

A systematic review of the effects of elevated CO₂ concentration on the growth of selected tropical trees

John Karlo C. Saddoy^{1*}

¹Department of Forest Biological Sciences, College of Forestry and Natural Resources, University of the Philippines Los Baños, College, Laguna, Philippines

ABSTRACT. The elevated CO₂ concentration causes drastic changes in the world's climatic conditions, affecting the growth and development of plants in their natural settings. Hence, scientists have been exploring this field to understand better the current trend of plant responses toward the intervention of elevated CO₂, and this systematic review created a generalized body of knowledge. The 27 out of 3,568 articles that passed the final selection process were selected and evaluated following the inclusion or exclusion Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines. The Population-Intervention-Comparison-Outcome (PICO) model was used to create Boolean search strings for the ScienceDirect and Scopus databases to find these included articles and Google Scholar for manual searching. These articles were downloaded as BibTeX and organized on Mendeley (version 1.19.8). The QGIS (version 3.16.15) was used to create the world map, and RStudio (version 4.2.2) was also used to visualize the descriptive statistics. The results showed that India (9 articles) has the highest number of reviewed articles, followed by the Republic of Panama and Brazil (4 articles each), Malaysia (3 articles), China and England (2 articles each), and Portugal, Australia, and Borneo (1 article each). Twenty-four articles had a controlled methodological approach, while three had an observational approach. The reviewed articles revealed that the elevated CO₂ affected the biomass (aboveground, belowground, dry, and total plant biomass) production, morphological (leaf characteristics, root characteristics, number of branches, stomatal characteristics, plant height, and stem diameter), and physiological (photosynthetic rates, transpiration rates, water use efficiency, stomatal conductance, intercellular CO₂ concentration, chlorophyll content, and biochemical activity) response of the tropical trees. Hence, it is justified that there are tropical tree species that can and cannot survive the worsening climate change.

Keywords: Review article, PRISMA protocol, Boolean search string, Climate change

Article Information

Received 19 January 2023

Accepted 26 May 2023

Published online 16 October 2023

*Email: jcsaddoy@up.edu.ph

INTRODUCTION

For over three decades, the world has been struggling against the adverse impacts of climate change, especially in tropical regions (Tang, 2019). Global warming is one of its effects, as scientists predicted a sudden increase in temperature by 2-5°C in 2100 (IPCC, 2013). Anthropogenic activities concerning greenhouse gas emissions (CO₂, N₂O, and CH₄) are the leading factor of global warming, associated with burning fossil fuels in developed countries such as China, the United States of America, and parts of Europe (Lacis *et al.*, 2013; Corlett, 2018). Specifically, the latest data on the CO₂ concentration in the atmosphere as of March 2021 has risen to 417 M ppm, considered the highest data for the past

800,000 years (Lindsey, 2007; Betts, 2021). Seeing this trend, it is interesting to determine how plants respond morphologically and physiologically to this emerging problem.

From the start of the 21st century, several scientific papers revealed that elevated CO₂ improves plant growth, leaf area, water use efficiency, and photosynthesis (Lovelock *et al.*, 1999; Khurana & Singh, 2001; Leakey *et al.*, 2002). After a decade, this topic has gained much attention as published studies have been emerging to broaden the understanding of the effects of elevated CO₂ concentration on plant growth, development, and other physiological activities (Janani *et al.*, 2016;

Singh *et al.*, 2019). Recent literature concluded that the rising atmospheric CO₂ also increased the production of biomass, leaf-level productivity, water efficiency, and plant C/N uptake (Needham *et al.*, 2020; Avila *et al.*, 2020; Rai *et al.*, 2020; Reichgelt *et al.*, 2020). Thus, both past and present literature show that the elevated CO₂ concentration has a significant relationship with plant growth, making it still relevant today.

However, there were studies in the same field that revealed alternative results. They found that elevated CO₂ did not significantly correlate with root growth, photosynthates, photosynthetic rates, plant height, and the number of leaves (Warrier *et al.*, 2013; Musa *et al.*, 2017; Tietze *et al.*, 2019). Thus, it is also a manifested notion that there is still needs to be a more specific understanding of this field of study. There are also limited reviews regarding the effects of the elevated CO₂ concentration on the growth of selected tropical trees, especially from 2010 to 2021, when drastic changes in CO₂ concentration in the atmosphere were observed (Betts, 2021). Most of the published meta-analyses about elevated CO₂ included other environmental factors, such as water stress and temperature, and discussed the broader scope of forest ecophysiology (Curtis & Wang, 1998; Kallarackal & Roby, 2012; Wang *et al.*, 2012; Cernusak *et al.*, 2013). Thus, it is necessary to have a comprehensive review of published papers concerning the topic at a finer scale, which can be used to distinguish the research gaps for future research.

The use of the Population-Intervention-Comparison-Outcome (PICO) model leads to credible and clarified answers because it shows the logical pathways of action needed, which helps the researchers to visualize the experiments conducted for the benefit of the population (Miller & Forrest, 2001; Booth *et al.*, 2019; Skivington *et al.*, 2021). This systematic review aids in the creation of the Boolean strings to target the needed articles for the results. On the other hand, the PRISMA protocol is used to understand the necessity for the review, reporting the findings of various authors and the results they achieved (Page *et al.*, 2021). Hence, applying the PRISMA protocol, the PICO model, and the Boolean search string to other fields

of science, especially forestry, aside from medical science, creates an opportunity to conduct more systematic reviews and a firm understanding of various topics.

This study aims to summarize through a systematic review the effects of the elevated CO₂ concentration on the growth of selected tropical trees within the 2010-2021 period in which drastic changes in the climate have been recorded. This study will also discuss the relationship between the elevated CO₂ concentration and the growth of tropical trees; distinguish the research gaps, especially in the Philippine context; and develop recommendations for the future progress of the research field.

METHODOLOGY

Research question

This systematic review addressed the primary question: "What are the effects of the elevated CO₂ concentration on the biomass, morphological growth, and physiological response of the selected tropical trees?" Adapting the protocol for an environmental PICO model in a systematic review of Livoreil *et al.* (2017), the research question was formulated as shown in **Table 1**.

Table 1. The research question of the systematic review using PICO.

Definitio	Description of the study
Population	Selected tropical trees
Intervention	Elevated CO ₂ concentration
Comparison	Control/No treatment
Outcome	Effects on the biomass, morphological growth, and physiological response of the tropical trees
Question	What are the effects of the elevated CO ₂ concentration on the biomass, morphological growth, and physiological response of the selected tropical trees?

Eligibility criteria

This systematic review was embedded in the PRISMA protocol based on Page *et al.* (2021). The final set of research articles included in this review was based on Figure 1 concerning the inclusion or exclusion criteria. The title-abstract-keyword advanced search strategy was utilized to identify the relevant research articles for the systematic review, implying that the match words should be in the pool of keywords in the search string. The research articles were the only document type needed for this systematic review. Other document types, such as conference papers, reviews, book chapters, books, notes, editorials, short surveys, and erratum were excluded. The publication period was from 2010 to 2021. The preferred language for article selection was English. In the ScienceDirect database (<https://www.sciencedirect.com/>), the included research articles were found in the open access and open archive, and the subject area should be 'environmental science.' Other subject areas unrelated to forestry or any field of environmental science were excluded as these may cause misleading results that lead to inappropriate conclusions.

Secondly, titles and abstracts of the compiled set of articles were further screened. The title must be compatible with the inclusion/exclusion criteria, with the relevant keywords used in the search query. Each research article is different because of the title and publication year. Otherwise, such research papers were excluded. In this stage, abstract screening was necessary to verify and validate the credibility of the remaining research articles. The article was only included if the abstract was relevant to the research question and the criteria presented below.

If the abstract clearly presents the methodology and result of the study, the last part of the screening process will push through. The full-text screening strategy was implemented for all the remaining research articles to examine the credibility of the methodology, and their presented results were inclined with the criteria and research question. Moreover, the screened research articles were derived from the ScienceDirect database under open access for full-text screening and in the

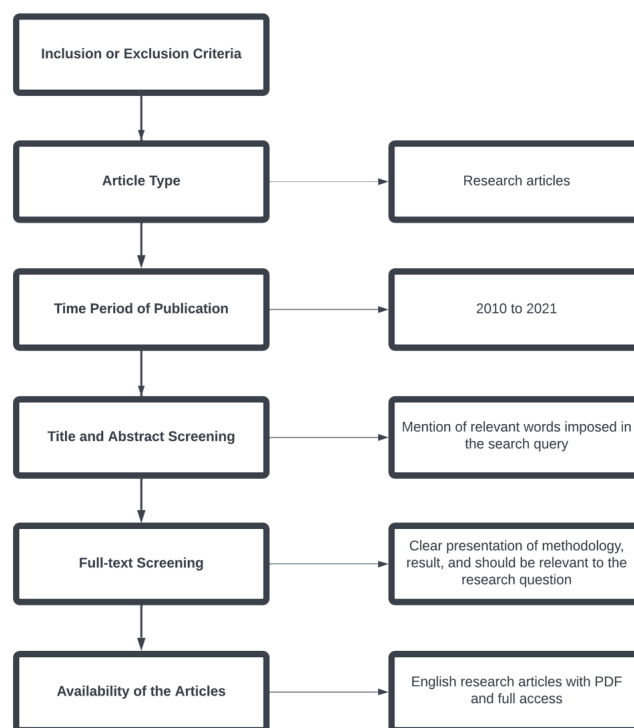


Figure 1. The inclusion or exclusion criteria based on the PRISMA protocol in Page *et al.* (2021).

Scopus database. They were exported to Mendeley (version 1.19.8) for proper organization. If the screened research articles were unavailable in the database, manual searching in any search engine, such as Google, was used to access the PDF file of the article.

Search strategy and selection process

The primary method for finding research articles needed for this systematic review was using Boolean operators and their principles based on Aliyu (2017). These search strings were anchored in the PICO model. In the search strings, the use of AND, OR, and quotation marks (") in the advanced search bar in the research database were maximized to target the research article directly for this systematic review. To address the limitation of ScienceDirect when using a Boolean search string, **Table 2** presents five (5) Boolean search strings to cover all the necessary research articles for this systematic review. In addition, the Scopus database has no restrictions for the Boolean connectors per field. Lastly, **Figure 2** summarizes the five-step procedure for finding the final articles to be reviewed for selection.

