

Drought Impact on Carbon Assimilation of A *Zelkova Serrata* Plantation

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Abstract

Background: 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*, an important plantation species, which extensively planted in low altitude of East Asia.

Results: We measured monthly gas exchange parameters and leaf area 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. However, drought led to lower daytime assimilation and higher night-time respiration, which caused a 43% decrease in carbon assimilation. Additionally, the poor site quality and environmental stress may impact the growth and carbon assimilation of this species.

Conclusions: *Z. serrata* may not be suitable for planting in a tropical monsoon climate area. Therefore, the effects of extreme weather on the forest carbon budget may be stronger in the future. Leaf area showed seasonal variation and serious defoliation caused by a typhoon in the summer. The monthly leaf assimilation rate was 0.88–4.17 μmol CO₂ m⁻² s⁻¹, which was estimated to assimilate 3.50 Mg C ha⁻¹ yr⁻¹ in the study area.

Background

Climate change is mainly caused by the emission of greenhouse gases through human activities and has extensive impacts on human and natural systems by increasing CO₂ concentration and air temperature, changing the precipitation pattern, and increasing the frequency and intensity of extreme weather events such as drought and typhoons. Moreover, climate change affects the physiology of Trees including photosynthesis, respiration, transpiration, decomposition, and nitrogen fixation. Simultaneously, it changes the ecosystem matter circulation, energy flow, and plant gross primary production, growth, flowering, and fruiting, affecting the animals that use plants (Desjardins et al. 2008; Gaboury et al. 2009; IPCC 2014; IPCC 2018).

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 (Sulman et al. 2016). In 2011, an intense drought impacted several regions around the world, causing a reduction in forest carbon sequestration (Flanagan et al. 2017). The severe drought suppressed plant photosynthesis, leading to a reduction of 0.23–0.53 petagrams carbon in the Amazon basin and turned the forest from a carbon sink to a source within a short period (Doughty et al. 2015). Additionally, the forest response to changing environmental conditions may affect the regional and global climate (Sulman et al. 2016).

Forests are the world's largest terrestrial carbon sink, which 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 enable sustainable livelihood generation. Therefore, a profound understanding of forest carbon budgets under extreme weather conditions is an urgent need (Lee et al. 2004; Solomon et al. 2017). However, plantations are subject to various environmental stresses in the field that may impact their photosynthetic efficiency, growth performance, and carbon sequestration potential (Lin et al. 2002; Chen et al. 2016). For example, environmental factors, such as precipitation and soil water content, may not be the main factors affecting carbon assimilation, whereas vapour pressure deficit and warming could strongly impact the forest carbon sink under drought conditions (Dai et al. 2015; Sulman et al. 2016).

Selection of plantation species that are valuable and adapted to the regional environmental conditions is a necessary prerequisite 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*, an important plantation species in East Asia with high woody carbon content and economical value. Our study aims were to clarify the drought impact on photosynthesis and carbon assimilation of *Z. serrata* plantation and estimate their suitability for tropical monsoon climates.

Methods

Study site and species

The data for this study was 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). Soil were classified as Entisols with over 60% parent material of sandstone and 45–55% gravel content, and the soil profile is shallow (< 40 cm depth) (Chen et al. 2012; Yu et al. 2012). In the study site, 14 species were used for afforestation from 2002 to 2005, with *Z. serrata* widely planted near the centre of the farm in 2003. *Z. serrata* is a pioneer species frequently used in lowland afforestation, having the second largest plantation area in Taiwan. The initial stand density was 1,500 seedlings ha⁻¹, with constant pruning and weed removal. A study plot (20 × 25 m) with 27 trees was set in 2010, where the average diameter at breast height and tree height were 3.89 ± 1.58 cm and 3.46 ± 1.28 m, respectively. The surrounding of the study plot was covered by the same species and size with the 77.4% of crown density in average.

Microclimate data were collected by a microclimate station from 400 m southeast of experimental plot with 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 lower (1,929 mm) than 2010 (2,848.5 mm) and 2012 (3,144.5 mm), 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 variation of precipitation, soil water content and air temperature in 2011 is shown in Fig. 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) and showed a similar pattern to that of precipitation, being lowest in March (8.8%) and highest in July (19.4%) in 2011.

