



Physiological and metabolic responses of the Amazonian Açaí palm (*Euterpe oleracea*) to elevated CO₂

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Received: 27 February 2025 / Accepted: 21 January 2026 / Published online: 2 February 2026
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Abstract

Key Message Elevated CO₂ boosts the growth of açaí plants mainly through increased carbon assimilation and starch accumulation, however, there are signs of acclimation by sugar sensing mechanisms.

Abstract Açaí (*Euterpe oleracea*) is an important sustainable crop in the Amazon region, used as a food supplement and widely consumed locally and exported globally. This study aimed to investigate the physiological and metabolic responses of açaí to elevated atmospheric CO₂, focusing on non-structural carbohydrate dynamics. Juvenile plants grew in open-top chambers under ambient (~380 ppm) and elevated (~760 ppm) CO₂ levels for 90 days, carbon assimilation, stomatal conductance, transpiration, growth, dry mass, and non-structural carbohydrate content (starch, sucrose, glucose, fructose, raffinose, and myo-inositol) were measured. Elevated CO₂ significantly increased carbon assimilation, particularly in the second leaf, while reducing stomatal conductance and transpiration. Starch accumulation in leaves increased by 180%, and overall dry mass was higher, although the area of the first leaf decreased. Non-structural carbohydrate levels varied among organs, with roots showing the lowest levels. These findings suggest that elevated CO₂ can promote growth in juvenile açaí plant due to high carbohydrate (starch) accumulation. However, signs of acclimation were observed over development, with declines in photosynthesis and relative growth rate. The pattern of carbohydrate metabolism, especially starch accumulation and slight raffinose transient decay, indicates that acclimation may involve sugar-sensing mechanisms.

Keywords Carbohydrate · Climate change · Carbon assimilation · Photosynthesis · Growth

Introduction

The açaí palm (*Euterpe oleracea* Mart.) is one of the most economically and ecologically important native plant species in the Amazon region. Its fruit pulp, known for its “superfood” properties, is rich in carbohydrates and antioxidants, drawing worldwide interest (Silveira et al. 2023). Economically, açaí Brazilian production has increased from about 130,000 tons in 2002 to over 240,000 tons in 2022 (IBGE 2024). Besides its nutritional benefits, the açaí palm plays a vital role in the Amazon ecosystem. It grows in

flood-prone areas of the Amazon River estuary, contributing to the reforestation and sustainability of these regions because of its tolerance to anoxia and its morphological and biochemical adaptations to seasonal flooding (Aguir and Mendonça 2003; Grandis et al. 2010; Gonçalves et al. 2010). However, the intensive management of açaí is causing significant changes in forest structure (Freitas et al. 2015).

Climate change presents significant challenges to açaí cultivation, as this flood-adapted palm is susceptible to both heat and water stress. According to the Intergovernmental Panel on Climate Change (IPCC), human activities have led to unprecedented atmospheric carbon dioxide (CO₂) levels, driving global temperature increases and changing precipitation patterns (IPCC 2021). In 2023, atmospheric CO₂ concentrations reached 420 ppm, the highest in at least 2 million years (NOAA 2024). Ongoing deforestation of the Amazon worsens these challenges by disturbing the fragile ecological balance (IPCC 2021; Flores et al. 2024). Experimental and field studies demonstrate that drought

Communicated by Amissah.

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and hotter years significantly decrease photosynthesis and fruit production in *E. oleraceae*, with producers reporting up to 40–45% losses (Calbo et al. 2000; Sousa et al. 2020; Tregidgo et al. 2020). Moreover, increasing extreme events, such as heat waves, droughts, and altered flood regimes, are expected to intensify these vulnerabilities, affecting both palm physiology and fruit yields (Menezes-Silva et al. 2019; Frank et al. 2015). Understanding the physiological and metabolic responses of açai to elevated CO₂ levels is essential for modeling and forecasting potential gains or declines in production.

The main responses of C3 plants to elevated CO₂ include enhanced photosynthesis, changes in carbohydrate dynamics, and increased growth. Elevated CO₂ significantly boosts photosynthetic rates by increasing carbon uptake and reducing stomatal conductance, which improves water use efficiency (WUE). This boost in WUE helps plants sustain high photosynthetic rates and carbohydrate production even under water-limited conditions, leading to higher dry mass accumulation in leaves, stems, and roots, and along with a notable rise in starch and soluble sugars as plants store more carbon. This accumulation suggests a finely tuned carbon metabolism that supports growth under elevated CO₂ conditions (Poorter et al. 2022). Regarding Brazilian species, a meta-analysis reveals that trees tend to accumulate more starch than herbs when exposed to elevated CO₂ (Fortirer et al. 2023). While herbs and other fast-growing plants display higher levels of soluble sugars, reflecting a strategy for rapid growth and metabolic activity, trees primarily accumulate starch, which acts as a long-term carbon reserve. The response of trees is crucial for supporting growth and resilience in changing environmental conditions (Fortirer et al. 2023). Elevated CO₂ also promotes greater carbon sequestration, helping plants resist the impacts of climate change.

Research on açai (*E. oleraceae*) shows that despite higher CO₂ levels boost CO₂ assimilation, the additional carbon was not converted into dry mass because of the high temperature and vapor-pressure deficit involved (Amaral et al. 2023). Although carbohydrate dynamics in açai have not been studied in relation to climate change, understanding these processes could offer insights into how its cultivation might be adapted to mitigate the negative impacts of climate change, ensuring sustainable agricultural practices, and maintain ecological benefits for açai palms.

This study aimed to investigate the physiological and metabolic responses of juvenile açai plants under elevated atmospheric CO₂ concentrations, focusing on non-structural carbohydrates dynamics and their allocation in different organs. We hypothesized that elevated CO₂ would increase carbon assimilation and starch accumulation triggering changes in source–sink balance mediated by sugar-signal-ing mechanisms.