Table 2. The research question of the systematic review using PICO.

Number	Search string
1	"Elevated CO ₂ " OR "Increased CO ₂ " OR "CO ₂ enrichment" OR "atmospheric CO ₂ " AND "ppm" AND "Growth response" OR "Growth" AND "Tropical Forest Tree" OR "Tropical Tree"
2	"Elevated atmospheric CO ₂ " OR "Increased CO ₂ " OR "CO ₂ enrichment" AND "Morphology" OR "Morphological response" OR "Morphological parameters" AND "Tropical Forest Tree" OR "Tropical Tree"
3	"Elevated atmospheric CO ₂ " OR "Increased CO ₂ " OR "CO ₂ enrichment" AND "ppm" AND "Physiology" OR "Physiological response" OR "Physiological parameters" AND "Tropical Forest Tree" OR "Tropical Tree"
4	"Elevated atmospheric CO ₂ " OR "CO ₂ enrichment" OR "Increased Air CO ₂ " AND "Plant height" OR "Root length" OR "Plant biomass" OR "Leaf length" AND "Tropical Tree" OR "Tropical Forest Tree"
5	"Elevated atmospheric CO ₂ " OR "CO ₂ enrichment" OR "Increased Air CO ₂ " AND "Photosynthesis" OR "Transpiration" OR "Stomatal Conductance" OR "Respiration" AND "Tropical Tree" OR "Tropical Forest Tree"

Data collection

The information sources of this systematic review included ScienceDirect and Scopus. The required articles for this systematic review were scanned and reviewed using the eligibility criteria in **Figure 1** and the selection process in **Figure 2**. The BibTeX file exported the articles from each Boolean search string. The downloaded BibTeX files will be uploaded to Mendeley (version 1.19.8) because it has a built-up mechanism to eliminate identical research papers. A manual search of relevant articles using a Boolean search string was done in ScienceDirect and Scopus (**Table 3**). **Figure 3** summarizes the combination of the mentioned databases and manual searching using Google Scholar, following the method by Hernandez *et al.* (2020) called chain searching. As mentioned in the eligibility criteria, other papers except research articles were excluded even in chain searching to ensure the consistency of the data. Hence, grey literature from the government, intergovernmental agencies, and non-governmental organizations was also excluded.

Data categorization

Articles were categorized based on the treatments of CO₂ being applied to the selected tropical tree species. The first category focused on ambient and elevated CO₂ concentrations. The 27 articles had different ranges of ambient levels of CO₂ by which a certain CO₂ level could be an ambient level in one study but could also be elevated in another study. Thus, using ambient (300–532 ppm) and elevated CO₂ (460–910 ppm) in this systematic review is justifiable. The experiment duration is another category knowing that the exposure

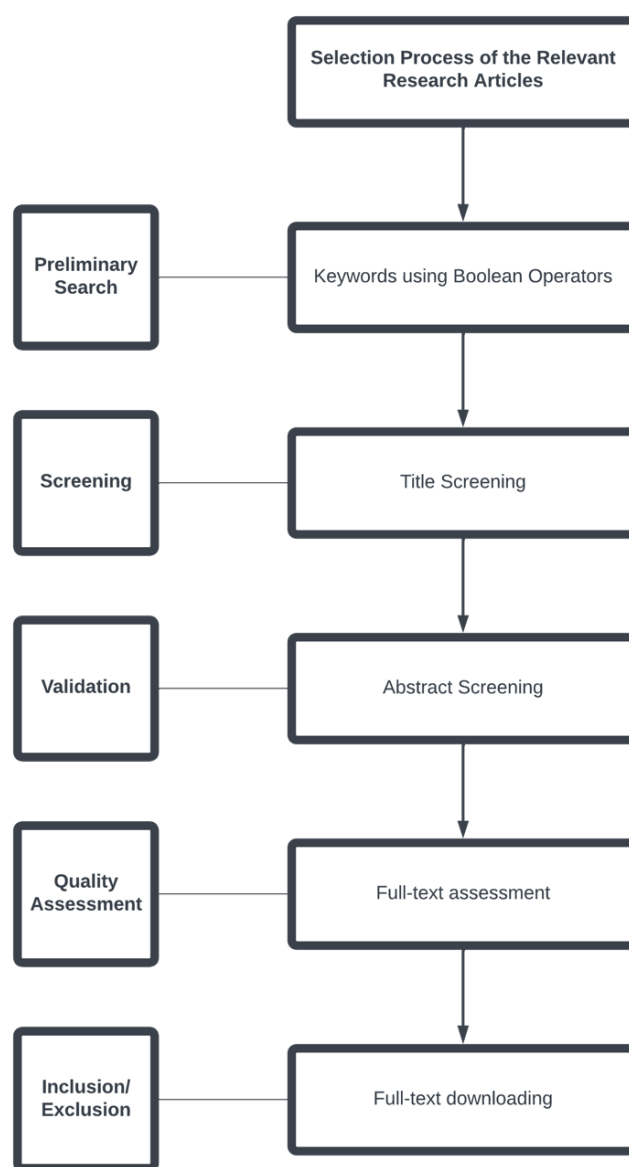
**Figure 2.** Step-by-step procedure of selection process based on PRISMA.

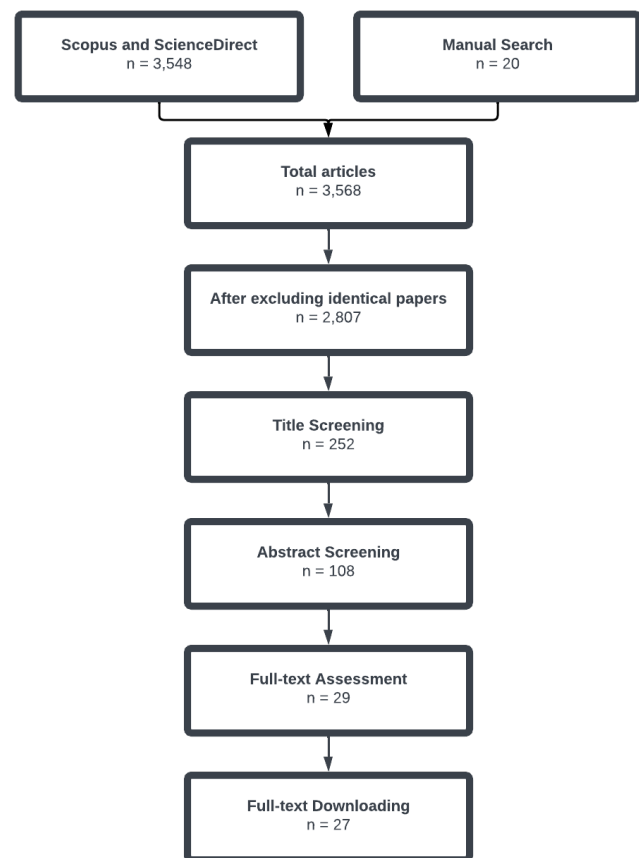
Table 3. The number of articles emerged using the search strings.

No.	Search string	No. of articles		Total
		ScienceDirect	Scopus	
1	"Elevated CO ₂ " OR "Increased CO ₂ " OR "CO ₂ enrichment" OR "atmospheric CO ₂ " AND "ppm" AND "Growth response" OR "Growth" AND "Tropical Forest Tree" OR "Tropical Tree"	175	15	190
2	"Elevated atmospheric CO ₂ " OR "Increased CO ₂ " OR "CO ₂ enrichment" AND "Morphology" OR "Morphological response" OR "Morphological parameters" AND "Tropical Forest Tree" OR "Tropical Tree"	182	9	191
3	"Elevated atmospheric CO ₂ " OR "Increased CO ₂ " OR "CO ₂ enrichment" AND "ppm" AND "Physiology" OR "Physiological response" OR "Physiological parameters" AND "Tropical Forest Tree" OR "Tropical Tree"	749	6	755
4	"Elevated atmospheric CO ₂ " OR "CO ₂ enrichment" OR "Increased Air CO ₂ " AND "Plant height" OR "Root length" OR "Plant biomass" OR "Leaf length" AND "Tropical Tree" OR "Tropical Forest Tree"	1,125	12	1,137
5	"Elevated atmospheric CO ₂ " OR "CO ₂ enrichment" OR "Increased Air CO ₂ " AND "Photosynthesis" OR "Transpiration" OR "Stomatal Conductance" OR "Respiration" AND "Tropical Tree" OR "Tropical Forest Tree"	1,230	45	1,275
TOTAL				3,548

duration of plants to elevated CO₂ can produce different results (Mndela *et al.*, 2022). Studies done in less than a year were considered short-term exposure, whereas those done in more than a year were regarded as long-term exposure. The articles were further divided into two subcategories based on their methodological approach: observational and controlled experiments. The observational approach included studies in the natural environment where elevated CO₂ exists. The controlled approach included studies highlighting a greenhouse, glasshouse, laboratory, or aided equipment to elevate the CO₂ within the area.

Data analysis and presentation

Microsoft Excel was used to organize the collected data for this systematic review. RStudio (version 4.2.2) was also utilized to visualize the descriptive statistics (*i.e.*, mean, range, counts, and percentages) for the identified categories and subcategories to homogenize the data. Multiple spell checks were done for each input under every category to minimize the doubling counting and error. Percentages were identified in terms of the number of chosen articles or the number of articles associated with each category and subcategory. Map layout was done in QGIS 3.16.15 software to plot the distribution of the reviewed research article.

**Figure 3.** Flow diagram of the result of the screening processes.

RESULTS

Study characteristics and approaches

Applying the inclusion or exclusion criteria based on the PRISMA protocol, 761 out of 3,568 were found as identical research articles. Titles of the articles were then examined, wherein only 108 remained after the screening. Then, 29 articles were retained after assessing abstracts (*i.e.*, a proper account of methodology and results). Only 27 articles were subject to data homogenization and analysis, as two were outside the open access or archive category.