Measurements of gas exchange and leaf area

Scaffolds (1.7 m height) were set near the sample trees with tripods so the leaf clamp reached the canopy leaves. Diurnal variations of leaf gas exchange were measured by portable photosynthesis systems (LI-6400; LI-COR, Lincoln, NE, USA) with a clear chamber bottom (LI-6400-08; LI-COR) one day per month for each sample tree during 2011 from three intact, fully expanded mature leaves on the same side of the canopy. Juvenile and ageing leaves were excluded from sampling. 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 maintain CO_2 concentration in the leaf chamber changing with ambient atmosphere. The air temperature (T_a), leaf temperature (T_l), vapour pressure deficit (VPD_a), and leaf vapour pressure deficit (VPD_l) were also recorded. The data gap in September 4 was caused by rain during 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 (photosynthetic photon flux density, PPFD) 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 minutes stabilization time in 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 $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ [15,16].

Total leaf area of the tree was estimated from the leaf area index (LAI), measured monthly at dusk from the top and under the canopy of three sample trees. LAI was measured by a plant canopy analyser (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 by measuring major and minor axis in two perpendicular directions as crown projection.

Data analysis

The single tree total leaf area was calculated by multiplying LAI by the canopy projection area, which was estimated as an ellipse. The crown projection area was calculated by measuring major and minor axes in two perpendicular directions.

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 (Sands 1995; Biswas et al. 2014). Therefore, the leaf carbon assimilation (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$) was calculated from the following equation:

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

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 model has been well-tested and extensively applied in several leaf carbon assimilation studies (Sands 1995; Thornley 2002; Biswas et al. 2014; Chen et al. 2019)

Several models to scale-up carbon assimilation from leaf to canopy level are already in use (Lambers et al. 1998). After calculating the leaf assimilation rate, we upscaled from leaf- to canopy-level assimilation using LAI as shown in (Chen et al. 2019). The estimation formulas were as follow:

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

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

Total daily canopy assimilation (A_c) can be calculated by considering total leaf area (L), day length (h), and leaf carbon assimilation (A) from formula (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 variations in air temperature during the nights of the study period were less than 6°C and 3°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 analyse 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.

Results

In the study area, precipitation in May – September was 94%, 92%, and 83% of the accumulated annual precipitation in 2009, 2010, and 2011, respectively. The soil water content was lowest in March (8.8%) and highest in July (19.4%) in 2011. Therefore, data from the dry and wet seasons were analysed separately.

The correlation between gas exchange parameters and environmental factors are shown in Table 1. 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 1). VPD greatly influenced stomatal opening/closure, especially under dry and high temperature conditions. In 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 CO₂ assimilation.

Table 1

Correlation coefficients for *Zelkova serrata* between gas exchange parameters (P_n : net photosynthetic rate, g_s : stomata conductance, C_i : intercellular CO₂ concentration, E: transpiration rate) and environmental factors (VPD_l: leaf to air vapour pressure deficit, VPD_a: vapour pressure deficit, T_l: leaf temperature, T_a: air temperature, CO₂: ambient CO₂ concentration, PPFD: photosynthesis photon flux density) in dry (grey) 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 variation in light intensity and VPD on leaf in different seasons are shown in Fig. 2 and gas exchange variation is shown in Fig. 3. We represented four days of diurnal data in January 28, May 31, September 4, and November 25 from monthly measurements in 2011. The PPFD and VPD were measured on the leaves. 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.

The daytime CO₂ assimilation, night-time respiration, and LAI are shown in Fig. 4. CO₂ assimilation in the wet season was 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 night-time respiration from January to March. In this study, the single tree night-time 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 (Fig. 5). The monthly leaf assimilation rate ranged from 0.88 to 4.17 μmol m⁻² 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 yr⁻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 night-time respiration in the wet season than those in the dry season (Fig. 6). Results also indicated that drought suppressed photosynthesis more than respiration.

Discussion

Gas exchange and environmental factors

A severe drought impacted many regions around the world in 2011 (Sulman et al. 2016; Flanagan et al. 2017). The 10-year average annual precipitation was 2,700.4 mm from 2005 to 2014 in southern Taiwan, thus the precipitation in 2011 (1,929 mm) was much lower than average. 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 (Colom and Vazzana 2003; Ogaya and Peñuelas 2003; Grzesiak et al. 2006; Li and Chen 2009). 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 (Ngugi et al. 2004; Ding et al. 2006; Jhou et al. 2017).

