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Seasonal Photosynthesis and Carbon Assimilation of Dynamics in a *Zelkova serrata* (Thunb.) Makino Plantation

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Abstract: As anthropogenic greenhouse gas emissions intensify global climate change, plantations have become an important tool to mitigate atmospheric CO₂. Our aim in this study was to estimate carbon assimilation and clarify the impact of environmental factors on the photosynthesis of *Zelkova serrata* (Thunb.) Makino, an important plantation species that is extensively planted in low altitude regions of East Asia. We measured monthly gas exchange parameters and leaf area index to estimate carbon assimilation. The results showed that gas exchange was significantly affected by vapor pressure deficit and temperature, especially in the dry season, and both photosynthetic rate and carbon assimilation decreased. Lower daytime assimilation and higher nighttime respiration during the dry season, which caused a 43% decrease in carbon assimilation in *Z. serrata* plantations. *Z. serrata* exhibited lower photosynthetic rate and lower carbon assimilation following planting in a tropical monsoon climate area. Therefore, the effects of extreme weather such as high temperature and vapor pressure deficit on *Z. serrata* forest carbon budget could be stronger in the future. Leaf area showed seasonal variation, and severe defoliation was caused by a typhoon in the summer. The annual carbon assimilation was estimated at 3.50 Mg C ha⁻¹ year⁻¹ in the study area.

Keywords: canopy; leaf area index; photosynthetic rate; vapor pressure deficit; water deficit

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1. Introduction

Forests are the world's largest terrestrial carbon sink and can sequester CO₂ from the atmosphere, modify atmospheric components, mitigate greenhouse effects, and provide ecosystem services such as provisioning of fodder and timber and non-timber products that facilitate sustainable livelihoods. Therefore, a profound understanding of forest carbon budgets under extreme weather conditions is required urgently [1,2]. However, plantations are subject to various environmental stresses in the field that may impact their photosynthetic efficiency, growth performance, and carbon sequestration potential [3,4]. For example, environmental factors such as precipitation and soil water content may not be the major factors affecting carbon assimilation, whereas vapor pressure deficit and warming could strongly impact forest carbon sinks under drought conditions [5,6].

Seasonality drives cycles of plant productivity in several ecosystems, and seasonal variation of photosynthesis and respiration are essential for ecosystem-atmosphere CO₂ exchange [7,8]. For example, photosynthetic light-use efficiency peaks in spring and then declines due to leaf aging or water stress, and night respiration gradually decreases during the growing season [7]. The impact of extreme weather on forests is becoming increasingly

severe under climate change, especially in seasonally dry ecosystems, due to cycles of prolonged drought and heavy rain. Drought is the primary cause of stress in forest ecosystems under climate change and may increase tree mortality under climatic warming [6]. In 2011, an intense drought impacted several regions around the world, causing a reduction in forest carbon sequestration [9]. Drought during the early growth season has long-lasting effects on photosynthesis and ecosystem carbon balance in plantations [3]. Severe drought suppressed tree photosynthesis more than respiration, leading to a reduction of 0.23–0.53 Pg of carbon in the Amazon Basin, turning the forest from a carbon sink to a source within a short period [10]. Drought usually accompanies high temperature and vapor pressure deficit, which influence forest carbon balance. For example, increasing vapor pressure deficit under climatic warming can reduce forest CO₂ uptake regardless of changes in soil water content, therefore warming may be the main climate factor that impacts carbon storage in tropical dry region [5,6]. Consequently, the influences of environmental factors on forest carbon balance require detailed multisite investigation [10]. Additionally, the forest response to changing environmental conditions may affect the regional and global climate [6].

Determining plantation species that are adapted to regional environmental conditions is necessary because of both limited plantation areas and climate change. In this study, we measured photosynthesis-related parameters to estimate the carbon assimilation of *Zelkova serrata* (Thunb.) Makino, an important plantation species in East Asia with high woody carbon content and economical value. *Z. serrata* mainly grows in the river valleys and sparse forest habitats beside streams, preferring fertile, moisture-laden, and well-drained soil conditions [11,12]. In addition, it exhibits considerable variation in growth performance under different growth site environments. Temperature seasonality, annual precipitation, annual mean temperature, and precipitation of the warmest quarter have been reported to be the key factors influencing its natural distribution in China [11]. The aims of the present study were to clarify the seasonal dynamic on photosynthesis and carbon assimilation dynamics of *Z. serrata* plantations and identify the key environmental factors influencing its growth performance under tropical monsoon climates.