Fifteen of 27 articles were published in Asia (India, China, Borneo, and Malaysia), as shown in **Figure 4**. Published papers in Portugal, England, and Australia used tropical species, making them relevant to this review. Specifically, India has the highest number of reviewed studies, followed by Brazil and the Republic of Panama (**Figure 5**). Conversely, the countries with the least reviewed studies were Portugal, Borneo, and

Australia. Interestingly, no research papers were found from the Philippines and other developing countries in Southeast Asia. Twenty-four articles that passed the final selection process had a controlled methodology wherein the tropical tree species were exposed to the manipulated CO₂ concentration using chambers, glasshouses, and greenhouses. Three articles followed observational methodology; hence, these studies used Free-Air CO₂ Enrichment (FACE) method, where plants were exposed to elevated CO₂ in their natural settings. Replications were done in every study to ensure the credibility of the results.

In the case of the publication year of reviewed articles, 2021 had the highest number of published articles (6), followed by 2013 and 2019 (4; **Figure 6**). No published papers were included in 2010, 2012, 2017, and 2020 as reviewed articles in these years were focused on weeds, crops, and ornamental plants in temperate regions.

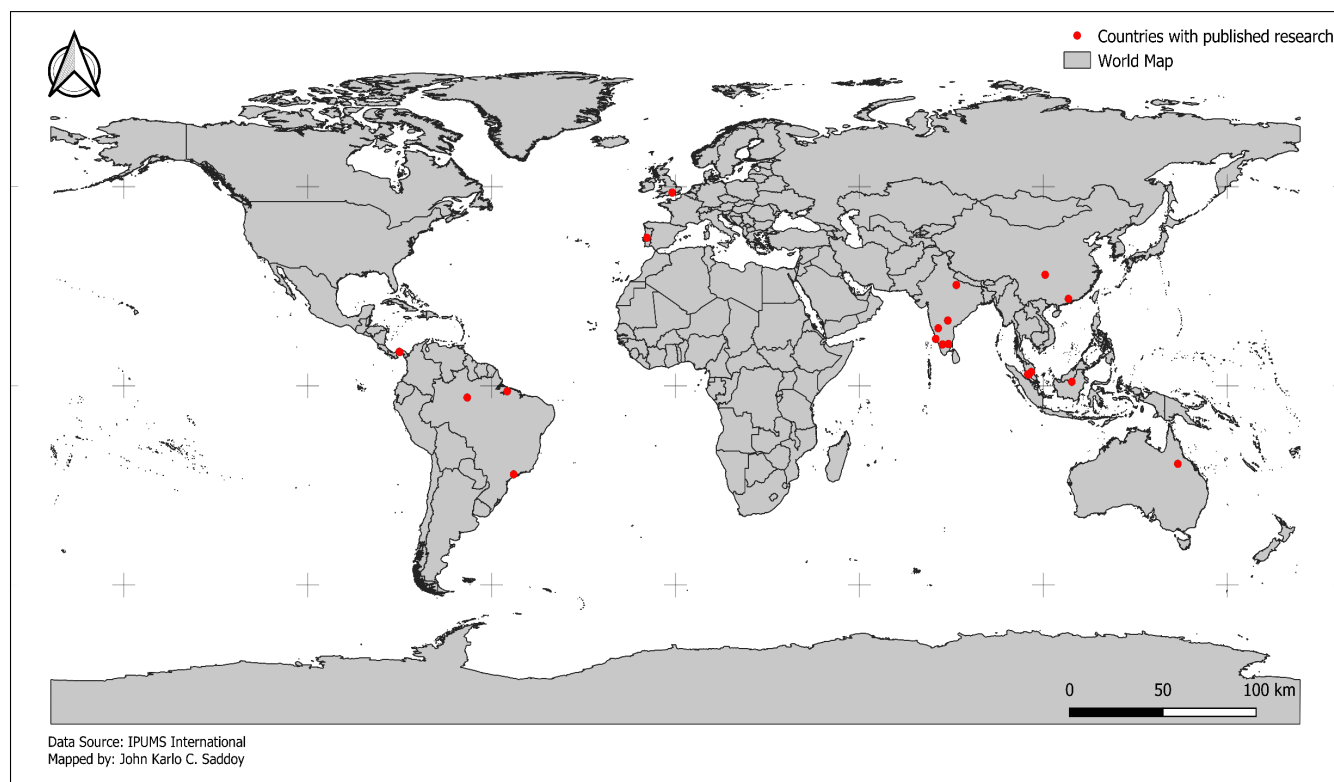


Figure 4. Geographical map distribution of the studies about the effects of elevated CO₂ on the growth of tropical trees with the bar plot of study approaches.

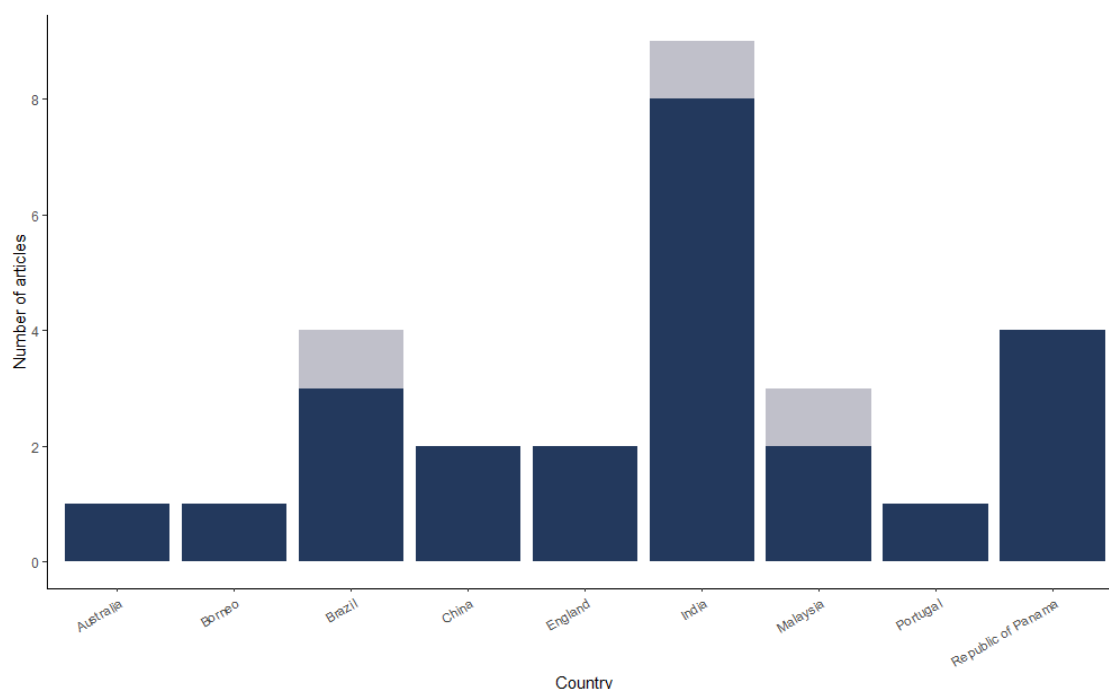


Figure 5. The number of articles per country and their corresponding methodological approaches.

Study duration

The mean and mode of the study duration among reviewed articles are 5.43 months and 3 months, respectively. Study duration ranged from 1 month to 60 months. Twenty out of 27 articles employed short-term exposure to the elevated CO₂ on the growth of the tropical tree species (**Figure 7**).

Life stages of the species used in the study

The species mentioned in the reviewed articles were categorized into seedlings, saplings, and trees (**Figure 8**). While five studies did not state the specific life stages of plants, the age, diameter, and height were nonetheless described, which allowed further categorization. About 59.26% of the total reviewed papers used seedlings in their study, 29.63% of papers used saplings, and the mature trees were the least life stages of the species used with 11.11%.

Biological parameters for analyses

The biomass (aboveground and belowground biomass, dry biomass, and total plant biomass), morphological characteristics, and physiological response were included to analyze the overall growth of study species (**Table 4**). Morphological parameters were leaf characteristics (leaf area,

leaf number, N and P leaf concentration), root characteristics (root weight and root length), number of branches, stomatal characteristics (stomatal density and stomatal size), plant height, and plant diameter. Physiological parameters included photosynthetic rates, transpiration rates, water use efficiency, stomatal conductance, intercellular CO₂ concentration, chlorophyll content, and biochemical activity (Rubisco activity and photosynthetic enzymes activity).

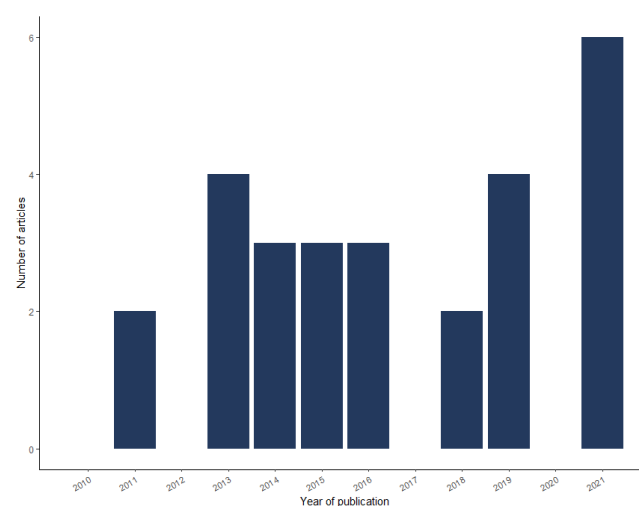


Figure 6. The number of articles per year of publication.

DISCUSSION

Positive response of the forest tree species under elevated CO₂

Increased production

Generally, the trend of biomass is directly related to the trend of CO₂ concentration. Warriar *et al.* (2013) agreed that the increased root biomass over low shoot biomass accounted for better adaptability of the species to the CO₂ concentration, while the increased shoot biomass is associated with the overall growth pattern of the species. The increased aerial and total plant biomass justified the narrative that *Gmelina arborea* Roxb. can accumulate more carbon (Rasineni & Reddy, 2013; Rasineni *et al.*, 2013). The increasing biomass trend in the tropical tree species used by Yan *et al.* (2014) was due to the increased mean annual net primary production. The increased leaf and root biomass were explained by the high physiological plasticity, which can adapt to various environments and has a greater capability for starch storage because of the utilization of transitory starch accumulation as a mechanism for carbon sink (Arenque *et al.*, 2014). This trend could be accounted for by the development of new carbon sinks in the plant system that can also explain the increasing morphological features of the plants and better utilization of photosynthates, which was revealed in the study of Sekhar *et al.*

(2015). Hence, the species they used also had high morphological plasticity by which they could adjust to the new challenges offered by the environment. Other notable species with increased biomass production under the influence of elevated CO₂ were presented in Table 5.