The diurnal variation of the net photosynthesis rate was high in the morning and decreased in the afternoon. Similar results were found by (Liao and Wang 2002) 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 (Gao et al. 2015; Hamada et al. 2016). The decrease in both P_n and g_s through the day appears to be the result of light-driven accumulations of photosynthesis products (Matthews et al. 2017). However, the P_n values recovered over the following morning showed that the damage to photosynthesis under environmental stress is impermanent. 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 (Arndt et al. 2015; Li et al. 2016). 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 (Yin et al. 2006; Zhang et al. 2013). 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 (Matthews et al. 2017). Both temperature and VPD presented a significant correlation with P_n in the dry season, showing that the responses of the leaf 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 (Koch et al. 1994; Li and Chen 2009; Cordeiro et al. 2009; Tucci et al. 2010; Sulman et al. 2016; Slot and Winter 2017).

Light intensity is one of the important factors affecting photosynthetic rate and therefore influenced the 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 (Yin et al. 2006; Lachapelle and Shipley 2012; Lang et al. 2013). These parameters varied both with internal plant factors (e.g., shade tolerance) and external environmental factors (e.g., water stress) (Kuo et al. 2004; Yin et al. 2006). 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 (Sands 1995; Lin et al. 2002; Biswas et al. 2014; Chen et al. 2019).

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 night-time respiration in the dry season. Several studies demonstrated that the photosynthetic rate was higher in the wet season than in the dry season (Colom and Vazzana 2003; Ogaya and Peñuelas 2003; Li and Chen 2009; Bucher et al. 2018). Kuo et al. (2004) showed that photosynthetic rate fluctuated (48–286%) during the dry and wet season in 30 broad-leaved tree species. Hu et al. (2008) 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. 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 (Way et al. 2015). Generally, the leaf respiration rate is greatly affected by temperature

and light intensity and, hence, shows seasonal variation (Way et al. 2015). However, Yin et al. (2006) 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 utilisation was reduced, which decreased the photosynthetic potential.

Total leaf area not only influences the amount of light availability 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 emission by respiration (Bonan 1993; Gond et al. 1999). 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 (Gond et al. 1999). Biswas et al. (2014) indicated that the LAI of seven young broadleaf tree species ranged from 1.22 to 3.26 in a plantation area. Chen et al. (2016) 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* in the study site may be caused by poor site quality, specific difference and plant pathology (Yeh et al. 2013; Cheng et al. 2016).

Seasonal carbon assimilation

The leaf assimilation rate can be upscaled to single-tree monthly CO_2 assimilation by considering total leaf area and day length (Fig. 5). The monthly leaf assimilation rate in *Z. serrata* was lower than that of *S. mukorossi* ($1.18\text{--}9.10 \mu\text{mol m}^{-2} \text{s}^{-1}$) in Southern Taiwan (Chen et al. 2016) and seven broad-leaved tree species ($1.37\text{--}11.61 \mu\text{mol m}^{-2} \text{s}^{-1}$) in Eastern India (Biswas et al. 2014). However, a previous study demonstrated that the poor site quality in the study area may be caused by a long-term monoculture of sugarcane (Chen et al. 2012). In addition, many trees showed symptoms of sooty mould in this area. Therefore, the effects of pathology on leaf photosynthesis could be an interesting field of research.

