

Article

Trends in Atmospheric CO₂ Fertilization Effects with Stand Age Based on Tree Rings

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Abstract: The increase in global carbon emissions has intensified the effects of CO₂ fertilization on the carbon cycle. CO₂ fertilization is shaped by several factors, including the physiological differences among trees of varied forest ages and types, as well as the influence of different climatic conditions. It is essential to investigate the differences in CO₂ fertilization effects across diverse climate zones and delve into the association between these effects and forest age and type. Such exploration will deepen our knowledge of forest responses to environmental changes. This study used annual ring width data from the International Tree-Ring Data Bank, employing the generalized additive mixed models and the Random Forest model to discern the pattern of the CO₂ fertilization effect concerning forest age in the Northern Hemisphere. This study also explored the variations in the effect of CO₂ fertilization across unique climate zones and the disparities among various forest types within the same climatic zone. The results indicated a link between forest age and the CO₂ fertilization effect: it tends to increase in sapling forests and middle-aged forests and diminish in mature forests. Warmer, drier environments had a more marked effect of increased CO₂ on tree fertilization. Additionally, coniferous forests demonstrated a more substantial CO₂ fertilization effect than broadleaf forests, and deciduous needle-leaf forests surpassed evergreen needle-leaf forests in this regard. This research is pivotal in understanding the shifting patterns of CO₂ fertilization effects and how forests respond to atmospheric changes.



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Keywords: CO₂ fertilization effect; ring width; stand age; northern hemisphere

1. Introduction

Since the industrial revolution, a significant amount of greenhouse gases (CO₂, CH₄, O₃, etc.) enters the atmosphere because of the combustion of fossil fuels such as coal and oil and the depletion of forest resources caused by human activities [1]. The concentration of atmospheric CO₂, the primary greenhouse gas, has increased from approximately 280 ppm before the start of the industrial era to more than 400 ppm currently [2]. This growing concentration of atmospheric CO₂ is the primary contributor to global warming [3]. The significance of global warming has captured the attention of nations worldwide. Countries are proactively taking measures and seeking solutions to mitigate global warming, combat climate change, and protect the environment. Utilizing terrestrial ecosystems for carbon sequestration has emerged as a significant area of global research, given its effectiveness in controlling greenhouse gas emissions and reducing the greenhouse effect [4]. Over the past six decades, terrestrial ecosystem carbon sinks have accounted for more than 50% of global carbon sinks, and this trend is on the increase, helping to lessen the effects of global warming [5]. Moreover, substantial evidence emphasizes the critical role of forest ecosystems in the process of terrestrial carbon sequestration [6,7]. Some research has associated the long-term increase in the terrestrial carbon sink with elevated atmospheric

CO₂ levels, which might boost photosynthesis and vegetation biomass growth. This phenomenon is commonly termed the “CO₂ fertilization effect” (β) [8].

In theory, atmospheric CO₂ molecules can be sequestered through the process of plant photosynthesis and react with water molecules to produce carbohydrates. Therefore, the fertilization effect of increasing atmospheric CO₂ concentration on vegetation growth manifests in two aspects: direct and indirect fertilization [9]. The higher concentration of CO₂ in the external environment will directly increase the content of CO₂ and the CO₂-to-O₂ ratio in the leaves of green vegetation, facilitating the carboxylation of enzymes and thus intensifying vegetation photosynthesis while inhibiting respiration, resulting in an increased net photosynthetic rate of vegetation. This is the direct fertilization effect of CO₂ [10]. On the other hand, the increasing atmospheric CO₂ concentration is likely to reduce the opening of leaf stomata, thereby decreasing water loss from transpiration and enhancing the water use efficiency of vegetation. This indirect effect of elevated CO₂ can extend the growth cycle of seasonally dry ecosystems, potentially stimulating continuous biomass accumulation in plants, known as the indirect fertilization effect of CO₂ [11]. With more than 80% of C3 plants on the global land surface still not reaching their CO₂ saturation point during photosynthesis, there is optimism that rising atmospheric CO₂ concentrations will further bolster global vegetation productivity [12]. The response of different plant species to increasing atmospheric CO₂ concentrations during photosynthesis is also anticipated to vary significantly [13].

Forests play a pivotal role in terrestrial ecosystems, constituting 45% and 50% of biomass and productivity, respectively, and serving as a crucial component in the global carbon cycle [14]. Trees, being a significant component of forest ecosystems, encapsulate historical adaptation records to fluctuating environmental factors within their annual rings [15,16]. The annual rings represent an essential data source for detecting the effects of CO₂ fertilization on tree growth [17]. Cook et al. were pioneers in analyzing the radial growth (ring width) of a tree, considering multiple factors such as internal stand disturbances, external disturbances, age-related factors, and climatic and atmospheric changes [18]. Among these, researchers postulated that stand-internal disturbances (e.g., stand windows created by downed trees) only affected a few trees around a downed tree at a specific moment. Subsequent averaging treatments mitigated this effect, provided sample sizes were sufficient. Conversely, external disturbances within the stand (e.g., forest fires, pests, diseases, and other disturbances) can be minimized by pre-selecting sample sites that are less disturbed. This allows for the detection of atmospheric CO₂ fertilization effects by eliminating interference from factors such as age in the tree annual rings' information. Tree whorl width is a concentric whorl structure formed by seasonal alternation in the process of inward differentiation of the tree formation layer, containing long-term climatic signals of various environmental factors and nonclimatic signals of the tree's growth and development, as well as internal disturbances [19]. Therefore, before reconstructing or predicting climate change using ring width sequences, age-related growth trends should be eliminated to maximize the retention of climate information [20]. Currently, many scholars have utilized tree annual rings' data under natural conditions to analyze the fertilization signal of atmospheric CO₂, presenting various perspectives. According to the theory of the fertilizing effect of atmospheric CO₂, numerous scholars have substantiated this hypothesis through various methods in different regions, utilizing data on the width of naturally growing trees' annual rings [21–23]. However, some studies have concluded that under natural conditions, the increase of atmospheric CO₂ concentration promotes only tree growth in specific regions (arid and semi-arid areas) or certain tree species [24,25]. By contrast, other studies have examined tree rings and deduced that at certain high latitudes, due to low temperatures and the limiting effect of atmospheric nitrogen deposition, the effect of elevated CO₂ concentrations on tree growth is minimal and challenging to detect [26]. Furthermore, it is plausible that atmospheric CO₂ concentrations have yet to reach the threshold for a fertilization effect, suggesting that increases in atmospheric CO₂ concentrations may not directly or indirectly enhance tree biomass growth [27].

In summary, the notable surge in CO₂ levels since the Industrial Revolution has, to some extent, influenced the radial growth of trees. However, current research using tree ring data to quantify the effects of atmospheric CO₂ fertilization faces challenges and disagreements. To accurately assess the influence of rising atmospheric CO₂ on the growth of tree annual rings, it is important to examine the relationship with forest age and perform a comparative analysis of the variations in CO₂ fertilization effects among distinct climatic zones and forest categories. The resulting data will improve the understanding of not only the influence of the fertilizing effect of atmospheric CO₂ on the radial growth of trees, possibly providing scientific evidence but also the mechanism underlying forests' response to atmospheric changes to enrich our perspectives on the global carbon cycle based on the annual rings of trees. Consequently, the carbon sequestration ability of forests can be improved. This study aimed to (1) minimize the influence of age on radial tree growth using optimal statistical techniques, while preserving the low-frequency signal of the atmospheric CO₂ fertilization effect to the greatest extent possible, (2) accurately quantify the atmospheric CO₂ fertilization effect, (3) investigate the association between forest age and the atmospheric CO₂ fertilization effect and compare the differences in this effect across various climate zones and forest types.

2. Materials and Methods

2.1. Annual Cycle Data

The annual tree ring data used in this study were sourced from the International Tree-Ring Data Bank (ITRDB). Currently, the ITRDB is the largest global database for tree rings, providing an open and freely accessible platform for both uploading and accessing data. Maintenance of the ITRDB has been overseen by NOAA and the World Data Center for Paleoclimatology since 1990. The ITRDB documents chronologies dating back to 6000 BC for all continents (excluding Antarctica due to the lack of trees), covering more than 4000 locations and spanning 226 species [28]. The ITRDB contains a variety of tree ring metadata, including width data, density data, stable isotope data, and other types. However, because each contributed dataset in the ITRDB might not have undergone rigorous verification, there are instances of formatting errors, unreadable files, and missing data. This study enhances database utility by downloading and organizing data from Zhao and the Global Annual Rotation Database (<https://www.ncdc.noaa.gov/paleo/study/25570>) (accessed on 10 May 2022) [28]. Due to the limited data distribution in the southern hemisphere, this study primarily focuses on the northern hemisphere, as illustrated in Figure 1.

