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Meta-analysis of the responses of tree and herb to elevated CO₂ in Brazil

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The CO₂ concentration has increased in the atmosphere due to fossil fuel consumption, deforestation, and land-use changes. Brazil represents one of the primary sources of food on the planet and is also the world's largest tropical rainforest, one of the hot spots of biodiversity in the world. In this work, a meta-analysis was conducted to compare several CO₂ Brazilian experiments displaying the diversity of plant responses according to life habits, such as trees (79% natives and 21% cultivated) and herbs (33% natives and 67% cultivated). We found that trees and herbs display different responses. The young trees tend to allocate carbon from increased photosynthetic rates and lower respiration in the dark—to organ development, increasing leaves, roots, and stem biomasses. In addition, more starch is accumulated in the young trees, denoting a fine control of carbon metabolism through carbohydrate storage. Herbs increased drastically in water use efficiency, controlled by stomatal conductance, with more soluble sugars, probably with a transient accumulation of carbon primarily stored in seeds as a response to elevated CO₂.

The carbon dioxide (CO₂) concentration has increased from ~ 280 to ~ 415 ppm in the atmosphere due to fossil fuel consumption, deforestation, and land-use changes^{1–5}. The Intergovernmental Panel on Climate Change (IPCC) stated that by 2100, CO₂ levels might reach the 1300 ppm mark² and consequently increase the global temperature, needing mitigation alternatives to restrain climate change. The IPCC's 2021 report provides valuable insights into the potential impacts of elevated CO₂ concentrations on plants, which can significantly improve plant growth and development. It highlights the need for further research to understand better the complex interactions between CO₂ and other climate change factors and their effects on plant physiology, growth, and ecosystem functioning⁵.

One of the manners to capture the CO₂ is forest maintenance and planting trees for carbon assimilation and biomass accumulation⁶. The increase in CO₂ concentration stimulates photosynthesis, resulting in a productivity gain and more carbon storage^{7–11}.

The photosynthesis parameters affected when plants grow under elevated CO₂ (eCO₂) are the reduction in stomatal conductance, leaf dark respiration rate, transpiration rate, maximum Rubisco enzyme carboxylation rate, and maximum transport of electrons rate that results in carbon assimilation increase^{2,6,12–18}. The increase in CO₂ concentration can stimulate photosynthesis in plants; consequently, the stimulation is influenced by various processes such as carboxylation and product synthesis¹⁹. The rate of photosynthesis can be controlled by Rubisco, which is sensitive to CO₂, and other less sensitive components¹⁹. In maize leaves, eCO₂ concentration decreased whole-leaf chlorophyll and protein content²⁰. The stomatal index was also significantly increased in plants grown at high CO₂ concentrations²⁰. Furthermore, eCO₂ reduced transpiration and water consumption in tomato plants, increasing water use efficiency²¹ and decreasing leaf transpiration rates²². The increase in leaf dark respiration can result from the direct instantaneous effect of increased CO₂ concentration and the longer-term indirect effect due to changes in leaf composition²³. The increased carbon assimilation resulting from elevated CO₂ concentrations has enhanced different crop species' growth, productivity, and biochemical constituents²⁴. In leguminous plants, eCO₂ concentrations have increased chlorophyll, total starch, sucrose, and total carbohydrate content²⁵.

Exposure to eCO₂ can lead to various biochemical changes in plants, including photosynthesis, respiration, chlorophyll content, and starch accumulation²⁶. Yelle et al.²⁷ investigated the acclimation of tomato plants to eCO₂, which observed an accumulation of starch in the chloroplasts. This suggests that starch alone can not fully

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explain the loss of photosynthetic efficiency in eCO₂-grown plants. To understand the biological adaptations to abiotic stress, such as eCO₂, it is important to select crops to verify their impact on plant development²⁶.

Several publications have widely identified changes in these parameters so that large amounts of data can be compiled to provide panels for understanding the climate change effect on plants. One way to analyze and summarize the data is meta-analysis, which affords a comparative analysis of several eCO₂ experiments displaying the diversity of plant responses according to life habits such as trees and herbs^{15,28}. Performing meta-analyses with data on leaf photosynthesis of forest trees and crops is important because such data are essential for modeling the future of carbon storage and sequestration on the planet^{29,30} and also the future changes in agriculture and food production^{31,32}.

The available data, including meta-analyses, is overwhelmed with temperate climate species^{6,12,13,18,28,33–35}, lacking data from tropical (cultivated/exotic or native) plants^{6,28,35–38} and preventing more accurate analysis of some key regions containing high biodiversity and food production in the world. Contrasting to the high proportion of publications focusing on temperate species, about 43% of all Earth's tree species occur in South America³⁹, with tropical and subtropical plants allocating 52% of the carbon on Earth's surface to biomass storage^{6,35}.

A recent meta-analysis about productivity and its potential for crop adaptation under eCO₂ included a single study from Brazil with coffee trees³⁵. However, considering that Brazil represents one of the primary sources of food on the planet⁴⁰ and is also the world's largest area of tropical rainforest³⁵, representing one of the hot spots of biodiversity in the world, it would be essential to include studies performed in the region to obtain a general and accurate view of the effects of CO₂ elevation for food production and biodiversity.

Plants in elevated CO₂ environments in neotropical regions are of great interest due to their importance for understanding the response of these plants to changes in atmospheric conditions. Levy-Varon et al.⁴¹ investigated how symbiotic nitrogen fixation influences the tropical forest carbon sink. They found that planted trees can double carbon accumulation early in succession and increase total carbon in mature forests by approximately 10%. It is important to consider the diversity of functional plant communities in understanding the carbon sequestration potential of neotropical plants at eCO₂. Rull and Vegas-Vilarrúbia⁴² performed simulations involving all known vascular flora of the neotropical Guayana Highlands and predicted the potential extinction of approximately 80% of species due to global warming by the end of this century. Despite these studies, there is still a gap in knowledge about the response of neotropical plants to elevated CO₂. Studies about the effects of eCO₂ on Brazilian plants have been carried out in the last couple of decades^{16,43–46}, and it has been recently pointed out that such data remain a gap in meta-analysis works⁴².

This work aimed to perform a meta-analysis on the eCO₂ responses in plant physiological parameters in Brazilian climates, representing a relevant portion of the neotropics. In these analyses, it was possible to: (I) estimate the size of the average effects of high atmospheric CO₂ on biomass, biochemical, and photosynthesis parameters and (II) verify whether the eCO₂ effects are influenced by the species' life habits (trees and herbs) with the hypothesis that trees and herbs would respond differently to elevated CO₂ concentrations.

Results

Photosynthetic parameters, biomass, and starch increased in leaves of tropical plants under elevated CO₂. The eCO₂ increased plants' assimilation rate by 44% (Fig. 1; Table 1). Overall, trees + herbs responses in biomass showed an average increase of 20% in leaves, 41% in stems, and 43% in roots (Fig. 2; Table 1). The results in non-structural carbohydrates composed of glucose, fructose, sucrose, and starch present in the leaves of trees and herbs under CO₂ are shown in Fig. 3. However, only total soluble sugars and starch content showed an increase of 7% and 47%, respectively (Fig. 3; Table 1).