The single-tree annual CO_2 assimilation was lower than those of other studies in Taiwan such as $96.14 \text{ kg CO}_2 \text{ yr}^{-1}$ in *Z. serrata* (Liao and Wang 2002), $100 \text{ kg CO}_2 \text{ yr}^{-1}$ in *Phyllostachys pubescens* (Tu et al. 2003), $230 \text{ kg CO}_2 \text{ yr}^{-1}$ in *Cinnamomum camphora* (Hong and Wang 2003) and $56.8 \text{ kg CO}_2 \text{ yr}^{-1}$ in *Alstonia scholaris* (Wang et al. 2005a). However, several studies showed similar CO_2 assimilation to that of *Z. serrata*, such as $18.0 \text{ kg CO}_2 \text{ yr}^{-1}$ in *Pongamia pinnata* (Wang et al. 2005b) and $19.1 \text{ kg CO}_2 \text{ yr}^{-1}$ in *Pterocarpus indicus* (Chen et al. 2019). The estimation methods of CO_2 assimilation in the studies mentioned above were also based on photosynthesis. The difference of annual CO_2 assimilation may be affected by interspecific differences, regional climate, and seasonal climatic shifts (Barford et al. 2001; Goulden et al. 2011; Grünzweig et al. 2003). Our study found a lower amount of CO_2 assimilation ($23.79 \text{ kg tree}^{-1} \text{ yr}^{-1}$) than another study ($96.14 \text{ kg tree}^{-1} \text{ yr}^{-1}$) (Liao and Wang 2002) 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 (Cheng et al. 2016).

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 (Grünzweig et al. 2003). 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 (Spannl et al. 2016). Collectively, the results of this study provide detailed information about the carbon assimilation of *Z. serrata* that can be useful for the assessment of plantation species and management in the future.

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. Under high VPD and temperature conditions during the dry season, *Z. serrata* plantations showed a low photosynthesis rate and stomata conductance. Although poor site quality and environmental stress may not increase plantation mortality, it caused the suppression of 43% of carbon assimilation. We suggest that *Z. serrata* are unsuitable for planting in poor quality sites in a tropical monsoon area, and the impact of prolonged drought and soil condition may suppress the growth and carbon assimilation.

Declarations

Author Contributions: CIC, YCC and YNW conceived of the study, and participated in its design and coordination and helped to draft the manuscript. CIC, HHL and JCY collected, analyzed and interpreted data. CIC and CWW wrote the manuscript. CWW and YNW advised throughout. All authors read and approved the final manuscript.