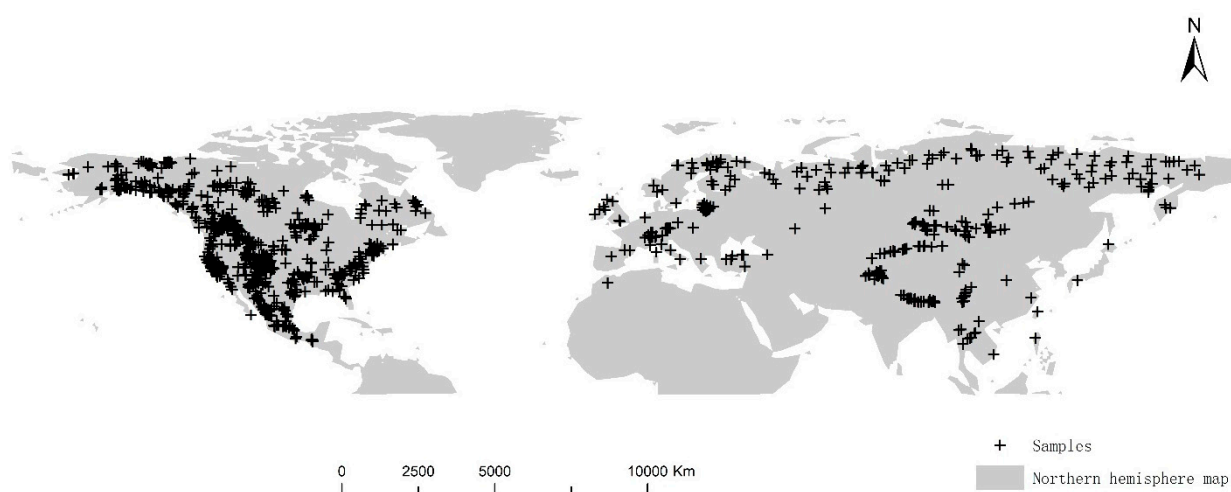


Figure 1. Distribution of tree rings in the Northern Hemisphere.

2.2. Atmospheric CO₂ Concentration Data

The study utilizes atmospheric CO₂ concentration data from 1901 to 1957, derived from the ice core CO₂ historical record [29]. Data from 1958 to 2020 are sourced from the Mauna Loa Observatory in Hawaii, USA, and are measured in parts per million (<https://www.esrl.noaa.gov/gmd/ccgg/trends/data.html>) (accessed on 20 June 2022) [30,31]. The change in atmospheric CO₂ concentration from 1901 to 2020 is shown in Figure 2.

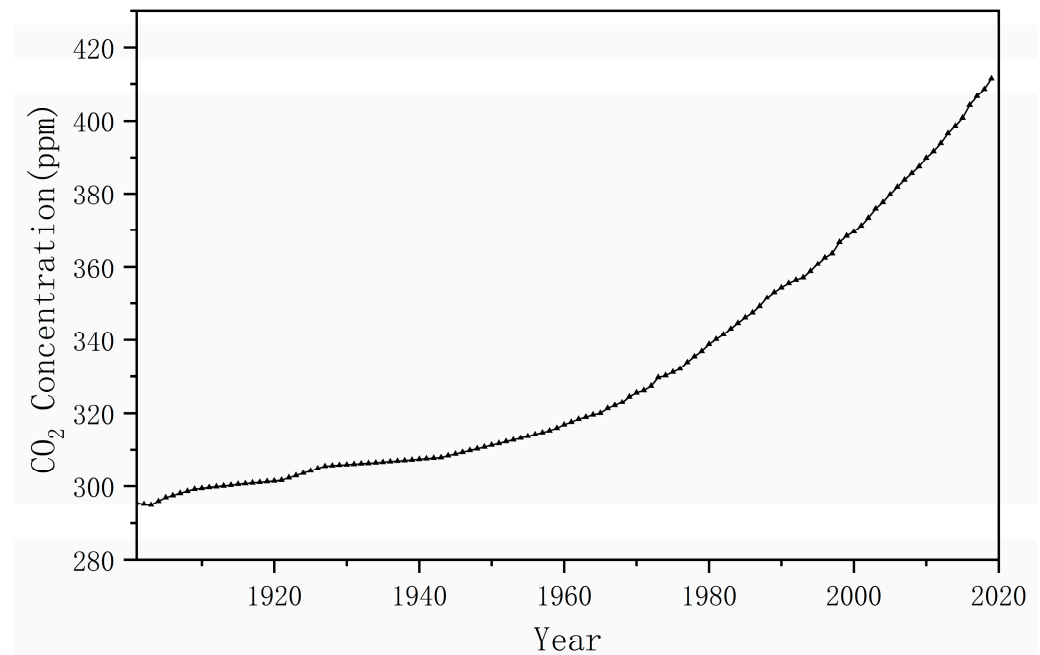


Figure 2. Atmospheric CO₂ concentration, 1901–2020.

2.3. Climate Data

The climate data for this research were obtained from the National Center for Atmospheric Sciences CRU TS (version 4.0.5) [32]. The study employs monthly mean temperature (TMP), monthly total precipitation (PRE), monthly water vapor pressure (VAP), and monthly water vapor pressure difference (VPD) as its primary data sources. The monthly VPD was calculated by subtracting the monthly saturated water vapor pressure (SVP) from the monthly VAP. The method for determining the monthly VPD was further explained through the provided formula. Equations (1)–(4).

$$VPD = SVP - VAP \quad (1)$$

$$SVP = 6.112 * f_w * e^{\frac{17.67T_{mean}}{T_{mean} + 243.5}} \quad (2)$$

$$f_w = 1 + 7 * 10^{-4} + 3.46 * 10^{-6} P_{mst} \quad (3)$$

$$P_{mst} = P_{msl} \left(\frac{(T_{mean} + 273.16)}{(T_a + 273.16) + 0.0065 * Z} \right)^{5.625} \quad (4)$$

where Tmean represents the mean temperature, Pmst denotes the sea-level pressure, Pmsl refers to the mean sea-level pressure (1013.25 hPa), and Z denotes the altitude.

2.4. Atmospheric Nitrogen Deposition Data

The global atmospheric nitrogen deposition (Ndep) data are sourced from CMIP6 driver data with a spatial resolution of 0.5° [33]. This dataset was generated using the NCAR-CCMI-2-0 model, which allows for a more accurate assessment of the effects of Ndep

changes on forest carbon sequestration. Data from the historical Ndep database (1850–2014) cover the period 1901–2014, while data from the future Ndep database (2015–2100) cover the period 2015–2020.

2.5. Koppen Climate Type Data

Climate type data were sourced from the Koppen Climate Classification dataset (<http://www.gloh2o.org/koppen/>) (accessed on 10 July 2022), published by Princeton University in 2018 [34]. The globe is divided into five climate zones: A (Tropical), B (Arid), C (Temperate), D (Continental), and E (Polar). These divisions are based on two metrics: temperature and precipitation, as depicted in Figure 3.

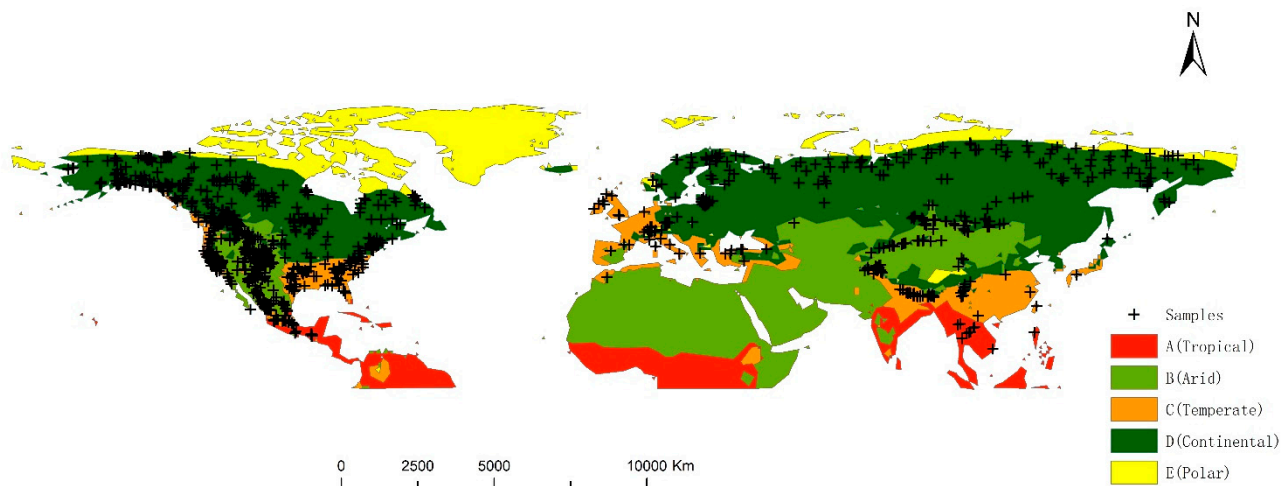


Figure 3. Spatial distribution of climate zones in the Northern Hemisphere.

2.6. Data Processing

For this study, the downloaded chronology data were specifically extracted for chronologies above the latitude of 0°N and for stands concluding after the year 1902. Chronologies not meeting these criteria were excluded. The final sample number and plant count for each climatic zone are detailed in Table 1.