Elevated CO₂ effect in trees and herbs according to life habits. The life habits were essential to distinguish responses in total biomass, stomatal conductance (*g_s*), transpiration foliar (*E*), water use efficiency (*WUE*), and maximum rate of electron transport (*J_{max}*) (Table 2). The biomass increase is different per organ between trees and herbs under eCO₂. The biomass increased more in trees than in the herbs category, being higher on leaves (194%), stems (245%), and roots (250%) (Fig. 2; Table 1). In herbs, the biomass increased by 28% and 77% in stems and roots, respectively. Furthermore, changes in the biomass of leaves were not significant in herbs (Fig. 2; Table 1). The grain biomasses were only measured in herbs, which had no alteration in plants cultivated under eCO₂ (Fig. 2). Starch increased by 61% in trees, while in the herbs, the fructose, sucrose, and soluble sugars increased by 13%, 15%, and 14%, respectively (Fig. 3; Table 1). When trees and herbs were analyzed separately, the assimilation increased by 39% and 52%, respectively (Fig. 3; Table 1). Stomatal conductance negatively affected herbs (*p* = 0.001; Table 2; Fig. 1). The reduction of *g_s* (39%) in herbs increased *WUE* (117%) (Fig. 3). Thus, the photosynthesis parameters *WUE*, *E*, and *J_{max}* differed among herbs and trees at eCO₂ (Fig. 1; Table 2). These results may reflect a tendency for the opposite effects of these variables in trees and herbs (Fig. 1; Table 1). On the other hand, the trees displayed no significant effect in *g_s*, *WUE*, and *E* at eCO₂ (Fig. 1; Table 1). Under eCO₂, trees significantly reduced dark respiration (17%). Furthermore, *Ci/Ca*, *J_{max}*, *V_{cmax}*, *Fv/Fm*, and total Chl in trees and herbs under eCO₂ did not change under eCO₂ (Figs. 1, 4). The lack of effect could reflect the small number of observations in those variables (Fig. 5), which calls for more studies to provide consistent analysis for these variables.

Heterogeneity and publication bias analysis. Heterogeneity (*I*²) analysis in the analytical models was used to evaluate the variation in results among observations. The high heterogeneity indicates variation in the effect of eCO₂ among observations. The heterogeneity was high (*I*² > 75) for total biomass, *A*, *g_s*, *R_d*, *E*, *WUE*, *Ci/Ca*, *J_{max}*, total chl, starch, and proteins (Table 2). High heterogeneity shows that external factors may influence the variation of the estimated effects among observations. The *V_{cmax}* showed moderate heterogeneity, and the

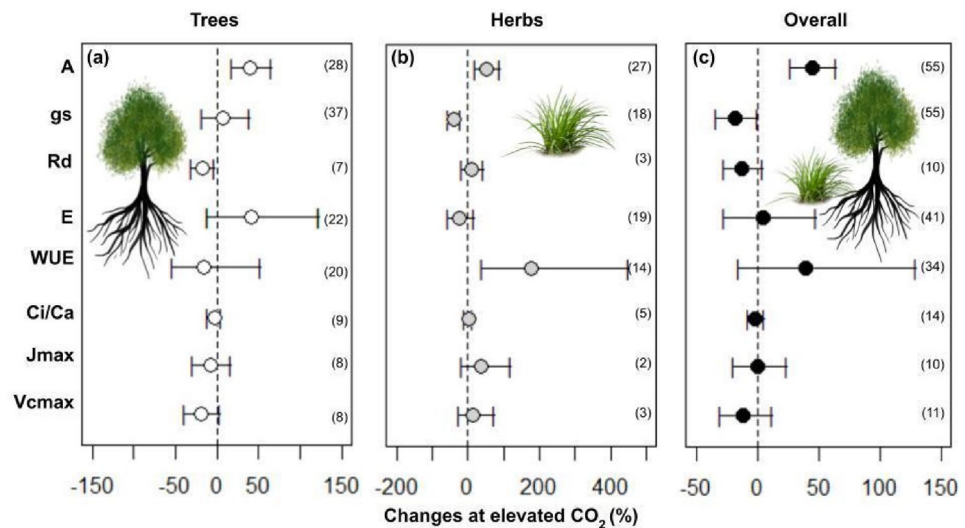


Figure 1. Responses of photosynthetic variables: Net CO₂ assimilation (A), stomatal conductance (gs), dark respiration (Rd), foliar transpiration (E), water use efficiency (WUE), intercellular/ambient CO₂ rate (Ci/Ca), maximum electron transport rate (J_{max}), and maximum Rubisco carboxylation rate (V_{cmax}) according to life habits: Trees (a), Herbs (b), and Overall (c) in plants grown in elevated CO₂. The circles represent the percentage changes in elevated CO₂. Error bars represent 95% confidence intervals. Study numbers for each variable are shown in parentheses.

Fv/Fm had low heterogeneity (Table 2). These results demonstrate less variation among observations in V_{cmax} and Fv/Fm variables.

No publication bias was found for net CO₂ assimilation, dark respiration, foliar transpiration, water use efficiency, intercellular/ambient CO₂ rate, maximum carboxylation rate, the potential quantum efficiency of PSII, total chlorophyll, and total soluble sugars (Table 2). However, the Egger test identified publication bias for biomass, gs, J_{max}, and starch (Table 2).

Discussion

Plants can be used to capture carbon to delay the effects of climate change through photosynthesis, which assimilates carbon in the form of CO₂ and accumulates it into the plant's biomass. Thus, higher carbon availability is expected to generate changes in these processes and intensify plant growth^{15,47}. In the meta-analysis presented in this work, data from species planted as crops and native species to the neotropics were examined. We confirmed previous literature observations regarding the physiology of temperate species, showing that several neotropical ones alter their photosynthesis parameters, biomass accumulation, and sugars (biochemicals) under eCO₂ (Fig. 6). The elevated CO₂ in plants through photosynthesis is directly connected to their growth and productivity⁴⁸. In addition, elevated CO₂ stimulated photosynthetic assimilation in neotropical herbs, improving WUE due to stomata closure and conductance reduction (Fig. 1). This behavior corroborates evidence reported in other meta-analyses^{12,28}, except that neotropical trees did not alter the stomatal conductance responses as happens in temperate trees¹³.

Stomatal conductance (gs) and assimilation rates control the intercellular/ambient CO₂ ratio, which dictates the internal carbon allocation in plants⁴⁹. Elevated CO₂ increases the concentration of intracellular CO₂ in leaves³⁸, but to continue the assimilation, the mesophyll CO₂ needs to display lower concentrations than the atmospheric partial pressure of CO₂⁵⁰. This regulation is performed by the closure and opening of the stomata, which leads to a decrease in stomatal conductance^{38,51}.

It has been reported that European forests grown in eCO₂ decreased J_{max} and V_{cmax} by 10%⁵². The authors attributed this decrease to the limiting levels of nitrogen in leaves. The Neotropical species examined in the present work did not decrease J_{max} and V_{cmax} changes (Fig. 1), possibly indicating that the leaf nitrogen status in the experiments used for this meta-analysis was not limited. According to Bonan et al.⁵³, the V_{cmax} parameter displays relevant implications for large-scale modeling. Carbon flux models show that simulated photosynthetic rates are particularly susceptible to V_{cmax} and J_{max}, with the former being pointed out by Bonan et al.⁵³ as a model-dependent parameter. Therefore, accuracy in these parameters is critical for a more effective prediction and modeling by the global panels.

