

Article

Diurnal, Seasonal, and Vertical Changes in Photosynthetic Rates in *Cinamomum camphora* Forests in Subtropical China

Zhiqiang Li ^{1,2}, Qinxiang Wu ¹, Yuanying Peng ³ , Junjie Lei ¹, Shuguang Liu ^{1,2}, Can Mao ¹, Xin Liu ¹, Jun Wang ^{1,2}, Wende Yan ^{1,2,*} and Xiaoyong Chen ^{4,*} 

¹ College of Life Science and Technology, Central South University of Forestry and Technology, Changsha 410004, China; lizhiqiang@csuft.edu.cn (Z.L.); 15971398770@163.com (J.L.); shuguang.liu@yahoo.com (S.L.)

² National Engineering Laboratory for Applied Forest Ecological Technology in Southern China, Changsha 410004, China

³ College of Arts and Sciences, Lewis University, Romeoville, IL 60446, USA; pengyu@lewisu.edu

⁴ College of Arts and Sciences, Governors State University, University Park, IL 60484, USA

* Correspondence: csfuywd@hotmail.com (W.Y.); xchen@govst.edu (X.C.)

Abstract: The increase in the global atmospheric CO₂ concentration is expected to increase the productivity of forests, but the dynamic processes of such increased productivity in the forest canopy remain unclear. In this study, diurnal and seasonal variations and vertical changes in photosynthetic rates were investigated in Camphor tree (*Cinamomum camphora*) forests in subtropical China. The effect of photosynthetically active radiation (PAR) and CO₂ concentrations on photosynthetic rates were also examined in the studied forests. Results showed the diurnal patterns of photosynthesis exhibited two peaks on sunny days, but only one peak on cloudy days. The daily average photosynthetic rate on cloudy days was approximately 74% of that on sunny days. The photosynthetic rate decreased along the vertical forest canopy profile. If the photosynthetic rate in the upper canopy layer was 100%, the corresponding rates were 83% and 25% in the middle and lower canopy layers, respectively. The rates of dark respiration derived from the PAR response curve were 1.73, 1.25, and 1.0 μmol m⁻² s⁻¹ for the upper, middle, and lower canopy layers, respectively. The apparent quantum yield of photosynthesis was 0.0183, 0.0186, and 0.0327 μmol CO₂ μmol⁻¹ PAR for the upper, middle, and lower canopy, respectively. The initial slope of the photosynthetic response curve to CO₂ was highest in the upper canopy and lowest in the lower canopy. The seasonal variation in photosynthetic rates exhibited a two-peaked pattern at all canopy positions, with the two peaks occurring in June and September. The stand biomass and biomass carbon storage were 144.7 t ha⁻¹ and 71.6 t C ha⁻¹ in the examined forests, respectively. The study provides a scientific reference for future research on accessing carbon sequestration and designing forest management practices, specifically in regulating canopy structure in subtropical regions.



Citation: Li, Z.; Wu, Q.; Peng, Y.; Lei, J.; Liu, S.; Mao, C.; Liu, X.; Wang, J.; Yan, W.; Chen, X. Diurnal, Seasonal, and Vertical Changes in Photosynthetic Rates in *Cinamomum camphora* Forests in Subtropical China. *Forests* **2024**, *15*, 183. <https://doi.org/10.3390/f15010183>

Academic Editor: Francois Girard

Received: 20 November 2023

Revised: 9 January 2024

Accepted: 15 January 2024

Published: 17 January 2024



Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

Keywords: photosynthetic rate; dynamic process; forest canopy; camphor tree

1. Introduction

Forests actively sequester atmospheric carbon dioxide through photosynthesis and play a vital role in offsetting anthropogenic carbon emissions and mitigating climate change [1]. Over the past two decades, there has been a growing worldwide concern regarding the rise in greenhouse gases and their potential impacts on global environmental change [2]. CO₂ stands as a major greenhouse gas and plays a pivotal role in global warming [3]. Due to the extensive coverage of forests across the planet, the study of CO₂ flux, carbon balance, and net productivity within forest ecosystems has become a central focus of research in the field of forest ecosystems [4,5]. It is widely recognized that photosynthesis is a crucial mechanism for removing CO₂ from the atmosphere and storing it in the

biosphere [6,7]. Therefore, understanding the photosynthetic characteristics of individual tree species and various forest ecosystems has become of imperative importance [8,9].

Photosynthesis is the process through which green plants capture solar energy and use it to convert carbon dioxide and water into reduced carbon compounds [10]. It stands as the most significant CO₂ flux within forest ecosystems and is the biological mechanism responsible for carbon sequestration by forests. Remarkably, it is estimated that photosynthetic organisms fix approximately 1.0×10^{14} kg of carbon into organic compounds annually. To put this in perspective, this amount is equivalent to about 1% of the world's known reserves of fossil fuels, including coal, gas, and oil, or roughly 10 times the world's current annual energy consumption [11]. Canopy photosynthetic productivity serves as the primary driver for promoting and sustaining forest formation and serves as the primary energy source for canopy carbon supply and metabolism [12,13]. The vertical distribution of the canopy directly influences trees' photosynthetic capacity and growth [14], consequently impacting the overall performance and productivity of the entire forest stand [15–17]. This dependence on photosynthetic productivity stems from the complex interplay of factors, including the three-dimensional forest stand structure, canopy leaf photosynthetic capacity, and the efficiency of light interception and conversion under specific environmental conditions [18–20]. Understanding the influence of canopy vertical distribution on photosynthetic productivity is crucial for comprehending forest productivity formation and enhancing the ecosystem's carbon sequestration capacity [21]. Therefore, it is important to develop forest management strategies and investigate forest productivity from an ecological and physiological perspective [22,23].

Significant variations exist in the vertical distribution of light within the layers of the forest canopy [24,25]. The light environment in forests varies significantly based on stand age, species composition, and stand structure [26]. For instance, in young forest stands, relative light intensity does not consistently decrease from the top to the bottom due to incomplete canopy closure and the presence of gaps between neighboring trees, allowing light to enter from various angles, not just from above [27]. In old Douglas fir trees, a local light intensity peak occurs near the middle canopy because of the lateral penetration of diffused light [19,24,25]. The utilization of forest light energy is influenced by the vertical distribution of the canopy [28]. Photosynthetic rates exhibited variability across canopy layers; in oak trees, the net assimilation of lower canopy leaves underwent a more significant decrease compared to sunlit leaves on the upper canopy [29]. Numerous studies have been conducted to examine the photosynthetic characteristics of selected tree species within evergreen broad-leaved forests in subtropical regions. For example, studies investigated the photosynthetic properties of two key tree species, evergreen Chinkapin (*Castanopsis fissa*) and Guger tree (*Schima superba* garden), in the subtropical region under varying CO₂ concentrations [30]. The findings revealed that, compared to values under 350 $\mu\text{mol mol}^{-1}$ CO₂, the photosynthetic rates of these species increased by 79% and 95%, respectively, under 500 $\mu\text{mol mol}^{-1}$ CO₂. In a separate study, light saturation points ranging from 1000 to 1900 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation (PAR), light compensation points ranging from 4.8 to 30.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of PAR, and a maximum photosynthetic rate of 13.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for mature Chinese fir were reported [31].

The environmental conditions, specifically the contrast between cloudy and sunny conditions, along with seasonal variations, play a crucial role in influencing the rate of photosynthesis. Numerous studies have explored the intricate interplay between light intensity, temperature, and atmospheric conditions on photosynthetic processes. Furthermore, the impact of seasonal changes, such as variations in temperature and day length, can significantly alter the overall photosynthetic activity of plants. For instance, a more even distribution of light among leaves across the vertical profile of the canopy is considered the most important factor contributing to this difference [32]. The cloud cover had a significant impact on carbon exchange between the biota and the atmosphere and an increase in the fraction of diffuse radiation enhances the photosynthetic efficiency of canopies [32]. A study reported that all physiological observations were 2–3 times lower under cloudy conditions

in the rainy season [33]. However, an observation found that on a daily timescale, Net ecosystem productivity (NEP) and gross primary production (GPP) were higher under both cloudy and sunny conditions compared to overcast conditions across seasons. Specifically, the daily NEP and GPP during the wet season peaked under cloudy skies [34]. Studies have demonstrated that net photosynthetic rates decline rapidly as temperatures increase above the optimal temperature [35,36]. Seasonal temperature changes also affected net photosynthetic rates; net photosynthetic rates were highest in spring and autumn, and lowest in July, August, and December–January in Douglas Fir Seedlings [37].