Table 1. Distribution of tree sample sites in the northern hemisphere across various climatic zones.

Climate Zone	No. of Samples	Plant Number
A (Tropical)	15	241
B (Arid)	235	7744
C (Temperate)	55	1657
D (Continental)	1085	25,033
E (Polar)	55	1657

The removal of the growth trend associated with tree age is crucial for examining the effects of atmospheric CO₂ and other climatic factors on tree radial growth. Hence, this study employed the GAMMs model to mitigate the influence of a tree's age and diameter at breast height (DBH) on its radial growth. This model has been shown to better preserve low-frequency signals, such as atmospheric CO₂ fertilization effects, compared with other detrending methods (e.g., linear, negative exponential, etc.). The initial step involved converting tree annual ring width data to basal area increment (BAI) using Equation (5).

$$BAI = \pi R_t^2 - \pi R_{t-1}^2 \quad (5)$$

where BAI represents the incremental cross-sectional area of the trunk, and R_t and R_{t-1} denote the cumulative sum of annual ring widths from tree growth up to year t and year $t - 1$, respectively.

The skewed distribution of BAI required a logarithmic transformation. Subsequently, the effects of age and DBH on BAI were fitted using the GAMM model for each sample plot. In the GAMMs model, each tree was modeled and analyzed individually. Chest diameter (DBH) and age of the tree formation layer (age) were treated as fixed effects, while tree number was viewed as a random effect. This model is represented by Equation (6).

$$\ln(BAI_{i,t} + 1) = s(DBH_{i,t}) + s(Age_{i,t}) + Z_{i,t}B_{i,t} + v_{i,t} + \varepsilon_{i,t} \quad (6)$$

where the symbol i denotes the tree number, t represents the year, ZB is the random effect, and v is the error term with a first-order autoregressive structure. The term ε signifies the residual term, and s is the smoothing function. In this context, the smoothing function employed is the cubic spline smoothing function. This study utilizes the gamm function from the mgcv package in the R language to model each sample of the annual cycle individually.

In this study, the reconstruction of BAI_res and the estimation of β were achieved using the Random Forest algorithm in machine learning. β is commonly used as a metric to gauge changes in vegetation productivity due to elevated atmospheric CO₂ concentrations, signifying the magnitude of the CO₂ fertilization effect. For the purpose of this research, BAI_res, the fractional area growth after eliminating the age trend, served as the observed variable. Influential factors, including the mean temperature (Tmean), total precipitation (Pre), VPD, and atmospheric nitrogen deposition (Ndep) in summer (June–September), were selected. Additionally, winter (December–February) precipitation and the temperature of the prior year's growing season (June–September) were integrated as influencing variables. BAI_res data for each global sample site was individually reconstructed for the study period spanning 1902–2020.

This study employed two scenarios to reconstruct the historical observation variable BAI_res, focusing on shifts in atmospheric CO₂ concentration. The first scenario accounted for genuine changes in all drivers over time, while the second scenario held the atmospheric CO₂ concentration constant at 1901 levels, permitting other drivers to undergo real-time changes. For example, the 1902 BAI_res was rebuilt, as shown in Equations (7)–(8).

Scenario 1:

$$BAI_{res1902} \sim CO2_{1902} + Tmean_{1902} + Pre_{1902} + VPD_{1902} + Ndpe_{1902} \quad (7)$$

Scenario 2:

$$BAI_{res1902} \sim CO2_{1901} + Tmean_{1902} + Pre_{1902} + VPD_{1902} + Ndpe_{1902} \quad (8)$$

The BAI_res for subsequent years was reconstructed following the same methodology. The variance between estimates yielded by the Random Forest algorithm simulation in both scenarios was leveraged to determine the fitting of the β -value, as shown in Equation (9).

$$\Delta BAI_{res} = \beta * \Delta CO_2 + \varepsilon \quad (9)$$

where ΔBAI_{res} indicates the difference between estimated values of the observed variables, modeled using the Random Forest algorithm, across different CO₂ concentration scenarios. β represents the response of BAI_res to the rise in atmospheric CO₂.

Trees aged 1–150 years were chosen to ascertain the β value associated with each tree's age. The average β value for each sampling point was derived by averaging the β values of trees of the same age within that point. With this approach, trends of β in relation to stand age in diverse climatic zones were established. For a comparative analysis, regions B (arid), C (temperate), and D (continental) with substantial sample sizes were selected. Trends of β concerning stand age for various tree species within these climatic zones were studied. In

this research, the relationship between β and stand age was mapped through nonlinear regression, as shown in Equation (10).

$$\beta_{tree} = a \left[1 + \frac{b \left(\frac{age}{c} \right)^d - 1}{e \left(\frac{age}{c} \right)} \right] \quad (10)$$

where a , b , c , and d are nonlinear regression model coefficients.

3. Results

3.1. Generalized Additive Mixed Model Results

To explore the correlation between tree annual rings, atmospheric CO₂, and other climatic factors, it is crucial to adjust the original tree rings to account for age-related patterns. This study assessed the significance of the nonparametric terms in the GAMMs model across each climate zone. The trend of tree BAI was analyzed by fitting it with tree age and DBH across sample plots in five distinct climate zones using the GAMMs model. The analysis revealed that all p -values were less than 0.01 (Table 2), pointing to a significant effect of both tree age and DBH on BAI. Concurrently, the adjusted coefficient of determination (R²) for the GAMMs model ranged between 0.75 and 0.93 for each sample point, indicating the model's effectiveness in capturing the influence of tree age on BAI.

Table 2. Generalized additive mixed model (GAMM) fitting results.

Climate Zone	Parameter Term				Nonparametric Term			
	Intercept	Standard Error	t -Value	p -Value	Variant	Freedom	p -Value	Radj2
A (Tropical)	0.89	0.33	43.82	<0.01	DBH	17.44	<0.01	0.83
					Age	3.21	<0.01	
B (Arid)	1.84	0.05	33.34	<0.01	DBH	16.46	<0.01	0.79
					Age	9.30	<0.01	
C (Temperate)	1.98	0.04	55.04	<0.01	DBH	25.89	<0.01	0.87
					Age	5.25	<0.01	
D (Continental)	1.78	0.72	24.49	<0.01	DBH	15.28	<0.01	0.75
					Age	4.49	<0.01	
E (Polar)	0.61	0.04	15.53	<0.01	DBH	18.30	<0.01	0.81
					Age	7.52	<0.01	

The biased residual plots of BAI against tree age for the five climate zones are provided in Figure 4. The figure demonstrates that the influence of tree age on the increment of BAI in all five zones follows a similar pattern: BAI increment decreases as tree age rises. The sharpest drop in the incremental trunk fracture area occurred between 0 and 60 years of tree age, after which the trend slowly stabilized.

3.2. Trends in CO₂ Fertilization Effects with Stand Age

Research findings indicate that the average atmospheric CO₂ fertilization effect on trees aged 1–150 years in the Northern Hemisphere shows a steady rise during early growth stages, slowing down in middle age. It peaks at a value of 53.85 cm²·100 ppm^{−1} at the age of 50 years and then declines annually as trees mature (Figure 5).

3.3. Differences in the Effects of CO₂ Fertilization in Different Climatic Zones

The study revealed that the CO₂ fertilization effect of trees exhibited a consistent pattern of an initial increase and a subsequent decrease across various climatic zones as the stand age increased (Figure 6). However, the rate of increase in the CO₂ fertilization effect and the strength of the response varied across different climatic zones.

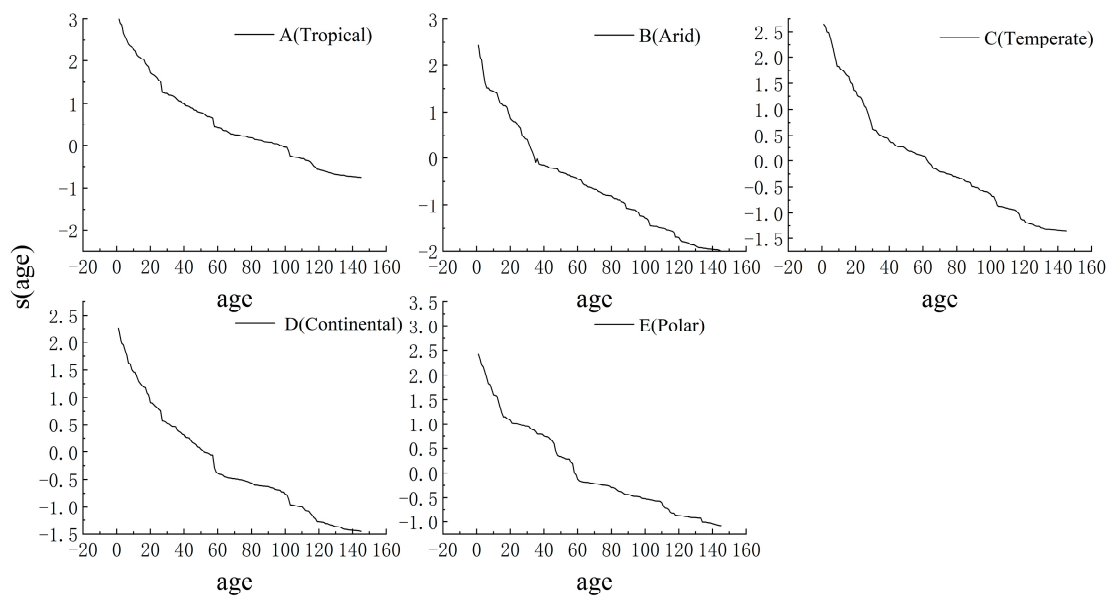


Figure 4. Effect of tree age on BAI. Note: The horizontal coordinate is age, referring to the age of the tree formation layer. The vertical coordinate is bias residual.