Materials and methods

Elevated CO₂ through juvenile plant development

Seed germination and early seedling establishment were monitored to ensure uniform growth before CO₂ treatments (Supplemental Fig. S1). At 105 days after germination, juvenile plants were distributed in four polycarbonate Open-Top- Chambers (OTCs—1.7 m height × 1.5 m diameter, with 90% of visible light transmittance up to 400 nm—Supplemental Fig. S1). We applied two treatments for 90 days (from February 01 to May 01, 2009): two OTCs for ambient CO₂ concentration (aCO₂) around 380 ppm and two for elevated CO₂ concentration (eCO₂) around 760 ppm. The pots were rotated weekly inside the chambers to prevent effects from micro-environmental differences. Microclimatic parameters (temperature and relative humidity) were measured daily in each OTC by a Remote Integrated Control System and weekly using a portable CO₂ measurer (Testo® model 435). The average temperature and relative humidity during the irrigation CO₂ experiment were 22.7 °C and 69.25%, respectively.

The experiment occurred 105 to 195 days after germination, allowing the evaluation of the final development of the first and second leaves, as well as the emergence and growth of the third leaf. Figure 1 shows the overall look of the juvenile plants at each harvest during the experiment. We referred to the combination of epicotyl and petioles as the epicotyl, and the leaf limb as the leaf, because the difference between the epicotyl and petiole was unclear.

Every 15 days, we perform non-destructive analyses to measure photosynthesis and growth, and on the next day, we conduct destructive harvests to investigate dry mass and non-structural carbohydrates. We had seven harvests: at 0 days of CO₂ exposure or 105 days after germination (start), and then at 15, 30, 45, 60, 75, and 90 days of eCO₂. All harvests took place between 9 and 11 am, with individuals randomly chosen from each OTC, totalling five individuals per treatment. These individuals were separated into organs: root, epicotyl, and leaves (first (L1), second (L2), and third leaf (L3)). All samples were frozen in liquid nitrogen, lyophilized, and weighed for growth calculations. Biochemical analyses used the same dry material for each organ and ground in a ball mill.

Gas-exchange measurements

Net photosynthesis (A), stomatal conductance (g_s), and transpiration (E) in leaves were measured biweekly in the first leaf using a portable open gas-exchange system (LI-6400 XT; Li-Cor). We measured the second leaf at 90 days of exposure, but it was not fully expanded. The conditions

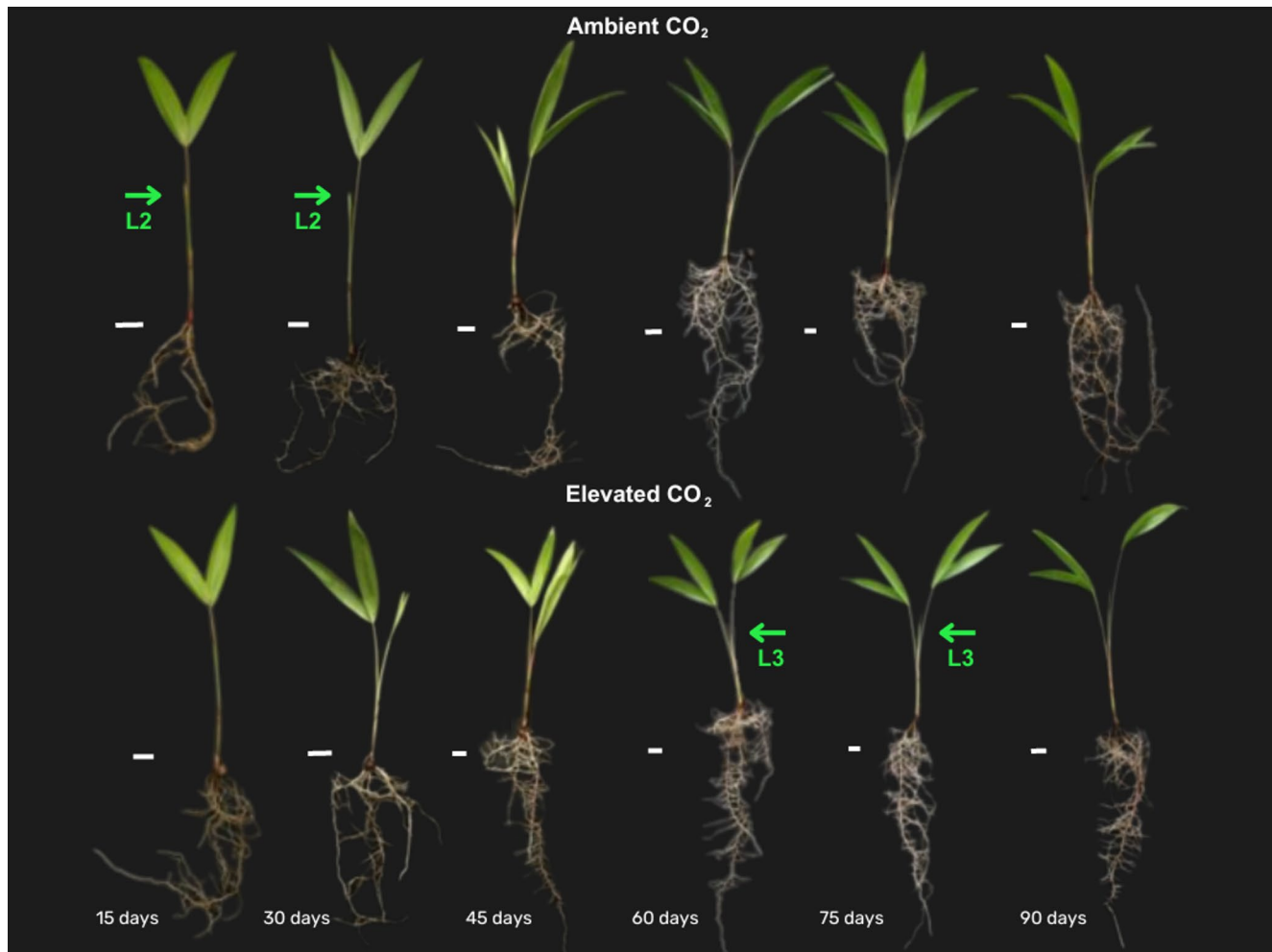


Fig. 1 Morphological aspects of *Euterpe oleracea* juvenile plants during each destructive harvest throughout the CO₂ fertilization experiment (15, 30, 45, 60, 75, and 90 days). White bars represent 2 cm; green arrows indicate the emergence of second (L2) and third leaves (L3)

were leaf temperature of 26 °C, saturating light intensity (500 $\mu\text{mol} \cdot \text{photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; Fig. S2), and CO₂ concentration 380 $\mu\text{mol} \cdot \text{CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (aCO₂ treatment) or 760 $\mu\text{mol} \cdot \text{CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (eCO₂ treatment).