As a native species in China, the Camphor tree (*Cinnamomum camphora* (L.) J. Presl) is an evergreen broadleaf tree species widely distributed in tropical and subtropical regions of the nation, with a history of exploitation and utilization spanning over a thousand years [38]. Characterized by relatively fast growth, high-quality timber, and abundant camphor oil production, the Camphor tree has been cultivated for various purposes, including timber, medicine, pesticides, and ornamental use. In addition, Camphor tree forests have been managed for urban landscaping, carbon sequestration, and ecosystem services, such as soil and water conservation, owing to their dense canopy, richness of fallen leaves, large biomass, and flourishing root systems [39]. Due to these attributes, the Camphor tree is regarded as a representative and valuable species in evergreen broadleaf forests, which constitute the typical climax forest community in subtropical regions of China [38,40]. These forests play a critical role in biodiversity conservation, regulating essential local ecological processes like energy flow, water balance, and nutrient cycling. Furthermore, they contribute significantly to the maintenance of regional landscape ecosystems in the subtropical zone [39,40]. However, despite their ecological importance, the photosynthetic characteristics of Camphor tree forests in subtropical zones remain poorly understood. Less is known about the dynamics of the photosynthesis process in Camphor tree forests. This information is crucial for gaining insights into the carbon sequestration potential of Camphor forests.

This study aimed to investigate the fundamental photosynthetic characteristics of camphor tree forests in subtropical China. The specific objectives of the current study were (1) to quantify the diurnal and seasonal patterns of photosynthetic rates under different weather conditions, (2) to investigate changes in photosynthetic rates along the forest canopy vertical profile, and (3) to examine the responses of photosynthesis to PAR and CO₂ concentration. Our study would provide a scientific reference for the further understanding of carbon sequestration in evergreen broadleaf forests and offer practical guidance for the sustainable management of forest ecosystems in subtropical regions.

2. Materials and Methods

2.1. Study Site

The study was conducted at Hunan Botanical Garden in Changsha city, Hunan Province, China (113°02′–113°03′ E, 28°06′–28°07′ N) (Figure 1). The climate of this study area was a typical moist subtropical climate. The annual mean temperature was 17.2 °C with a mean monthly temperature of 4.7 °C in January and 29.4 °C in July. Annual mean precipitation was 1422 mm, most of which occurred from April to August. Annual mean relative humidity was >80%. The frost-free period ranged across 270–310 days per year. The elevation was 50–110 m with a slope of 5–15°. Soil was classified as a typical red earth and soil texture ranged from clay loam to sandy loam. Soil pH on the topsoil (0–10 cm) was acidic with an average pH of 5.0.

The Camphor tree forests were planted using one-year seedlings in 2000, with an initial stand density of 2 × 3 m (Figure 1). The main plant species in the understorey were *Clerodendron cyrtophyllum* Turcz., *Lophantherum gracile* Brengn., *Nephrolepis auriculata* Trimen., *Sassafras tsumu* Hemsl., and *Symplocos caudata* Wall. ex A. DC.

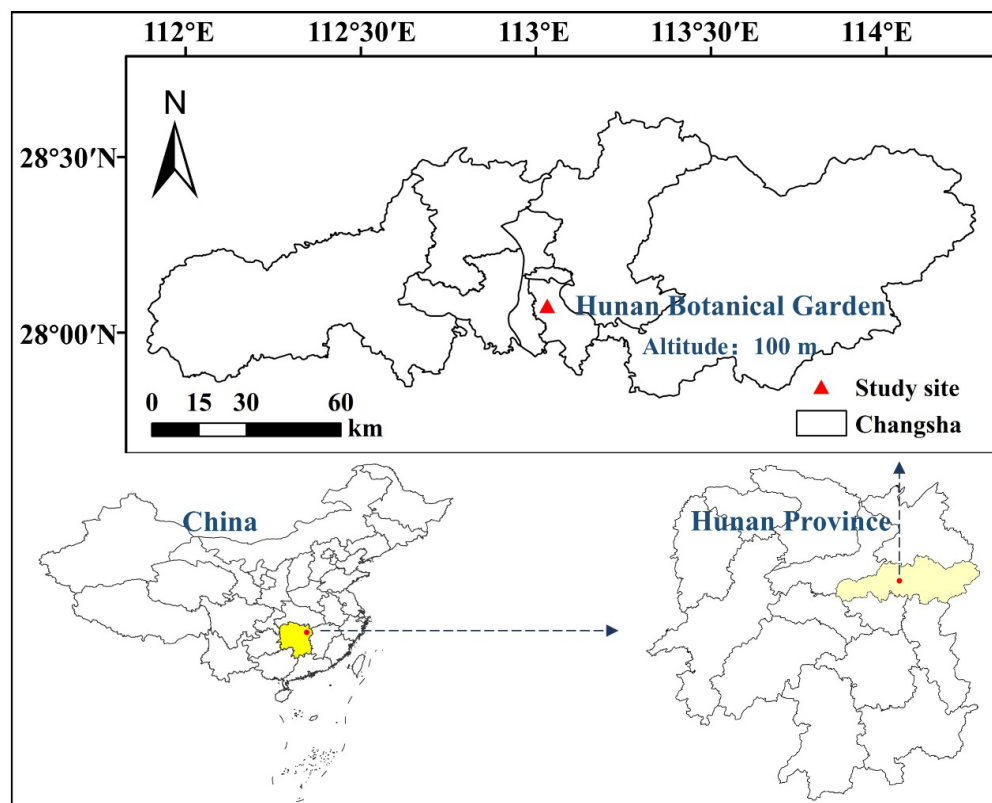


Figure 1. Geographic location of the study site in the Hunan Botanical Garden, Changsha city, Hunan Province, China.

2.2. Experimental Design and Measurements

A randomized complete block design (RCBD) was employed in this study. Twenty-year-old Camphor tree forests were chosen as the research focus in the designated region. Three plots, each measuring 20 m by 20 m, were set up in the forests with nearly identical slopes and aspects. We measured the diameter at breast height (DBH) and tree height (H) of every tree within the plot. The characteristics of the studied Camphor tree forests are shown in Table 1. Based on the tree size measurements, three trees (from small to large size of DBH and tree height) were selected as the sample trees for the photosynthesis measurements for each plot. For the investigation of vertical variations in photosynthesis along the canopy profiles, we divided the canopy into three distinct layers: upper, middle, and lower positions, each measured separately. This configuration led to a total of 27 measurement points (3 plots \times 3 trees \times 3 layers) for assessing photosynthesis rates in the Camphor tree forests. Three fully expanded leaves per measurement point were randomly selected for measurements and the average value was obtained for each point for each measurement time at that point.

Table 1. Characteristics of Camphor tree forests in the study site*.

Forest Type	Stand Density (Tree ha ⁻¹)	Mean DBH (cm)	Mean Tree Height (m)	Crown Diameter (m)	Stand Biomass (t ha ⁻¹)	Biomass Carbon Storage (t C ha ⁻¹)	Litterfall (t ha ⁻¹)
Camphor tree	1600	15.1 \pm 1.1	12.9 \pm 0.6	6.2 \pm 0.4	144.7 \pm 11.8	71.6 \pm 6.2	3.28 \pm 0.4

* Values: mean \pm S.E.