The sugars produced during photosynthesis can be metabolized for maintenance and developmental processes. Catabolism of sugars leads to the consumption of ATP by respiration, which may increase or decrease, depending on the species, when plants are exposed to unfavorable conditions⁵⁴. When neotropical plant species were subjected to elevated CO₂ during growth, they displayed a decrease in dark respiration (Rd) (see Overall in Fig. 1), which is expected to increase the efficiency of the net productivity of carbon gain^{55,56}. Thus, the efficiency of the carbon metabolism increases under eCO₂. The decrease in Rd may be associated with the higher

| | | k | Mean (LnRR) | Lower CI | Upper CI | %change | p-value |
|---|---------|----|--------------|--------------|--------------|-------------|-----------------|
| Biomass variables | | | | | | | |
| Leaves | Trees | 8 | 1.07 | 0.23 | 1.92 | 194% | 0.01 |
| | Herbs | 7 | 0.04 | -0.03 | 0.31 | 4% | 0.67 |
| | Overall | 15 | 0.18 | 0.00 | 0.36 | 20% | <0.05 |
| Stems | Trees | 8 | 1.23 | 0.39 | 2.08 | 245% | <0.01 |
| | Herbs | 5 | 0.24 | 0.01 | 0.48 | 28% | 0.03 |
| | Overall | 13 | 0.34 | 0.16 | 0.52 | 41% | <0.01 |
| Roots | Trees | 8 | 1.25 | 0.40 | 2.09 | 250% | <0.01 |
| | Herbs | 2 | 0.57 | 0.20 | 0.93 | 77% | <0.01 |
| | Overall | 10 | 0.35 | 0.17 | 0.53 | 43% | <0.01 |
| Grains | Trees | - | - | - | - | - | - |
| | Herbs | 4 | 0.09 | -0.42 | 0.61 | 10% | 0.71 |
| | Overall | 4 | 0.09 | -0.42 | 0.61 | 10% | 0.71 |
| Total | Trees | 22 | 0.36 | -0.29 | 1.03 | 44% | 0.27 |
| | Herbs | 15 | 0.14 | -0.03 | 0.31 | 15% | 0.11 |
| | Overall | 37 | 0.21 | -0.07 | 0.35 | 24% | 0.18 |
| Photosynthesis variables | | | | | | | |
| Net CO ₂ assimilation (A) | Trees | 28 | 0.33 | 0.16 | 0.50 | 39% | <0.05 |
| | Herbs | 27 | 0.42 | 0.21 | 0.63 | 52% | <0.05 |
| | Overall | 55 | 0.36 | 0.23 | 0.49 | 44% | <0.05 |
| Stomatal conductance (gs) | Trees | 37 | 0.06 | -0.19 | 0.33 | 7% | 0.6 |
| | Herbs | 18 | -0.50 | -0.78 | -0.22 | -39% | <0.05 |
| | Overall | 55 | -0.19 | -0.39 | 0.00 | -17% | 0.05 |
| Dark respiration (Rd) | Trees | 7 | -0.19 | -0.36 | -0.02 | -17% | <0.05 |
| | Herbs | 3 | 0.09 | -0.17 | 0.37 | 10% | 0.48 |
| | Overall | 10 | -0.13 | -0.31 | 0.04 | -12% | 0.13 |
| Foliar transpiration (E) | Trees | 22 | 0.34 | -0.10 | 0.79 | 41% | 0.13 |
| | Herbs | 19 | -0.29 | -0.77 | 0.17 | -25% | 0.21 |
| | Overall | 41 | 0.04 | -0.30 | 0.38 | 4% | 0.81 |
| Water use efficiency (WUE) | Trees | 20 | -0.16 | -0.76 | 0.42 | -15% | 0.58 |
| | Herbs | 14 | 1.02 | 0.33 | 1.70 | 117% | <0.05 |
| | Overall | 34 | 0.33 | -0.16 | 0.83 | 39% | 0.19 |
| Intercellular/ambient CO ₂ ratio (Ci/Ca) | Trees | 9 | -0.03 | -0.12 | 0.05 | -3% | 0.43 |
| | Herbs | 5 | 0.01 | -0.08 | 0.12 | 1% | 0.71 |
| | Overall | 14 | -0.01 | -0.08 | 0.05 | -1% | 0.68 |
| Potential quantum efficiency of PSII (Fv/Fm) | Trees | 12 | 0.07 | 0.01 | 0.16 | 7% | 0.11 |
| | Herbs | 11 | 0.01 | -0.10 | 0.13 | 1% | 0.78 |
| | Overall | 23 | 0.05 | -0.01 | 0.11 | 5% | 0.14 |
| Total chlorophyll (Chl total) | Trees | 14 | 0.06 | -0.03 | -0.15 | 6% | 0.22 |
| | Herbs | 12 | 0.05 | -0.05 | 0.15 | 5% | 0.35 |
| | Overall | 26 | 0.05 | -0.01 | 0.12 | 5% | 0.11 |
| Maximum rate of electron transport (Jmax) | Trees | 8 | -0.08 | -0.33 | 0.15 | -8% | 0.48 |
| | Herbs | 2 | 0.31 | -0.15 | 0.79 | 37% | 0.18 |
| | Overall | 10 | -0.00 | -0.21 | 0.21 | 0% | 0.99 |
| Maximum rate of Rubisco carboxylation (Vcmax) | Trees | 8 | -0.22 | -0.48 | 0.04 | -19% | 0.09 |
| | Herbs | 3 | 0.13 | -0.28 | 0.55 | 14% | 0.53 |
| | Overall | 11 | -0.12 | -0.35 | 0.11 | -11% | 0.31 |
| Biochemical variables | | | | | | | |
| Glucose | Trees | 8 | 0.10 | -0.04 | 0.25 | 10% | 0.17 |
| | Herbs | 7 | -0.09 | -0.20 | 0.01 | -9% | 0.07 |
| | Overall | 15 | -0.04 | -0.14 | 0.04 | -4% | 0.28 |
| Fructose | Trees | 6 | 0.03 | -0.10 | 0.17 | 3% | 0.6 |
| | Herbs | 7 | 0.12 | 0.03 | 0.21 | 13% | <0.01 |
| | Overall | 13 | 0.06 | -0.05 | 0.14 | 7% | 0.06 |
| Continued | | | | | | | |

| | | k | Mean (LnRR) | Lower CI | Upper CI | %change | p-value |
|----------------------|---------|----|-------------|-------------|-------------|------------|-----------------|
| Sucrose | Trees | 7 | 0.02 | -0.10 | 0.15 | 2% | 0.6 |
| | Herbs | 6 | 0.14 | 0.05 | 0.22 | 15% | <0.01 |
| | Overall | 13 | 0.08 | 0.01 | 0.15 | 8% | 0.01 |
| Total soluble sugars | Trees | 6 | -0.00 | -0.15 | 0.13 | 0% | 0.89 |
| | Herbs | 4 | 0.13 | 0.04 | 0.21 | 14% | <0.01 |
| | Overall | 10 | 0.07 | 0.00 | 0.14 | 7% | 0.04 |
| Starch | Trees | 7 | 0.47 | 0.08 | 0.87 | 61% | 0.01 |
| | Herbs | 14 | 0.29 | -0.09 | 0.69 | 34% | 0.14 |
| | Overall | 21 | 0.38 | 0.11 | 0.65 | 47% | <0.01 |
| Proteins | Trees | 4 | 0.10 | -0.39 | 0.61 | 11% | 0.67 |
| | Herbs | 3 | 0.03 | -0.04 | 0.46 | 3% | 0.88 |
| | Overall | 7 | 0.06 | -0.23 | 0.35 | 6% | 0.68 |

Table 1. Meta-analysis with the percentage change of the biomass, photosynthesis, and biochemical variables measured in Trees and Herbs under elevated CO₂. Observation numbers (k). The effect size values are represented as Log response rate (LnRR) and percentage. Average estimates with lower and upper Confidence Intervals (CI). Bold letters represent significant differences (p < 0.05).