Growth and dry mass accumulation and allocation

In non-destructive analyses, we measured plant height and leaf area. Leaf height was measured from the seed insertion of the epicotyl to the leaf apex (Supplemental Fig. S3a), which corresponds to the overall plant height. At this developmental stage (bifid leaves), we measured the length (L) and width (W) of the leaf limb to estimate the apparent leaf area. ($L \times W$). Subsequently, we summed the areas of the two ellipses (Fig. S3b). To determine the ellipse Real Area (RA), leaves were scanned, and each ellipse was measured with an area recognition program (Image-Pro Plus® Version 6.3). We used 110 leaves (220 lanceolate ellipses) to obtain a correction factor (CF) by linear regression ($y = 0.7242x + 0.829$;

$R^2 = 0.951$) between the apparent area and the actual area, resulting in a CF of 0.7242 (Percentage Relative Standard Error = 1.8%). The linear regression between the apparent area ($L \times W$) and the RA produced a fitting Eq. 1:

$$RA = (L \cdot W) \cdot 0.7242 \quad (1)$$

In destructive harvests, we measured the root length (Supplemental Fig. S2a and Table S3), and the dry mass of each organ was calculated by weighing the dried material obtained from these harvests. To calculate the relative growth rate (RGR) we applied the following Eq. 2 (Hoffmann and Poorter 2002):

$$\text{RGR} = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1} \quad (2)$$

where: RGR represents the relative growth rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$). W_1 and W_2 correspond to the mean dry mass of the

plants (g) at times t_1 and t_2 , respectively. The natural logarithm of plant mass ($\ln W$) is used to linearize growth over time, and the difference between $\ln(W_2)$ and $\ln(W_1)$, divided by the time interval ($t_2 - t_1$), in days.

Non-structural carbohydrates quantifications

The total non-structural carbohydrate (NSC) content was quantified following Arenque et al. (2014). Ten milligrams of each sample were washed three times with 1.5 mL of 80% ethanol at 80 °C for 20 min to analyze soluble sugars. After centrifuge (10,000 g x 5 min), the supernatants were dried under vacuum and re-suspended in deionized water. Each sample was analyzed using High-Performance Anion Exchange Chromatography with Pulsed Amperometric Detection (HPAEC/PAD) on a Carbopac PA1 column (Dionex ICS3000, Dionex, CA, USA). Glucose, fructose, sucrose, raffinose, and myo-inositol were separated with an isocratic method (100 mM NaOH) and quantified by a standard curve. The pellet residues were dried for starch extraction and quantification. They were treated twice with α -amylase (120 U mL⁻¹) from *Bacillus licheniformis* and twice with amyloglucosidase from *Aspergillus niger* (30 U mL⁻¹). Aliquots of the supernatant were incubated with 250 μ L of glucose oxidase/peroxidase (GOD/POD-Centerlab/Brazil) at 30 °C for 15 min, and the glucose content was measured at 490 nm by comparison with the glucose standard curve (20 to 300 mg.mL⁻¹).

Statistical analysis

To evaluate the significance of the differences between the means at each sampling point for the aCO₂ and eCO₂ treatments, we first performed the Shapiro-Wilk test to assess data normality. We also used an F-test to evaluate the

homogeneity of variances. Based on these results, we conducted an independent samples Student's t-test ($\alpha=0.05$) to compare the treatments. The points and bars shown in the graphs represent the mean $\pm$ standard error of the mean ($n=5$). Additionally, we calculated a Pearson Correlation Coefficient, across all parameters to examine the linear relationship between the datasets (Supplemental Table S4).

Results

Net Photosynthesis (A) in juvenile açai plants ranged from 4 to 5 $\mu\text{mol.CO}_2\text{.m}^{-2}\text{s}^{-1}$, with stomatal conductance (g_s) lower than 0.06 $\text{mol.H}_2\text{O. m}^{-2}\text{s}^{-1}$ throughout all periods of the experiment in ambient CO₂ treatment. When the CO₂ concentration was doubled, A increased on all harvest days, but a significant difference was only observed only at 60 days of eCO₂ exposure (38% in the first leaf). At 90 days, net photosynthesis in the first leaf decreased in both treatments, while it increased about 89% in the second leaf compared to ambient condition (Fig. 2a). Conversely, g_s and transpiration (E) decreased by approximately 50% from 45 days of exposure to elevated CO₂, which remained until the end of the experiment (Fig. 2b and c, respectively). Chlorophyll levels (a, b, or a+b) did not change significantly between treatments under eCO₂ (Supplemental Table S1). The assimilation reduction in the first leaf at 90 days (Fig. 2) suggests integrated sugar signaling (Fig. 3) from the expansion of the second leaf (Fig. 4b), with photosynthetic assimilation starting in L2 (Fig. 3a), and growth stimulation (Fig. 5).