To assess seasonal and diurnal variations in photosynthesis, we employed a Li-6400 gas exchange system (LICOR Inc., Lincoln, NE, USA) [30]. Diurnal measurements were conducted from 8:00 to 18:00 h at one-hour intervals. These measurements were carried out twice a month, spanning from May to October of 2021. All measurements were consistently taken on south-facing leaves. During the measurements, the light intensity of the Li-Cor 6400 instrument was adjusted to $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and the CO_2 concentration was maintained at $400 \mu\text{mol}\cdot\text{mol}^{-1}$. The air temperatures within the leaf chamber were regulated within the range of 25°C to 30°C . The humidity within the leaf chamber was kept at 45–65%, depending on the air temperature and moisture levels during the measurements [41]. Photosynthetically active radiation (PAR) referred to light within the 400–700 nm wavelength range, which was the portion of the light spectrum that plants utilize for photosynthesis. Photosynthetic response curves were measured on fully expanded leaves of the Camphor tree using eleven gradient change points of PAR between 0 and $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$. We conducted light and CO_2 response curve measurements for all three canopy layers. The upper canopy was assessed at 0, 100, 200, 400, 600, 800, 1200, 1400, 1600, 1800, and $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ of PAR. For the middle and lower leaves, PAR measurements ranged from 0, 50, 100, 200, 300, 500, 700, 800, and 1000 to $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$. PAR responses were measured under ambient CO_2 concentrations. Photosynthetic light response curves were fitted to a nonrectangular hyperbola, and from these curves, the asymptotic light-saturated rate of net photosynthesis, apparent quantum yield, near-light saturation point, light compensation point, and dark respiration rate were determined [42]. In the case of CO_2 response curves, measurements were conducted under saturation PAR and various CO_2 concentrations including 400, 300, 200, 100, 50, 100, 200, 300, 400, 600, 800, 1000, 1200, 1400, 1600, and $1800 \mu\text{mol mol}^{-1}$ in the air passing through the leaf chamber [30].

2.3. Data Analysis

The three-way analysis of variance (ANOVA) was conducted to assess the effects of daily variations at different periods of time in a day, seasonal/temporal variations (month-to-month), and positional/spatial variations (different canopy layers), as well as their triple interactions, on photosynthesis rates. To meet the normality and homoscedasticity assumptions of ANOVA, we applied a log transformation to the original data. Furthermore, multiple comparisons were carried out to identify differences in photosynthetic rates among different months and seasons. For examining differences among the top, middle, and low canopy levels, Duncan's new multiple range method was employed for multiple comparisons. All statistical comparisons were considered significant at $p < 0.05$. Regression analysis was employed to examine the relationships between the photosynthetic rates and PAR. This analysis was used to explore the effects of PAR and ambient CO_2 concentration on photosynthetic rates in Camphor tree forests. All statistical analyses were performed using the SAS v9.4 statistical package (SAS Institute, Inc., Cary, NC, USA).

3. Results

The overall photosynthesis rates were significantly changed with the layers of the canopy, daily time, and the month ($p < 0.05$). Triple interactions also had significant effects on photosynthesis rates ($p < 0.05$, three-way ANOVA, Tukey–Kramer).

Figure 2 displayed the overall average of photosynthetic rates during both sunny and cloudy days, as well as the seasonal pattern. On average, the photosynthetic rate was marginally significantly higher on sunny days than on cloudy days ($p = 0.055$) (Figure 2b). The maximum rate of photosynthesis recorded was $18.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for sunny days and $13.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for cloudy days. Additionally, the diurnal pattern of the photosynthesis process on cloudy days exhibited significant differences from that on sunny days.

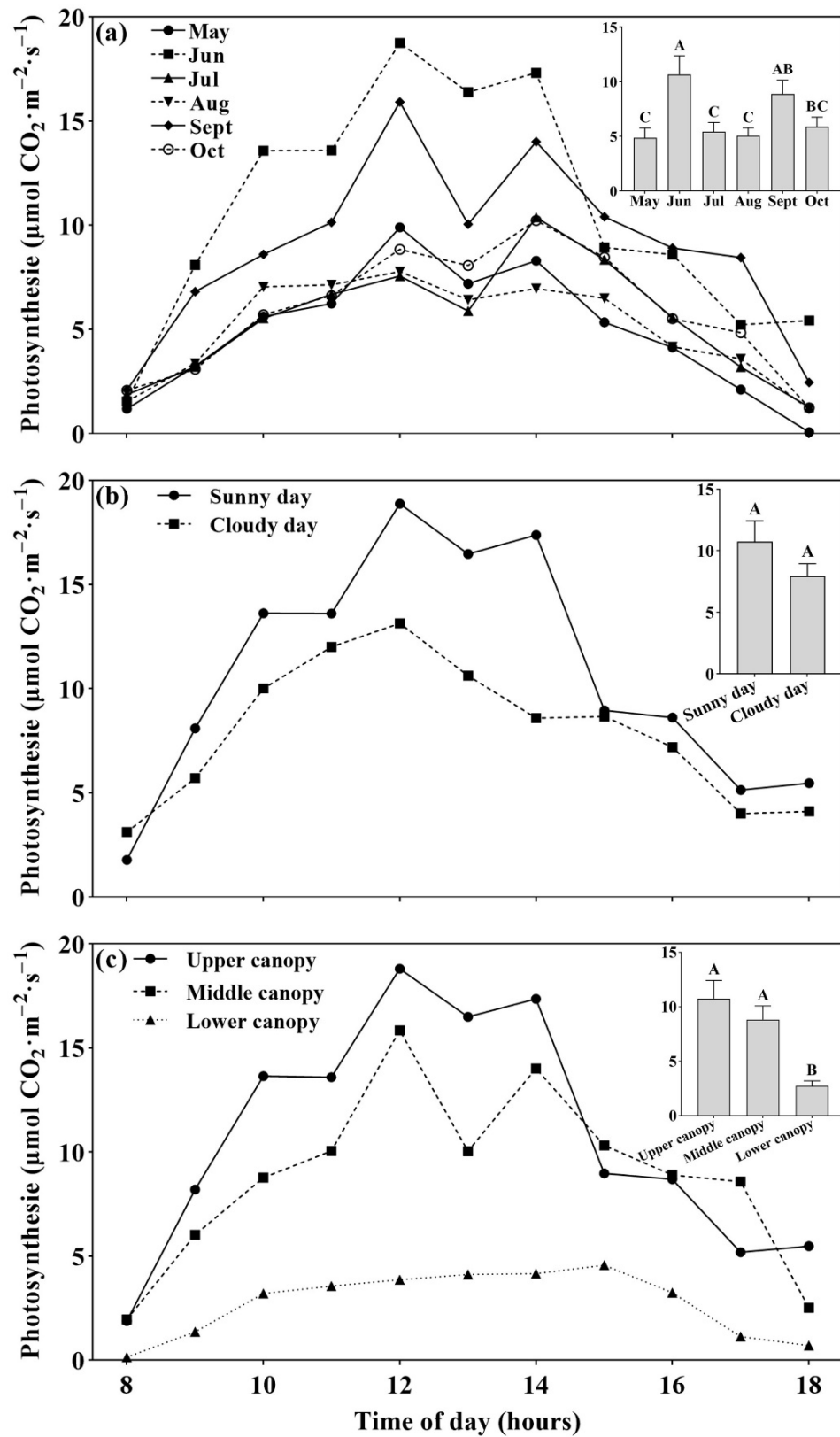


Figure 2. Diurnal variations in photosynthesis in the studied Camphor tree forests: (a) during the growing season (May to October), (b) under different weather conditions, and (c) at different canopy levels. All the measurements were taken from south-facing leaves. The measurements in (b,c) were collected in June. The different letters labeled with bar charts represent significantly difference at $p < 0.05$.