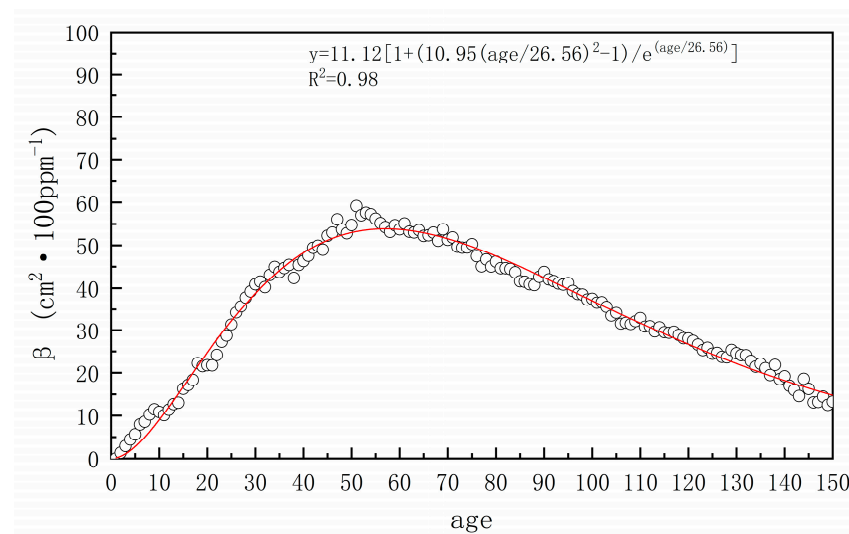


Figure 5. Trends in CO₂ fertilization effect with stand age in the Northern Hemisphere.

The effect of CO₂ fertilization on trees across different climatic zones is ranked as follows: A (tropical) > C (temperate) > B (arid) > D (continental) > E (polar). Trees in the A (tropical) zone experience the most pronounced CO₂ effect, peaking at 48 years ($\beta_A = 156.58 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$). When comparing trees in the B (arid) and C (temperate) regions, no significant difference was observed during the ascending stage, with both reaching maximum growth at 45 years ($\beta_B = 84.44 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$, $\beta_C = 89.22 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$). During the declining stage, as tree age increased, the β value of B (arid) declined more significantly than that of the C (temperate). Compared with B (arid) and C (temperate) regions, trees in the D (continental) region exhibited a lower intensity of response to CO₂ fertilization, peaking at 54 years ($\beta_D = 48.23 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$), but ultimately aligning with the values of the B (arid) region as trees matured. Trees in the E (polar) zone showed the mildest response, peaking at 50 years ($\beta_E = 32.88 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$) and gradually declined annually after that. Table 3 presents results from fitting the model parameters for the various climate zones.

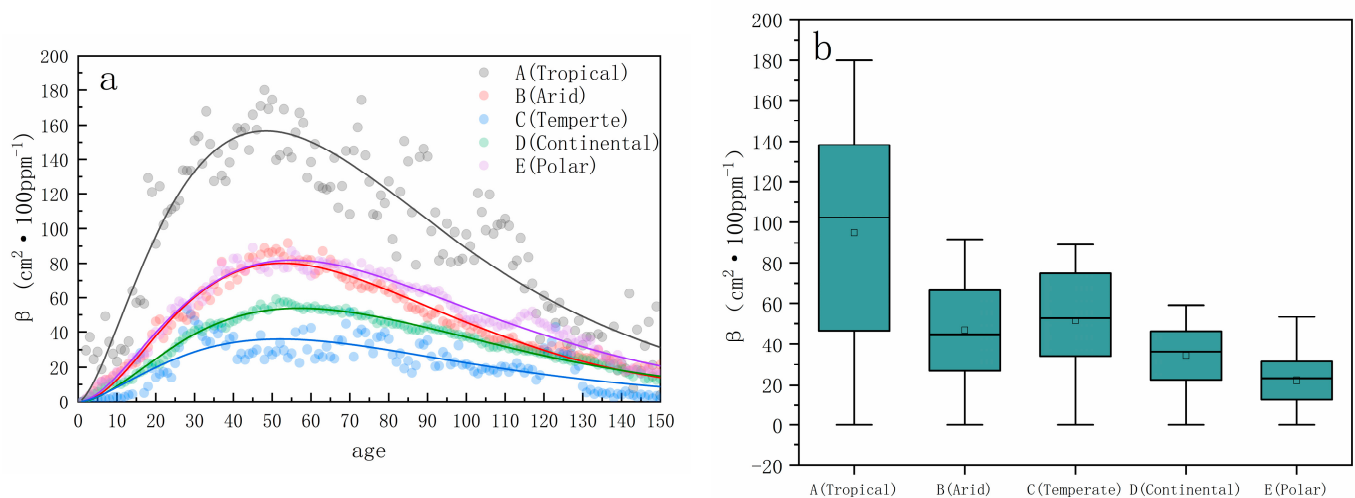


Figure 6. Trends in CO₂ fertilization effect with forest age under different climate zones in the northern hemisphere (a). Comparison of CO₂ fertilization in different Climatic Zones. Boxes represent the interquartile range of the β values (solid lines represent medians, and empty rectangles represent the average value). The upper and lower extension lines extend to 1.5 times the interquartile spacing (b).

Table 3. Fitting results of model parameters for different climate zones.

Climate Zone	Parameters				R ²	SSE	RMSE	RF
	a	b	c	d				
A (Tropical)	26.67	13.29	29.10	1.66	0.86	49508.65	18.41	146
B (Arid)	9.73	13.41	24.22	2.17	0.96	2784.55	4.37	146
C (Temperate)	9.46	16.92	28.85	1.92	0.97	9828.68	8.20	146
D (Continental)	11.25	9.14	29.25	1.95	0.98	521.96	1.89	146
E (Polar)	8.08	9.69	29.99	1.73	0.63	2626.73	4.08	146

3.4. Differences in CO₂ Fertilization Effects across Forest Types

To investigate the response of various stand types to CO₂ fertilization, three climatic zones were chosen: B (arid), C (temperate), and D (continental). The selection ensured adequate sample sizes for each zone. The B (arid) region includes three distinct forest types: evergreen needle-leaved forest (ENF), deciduous needle-leaf forest (DNF), and deciduous broad-leaved forest (DBF). The C (temperate) region features two forest types: ENF and DBF. The D (continental) region encompasses the same three distinct types of forests: ENF, DNF, and DBF.

In the B (arid) region, the effects of CO₂ fertilization on various stand types rank as follows: DNF > ENF > DBF. The DNF reached its peak value at the age of 53 years ($\beta_{\text{DNF}} = 85.35 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$), the ENF peaked at the age of 52 years ($\beta_{\text{ENF}} = 58.48 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$), and the DBF peaked at the age of 47 years ($\beta_{\text{DBF}} = 45.77 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$) (Figure 7).

For the C (temperate) region, the effect of CO₂ fertilization on various stand types is ENF > DBF. The ENF peaked at the age of 55 years ($\beta_{\text{ENF}} = 93.11 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$), and the DBF peaked at the age of 53 years ($\beta_{\text{DBF}} = 51.58 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$) (Figure 8).

In the D (continental) region, the ranking of CO₂ fertilization effects is: DNF > ENF > DBF. The DNF peaked at the age of 50 years ($\beta_{\text{DNF}} = 71.13 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$), the ENF peaked at the age of 57 years ($\beta_{\text{ENF}} = 53.84 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$), and the DBF peaked at the age of 50 years ($\beta_{\text{DBF}} = 45.98 \text{ cm}^2 \cdot 100 \text{ ppm}^{-1}$) (Figure 9).

Across all examined climate zones, needle-leaf forests demonstrated a more pronounced CO₂ fertilization effect compared to broad-leaved forests. Additionally, the CO₂

fertilization effects were more distinct in deciduous forests than in evergreen ones. Table 4 presents the results of model parameter fitting for different stand types.