Non-structural carbohydrates (NSC) changed over time and among different organ (Fig. 3). In general, roots had the lowest NSC content than leaves and epicotyl, except for sucrose, whose levels were similar across all organs (Fig. 3 and Supplemental Table S2). Soluble sugars, such

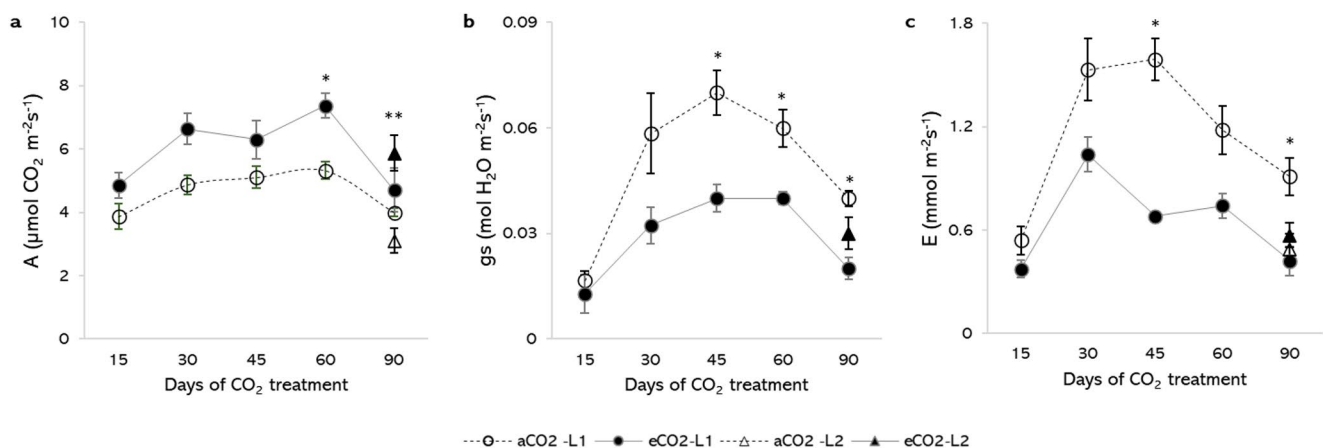


Fig. 2 Gas exchange parameters in the first leaf (circles) and second leaf (triangles) of *Euterpe oleracea* under ambient (aCO₂ - open form) and elevated CO₂ (eCO₂ - close form) concentrations during 90 days of treatment (105 to 195 days after germination). (a) Leaf net carbon

assimilation (A); (b) Stomatal conductance (g_s); (c) Transpiration (E). Circles and triangles represent the mean $\pm$ standard error ($n=5$) for the first and second leaves, respectively. Asterisks indicate a significant difference between treatments at each harvest period ($p < 0.05$)

as sucrose, glucose, fructose, raffinose, myo-inositol, and starch are less than 1% of root dry mass. Starch is the main NSC in leaves and epicotyl, while sucrose is the dominant sugar in the roots.

The most remarkable effect of the eCO₂ was the progressive and significant starch accumulation in leaves (180% increase over 90 days of the experiment) (Fig. 3a). Starch content also increased significantly in the epicotyl (100%) and roots (66%) after 15 days of eCO₂ exposure, as a short-term CO₂ response. However, only in the roots at 75–90 days was an inversion in starch root content between treatments detected. This is negatively linked to the high investment in root growth in the eCO₂ treatment (Fig. 5d), which is a long-term CO₂ response. The reduction in all NSC at 75 days is most notable in the epicotyl in both treatments, possibly due to sugar mobilization, epicotyl growth, new leaves (Fig. 4a) and root development (Fig. 5C and D), along with decreased sucrose transport from the first leaf because of lower photosynthesis. In leaves, the reduction is only seen in glucose, fructose, and raffinose (Fig. 3g, j, m), while sucrose levels remain stable and do not differ under eCO₂.

Raffinose and myo-inositol appeared in the lowest concentrations in all organs, and in leaves the levels decreased under eCO₂. We observe an effect of eCO₂ treatment on raffinose content, which increased in the epicotyl at 15 and 75 days but decreased at 60 and 90 days. Raffinose levels peaked at 15 days in leaves (source) and at 60 days in leaves and epicotyl (sink), indicating the raffinose translocation to sink organs. At day 75, the myo-inositol concentration in leaves was significantly lower under eCO₂ compared to aCO₂, while no differences were observed in other organs and sampling times (Fig. 3p–r).

The height, measured by the tip of the first leaf, was 3% lower under eCO₂ at the first harvest (15 days of exposure), and this trend persisted throughout the experiment (Fig. 4a and Supplemental Table S3). In contrast, the second and third leaves completed their development during eCO₂ exposure, with height increases of 11% at 30 and 9% at 60 days for the second leaf, and 16% at 60 days for the third leaf, while the ambient treatment reached the same size by 90 days. This investment in height under eCO₂ appears to be associated with greater NSC accumulation, which promotes faster leaf development. The leaf area of the first leaf was consistently smaller, with significant reductions of 6%, 5%, and 5% at 15, 30, and 60 days of eCO₂ treatment (Fig. 4b).

Açaí exposed to eCO₂ treatment showed higher total dry mass, with significant increases of 24%, 28%, 47% and 34% at 30, 60, 75, and 90 days, respectively, (Fig. 5) compared to aCO₂. At 30 days, the increase in total dry mass was mainly due to leaf dry mass. After 45 days, all organs (leaves, epicotyl, and roots) contributed similarly to the total dry mass

increment, with the most substantial increases observed in the roots: 71% (45 days), 43% (60 days), 73% (75 days) and 38% (90 days) (Fig. 5d). Overall, eCO₂ treatment resulted in higher relative growth rates (RGR) at 15, 30, 60, and 75 days, and lower rates at 45 and 90 days, while aCO₂ treatment maintained a constant RGR (Fig. 5e). This suggests an early investment in dry mass under high CO₂ conditions (15 to 30, 60 to 75 days), followed by reduced growth investments at 45 and 90 days. Under ambient conditions, this pattern is less pronounced but remained consistent.

Under eCO₂, there is a strong positive correlation between leaf starch content and total dry mass (Fig. 6 and Supplemental Table S4). The slope of the regression line for eCO₂ is significantly steeper than that for aCO₂, indicating that for a given increase in dry mass, leaf starch accumulation is much higher under eCO₂ conditions. This leaf starch correlation is significant across all dry mass parameters (total, leaves, epicotyl, and roots), highlighting the importance of starch in dry mass accumulation under eCO₂ compared to the ambient treatment. Root dry mass is correlated with leaf starch in both treatments, and it was shown that starch in leaves can serve as a significant signal to redistribute sugars to growing roots.