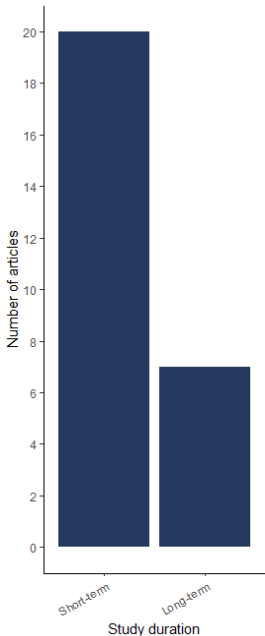


Figure 7. The number of articles per country and their corresponding methodological approaches.

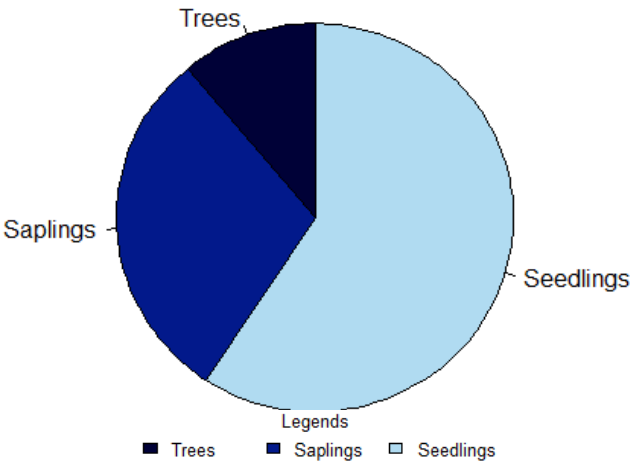


Figure 8. Life stages of the species used in the study.

Table 4. Growth parameters used in the study.

Biomass	Morphological parameter	Physiological parameter
Aboveground biomass	Leaf characteristics	Photosynthetic rates
Belowground biomass	Root characteristics	Transpiration rates
Dry biomass	Number of branches	Water use efficiency
Total plant biomass	Stomatal characteristics	Stomatal conductance
	Plant height	Intercellular CO ₂ concentration
	Stem diameter	Chlorophyll content
		Biochemical activity

Increased morphological growth

Increased leaf area increased carboxylation efficiency using phosphoglyceric acid as the indicator and increased CO₂ assimilation (Bassham, 2003; Lamani *et al.*, 2016). Vogado *et al.* (2022) reported that the increased leaf area had a log-linear relationship with chlorophyll content and water-use efficiency. Conversely, the leaf number had increased under elevated CO₂ in the species presented in Table 5. These phenomena were due to species' expanding carbon sink and utilization of photosynthesis products, an adaptive mechanism for maximizing photosynthetic ability, increasing starch storage, and fresh and dry aboveground biomass production (Farquhar & Sharkey, 1982; Kumar *et al.*, 2014; Sekhar *et al.*,

2015; Lahive *et al.*, 2018). Meanwhile, the increased root length under elevated CO₂ was attributed to root biomass increment connected with the better biomass allocation in the root system and the increasing soluble sugars, photosynthetic rates, and non-structural carbohydrates (Dickson *et al.*, 1998; Zak *et al.*, 2000; Janani *et al.*, 2016).

Most results claimed that plant height is directly related to elevated CO₂. The list of species presented in **Table 5** with a positive response in plant height had increased biomass and biomass allocation to the root and shoot system (Zhu *et al.*, 2016; Janani *et al.*, 2016; Lamani *et al.*, 2016; Shi *et al.*, 2021). Other authors hypothesized that the increased plant height was linked with better photosynthates utilization, increased phenolic substances, transpiration rates, and soluble sugar concentration (Onoda *et al.*, 2009; Ghasemzadeh *et al.*, 2010; Ghasemzadeh & Jaafar, 2011; Kumar *et al.*, 2014; Ghini *et al.*, 2015). Rasineni *et al.* (2013) claimed that an increase in plant height resulted in the sink's increased size, which further implied a new potential creation of the sink for carbohydrates and photosynthates allocation. Moreover, stem diameter also increased under the influence of elevated CO₂ (Musa *et al.*, 2016), but they argued it was explained by the heterogeneity of the species used.

Species with notable stomatal responses are presented in **Table 5**. It was found that stomatal conductance has a direct relationship with stomatal density because stomatal size and density are considered the baseline of maximum stomatal conductance (Ramalho *et al.*, 2013; Lahive *et al.*, 2018). The increased stomatal density could be an evolution to withstand the humid understory of tropical rainforests where water deficit is evident (Lahive *et al.*, 2018).

Increased physiological response

The photosynthetic rate also generally improved under elevated CO₂. For example, *Acacia mangium* Willd. can adapt to a higher temperature, a higher concentration of CO₂, and higher light intensity due to their adaptive mechanism of photosystem II and the balance between RuBP carboxylation and regeneration, which are dependent on the

photosynthetic processes (Yu & Ong, 2002; Hikosaka *et al.*, 2016; Lee *et al.*, 2019; Ibrahim *et al.*, 2021). This increasing photosynthetic rate may be likely due to the genotypic variations in RuBP carboxylation and the competitive inhibition of oxygenation that improved the Rubisco efficiency (Farquhar & Sharkey, 1982; Liberloo *et al.*, 2007; Darbah *et al.*, 2010). A direct relationship was found between photosynthesis and transpiration, stomatal conductance, and water available for the plant, as mentioned by Lion *et al.* (2019) and De Oliveira & Marengo (2019). The trend can also be explained by knowing that mature leaves of the species have a completely functionally developed organ that can allocate nitrogen resources compared with the younger leaves (Vogado *et al.*, 2021). The changes in the photosynthetic trend in the tropical tree species were due to the additional carbon and the assimilated carbon over the plant's ability to create sinks; hence, the species' response to elevated CO₂ would be to create a new carbon sink (Amthor, 1995; Ceulemans *et al.*, 1999).

Increased transpiration can imply that they could adapt based on water availability and regulate their water potential (Rouhi *et al.*, 2007; Camposeo *et al.*, 2011). This increasing trend can also be directly associated with water vapor pressure and stomatal conductance (Lion *et al.*, 2019). However, an increased transpiration rate under elevated CO₂ can be stressful for the plants knowing that they are losing too much water in their system. Hence, the general response of the plants in this systematic review is inverse because they have an adaptive mechanism for controlling water resources. In the case of water-use efficiency, most species mentioned in the 27 articles, as presented in **Table 5**, highlight that this physiological parameter exhibited an increasing trend under elevated CO₂. The water-use efficiency has an inverse relationship with transpiration and stomatal conductance because those species have a better water conservation mechanism to survive the environmental stress and better carbon assimilation (Amthor, 1995; Ainsworth & Rogers, 2007; Shi *et al.*, 2021). Lahive *et al.* (2018) & Hebbar *et al.* (2020) argued that this increase is attributable to enhanced biomass production rather than lesser water loss by reduced stomatal opening.

Interestingly, the increased water-use efficiency in some trees like *Theobroma cacao* L. did not automatically mean it can tolerate drought stress, specifically when the water is not lost through leaf pathways; hence, not all species with increased water-use efficiency have an adaptive mechanism to drought stress corresponding to the trend among the water-use efficiency, transpiration, and stomatal conductance (Lahive *et al.*, 2018).

Species with positive stomatal conductance response showed adaptive and stable mechanisms to withstand the stress brought by the increasing CO₂ concentration (Lamani *et al.*, 2016). Vu (2005) and Darke *et al.* (1997) mentioned that the changes in stomatal conductance were caused by the indirect effects of CO₂ rather than the direct effect on stomatal aperture, promoting reduced transpiration, improved water use efficiency, and status of tissue water. On the other hand, most species mentioned with intercellular CO₂ concentration as growth parameters showed a positive response. These changes in intercellular CO₂ concentration were associated with the downregulation of photosynthetic rates and sink capacity of photosynthetic products (Flexas *et al.*, 2008; Bader *et al.*, 2010). The trend of intercellular CO₂ concentration is the basis of mesophyll efficiency and net assimilation rates (Sheshshayee *et al.*, 1996; Ogren, 2003). Hence, it was proven that intercellular CO₂ concentration increases as the photosynthetic rate increases (Ramalho *et al.*, 2013; Sekhar *et al.*, 2015). Lastly, an increased Rubisco also increased intercellular CO₂ concentration and carbonic anhydrase activity (Rasineni & Reddy, 2013). The increased trends of RuBisCo and Ru5PK enzymes hint at the potential biochemical capacity reinforcement for the respiration and photosynthetic processes of the species (Ramalho *et al.*, 2013). Hence, the physiological processes in plants affect the trend of biochemical activity.

Negative response of the forest tree species under elevated CO₂

Decreased biomass and morphological growth

Considerably, there were alternative results, given that most trends showed otherwise in the 27 articles. When plants have decreased in height, most of the allocated resources were accumulated

in the leaf area of the species (Warrier *et al.*, 2013). Hence, the inverse trend was associated with decreased photosynthetic rates, low carbon fixation, the inability to stimulate greater carbon sinks associated with biomass, and the alteration in the photosynthate distribution in the plant system (Bhatt *et al.*, 2010; Prior *et al.*, 2011). Whereas in some cases, the reduced leaf area and number of leaves under elevated CO₂ was due to the decreasing aboveground biomass simulation and photosynthetic rate as well as the inability to stimulate greater carbon sinks (Rasineni *et al.*, 2013; Musa *et al.*, 2021).

In the reviewed articles, a negative correlation between leaf N/P concentration and leaf biomass production was due to the high accumulation of carbohydrates that led to the dilution of leaf nutrient concentration, reduced resources available for the plant, and reduced allocation of N to Rubisco during photosynthesis (Sakai *et al.*, 2006; Shi *et al.*, 2021). The delayed greening of plants under elevated CO₂ was related to the decreased trend of leaf N content resulting in low nutritional value in the plant system and underdeveloped photosynthetic apparatus (Vogado *et al.*, 2021; Kursar & Coley, 2003). Some species with reduced leaf N content are also presented in **Table 5**. In the case of branch numbers, the reduction in branches stimulated the apical dominance promoting jorquetting in trees (Hebbar *et al.*, 2020). Hence, in general, the reduction of morphological characteristics of the plants was attributed to reduced biomass production and physiological processes such as photosynthesis, transpiration, and respiration, among others.