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Figures

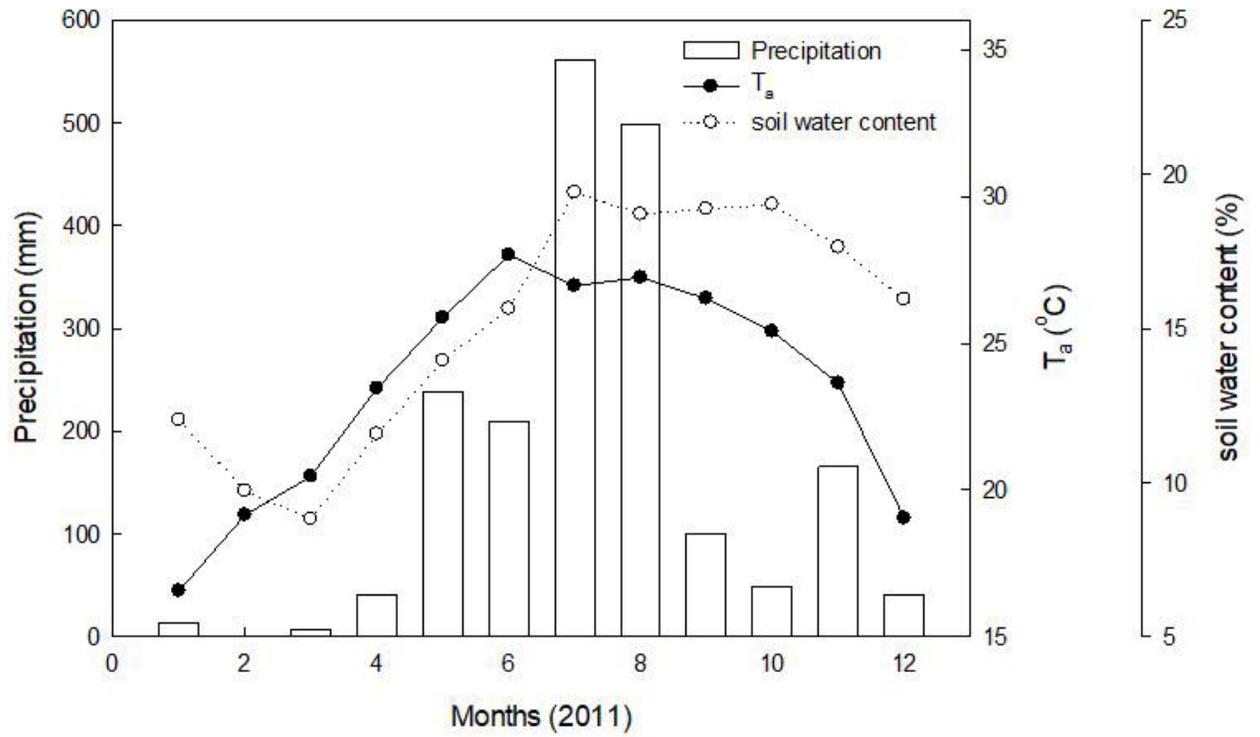


Figure 1

The monthly average air temperature (Ta), soil water content and accumulated precipitation in 2011