Discussion

Few studies investigated palm trees under elevated CO₂. Our results align with observations in oil palm (*Elaeis guineensis* Jacq) and açai (*E. oleraceae*) (Ibrahim et al. 2017; Amaral et al. 2023). The first leaf exhibited 38% higher A values at 60 days under eCO₂. The second leaf started developing with 84% higher A in eCO₂ compared to aCO₂ (Fig. 2). Conversely, g_s and E values were lower under eCO₂ only in the first leaf, resulting in improved water use efficiency (A/g_s). These responses are typical of C3 plants grown under eCO₂, in which increased carbon assimilation results from higher CO₂ concentration at the active site of Rubisco. This enhances quantum yield and reduces photorespiration, leading to improved water use efficiency (Ainsworth and Rogers 2007). The higher CO₂ gradient across the leaf allows more efficient diffusion through stomata. This may enable plants to reduce stomatal number per unit leaf area, which is reflected in lower g_s (Poorter et al. 2022), and consequently reduced evapotranspiration.

As a consequence of increased photosynthetic assimilation, the most notable effect observed during the 90 days eCO₂ experiment was starch accumulation and relatively low levels of soluble sugars in leaves (Fig. 3). This pattern supports findings in other species (Poorter et al. 2022; Fortier et al. 2023), including palms such as *E. guineenses* (Ibrahim and Jaafar 2012). Short-term CO₂ fertilization

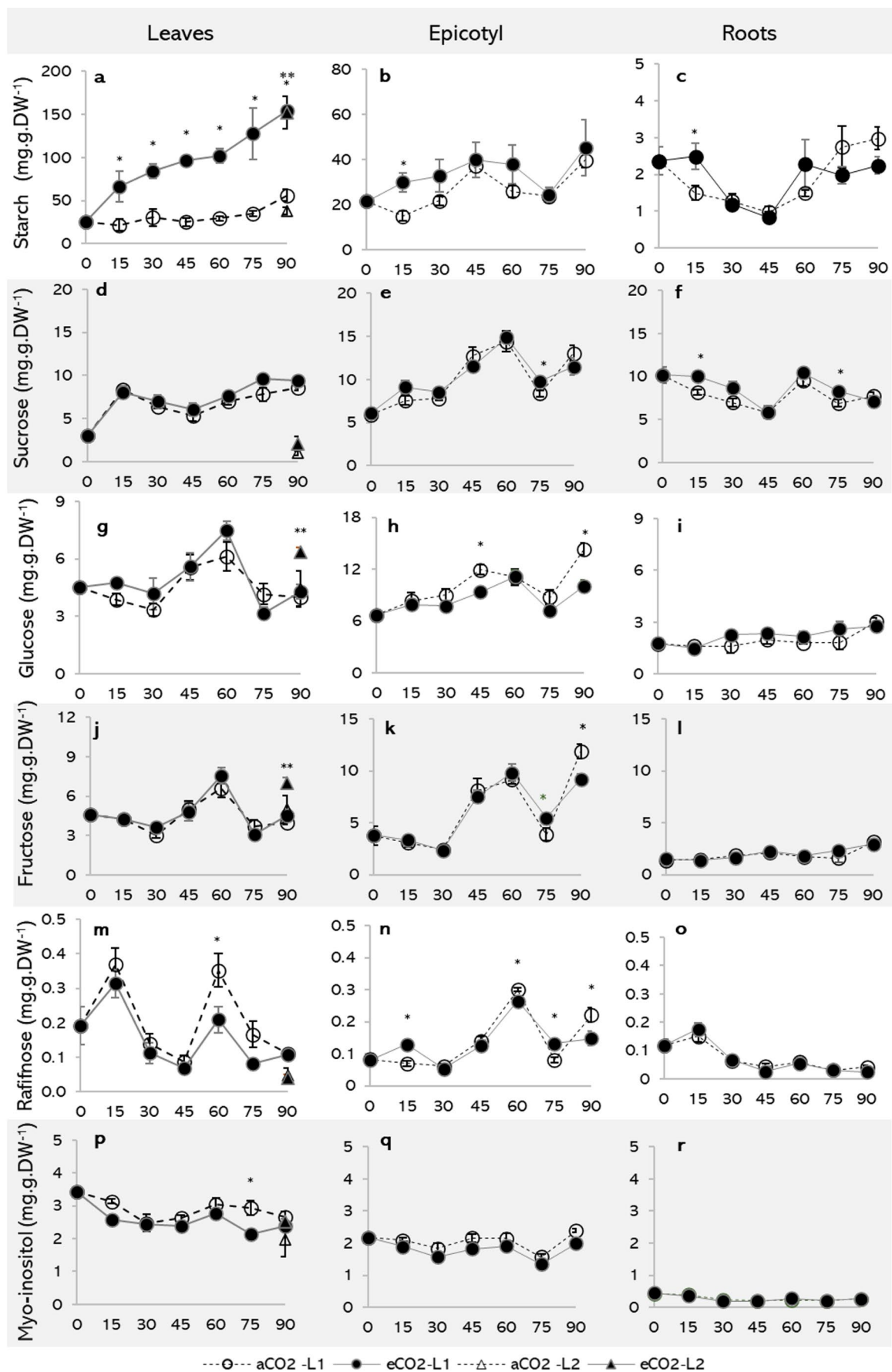


Fig. 3 Non-structural carbohydrates of *Euterpe oleracea* under ambient ($a\text{CO}_2$ - open form) and elevated CO_2 ($e\text{CO}_2$ - close form) conditions over 90 days of treatments (105 to 195 days after germination). Graph columns indicate organs: leaves (a, d, g, j, m, p), epicotyl (b, e, h, k, n, q) and roots (c, f, i, l, o, r); while graph lines show soluble sugars: starch (a–c), sucrose (d–f), glucose (g–i), fructose (j–l), raffinose (m–o), and myo-inositol (p–r). DW- dry weight. In leaves columns circles represent the first leaf and triangles the second leaf, with mean $\pm$ standard error ($n=5$). Asterisks indicate significant differences between treatments at each harvest period ($p<0.05$)

often increases starch accumulation within 15 days, but plants exposed to $e\text{CO}_2$ for longer periods may show photosynthetic (Sage 1994). Studies in *Arabidopsis* indicate that starch plays a key role in negatively regulating photosynthesis under $e\text{CO}_2$. These findings agree with earlier hypotheses proposing that acclimation results from accelerated senescence and reduced CO_2 diffusion to the stroma due to the accumulation of large starch granules (Gibson et al. 2011; Jauregui et al. 2018). However, in coffee leaves, starch accumulation did not lead to photosynthetic down-regulation (Avila et al. 2020). Several biochemical changes also occur under $e\text{CO}_2$, affecting respiration, chlorophyll content, and secondary metabolism. This suggests that starch accumulation alone may not fully explain the decline in photosynthetic efficiency observed in plants growing in $e\text{CO}_2$ environments (Fortier et al. 2023).