2. Materials and Methods

2.1. Study Site and Species

The data for this study were collected in 2011 at Wan-Long Farm, a lowland former sugarcane plantation owned by the Taiwan Sugar Corporation in Sinpi Township, Pingtung, Taiwan (120°36'30'' E, 22°31'26'' N, 69 m above sea level). The soils are classified as Entisols with more than 60% sandstone parent material and 45%–55% gravel content, and the soil profile is shallow (<40 cm depth) [12,13]. In the study site, 14 species were used for afforestation from 2002 to 2005, with *Z. serrata* widely planted near the center of the farm in 2003. *Z. serrata* is a pioneer species frequently used in lowland afforestation, with the second largest plantation area in Taiwan. The initial stand density was 1500 seedlings ha^{−1} (2.5 × 2.5 m tree spacing), with constant pruning and weed removal. Mean diameter at breast height was calculated in a 20 × 25 m area in 2010, which was 3.89 ± 1.58 cm (*N* = 27). Mean tree height was 3.46 ± 1.28 m (*N* = 27). The surrounding area of the study plot had the same species and similar size, which had 77.4% of crown density on average.

Microclimate data were collected at a microclimate station 400 m southeast of experimental plot from 2009 to 2011, which had a rain gauge and a temperature and relative humidity probe (HMP45C, Vaisala, Finland). The region has a typical tropical monsoon climate, with a high frequency of typhoons and afternoon thundershowers during summer. However, the annual precipitation in 2011 was the lowest (1929 mm) during the study period and represented an intense drought event. In 2011, the January and June mean air temperature were 16.6 and 28.0 °C, respectively; annual precipitation was concentrated from May to September (wet season). The monthly precipitation, soil water content, and average maximum temperature variation in 2011 are shown in Figure 1. Data on soil water content were collected by the microclimate station using a time-domain reflectometer

(TDR, CS616, Campbell Scientific Inc., Logan, UT, USA) installed 20 cm underground, and showed a pattern similar to that of precipitation, being the lowest in March (8.8%) and the highest in July (19.4%) in 2011.

Figure 1. The monthly average maximum temperature ($T_{\max}$), soil water content, and accumulated precipitation in 2011.

2.2. Measurements of Gas Exchange and Leaf Area

The crowns of shade-intolerant species, such as *Z. serrata*, are usually mono-level of canopies, which is indicated by a leaf area index (LAI) = 1.07, and monthly variation in the 0.4–2.1 range in 2011. To enable convenient transportation of instruments, we selected three nearby trees for gas exchange measurements. Scaffolds (1.7 m height) were set near the sample trees with tripods so the leaf clamp reached the canopy leaves. Diurnal variations in leaf gas exchange were measured using portable photosynthesis systems (LI-6400; LI-COR, Lincoln, NE, USA) with a clear chamber top (LI-6400-08; LI-COR) one day per month for each sample tree in 2011 from three intact, fully expanded mature leaves on the same side of the canopy. The 5–7th leaf from the top was selected for measurement to prevent sampling juvenile and aging leaves. The sampled leaves were fully placed in the 2×3 cm leaf chamber of the instrument. Measurements were taken hourly from 8:00 a.m. to 4:00 p.m. (mean solar time), and net photosynthesis rate (P_n), stomatal conductance (g_s), transpiration rate (E), and intercellular CO_2 concentration (C_i) were recorded. The flow rate was set to $500 \mu\text{mol s}^{-1}$ and the air inlet of the LI-6400 was connected to a plastic tube (2–3 m in length), with the end set away from the operator to prevent the influence of human activities, and the CO_2 concentration in the leaf chamber was maintained at the level of the ambient atmosphere. The CO_2 sample concentrations ranged from 382.4 to 395.9 ppm during max photosynthesis in summer. The air temperature (T_a), leaf temperature (T_l), vapor pressure deficit (VPD_a), and leaf vapor pressure deficit (VPD_l) were also recorded. We represented four days of diurnal data in January 28, May 31, September 4, and November 25 from monthly measurements in 2011. Photosynthetic photon flux density (PPFD) and VPD were measured on the leaves. The data gap in September 4 was caused by rain in the afternoon.