Decreased physiological response

Concerning the physiological parameters, the reduced photosynthetic rate per total leaf area was elaborated by the fact that the plant growth was not maintained in the long run because exposure to elevated CO₂ can require losses in carbon assimilation (Korner & Miglietta, 1994; Arenque, 2014). In another case, the low pot space accounted for low nutrient uptake resulting in the reduced movement of photosynthetic products to the root system of their study species (Shi *et al.*, 2021).

Table 5. Summary table of the species' response to elevated CO₂ as mentioned in the 27 articles.

Tree species	Positive response	Negative response	No response	Reference
<i>Tectona grandis</i> Linn. F., (Lamiaceae)	RB; RL; TPB; PR; ICC	H		Warrier <i>et al.</i> (2013); Raj <i>et al.</i> (2014)
<i>Ailanthus excelsa</i> Roxb. (Simaroubaceae)	SB; RL; TR	CC		
<i>Casuarina equisetifolia</i> L. (Casuarinaceae)	SB		RL	Warrier <i>et al.</i> (2013)
<i>Gmelina arborea</i> Roxb. (Lamiaceae)	TPB; NB; H; SDi; RW; ICC; RA	TR		Rasineni & Reddy 2013; Rasineni <i>et al.</i> 2013)
<i>Schima superba</i> Gardn. & Champ. (Theaceae); <i>Syzygium hancei</i> Merr. & Perry (Myrtaceae); <i>Ormosia pinnata</i> (Lour.) Merr. (Fabaceae); <i>Castanopsis hystrix</i> J. D. Hooker & Thomson ex A. de Candolle (Fagaceae); <i>Acmena acuminatissima</i> (Bl.) Merr. et Perry (Myrtaceae)	TPB			Yan <i>et al.</i> (2014)
<i>Senna reticulata</i> (Willd.) H. S. Irwin & Barneby (Fabaceae)	TPB	PR; LN	LA; SC	Arenque <i>et al.</i> (2014)
<i>Morus alba</i> L. (Moraceae)	TPB; LN; H; PR; ICC	TR		Sekhar <i>et al.</i> (2015); Shi <i>et al.</i> (2021)
<i>Azadirachta indica</i> A. Juss. (Meliaceae)	TPB; LN; RL; RW; PR; SC; ICC			Raj <i>et al.</i> (2014); Janani <i>et al.</i> (2016)
<i>Melia dubia</i> Cav. (Meliaceae)	TPB; LN; PR; SC	RW; ICC		Janani <i>et al.</i> (2016)
<i>Theobroma cacao</i> L. (Malvaceae)	TPB; LN; SD; PR; WUE	NB	LA; SL; SC; TR; CC	Lahive <i>et al.</i> (2018); Lahive <i>et al.</i> (2020); Hebbbar <i>et al.</i> (2020)
<i>Shorea platycarpa</i> F.Heim. (Dipterocarpaceae)	H; SDi	SB; LA	TPB	Musa <i>et al.</i> (2016); Musa <i>et al.</i> (2021)
<i>Macaranga pruinosa</i> (Miq.) Mull.Arg. (Euphorbiaceae)	TPB; H; SDi			Musa <i>et al.</i> (2021)
<i>Trichospermum galeottii</i> (Turcz.) Kosterm (Malvaceae); <i>Cecropia insignis</i> Liebm. (Urticaceae); <i>Ochroma pyramidale</i> (Cav.) Urban. (Malvaceae); <i>Trema micrantha</i> L. (Cannabaceae); <i>Ficus insipida</i> Willd. (Moraceae); <i>Guazuma ulmifolia</i> Lam. (Malvaceae); <i>Cecropia peltata</i> L. (Moraceae); <i>Cecropia longipes</i> Pitt. (Urticaceae)	TPB; PR	TR		Thompson <i>et al.</i> (2019)
<i>Santalum album</i> L. (Santalaceae)	LA; H; PR; TR; SC			Lamani <i>et al.</i> (2016)
<i>Coffea arabica</i> cv. <i>catuai</i> L. (Rubiaceae)	H; PR; WUE		SC; LNC	Ghini <i>et al.</i> (2015)
<i>Coffea arabica</i> cv. <i>obata</i> L. (Rubiaceae)	H; PR; WUE	LNC	SC	
<i>Coffea arabica</i> L. (Rubiaceae); <i>Coffea canephora</i> P. ex Fr. (Rubiaceae)	SS; PR; WUE; RuBisCo and Ru5PK enzymes	SD	LA; SC; CC	Ramvalho <i>et al.</i> (2013)
<i>Morus multicaulis</i> Perr. var. <i>QiangSang</i> (Moraceae)	TPB; LN; H; SDi	CC; PR; SC; TR; Leaf P content; LNC		Shi <i>et al.</i> (2021)
<i>Morus multicaulis</i> Perr. var. <i>NongSang</i> (Moraceae)	TPB; LN; H	CC; PR; SC; TR	SDi	
<i>Butea monosperma</i> (Lam.) Taub. (Fabaceae)			H; TPB	Singh <i>et al.</i> (2019)

Table 5. (Con't)

Tree species	Positive response	Negative response	No response	Reference
<i>Carapa surinamensis</i> Miq. (Meliaceae)	TPB; PR; WUE	SC	LA; ICC	De Oliveira & Marengo (2019)
<i>Acacia mangium</i> Willd. (Fabaceae)	PR; WUE		TR; SC	Ibrahim <i>et al.</i> (2021)
<i>Buchanania arborescens</i> (Blume) Blume (Anacardiaceae)	WUE	TR	PR; SC	
<i>Dillenia suffruticosa</i> (Griffth) Martelli	WUE	TR; SC	PR	
<i>Calophyllum inophyllum</i> L.	WUE	TR	PR; SC	
<i>Ploiarium alternifolium</i> (Vahl) Melch.	PR; SC; WUE		TR	
<i>Shorea parvifolia</i> Dyer (Dipterocarpaceae)	PR; TR; SC	WUE		Lion <i>et al.</i> (2019)
<i>Dalbergia retusa</i> Hemsl. (Fabaceae); <i>Inga punctata</i> Willd. (Fabaceae); <i>Ormosia macrocalyx</i> Ducke (Fabaceae); <i>Schizolobium parahyba</i> (Vell.) S. F. Blake (Fabaceae); <i>Chrysophyllum cainito</i> L. (Sapotaceae); <i>Coccoloba uvifera</i> (L.) L. (Polygonaceae); <i>Hieronyma alchorneoides</i> Allemão (Euphorbiaceae); <i>Pachira quinate</i> W.S. Alverson (Malvaceae); <i>Swietenia macrophylla</i> King. (Meliaceae)	TPB; PR; WUE	SC		Cernusak <i>et al.</i> (2011); Trierweiler <i>et al.</i> (2018)
<i>Brachychiton acerifolius</i> (A.Cunn. ex G.Don) Macarthur & C.Moore (Malvaceae)	LA; PR; SC; WUE; CC			Vogado <i>et al.</i> (2022)
<i>Phaleria clarodendron</i> (F.Muell.) Benth. (Thymelaeaceae)	LA; PR; SC; WUE; CC			
<i>Terminalia catappa</i> L. (Combataceae)	PR; SC; WUE; CC	LNC	LA	
<i>Psidium guajava</i> L. cv. Pedro Sato (Myrtaceae)			TPB; H; LN; RL; Total phenolic compounds	De Rezende <i>et al.</i> (2014)
<i>Tabebuia rosea</i> (Bertol.) DC. (Bignoniaceae)	PR	SC	LNC; SD	Slot <i>et al.</i> 2020

Note: CC: Chlorophyll content; H: Height; ICC: Intercellular CO₂ concentration; LA: Leaf area; LN: Leaf number; LNC: Leaf Nitrogen content; NB: Number of branches; PR: Photosynthetic rate; RA: Rubisco activity; RB: Root biomass; RL: Root length; RW: Root weight; SB: Shoot biomass; SC: Stomatal conductance; SD: Stomatal density; SDi: Stem diameter; SL: Stomatal length; SS: Stomatal Size; TPB: Total plant biomass; TR: Transpiration rate; WUE: Water-use efficiency

A reduction in transpiration rate under elevated CO₂ means plants can withstand climate change scenarios, specifically high CO₂ concentration and drought, because of their water conservation mechanism (Dang *et al.*, 2008; Onoda *et al.*, 2009; Rasineni *et al.*, 2013; Sekhar *et al.*, 2015). Moreover, Thompson *et al.* (2019) revealed that the average transpiration rate of the eight tropical tree seedlings presented in **Table 5** was reduced significantly under 800 ppm, and this would furtherly reduce the foliar Phosphorus concentration in some tropical trees. Thompson *et al.* (2019) also reported the reduced stomatal conductance as well as the

leguminous and non-leguminous tropical tree species used by Cernusak *et al.* (2011) under elevated CO₂. It explained the increasing leaf temperature during photosynthesis, increasing leaf-to-air vapor pressure difference. Moreover, the transpiration rate and stomatal conductance have a direct relationship, but the water use efficiency is inversely related. Generally, if a species exhibited increasing water use efficiency and decreasing transpiration rate and stomatal conductance, they have a higher chance of adapting and surviving drought and elevated CO₂ stresses, as mentioned in the reviewed papers (Warrier *et al.*, 2013; Raj

et al., 2014; Sekhar *et al.*, 2015; Janani *et al.*, 2016; Shi *et al.*, 2021). Hence, the lower transpiration and stomatal conductance can be a parameter to distinguish which species can withstand future climate change.

Furthermore, decreasing intercellular CO₂ concentration altered the mesophyll efficiency and net assimilation rates (Sheshshayee *et al.*, 1996; Ogren, 2003; Janani *et al.*, 2016). Lastly, reduced chlorophyll content affected the stability of the non-structural carbohydrates that inhibit the production of chloroplasts and reduced Nitrogen investment in photosynthesis when exposed to elevated CO₂ (Delucia *et al.*, 1985; Epron *et al.*, 1996; Warriar *et al.*, 2013; Vogado *et al.*, 2021). Other notable species mentioned in the 27 articles with reduced photosynthetic rate, transpiration rate, stomatal density, and water-use efficiency are also presented in **Table 5**.

