sub> storage cylinders with a capacity of 25 kg each were used. The primary flow of CO<sub>2</sub> into the chambers was regulated by a special pressure gauge (White Martins—R201C). The flow was regulated and directed to the chambers through high pressure hoses (500 psi). Plants were exposed to elevated [CO<sub>2</sub>] during the day (6:00 am to 6:00 pm) and monitored with a CO<sub>2</sub> meter (Testo 535). Inside OTCs, fans worked during the day, avoiding excess moisture and temperature rise inside OTCs. The OTCs were monitored periodically by measuring air temperature (thermo-hygrometer, model INCOTERM 7666.02.0.00).

### Plant material and soil properties

The five native species studied were classified according to their corresponding leaf persistence group (Souza et al. 2009a, b; Souza et al. 2011; Borges and Prado 2014): deciduous (DE) *Anadenanthera peregrina* var. *falcata* (Benth.) Altschul and *Tabebuia aurea* (Silva Manso) Benth & Hook. f. ex. Moore, and evergreen (EV) *Hymenaea stigonocarpa* Mart. ex Hayne, *Stryphnodendron adstringens* Mart., and *Stryphnodendron polyphyllum* Mart.

*Anadenanthera peregrina* var. *falcata* (Benth.) Altschul, popularly known as angico-do-cerrado, belongs to the Fabaceae family and is a tree species that can reach 15 m in

height (Silva et al. 2020). *Tabebuia aurea* (Manso) Benth. & Hook f. ex S. Moore, species native to Brazil belonging to the Bignoniaceae Family, occurs in the Amazon Region, Northeast, Midwest, and Southeast, in several vegetation formations, being popularly known as paratudo, caraíba, ipê-do-cerrado (Lorenzi 2002; Santos et al. 2019). *Hymenaea stigonocarpa* Mart. ex Hayne, known as jatobá-do-cerrado, jutaí, jatobá-capo, jatobá-de-cascafina, jitaí or jutaicaica, being common in the open formations of the cerrado and campo cerrado (Lorenzi 1992). *Stryphnodendron adstringens* (Mart.), known as barbatimão, has a wide geographic distribution, occurring from Pará, through the central plateau, to Minas Gerais and São Paulo (Felfili et al. 1999). *Stryphnodendron polyphyllum* Mart. is a plant with 4–6 m high, deciduous, heliophyte, pioneer and characteristic of the cerrado, whose distribution extends from the cerrado of Central Brazil to Paraná and Mato Grosso do Sul (Lorenzi 2000).

The soil used for the species growth was typical of cerrado areas in the State of Minas Gerais (Haridasan et al. 2000). The chemical characteristics were: pH in H<sub>2</sub>O = 6.1; H + Al = 3.54 cmol.charge/dm<sup>3</sup>; Al<sup>3+</sup> = 1.83 cmol.charge/dm<sup>3</sup>; Ca<sup>2+</sup> = 0.33 cmol.charge/dm<sup>3</sup>; Mg<sup>2+</sup> = 0.07 cmol.charge/dm<sup>3</sup>; P = 0.8 mg/dm<sup>3</sup>; K = 8 mg/dm<sup>3</sup>; Sum of bases = 0.42 cmol.charge/dm<sup>3</sup>; Cation exchange capacity = 3.96 cmol.charge/dm<sup>3</sup>; effective cation exchange capacity = 2.25 cmol.charge/dm<sup>3</sup>; Aluminum saturation index = 81.20%, and base saturation index = 10.68%. Soil analysis was carried out in the Agricultural Chemistry Laboratory of the Minas Gerais Institute of Agriculture (IMA).

### Pre-germination treatment and experimental design

Seeds of *A. peregrina*, *T. aurea*, *H. stigonocarpa*, *S. adstringens*, and *S. polyphyllum* were treated with 2% sodium hypochlorite, for five minutes (De Lemos Filho et al. 1997; Botelho et al. 2000; Cabral et al. 2003; Miranda et al. 2012) and then washed with water. The following species were mechanically scarified to break the physical dormancy of seeds: *H. stigonocarpa*, *S. adstringens*, and *S. polyphyllum*. Seeds of all species germinated on filter paper, in a germination chamber Solab (SL.225). Seeds of *H. stigonocarpa*, *S. adstringens*, and *T. aurea* remained at alternating temperatures of 25–30 °C (night and day, respectively) and 12 h of photoperiod (Botelho et al. 2000; Cabral et al. 2003) and the seeds of *S. polyphyllum* and *A. peregrina* at constant light and temperatures of 30 °C (De Lemos Filho et al. 1997; Miranda et al. 2012). After germination, the seedlings were transferred to 8.0 L plastic pots filled with soil. The treatment with eCO<sub>2</sub> started when the seedlings were 190 days old.

