

Article

# Three-Year Study on Diurnal and Seasonal CO<sub>2</sub> Sequestration of a Young *Fraxinus griffithii* Plantation in Southern Taiwan

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**Abstract:** This study examined monthly carbon sequestration of the Himalayan ash (*Fraxinus griffithii* C. B. Clarke), an important plantation species in Taiwan. From January 2010 to December 2012, data were collected from an *F. griffithii* plantation in southern Taiwan, which experiences a typical Southeast Asia monsoon climate. To estimate CO<sub>2</sub> sequestration rate, we conducted diurnal measurements of photosynthetic rates and seasonal measurements of photosynthetic light response curves. We also calculated leaf area index to estimate the total leaf area of individual trees. The diurnal variation in photosynthetic rate, stomatal conductance, and transpiration exhibited seasonal and annual differences. The range of net CO<sub>2</sub> assimilation rates was 1.34–8.68 μmol·m<sup>-2</sup>·s<sup>-1</sup> in 2010, 1.02–6.60 μmol·m<sup>-2</sup>·s<sup>-1</sup> in 2011, and 1.13–4.45 μmol·m<sup>-2</sup>·s<sup>-1</sup> in 2012. A single *F. griffithii* tree sequestered 12.21 kg·year<sup>-1</sup> CO<sub>2</sub> on average. Annual CO<sub>2</sub> sequestration occurred primarily during the summer for all years, averaging 14.89 Mg·ha<sup>-1</sup>·year<sup>-1</sup> for three years. Correlation analyses between various environmental variables and CO<sub>2</sub> sequestration rates indicated that air temperature and soil water content were likely the main factors influencing carbon sequestration of *F. griffithii* at this study site.

**Keywords:** carbon assimilation; canopy; leaf area index; light response curve; photosynthesis

## 1. Introduction

Afforestation is an important contributor to the mitigation of the greenhouse effect, as young forests can sequester more CO<sub>2</sub> from the atmosphere than mature forests [1,2]. However, climate change has heightened the incidence and severity of extreme climate events such as droughts, typhoons, and high temperatures [3–5]. Such climatic pressures affect plant physiology and growth, potentially decreasing photosynthetic efficiency and reducing carbon sequestration in forests [6,7]. Thus, quantification of annual carbon sequestration is critical to estimating forest ecosystem function and response under climate change [8].

*Fraxinus griffithii* C. B. Clarke, a semi-deciduous tree endemic to Taiwan, is a major species used for afforestation on the island. Widely planted in central and southern regions of Taiwan, the tree has high economic value due to its fast growth and quality lumber [9,10]. Recently, however, *F. griffithii* plantations in southern Taiwan have suffered from increasingly frequent typhoons during the summer and prolonged droughts from winter to spring. The length and severity of these extreme weather conditions have negatively affected the photosynthetic productivity of trees in these plantations [11].

To improve plantation management under severe weather stress and estimate their carbon sequestration, we require more instantaneous measurements of photosynthesis. Previous work

has demonstrated that diurnal and seasonal dynamic gas exchanges are more reliable indicators of photosynthetic efficiency than long-term evaluation based on biomass [12]. However, the latter approach dominates research on forest carbon storage, and relatively few studies have examined short-term fluctuations in carbon sequestration of individual trees resulting from rapid environmental change. Thus, the objective of this study was to provide an accurate, faster method for calculating canopy carbon sequestration and to understand the influence of environmental stress. In an *F. griffithii* plantation, we monitored several environmental factors at the leaf to canopy levels, related them to diurnal and seasonal variations in photosynthesis, and then estimated canopy-level carbon sequestration.

## 2. Materials and Methods

### 2.1. Plants and Growing Conditions

The study took place from 2010 to 2012 on a lowland plantation located in the Wan-Long Farm, 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 total area of the farm is approximately 291 ha and the soil texture is sandy loam.

The study region has a typical Southeast Asia monsoon climate, with a high frequency of typhoons and afternoon thundershowers during summer. In 2010–2012, January mean air temperatures were 19.4 °C, 16.6 °C, and 18.2 °C, and July mean air temperatures were 27.5 °C, 27.0 °C, and 27.8 °C, respectively. Annual precipitation was concentrated during May through September and accumulated to 2848.5 mm in 2010, 1929 mm in 2011, and 3144.5 mm in 2012. From 2002 to 2005, 14 species were afforested in the study site, with *F. griffithii* widely planted in 2003. The stand density of *F. griffithii* in the area was 1220 trees per hectare.

Typically, *F. griffithii* half-defoliates during February to April and sprouts new leaves in May, but in the last third of April 2011, full defoliation occurred, likely due to decreased precipitation earlier in the year. For this study, we sampled three randomly selected trees from a monoculture plot of *F. griffithii*. All three trees were close to the average diameter-at-breast-height (5.63 cm) of the plot.