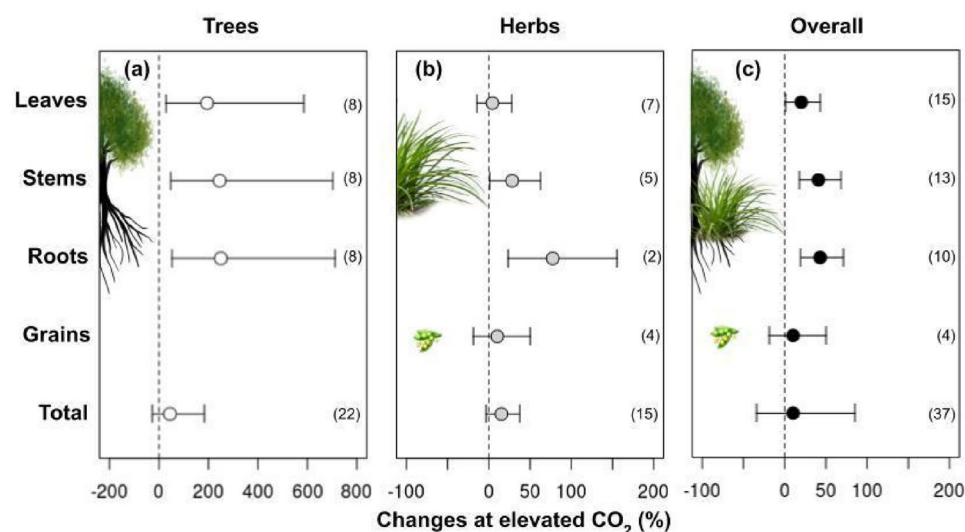


Figure 2. Biomass responses in each plant organ (leaf, stem, root, grain, and total) in plants grown into elevated CO₂ according to life habits: Trees (a), Herbs (b), and Overall (c). The circles represent the percentage changes in elevated CO₂. Error bars represent 95% confidence intervals. Study numbers for each variable are shown in parentheses.

concentrations of foliar starch found in plants grown under eCO₂ analyzed in Overall (Table 1). The same pattern of reduction of *Rd* was observed for temperate trees¹². However, no meta-analysis has been performed considering sugar metabolism and photosynthesis, so temperate and neotropical species could not be directly compared via meta-analysis.

An explanation for the higher accumulation of starch in leaves of neotropical species growing under eCO₂ is that the photosynthetic assimilation rate can exceed the growth capacity, leading to the accumulation of non-structural carbohydrates^{19,57,58}. We found that starch increase (47%) represents the primary non-structural carbohydrate in plant leaves under eCO₂ (Fig. 2).

The increased starch levels in eCO₂ are usually the main element responsible for increasing the content of total non-structural carbohydrates⁵⁹. Starch is composed of insoluble and long-term storage polysaccharides (amylose and amylopectin) that are not readily available to participate in plant metabolic processes⁶⁰ but can be used to increase biomass in leaves, stems, and roots, as observed in this meta-analysis (Fig. 2). The carbohydrates synthesized in leaves from extra CO₂ supply were translocated into tree stems (Fig. 2), suggesting that the reserve biomass is driven to this organ, boosting secondary growth⁶¹. Furthermore, stimulation of photosynthesis with eCO₂ had a response in the biomass increase different in the development of organs and plant seed mass⁶². Li et al.⁶³ synthesized 71 tree species and data of a more significant increase in starch than soluble sugars in leaves under eCO₂.

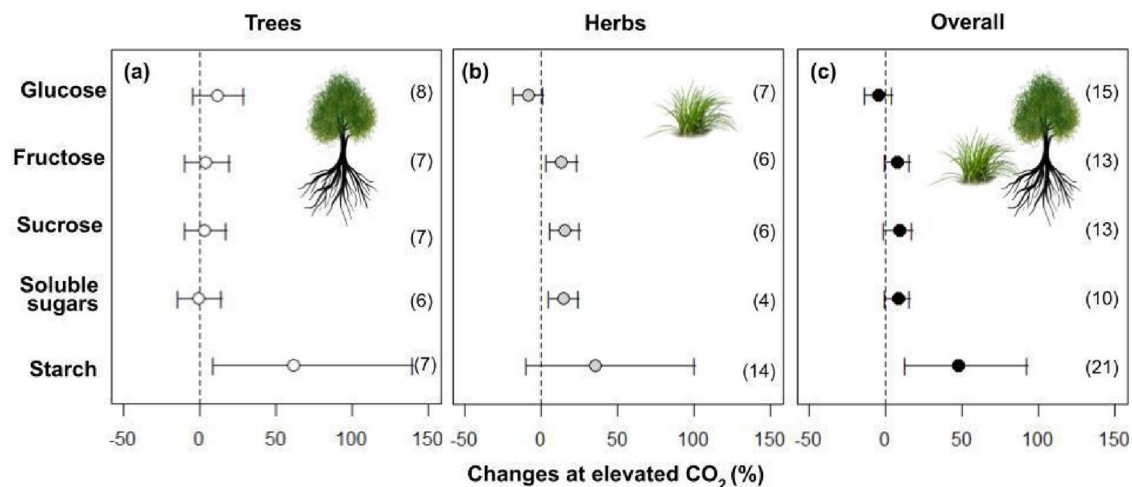


Figure 3. Responses of non-structural carbohydrates (glucose, fructose, sucrose, total soluble sugars, and starch) in plants grown to elevated CO_2 , according to life habits: Tree (a), Herbs (b), and Overall (c). The circles represent the percentage changes to elevated CO_2 . Error bars represent 95% confidence intervals. Study numbers for each variable are shown in parentheses.

| | Life habits | Publication bias | Heterogeneity (%) |
|---|-------------|------------------|-------------------|
| Total biomass | < 0.01 | 0.01 | 95 |
| Net CO_2 assimilation (A) | 0.89 | 0.92 | 99 |
| Stomatal conductance (gs) | < 0.01 | < 0.01 | 96 |
| Dark respiration (Rd) | 0.07 | 0.08 | 92 |
| Foliar transpiration (E) | 0.05 | 0.14 | 98 |
| Water use efficiency (WUE) | < 0.01 | 0.11 | 90 |
| Intercellular/ambient CO_2 ratio (Ci/Ca) | 0.43 | 0.52 | 81 |
| Maximum rate of electron transport (J_{max}) | 0.05 | < 0.01 | 88 |
| Maximum rate of Rubisco carboxylation (V_{cmax}) | 0.16 | 0.31 | 63 |
| Potential quantum efficiency of PSII (Fv/Fm) | 0.46 | 0.75 | 13 |
| Total chlorophyll (Chl total) | 0.89 | 0.24 | 93 |
| Total soluble sugars | 0.29 | 0.33 | 89 |
| Starch | 0.23 | 0.01 | 91 |
| Proteins | 0.74 | 0.74 | 99 |

Table 2. Meta-analyses result in different variables according to life habits: Trees and Herbs, publication bias, and heterogeneity. Bold letters represent significant differences between Trees and Herbs $p < 0.05$. For data from the column in publication bias, the p -value < 0.05 does not indicate publication bias. For heterogeneity, analyses were considered $I^2 \leq 25$ low, $I^2 > 25$ to 75 moderate, and $I^2 > 75$ high heterogeneity.