Young plants were assigned in two treatments with different  $[\text{CO}_2]$ : 25 plants of each species divided in four OTC growing under elevated  $\text{CO}_2$  ( $\text{eCO}_2$ ,  $\sim 700 \pm 5.10$  ppm) and 25 plants of each species divided in four OTC growing under ambient  $\text{CO}_2$  ( $\text{aCO}_2$ ,  $\sim 430 \pm 7.20$  ppm, without  $\text{CO}_2$  enrichment). The plants in both  $\text{CO}_2$  treatments were daily watered.

### Leaf area, and leaf, stem, and root dry mass

The morphological measurements were taken in four individuals of each species in each  $\text{CO}_2$  treatment in each measurement date ( $n=4$  individuals per species in each treatment). These measurements were carried out when the young plants were 294, 379, and 466 days old and growing under  $\text{eCO}_2$  for 104, 189, and 276 days. All leaves were separated from the stem and petioles and then scanned in black and white with the help of a table scanner to determine leaf area. Subsequently, the leaf area was calculated using the Image-Pro 5.0 software (Media Cybernetics, Inc., Silver Spring, MD, USA). The root length (measurement of the largest root) was determined with a 30 cm millimeter plastic ruler. The dry mass of each stem was determined after removing all buds and leaves when the leaf mass was also determined (the same leaves detached from the stems to leaf area determination). Leaves, stems, and roots were dried in an oven (Tecnal TE-394/3, Piracicaba, São Paulo, BR) at  $60^\circ\text{C}$  for 72 h (Pérez-Harguindeguy et al. 2013) and had their masses measured using an analytical balance (Shimadzu-BL Series—20H, Tokyo, Japan). The total dry mass was the sum of the dry masses of root, stem, and leaves in the same individual.

### Growth indices and vegetative morphometry

After determining the morphological traits, the following growth indices were calculated: relative growth rate (RGR,  $\text{g g}^{-1} \text{days}^{-1}$ ), leaf area index (LAI,  $\text{cm}^2 \text{days}^{-1}$ ), leaf area ratio (LAR, total leaf area/total dry mass,  $\text{cm}^2 \text{g}^{-1}$ ), specific leaf area (SLA, total leaf area/total leaf dry mass,  $\text{cm}^2 \text{g}^{-1}$ ), and root/stem ratio (RSR, root dry mass/stem dry mass,  $\text{g g}^{-1}$ ) in four individuals of each species in each treatment and measurement date.

Relative growth rates (RGR,  $\text{g g}^{-1} \text{days}^{-1}$ ) were calculated using the following equation:

$$\text{RGR} = (1 / \text{total dry mass at time 1}) \\ * [(\text{total dry mass at time 2}) - (\text{total dry mass at time 1}) / (\text{time 2})]$$

Leaf area index (LAI,  $\text{cm}^2 \text{days}^{-1}$ ) were calculated using the following equation:

$$\text{LAI} = [(\text{total leaf area at time 1}) + (\text{total leaf area at time 2})] * (1/2)$$

The leaf number (LN), stem length (SL, cm), and stem diameter (SD, cm) were monitored weekly throughout the experiment, up to 283 days after the beginning of the experiment (DBE) in 25 individuals of each species in each  $[\text{CO}_2]$ . We analyzed the leaf development in five leaves from five individuals ( $n=5$  plants per species in each treatment) to determine the leaf expansion interval (LEI, days) and leaf expansion rate (LER,  $\text{cm days}^{-1}$ ). The length and width of each marked leaf (or leaflet) were monitored weekly. When the leaf stabilized the growth, the LEI was determined. Using the leaf expansion interval, we estimated LER by dividing the stabilized leaf area by the leaf expansion interval ( $\text{LER} = \text{LEA}/\text{LEI}$ ).

### Non-structural carbohydrates

The same individuals used for growth measures were used to quantify non-structural carbohydrates (NSC) in the roots using the sulfuric phenol method (Dubois et al. 1956). 0.5 g of root dry biomass was ground with liquid nitrogen, then mixed in ethanol 80% (5 ml) and incubated in a water bath at  $75^\circ\text{C}$  for 30 min. Afterward, the sample was quickly placed on ice. Subsequently, the material was centrifuged at  $3000 \times g$  for 15 min then the supernatant was collected. This procedure was performed twice. We collected 1 ml of the supernatant from the alcoholic extraction and incubated it in a water bath at  $75^\circ\text{C}$ . The evaporates were hydrolyzed in 1 ml of distilled water, added 1 ml of hydrochloric acid (HCL 2.5N), and placed in a water bath at  $100^\circ\text{C}$  for 60 min. After 60 min, this material was placed on ice for 10 min and centrifuged at 10000 rpm for 5 min. We collected 0.1 ml of extraction solution with new tubes with more 0.9 ml of deionized water and added 0.5 ml of 5% phenol solution and 2.5 ml of 96% sulfuric acid in each tube. After 10 min, the tube content was incubated in a water bath at  $25\text{--}30^\circ\text{C}$  for 20 min. The absorbance reading was performed on a spectrophotometer (Shimadzu, Model UV-1800 120 V Tokyo, Japan) with a wavelength of 490 nm. We calculate the amount of total carbohydrate present in the sample solution using the standard graph.