In general, $e\text{CO}_2$ increases photosynthetic rates, leading to greater carbon assimilation and faster growth. This phase is marked by a positive feedback loop where more carbon mobilization enhances photosynthesis and growth stimulation. Over time, as non-structural carbohydrates, such as sucrose, accumulate, plants may experience a reduction in photosynthesis. This negative feedback is triggered by sugar sensing mechanisms that detect high internal sugar levels and signal the plant to decrease photosynthetic activity to prevent an over-accumulation of carbohydrates, which can be harmful (Rolland et al. 2006). Our results indicates that the high leaf starch accumulation under $e\text{CO}_2$ does not immediately cause negative feedback on photosynthesis within 90 days. Instead, the increased starch storage may serve as a buffer to protect the plant from metabolic imbalances, supporting sustained high photosynthetic rates, as observed in the second leaf (Figs. 2a and 3a). When plants mobilize the NSC for growth, first in roots from day 45, and later in leaves and epicotyl from day 60 (Fig. 5), this sugar mobilization signals the system to use the higher starch levels in the leaves. The authors suggest this process helps maintain the sucrose flow homeostasis while reducing glucose, fructose, and raffinose levels in the leaves and epicotyl (Fig. 3). Starch and sucrose in the epicotyl and roots decrease at 75 days, which is inversely related to increased dry mass in these organs.

Regarding sugars and signaling, it is interesting to note that raffinose peaks at 15 and 60 days, which may be linked to the emergence of the second and third leaves (Figs. 3 and 4). Studies on raffinose influencing plant growth, development, and stress response are increasing (Unda et al. 2017; Liu et al. 2021, 2024). For example, raffinose production has been shown to act as a molecular signal for metabolic changes affecting cell wall development and xylem tension formation (Unda et al. 2017). The raffinose oligosaccharide family has the potential to improve sugar export to the phloem and enhance crop performance under $e\text{CO}_2$ levels (Sanyal et al. 2023). Additionally, raffinose is associated with responses to osmotic stress (Pluskota et al. 2015; Sanyal et al. 2023). Therefore, in açai, the slight transient decline in raffinose levels, along with the reduction in stomatal conductance, suggests this sugar may play a role in osmotic adjustments under elevated CO_2 conditions. This supports with Kikuzawa's theory, which states that plants optimize resource use, including water and sugars, in response to environmental stresses. The decreased stomatal conductance and the possible role of raffinose in osmotic regulation under elevated CO_2 might reflect an adaptive strategy by açai to conserve water and maintain physiological balance, as observed in other species that modulate leaf longevity to optimize resource use across different environments (Kikuzawa 1991).

Along with starch accumulation and raffinose dynamics, a temporary decrease in myo-inositol levels was observed in leaves at day 75 under $e\text{CO}_2$. Given its role in cell wall precursors, phosphate storage, and signaling pathways (Loewus and Murthy 2000), this decrease probably indicates a temporary shift in carbon allocation, suggesting that myo-inositol metabolism is dynamically modulated during acclimation to elevated CO_2 .

Sucrose was found in similar amounts across all organs and is vital in source-sink relationships, as it is produced in the source (leaves) and transported via phloem to other organs. During the sink phase, carbon is mainly allocated to protein, starch, and structural carbohydrates, resulting in a relatively low sucrose to monosaccharides ratio (Lal et al. 2022). As photosynthetic capacity matures, the demand for assimilates decreases, making them available to export. In açai juvenile plants, the high levels of glucose, fructose, and a small amount of sucrose (Fig. 3 and Supplemental Table S2) suggest that leaves produce enough carbon compounds for immediate use, with little to no export to sink organs. The high and negative correlation between sucrose and net carbon assimilation in $a\text{CO}_2$ indicates sucrose consumption (Supplemental Table S4). In contrast, in $e\text{CO}_2$, this correlation disappears, likely due to starch accumulation and growth investments.