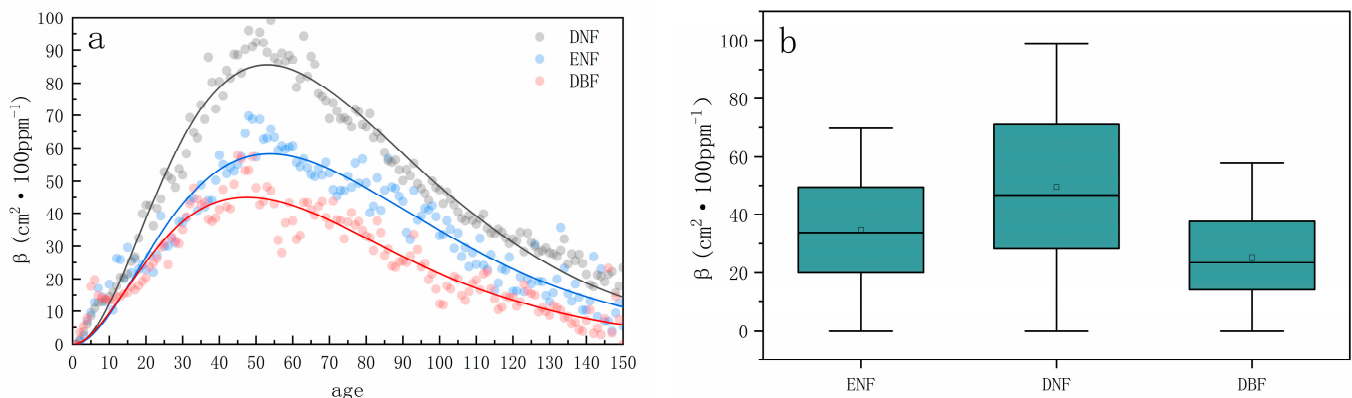


Figure 7. Trends in CO₂ fertilization effect with stand age for different forest types in the B (arid) region (a). Comparison of CO₂ fertilization for different forest types in the B (arid) region. Boxes represent the interquartile range of the β values (solid lines represent medians, and empty rectangles represent the average value). The upper and lower extension lines extend to 1.5 times the interquartile spacing (b).

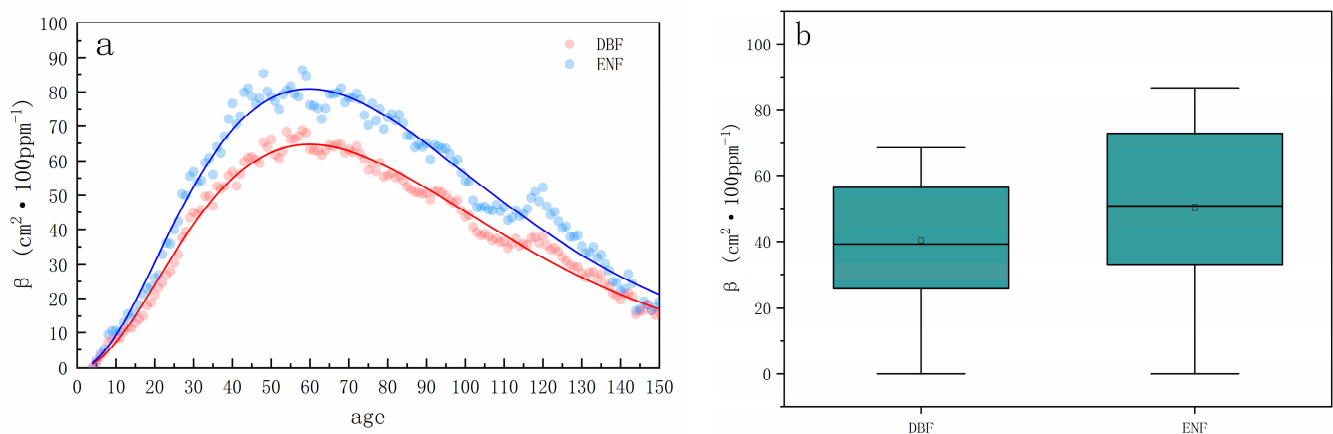


Figure 8. Trends in CO₂ fertilization effect with forest age for different forest types in the C (temperate) region (a). Comparison of CO₂ fertilization for different forest types in the C (temperate) region. Boxes represent the interquartile range of the β values (solid lines represent medians, and empty rectangles represent the average value). The upper and lower extension lines extend to 1.5 times the interquartile spacing (b).

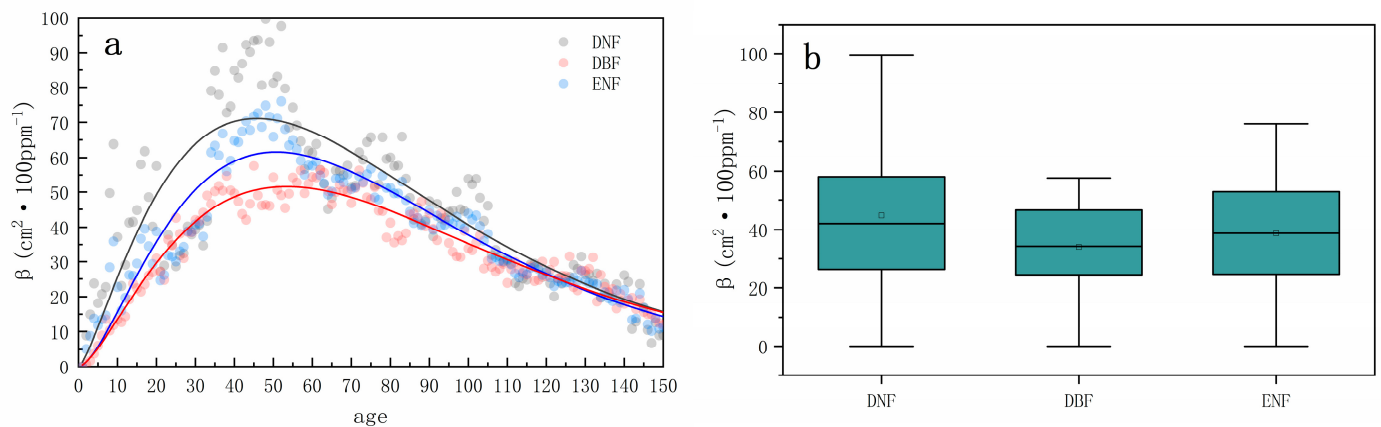


Figure 9. Trends in CO₂ fertilization effect with forest age for different forest types in the D (continental) region (a). Comparison of CO₂ fertilization for different forest types in the D (continental) region. Boxes represent the interquartile range of the β values (solid lines represent medians, and empty rectangles represent the average value). The upper and lower extension lines extend to 1.5 times the interquartile spacing (b).

Table 4. Fitting results of model parameters for different forest types.

Climatic Zone	Stand Type	Parameters				R^2	SSE	RMSE	RF
		a	b	c	d				
B (Arid)	ENF	11.20	11.53	23.42	2.26	0.96	3492.39	4.89	146
	DNF	9.69	9.92	24.96	2.15	0.89	4747.05	5.70	146
	DBF	9.44	8.64	23.45	2.03	0.87	3797.77	5.10	146
C (Temperate)	ENF	13.75	12.52	27.93	1.99	0.96	4287.93	5.42	146
	DBF	10.01	9.42	27.72	2.04	0.97	725.73	2.23	146
	ENF	11.41	12.18	30.35	1.67	0.88	5610.83	6.20	146
D (Continental)	DNF	13.29	13.60	33.01	1.39	0.70	2244.25	12.40	146
	DBF	10.67	11.54	34.43	1.55	0.93	2024.99	3.72	146

4. Discussion

The examination of annual tree rings in the northern hemisphere revealed a pattern in the impact of CO₂ fertilization on trees. This effect was most pronounced during the sapling forest phase, peaked in the middle-aged forest stage, and gradually diminished with the trees' age. When comparing tree responses to increasing atmospheric CO₂ concentrations across various climatic zones, distinct variations were observed. The A (tropical) region demonstrated the most significant effect, followed by the B (arid) and C (temperate) regions, with an average effect in the D (continental) region, and the weakest effect in the E (polar) region. Furthermore, the fertilization effect of atmospheric CO₂ varied among different stand types within the same climatic zones. Needle-leaved forests exhibited a more substantial effect than broad-leaved forests, with deciduous needle-leaf forests displaying the highest CO₂ fertilization effect, while the lowest effect was observed in deciduous broad-leaved forests.

The substrate for plant photosynthesis is atmospheric CO₂; therefore, an increase in atmospheric CO₂ concentration directly enhances the rate of plant photosynthesis by facilitating greater CO₂ uptake [35,36]. Elevated concentrations of atmospheric CO₂ prompt stomatal closure, leading to reduced water evaporation and improved water utilization [11,37,38]. This, in turn, extends the growing season in seasonally arid ecosystems, promoting the accumulation of plant biomass [39,40]. In this study, we consider the combined effect of several factors, encompassing not only the direct impact of carbon dioxide on photosynthesis but also the indirect effects resulting from increased temperatures.