Non-structural carbohydrates were calculated using the following equation:

Absorbance corresponds to 0.1 ml of the test =  $\chi$  mg of glucose

$$10 \text{ ml contains} = (\chi \times 10 \text{ mg of glucose}) / 0.1 \\ = \% \text{ of total carbohydrate present}$$

### Data analysis

Principal component analysis (PCA) was performed with all variables: total leaf area (TLA), root length (RL), leaf dry mass (LDM), stem dry mass (SDM), root dry mass (RDM), total dry mass (TDM), relative growth rate (RGR), leaf area



index (LAI), leaf area ratio (LAR), specific leaf area (SLA), root/stem ratio (RSR), non-structural carbohydrates (NSC), leaf number (LN), stem length (SL), stem diameter (SD), leaf expansion interval (LEI), and leaf expansion rate (LER). For PCA analysis, we utilized the average values of each variable in every species and CO<sub>2</sub> treatment.

We calculated the mean and standard deviation for all physiological, morphological, and morphometrical parameters. The Shapiro–Wilk test was used to evaluate the normal distribution in each dataset. The data which did not show normal distribution (RGR, NSC, LER) were log-transformed. Afterward, the Levene test was used to verify variance homogeneity. For TDM, RGR, LAI, SLA, RSR, and NSC, we used Mixed Design Analysis of Variance (MIXED ANOVA) with two factors and repeated measures, considering species and [CO<sub>2</sub>] between-subjects factors and time as within-subject factor. We used a posteriori Tukey's posthoc test to investigate significant differences ( $p < 0.05$ ) between the means of the species, [CO<sub>2</sub>], and time interval (days after the beginning of the experiment, DBE). For LER, we used Analysis of variance (two-way ANOVA), and a posteriori Tukey's test was also applied to investigate significant differences ( $p < 0.05$ ) between the means of the species and [CO<sub>2</sub>]. All analyses were performed in the R program, version 3.0.0 (R Core Team 2019).

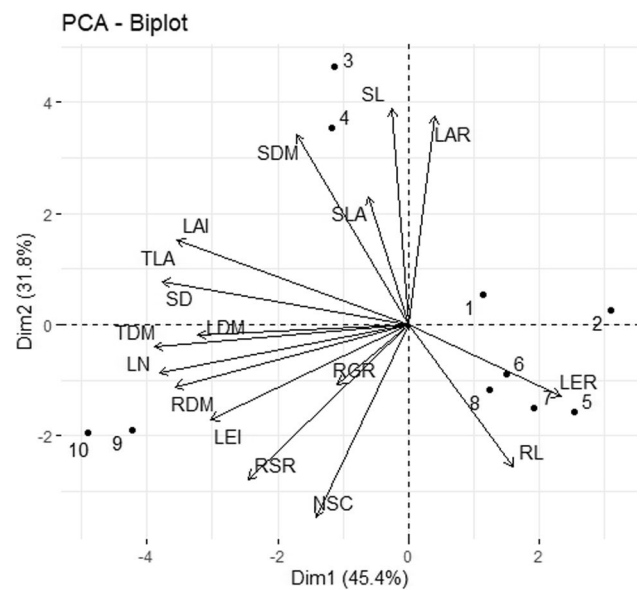
## Results

### Principal component analysis

The ordination diagram resulting from the principal component analysis (PCA) summarized 77% total variation of the data in the first two dimensions (Dim1 and Dim2), with 45% and 32% variation explained by Dim1 and Dim2, respectively (Figure 1). EV *H. stigonocarpa* independent of [CO<sub>2</sub>] had a positive relationship with the characteristics: LDM, SDM, RDM, TDM, LEA, RGR, LAI, SLA, RSR, LAR, LN, SL, SD, and LEI and were distributed along Dim1 (Figure 1). The distribution of EV species *S. polyphyllum* and *S. adstringens* were more influenced by RL and LER (Figure 1). The PCA ordination diagram indicated that species were separated by growth characteristics in relation to CO<sub>2</sub> concentration (~ 430 and ~ 700 ppm).