The photosynthesis response to different light intensity gradients was measured to construct photosynthetic light response curves. Measurements were taken for three leaves per sampled tree in each season using an LI-6400 with an artificial LED light chamber (LI-6400-02B; LI-COR). The leaf selection criteria were the same for the diurnal measurement. Sample leaves were exposed to $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ artificial PPFD for a few minutes before measurements were taken to induce leaf stomatal opening. The artificial light intensities were set at 0, 5, 10, 20, 50, 100, 200, 500, 750, 1000, 1500, and $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ in sequence with about 10–20 min of stabilization time under each light intensity. Seasonal measurements of photosynthetic light response curves were used to calculate maximum assimilation rate ($A_{\max}$) and shape parameter (θ). Simultaneously, quantum efficiency (α)

and dark respiration rate (R_d) were calculated from the initial slope of the photosynthetic light response curve, at light intensities lower than $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ [14,15].

Tree total leaf area was estimated from the LAI, measured monthly at dusk from the top and under the canopy in three sample trees [15,16]. LAI was measured using a plant canopy analyzer (LAI-2200; LI-COR) in four directions under each sample tree. The sensor was covered with a lens cap (90° opening) to prevent overestimation of the canopy leaf area owing to shading by the main branch and trunk. The total leaf area of each sample tree was calculated as LAI multiplying canopy projected area of an individual tree's canopy. The canopy projected area was calculated as an ellipse area following measurement of the major and minor axis in two perpendicular directions as crown projection.

2.3. Data Processing and Analysis

According to several studies, the light response curve can demonstrate the effects of environmental factors such as nutrient levels, temperature, and water variables on leaf photosynthesis [16–18]. Therefore, the leaf carbon assimilation (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$) was calculated from the following equation:

$$A(A_{\max}, I_l) = A_{\max} \frac{2\alpha I_l / A_{\max}}{1 + \frac{\alpha I_l}{A_{\max}} + \sqrt{\left(1 + \frac{\alpha I_l}{A_{\max}}\right)^2 - 4\theta \frac{\alpha I_l}{A_{\max}}}} \quad (1)$$

where $A_{\max}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the maximum net assimilation of CO_2 , α is the quantum efficiency, I_l ($\mu\text{mol m}^{-2} \text{s}^{-1}$) represents leaf-level light intensity, which is derived from the measurements at the canopy top according to Beer's Law, and θ is the shape parameter of the photosynthetic light response curve, calculated as the slope of the tangent at the light saturation point. The associated parameters are listed in Table 1. The model has been well-tested and extensively applied in several leaf carbon assimilation studies [14,16–18]. In addition, the model is used as upscaling from leaf to canopy level estimation by considering the light extinction in canopy.

Table 1. Average values ($\pm$ standard error) of quantum efficiency (α), shape parameter (θ), maximum net assimilation rate ($A_{\max}$), and dark respiration rate (R_d) of *Zelkova serrata* (Thunb.) Makino across different seasons.

	Winter	Spring	Summer	Autumn
α ($\text{mol} \cdot \text{mol}^{-1}$)	0.038 ± 0.007	0.041 ± 0.001	0.036 ± 0.006	0.032 ± 0.008
θ	0.004 ± 0.001	0.005 ± 0.001	0.005 ± 0.001	0.006 ± 0.002
$A_{\max}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.92 ± 0.43	3.01 ± 0.78	4.99 ± 1.21	5.57 ± 1.94
R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	3.96 ± 0.75	2.43 ± 0.55	1.79 ± 0.30	0.94 ± 0.25