The Investigation into tree annual rings in the northern hemisphere revealed that the effect of CO₂ fertilization on trees peaks during the middle-aged forest stage. It becomes more pronounced during the sapling forest phase and then slowly diminishes as the trees age. The study indicates that while young trees can help offset atmospheric CO₂ concentrations, this ability lessens as they mature. Various CO₂ enrichment experiments have demonstrated that elevated CO₂ levels significantly influence juvenile trees or seedlings. In high CO₂ environments, seedlings or young trees often grow faster than their mature counterparts. This rapid growth is due to young trees having a greater ability for photosynthesis [40–43]. Elevated CO₂ levels promote photosynthesis, increase nutrient uptake and utilization efficiency, and thus support faster growth and development [44]. At the same time, research indicates that higher CO₂ levels notably enhance water use efficiency in trees during their early growth stage and promote increased biomass [22]. Trees in sapling and middle-aged forest stages are more sensitive to increased atmospheric CO₂ concentrations [9,22]. However, as trees grow older, they face greater nutrient and water constraints [41,45–47]. Elevated concentrations of CO₂ [48–50] can exacerbate these limitations, reducing the benefits of CO₂ fertilization [51–53]. Some studies suggest that tree growth might adapt to these higher CO₂ concentrations over time [54].

Comparing the response of trees to increasing atmospheric CO₂ levels across different climatic regions, we noted variations in the CO₂ fertilization effect. The A (tropical) region displayed the most noticeable effect, followed by the B (arid) and C (temperate) regions with even more pronounced effects, while the D (continental) region exhibited an average effect, and the E (polar) region showed the least discernible effect. The factors contributing to this outcome are as follows: Firstly, analyzing from the perspective of temperature. When examining the interaction between increasing CO₂ concentrations and temperature, researchers found that the potential carbon uptake lost to photorespiration increases as temperature rises [55]. The influence of CO₂ concentration on plant growth affects both leaf photosynthesis and overall plant respiration [56]. As dark respiration depends on temperature, increased temperatures amplify plant respiration rates. This, in turn, reduces the plant's carbohydrate content, limiting respiration and stunting growth [55,57]. Nevertheless, some studies suggest that the CO₂ fertilization effect is negligible in tropical regions or has a minimal effect on tree growth in the tropics [17,58]; this finding diverges from the current study, potentially due to the limited number of sampling locations in tropical areas, uneven distribution causing an incomplete representation of the climatic zone, and variances in the tree species studied. In high-CO₂ environments, upregulation of photosynthesis produces extra carbohydrates, which can meet the increased energy demand for respiration in warmer conditions [54]. Low temperatures might hamper carboxylase activity, offsetting the effects of rising atmospheric CO₂ levels on plant growth [59,60]. Trees in subtropical regions, characterized by warmer and wetter conditions, experience a more pronounced CO₂ fertilization effect, which diminishes in cooler temperatures. Secondly, taking into account the water-use efficiency. With higher atmospheric CO₂ concentrations, trees under drought stress might benefit from increased water-use efficiency, helping to alleviate drought effects and postpone the decrease in photosynthesis due to stomatal closure [61]. This allows for a prolonged growing season [25]. Several studies emphasize that in dry ecosystems, raised CO₂ levels can enhance water use efficiency, subsequently increasing plant biomass [39,42,48,49,62]. Ecosystems in warm, somewhat dry regions with adequate nitrogen supply might show the most significant responsiveness to CO₂ [9]. Elevated CO₂ concentrations' most noticeable effect on tree radial growth appears in areas with the most limited water resources, as confirmed by research [50]. The collective findings from these studies consistently highlight a more noticeable CO₂ fertilization effect on trees in dry areas.

Regarding different forest stand types, the study unveiled a more prominent CO₂ fertilization effect in needle-leaved forests compared to broad-leaved forests. According to a study, the distinct physiological and ecological traits of needle-leaved forests and broad-leaved forests result in heightened water utilization in needle-leaf forests compared with their broad-leaved counterparts [63]. Simultaneously, the higher leaf build-up efficiency of needle-leaved forests leads to the ability to induce faster and stronger growth of LAI when stimulated by CO₂ growth, subsequently resulting in enhanced photosynthesis in needle-leaf forests [64,65]. All indications point to a more pronounced atmospheric CO₂ fertilization effect in needle-leaved forests than in broad-leaved forests under identical environmental conditions. This study found that the CO₂ fertilization effect was more pronounced in deciduous needle-leaf forests than in evergreen needle-leaf forests in both B (arid) and D (continental) regions. The radial growth of both coniferous and deciduous trees peaks a few weeks after needle lengthening, largely relying on assimilates from the current year [66,67]. Conversely, evergreen conifers begin radial growth before needle development, drawing on stored carbon [68]. deciduous needle-leaf forests have shown more efficient utilization of carbon in the current year. The effects of climate change on photosynthesis are more detrimental to evergreen species more than deciduous species [69–72]. With global warming, deciduous needle-leaf forests demonstrate stronger photosynthetic activity than that in evergreen needle-leaf forests.

This study leverages the existing international tree ring database in the northern hemisphere to conduct a comprehensive analysis of the relationship between forest age changes and the atmospheric CO₂ fertilization effect. Additionally, it explores changes in different climatic zones and forest types, contributing to our understanding of future carbon sink dynamics. However, some limitations still need to be acknowledged. (1) A multitude of studies have demonstrated that elevated carbon dioxide concentrations hasten the senescence of trees and reduce their turnover times [73,74]. However, due to a lack of sufficient data, these variables were not taken into account in this research. Consequently, this study solely represents the average response of individual trees to carbon dioxide across different climate zones and forest types and should not be taken as indicative of entire forest ecosystems. In future research, we intend to collect additional data to enable a more thorough discussion and analysis. (2) Due to limited data available in the ITRDB regarding broad-leaf forests, a comparison between broad-leaf deciduous forests and broad-leaf evergreen forests was not feasible. Gathering more extensive data in the future is imperative to evaluate the effect of CO₂ fertilization on various stand types.

5. Conclusions

This study utilizes the ITRDB to examine the correlation between the CO₂ fertilization effect and forest age. It aimed to compare variations in the CO₂ fertilization effect across diverse climatic zones and stand types. The results of the study are as follows: (a) The effect of CO₂ fertilization increases with forest age, showing an ascending pattern from sapling forests to middle-aged forests. However, this effect declines as the trees mature. Notably, young forests exhibit a higher CO₂ fertilization effect than their older counterparts. (b) The effect of trees on CO₂ fertilization is more pronounced in warm and arid environments. (c) Coniferous forests display a greater CO₂ fertilization effect than broad-leaf forests. Additionally, deciduous needle-leaf forests have a more pronounced CO₂ fertilization effect than evergreen needle-leaf forests. The findings suggest that younger trees have the potential to significantly mitigate the increase in atmospheric CO₂ levels. Moreover, trees in hotter and drier climates show a heightened response to increased CO₂ concentrations, enhancing their ability to offset carbon emissions. Conifer species have a superior ability to mitigate carbon emissions in comparison to broad-leaved species. This research broadens the global carbon cycle perspective through the analysis of tree annual rings and investigates the response of forests to escalating CO₂ levels.