### 2.2. Measurements of Photosynthesis and Leaf Area

The diurnal net photosynthetic rate ( $P_N$ ), stomatal conductance ( $g_s$ ), and transpiration rate ( $E$ ) were measured using a portable photosynthesis system (LI-6400-08, LI-COR, Lincoln, NE, USA). For each tree, measurements were taken with an air flow rate of 500  $\mu\text{mol}\cdot\text{s}^{-1}$  from three randomly selected, intact, fully expanded mature leaves on the same side of the canopy. The average tree height of the stand is approximately 4.3 m, allowing easy access to canopy leaves when the instrument was set on a 3.5-m-high scaffold. Light intensity,  $\text{CO}_2$  concentration, and temperature inside the cuvette were set to fluctuate with ambient conditions. Ambient light intensity, humidity, and air temperature were also recorded with the LI-6400. Measurements were taken one day per month for each examined tree, hourly from 0800 to 1600 (mean solar time) for the entirety of the study.

In 2011, photosynthetic light response curves were constructed by measuring three leaves of each selected tree during winter (January), spring (April), summer (July), and autumn (October), with a LI-6400-02B LED Light Source (LI-COR). The light intensities (artificial photosynthetic photon flux density (PPFD)) were set at 0, 5, 10, 20, 50, 100, 200, 500, 750, 1000, 1500, and 2000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in sequence. Before measuring, sample leaves were exposed to 500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  artificial PPFD for several minutes to induce stomatal opening. The light response curves were fitted to a non-rectangular hyperbolic curve for determining the seasonal maximum assimilation rate ( $A_{max}$ ), dark respiration ( $R_D$ ), light compensation point (LCP), quantum efficiency ( $\alpha$ ), and shape parameter ( $\theta$ ). These parameters were used to estimate  $\text{CO}_2$  assimilation in the following equations.

Leaf area index (LAI) is a dimensionless quantity parameter that describes the forest canopy and is frequently used in calculations of canopy assimilation from the leaf [2]. It measures the one-sided leaf surface area per ground surface area; the amount of canopy leaves can be deduced from measuring how quickly radiation is attenuated as it passes through the canopy. Simultaneous LAI measurements

on the top and under canopy of the three sample trees were made monthly with a plant canopy analyzer (LAI-2200, LI-COR) at dusk. The total leaf area of an individual tree was estimated via multiplying LAI with the projected area of that tree's canopy.

Environmental data were monitored at a meteorological station located 100 m from the sampled trees. Relevant variables included air temperature ( $T_a$ ), soil temperature ( $T_s$ ), soil water content (SWC), relative humidity (RH), daytime photosynthetic photon flux density (PPFD<sub>d</sub>), vapor pressure deficit (VPD), and ambient CO<sub>2</sub> concentration. These data had been continuously recorded since 2009 at a frequency of 10 Hz and averaged over 30 min. RH and SWC, respectively, were measured using a relative humidity probe (HMP45C, Vaisala, Finland) and a time-domain reflectometer (TDR, CS616, Campbell Scientific Inc., Logan, UT, USA) set 20 cm belowground. Subsequently, these environmental data were applied to estimate CO<sub>2</sub> assimilation and subjected to correlation analysis.

### 2.3. Estimation of CO<sub>2</sub> Assimilation

A number of well-tested and extensively researched models are available for extrapolating from leaf measurements to canopy-wide photosynthesis [13,14]. The photosynthetic light response curve is important for predicting carbon sequestration in nature because light variation in a leaf's environment affects photosynthetic rates [15]. According to previous modeling [13], the leaf-level assimilation rate ( $A_l$ ) can be calculated with the following formula for non-rectangular hyperbolic light response:

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

where  $A_{max}$  ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) is the maximum net assimilation of CO<sub>2</sub>,  $\alpha$  is the quantum efficiency (slope of the linear part of light response curves),  $I_l$  ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) is leaf-level light intensity from the diurnal measurement, and  $\theta$  is the shape (slope of the tangent at light saturation point) of the light response curve. Environmental factors (e.g., temperature, nutrient levels, and water variables) affect single-leaf photosynthetic rate through their interaction with  $A_{max}$ ,  $\alpha$ , and  $\theta$  [13]. Whole canopy assimilation can be obtained from leaf assimilation rate through integrating time and canopy leaf area.

The following model relies on two assumptions: a closed (horizontally uniform) canopy and the same decay constant between the exponential light profile on the canopy and light from various parts of the sky [14]. Total daily canopy assimilation ( $A_c$ ,  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ) was calculated with the following equation:

$$A_c = \int_0^h \int_0^L A_l dL dt, \quad (2)$$

where  $L$  is the total leaf area,  $h$  ( $\text{s}\cdot\text{day}^{-1}$ ) is the day length, and  $A_l$  ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) is the leaf-level assimilation rate [2].