The results obtained in this work show that the responses of neotropical plant species to eCO_2 are consistent with those on the global scale (temperate climates mainly), suggesting that the predictions made by models of climate change would answer similarly to temperate and neotropical species^{13,47,52}. However, in Brazil, relatively few experiments were carried out with eCO_2 in plants from the biomes Pantanal, Caatinga, Cerrado, Amazon, and the Pampas, the latter in a temperate region (Table 3). Thus, more profound exploration should provide relevant information on how different biomes could answer to eCO_2 and climate change^{64,65}. Also, establishing long-term experiments to test the effect of eCO_2 on plants over time in Brazil is needed once a significant portion of the neotropical plants is located there. This would allow an understanding of the physiological responses to climate change⁶⁶.

Native plants in neotropical regions have evolved to adapt to their specific environmental conditions, including CO_2 levels. Elevated CO_2 can positively affect native plants by increasing photosynthesis, promoting plant growth, increasing carbon sequestration, and potentially acting as a CO_2 sink¹⁶. In contrast, plants grown in neotropical regions are often grown for agricultural purposes. They may have different responses to eCO_2 compared to native plants, although this hypothesis needs to be checked in further studies with more species. Cultivated plants can exhibit increased photosynthetic rates and grow under elevated CO_2 ³⁵. This can benefit crop productivity and potentially increase carbon sequestration in farming systems⁶⁷. However, the response of cultivated plants to elevated CO_2 may vary depending on factors such as plant species, nutrient availability, management

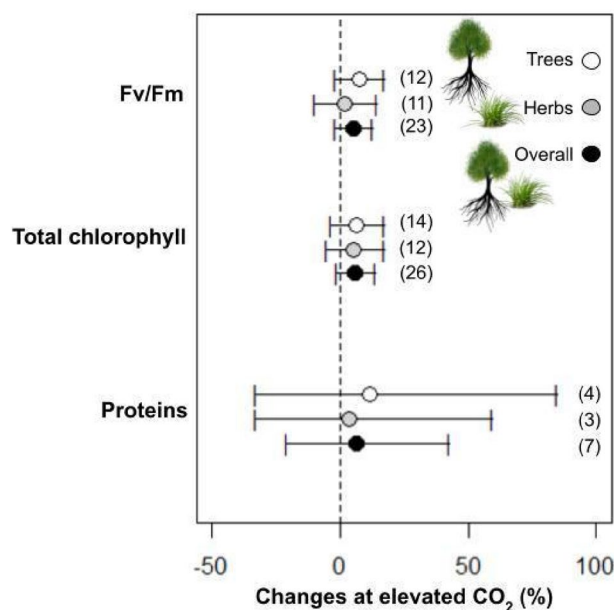


Figure 4. Responses of potential quantum efficiency of photosystem II (Fv/Fm), total chlorophyll content, and proteins in plants grown in elevated CO₂, according to life habits: Trees (white), Herbs (gray), and Overall (black). The circles represent the percentage change in elevated CO₂. Error bars represent 95% confidence intervals. Study numbers for each variable are shown in parentheses.

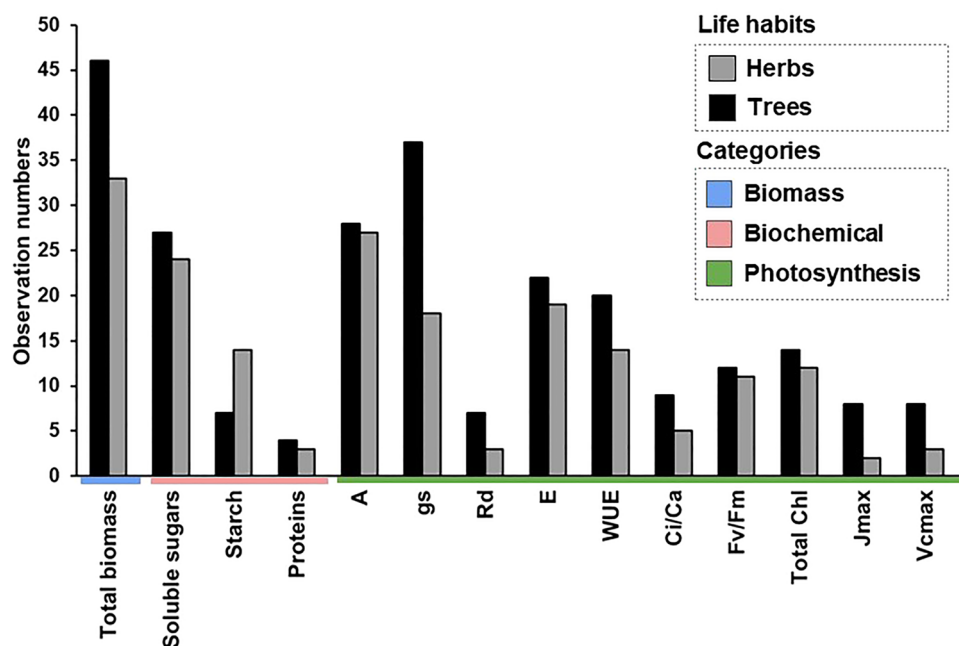


Figure 5. Observation numbers from the literature extracted were divided into biomass, biochemical, and photosynthesis components according to life habits: Trees (black) and Herbs (gray) in experiments with elevated CO₂. The variables correspond to total biomass, total soluble sugars, starch, proteins, net CO₂ assimilation (A), stomatal conductance (gs), foliar transpiration (E), water use efficiency (WUE), dark respiration (Rd), intercellular/ambient CO₂ ratio (Ci/Ca), the potential quantum efficiency of PSII (Fv/Fm), total chlorophyll (total Chl) maximum Rubisco carboxylation rate (V_{cmax}), and maximum electron transport rate (J_{max}).

practices, and genetic improvement techniques⁶⁸. Therefore, it is important to note that the potential of native and cultivated plants to act as CO₂ sources or sinks is influenced by several factors. These include the specific plant species, their physiological characteristics, duration of exposure to elevated CO₂, and general ecosystem

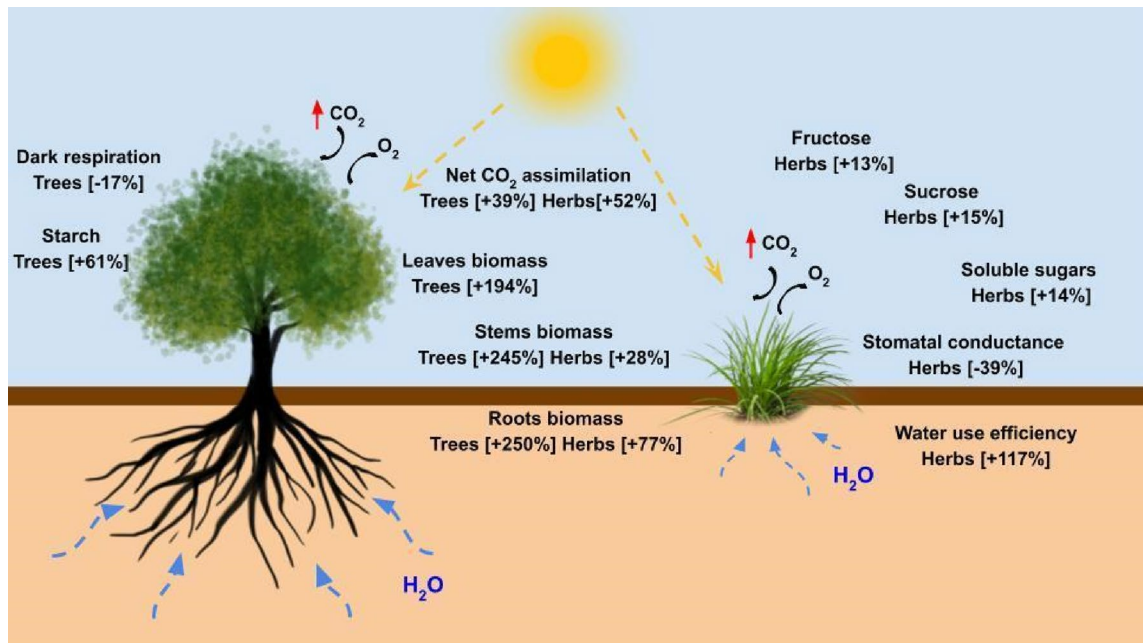


Figure 6. Tropical climate trees and herbs responses to elevated CO₂.

dynamics. To understand the potential of native and cultivated plants in neotropical regions as sources or sinks of CO₂, more research is needed.