On sunny days, the rate of photosynthesis exhibited a characteristic pattern, with an increase in the morning followed by a decline in the afternoon (Figure 2a). This diurnal variation was consistent throughout the growing season, spanning from May to October, and featured a distinct midday depression in photosynthesis around 13:00 h. Particularly, photosynthesis displayed two peaks, with the first occurring around 12:00 noon and the second around 14:00 h (Figure 2a). The maximum rates of photosynthesis for each month were as follows: May ($10.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), June ($18.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), July ($10.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), August ($8.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), September ($15.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and October ($10.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Notably, the values measured between 9:00 and 10:00 h and between 15:00 and 16:00 h closely approximated the daily average photosynthetic rate, as calculated from the hourly measurements taken between 8:00 and 18:00 h. Furthermore, photosynthetic production during the peak periods (10:00 to 12:00 h and 14:00 to 16:00 h) accounted for approximately 80% of the total daily photosynthetic production observed between 8:00 and 18:00 h. Cloudy days lacked the midday depression typically observed in photosynthesis, displaying only one peak occurring around 12:00 noon (Figure 2b). Interestingly, photosynthesis on cloudy days still followed a morning increase and an afternoon decrease, resembling the general pattern of photosynthesis observed on sunny days (Figure 2a,b). The daily average rate of photosynthesis on cloudy days amounted to approximately 74% of that on sunny days.

Photosynthetic rates were significantly higher in the upper and middle canopy layers than in the lower canopy layer ($p < 0.05$) (Figure 2c). Specifically, the upper canopy layers exhibited higher photosynthetic rates than the middle canopy layer, although no significant differences were found between these two canopy layers ($p > 0.05$).

The maximum rates of photosynthesis recorded were $18.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the upper canopy, $15.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the middle canopy, and $4.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the lower canopy. Furthermore, the daily average rate of photosynthesis in the middle and lower canopies amounted to approximately 83% and 25% of that observed in the upper canopy, respectively. The diurnal patterns of photosynthesis exhibited notable differences among different canopy layers. Specifically, the upper and middle canopy layers displayed similar patterns, as previously described, with distinct peaks and a midday depression (Figure 2c). However, the photosynthesis of leaves in the lower canopy layer presented a distinct pattern, devoid of obvious peaks or midday depression (Figure 1c). Between 9:00 and 15:00 h, there were minimal variations in the rate of photosynthesis in the lower canopy, whereas an increasing trend was observed between 8:00 and 9:00 h, followed by a decreasing trend between 15:00 and 18:00 h (Figure 2c).

The upper canopy displayed the highest PAR-saturated rate of net photosynthesis, which was significantly higher than that in the middle and lower canopy layers ($p < 0.05$), while the lower canopy exhibited the lowest (Figure 3). In the lower canopy, photosynthesis began to decline as PAR levels increased, particularly in the range of 300 to 400 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Conversely, the middle canopy started to experience a decrease in photosynthesis at higher PAR levels, typically around 700 to 800 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Intriguingly, the photosynthesis of leaves in the upper canopy layer remained unaffected by increasing PAR until it exceeded 1200 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Furthermore, the light compensation points were measured at 95, 67, and 31 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR for the upper, middle, and lower canopy layers, respectively. The rates of dark respiration derived from the PAR response curve were found to be $1.73 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for the upper canopy, $1.25 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for the middle canopy, and $1.0 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for the lower canopy layer. Additionally, the apparent quantum yield of photosynthesis was calculated as $0.0183 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ PAR}$ for the upper canopy, $0.0186 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ PAR}$ for the middle canopy, and $0.0327 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ PAR}$ for the lower canopy (Figure 3). Interestingly, the mean photosynthetic rate was significantly higher in the upper canopy than in the middle and lower canopy layers, but under the 300 to 400 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ of PAR, the photosynthetic rates in the middle and lower canopy layers exceed that in the upper canopy layer (Figure 3).

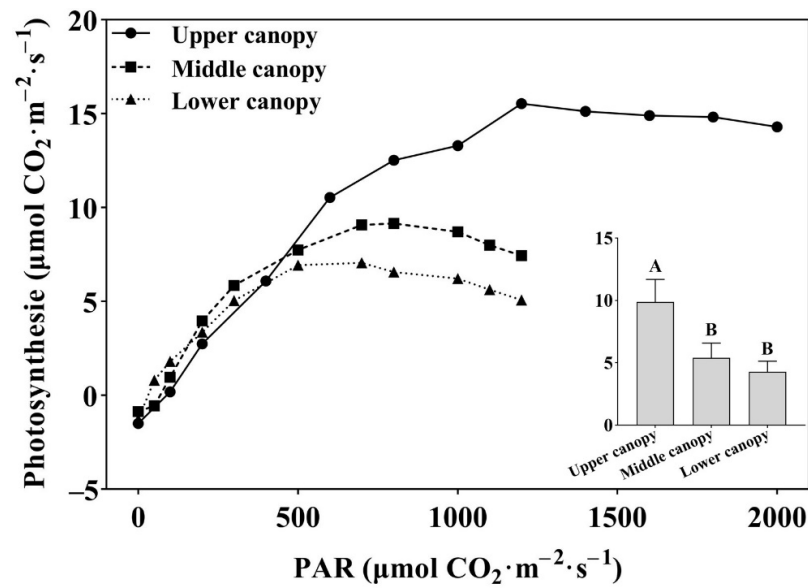


Figure 3. The response of photosynthetic rates to photosynthetically active radiation. PAR at three distinct canopy levels within the Camphor tree forests. Measurements were collected on south-facing leaves in June. The different letters labeled with bar charts represent significantly difference at $p < 0.05$.

Among the different canopy positions, the upper canopy consistently exhibited the highest photosynthesis rate, while the lower canopy consistently displayed the lowest, except under very low CO_2 concentrations (Figure 4). On average, photosynthesis rates were significantly higher in the upper canopy layer than in the lower canopy layer ($p < 0.05$), but the photosynthesis rates did not significantly differ between the upper canopy layer and the middle canopy layer, and between the middle canopy layer and the lower canopy layer ($p > 0.05$). The CO_2 compensation points were found to be $52 \mu\text{mol mol}^{-1}$ for the upper, $51 \mu\text{mol mol}^{-1}$ for the middle, and $52 \mu\text{mol mol}^{-1}$ for the lower canopy layer. Additionally, the initial slope of the response curve was calculated as $0.0354 \text{ mol m}^{-2} \text{ s}^{-1}$ for the upper canopy, $0.0186 \text{ mol m}^{-2} \text{ s}^{-1}$ for the middle canopy, and $0.0144 \text{ mol m}^{-2} \text{ s}^{-1}$ for the lower canopy.

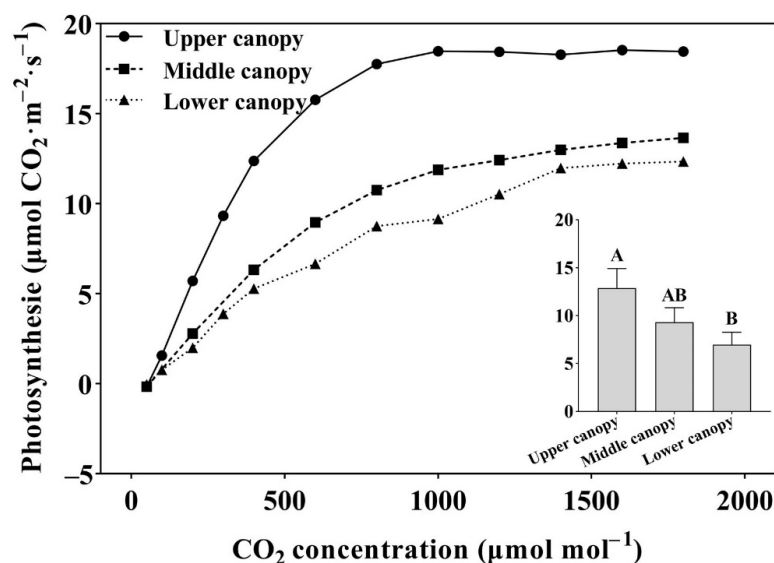


Figure 4. The response of photosynthetic rates to CO_2 concentration at three different canopy levels of the Camphor tree forests. The measurements were taken on south-facing leaves in June. The different letters labeled with bar charts represent significantly difference at $p < 0.05$.