### Leaf responses to eCO<sub>2</sub>

Deciduous *A. peregrina* and evergreen *H. stigonocarpa* independent of [CO<sub>2</sub>], showed a significant increase in the specific leaf area (SLA) at the middle of the experiment (189th day, Fig. 2a,  $F$ -test = 7.62,  $p < 0.05$ ) than other species. Leaf area index (LAI) peaked at the middle of the experiment (189th day) under eCO<sub>2</sub> compared to

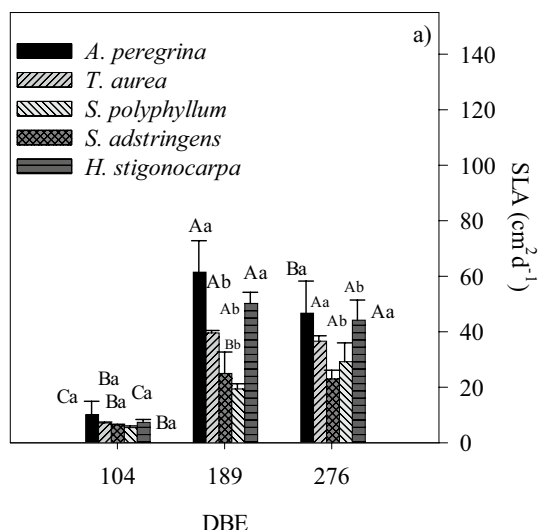


**Fig. 1** Principal component analysis (PCA) showing the distribution of all features according to the five Cerrado woody species growing under ambient (430 ppm) and elevated (700 ppm) CO<sub>2</sub> concentrations in open-top chambers. *LDM* Leaf dry mass, *SDM* stem dry mass, *RDM* root dry mass, *TDM* total dry mass, *TLA* total leaf area, *RL* root length, *RGR* relative growth rate, *LAI* leaf area index, *LAR* leaf area ratio, *SLA* specific leaf area, *RSR* root/stem ratio, *NSC* non-structural carbohydrates, *LN* leaf number, *SL* stem length, *SD* stem diameter, *LEI* leaf expansion interval, and *LER* leaf expansion rate. 1 = *A. peregrina* 700 ppm, 2 = *A. peregrina* 430 ppm, 3 = *H. stigonocarpa* 700 ppm, 4 = *H. stigonocarpa* 430 ppm, 5 = *S. adstringens* 700 ppm, 6 = *S. adstringens* 430 ppm, 7 = *S. polyphyllum* 700 ppm, 8 = *S. polyphyllum* 430 ppm, 9 = *T. aurea* 700 ppm, 10 = *T. aurea* 430 ppm. Dimensions 1 and 2 are responsible for 45.4% and 31.8% of the total data variation, respectively

the beginning (104th day) and at the end of the experiment (276th day, Fig. 3b,  $F$ -test = 3.70,  $p < 0.05$  interaction between CO<sub>2</sub> and DBE). The species did not show significant differences in LAI between [CO<sub>2</sub>] in the same DBE (Fig. 3b). *S. polyphyllum* and *S. adstringens* plants in eCO<sub>2</sub> showed higher leaf expansion rate (LER) than their plants in aCO<sub>2</sub> (Table 1,  $F$ -test = 8.90,  $p < 0.05$ ). Also, *S. polyphyllum* and *S. adstringens* in eCO<sub>2</sub> showed higher LER than plants of other species in eCO<sub>2</sub> (Table 1,  $F$ -test = 8.90,  $p < 0.05$ ).