Figure 6 summarizes the responses of the neotropical species analyzed in this work. Temperate and neotropical species respond similarly to eCO₂, which is likely to reflect directly in the consistency of modeling regarding the adjustment of parameters. Trees and herbs display different responses. The trees studied are primarily young and, therefore, rapidly growing. As they are not yet at the reproductive stage, young trees tend to allocate carbon—from increased photosynthetic rates and lower respiration in the dark—to organ development, significantly increasing leaves, roots, and stem biomasses. As growth rates are limited in comparison with the growth capacity of most herbs, more starch is accumulated in trees, denoting a tight control of carbon metabolism through carbohydrate storage. Herbs, mainly crop plants, reached reproductive maturity during the experiments. Their strategy to respond to eCO₂ involved a drastic increase in water use efficiency, controlled by stomatal conductance. In addition, the plants tend to display more soluble sugars, probably with a transient accumulation of carbon primarily stored in seeds.

Conclusion

The responses of species native or cultivated in the neotropics to eCO₂ can be attributed to contrasting growth strategies and physiological features of trees and herbs. Trees display greater carbon sink capacity and can allocate more resources for growth and storage. The higher rates of photosynthesis in response to eCO₂ (39%) led to greater starch storage (61%) and a more significant biomass accumulation in tree organs (Table 1). This behavior may be attributed to the tree's long lifespan and ability to allocate resources for growth and storage.

In contrast, herbs, which display shorter lifespans, prioritize rapid growth and reproduction and tend to allocate resources that would support higher water use efficiency (117%) due to decreased stomatal conductance (-39%) under conditions of eCO₂. Herbs responded differently, increasing net CO₂ assimilation (52%) and soluble sugars such as sucrose and fructose (14%, 15%, and 13%). Understanding these responses would be crucial to predicting the impacts of increased CO₂ levels on different types of plants in the face of eCO₂ increases.

Finally, it is essential to note that eCO₂ alone does not represent the complete response of plants to climate change. Combinations of eCO₂ with stresses of temperature and water will be necessary to assess the systemic response of plants to global climate change. Thus, more experiments are needed using these parameters that, together with modeling work, could help understand how the neotropics, with their rather large proportion of world biodiversity, will respond to climate change in this century.

Materials and methods

Data collection. For data collection, a systematic review was performed. A systematic review is a technique that selects primary studies on a given subject⁶⁹. For the elaboration of the systematic review, it is necessary to identify and describe the steps taken to study selection and data extraction. These steps must follow a protocol that can be consulted and reproducible⁶⁹. The flowchart with steps for data collection is shown in Supplementary Fig. 1. Literature search for the data collection on the effect of the elevated CO₂ on plants was performed in three databases: *Web of Science*, *Scielo*, and *Brazilian Digital Library of Theses and Dissertations* (<https://bdtd.ibict.br>)^{70–72}. For each database, a combination of keywords was used (Supplementary Table 1) that recovered 2096 works on the eCO₂. In addition, 35 studies were manually included from leading Brazilian researchers by Lattes search (<https://lattes.cnpq.br>)⁷². Lattes is a Brazilian platform for integrating Curriculum, Research Groups, and

| Species | aCO ₂ | eCO ₂ | Functional group | Native/exotic/ cultivated | Experiment | Reference |
|--------------------------------------|------------------|------------------|------------------|------------------------------|------------|--------------------------|
| <i>Acrocomia aculeata</i> | 400 | 700 | Tree | Native | OTC | Rosa et al. 2019 |
| <i>Alchornea glandulosa</i> | 400 | 800 | Tree | Native | OTC | Fauset et al. 2019 |
| <i>Anacardium occidentale</i> | 380 | 720 | Tree | Native/cultivated | GC | Souza, 2012 |
| <i>Anacardium occidentale</i> | 380 | 760 | Tree | Native/cultivated | GC | Souza et al. 2019 |
| <i>Anadenanthera peregrina</i> | 430 | 700 | Tree | Native | OTC | Melo, 2020 |
| <i>Baccharis dracunculifolia</i> | 360 | 720 | Tree | Exotic/cultivated | OTC | Sá et al. 2014 |
| <i>Carapa surinamensis</i> | 400 | 700 | Tree | Native | GC | Oliveira, 2016 |
| <i>Carapa surinamensis</i> | 350 | 1000 | Tree | Native | OTC | Oliveira, 2017 |
| <i>Cariniana legalis</i> | 380 | 740 | Tree | Native | OTC | Martinez et al. 2008 |
| <i>Cariniana legalis</i> | 380 | 760 | Tree | Native | OTC | Oliveira et al. 2012 |
| <i>Coffea arabica</i> | 400 | 700 | Tree | Exotic/cultivated | OTC | Avila et al. 2020 |
| <i>Coffea arabica</i> | 400 | 550 | Tree | Exotic/cultivated | FACE | Bianconi, 2014 |
| <i>Coffea arabica</i> | 390 | 550 | Tree | Exotic/cultivated | FACE | Ghini et al. 2015 |
| <i>Coffea arabica</i> | 380 | 740 | Tree | Exotic/cultivated | OTC | Marçal et al. 2021 |
| <i>Coffea arabica</i> | 380 | 700 | Tree | Exotic/cultivated | GC | Martins et al. 2016 |
| <i>Coffea arabica</i> | 390 | 590 | Tree | Exotic/cultivated | FACE | Rakocevic et al. 2016 |
| <i>Coffea arabica</i> | 390 | 590 | Tree | Exotic/cultivated | FACE | Rakocevic et al. 2018 |
| <i>Coffea arabica</i> | 380 | 700 | Tree | Exotic/cultivated | GC | Ramvalho et al. 2018 |
| <i>Coffea arabica</i> | 380 | 760 | Tree | Exotic/cultivated | OTC | Reis, 2015 |
| <i>Coffea arabica</i> | 380 | 700 | Tree | Exotic/cultivated | GC | Rodrigues et al. 2016 |
| <i>Coffea arabica</i> | 400 | 760 | Tree | Exotic/cultivated | OTC | Sanches et al. 2017 |
| <i>Coffea arabica</i> | 380 | 700 | Tree | Exotic/cultivated | GC | Semedo et al. 2021 |
| <i>Coffea canephora</i> | 380 | 700 | Tree | Exotic/cultivated | GC | Martins et al. 2016 |
| <i>Coffea canephora</i> | 380 | 700 | Tree | Exotic/cultivated | GC | Rodrigues et al. 2016 |
| <i>Coffea canephora</i> | 380 | 700 | Tree | Exotic/cultivated | GC | Semedo et al. 2021 |
| <i>Coffea sp.</i> | 390 | 550 | Tree | Exotic/cultivated | FACE | DaMatta et al. 2015 |
| <i>Croton urucurana</i> | 380 | 740 | Tree | Native | OTC | Martinez et al. 2008 |
| <i>Croton urucurana</i> | 380 | 760 | Tree | Native | OTC | Oliveira et al. 2012 |
| <i>Dalbergia nigra</i> | 360 | 720 | Tree | Native | OTC | Godoy, 2007 |
| <i>Enterolobium contortisiliquum</i> | 380 | 700 | Tree | Native | OTC | Melo, 2015 |
| <i>Enterolobium contortisiliquum</i> | 400 | 700 | Tree | Native | OTC | Melo et al. 2018 |
| <i>Eucalyptus sp</i> | 380 | 700 | Tree | Exotic/cultivated | FACE | Fontes, 2017 |
| <i>Eucalyptus sp.</i> | 400 | 760 | Tree | Exotic/cultivated | OTC | Baesso, 2017 |
| <i>Euterpe oleracea</i> | 380 | 760 | Tree | Native/cultivated | OTC | Mortari, 2015 |
| <i>Hymenaea courbaril</i> | 360 | 720 | Tree | Native | OTC | Godoy, 2007 |
| <i>Hymenaea courbaril</i> | 360 | 720 | Tree | Native | OTC | Aidar et al. 2002 |
| <i>Hymenaea courbaril</i> | 360 | 720 | Tree | Native | OTC | Costa, 2004 |
| <i>Hymenaea courbaril</i> | 370 | 720 | Tree | Native | OTC | Machado, 2007 |
| <i>Hymenaea courbaril</i> | 380 | 760 | Tree | Native | OTC | Mayorga, 2010 |
| <i>Hymenaea stigonocarpa</i> | 370 | 720 | Tree | Native | OTC | Machado, 2007 |
| <i>Hymenaea stigonocarpa</i> | 390 | 1000 | Tree | Native | OTC | Maia, 2016 |
| <i>Hymenaea stigonocarpa</i> | 380 | 700 | Tree | Native | OTC | Melo, 2015 |
| <i>Hymenaea stigonocarpa</i> | 430 | 700 | Tree | Native | OTC | Melo, 2020 |
| <i>Hymenaea stigonocarpa</i> | 400 | 700 | Tree | Native | OTC | Souza et al. 2018 |
| <i>Lafoensia pacari</i> | 430 | 700 | Tree | Native | OTC | Souza et al. 2019 |
| <i>Piptadenia gonoacantha</i> | 360 | 720 | Tree | Native | OTC | Godoy, 2007 |
| <i>Psidium guajava</i> | 390 | 780 | Tree | Native/cultivated | OTC | Rezende et al. 2015 |
| <i>Schizolobium parahyba</i> | 360 | 720 | Tree | Native | OTC | Godoy, 2007 |
| <i>Schizolobium parahyba</i> | 360 | 720 | Tree | Native | OTC | Godoy, 2007 |
| <i>Senna alata</i> | 380 | 700 | Tree | Native | OTC | Marabesi, 2007 |
| <i>Senna reticulata</i> | 380 | 760 | Tree | Native | OTC | Arenque-Musa, 2010 |
| <i>Senna reticulata</i> | 380 | 760 | Tree | Native | OTC | Arenque-Musa et al. 2014 |
| Continued | | | | | | |