No significant response of the forest tree species under elevated CO₂

Some species did not respond significantly to the elevated CO₂. In the case of biomass production, De Rezende *et al.* (2014) countered the previous results and revealed that the changes in dry biomass had no significant differences from the increasing CO₂ concentration. However, exposure to different levels of CO₂ can lead to the accumulation of starch and tannins, as mentioned in their paper.

Morphologically, the leaf area of species in reviewed articles (**Table 5**) showed insignificant differences among the CO₂ treatments. In root length, Warriar *et al.* (2013) and De Rezende *et al.* (2014) reported no significant differences between control and experimental treatments. Furthermore, the stomatal length, index, and density had no significant differences between ambient and elevated CO₂ (Cernusak *et al.*, 2011; Lahive *et al.*, 2018).

Physiologically, there were parameters mentioned that also did not exhibit any significant differences. Three papers agreed that the transpiration rate of plant species had no significant changes in elevated CO₂ (Lahive *et al.*, 2018; Lahive *et al.*, 2020; Hebbar *et al.*, 2020). There were also reported cases

that the stomatal conductance had no significant differences with elevated CO₂ concentration (Ramalho *et al.*, 2013; Arenque *et al.*, 2014; Ghini *et al.*, 2015; De Oliveira & Marengo, 2019; Slot *et al.*, 2021), same case with the biochemical activity such as chlorophyll content, chlorophyll a+b, and total carotenoids (Lahive *et al.*, 2018). Moreover, the phenolic compounds and flavonoids found in the roots, stems, and leaves had no significant differences between ambient and elevated CO₂, but there were higher levels of these substances in the root system of the species (De Rezende *et al.*, 2014). Other species with no significant response on their grown parameters are also shown in **Table 5**.

Research gaps

One of the prominent research gaps in this study is the limited studies in the Philippines about the effect of elevated CO₂ in plants. While most research papers in research databases were conducted and published within the tropical region, they have yet to be done in the Philippines. If there are studies about elevated CO₂, they were using crops such as rice and corn, that did not qualify for the screening method because they should be tropical trees. Hence, a developing country with megadiverse biodiversity and a biodiversity hotspot must conduct various research about the effects of CO₂ enrichment on the growth of tropical forest trees.

On the other hand, the study duration of the effects of the elevated CO₂ in trees was identified as another research gap. The structure, morphology, and physiological responses of the younger plant are different from the mature plants that already underwent secondary growth, development of an adaptive mechanism to various environmental stresses, and establishment of their firm shape and form (Baucher *et al.*, 2007; Spicer & Groover, 2010; Ragni & Greb, 2018). The result inconsistencies were found in the reviewed articles (Ramalho *et al.*, 2013; Warriar *et al.*, 2013; Raj *et al.*, 2014; Ghini *et al.*, 2015; Janani *et al.*, 2016) concerning the plant height, transpiration rate, and stomatal conductance. There was still a vague understanding of the short-term and long-term effects of the elevated CO₂ and the steps needed to

eradicate this, knowing that the plants underwent the principle of hormesis that generally alters their metabolic processes. Fortunately, Cernusak *et al.* (2013) provided some opportunities and recommendations to diminish the variability and uncertainty in the study of CO₂ enrichment.

Lastly, the methodology of CO₂ enrichment in plant study was one of the critical research gaps in reviewed articles. Twenty-four articles had a controlled approach to elevated CO₂, while three articles used an observational approach using solely the FACE method. The systematic reviews about the impacts of the FACE method on plants have a well-studied reputation (Ainsworth & Long *et al.*, 2004 & 2020; Allen *et al.*, 2020). Drake *et al.* (1985) pointed out that the FACE method has the closest simulation to the environmental settings compared with the other methods. However, organizing and implementing the FACE method requires high maintenance and cost. The question is how instantaneous the potential development of a low-cost, high-efficient, and sustainable CO₂ enrichment method with a lesser error of comparison in a natural environmental setting is possible. Providing solutions to this gap can change our understanding of the impacts of elevated CO₂ on plants' physiology, morphology, and biomass production.

CONCLUSIONS AND RECOMMENDATIONS

Tropical forest trees are excellent at capturing and storing vast amounts of atmospheric carbon. However, elevated CO₂ concentration affects biomass production as well as the morphological and physiological processes of tropical trees, as verified in this systematic review. Variability in biomass production and physiological and morphological responses of tropical trees have shown that some species can withstand worsening climate change, but others cannot. Generally, species with adaptive mechanisms to climate change follow a trend of reduced transpiration and stomatal conductance while exhibiting positive water use efficiency. It was also found that the specific changes in biomass production and morphological responses complemented

the physiological response of the tropical tree species under the elevated CO₂ treatment. If biomass production decreases, morphological and physiological responses also decrease. Hence, these parameters are useful in determining the responses of plants to any environmental stresses.

This systematic review further highlighted the gaps in CO₂ enrichment research, which can be opportunities for future research. To understand current research trends, a consistent, systematic review of the effects of elevated CO₂ concentration must be conducted once every decade. The scope of the future systematic review should be in a more extended period (> 11 yr) and include different biomes to generate a more comprehensive knowledge about the field. In addition, a wide range of literature, such as conference papers, book chapters, or gray literature, can also be explored to create a more extensive systematic review concerning climate research. Lastly, more climate-related research can lessen the impact of climate change through successful policy formulation, sustainable economic development, and food security enhancement.

ACKNOWLEDGMENTS

The author would like to extend his sincerest gratitude to Dr. Marilyn S. Combalicer, his academic adviser, for guidance and for providing the opportunity to publish. The author would also like to thank the Department of Forest Biological Science and colleagues for their support.

LITERATURE CITED

- Ainsworth, E. A. & Rogers, A. (2007). The response of photosynthesis and stomatal conductance to rising [CO₂]: Mechanisms and environmental interactions. *Plant Cell Environment*, 30, 258–270.
- Ainsworth, E. A., & Long, S. P. (2005). What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy

- properties and plant production to rising CO₂. *New Phytologist*, 165(2), 351–372.
- Ainsworth, E. A., & Long, S. P. (2021). 30 years of free-air carbon dioxide enrichment (FACE): What have we learned about future crop productivity and its potential for adaptation? *Global change biology*, 27(1), 27–49.
- Aliyu, M. B. (2017). Efficiency of Boolean search strings for information retrieval. *American Journal of Engineering Research*, 6(11), 216–222.
- Allen, L., Kimball, B., Bunce, J., Yoshimoto, M., Harazono, Y., Baker, J., Boote, K., & White, J. (2020). Fluctuations of CO₂ in Free-Air CO₂ Enrichment (FACE) depress plant photosynthesis, growth, and yield. *Agricultural and Forest Meteorology*, 284, 107899. doi:10.1016/j.agrformet.2020.107899
- Amthor, J. S. (1995). Predicting effects of atmospheric CO₂ partial pressure on forest photosynthesis. *Global Ecology and Biogeography Letters*, 22, 243–274.
- Arenque, B. C., Grandis, A., Pocius, O., de Souza, A. P., & Buckeridge, M. S. (2014). Responses of *Senna reticulata*, a legume tree from the amazonian floodplains, to elevated atmospheric CO₂ concentration and waterlogging. *Trees - Structure and Function*, 28(4), 1021–1034.
- Avila, R. T., de Almeida, W. L., Costa, L. C., Machado, K. L. G., Barbosa, M. L., de Souza, R. P. B., Martino, P. B., Juárez, M. A. T., Marçal, D. M. S., Martins, S. C. V., Ramalho, J. D. C., & DaMatta, F. M. (2020). Elevated air [CO₂] improves photosynthetic performance and alters biomass accumulation and partitioning in drought-stressed coffee plants. *Environmental and Experimental Botany*, 177, 104137. doi:10.1016/j.envexpbot.2020.104137.
- Bader, K-F. M., Siegwolf, R., & Korner, C. (2010). Sustained enhancement of photosynthesis in mature deciduous forest trees after 8 years of free air CO₂ enrichment. *Planta*, 232, 1115–1125.
- Bassham, J. A. (2003). Mapping the carbon reduction cycle: a personal retrospective. *Photosynthesis Research*, 76, 35–52.
- Baucher, M., Jaziri, M. E., & Vandeputte, O. (2007). From primary to secondary growth: origin and development of the vascular system. *Journal of Experimental Botany*, 58(13), 3485–3501.
- Betts, R. (2021). Met Office: Atmospheric CO₂ now hitting 50% higher than preindustrial levels. Retrieved from: <<https://www.carbonbrief.org/met-office-atmospheric-co2-now-hitting-50-higherthan-pre-industrial-levels>>.
- Bhatt, R. K., Baig, M. J., Tiwari, H. S., & Roy, S. (2010). Growth, yield and photosynthesis of *Panicum maximum* and *Stylosanthes hamata* under elevated CO₂. *Journal of Environmental Biology*, 31, 549–552.
- Booth, A., Noyes, J., Flemming, K., Moore, G., Tuncalp, O., & Shakibazadeh, E. (2019). Formulating questions to explore complex interventions within qualitative evidence synthesis. *BMJ Global Health*, 4(Suppl 1): e001107. doi:10.1136/bmjgh-2018-001107.
- Camposeo, S., Palasciano, M., Vivaldi, G. A., & Godini, A. (2011). Effect of increasing climatic water deficit on some leaf and stomatal parameters of wild and cultivated almonds under Mediterranean conditions. *Scientia Horticulturae*, 127(3), 234–241.
- Cernusak, L. A., Winter, K., Dalling, J. W., Holtum, J. A., & Wright, S. J. (2013). Tropical forest responses to increasing atmospheric CO₂: current knowledge and opportunities for future research. *Functional Plant Biology*, 40, 531–551.
- Cernusak, L. A., Winter, K., Martínez, C., Correa, E., Aranda, J., Garcia, M., Jaramillo, C. & Turner, B. L. (2011). Responses of legume versus nonlegume tropical tree seedlings to elevated CO₂ concentration. *Plant Physiology*, 157(1), 372–385.
- Ceulemans, R., Janssens, I. A., & Jach, M. E. (1999). Effects of CO₂ enrichment on trees and forests: Lessons to be learned in view of future ecosystem studies. *Annals of Botany*, 84, 577–590.
- Corlett, R. T. (2018). Tropical Rainforests and Climate Change. Yunnan, China: Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