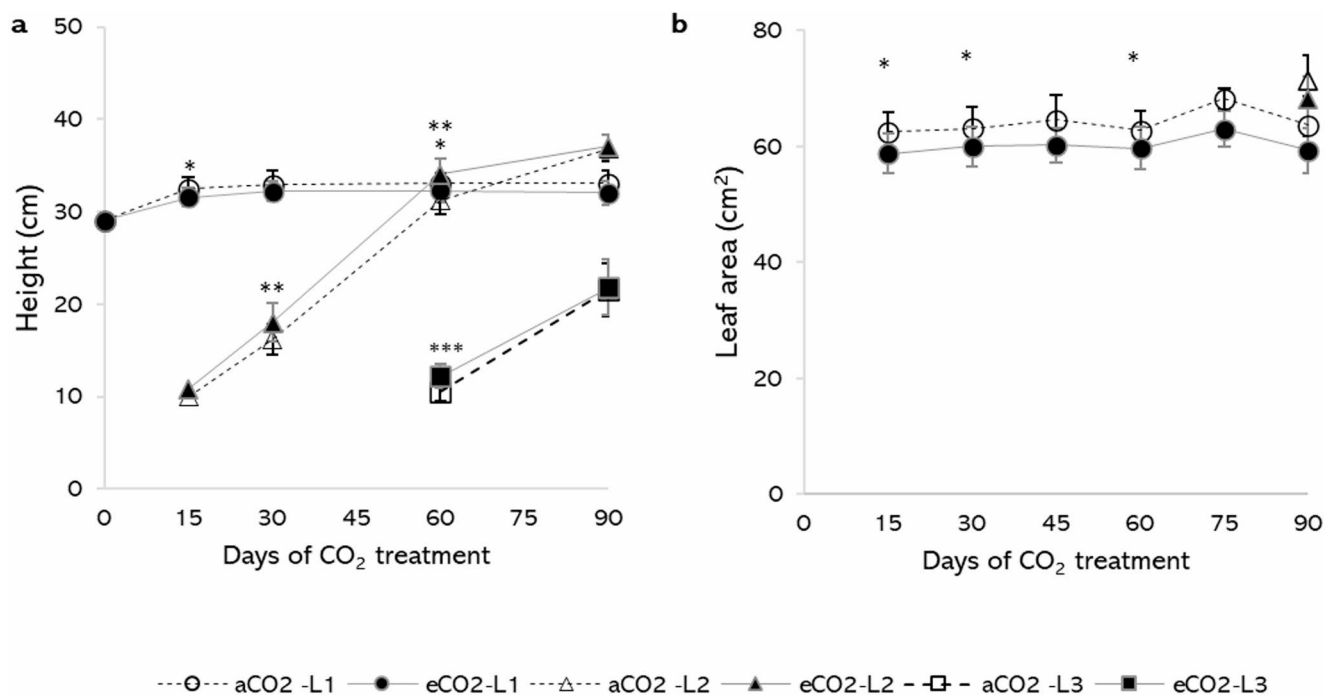


Fig. 4 Growth parameters of *Euterpe oleracea* under ambient (aCO₂ - open form) and high CO₂ (eCO₂ - close form) concentrations during over 90 days of treatment. **(a)** Height (cm) of the first (circle), second

(triangle), and third leaves (squares). **(b)** Leaf area (cm²) of the first leaf. Asterisks indicate a significant difference between treatments at each harvest period ($p < 0.05$)

The ability of açai to accumulate high starch levels indicates it has a high degree of physiological plasticity to store carbon. This plasticity enables the plant to adapt to rising CO₂ atmospheric levels by adjusting its metabolism and storage capacity. The stronger, positive correlation and linear regression between dry mass and leaf starch content under eCO₂ (Fig. 6 and Supplemental Table S4) suggest that açai can sustain higher growth rates and dry mass accumulation by efficiently storing excess carbon as starch, contributing to greater overall productivity under eCO₂ conditions.

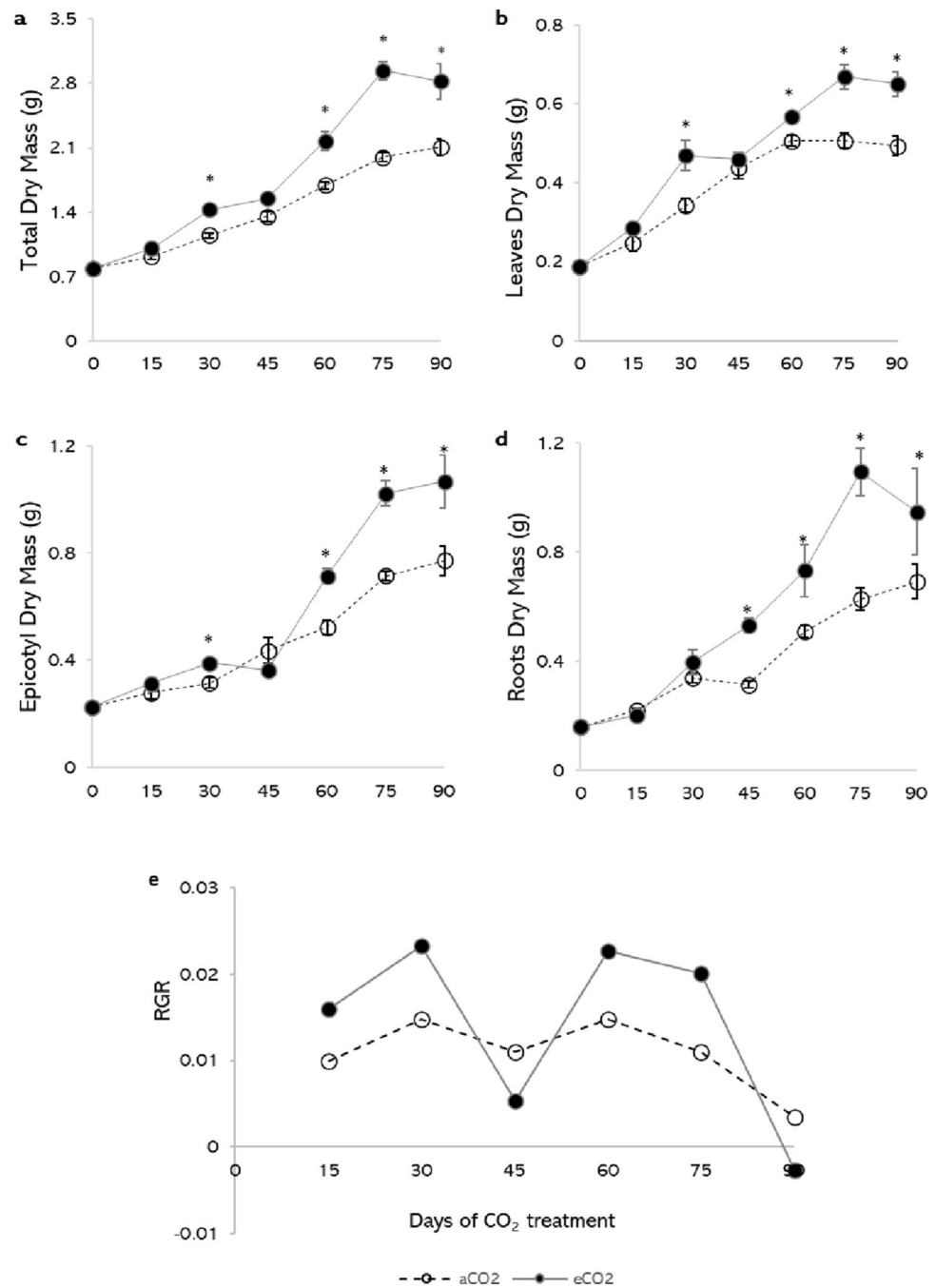
Growth was positively influenced by increased photosynthesis under eCO₂, as shown by height and dry mass increase in all organs (Figs. 4a and 5). In contrast, the leaf area decreased in the first leaf, and the second leaf exhibited a delay in the expansion of limb area (Fig. 4b). Leaves dry mass increased, while leaf area decreased, leading to a lower leaf area ratio (LAR) and specific leaf area (SLA) (Supplemental Table S3). The reduction in LAR and SLA suggests a shift in carbon allocation under eCO₂, with the plant investing more in dry mass accumulation rather than expanding the leaf area. This may be a strategy to optimize resource use, as a smaller leaf area can reduce water loss through transpiration while maintaining a higher carbon assimilation capacity. Although eCO₂ boosts photosynthesis, acclimation may occur over time, resulting in decreased leaf expansion rates as the plant adjusts its growth strategies to balance carbon gain with other physiological needs,