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References

- MacCracken, M.C. Prospects for Future Climate Change and the Reasons for Early Action. *J. Air Waste Manag. Assoc.* **2008**, *58*, 735–786. [[CrossRef](#)] [[PubMed](#)]
- Friedlingstein, P.; O’Sullivan, M.; Jones, M.W.; Andrew, R.M.; Luke, G.; Hauck, J.; Le Corinne, Q.; Luijkx, I.T.; Olsen, A.; Peters, G.P.; et al. Global Carbon Budget 2022. *Earth Syst. Sci. Data* **2022**, *14*, 4811–4900. [[CrossRef](#)]
- He, M.; Piao, S.; Huntingford, C.; Xu, H.; Wang, X.; Bastos, A.; Cui, J.; Gasser, T. Amplified warming from physiological responses to carbon dioxide reduces the potential of vegetation for climate change mitigation. *Commun. Earth Environ.* **2022**, *3*, 160. [[CrossRef](#)]
- Gifford, L. See the Carbon through the Trees: Market-Based Climate Change Mitigation, Forest Carbon Offsets and the Uneven Power of Carbon Accounting. Ph.D. Thesis, University of Colorado, Boulder, CO, USA, 2018.
- Yue, C.; Ciais, P.; Cadule, P.; Thonicke, K.; van Leeuwen, T.T. Modelling the role of fires in the terrestrial carbon balance by incorporating SPITFIRE into the global vegetation model ORCHIDEE—Part 2: Carbon emissions and the role of fires in the global carbon balance. *Geosci. Model Dev.* **2015**, *8*, 1321–1338. [[CrossRef](#)]
- Gampe, D.; Zscheischler, J.; Reichstein, M.; O’Sullivan, M.; Smith, W.K.; Sitch, S.; Buermann, W. Increasing impact of warm droughts on northern ecosystem productivity over recent decades. *Nat. Clim. Change* **2021**, *11*, 772–779. [[CrossRef](#)]
- Piao, S.; Sitch, S.; Ciais, P.; Friedlingstein, P.; Peylin, P.; Wang, X.; Ahlström, A.; Anav, A.; Canadell, J.G.; Cong, N. Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO₂ trends. *Glob. Change Biol.* **2013**, *19*, 2117–2132. [[CrossRef](#)] [[PubMed](#)]
- Bacastow, R.; Keeling, C.D. Atmospheric carbon dioxide and radiocarbon in the natural carbon cycle: II. Changes from AD 1700 to 2070 as deduced from a geochemical model. In Proceedings of the Brookhaven Symposia in Biology, Upton, NY, USA, 16–18 May 1972; pp. 86–135.
- Huang, J.-G.; Bergeron, Y.; Denneler, B.; Berninger, F.; Tardif, J. Response of forest trees to increased atmospheric CO₂. *Crit. Rev. Plant Sci.* **2007**, *26*, 265–283. [[CrossRef](#)]
- Bazzaz, F.A. The response of natural ecosystems to the rising global CO₂ levels. *Annu. Rev. Ecol. Syst.* **1990**, *21*, 167–196. [[CrossRef](#)]
- Field, C.B.; Jackson, R.B.; Mooney, H.A. Stomatal responses to increased CO₂: Implications from the plant to the global scale. *Plant Cell Environ.* **1995**, *18*, 1214–1225. [[CrossRef](#)]
- Norby, R.J.; Zak, D.R. Ecological lessons from free-air CO₂ enrichment (FACE) experiments. *Annu. Rev. Ecol. Syst.* **2011**, *42*, 181–203. [[CrossRef](#)]
- Jiang, G.; Qu, C. Photosynthetic response of six woody species to elevated CO₂ in quercus liaotungensis forest in the beijing mountainous areas. *Chin. J. Plant Ecol.* **2000**, *24*, 204–208.
- Li, Z.; Chen, W.; Wei, J.; Keyimu, M.; Zhang, Y.; Zhang, S.; Wang, X. Tree-ring growth responses of Liaodong Oak (*Quercus wutaishanica*) to climate in the Beijing Dongling Mountain of China. *Acta Ecol. Sin.* **2021**, *41*, 27–37.
- Babst, F.; Alexander, M.R.; Szejner, P.; Bouriaud, O.; Klesse, S.; Roden, J.; Ciais, P.; Poulter, B.; Frank, D.; Moore, D.J. A tree-ring perspective on the terrestrial carbon cycle. *Oecologia* **2014**, *176*, 307–322. [[CrossRef](#)] [[PubMed](#)]
- Fritts, H. *Tree Rings and Climate*; Elsevier: Amsterdam, The Netherlands, 2012.
- Battipaglia, G.; Zalloni, E.; Castaldi, S.; Marzaioli, F.; Cazzolla-Gatti, R.; Lasserre, B.; Tognetti, R.; Marchetti, M.; Valentini, R.J. Long tree-ring chronologies provide evidence of recent tree growth decrease in a central African tropical forest. *PLoS ONE* **2015**, *10*, e0120962. [[CrossRef](#)] [[PubMed](#)]
- Cook, E.R.; Peters, K. The smoothing spline: A new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bull.* **1981**, *41*, 45–53.
- Biondi, F.; Qeadan, F.J. A theory-driven approach to tree-ring standardization: Defining the biological trend from expected basal area increment. *Tree-Ring Res.* **2008**, *64*, 81–96. [[CrossRef](#)]

20. Wu, X.; Shao, X. Status of dendroclimatological study and its prospects in China. *Adv. Earth Sci.* **1993**, *8*, 31–35.
21. Chen, Z.; Zhang, X.; He, X.; Davi, N.K.; Li, L.; Bai, X. Response of radial growth to warming and CO₂ enrichment in southern Northeast China: A case of *Pinus tabulaeformis*. *Clim. Change* **2015**, *130*, 559–571. [\[CrossRef\]](#)
22. Geoff Wang, G.; Chhin, S.; Bauerle, W.L. Effect of natural atmospheric CO₂ fertilization suggested by open-grown white spruce in a dry environment. *Glob. Change Biol.* **2006**, *12*, 601–610. [\[CrossRef\]](#)
23. Huang, J.-G.; Zhang, Q.-B. Tree rings and climate for the last 680 years in Wulan area of northeastern Qinghai-Tibetan Plateau. *Clim. Change* **2007**, *80*, 369–377. [\[CrossRef\]](#)
24. Graybill, D.A.; Idso, S.B. Detecting the aerial fertilization effect of atmospheric CO₂ enrichment in tree-ring chronologies. *Glob. Biogeochem. Cycles* **1993**, *7*, 81–95. [\[CrossRef\]](#)
25. Knapp, P.A.; Soule, P.T.; Grissino-Mayer, H.D. Detecting potential regional effects of increased atmospheric CO₂ on growth rates of western juniper. *Glob. Change Biol.* **2001**, *7*, 903–917. [\[CrossRef\]](#)
26. Schweingruber, F.; Briffa, K.; Nogler, P. A tree-ring densitometric transect from Alaska to Labrador: Comparison of ring-width and maximum-latewood-density chronologies in the conifer belt of northern North America. *Int. J. Biometeorol.* **1993**, *37*, 151–169. [\[CrossRef\]](#)
27. Girardin, M.P.; Bernier, P.Y.; Raulier, F.; Tardif, J.C.; Conciatori, F.; Guo, X.J. Testing for a CO₂ fertilization effect on growth of Canadian boreal forests. *J. Geophys. Res. Biogeosci.* **2011**, *116*, G01012. [\[CrossRef\]](#)
28. Zhao, S.; Pederson, N.; D'Orangeville, L.; HilleRisLambers, J.; Boose, E.; Penone, C.; Bauer, B.; Jiang, Y.; Manzanedo, R.D. The International Tree-Ring Data Bank (ITRDB) revisited: Data availability and global ecological representativity. *J. Biogeogr.* **2019**, *46*, 355–368. [\[CrossRef\]](#)
29. Neftel, A.; Friedli, H.; Moor, E.; Lötscher, H.; Oeschger, H.; Siegenthaler, U.; Stauffer, B.J.T. Historical carbon dioxide record from the Siple Station ice core. *J. Geophys. Res. Atmos.* **1994**, *93*, 92093–0444.
30. Girardin, M.P.; Bouriaud, O.; Hogg, E.H.; Kurz, W.; Zimmermann, N.E.; Metsaranta, J.M.; de Jong, R.; Frank, D.C.; Esper, J.; Büntgen, U. No growth stimulation of Canada's boreal forest under half-century of combined warming and CO₂ fertilization. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, E8406–E8414. [\[CrossRef\]](#) [\[PubMed\]](#)
31. Wang, S.; Zhang, Y.; Ju, W.; Chen, J.M.; Ciais, P.; Cescatti, A.; Sardans, J.; Janssens, I.A.; Wu, M.; Berry, J.A. Recent global decline of CO₂ fertilization effects on vegetation photosynthesis. *Science* **2020**, *370*, 1295–1300. [\[CrossRef\]](#)
32. Climatic Research Unit, Met Office. CRU TS Version 4.05. Available online: https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.05/ (accessed on 20 June 2022).
33. Hegglin, M.; Kinnison, D.; Lamarque, J.-F. CCMi nitrogen surface fluxes in support of CMIP6—Version 2.0. Version 20160706. Earth Syst. Grid Fed. Available online: <https://www.wdc-climate.de/ui/cmip6?input=input4MIPs.CMIP6.CMIP.NCAR.NCAR-CCMI-2-0> (accessed on 20 June 2022).
34. Beck, H.E.; Zimmermann, N.E.; McVicar, T.R.; Vergopolan, N.; Berg, A.; Wood, E.F. Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Sci. Data* **2018**, *5*, 180214. [\[CrossRef\]](#)
35. Amthor, J.S. Terrestrial higher-plant response to increasing atmospheric [CO₂] in relation to the global carbon cycle. *Glob. Change Biol.* **1995**, *1*, 243–274. [\[CrossRef\]](#)
36. Arp, W. Effects of source-sink relations on photosynthetic acclimation to elevated CO₂. *Plant Cell Environ.* **1991**, *14*, 869–875. [\[CrossRef\]](#)
37. Bowes, G. Facing the inevitable: Plants and increasing atmospheric CO₂. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **1993**, *44*, 309–332. [\[CrossRef\]](#)
38. Farquhar, G.D.; Ehleringer, J.R.; Hubick, K.T. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **1989**, *40*, 503–537. [\[CrossRef\]](#)
39. Ceulemans, R.; Mousseau, M. Tansley Review No. 71 Effects of elevated atmospheric CO₂ on woody plants. *New Phytol.* **1994**, *127*, 425–446. [\[CrossRef\]](#)
40. Saxe, H.; Ellsworth, D.S.; Heath, J. Tree and forest functioning in an enriched CO₂ atmosphere. *New Phytol.* **1998**, *139*, 395–436. [\[CrossRef\]](#)
41. Körner, C. Plant CO₂ responses: An issue of definition, time and resource supply. *New Phytol.* **2006**, *172*, 393–411. [\[CrossRef\]](#) [\[PubMed\]](#)
42. Norby, R.J.; Wullschlegel, S.D.; Gunderson, C.A.; Johnson, D.W.; Ceulemans, R. Tree responses to rising CO₂ in field experiments: Implications for the future forest. *Plant Cell Environ.* **1999**, *22*, 683–714. [\[CrossRef\]](#)
43. Wang, X. Effects of species richness and elevated carbon dioxide on biomass accumulation: A synthesis using meta-analysis. *Oecologia* **2007**, *152*, 595–605. [\[CrossRef\]](#)
44. Ryan, M.G.; Binkley, D.; Fownes, J.H. Age-related decline in forest productivity: Pattern and process. *Adv. Ecol. Res.* **1997**, *27*, 213–262.
45. Ellsworth, D.S.; Anderson, I.C.; Crous, K.Y.; Cooke, J.; Drake, J.E.; Gherlenda, A.N.; Gimeno, T.E.; Macdonald, C.A.; Medlyn, B.E.; Powell, J.R. Elevated CO₂ does not increase eucalypt forest productivity on a low-phosphorus soil. *Nat. Commun.* **2017**, *7*, 279–282. [\[CrossRef\]](#)