The dark respiration rate was calculated from the initial linear part of the light response curve. Air temperature fluctuations during nights of the experimental period were less than 5 °C and 3 °C in winter and summer, respectively. Total night canopy respiration ( $R_c$ ,  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ) was modified from Biswas et al. [2]:

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

where  $L$  is the total leaf area,  $n$  ( $\text{s}\cdot\text{day}^{-1}$ ) is the night length, and  $R_D$  ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) is the leaf-level dark respiration rate calculated by the linear part of light response curves.

After obtaining the canopy assimilation of an individual tree for an entire day, the monthly CO<sub>2</sub> assimilation ( $A_m$ ,  $\mu\text{mol}$ ) was calculated as follows:

$$A_m = D_i (A_c - R_c) \times C, \quad (4)$$

where  $D_i$  is the number of days in a month and  $C$  ( $4.4 \times 10^{-7}$ ) is a unit-conversion constant ( $\mu\text{mol}$  CO<sub>2</sub> to g CO<sub>2</sub>). Summing all  $A_m$  in a year yielded the annual assimilation of individual trees. Annual

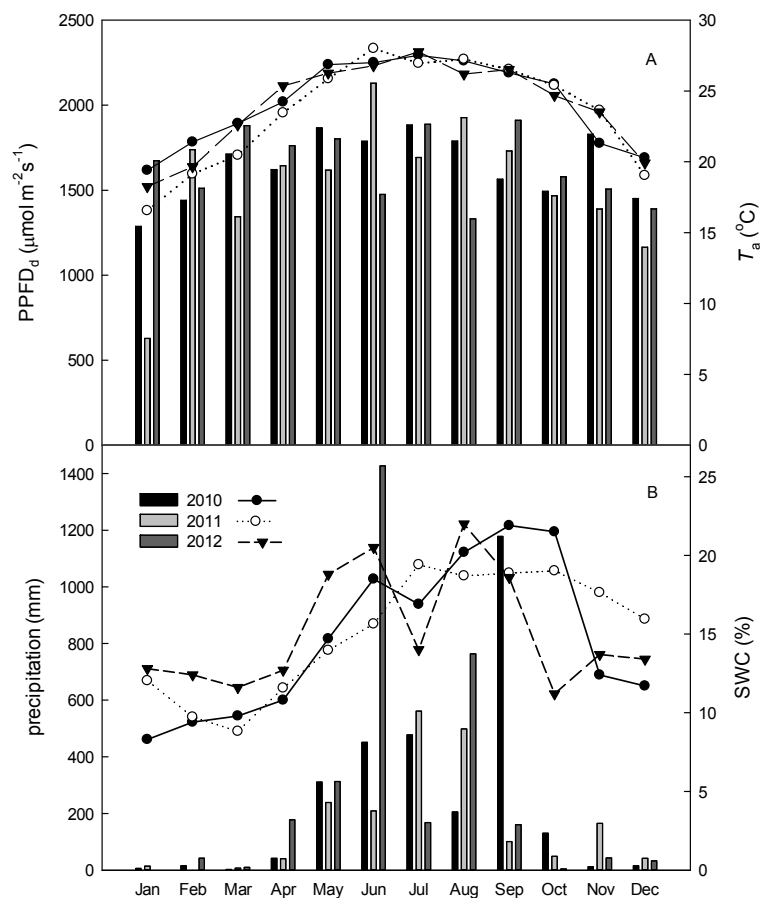
CO<sub>2</sub> assimilation of *F. griffithii* was estimated via multiplying total  $A_m$  with stand density (1220 trees per hectare).

Data were analyzed in SAS 9.4. (SAS Inc., Cary, NC, USA) Significant relationships between CO<sub>2</sub> sequestration and environmental variables were tested with Pearson's correlations, and Duncan's multiple range tests were run a posteriori. Significance was set at  $p < 0.05$  for all analyses. Curve fitting of data was performed using *SigmaPlot 12.0* (Systat Software Inc., Chicago, IL, USA). Data are presented as means  $\pm$  standard error.