Several models to scale-up carbon assimilation from leaf to canopy level are already in use [14,16,18]. After calculating the leaf assimilation rate, we upscaled from leaf- to canopy-level assimilation using LAI as shown in [16]. According to [16,18] the estimation formulas were as follow:

$$A_c = \int_0^h \int_0^L A(A_{\max}, I_l) dL dt \quad (2)$$

$$R_c = \int_0^n \int_0^L R_d dL dt \quad (3)$$

Total daily canopy assimilation (A_c) can be calculated by considering total leaf area (L), day length (h), and leaf carbon assimilation (A) from Equation (1). Total night canopy respiration (R_c) can be calculated by considering total leaf area (L), night length (n), and dark respiration rate (R_d) from light response curves. The differences in mean temperature between day and night in the study period were less than 3 and 4 $^\circ\text{C}$ in winter and

summer, respectively. Additionally, we calculated monthly assimilation and respiration by considering days in each month, and annual carbon assimilation of *Z. serrata* was calculated by summing up monthly carbon assimilations.

SAS 9.4. statistical software (SAS Inc., Cary, NC, USA) was used to analyze the Pearson correlation between gas exchange and environmental variables. Correlation analysis data were collected from monthly measurement of diurnal variation. Significance was set at $p < 0.05$. Data in figures are presented as means $\pm$ standard error.

3. Results

In the study area, precipitation from May–September was 94%, 92%, and 83% of the accumulated annual precipitation in 2009, 2010, and 2011, respectively. Soil water content was the lowest in March (8.8%) and the highest in July (19.4%) in 2011. Therefore, data from the dry and wet seasons were analyzed separately. The correlations between gas exchange parameters and environmental factors are shown in Table 2. The data showed a significant correlation between g_s and E during dry and wet seasons but not between P_n and g_s . The results demonstrated that the leaf transpiration rate was controlled by stomatal closure, but the decrease in P_n may be caused by non-stomatal limitation. In both dry and wet seasons, P_n had no significant correlation with PPFD, but showed significant negative correlations with VPD and temperature in the dry season (Table 2). VPD greatly influenced stomatal opening/closure, especially under dry and high temperature conditions. At the study site, the dry season was over six months and the highest VPD (up to 5.14 kPa) occurred at noon in March during 2011, demonstrating its impact on plant CO_2 assimilation.

Table 2. Correlation coefficients for *Zelkova serrata* (Thunb.) Makino between gas exchange parameters (P_n : net photosynthetic rate, g_s : stomata conductance, C_i : intercellular CO_2 concentration, E : transpiration rate) and environmental factors (VPD_l: leaf to air vapor pressure deficit, VPD_a: vapor pressure deficit, T_l : leaf temperature, T_a : air temperature, CO_2 : ambient CO_2 concentration, PPFD: photosynthesis photon flux density) in dry (gray) and wet (white) season.

	P_n	g_s	C_i	E	VPD _l	VPD _a	T_l	T_a	CO_2	PPFD
P_n	-	0.14	-0.55 **	0.03	-0.30 **	-0.33 **	-0.25 **	-0.29 **	-0.08	0.05
g_s	-0.11	-	0.34 **	0.81 **	-0.32 **	-0.25 **	-0.13	-0.08	-0.10	-0.04
C_i	-0.86 **	0.28	-	0.26 **	-0.14	-0.05	0.00	0.09	0.15	-0.25 **
E	0.22	0.77 **	0.02	-	0.16	0.21 *	0.30 **	0.35 **	-0.23 **	0.25 **
VPD _l	0.19	-0.56 **	-0.36 *	-0.12	-	0.93 **	0.83 **	0.80 **	-0.36 **	0.56 **
VPD _a	0.14	-0.50 **	-0.33 *	-0.18	0.87 **	-	0.87 **	0.88 **	-0.35 **	0.43 **
T_l	0.20	0.06	-0.30 *	0.37 **	0.60 **	0.63 **	-	0.96 **	-0.56 **	0.28 **
T_a	0.15	0.12	-0.26	0.39 **	0.51 **	0.60 **	0.97 **	-	-0.48 **	0.26 **
CO_2	0.05	-0.59 **	-0.11	-0.56 **	0.35 *	0.43 **	-0.29 *	-0.32 *	-	-0.12
PPFD	0.14	-0.07	-0.17	0.29 *	0.61 **	0.32 *	0.40 **	0.29 *	-0.08	-

*, ** means $p < 0.05$ and $p < 0.01$. $N = 138$ (dry season), $N = 49$ (wet season).