| Species | aCO ₂ | eCO ₂ | Functional group | Native/exotic/ cultivated | Experiment | Reference |
|------------------------------------|------------------|------------------|------------------|------------------------------|------------|-------------------------|
| <i>Senna reticulata</i> | 400 | 800 | Tree | Native | OTC | Arenque-Musa, 2014 |
| <i>Senna reticulata</i> | 380 | 760 | Tree | Native | OTC | Grandis, 2010 |
| <i>Sesbania virgata</i> | 360 | 720 | Tree | Native | OTC | Godoy, 2007 |
| <i>Sesbania virgata</i> | 360 | 720 | Tree | Native | OTC | Godoy, 2007 |
| <i>Solanum lycocarpum</i> | 400 | 700 | Tree | Exotic/cultivated | OTC | Souza et al. 2018 |
| <i>Stryphnodendron adstringens</i> | 430 | 700 | Tree | Native | OTC | Melo, 2020 |
| <i>Stryphnodendron polyphyllum</i> | 430 | 700 | Tree | Native | OTC | Melo, 2020 |
| <i>Tabebuia aurea</i> | 430 | 700 | Tree | Native | OTC | Melo, 2020 |
| <i>Tabebuia aurea</i> | 400 | 700 | Tree | Native | OTC | Souza et al. 2018 |
| <i>Brachiaria decumbens</i> | 390 | 550 | Herbaceous | Exotic/cultivated | FACE | Abdalla, 2018 |
| <i>Chrysolea obovata</i> | 380 | 760 | Herbaceous | Native | OTC | Oliveira et al. 2016 |
| <i>Glycine max</i> | 360 | 720 | Herbaceous | Exotic/cultivated | OTC | Braga et al. 2006 |
| <i>Glycine max</i> | 360 | 720 | Herbaceous | Exotic/cultivated | OTC | Costa, 2003 |
| <i>Glycine max</i> | 380 | 760 | Herbaceous | Exotic/cultivated | OTC | Kretzschmar, 2007 |
| <i>Glycine max</i> | 380 | 760 | Herbaceous | Exotic/cultivated | OTC | Kretzschmar et al. 2009 |
| <i>Glycine max</i> | 360 | 720 | Herbaceous | Exotic/cultivated | OTC | Lobo, 2003 |
| <i>Melinis minutiflora</i> | 380 | 700 | Herbaceous | Exotic/cultivated | OTC | Melo, 2015 |
| <i>Melinis minutiflora</i> | 350 | 1000 | Herbaceous | Exotic/cultivated | OTC | Oliveira, 2017 |
| <i>Oryza sativa</i> | 400 | 700 | Herbaceous | Exotic/cultivated | OTC | Barbosa, 2019 |
| <i>Oryza sativa</i> | 400 | 700 | Herbaceous | Exotic/cultivated | OTC | Dorneles et al. 2020 |
| <i>Panicum maximum</i> | 390 | 600 | Herbaceous | Exotic/cultivated | FACE | Approbato, 2015 |
| <i>Panicum maximum</i> | 400 | 600 | Herbaceous | Exotic/cultivated | FACE | Bortolin, 2016 |
| <i>Panicum maximum</i> | 400 | 600 | Herbaceous | Exotic/cultivated | FACE | Britto, 2016 |
| <i>Panicum maximum</i> | 400 | 600 | Herbaceous | Exotic/cultivated | FACE | Habermann et al. 2019 |
| <i>Panicum maximum</i> | 400 | 600 | Herbaceous | Exotic/cultivated | FACE | Habermann et al. 2020 |
| <i>Panicum maximum</i> | 385 | 600 | Herbaceous | Exotic/cultivated | FACE | Oliveira et al. 2020 |
| <i>Phaseolus vulgaris</i> | 380 | 700 | Herbaceous | Exotic/cultivated | OTC | Silva, 2010 |
| <i>Saccharum sp.</i> | 370 | 720 | Herbaceous | Exotic/cultivated | OTC | De Souza, 2007 |
| <i>Saccharum sp.</i> | 370 | 720 | Herbaceous | Exotic/cultivated | OTC | De Souza et al. 2008 |
| <i>Saccharum sp.</i> | 390 | 750 | Herbaceous | Exotic/cultivated | OTC | De Souza, 2011 |
| <i>Solanum curtilobum</i> | 360 | 720 | Herbaceous | Exotic/cultivated | OTC | Olivo et. 2002 |
| <i>Solanum lycopersicum</i> | 400 | 750 | Herbaceous | Exotic/cultivated | OTC | Brito, 2016 |
| <i>Solanum lycopersicum</i> | 400 | 750 | Herbaceous | Exotic/cultivated | OTC | Pimenta, 2017 |
| <i>Solanum tuberosum</i> | 360 | 720 | Herbaceous | Exotic/cultivated | OTC | Olivo et. 2002 |
| <i>Stylosanthes capitata</i> | 400 | 600 | Herbaceous | Native | FACE | Habermann et al. 2019 |
| <i>Urochloa brizantha</i> | 360 | 550 | Herbaceous | Native | OTC | Faria et al. 2015 |
| <i>Vernonia herbacea</i> | 380 | 720 | Herbaceous | Native | OTC | Oliveira, 2007 |
| <i>Vernonia herbacea</i> | 380 | 760 | Herbaceous | Native | OTC | Oliveira et al. 2010 |
| <i>Vernonia herbacea</i> | 360 | 760 | Herbaceous | Native | OTC | Oliveira, 2012 |
| <i>Viguiera discolor</i> | 380 | 760 | Herbaceous | Native | OTC | Oliveira et al. 2013 |
| <i>Zea mays</i> | 380 | 700 | Herbaceous | Exotic/cultivated | OTC | Silva, 2010 |