Photosynthesis rates exhibited significant seasonal variations throughout the growing season. Peaks in photosynthesis were observed during two distinct periods in June and September, with considerably lower rates during non-peak periods (Figure 5). In particular, the peak photosynthesis rates in June generally surpassed those recorded in September. While leaves in different canopy layers displayed similar seasonal patterns, the magnitude of variation in the lower canopy layer was notably smaller compared to the upper and middle canopy layers (Figure 5). On average, monthly photosynthesis rates were significantly higher in the upper and middle canopy layers than in the lower canopy layers ($p < 0.05$). In addition, photosynthesis rates during the peak periods were approximately 1.8 times higher than the mean rates during non-peak periods for the upper and middle canopy layers, and 1.5 times higher for the lower canopy layer. In the examined Camphor tree forests, the standing biomass and carbon storage in biomass were recorded at 144.7 t ha^{-1} and 71.6 t C ha^{-1} , respectively.

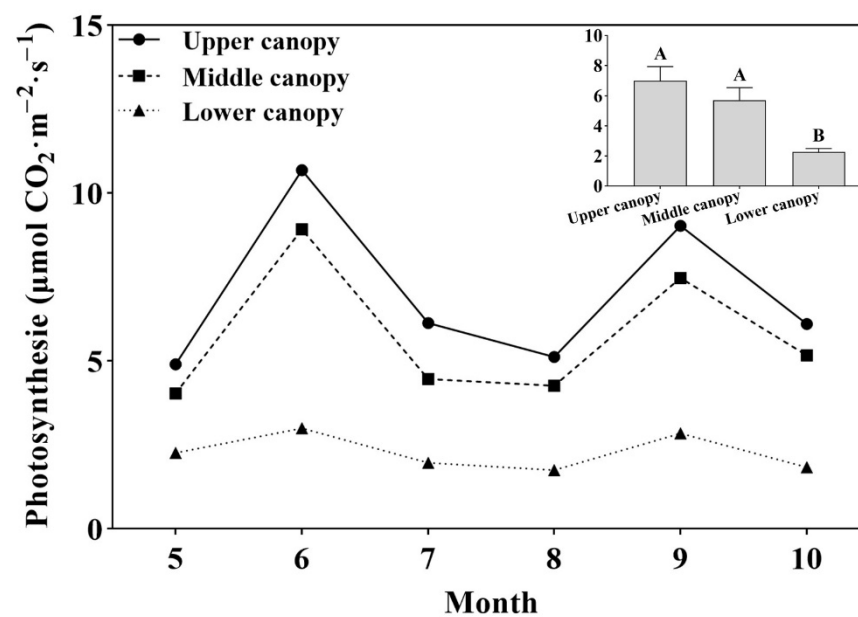


Figure 5. Seasonal variations in photosynthesis in the studied Camphor tree forests. Each value in the figure represents the average of eleven measurements taken at one-hour intervals from 8:00 to 18:00 h on south-facing leaves in the upper canopy. The different letters labeled with bar charts represent significantly difference at $p < 0.05$.

4. Discussion

This study highlights that the diurnal patterns of net photosynthesis remained consistent throughout the growing season, spanning from May to October. However, these patterns exhibited variations dependent on weather conditions and the vertical position within the canopy. On sunny days, the rate of net photosynthesis typically increased in the morning, followed by a decrease in the afternoon, characterized by a midday depression around 13:00 h, with two peak values observed at 12:00 and 14:00 h. This diurnal pattern aligns with the findings of Leverenz [31]. Conversely, on cloudy days, no midday depression was observed. Interestingly, leaves in the lower canopy also did not display a midday depression. The diurnal variation in photosynthesis can be influenced by various environmental and physiological/biochemical factors [43]. For instance, this study found that photosynthesis rates were generally positively correlated with PAR, while an inverse relationship was observed with ambient CO₂ concentration (Figure 6). However, the remarkably consistent diurnal pattern of photosynthesis observed throughout the growing season suggests that the regulation of photosynthesis in Camphor tree forests follows a robust internal rhythm [44]. Moreover, the fact that the midday depression of photosynthesis occurred exclusively on sunny days but not on cloudy days implies that this depression re-

sults from intricate interactions between internal regulatory mechanisms of photosynthesis and external environmental conditions, particularly PAR. These interactions, along with the underlying physiological and biochemical mechanisms governing the internal rhythm of photosynthesis in this species, warrant further investigation [45].

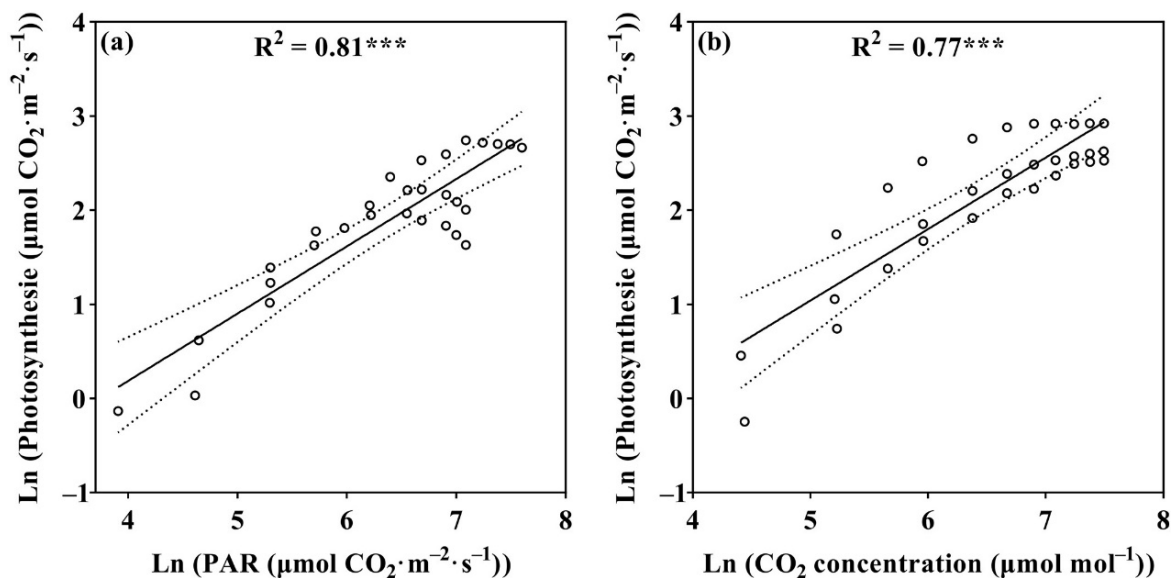


Figure 6. Relationships between the photosynthetic rates and photosynthetically active radiation (PAR) (a), and ambient CO₂ concentration (b) in the studied Camphor tree forests. The *** labeled with R^2 represents significant at $p < 0.01$.