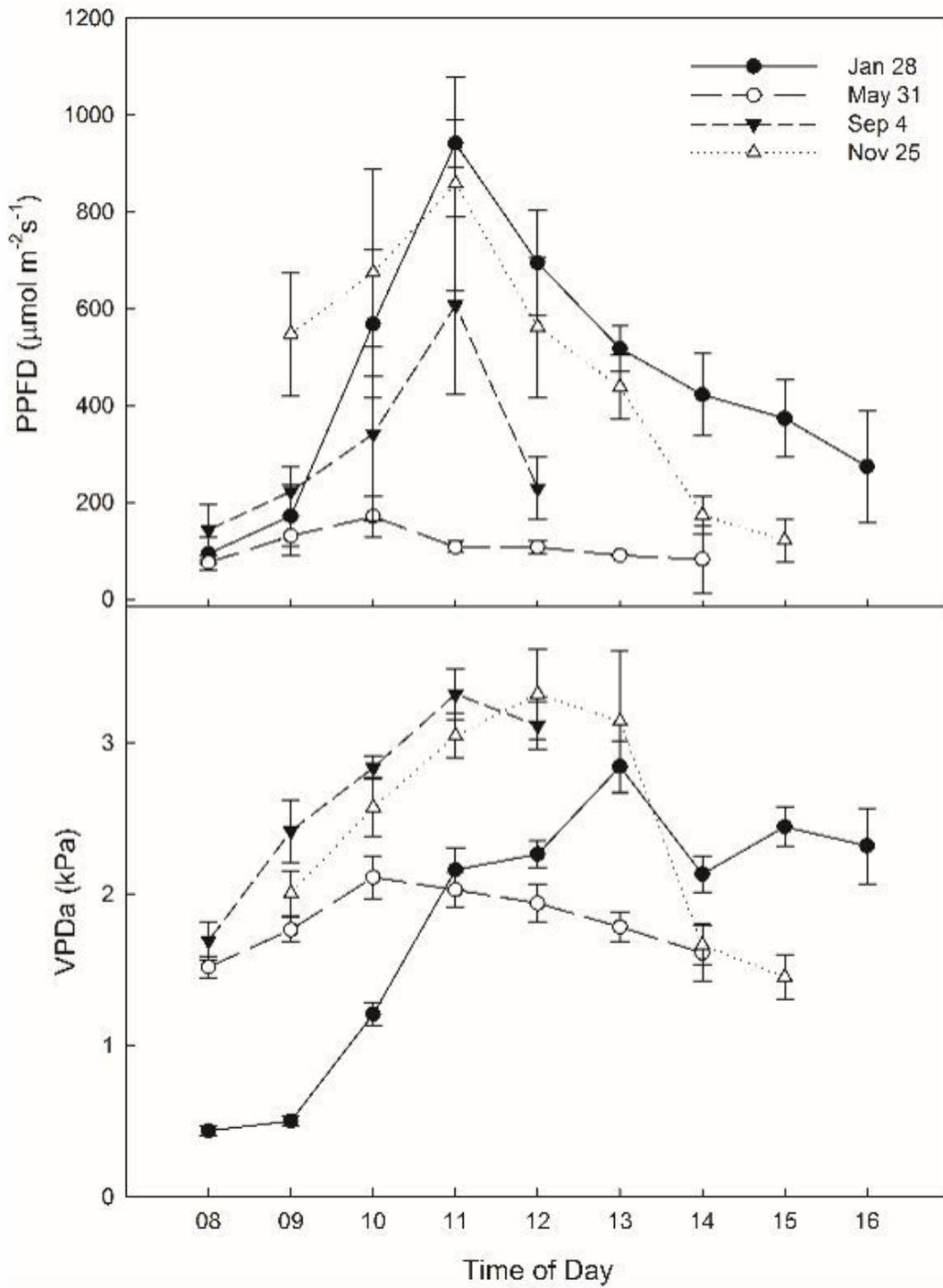


Figure 2

Diurnal variation of light intensity (PPFD) and vapor pressure deficit (VPDa) on January 28, May 31, September 4, and November 25, 2011. Bars indicate \pm SE.

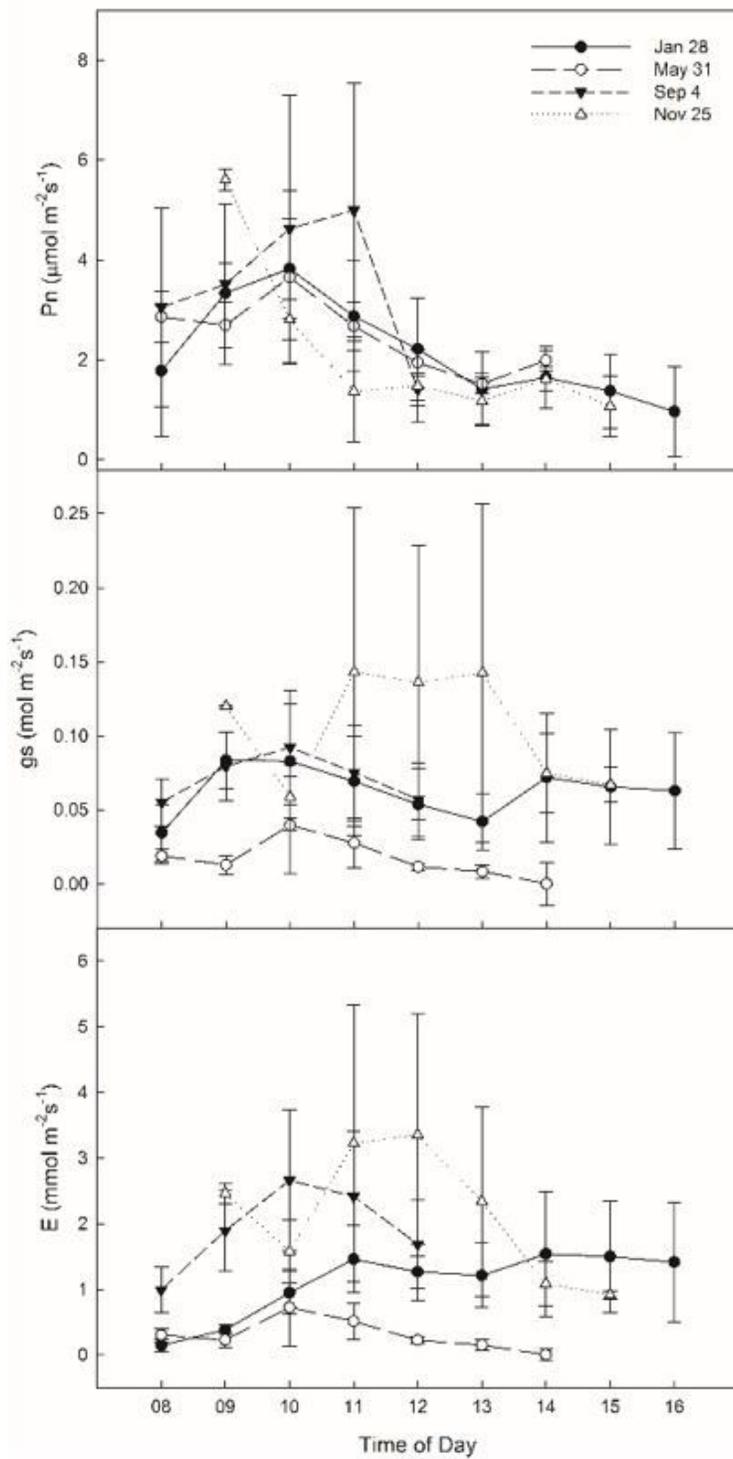


Figure 3

Diurnal variation of net photosynthetic rate (Pn), stomata conductance (gs) and transpiration rate (E) on January 28, May 31, September 4, and November 25, 2011. Bars indicate \pm SE.