such as water uptake and nutrient allocation. This dynamic, along with increased starch, highlights the complex feedback mechanisms regulating plant responses to long-term exposure to elevated CO₂ (Rogers and Ainsworth 2006; Poorter et al. 2022).

Plants' ability to withstand waterlogged conditions is often linked to their capacity to store carbohydrates in their roots (Scarano et al. 1994; Gravatt and Kirby 1998; Arpagaus and Braendle 2000; Ferreira et al. 2009). Typically, species from waterlogged areas are expected to have high root NSC levels. However, in açai, our study found low NSC concentrations, mainly starch, in the roots and higher levels in the leaves and stems. The same pattern was observed in another Amazonian species, *Senna reticulata*, which also shows higher starch in its aerial parts (Arenque et al. 2014), indicating a different adaptation strategy to survive environmental stresses by producing new roots to support extended periods of hypoxia.

In this study, eCO₂ showed a fertilizing effect on açai juvenile plants, increasing assimilation and starch production, which enhanced growth rates. However, it is important to recognize that eCO₂ also interacts with other climate-change stressors, such as high temperatures and water deficits, which are predicted to intensify in the Amazon region. The açai palm is vital to the local economy in the Amazon region, and the disruptions in production could threaten the survival of local communities, highlighting the

Fig. 5 Dry mass of *Euterpe oleracea* juvenile plants under ambient ($a\text{CO}_2$ - open form) and high CO_2 ($e\text{CO}_2$ - close form) concentrations during over 90 days of treatments. **(a)** Total dry mass, **(b)** Leaves dry mass, **(c)** Epicotyl dry mass, **(d)** Roots dry mass, and **(e)** Relative Growth Rate (RGR - $\text{g g}^{-1} \cdot \text{day}^{-1}$) calculated from dry mass averages. Circles represent means $\pm$ standard error ($n=5$). Asterisks indicate significant differences between treatments at each harvest period ($p < 0.05$)



need of understand how these plants function. This study demonstrated positive effects, but when combined with high temperatures (up to 40°C) and water stress, açai is negatively affected, decreasing the photosynthetic rates and fruit production (Neves et al. 2019; Oliveira et al. 2019). When $e\text{CO}_2$ is combined with elevated temperature and water stress, the buffer effect of $e\text{CO}_2$ weakens, resulting in negative responses to climate change (Arenque et al. 2014; Amaral et al. 2023).

In summary, the growth of the Amazonian palm species *Euterpe oleracea* (açai palm) accelerates with the increased

atmospheric CO_2 , leading to a twofold in starch accumulation in leaves. However, starch levels in other examined organs, such as the epicotyl and roots, did not explain dry mass accumulation. This indicates that dry mass gain is related to the presence of more cells with additional cell walls in the epicotyl and roots. The carbohydrate profile changes throughout development, with peaks observed at 15 and 60 days of the experiment (Fig. 3). The most prominent peaks are for raffinose, which is known to be involved in plant signalling systems. The fast growth in early development probably triggers acclimation by 60 days (Fig. 2

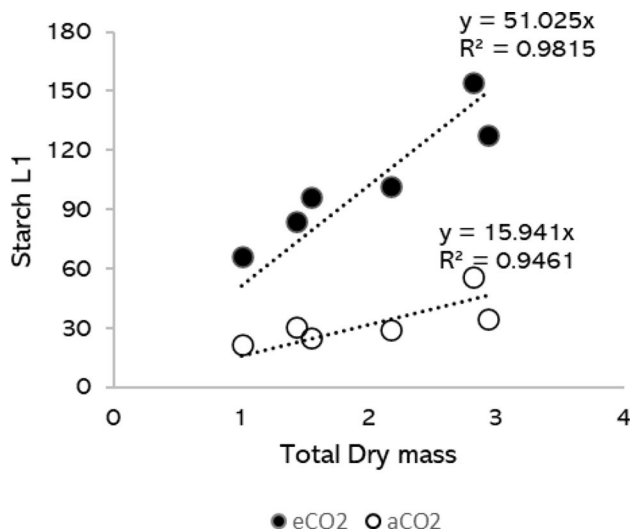


Fig. 6 Linear regression between leaf starch (mg of dry weight) and total dry mass (g) of *Euterpe oleracea* under ambient (aCO₂ - open form) and high CO₂ (eCO₂ - close form) concentrations during over 90 days of treatments

for photosynthesis) and 75 days (Fig. 5 for dry mass). Our findings suggest that the initial boost in growth caused by elevated CO₂ may not be sustained over time due to photosynthetic acclimation and sugar sensing mechanisms.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00468-026-02732-3>.

Author contributions LCM (MSc dissertation under MSB supervision) conducted the experiments and performed the basic data analyses. FMR, AG, and BCA complemented the data analyses and drafted the manuscript. MSB led the research team and edited the final version of the manuscript. All authors have read and approved to the published version of the manuscript.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). Fellowships for Scientific Initiation and MSc to LCM FAPESP (2007/04686-3 and 2009/04038-7). Authors thank Eglee Igarashi and Viviane Lopes Costa for the technical support. This work was supported by FAPESP (Grant Number 07/59708-1), CNPq and the Ministry of Science and Technology of Brazil. This work was partly supported by Eletronorte (Pará State, Brazil).

Data availability Supplementary file, the following are available online.

Declarations

Conflict of interest The authors declare no conflicts of interest.

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