Diurnal variations in PPFD and VPD on leaves in different seasons are illustrated in Figure 2 and gas exchange variation is shown in Figure 3. Diurnal variations in gas exchange represent the fluctuations in gas exchange during the day and the recovery overnight. The net photosynthesis rate in the four seasons was high in the morning and decreased in the afternoon. In the morning, P_n reached 3.8 and 5.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the dry and wet seasons, respectively.

Figure 2. Diurnal variation of light intensity (PPFD) and vapor pressure deficit (VPD_a) on 28 January, 31 May, 4 September, and 25 November, 2011. $N = 3$, bars indicate $\pm$ standard error.

The daytime CO₂ assimilation, nighttime respiration, and LAI are shown in Figure 4. CO₂ assimilation in the wet season was significantly higher than that in the dry season, with the yearly maximum in September (160.9 g CO₂) and the minimum in February (6.7 g CO₂). The daytime carbon sink capacity of trees was lower than the nighttime respiration from January to March. In this study, the single tree nighttime respiration ranged from 14.6 to 85.6 g CO₂. Higher dark respiration and light compensation point values with lower $A_{\max}$ and light saturation point were observed in the dry season. LAI represented the tree canopy dynamics and frequently fluctuated with seasons. LAI showed high values in spring and summer, thus represented seasonal variation in *Z. serrata*. However, the experimental area was struck by an intense typhoon in August, causing serious defoliation and low LAI. The difference between the fluctuations in leaf assimilation and monthly CO₂ assimilation was mainly caused by the monthly variation in leaf area (Figure 5). The monthly leaf assimilation rate ranged from 0.88 to 4.17 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The single-tree annual CO₂ assimilation was 23.79 kg. *Z. serrata* carbon assimilation was estimated as 3.50 Mg C ha⁻¹ year⁻¹ in the study area. CO₂ assimilation in the dry season was 56% that of the wet season, mainly caused by higher daytime assimilation and lower nighttime respiration in the wet season than in the dry season (Figure 6). Results also indicated that drought suppressed photosynthesis more than respiration.

Figure 3. Diurnal variation of net photosynthetic rate (P_n), stomata conductance (g_s), and transpiration rate (E) on 28 January, 31 May, 4 September, and 25 November, 2011. $N = 3$, bars indicate $\pm$ standard error.

Figure 4. Monthly daytime CO_2 assimilation (CS), night respiration (RD), and leaf area index (LAI) of *Zelkova serrata* (Thunb.) Makino. $N = 3$, bars indicate $\pm$ standard error.

Figure 5. The monthly leaf assimilation rate (A) and monthly CO₂ assimilation (Am) of *Zelkova serrata* (Thunb.) Makino.

Figure 6. Ratio of day CO₂ assimilation (Day CS) and night respiration (Night RD) in wet and dry seasons.

4. Discussion

4.1. Gas exchange and Environmental Factors

The 10-year average annual precipitation was 2700.4 mm from 2005 to 2014 in southern Taiwan, thus the precipitation in 2011 (1929 mm) was much lower than average. The annual evaporation in 2011 (1756.9 mm) was measured by the central weather bureau in southern Taiwan. Plant gas exchange was sensitive to environmental factors such as light intensity, water availability, humidity, and temperature. For example, a water deficit may cause the reduction of stomata conductance, photosynthetic rate, and transpiration, leading to negative effects on plant growth [19–22]. Water deficit is likely to be more severe in the seasonal drought regions; therefore, the selection of plantation species adapted to such environmental stress factors is essential. Different trees species may show different physiological responses to microclimate factors and their interaction in plantation areas. Diurnal variation of gas exchange could be the indicator of maintained photosynthetic capacity in various environmental conditions [23–25].