### 3. Results

#### 3.1. Environmental Conditions

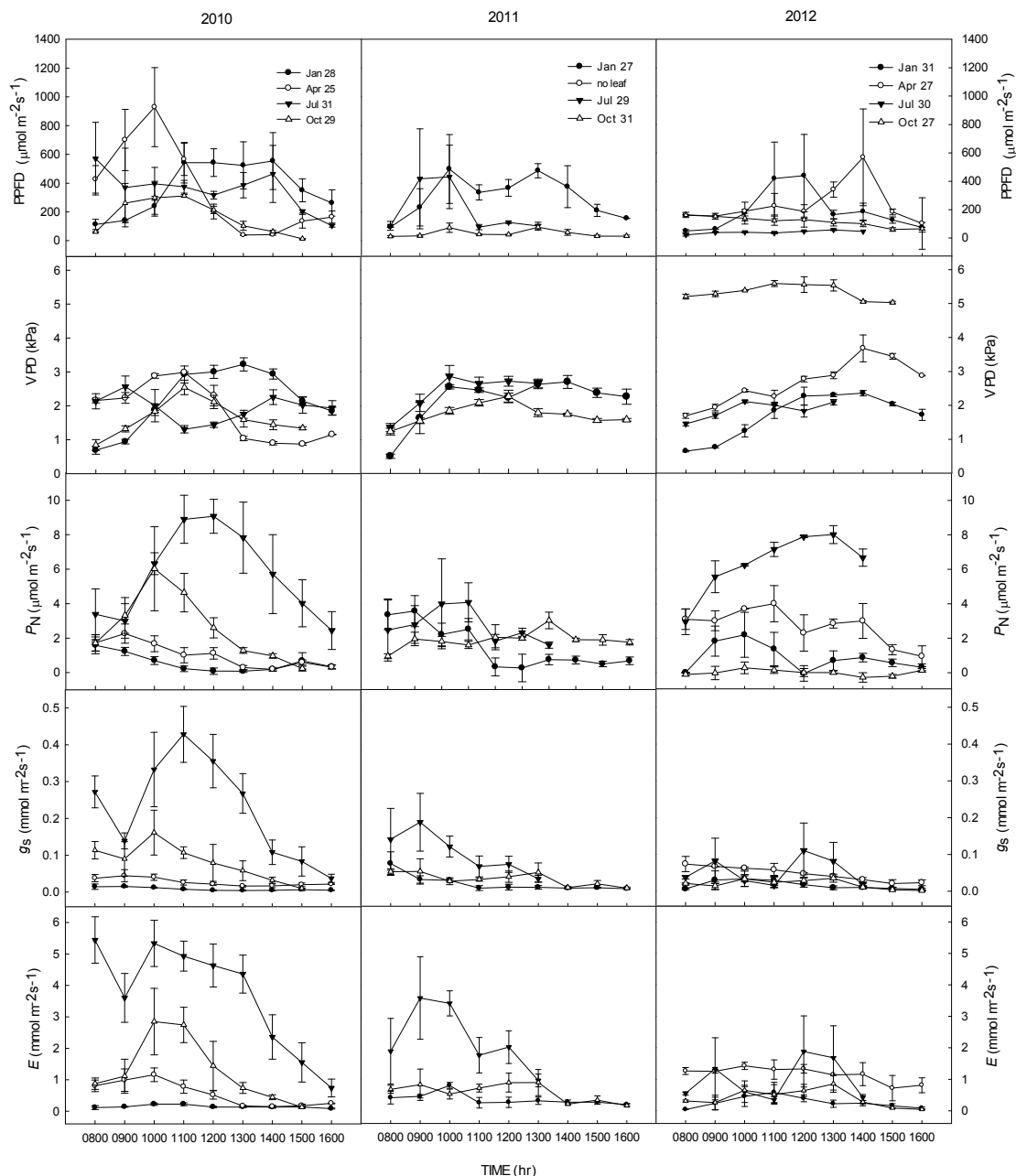
Annual precipitation was highest in 2012 (3144.5 mm), followed by 2010 (2848.5 mm) and 2011 (1929 mm). Heavy typhoons during 2010 and 2012 generally resulted in concentrated rainfall during May through September, but July and October 2012 experienced lower precipitation and SWC. Annual precipitation in 2011 was the lowest of all three years because typhoons did not occur (Figure 1). The maximum and minimum rainfall during the experimental period was 1427.5 mm in June 2012 and 0.5 mm in January 2012, respectively. Seasonal SWC varied with precipitation and reached the lowest levels from January to March in all three years: 8.3%–21.9% in 2010, 8.8%–19.4% in 2011, and 11.2%–22.0% in 2012. The mean annual daytime PPFD above canopy level was 1645.89, 1539.67, and 1642.64  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in 2010, 2011, and 2012, respectively. The mean annual  $T_a$  was 24.14, 23.53, and 23.96 °C in 2010, 2011, and 2012, respectively.



**Figure 1.** Monthly precipitation (bars), soil water content (SWC, lines), daytime light intensity (photosynthetic photon flux density (PPFD<sub>d</sub>), bars), and air temperature ( $T_a$ , lines) from 2010 to 2012 at the Wan-Long Farm study site.