Table 3. Species found in a literature search with plants grown at different CO₂ atmospheric concentrations (ambient CO₂ = aCO₂ and elevated CO₂ = eCO₂), classified according to life habits: Tree and Herbs. OTC Open top chambers, FACE Free Air Carbon Enrichment, and GC Glasshouse, ppm parts per million.

Institution databases into a single information system⁷². The search resulted in a total of 2127 analyzed works in the systematic review (Supplementary Fig. 1). A database was assembled with 68 studies published before October 1st, 2021 (see Table 3; Supplementary Fig. 1). The included works were: (a) studies on Brazilian manipulative experimentation, reporting results from both the treatment groups (eCO₂) and the control groups (ambient CO₂ = aCO₂); (b) studies on trees or herbs; and (c) studies with the mean, sample size, and standard deviation of error of the selected variables. The data from articles were grouped as trees and herbs on 28 and 16 species, respectively (Table 3). The collected data were extracted in three theoretical categories: growth (biomass), biochemical (total soluble sugars, starch, and proteins), and photosynthesis-related parameters [net CO₂ assimilation (*A*), stomatal conductance (*g_s*), transpiration foliar (*E*), water use efficiency (*WUE*), dark respiration (*R_d*), intercellular/ambient CO₂ ratio (*C_i/C_a*), the potential quantum efficiency of PSII (*F_v/F_m*), total chlorophyll content (*Chl*), maximum carboxylation rate (*V_{c,max}*), and maximum rate of electron transport (*J_{max}*)]. The biomass

data were collected from total biomass or biomass per plant organ. Each biomass result per organ was considered a biomass observation. Each soluble sugar (glucose, fructose, sucrose, raffinose, and myoinositol) was considered an observation for the biochemical category. A dataset contemplated a total of 437 observations. In general, the duration of the studies was 90 days. The average high CO₂ concentration was from ~400 to ~800 ppm. Fifty studies were performed in Open Top Chambers (OTC), 13 in Free Air CO₂ Enrichment (FACE), and 7 in Glasshouse (GC). The most frequently studied species among trees was *Coffea arabica*, with 12 different studies. On the other hand, among herbs was *Panicum maximum* with six different studies. Fourteen variables were analyzed [*A*, *gs*, *E*, *WUE*, *Rd*, *Ci/Ca*, *biomass*, *total soluble sugars*, *starch*, *proteins*, *Fv/Fm*, *total Chl*, *V_{cmax}*, *J_{max}*] (Fig. 5). The most frequent variables were biomass (79), with 46 observations for trees and 33 for herbs (Fig. 5). From the total species analyzed, 30% represent cultivated ones. Among the trees, 21% are cultivated, and 79% are native species. Among herbs, 33% are native, and 67% are cultivated. The experiments were considered unstressed unless the author had identified some stress factor. In the case of stress treatments, data from the control treatments were used. Most of the works had an average duration of experimentation of 90 days. The plants were grown in pots. Plants that received fertilizer treatment were not included in this analysis. The plants were watered regularly and exposed to natural light.

Observations of each study at the end of the experiment were grouped, and there was no categorization by experiment period. There was also the group for the elevated CO₂ levels of the different studies. Curtis and Wang¹³ examines each subgroup for categorical divisions such as pot size and exposure time. However, a meta-analysis by these authors did not find significant differences among the groups by pot size and experiment time. This is an example that, throughout all studies, suggests significant differences in the response of plants under the CO₂ environment and, however, not among those grown in different pot sizes or experiment duration.

Mean values, standard deviation/error, and sample size under eCO₂ and aCO₂ were collected for each observation. WebPlotDigitizer v4.1⁷³ was used to obtain the numerical data from the figures. For works that showed only the standard error value, the following equation was used: (SD = SE × √n) (n is the sample size, SE is the standard error, and SD is the standard deviation)⁷⁴. Data from temporal experiments were considered only the last harvest to represent the maximum exposure of these plants to eCO₂ cultivation.

Meta-analysis. Meta-analysis assessed plant responses to eCO₂ in growth, biochemical composition, and photosynthesis categories. To evaluate the relative changes of these responses between treatment (eCO₂) versus control (aCO₂), it was applied the logarithmic response ratio ln (RR), calculated as the size effect, where \bar{X}_t is the mean of the experimental/treatment group, and \bar{X}_c is the mean of the control group⁶⁸. The natural log of the response ratio (lnRR = \bar{X}_t/\bar{X}_c) was used and is reported as the mean percentage change [(lnRR - 1) × 100]⁷⁵. Values of lnRR higher than zero indicate that the eCO₂ effect increases, while negative values indicate that the eCO₂ effect decreases concerning aCO₂. A hierarchical mixed-effects model was used to estimate the mean and 95% confidence interval (CI) of the lnRR for each type of response variable. If the 95% CI of a response variable overlaps zero, the lnRR of the treatment is not significantly different from the control⁷⁶. The effect was reported as a percentage change from the control: ((e^{lnRR} - 1) × 100). In addition, life habits were used as a fixed predictor variable while the study and species were considered random variables to control for the lack of independence of observations from the same study or/and carried out with the same plant species^{77,78}. Furthermore, heterogeneity (I²) was tested to verify the variation in results between studies^{77,79}. The Egger regression test was used to identify publication bias^{80,81}. Bias analyses for the multilevel models were conducted with meta-analytic residuals⁷⁷. Analyses were performed using the package "metafor"⁸², and the graphics were generated using the package "ggplot2"⁷⁸, both in R version program 3.6.0⁸³.

Data availability

All data generated or analyzed during this study are included in this published article as supplementary information file (excel) named "Supplementary Table 2".

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Author contributions

J.S.F., A.G., C.T.C., and M.S.B. conceived the study. J.S.F., D.P., and A.G. collected the data and conducted statistical analysis. All authors participated in the writing. M.S.B. consolidated writing and produced the final version of the manuscript.

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Competing interests

The authors declare no competing interests.

Additional information

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