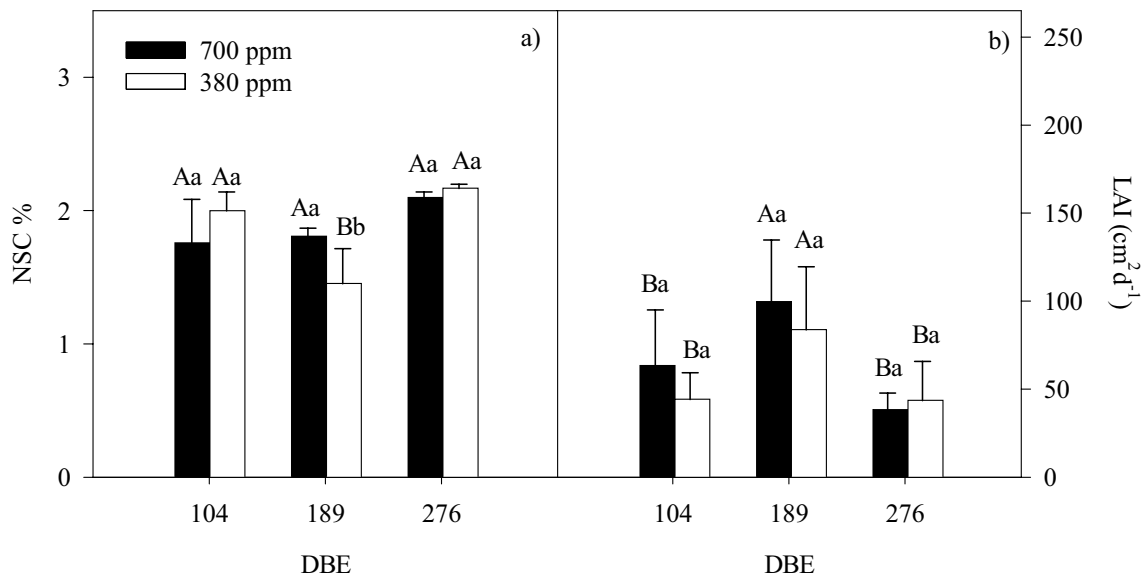
### Root responses to eCO<sub>2</sub>

There was a decrease in non-structural carbohydrates (NSC) at the middle of the experiment (189th day) under aCO<sub>2</sub> (Fig. 2e,  $F$ -test < 0.0001,  $p < 0.05$  interaction between CO<sub>2</sub> and DBE). However, under eCO<sub>2</sub> there were no significant differences in NSC across species over time (Fig. 3a). However, at the middle of the experiment (189th



**Fig. 2 a** Specific leaf area (SLA) in five Cerrado woody species growing under ambient (430 ppm) and elevated (700 ppm)  $\text{CO}_2$  concentrations in open-top chambers. Symbols represent averages ( $n=4$ ), and bars indicate standard deviation. Capital letters compare significant differences within the same species in different DBE. Lowercase letters compare significant differences between species in the same DBE ( $p < 0.05$ , Tukey's test)

day) the species under  $\text{eCO}_2$  showed higher NSC (Fig. 3a,  $F$ -test  $< 0.0001$ ,  $p < 0.05$  interaction between  $\text{CO}_2$  and DBE) than under  $\text{aCO}_2$ .



**Fig. 3 a** NSC=non-structural carbohydrates and **b** LAI=leaf area index in five Cerrado woody species growing under ambient (430 ppm) and elevated (700 ppm)  $\text{CO}_2$  concentrations in open-top chambers. Symbols represent averages ( $n=4$ ), and bars indicate

## Individual-level responses to $\text{eCO}_2$

All species showed greater total dry mass (TDM) at the middle of the experiment (189th day) remained higher at the end of the experiment (276th day, Fig. 4a,  $F$ -test = 23.06,  $p < 0.05$ ), regardless of  $[\text{CO}_2]$ .

The individuals of deciduous species, *A. peregrina* and *T. aurea*, under  $\text{eCO}_2$  at beginning of the experiment (104th day) showed higher relative growth rate (RGR, Fig. 5a) than their plants under  $\text{eCO}_2$  at the middle of the experiment (189th day). Furthermore, *A. peregrina* and *T. aurea* plants (Fig. 5a,  $F$ -test = 3.01,  $p < 0.05$  interaction among  $\text{CO}_2$ , species, and DBE) under  $\text{eCO}_2$  at beginning of the experiment (104th day) showed higher RGR than all species under  $\text{eCO}_2$  at beginning of the experiment (104th day). Also, *A. peregrina* and *T. aurea* plants (Fig. 5a,  $F$ -test = 3.01,  $p < 0.05$  interaction among  $\text{CO}_2$ , species, and DBE) under  $\text{eCO}_2$  at the beginning of the experiment (104th day) showed higher RGR than their plants under  $\text{aCO}_2$  at beginning of the experiment (104th day).

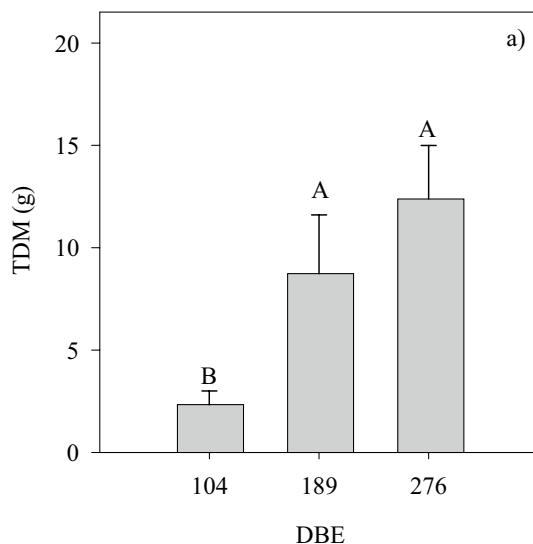
*T. aurea* plants at the middle of the experiment (189th day) under  $\text{aCO}_2$  showed a higher root/stem ratio (RSR) than their plants under  $\text{aCO}_2$  at beginning (104th day) and at the end of the experiment (276th day) Fig. 5b,  $F$ -test  $< 0.0001$ ,  $p < 0.05$  interaction among  $\text{CO}_2$ , species, and DBE). At end of the experiment (276th day), *T. aurea* plants under  $\text{eCO}_2$  showed higher RSR than plants of the other species under  $\text{eCO}_2$  (Fig. 5b,  $F$ -test  $< 0.0001$ ,  $p < 0.05$  interaction among  $\text{CO}_2$ , species, and DBE). Also,