- Curtis, P. S. & Wang, X. (1998). A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia*, 113, 299–313.
- Dang, Q. L., Maepea, J. M., & Parker, W. H. (2008). Genetic variation of ecophysiological responses to CO₂ in *Picea glauca* seedlings. *Open Forest Science Journal*, 1, 68–79.
- Darbah, J. N. T., Kubiske, M. E., Nelson, N., Kets, K., Riikonen, J., Sober, A., Rouse, L., & Karnosky, D. F. (2010). Will photosynthetic capacity of aspen trees acclimate after long-term exposure to elevated CO₂ and O₃? *Environmental Pollution*, 158, 983–991.
- Darke, B. G., Gonzales-Meler, M., & Long, S. P. (1997). More efficient plants: A consequence of rising atmospheric CO₂? *Annual Review of Plant Physiology and Plant Molecular Biology*, 48, 609–639.
- De Oliveira, M. F. & Marengo, R. A. (2019). Gas exchange, biomass allocation and water-use efficiency in response to elevated CO₂ and drought in andiroba (*Carapa surinamensis*, Meliaceae). *iForest*, 12, 61–68.
- De Rezende, F. M., Pereira de Souza, A., Silveira Buckeridge, M., & Maria Furlan, C. (2014). Is guava phenolic metabolism influenced by elevated atmospheric CO₂? *Environmental Pollution*, 196, 483–488.
- Delucia, E. H., Sasek, T. W., & Strain, B. R. (1985). Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. *Photosynthesis Research*, 7, 175–84.
- Dickson, R. E., Coleman, M. D., Riemenschneider, D. E., Isebrands, J. G., Hogan, G. D., & Karnosky, D. F. (1998). Growth of five hybrid poplar genotypes exposed to interacting elevated CO₂ and O₃. *Canadian Journal of Forest Research*, 28, 1706–1716.
- Epron D., Liozon R., & Mousseau M. (1996). Effects of elevated CO₂ concentration on leaf characteristics and photosynthetic capacity of beech (*Fagus sylvatica*) during the growing season. *Tree Physiology*, 16, 425–32.
- Farquhar, G. D. & Sharkey, T. D. (1982). Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology*, 33, 317–345.
- Flexas, J., Ribas-Carbo, M., Diaz-Espejo, A., Galmés, J., & Medrano, H. (2008). Mesophyll conductance to CO₂: current knowledge and future prospects. *Plant, Cell & Environment*, 31, 601–621.
- Ghasemzadeh, A., Jaafar, H. Z. E., & Rahmat, A. (2010). Antioxidant activities, total phenolics and flavonoids content in two varieties of Malaysia young ginger (*Zingiber officinale* Roscoe). *Molecules*, 15(6), 4324–4333.
- Ghasemzadeh, A. & Jaafar, H. Z. E. (2011). Effect of CO₂ enrichment on some primary and secondary metabolites synthesis in Ginger (*Zingiber officinale* Roscoe). *International Journal of Molecular Science*, 12(2), 1101–1114.
- Ghini, R., Torre-Neto, A., Dentzien, A. F. M., Guerreiro-Filho, O., Iost, R., Patrício, F. R. A., Prado, J. S. M., Thomaziello, R. A., Bettiol, W., & DaMatta, F. M. (2015). Coffee growth, pest and yield responses to free-air CO₂ enrichment. *Climatic Change*, 132(2), 307–320.
- Hebbar, K. B., Apshara, E., Chandran, K. P., & Prasad, P. V. V. (2020). Effect of elevated CO₂, high temperature, and water deficit on growth, photosynthesis, and whole plant water use efficiency of cocoa (*Theobroma cacao* L.). *International Journal of Biometeorology*, 64(1): 47–57.
- Hernandez, J. O., Maldia, L. S. J., & Park, B. B. (2020) Research trends and methodological approaches of the impacts of windstorms on forests in tropical, subtropical, and temperate zones: Where are we now and how should research move forward? *Plants*, 9, 1709; doi:10.3390/plants9121709.
- Hikosaka, K., Noguchi, K., & Terashima, I. (2016). Modeling leaf gas exchange. In: Hikosaka, K., Niinemets, Ü., & Anten, N. P. R. (eds.). *Canopy Photosynthesis: From Basics to Applications*. pp. 61–100. Springer.
- Ibrahim, M. H., Sukri, R. S., Tennakoon, K. U., Le, Q. V., & Metali, F. (2021). Photosynthetic responses of invasive *Acacia mangium* and co-existing native heath forest species to elevated temperature and CO₂ concentrations. *Journal of Sustainable Forestry*, 40(6), 573–593.

- IPCC [Intergovernmental Panel on Climate Change]. (2013). Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press.
- Janani, S., Priyadharshini, P., Jayaraj, R., Buvaneshwaran, C., & Warriar, R. (2016). Growth, physiological and biochemical responses of Meliaceae species - *Azadirachta indica* and *Melia dubia* to elevated CO₂ concentrations. *Journal of Applied Biology and Biotechnology*, 4, 052–060.
- Kallarackal, J. & Roby, T. J. (2012). Responses of trees to elevated carbon dioxide. *Biodiversity Conservation*, 21, 1327–1342.
- Khurana, E. & Singh, J. S. (2001). Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: A review. *Environmental Conservation*. doi:10.1017/S0376892901000042.
- Korner, C. & Miglietta, F. (1994). Long-term effects of naturally elevated CO₂ on Mediterranean grassland and forest trees. *Oecologia*, 99, 343–351.
- Kumar, S., Chaitanya, B. S. K., Ghatti, S., & Reddy, A. R. (2014). Growth, reproductive phenology and yield responses of a potential biofuel plant, *Jatropha curcas* grown under projected 2050 levels of elevated CO₂. *Physiologia Plantarum*, 152, 501–519.
- Kursar, T. A. & Coley, P. D. (2003). Convergence in defense syndromes of young leaves in tropical rainforests. *Biochemical Systematics & Ecology*, 31, 929–49.
- Lacis, A. A., Hansen, J. E., Russell, G. L., Oinas, V., & Jonas, J. (2013). The role of long-lived greenhouse gases as principal LW control knob that governs the global surface temperature for past and future climate change. *Tellus B*, 65, 19734. doi:10.3402/tellusb.v65i0.19734.
- Lahive, F., Hadley, P., & Daymond, A. J. (2018). The impact of elevated CO₂ and water deficit stress on growth and photosynthesis of juvenile cacao (*Theobroma cacao* L.). *Photosynthetica*, 56, 911–920.
- Lamani, N., Shivaprasad, D., & Swamy, K. R. (2016). Effect of elevated carbon dioxide concentration on photosynthetic and transpiration rate in Sandal (*Santalum album* L.). *Proceedings of the International Academy of Ecology and Environmental Sciences*, 6(2), 44–52.
- Leakey, A. D. B., Press, M. C., Scholes, J. D., & Watling, J. R. (2002). Relative enhancement of photosynthesis and growth at elevated CO₂ is greater under sunflecks than uniform irradiance in a tropical rain forest tree seedling. *Plant, Cell & Environment*, 25(12), 1701–1714.
- Lee, Q. V., Tennakoon, K. U., Metali, F., & Sukri, R. S. (2019). Photosynthesis in co-occurring invasive *Acacia* spp. and native Bornean heath forest trees at the post-establishment invasion stage. *Journal of Sustainable Forestry*, 38(3), 230–243.
- Liberloo, M., Tulva, I., Raim, O., Kull, O., & Ceulemans, R. (2007). Photosynthetic stimulation under long-term CO₂ enrichment and fertilization is sustained across a closed populous canopy profile (EUROFACE). *New Phytologist*, 173, 537–549.
- Lindsey, R. (2007). Tropical Deforestation. Earth Observatory – NASA. Retrieved on 15 May 2021 from: <<https://earthobservatory.nasa.gov/features/Deforestation>>.
- Lion, M., Remperi, S., Chuah, N. J. & Shamsuddin, S.A. (2019). The study on transpiration and water use efficiency of *Shorea parvifolia* under elevated carbon dioxide concentration in the tropical forest. *International Journal of Agriculture, Forestry and Plantation*, 8, 98–105.
- Livoreil, B., Glanville, J., Haddaway, N. R., Bayliss, H., Bethel, A., de Lachapelle, F. F., Robalino, S., Savilaakso, S., Zhou, W., Petrokofsky, G., & Frampton, G. (2017). Systematic searching for environmental evidence using multiple tools and sources. *Environmental Evidence*, 6(1), 23. doi:10.1186/s13750-017-0099-6.
- Lloyd, J. & Farquhar, G. D. (2008). Effects of rising temperatures and CO₂ on the physiology of tropical forest trees. *Philosophical Transactions of Royal Society B*, 363, 1811–1817.
- Lovelock, C. E., Virgo, A., Popp, M., & Winter, K. (1999). Effects of elevated CO₂ concentrations on photosynthesis, growth and reproduction