We observed that the rates of photosynthesis declined along the vertical canopy profile in the studied forests. The daily average of photosynthetic rates in the middle and lower canopies accounted for approximately 83% and 25% of that observed in the upper canopy, respectively. Our results were consistent with the findings from other studies. It was found that the light-saturated photosynthetic rate declined by 27% and 36% in Douglas fir and western hemlock, respectively, between the upper canopy and the lower canopy [46]. Leaf photosynthesis decreased from the top of the canopy downwards, showing a significant vertical gradient in a poplar plantation [47]. The observation that the magnitude of diurnal fluctuations in photosynthesis in camphor trees was smaller on cloudy days than on sunny days, as well as smaller in the lower canopy compared to higher canopy positions, raises interesting considerations. The reduced fluctuations in photosynthesis on cloudy days may be linked to the relatively stable levels of PAR experienced on overcast days. Studies have indicated that PAR levels within the forest canopy are more consistent on cloudy days compared to sunny days [48,49]. Additionally, other environmental factors, such as temperature, often vary with light levels and are also presumed to be more stable on cloudy days. These combined factors could contribute to the smaller fluctuations in photosynthesis on cloudy days in comparison to sunny days [50]. However, the smaller fluctuations in photosynthesis observed in leaves in the lower canopy, as opposed to what might be expected, raise intriguing questions. Despite the study site's relatively low latitude ($27^{\circ}50'$ N), resulting in a smaller sun angle, one might anticipate that the PAR level beneath the forest canopy would exhibit more variability at the lower canopy positions [51]. This expectation stems from the notion that the shading effect of the forest canopy should be more pronounced in the early morning and late afternoon. Consequently, one might expect the rate of photosynthesis in lower canopy leaves to exhibit greater fluctuations rather than smaller ones when compared to higher canopy positions [52]. The study suggests that the smaller fluctuations in photosynthesis in the lower canopy could reflect the acclimation of these leaves to lower light conditions. Data from the study indeed demonstrate that lower canopy leaves exhibit an acclimation to reduced light conditions. For instance, when

compared to leaves at higher canopy positions, lower canopy leaves displayed a lower light compensation point, a lower light-saturated rate of photosynthesis, a lower respiration rate, and a lower initial slope in response to changes in CO₂ concentration, but they exhibited a greater apparent quantum yield (Figures 3 and 4). It is also possible that morphological adaptations occurred. These acclimations allow lower canopy leaves to efficiently utilize low PAR levels, particularly during the early morning and late afternoon, but may render them less efficient in harnessing higher PAR levels, which occur during late morning to early afternoon [51,53]. This contrasts with leaves in higher canopy positions, which appear to exhibit the opposite response. Consequently, lower canopy leaves exhibit smaller diurnal fluctuations in photosynthesis compared to those at higher canopy positions.

The data collected in this study revealed that camphor trees have strategically optimized their allocation of nitrogen resources within the photosynthetic apparatus across different vertical layers of the canopy. This adaptation allows them to efficiently harness varying light conditions at different canopy positions. Leaves in the lower canopy exhibit a remarkable ability to utilize limited light resources, with an apparent quantum yield of photosynthesis nearly twice as high as their counterparts in the upper canopy [54]. These lower canopy leaves also display reduced dark respiration rates, conserving carbon during periods of low light availability. Moreover, their lower light compensation point indicates efficient photosynthesis initiation under reduced light levels. Conversely, upper canopy leaves are adept at maximizing photosynthetic productivity in high-light conditions. They allocate more resources to capture and assimilate carbon efficiently [55]. These findings underscore the importance of an optimized nitrogen allocation strategy in camphor trees, enhancing their adaptation to varying light conditions throughout the canopy layers, and aligning with the concept of functional convergence observed in other tree species [49]. Overall, the mean values for stand biomass (144.7 t ha⁻¹) and biomass carbon storage (71.6 t C ha⁻¹) in the surveyed Camphor tree forests were consistent with previous research findings. Notably, Wang et al. [48] reported an average individual tree carbon storage of 0.05 t tree⁻¹ in the Taiwan region, equivalent to approximately 80 t C ha⁻¹ at a stand density of 1600 trees per hectare. Additionally, Lei et al. [49] observed a carbon storage of 45.1 t C ha⁻¹ in the overstory tree layer of 18-year-old Camphor tree forests in tropical regions. The photosynthesis patterns in camphor trees displayed a seasonal variation characterized by two peaks in June and September, with the June peak being more pronounced. Notably, there was a significant “mid-summer depression” in photosynthesis during July and August. This seasonal pattern bears similarity to observations made in a nine-year-old loblolly pine forest [50]. However, it contrasts with findings from black spruce seedlings in a semi-natural environment, where the rate of photosynthesis steadily declined throughout the growing season [56]. This seasonal pattern likely results from complex interactions between leaf physiology and environmental conditions. From March to June, the region experiences increasingly favorable environmental conditions for tree physiology and growth, leading to a steady rise in physiological activity and growth. However, this active growth phase may rapidly deplete soil moisture and other essential resources. Moreover, July and August represent the hottest months with the highest solar radiation levels in the region, creating stressful conditions that could reduce the photosynthetic activity and the effectiveness of certain protective mechanisms, further depressing photosynthesis [57]. Notably, the “mid-summer depression” in photosynthesis observed by Murthy et al. (1997) coincides with the peak air temperatures in the season [50]. The second peak of photosynthesis in September is likely attributed to increased rainfall and cooler temperatures. However, as October and November approach, trees in the region typically initiate cold-hardening processes and bud setting. With these processes occurring alongside less favorable environmental conditions, it is expected that the rate of photosynthesis would decline during these months.

It is important to exercise caution when extrapolating the findings of this study to natural forests. This research was conducted in a plantation forest, which exhibits structural differences when compared to natural forests. These distinctions include lower

stem density and reduced crown closure in plantations relative to natural forests, as well as a more uniform size and genetic composition in plantations [58]. While the specific variances in the seasonal and vertical patterns of physiological traits between plantations and natural forests of the same species remain poorly understood, it is reasonable to suspect significant differences. For instance, in natural forests, there is typically a gradual decline in photosynthetic capacity from the upper to the lower canopy [49]. In contrast, the disparity in photosynthesis between the upper and middle canopy layers was relatively minor compared to the abrupt reduction observed from the middle to the lower canopy in the camphor tree plantation of this study (Figures 2c and 5). This dramatic drop in photosynthesis in the lower canopy may be attributed to the shading effect of understory vegetation growing beneath the relatively open canopy of the plantation. Such disparities should be thoroughly investigated and carefully considered when applying the study's results, particularly in cases where findings at the leaf level are extrapolated to the canopy or broader landscape.

5. Conclusions

In this study, the daily, seasonal, and vertical patterns of photosynthetic rates in a Camphor tree forest were examined in a tropical region of China. The results indicated that both sunny and cloudy weather conditions, along with the vertical variations in the canopy, significantly influence the dynamics of the photosynthetic process of Camphor tree forests in the study region. The fluctuational magnitude of photosynthetic rates was larger on sunny days than on cloudy days, and in upper canopy positions than in lower canopy positions. Additionally, photosynthetic rates were positively correlated with PAR but inversely related to ambient CO₂ concentration. The overall average standing biomass and carbon storage in biomass were 144.7 t ha⁻¹ and 71.6 t C ha⁻¹, respectively, in the studied forests. Our findings suggest that variations in photosynthesis rates at different canopy levels have potential applications in regulating the tree crown and forest canopy to enhance the photosynthesis capacity, biomass yield, and carbon sequestration in Camphor tree forests. This study provides a scientific reference and practical guidance for the sustainable management of forest ecosystems in subtropical regions.

Author Contributions: Conceptualization, Z.L., Q.W., S.L., W.Y. and X.C.; methodology, Z.L., Y.P. and W.Y.; validation, Z.L., Q.W., C.M. and X.L.; formal analysis, J.L., Y.P. and J.W.; investigation, Z.L., Q.W., J.L., C.M. and X.L.; resources, J.L., Q.W., C.M. and X.L.; writing—original draft preparation, Z.L., Q.W. and Y.P.; writing—review and editing, Z.L., Y.P., W.Y. and X.C.; visualization, J.L. and J.W.; supervision, S.L., W.Y. and X.C.; project administration, Z.L. and W.Y.; funding acquisition, S.L. and W.Y. All authors have read and agreed to the published version of the manuscript.

Funding: This study was funded by the National Key R&D Program of China (grant number: 2020YFA0608100), Joint Funds of the National Natural Science Foundation of China (grant number: U21A20187), and the Key Research and Development Program of Hunan Province (2020NK2022).

Data Availability Statement: The data presented in this study are available upon request from the corresponding author.