standard deviation. Capital letters compare significant differences within the same  $[\text{CO}_2]$  in different DBE. Lowercase letters compare significant differences between  $[\text{CO}_2]$  in the same DBE ( $p < 0.05$ , Tukey's test)

**Table 1** Mean values  $\pm$  standard deviation of leaf expansion rate (LER), in five Cerrado woody species growing under ambient (430 ppm) and elevated (700 ppm) CO<sub>2</sub> concentrations in open-top chambers

PG	Species	CO <sub>2</sub>	LER (cm d <sup>-1</sup> )
Deciduous	<i>A. peregrina</i>	430 ppm	1.03 $\pm$ 0.95 Aa
		700 ppm	0.81 $\pm$ 0.73 Ab
	<i>T. aurea</i>	430 ppm	0.18 $\pm$ 0.06 Aa
		700 ppm	0.47 $\pm$ 0.50 Ab
Evergreens	<i>H. stigonocarpa</i>	430 ppm	0.48 $\pm$ 0.23 Aa
		700 ppm	0.53 $\pm$ 0.29 Ab
	<i>S. adstringens</i>	430 ppm	0.47 $\pm$ 0.75 Ba
		700 ppm	3.71 $\pm$ 3.99 Aa
	<i>S. polyphyllum</i>	430 ppm	1.11 $\pm$ 1.19 Ba
		700 ppm	2.32 $\pm$ 3.77 Aa

Capital letters compare differences between [CO<sub>2</sub>] in the same species. Lowercase letters compared differences between species in the same [CO<sub>2</sub>] ( $p < 0.05$ , Tukey's test).  $n = 5$  leaves per species. PG phenological group,  $d$  days



**Fig. 4 a** TDM = total dry mass in five Cerrado woody species growing under ambient (430 ppm) and elevated (700 ppm) CO<sub>2</sub> concentrations in open-top chambers. Symbols represent averages ( $n = 4$ ), and bars indicate standard deviation. Capital letters compare significant differences between days after the beginning of the experiment (DBE) ( $p < 0.05$ , Tukey's test)

*T. aurea* plants under aCO<sub>2</sub> at the middle of the experiment (189th day) showed a higher RSR than plants of the other species under aCO<sub>2</sub> (Fig. 5b,  $F$ -test  $< 0.0001$ ,  $p < 0.05$  interaction among CO<sub>2</sub>, species, and DBE). At the middle of the experiment (189th day) *T. aurea* plants under aCO<sub>2</sub> showed a higher RSR than their plants under eCO<sub>2</sub> (Fig. 5b,  $F$ -test  $< 0.0001$ ,  $p < 0.05$  interaction among CO<sub>2</sub>, species, and DBE).