46. Oren, R.; Ellsworth, D.S.; Johnsen, K.H.; Phillips, N.; Ewers, B.E.; Maier, C.; Schäfer, K.V.; McCarthy, H.; Hendrey, G.; McNulty, S.G. Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature* **2001**, *411*, 469–472. [\[CrossRef\]](#)
47. Sigurdsson, B.D.; Medhurst, J.L.; Wallin, G.; Eggertsson, O.; Linder, S.J. Growth of mature boreal Norway spruce was not affected by elevated [CO₂] and/or air temperature unless nutrient availability was improved. *Tree Physiol.* **2013**, *33*, 1192–1205. [\[CrossRef\]](#)
48. Lloyd, J.; Farquhar, G. The CO₂ dependence of photosynthesis, plant growth responses to elevated atmospheric CO₂ concentrations and their interaction with soil nutrient status. I. General principles and forest ecosystems. *Funct. Ecol.* **1996**, *10*, 4–32. [\[CrossRef\]](#)
49. Schlesinger, W.H.; Lichter, J. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂. *Nature* **2001**, *411*, 466–469. [\[CrossRef\]](#) [\[PubMed\]](#)
50. Soulé, P.T.; Knapp, P.A. Radial growth rate increases in naturally occurring ponderosa pine trees: A late-20th century CO₂ fertilization effect? *Glob. Change Biol.* **2006**, *171*, 379–390. [\[CrossRef\]](#) [\[PubMed\]](#)
51. Cotrufo, M.F.; Ineson, P.; Scott, A. Elevated CO₂ reduces the nitrogen concentration of plant tissues. *Glob. Change Biol.* **1998**, *4*, 43–54. [\[CrossRef\]](#)
52. Luo, Y.; Su, B.; Currie, W.S.; Dukes, J.S.; Finzi, A.; Hartwig, U.; Hungate, B.; McMurtrie, R.E.; Oren, R.; Parton, W.J. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* **2004**, *54*, 731–739. [\[CrossRef\]](#)
53. Norby, R.J.; Warren, J.M.; Iversen, C.M.; Medlyn, B.E.; McMurtrie, R.E. CO₂ enhancement of forest productivity constrained by limited nitrogen availability. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 19368–19373. [\[CrossRef\]](#) [\[PubMed\]](#)
54. Loehle, C. Anomalous responses of plants to CO₂ enrichment. *Oikos* **1995**, *73*, 181–187. [\[CrossRef\]](#)
55. Long, S. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated? *Plant Cell Environ.* **1991**, *14*, 729–739. [\[CrossRef\]](#)
56. Desjardins, R.; Gifford, R.; Nilson, T.; Greenwood, E.; Gifford, R. Interaction of carbon dioxide with growth-limiting environmental factors in vegetation productivity: Implications for the global carbon cycle. In *Advances in Bioclimatology*; Springer: Berlin/Heidelberg, Germany, 1992; pp. 24–58.
57. Rowland-Bamford, A.; Baker, J.; Allen, L., Jr.; Bowes, G. Interactions of CO₂ enrichment and temperature on carbohydrate accumulation and partitioning in rice. *Environ. Exp. Bot.* **1996**, *36*, 111–124. [\[CrossRef\]](#)
58. Van Der Sleen, P.; Groenendijk, P.; Vlam, M.; Anten, N.P.; Boom, A.; Bongers, F.; Pons, T.L.; Terburg, G.; Zuidema, P.A. No growth stimulation of tropical trees by 150 years of CO₂ fertilization but water-use efficiency increased. *Nat. Geosci.* **2015**, *8*, 24–28. [\[CrossRef\]](#)
59. Hendrickson, L.; Ball, M.; Wood, J.; Chow, W.; Furbank, R.T. Low temperature effects on photosynthesis and growth of grapevine. *Plant Cell Environ.* **2004**, *27*, 795–809. [\[CrossRef\]](#)
60. Sage, R.F.; Kubien, D.S. The temperature response of C3 and C4 photosynthesis. *Plant Cell Environ.* **2007**, *30*, 1086–1106. [\[CrossRef\]](#) [\[PubMed\]](#)
61. Owensby, C.E.; Ham, J.M.; Knapp, A.K.; Auen, L.M. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO₂. *Glob. Change Biol.* **1999**, *5*, 497–506. [\[CrossRef\]](#)
62. Curtis, P.S.; Wang, X. A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* **1998**, *113*, 299–313. [\[CrossRef\]](#) [\[PubMed\]](#)
63. Li, X.; Piao, S.; Wang, K.; Wang, X.; Wang, T.; Ciais, P.; Chen, A.; Lian, X.; Peng, S.; Peñuelas, J.; et al. Temporal trade-off between gymnosperm resistance and resilience increases forest sensitivity to extreme drought. *Nat. Ecol. Evol.* **2020**, *4*, 1075–1083. [\[CrossRef\]](#)
64. McGroddy, M.E.; Daufresne, T.; Hedin, L.O. Scaling of C:N:P stoichiometry in forests worldwide: Implications of terrestrial redfield-type ratios. *Ecology* **2004**, *85*, 2390–2401. [\[CrossRef\]](#)
65. Niklas, K.J. Plant allometry, leaf nitrogen and phosphorus stoichiometry, and interspecific trends in annual growth rates. *Ann. Bot.* **2006**, *97*, 155–163. [\[CrossRef\]](#)
66. Hansen, J.; Beck, E. The fate and path of assimilation products in the stem of 8-year-old Scots pine (*Pinus sylvestris* L.) trees. *Trees* **1990**, *4*, 16–21. [\[CrossRef\]](#)
67. Oribe, Y.; Funada, R.; Kubo, T. Relationships between cambial activity, cell differentiation and the localization of starch in storage tissues around the cambium in locally heated stems of *Abies sachalinensis* (Schmidt) Masters. *Trees* **2003**, *17*, 185–192. [\[CrossRef\]](#)
68. Oberhuber, W.; Swidrak, I.; Pirkebner, D.; Gruber, A. Temporal dynamics of nonstructural carbohydrates and xylem growth in *Pinus sylvestris* exposed to drought. *Can. J. For. Res.* **2011**, *41*, 1590–1597. [\[CrossRef\]](#) [\[PubMed\]](#)
69. Kurepin, L.V.; Stangl, Z.R.; Ivanov, A.G.; Bui, V.; Mema, M.; Hüner, N.P.; Öquist, G.; Way, D.; Hurry, V. Contrasting acclimation abilities of two dominant boreal conifers to elevated CO₂ and temperature. *Plant Cell Environ.* **2018**, *41*, 1331–1345. [\[CrossRef\]](#) [\[PubMed\]](#)
70. Way, D.A.; Sage, R.F. Elevated growth temperatures reduce the carbon gain of black spruce [*Picea mariana* (Mill.) BSP]. *Glob. Change Biol.* **2008**, *14*, 624–636. [\[CrossRef\]](#)
71. Way, D.A.; Sage, R.F. Thermal acclimation of photosynthesis in black spruce [*Picea mariana* (Mill.) BSP]. *Plant Cell Environ.* **2008**, *31*, 1250–1262. [\[CrossRef\]](#)
72. Zhang, X.W.; Wang, J.R.; Ji, M.F.; Milne, R.I.; Wang, M.H.; Liu, J.-Q.; Shi, S.; Yang, S.-L.; Zhao, C.-M. Higher thermal acclimation potential of respiration but not photosynthesis in two alpine *Picea* taxa in contrast to two lowland congeners. *PLoS ONE* **2015**, *10*, e0123248. [\[CrossRef\]](#)

73. Needham, J.F.; Chambers, J.; Fisher, R.; Knox, R.; Koven, C.D. Forest responses to simulated elevated CO₂ under alternate hypotheses of size-and age-dependent mortality. *Glob. Change Biol.* **2020**, *26*, 5734–5753. [[CrossRef](#)]
74. Yu, K.; Smith, W.K.; Trugman, A.T.; Condit, R.; Hubbell, S.P.; Sardans, J.; Peng, C.; Zhu, K.; Peñuelas, J.; Cailleret, M.; et al. Pervasive decreases in living vegetation carbon turnover time across forest climate zones. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 24662–24667. [[CrossRef](#)]

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