Acknowledgments: The authors thank Li Zhang, Xiaocui Liang, and Piaoyun Deng for their help with fieldwork and data calculation.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Green, J.K.; Keenan, T.F. The limits of forest carbon sequestration. *Science* **2022**, *376*, 692–693. [[CrossRef](#)]
2. Searchinger, T.; Heimlich, R.; Houghton, R.A.; Dong, F.; Elobeid, A.; Fabiosa, J. Use of US croplands for biofuels increases greenhouse gases through emissions from land-use change. *Science* **2008**, *319*, 1238–1240. [[CrossRef](#)] [[PubMed](#)]
3. Kweku, D.W.; Bismark, O.; Maxwell, A.; Desmond, K.A.; Danso, K.B.; Oti-Mensah, E.A.; Quachie, A.T.; Adormaa, B.B. Greenhouse effect: Greenhouse gases and their impact on global warming. *J. Sci. Res. Rep.* **2018**, *17*, 1–9. [[CrossRef](#)]
4. Litton, C.M.; Raich, J.W.; Ryan, M.G. Carbon allocation in forest ecosystems. *Glob. Chang. Biol.* **2007**, *13*, 2089–2109. [[CrossRef](#)]

5. Song, J.; Wan, S.; Piao, S.; Knapp, A.K.; Classen, A.T.; Vicca, S.; Ciais, P.; Hovenden, M.J.; Leuzinger, S.; Beier, C. A meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling responses to global change. *Nat. Ecol. Evol.* **2019**, *3*, 1309–1320. [[CrossRef](#)] [[PubMed](#)]
6. Beer, C.; Reichstein, M.; Tomelleri, E.; Ciais, P.; Jung, M.; Carvalhais, N.; Rödenbeck, C.; Arain, M.A.; Baldocchi, D.; Bonan, G.B. Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science* **2010**, *329*, 834–838. [[CrossRef](#)] [[PubMed](#)]
7. Wang, S.; Zhang, Y.; Ju, W.; Chen, J.; Ciais, P.; Cescatti, A.; Sardans, J.; Janssens, I.; Wu, M.; Berry, J. Recent global decline of CO₂ fertilization effects on vegetation photosynthesis (vol 370, pg 1295, 2020). *Science* **2021**, *371*, 1295–1300.
8. Niinemets, Ü.; Keenan, T.F.; Hallik, L. A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. *New Phytol.* **2015**, *205*, 973–993. [[CrossRef](#)]
9. Chen, C.; Riley, W.J.; Prentice, I.C.; Keenan, T.F. CO₂ fertilization of terrestrial photosynthesis inferred from site to global scales. *Proc. Natl. Acad. Sci. USA* **2022**, *119*, e2115627119. [[CrossRef](#)]
10. Martens, J.A.; Bogaerts, A.; De Kimpe, N.; Jacobs, P.A.; Marin, G.B.; Rabaey, K.; Saeys, M.; Verhelst, S. The chemical route to a carbon dioxide neutral world. *ChemSusChem* **2017**, *10*, 1039–1055. [[CrossRef](#)]
11. Nobel, P.S. *Physicochemical & Environmental Plant Physiology*; Academic Press: Cambridge, MA, USA, 1999.
12. Badgley, G.; Field, C.; Berry, J. Canopy near-infrared reflectance and terrestrial photosynthesis. *Sci. Adv.* **2017**, *3*, e1602244. [[CrossRef](#)] [[PubMed](#)]
13. Bar-Even, A. Daring metabolic designs for enhanced plant carbon fixation. *Plant Sci.* **2018**, *273*, 71–83. [[CrossRef](#)] [[PubMed](#)]
14. Smith, W.K.; Bell, D.T.; Shepherd, K.A. Associations between leaf structure, orientation, and sunlight exposure in five Western Australian communities. *Am. J. Bot.* **1998**, *85*, 56–63. [[CrossRef](#)] [[PubMed](#)]
15. Lowman, M.D.; Schowalter, T.D. Plant science in forest canopies—the first 30 years of advances and challenges (1980–2010). *New Phytol.* **2012**, *194*, 12–27. [[CrossRef](#)] [[PubMed](#)]
16. Slot, M.; Winter, K. In situ temperature response of photosynthesis of 42 tree and liana species in the canopy of two Panamanian lowland tropical forests with contrasting rainfall regimes. *New Phytol.* **2017**, *214*, 1103–1117. [[CrossRef](#)]
17. Meir, P.; Mencuccini, M.; Binks, O.; Da Costa, A.L.; Ferreira, L.; Rowland, L. Short-term effects of drought on tropical forest do not fully predict impacts of repeated or long-term drought: Gas exchange versus growth. *Philos. Trans. R. Soc. B Biol. Sci.* **2018**, *373*, 20170311. [[CrossRef](#)] [[PubMed](#)]
18. Kira, T.; Shinozaki, K.; Hozumi, K. Structure of forest canopies as related to their primary productivity. *Plant Cell Physiol.* **1969**, *10*, 129–142.
19. Kurachi, N.; Hagihara, A.; Hozumi, K. Evaluation of the light interception by non-photosynthetic organs in a Larix leptolepis plantation. *Ecol. Res.* **1986**, *1*, 173–183. [[CrossRef](#)]
20. Parker, G.G. Structure and microclimate of forest canopies. In *Forest Canopies*; Academic Press: Cambridge, MA, USA, 1995.
21. Kurachi, N.; Hagihara, A.; Hozumi, K. Canopy photosynthetic production in a Japanese larch stand. I. Seasonal and vertical changes of leaf characteristics along the light gradient in a canopy. *Ecol. Res.* **1992**, *7*, 255–265. [[CrossRef](#)]
22. Ren, Y.; Zhang, C.; Zuo, S.; Li, Z. Scaling up of biomass simulation for Eucalyptus plantations based on landsense ecology. *Int. J. Sustain. Dev. World Ecol.* **2017**, *24*, 135–148. [[CrossRef](#)]
23. Fien, E.K.; Fraver, S.; Teets, A.; Weiskittel, A.R.; Hollinger, D.Y. Drivers of individual tree growth and mortality in an uneven-aged, mixed-species conifer forest. *For. Ecol. Manag.* **2019**, *449*, 117446. [[CrossRef](#)]
24. Denison, W.C.; Tracy, D.M.; Rhoades, F.M.; Sherwood, M. Direct, non-destructive measurement of biomass and structure in living old-growth Douglas-fir. In *Proceedings of the Research on Coniferous Forest Ecosystems—A Symposium*, Bellingham, WA, USA, 23–24 March 1972; pp. 23–24.
25. Ishii, H.T.; Tanabe, S.-I.; Hiura, T. Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. *For. Sci.* **2004**, *50*, 342–355.
26. Angelini, A.; Corona, P.; Chianucci, F.; Portoghesi, L. Structural attributes of stand overstorey and light under the canopy. *Ann. Silv. Res.* **2015**, *39*, 23–31.
27. Kovács, B.; Tinya, F.; Ódor, P. Stand structural drivers of microclimate in mature temperate mixed forests. *Agric. For. Meteorol.* **2017**, *234*, 11–21. [[CrossRef](#)]
28. Wang, N.; Palmroth, S.; Maier, C.A.; Domec, J.C.; Oren, R. Anatomical changes with needle length are correlated with leaf structural and physiological traits across five Pinus species. *Plant Cell Environ.* **2019**, *42*, 1690–1704. [[CrossRef](#)] [[PubMed](#)]
29. Cano, F.J.; Sanchez-Gomez, D.; Rodriguez-Calcerrada, J.; Warren, C.R.; Gil, L.; Aranda, I. Effects of drought on mesophyll conductance and photosynthetic limitations at different tree canopy layers. *Plant Cell Environ.* **2013**, *36*, 1961–1980. [[CrossRef](#)]
30. Flexas, J.; Díaz-Espejo, A.; Berry, J.; Cifre, J.; Galmés, J.; Kaldenhoff, R.; Medrano, H.; Ribas-Carbó, M. Analysis of leakage in IRGA's leaf chambers of open gas exchange systems: Quantification and its effects in photosynthesis parameterization. *J. Exp. Bot.* **2007**, *58*, 1533–1543. [[CrossRef](#)]
31. Leverenz, J.W. Photosynthesis and transpiration in large forest-grown Douglas-fir: Diurnal variation. *Can. J. Bot.* **1981**, *59*, 349–356. [[CrossRef](#)]
32. Urban, O.; Klem, K.; Ač, A.; Havránková, K.; Holišová, P.; Navrátil, M.; Zitová, M.; Kozlová, K.; Pokorný, R.; Šprtová, M. Impact of clear and cloudy sky conditions on the vertical distribution of photosynthetic CO₂ uptake within a spruce canopy. *Funct. Ecol.* **2012**, *26*, 46–55. [[CrossRef](#)]