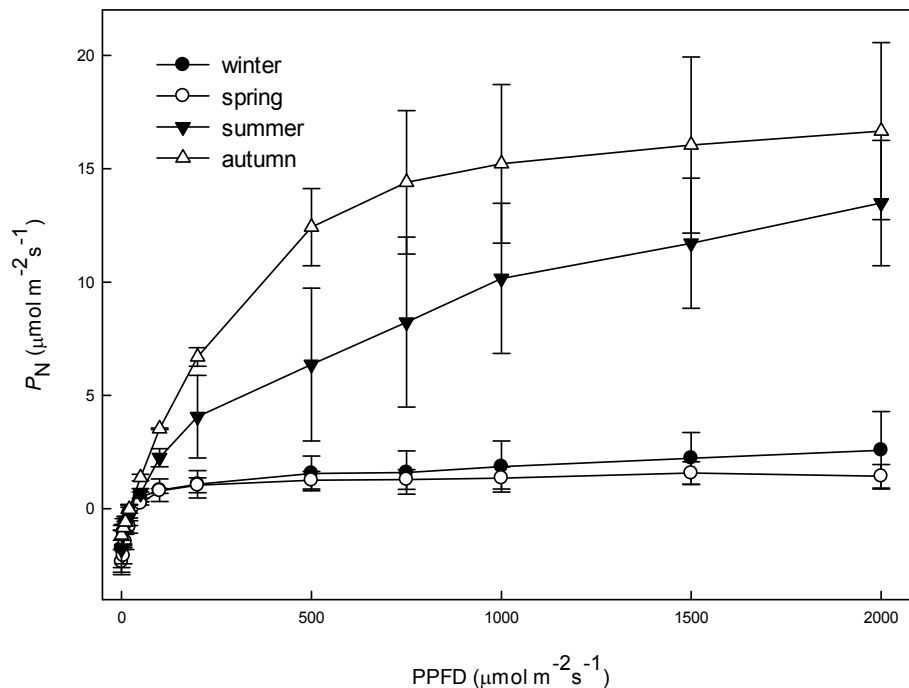
### 3.2. Photosynthesis and Related Parameters

The diurnal PPFD, VPD,  $P_N$ ,  $g_s$ , and  $E$  were measured monthly from 2010 to 2012; representative data in January, April, July, and October of each year are shown (Figure 2). Although differing across seasons,  $P_N$ ,  $g_s$ , and  $E$  were generally higher in the morning, with a gradual decrease throughout the day (Figure 2). One exception was in July 2012, when  $P_N$ ,  $g_s$ , and  $E$  were highest in the afternoon, with lower PPFD. The highest seasonal  $P_N$  occurred in July of all three years, whereas the lowest  $P_N$  occurred in January 2010 and 2011. The lower precipitation and RH in October 2012 resulted in the highest VPD of the study period.



**Figure 2.** Diurnal changes in light intensity (PPFD), vapor pressure deficit (VPD), net photosynthetic rate ( $P_N$ ), stomatal conductance ( $g_s$ ), and transpiration rate ( $E$ ) of *Fraxinus griffithii* across different seasons from 2010 to 2012. The data gap in 2011 and 2012 occurred due to full defoliation in April 2011 and thunderstorms in July of both years. Bars indicate  $\pm$  standard error.

The light response curve differed across seasons, and was generally higher in summer and autumn (Figure 3). Table 1 shows the parameters calculated with the light response curve. No significant differences were found in  $\alpha$  or  $R_D$  across seasons. However,  $A_{max}$  was significantly lower in the winter ( $2.69 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) and spring ( $1.57 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) than in the other seasons. In addition, the LCP was significantly higher in spring than in other seasons. Finally, LAI was consistent across all three years and was highest (3.70) in August and lowest (0.69) in March.



**Figure 3.** Light response curve of net photosynthetic rate ( $P_N$ ) of *Fraxinus griffithii* across different seasons in 2011. PPFD: photosynthetic photon flux density. Bars indicate  $\pm$  SE.

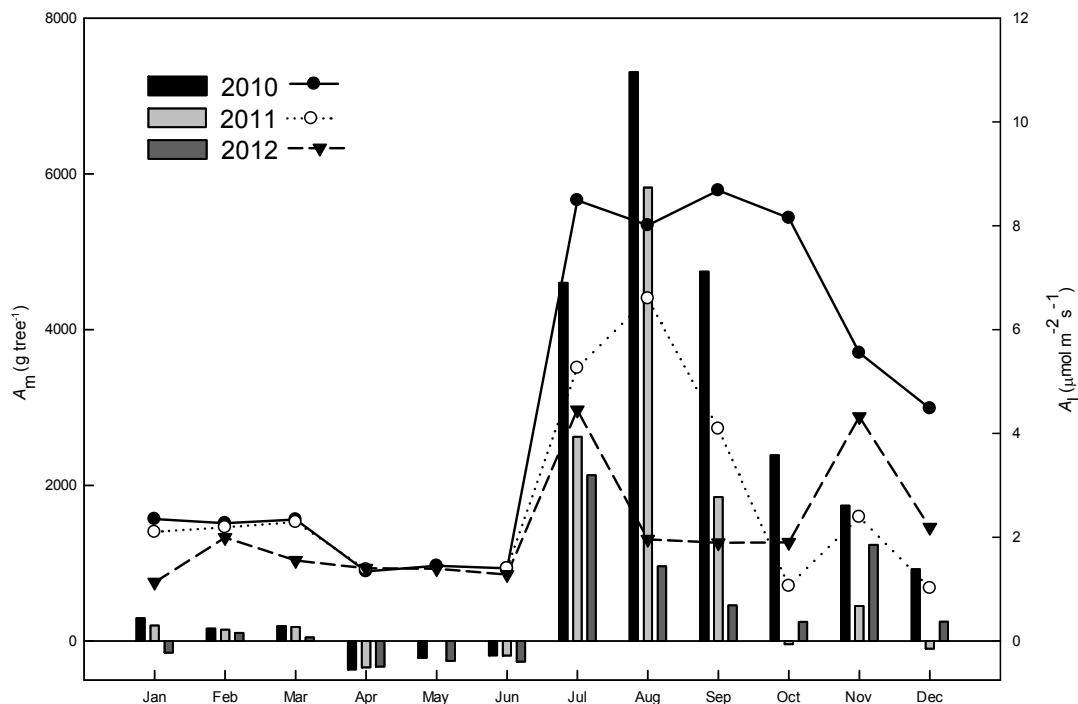
**Table 1.** Average values ( $\pm$  standard error) of quantum efficiency ( $\alpha$ ), shape parameter ( $\theta$ ), light compensation point (LCP), maximum assimilation rate ( $A_{max}$ ), dark respiration ( $R_D$ ), and leaf area index (LAI) of *Fraxinus griffithii* across different seasons.