- of branches of the tropical canopy tree species, *Luehea seemannii* Tr. and Planch. *Plant, Cell & Environment*, 22(1), 49–59.
- Miller, S. A. & Forrest, J. L. (2001). Enhancing your practice through evidence-based decision making: PICO, learning how to ask good questions. *Journal of Evidence Based Dental Practice*, 1, 136–141.
- Minnesota Population Center (2020). Integrated Public Use Microdata Series, International: Version 7.3 [World Map dataset]. Minneapolis, MN: IPUMS. doi:10.18128/D020.V7.3
- Mndela, M., Tjelele, J. T., Madakadze, I. C., Mangwane, M., Samuels, I. M., Muller, F., & Pule, H. T. (2022). A global meta-analysis of woody plant responses to elevated CO₂: implications on biomass, growth, leaf N content, photosynthesis and water relations. *Ecological Processes*, 11, 52. doi:10.1186/s13717-022-00397-7
- Musa, N. L. W., Nizam, M. S., Radziah, C. M. Z. C., & Juliana, W. A. W. (2021). Growth responses of light demanding and shade tolerant peat swamp forest saplings to elevated CO₂. *Journal of Environmental Biology*, 42(3), 735–743.
- Musa, N. L. W., Wan Juliana, W. A., Nizam, M. S., & Che Radziah, C. M. Z. (2017). Effects of elevated atmospheric CO₂ on photosynthesis, growth and biomass in *Shorea platycarpa* F. Heim (Meranti Paya). *Sains Malaysiana*, 46(9), 1421–1428.
- Needham, J. F., Chambers, J., Fisher, R., Knox, R., & Koven, C. D. (2020). Forest responses to simulated elevated CO₂ under alternate hypotheses of size- and age-dependent mortality. *Global Change Biology*, 26(10), 5734–5753.
- Ogren, W. L. (2003). Affixing the O to RuBisCo: Discovering the source of photorespiratory glycolate and its regulation. *Photosynthesis Research*, 76, 53–63.
- Onoda, Y., Hirose, T., & Hikosaka, K. (2009). Does leaf photosynthesis adapt to CO₂-enriched environments? An experiment on plants originating from three natural CO₂ springs. *New Phytologist*, 182, 698–709.
- Page, M. J., McKenzie, J. E., Bossuyt, P. M., Boutron, I., Hoffmann, T. C., Mulrow, C. D., Shamseer, L., Tetzlaff, J. M., Akl, E. A., Brennan, S. E., Chou, R., Glanville, J., Grimshaw, J. M., Hróbjartsson, A., Lalu, M. M., Li, T., Loder, E. W., Mayo-Wilson, E., McDonald, S., & Moher, D. (2021). The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *British Medical Journal*, 372. doi:10.1136/bmj.n7.
- Prior, S. A., Runion, G. B., Marble, S. C., Rogers, H. H., Gilliam, C. H., & Torbert, H. A. (2011). A review of elevated atmospheric CO₂ effects on plant growth and water relations: Implications for horticulture. *Horticulture & Horticultural Science*, 46(2), 158–162.
- QGIS Development Team. (2020). QGIS Geographic Information System. Open-Source Geospatial Foundation Project. Retrieved from: <http://qgis.osgeo.org>.
- Ragni, L. & Greb, T. (2018). Secondary growth as a determinant of plant shape and form. *Seminars in Cell & Developmental Biology*, 79, 58–67.
- Rai, A., Singh, A.K., Singh, N., & Ghoshal, N. (2020). Effect of elevated CO₂ on litter functional traits, mass loss and nutrient release of two subtropical species in free air carbon enrichment facility. *Environmental and Experimental Botany*, 172, doi:10.1016/j.envexpbot.2020.103994.
- Raj, E. E., Buvaneswaran, C., Menason, E., & Vijayalakshmi, C. (2014). Physiological response of tropical tree species to elevated CO₂ levels at seedling stage. *Indian Journal of Ecology*, 41(1), 16–22.
- Ramvalho, J. C., Rodrigues, A. P., Semedo, J. N., Pais, I. P., Martins, L. D., Simões-Costa, M. C., Leitão, A. E., Fortunato, A. S., Batista-Santos, P., Palos, I. M., Tomaz, M. A., Scotti-Campos, P., Lidon, F. C., & DaMatta, F. M. (2013). Sustained photosynthetic performance of *Coffea* spp. under long-term enhanced CO₂. *PLOS ONE*, 8(12). doi:10.1371/journal.pone.0082712

- Rasineni, G. K. & Reddy, A. R. (2013). Influence of Elevated CO₂ Concentration on Photosynthesis and Biomass Yields in a Tree Species, *Gmelina arborea* Roxb. Springer, Berlin, Heidelberg. doi:10.1007/978-3-642-32034-7_167
- Rasineni, G. K., Guha, A., & Reddy, A. R. (2013). Elevated CO₂ atmosphere significantly increased photosynthesis and productivity in a fast growing tree species, *Gmelina arborea* Roxb. *Climate Change and Environmental Sustainability*, 1(1), 81–94.
- Reichgelt, T., D'Andrea, W. J., Valdivia-McCarthy, A. C., Fox, B. R. S., Bannister, J. M., Conran, J. G., Lee, W. G., & Lee, D. E. (2020). Elevated CO₂ increased leaf-level productivity, and water-use efficiency during the early Miocene. *Climate of the Past*, 16(4), 1509–1521.
- Rouhi, V., Samson, R., Lemeur, R., & Damme, V. (2007). Photosynthetic gas exchange characteristics in three different almond species during drought stress and subsequent recovery. *Environmental and Experimental Botany*, 59, 117–129.
- Sakai, H., Hasegawa, T., & Kobayashi, K. (2006). Enhancement of rice canopy carbon gain by elevated CO₂ is sensitive to growth stage and leaf nitrogen concentration. *New Phytologist*, 170, 321–332.
- Sekhar, K. M., Sreeharsha, R. V., & Reddy, A. R. (2015). Differential responses in photosynthesis, growth and biomass yields in two mulberry genotypes grown under elevated CO₂ atmosphere. *Journal of Photochemistry and Photobiology*, 151, 172–179.
- Sheshshayee, M. S., Krishna Prasad, B. T., Natraj, K. N., Shankar, A. G., Prasad, T. G., & Uday Kumar, M. (1996). Ratio of intercellular CO₂ concentration to stomatal conductance is a reflection of mesophyll efficiency. *Current Science*, 70(7), 672–675.
- Shi, S., Xu, X., Dong, X., Xu, C., Qiu, Y., & He, X. (2021). Photosynthetic acclimation and growth responses to elevated CO₂ associate with leaf nitrogen and phosphorus concentrations in mulberry (*Morus multicaulis* Perr.). *Forests*, 12(6), 660. MDPI AG. doi:10.3390/f12060660.
- Singh, A. K., Rai, A., Kushwaha, M., Chauhan, P. S., Pandey, V., & Singh, N. (2019). Tree growth rate regulate the influence of elevated CO₂ on soil biochemical responses under tropical condition. *Journal of Environmental Management*, 231, 1211–1221.
- Skivington, K., Matthews, L., Simpson, S. A., Craig, P., Baird, J., Blazeby, J. M., Boyd, K. A., Craig, N., French, D. P., McIntosh, E., Petticrew, M., Rycroft-Malone, J., White, M., & Moore, L. (2021). Framework for the development and evaluation of complex interventions: gap analysis, workshop and consultation-informed update. *Health Technology Assessment* (Winchester, England), 25(57), 1–132.
- Slot, M., Rifai, S. W., & Winter, K. (2021). Photosynthetic plasticity of a tropical tree species, *Tabebuia rosea*, in response to elevated temperature and [CO₂]. *Plant, Cell & Environment*, 44, 2347–2364.
- Sohrabi, C., Franchi, T., Mathew, G., Kerwan, A., Nicola, M., Griffin, M., Agha, M., & Agha, R. (2021). PRISMA 2020 statement: What's new and the importance of reporting guidelines. *International Journal of Surgery*, 88, 105918. doi:10.1016/j.ijssu.2021.105918.
- Spicer, R. & Groover, A. (2010). Evolution of development of vascular cambia and secondary growth. *New Phytologist*, 186, 577–592.
- Drake, B. G., Rogers, H. H., & Allen, L. H., Jr. (1985). Methods of exposing plants to elevated Carbon dioxide. In B. R. Strain & J. D. Cure (Eds.), *Direct effects of increasing carbon dioxide on vegetation* (pp. 13–31). United States. doi:10.2172/6134866
- Tang, K. H. D. (2019). Impacts of climate change on tropical rainforest's adaptive capacity and ecological plasticity. *Climate Change Facts, Impacts and Solutions*, 1, 1–5.
- Thompson, J. B., Slot, M., Dalling, J. W., Winter, K., Turner, B. L., & Zalamea, P. C. (2019). Species-specific effects of phosphorus addition on tropical tree seedling response to elevated CO₂. *Functional Ecology*, 33, 1871–1881.
- Tietze, H. S. E., Joshi, J., Pugnaire, F. I., & Dechoum, M. dS. (2019). Seed germination and seedling establishment of an invasive tropical

- tree species under different climate change scenarios. *Australia Ecology*, 44(16). doi:10.1111/aec.12809.
- Vogado, N. O., Cheesman, A. W., & Cernusak, L. A. (2021). Delayed greening during leaf expansion under ambient and elevated CO₂ in tropical tree seedlings. *Australian Ecology*, 47, 530–540.
- Vu, J. C. V. (2005). Acclimation of peanut (*Arachis hypogaea* L.) leaf photosynthesis to elevated growth CO₂ and temperature. *Environmental and Experimental Botany*, 53, 85–95.
- Wang, D., Heckathorn, S. A., Wang, X., & Philpott, S. M. (2012). A meta-analysis of plant physiological and growth responses to temperature and elevated CO₂. *Oecologia*, 169, 1–13.
- Warrier, R. R., Buvaneswaran, C., Priyadharshini, P., & Jayaraj, R. S. C. (2013). Growth response of three plantation species of the tropics exposed to elevated CO₂ levels. *Journal of Forestry Research*, 24(3), 449–456.
- Yan, J., Zhang, D., Liu, J., & Zhou, G. (2014). Interactions between CO₂ enhancement and N addition on net primary productivity and water-use efficiency in a mesocosm with multiple subtropical tree species. *Global Change Biology*, 20(7), 2230–2239.
- Yu, H. & Ong, B. L. (2002). The effect of phyllode temperature on gas exchange and chlorophyll fluorescence of *Acacia mangium*. *Photosynthetica*, 40(4), 635–639.
- Zak, D. R., Pregitzer, K. S., Curtis, P. S., Vogel, C. S., Holmes, W. E., & Lussenhop, J. (2000). Atmospheric CO₂, soil-N availability, and allocation of biomass and nitrogen by *Populus tremuloides*. *Ecological Applications*, 10(1), 34–46.
- Zhu, C., Zeng, Q., Yu, H., Liu, S., Dong, G., & Zhu, J. (2016). Effect of elevated CO₂ on the growth and macronutrient (N, P, and K) uptake of annual wormwood (*Artemisia annua* L.). *Pedosphere*, 26, 235–242.