The diurnal variation of the net photosynthesis rate was high in the morning and decreased in the afternoon. Similar results were found by [26] in young *Cinnamomum camphora* and *Z. serrata* in central Taiwan. High values of P_n in the morning, which decreased after noon without recovery until sunset, were shown occasionally in the field owing to high light intensity, air temperature, and VPD at noon [27,28]. The decrease in both P_n and g_s through the day appears to be the result of light-driven accumulations of photosynthesis products [29]. However, the P_n values recovered over the following morning, showing that the damage to photosynthesis under environmental stress is transient. We found

that g_s and E showed similar diurnal fluctuation and the values in the wet season were higher than those in the dry season. These results demonstrated that leaf transpiration was controlled by stomatal opening/closure in *Z. serrata*, as shown in Table 1. Several studies also demonstrated a similar relationship between stomata and water loss during the dry and wet seasons [30,31]. The effects of stomatal or non-stomatal limitation on the reduction of photosynthetic rate can be determined by the correlation between P_n , g_s , and C_i [32,33]. For example, the positive correlation between P_n and g_s and the negative correlation between P_n and C_i were determined as the effect of stomata limitation. Stomata regulation can prevent excess water loss from leaves, but also limit the carbon uptake. The non-significant relation between P_n and g_s and the significant relation between g_s and E demonstrated that the maintenance of leaf water status under drought is more important than carbon uptake [29]. Both temperature and VPD presented a significant correlation with P_n in the dry season, showing that the responses of the leaves were directly affected by the high temperature and dry air. Several studies demonstrated that the influence of temperature and VPD on photosynthetic rate was occasionally larger than that of light intensity and soil water content. Thus, the variation of VPD and stomata conductance may influence leaf gas exchange and CO_2 assimilation [6,21,34–37]. Harsh environmental conditions could become more severe in the future since climate change could intensify high temperature and drought conditions, causing higher VPD.

Light intensity is one of the key factors influencing photosynthetic rate and, therefore, the forest carbon sink. The optimum range of light intensity is species-specific. However, the photosynthetic light response curve demonstrated the relationship between light intensity and P_n on leaves and could calculate the light compensation point, A_{max} , R_d , and α [32,38,39]. These parameters varied both with internal plant factors (e.g., shade tolerance) and external environmental factors (e.g., water stress) [32,40]. In addition, several studies have shown that these parameters can be used to calculate the mean leaf carbon assimilation rate and upscale to the daily carbon assimilation of the whole tree [4,16–18].

4.2. Leaf Carbon Assimilation and Leaf Area Index

The mean leaf carbon assimilation rate can be upscaled to the tree and stand level by considering LAI. The results showed that the daytime carbon assimilation was lower than the nighttime respiration in the dry season. Several studies demonstrated that the photosynthetic rate was higher in the wet season than in the dry season [19,21,22,41]. Kuo et al. [40] showed that mean light-saturated photosynthetic rate and stomatal conductance measured in the rainy season increased 48% and 286%, respectively, when compared with the dry season in 30 broad-leaved tree species, demonstrating that stomatal opening was severely restricted during the dry season. Hu et al. [42] showed that the maximum photosynthetic rate may fluctuate 2.2–3.1-fold under different light regimes in subtropical broad-leaved tree species. Moreover, the variation of photosynthetic rate under different environmental conditions also represented the variation of carbon sequestration potential.

A higher R_d and light compensation point with lower A_{max} and light saturation point were observed in the dry season. Generally, the leaf respiration rate is greatly affected by temperature and light intensity and, hence, shows seasonal variation [43]. However, Yin et al. [32] demonstrated that drought impacted the pattern of the photosynthetic light response curve, which increased the dark respiration and light compensation point and decreased A_{max} and light saturation point. Therefore, the light range utilization was reduced, which decreased the photosynthetic potential. The leaf respiration in the dark is usually higher than in the light, however, the light suppression of respiration may reduce in high temperature conditions [43]. Plant respiration plays an important role in the global carbon cycle, with 120 billion tonnes of carbon sequestered by terrestrial plants compared with 60 billion tonnes of carbon released by plant respiration annually [43]. Additionally, severe drought and increasing temperatures in the future could suppress the photosynthesis and increase respiration in plantations under climate change.