	Winter	Spring	Summer	Autumn
$\alpha$ ( $\text{mol}\cdot\text{mol}^{-1}$ )	$0.040 \pm 0.011$ <sup>a,*</sup>	$0.051 \pm 0.007$ <sup>a</sup>	$0.056 \pm 0.004$ <sup>a</sup>	$0.050 \pm 0.001$ <sup>a</sup>
$\theta$	$0.003 \pm 0.001$ <sup>b</sup>	$0.004 \pm 0.001$ <sup>b</sup>	$0.006 \pm 0.001$ <sup>b</sup>	$0.013 \pm 0.001$ <sup>a</sup>
LCP ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	$30.20 \pm 4.67$ <sup>a,b</sup>	$41.86 \pm 2.28$ <sup>a</sup>	$21.46 \pm 4.78$ <sup>b</sup>	$21.88 \pm 2.57$ <sup>b</sup>
$A_{max}$ ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	$2.69 \pm 1.33$ <sup>b</sup>	$1.57 \pm 0.41$ <sup>b</sup>	$13.49 \pm 2.26$ <sup>a</sup>	$16.66 \pm 3.19$ <sup>a</sup>
$R_D$ ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	$1.29 \pm 0.56$ <sup>a</sup>	$2.16 \pm 0.36$ <sup>a</sup>	$1.22 \pm 0.35$ <sup>a</sup>	$1.10 \pm 0.14$ <sup>a</sup>
LAI ( $\text{m}^2\cdot\text{m}^{-2}$ )	$1.02 \pm 0.26$ <sup>c</sup>	$2.31 \pm 0.03$ <sup>a,b</sup>	$2.73 \pm 0.49$ <sup>a</sup>	$1.44 \pm 0.15$ <sup>b,c</sup>

\* Means followed by different lowercase letters differ significantly between seasons ( $p < 0.05$ ).

### 3.3. $\text{CO}_2$ Assimilation and Environmental Factors

Seasonal variation in  $A_l$  was apparent, with rates peaking at different months across the study period (Figure 4). In 2010, for example, the highest  $A_l$  occurred from July to October, while in 2012, the highest  $A_l$  values occurred in July and November. Seasonal variation in  $A_m$  was also observed: negative  $A_m$  was recorded from April to June 2010, April, June, October, and December 2011, as well as in January and April to June 2012.



**Figure 4.** The leaf-level CO<sub>2</sub> assimilation rate ( $A_1$ , lines) and tree-level monthly CO<sub>2</sub> assimilation ( $A_m$ , bars) of *Fraxinus griffithii* from 2010 to 2012.

The maximum  $A_m$  of a single tree from 2010 to 2012 was 7308.12 g in August 2010, 5823.86 g in August 2011, and 2129.92 g in July 2012. Annual CO<sub>2</sub> assimilation of *F. griffithii* was 26.33 Mg·ha<sup>-1</sup>·year<sup>-1</sup> in 2010, 12.94 Mg·ha<sup>-1</sup>·year<sup>-1</sup> in 2011, and 5.41 Mg·ha<sup>-1</sup>·year<sup>-1</sup> in 2012. The  $A_m$  from July to September was 77.15%, 97.05%, and 79.97% of annual CO<sub>2</sub> assimilation in 2010, 2011, and 2012, respectively. The tree-level and stand-level CO<sub>2</sub> sequestration for *F. griffithii* averaged 12.21 kg·year<sup>-1</sup> and 14.89 Mg·ha<sup>-1</sup>·year<sup>-1</sup>, respectively. Finally, CO<sub>2</sub> assimilation of *F. griffithii* was significantly correlated with SWC ( $p < 0.01$ ) and  $T_a$  ( $p < 0.05$ ), indicating that some environmental factors affected CO<sub>2</sub> sequestration rates (Table 2). The SWC was significantly correlated with all environmental factors except ambient CO<sub>2</sub> concentration.