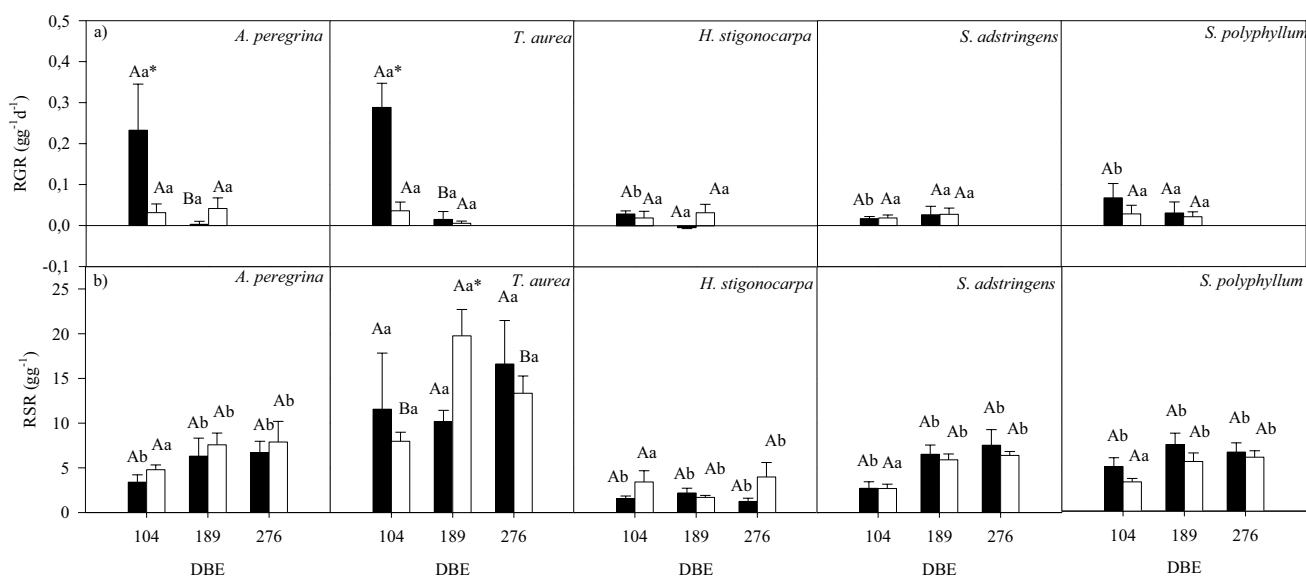
All significances and interactions between species and DBE, and correlation matrix of principal component analysis were presented in the supplementary material (Table S1, S2, and S3).

## Discussion

Our results confirmed contrasting strategies for resource allocation and growth rate in woody species of distinct leaf persistence groups growing under eCO<sub>2</sub>. Under eCO<sub>2</sub>, the higher relative growth rate of the deciduous species (*T. aurea* and *A. peregrina*) in the first harvest, with a decrease in the next harvest, was probably due to the rapid accumulation of leaf mass at the beginning of exposure to eCO<sub>2</sub>, followed by a decline over time. There is an expectation that the increase in [CO<sub>2</sub>] will stimulate the initial growth of woody species. Poorter and Navas (2003) observed that fast-growing species responded better to the increase in [CO<sub>2</sub>] than slow-growing species. However, Lloyd and Farquhar (1996) presented an alternative hypothesis, suggesting that slow-growing species tend to consume a pronounced proportion of their daily CO<sub>2</sub> assimilation in maintenance respiration. In our results we found more acquisitive strategies in deciduous trees, surpassing evergreen ones with more conservative strategies under eCO<sub>2</sub> in the short term, supporting Poorter and Navas (2003). Thus, evergreens could be more responsive to eCO<sub>2</sub> in the long-term because of the more conservative strategy of acquisition and resource use (Niinemets et al. 2011; Krishna and Garkoti 2022). However, deciduous cerrado species could show advantages over evergreens under eCO<sub>2</sub> due to their fast growth and more acquisitive resource use strategy (Krishna and Garkoti 2022).

The faster leaf expansion found out of five species under eCO<sub>2</sub> allowed the leaves to mature quickly. This ecological strategy of rapidly expanding the leaves developed under eCO<sub>2</sub> maximizes carbon gain to the whole plant in less time, so the entire photosynthetic apparatus is ready and mature to carry out photosynthesis at high levels during the leaf life span (Reich et al. 1991; Edwards et al. 2014). Only the evergreen species *S. polyphyllum* and *S. adstringens* showed a higher leaf expansion rate under eCO<sub>2</sub> than under aCO<sub>2</sub>. This shift in the amount of leaf area produced by day could accelerate the leaf development and becoming these leaves mature faster over time. However, this faster leaf development could desynchronize leaf production to the increase in rain and temperature over the growing season.

Deciduous and evergreen Cerrado species studied in our experiment growing under eCO<sub>2</sub> in 189 DBE showed an increase in stem and leaf dry mass, total leaf area, and non-structural carbohydrates than deciduous and evergreen species growing under aCO<sub>2</sub> at 189 DBE. This result is contrary to the results found by Curtis and Wang (1998), Reich