Total leaf area not only influences the amount of light available but also affects the carbon sequestration of trees because it is the key factor for upscaling from leaf to stand level. High leaf area increases the amount of carbon sequestration by photosynthesis but also increases the amount of carbon emitted by respiration [44,45]. The variation of leaf area may be affected by internal factors such as the phenology of each species and external factors such as typhoons and tree pathology [45]. Biswas et al. [16] indicated that the LAI of seven young broadleaf tree species ranged from 1.22 to 3.26 in a plantation area. Chen et al. [46] found that the LAI of *Sapindus mukorossi* in the plain area ranged from 0.75 to 3.74. Compared with previous studies, the lower LAI (0.39–2.16) in *Z. serrata* at the study site may be caused by poor site quality, specific difference, and plant pathology [47,48].

4.3. Seasonal Carbon Assimilation

The leaf assimilation rate can be upscaled to single-tree monthly CO₂ assimilation by considering total leaf area and day length (Figure 5). The monthly leaf assimilation rate in *Z. serrata* was lower than that of *S. mukorossi* (1.18–9.10 $\mu\text{mol m}^{-2} \text{s}^{-1}$) in Southern Taiwan [46] and seven broad-leaved tree species (1.37–11.61 $\mu\text{mol m}^{-2} \text{s}^{-1}$) in Eastern India [16]. However, a previous study demonstrated that the poor site quality in the study area may be caused by a long-term monoculture of sugarcane [12]. In addition, many trees showed symptoms of sooty mold in this area. Therefore, the effects of pathology on leaf photosynthesis could be an interesting field of research.

The single-tree annual CO₂ assimilation rates were lower than those of other studies in Taiwan such as 96.14 kg CO₂ year^{−1} in *Z. serrata* [26], 100 kg CO₂ year^{−1} in *Phyllostachys pubescens* [49], 230 kg CO₂ year^{−1} in *Cinnamomum camphora* [50], and 56.8 kg CO₂ year^{−1} in *Alstonia scholaris* [51]. However, several studies showed similar CO₂ assimilation to that of *Z. serrata*, such as 18.0 kg CO₂ year^{−1} in *Pongamia pinnata* [52] and 19.1 kg CO₂ year^{−1} in *Pterocarpus indicus* [17]. The estimation methods of CO₂ assimilation in the studies mentioned above were also based on photosynthesis. The difference of annual CO₂ assimilation may be affected by interspecific differences, regional climate, and seasonal climatic shifts [53–55]. Our study found a lower amount of CO₂ assimilation (23.79 kg tree^{−1} year^{−1}) than another study (96.14 kg tree^{−1} year^{−1}) [26] conducted in secondary forest in central Taiwan. The difference may be caused by the poor site quality, including shallow soils, high gravel content, long-term tillage, and prolonged drought in our study site. Plantations in shallow and rocky soils may have a lower growth rate and carbon accumulation potential. For example, the aboveground biomass of *Z. serrata* in deep and shallow soils was 32 Mg C ha^{−1} and 9 Mg C ha^{−1}, respectively [48].

The balance between CO₂ sink and source during drought is important because future drought in tropical regions may increase in frequency and severity because of global climate change [55]. These adverse weather conditions cause a reduction in tree growth, showing the serious impact of such climate extremes on carbon sequestration in dry tropical forest ecosystems [56]. Collectively, the results of the present study offer insights on photosynthesis and carbon assimilation dynamics in *Z. serrata* plantations, which could facilitate the assessment and management of plantation species under projected climate change.

5. Conclusions

Forests play a crucial role in terrestrial carbon budgets under climate change and provide several important ecosystem service functions. Extreme weather events such as prolonged drought and high temperature strongly impact the growth and carbon sink capacity of plantations. High VPD and high temperature conditions considerably influence the net photosynthesis rate of *Z. serrata* plantations in the dry season. However, the gas exchange rate recovered over the following morning, showing that the environmental stresses may not permanently suppress carbon assimilation by plantations. The environmental stress factors that are prominent during the dry season suppressed carbon assimilation

by 43%. Additionally, the relatively low carbon assimilation by *Z. serrata* plantation at the study site could be attributed to poor site quality.

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