**Table 2.** The correlation coefficients between monthly CO<sub>2</sub> assimilation ( $A_m$ ) and environmental factors ( $T_a$ : air temperature,  $T_s$ : soil temperature, SWC: soil water content, CO<sub>2</sub>: ambient CO<sub>2</sub> concentration, PPFD: photosynthetic photon flux density, VPD: vapor pressure deficit) of *Fraxinus griffithii* ( $n = 35$ ).

	$T_a$	$T_s$	Precipitation	SWC	CO <sub>2</sub>	PPFD	VPD
$A_m$	0.405 *	0.241	0.316	0.472 **	0.267	0.240	0.133
$T_a$	-	0.827 **	0.538 **	0.672 **	-0.081	0.632 **	0.135
$T_s$		-	0.400 *	0.346 *	-0.037	0.654 **	-0.097
Precipitation			-	0.670 **	0.079	0.087	-0.026
SWC				-	0.327	0.157	0.047
CO <sub>2</sub>					-	-0.112	-0.428 *
PPFD						-	-0.031

\* indicates  $p < 0.05$ , \*\* indicates  $p < 0.01$ .

#### 4. Discussion

Our results show that SWC and  $T_a$  were the primary factors affecting carbon sequestration of a Southeast Asian *F. griffithii* plantation experiencing a monsoon climate. In 2010, over 92% of the annual precipitation occurred during March to September, and the dry season lasted longer than half

a year. Our results demonstrated that droughts have long-lasting consequences on photosynthesis in *F. griffithii*, which support previous research indicating that water stress limits tree growth and decreases photosynthetic efficiency [16,17]. The extended dry seasons in our study period occurred during the early growth season of *F. griffithii* (March to April). Moreover, a previous study had demonstrated that a spring drought may suppress canopy development and exert long-lasting effects on annual ecosystem carbon balance that remains even when soil water availability improves [3]. Here, we also found that repeated measurements significantly affected  $P_N$  and carbon sequestration, and the interaction between those repeats and the year was significant as well. Thus, despite heavy summer precipitation in all three years leading to high SWC, 2012 still experienced a low photosynthetic rate might because overall precipitation levels decreased in the previous year. However, the quantitative understanding of these effects remains limited because the lags and feedbacks between different processes depend on soil and other site-specific factors [3].

Precipitation varied seasonally during every study year, and environmental factors such as PPFD, SWC, and RH fluctuated depending on that variation. Precipitation from May to September was approximately 92%, 83%, and 90% of the annual amount in 2010–2012, respectively. During the study period, southern Taiwan experienced four typhoons that became the major source of soil water per year and led to higher precipitation. Although the typhoon also caused damage (defoliation, snapped boles, uprooting), these effects ultimately did not affect photosynthetic rate more than the increase in soil moisture. The SWC exhibited variations similar to precipitation during the experimental period, but remained high even when precipitation decreased in October 2010 and 2011. SWC was the lowest in October 2012 and resulted in a lower photosynthetic rate during this season. In contrast, on 30 July 2012, an afternoon thundershower (increasing SWC) was associated with higher photosynthetic rate.

The lower precipitation in 2011 likely caused the full tree defoliation that occurred in April of that year, a phenomenon also observed in tropical dry forests [18]. The diurnal dynamics of gas exchange might reflect the ability to maintain photosynthesis under different environmental conditions [19,20]. Generally, photosynthetic rate increased with PPFD and was higher in the morning. However, July  $P_N$  increased from morning and decreased later in the day for all three years but rarely fluctuated with PPFD, likely because of high summer temperatures. The lack of correlation between  $P_N$  and PPFD may affect photosynthetic rate through numerous individual environmental factors, such as air temperature, SWC, and vapor pressure deficit, or a combination of these [21,22]. In particular, because VPD strongly influences stomatal opening and closing, the variable is an important factor in gas exchange [21,22]. Lower  $g_s$  with high VPD in the afternoons represented stomatal closure to prevent water loss. Correspondingly, we observed a midday depression of leaf photosynthesis throughout the experimental period (regardless of season), except July 2010 and 2012, when overcast days dampened photosynthesis at all hours. Such midday photosynthetic decreases are common to tropical forest canopies and may result from stomatal or non-stomatal limitations, which in turn are caused by high temperature, irradiance, or VPD [20,21].