**Fig. 5** **a** RGR=relative growth rate (RGR) and **b** RSR=root/stem ratio in five Cerrado tree species growing under ambient (430 ppm) and elevated (700 ppm)  $\text{CO}_2$  concentrations of  $\text{CO}$  [ $\text{CO}_2$ ] in open-top chambers. Symbols represent averages ( $n=4$ ), and bars indicate standard deviation. Capital letters compare differences within the

same [ $\text{CO}_2$ ] and species in different DBE. Lowercase letters compare differences within the same [ $\text{CO}_2$ ] and DBE in different species. Asterisks indicate differences within the same species and DBE at different [ $\text{CO}_2$ ] ( $p < 0.05$ , Tukey's test)

and Hobbie (2014), Reich et al. (2014), and Terrer et al. (2018), that at  $e\text{CO}_2$ , growth in poor soil (as the soil used in our experiment) reduces biomass gain in woody species due to low soil nutrient availability. However, in a previous study, Souza et al. (2016) investigated the ecophysiological responses of three woody species from the Cerrado to the  $e\text{CO}_2$  and found increased biomass production. This response indicates the ability to uptake resources in this deciduous and evergreen species, even growing in poor soil and a relatively short time of exposure to greater  $\text{CO}_2$  availability. Furthermore, according to Reich et al. (2006), in the early developmental stages, even in poor soils, the high stimulus of biomass production may be more a characteristic of seedlings than of adult plants. In addition, Fox (1978), defined that a plant is efficient in the absorption and use of phosphorus when it produces a large amount of dry matter per unit of time and area, even when the environment (e.g., soil used in our study) has less phosphorus available for maximum productivity as found in our study.

The change in root/stem ratio only observed in the deciduous *T. aurea*, with a decrease in the biomass accumulation in roots at the expense of stems under  $e\text{CO}_2$ , could impair the competitive capacity of this species for water and nutrients in the soil with other woody and herbaceous species (Melo et al. 2018). This change in biomass allocation in favor of stems seems more frequent in cerrado woody plants (Souza et al. 2016; Melo et al. 2018) compared gramineous plants. The higher biomass allocation favoring the shoots could benefit the species in light capture among dense gramineous

strata in Cerrado areas (Melo et al. 2018). However, high efficiency of resource uptake from the soil is of great importance in cerrado areas because the seedlings and young woody plants need to capture water and nutrients in competition with efficient root systems of grass species (Oliveira et al. 2005). In the Cerrado, which is a domain marked by seasonal rainfall, it is commonly proposed that trees develop deep root systems that provide access to deeper, more humid layers of the soil (Rossato et al. 2013). Furthermore, Cerrado trees are capable of adjusting their hydraulic architecture and water characteristics (Bucci et al. 2005, 2008) to minimize seasonal imbalances. Therefore, the greater investment in growth of the aerial part than the belowground part in plants growing under  $e\text{CO}_2$  indicates a change in the biomass allocation pattern (Melo et al. 2018) which can make it difficult for savanna trees to resist the increase in seasonal droughts resulting from climate change (IPCC 2019).

All species studied showed similar responses in non-structural carbohydrates in roots. Although the roots did not increase the NSC under  $e\text{CO}_2$ , it guaranteed the maintenance of the levels during the initial growth of all species compared to the lower values at 189 DBE in  $a\text{CO}_2$  plants. Even without an increase over time, maintaining a stock of non-structural carbohydrates in the roots could benefit these species after disturbances such as fire events or loss of aerial parts by herbivory. However, according to Manea and Leishman (2019),  $e\text{CO}_2$  could increase the woody species encroachment in grassland environments. According to Bond and Midgley (2000), the enhanced



potential to resprout in woody plant species under eCO<sub>2</sub> may also contribute to the invasion of these plants in pastures after events such as fire and herbivory. This potential change could favor the invasion of native (and alien) species over field formation, modifying the floristic and functional diversity of the Cerrado.

In the future, the establishment of woody seedlings in cerrado physiognomies would be strongly associated with CO<sub>2</sub> plant responses and the subsequent competitive effect of grass species in these systems (Manea and Leishman 2015; Melo et al. 2018). Also, it is necessary to take into account that these species have a long life cycle, and therefore, the time required for exposure to eCO<sub>2</sub> to produce significant effects on carbohydrate accumulation may be longer than the one observed in our work. However, it is important to investigate the interactions between increased [CO<sub>2</sub>], regrowth capacity, and vegetative growth in woody species from the Cerrado, as these factors may have an impact on the global carbon cycle and on responses to climate change (Bradley and Pregitzer 2007). Therefore, long-term studies are needed using, for example, open-air CO<sub>2</sub> enrichment technologies (FACE), and experiments in open-top chambers (OTC) with trees cultivated with interaction of stresses and in small places with an element of competition or forests stands around natural sources of CO<sub>2</sub> to increase the knowledge base on ecosystem responses to elevated atmospheric CO<sub>2</sub>. Also, understanding the regrowth capacity associated with carbon allocation and storage in woody plants growing under eCO<sub>2</sub> is fundamental for the development of dynamic models for Cerrado vegetation in the face of climate change.

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**Data availability** The data set is being prepared for upload in the Plant Trait Database - TRY (<https://www.try-db.org/TryWeb/Home.php>).

## Declarations

**Conflict of interest** The authors declare no conflicts of interest.

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