33. Kelkar, K.; Kulkarni, M.; Burondkar, M.; Haldavnekar, P.; Gokhale, N.; Haldankar, P.; Bhuwad, A. Light Response Curve of Mango (*Mangifera indica* L.) Cv. Alphonso under Cloudy and Sunny Conditions of Rainy Season of Konkan Agro-climatic Conditions. *Int. J. Curr. Microbiol. App. Sci.* **2020**, *11*, 2052–2058.
34. Shao, Y.; Liu, H.; Du, Q.; Liu, Y.; Sun, J.; Li, Y.; Li, J. Impact of Sky Conditions on Net Ecosystem Productivity over a “Floating Blanket” Wetland in Southwest China. *Adv. Atmos. Sci.* **2024**, *41*, 355–368. [[CrossRef](#)]
35. Larcher, W. *Physiological Plant Ecology*; Springer: Berlin/Heidelberg, Germany, 1980.
36. Kozłowski, T.T.; Pallardy, S.G. *Physiology of Woody Plants*; Elsevier: Amsterdam, The Netherlands, 1996.
37. Lewis, J.D.; Lucash, M.; Olszyk, D.; Tingey, D.T. Seasonal patterns of photosynthesis in Douglas fir seedlings during the third and fourth year of exposure to elevated CO₂ and temperature. *Plant Cell Environ.* **2001**, *24*, 539–548. [[CrossRef](#)]
38. Hou, H.Y.; Xue-Yu, H. Vegetation of China with reference to its geographical distribution. *Ann. Mo. Bot. Gard.* **1983**, *70*, 509–549. [[CrossRef](#)]
39. Li, Z.; Yang, M.; Luan, X.; Zhong, Y.; Xu, M. Genetic diversity and geographic distribution patterns of *Cinnamomum camphora* under climate change in China. *Glob. Ecol. Conserv.* **2023**, *46*, e02619. [[CrossRef](#)]
40. Wang, X.H.; Kent, M.; Fang, X.F. Evergreen broad-leaved forest in Eastern China: Its ecology and conservation and the importance of resprouting in forest restoration. *For. Ecol. Manag.* **2007**, *245*, 76–87. [[CrossRef](#)]
41. Perez-Harguindeguy, N.; Diaz, S.; Garnier, E.; Lavorel, S.; Poorter, H.; Jaureguiberry, P.; Bret-Harte, M.; Cornwell, W.; Craine, J.; Gurvich, D. New handbook for standardised measurement of plant functional traits worldwide. *Aust. Bot.* **2013**, *61*, 167–234. [[CrossRef](#)]
42. Zhang, Q.; Zhang, T.J.; Chow, W.S.; Xie, X.; Chen, Y.J.; Peng, C.L. Photosynthetic characteristics and light energy conversions under different light environments in five tree species occupying dominant status at different stages of subtropical forest succession. *Funct. Plant Biol.* **2015**, *42*, 609–619. [[CrossRef](#)] [[PubMed](#)]
43. Dang, Q.; Lieffers, V.; Rothwell, R.; Macdonald, S. Diurnal variation and interrelations of ecophysiological parameters in three peatland woody species under different weather and soil moisture conditions. *Oecologia* **1991**, *88*, 317–324. [[CrossRef](#)]
44. Singaas, E.L.; Ort, D.R.; DeLUCIA, E.H. Diurnal regulation of photosynthesis in understory saplings. *New Phytol.* **2000**, *145*, 39–49. [[CrossRef](#)]
45. Muhammad, I.; Shalmani, A.; Ali, M.; Yang, Q.H.; Ahmad, H.; Li, F.B. Mechanisms regulating the dynamics of photosynthesis under abiotic stresses. *Front. Plant Sci.* **2021**, *11*, 615942. [[CrossRef](#)]
46. Lewis, J.; McKane, R.; Tingey, D.; Beedlow, P. Vertical gradients in photosynthetic light response within an old-growth Douglas-fir and western hemlock canopy. *Tree Physiol.* **2000**, *20*, 447–456. [[CrossRef](#)] [[PubMed](#)]
47. Liberloo, M.; Tulva, I.; Raïm, O.; Kull, O.; Ceulemans, R. Photosynthetic stimulation under long-term CO₂ enrichment and fertilization is sustained across a closed *Populus* canopy profile (EUROFACE). *New Phytol.* **2007**, *173*, 537–549. [[CrossRef](#)]
48. Messier, C.; Puttonen, P. Spatial and temporal variation in the Bight environment of developing Scots pine stands: The basis for a quick and efficient method of characterizing Bight. *Can. J. For. Res.* **1995**, *25*, 343–354. [[CrossRef](#)]
49. Dang, Q.L.; Margolis, H.A.; Sy, M.; Coyea, M.R.; Collatz, G.J.; Walthall, C.L. Profiles of photosynthetically active radiation, nitrogen and photosynthetic capacity in the boreal forest: Implications for scaling from leaf to canopy. *J. Geophys. Res. Atmos.* **1997**, *102*, 28845–28859. [[CrossRef](#)]
50. Murthy, R.; Zarnoch, S.; Dougherty, P. Seasonal trends of light-saturated net photosynthesis and stomatal conductance of loblolly pine trees grown in contrasting environments of nutrition, water and carbon dioxide. *Plant Cell Environ.* **1997**, *20*, 558–568. [[CrossRef](#)]
51. Ellsworth, D.; Reich, P. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* **1993**, *96*, 169–178. [[CrossRef](#)] [[PubMed](#)]
52. Stenberg, P. Implications of shoot structure on the rate of photosynthesis at different levels in a coniferous canopy using a model incorporating grouping and penumbra. *Funct. Ecol.* **1998**, *12*, 82–91. [[CrossRef](#)]
53. Whitehead, D.; Griffin, K.L.; Turnbull, M.H.; Tissue, D.T.; Engel, V.C.; Brown, K.J.; Schuster, W.S.; Walcroft, A.S. Response of total night-time respiration to differences in total daily photosynthesis for leaves in a *Quercus rubra* L. canopy: Implications for modelling canopy CO₂ exchange. *Glob. Chang. Biol.* **2004**, *10*, 925–938. [[CrossRef](#)]
54. Stoy, P.C.; Trowbridge, A.M.; Bauerle, W.L. Controls on seasonal patterns of maximum ecosystem carbon uptake and canopy-scale photosynthetic light response: Contributions from both temperature and photoperiod. *Photosynth. Res.* **2014**, *119*, 49–64. [[CrossRef](#)]
55. Hirose, T. Development of the Monsi-Saeki theory on canopy structure and function. *Ann. Bot.* **2005**, *95*, 483–494. [[CrossRef](#)]
56. Abidine, A.Z.E.; Stewart, J.D.; Plamondon, A.P.; Bernier, P.Y. Diurnal and seasonal variations in gas exchange and water relations of lowland and upland black spruce ecotypes. *Can. J. Bot.* **1995**, *73*, 716–722. [[CrossRef](#)]
57. Demmig-Adams, B.; Adams Iii, W. Photoprotection and other responses of plants to high light stress. *Annu. Rev. Plant Biol.* **1992**, *43*, 599–626. [[CrossRef](#)]
58. Bowersox, T.W. *The Practice of Silviculture—Applied Forest Ecology*; John Wiley & Sons: Hoboken, NJ, USA, 1997.

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.