Understanding environmental controls on leaf photosynthetic activity is fundamental for evaluating the large-scale behavior of an ecosystem. The photosynthetic light response curve, which describes the relationship between leaf photosynthetic rate and light levels (PPFD), helps to characterize plant photosynthetic capacity [15,23]. Here, we used this method to estimate carbon assimilation variables across different seasons and found that the light response curve was saturated at a lower PPFD during the dry season. This result corroborates previous research showing that variation in SWC influences photosynthetic rate [24]. Furthermore, we found that the  $A_{max}$  of *F. griffithii* was higher in summer than in spring, while the LCP was lower in the summer than in spring. This pattern indicates that *F. griffithii* photosynthesizes across a wider range of irradiance conditions in summer. We should note that the LCP,  $A_{max}$ , and  $R_D$  values obtained in this study were slightly lower than previous reports for *F. griffithii* [25], and we suggest that these differences may be due to differing environmental conditions and sample ages across studies.



Leaf area index varies during the year and influences carbon sequestration via determining the amount of PPFD absorbed by the leaves, and thus, the canopy as a whole [26,27]. We observed that LAI began to increase during spring with the development of new leaves, and continued to increase until late summer. As can be expected from the lower LAI in spring versus summer, CO<sub>2</sub> assimilation was negative during spring of all three years and reached maximum positive values during summer, reflected in low and high  $A_{max}$ , respectively, over the two seasons. Additionally,  $R_D$  was high during spring and low during summer. Thus, greater LAI increases carbon assimilation through photosynthesis and carbon emission through dark respiration.

In terms of CO<sub>2</sub> assimilation rates, we found that  $A_l$  exhibited different patterns from  $A_m$ . This outcome is likely because total assimilation depends not only on  $\alpha$  or spontaneous net assimilation rate, but also on factors such as dark respiration, effective leaf area, water availability, and proximity to other trees. Accordingly, we found that air temperature and SWC strongly affected CO<sub>2</sub> assimilation rates. Moreover, most environmental factors significantly correlated with SWC. For example, the low precipitation in October and December 2011 dropped annual CO<sub>2</sub> assimilation for that year. In 2012, the 18 and 27 days of precipitation during June and August, respectively, comprised approximately 70% of the annual precipitation, leading to weaker light intensity. Furthermore, an unusually arid July decreased CO<sub>2</sub> assimilation during summer, ultimately lowering total CO<sub>2</sub> assimilation for 2012 compared with other years. Numerous reports emphasize that water stress influences gas exchange, frequently causing decreased photosynthetic efficiency, stomata conductance, and transpiration [17,28–30]. Photosynthetic efficiency may decline because the correlated variables [31] of high temperature and water stress [32] lead to photo-inhibition. In other words, under low water conditions, evaporative cooling will decrease and leaf temperatures will increase.

Notably, for all three years, maximum  $A_l$  and  $A_m$  occurred in the summer, likely because of higher SWC and LAI during that season. In comparison with other studies, our calculated carbon sequestration rates exhibited similar levels of between-year variation. Specifically, annual carbon sequestration was 80.5 g·m<sup>-2</sup> in 1999 and 57.6 g·m<sup>-2</sup> in 2000 [33] for a subalpine forest, and 144, 80, 116, and 290 g·m<sup>-2</sup>·year<sup>-1</sup>, respectively, in 1994, 1996, 1997 and 1998 for a boreal deciduous forest [34]. In addition, another study examining seven broadleaved species in India [2] used the same method for estimating carbon sequestration as the present work, and found similar annual rates ranging from 171.71 to 555.05 g·m<sup>-2</sup> in 2011. Several studies also described the interannual variability of CO<sub>2</sub> sequestration, likely caused by seasonal climatic shifts (e.g., growing-season length, cloudiness) [35,36]. However, Grünzweig et al. [37] showed that forests in the Mediterranean region accumulated noticeably lower amounts of carbon (130–240 g·m<sup>-2</sup>·year<sup>-1</sup>) than our study, likely because of interspecific differences and the arid climate.

When we compared the average annual carbon sequestration of *F. griffithii* (406.18 g·m<sup>-2</sup>) with results from previous research in Taiwan, we noted that our average rates tended to be higher. We believe this disparity stems primarily from variation in study site characteristics. For instance, one study on the same species used biomass to estimate carbon sequestration rates, and collected data from an older plantation, with higher stand density [10], than our site. Another study on *Acacia confusa* and *Liquidambar formosana* in southeast Taiwan examined mature stands aged approximately 25–30 years [38], considerably older than our sample trees.

## 5. Conclusions

Our results demonstrate that air temperature, soil water content, and leaf area are the major factors affecting CO<sub>2</sub> sequestration in *F. griffithii*. Their effects may be exacerbated by manifestations of global climate change, such as high temperature, extreme drought, and frequent typhoons. These findings should be applicable to other forests and help improve our understanding of the processes involved in plant assimilation of CO<sub>2</sub>, thereby allowing better forest management procedures to be developed.

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