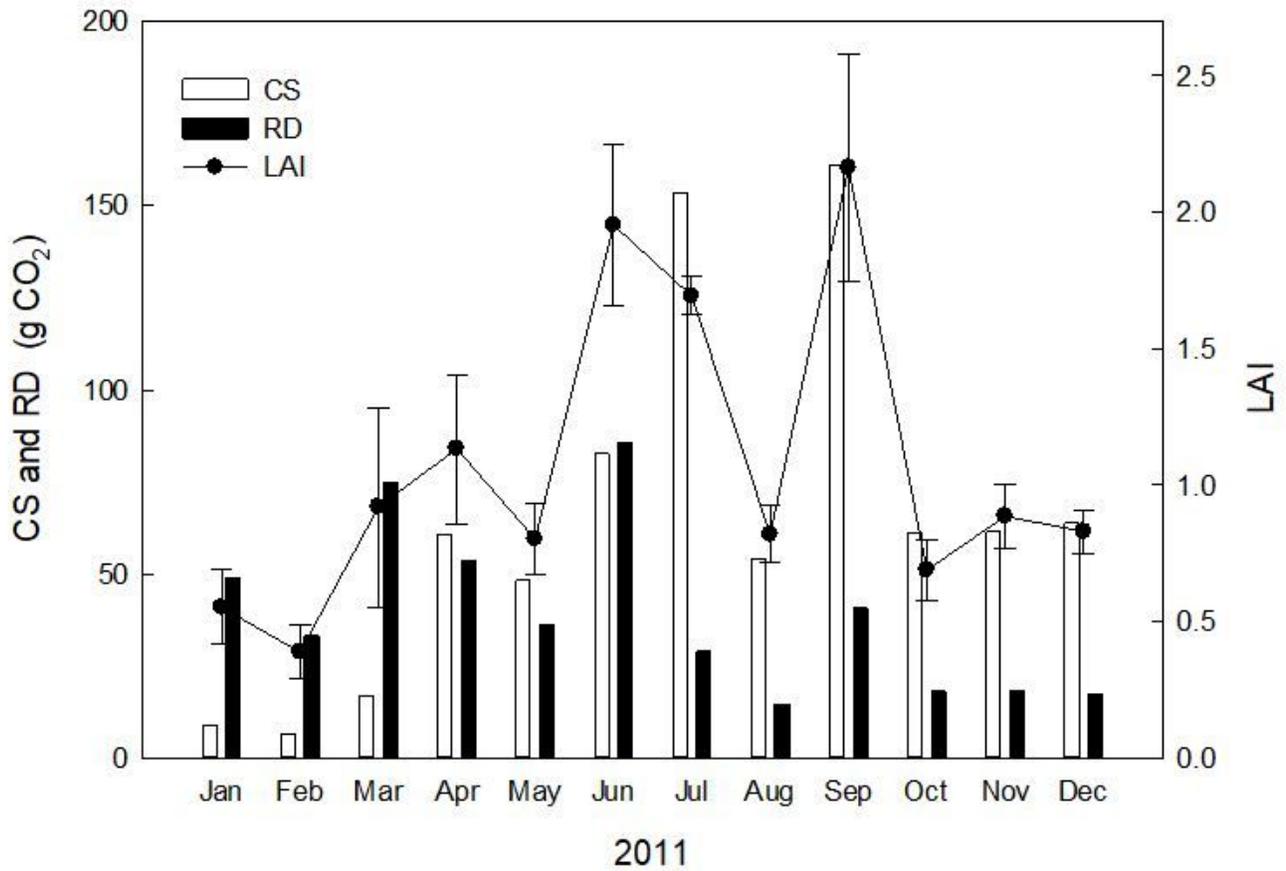


Figure 4

Monthly daytime CO₂ assimilation (CS), night respiration (RD) and leaf area index (LAI) of *Zelkova serrata*

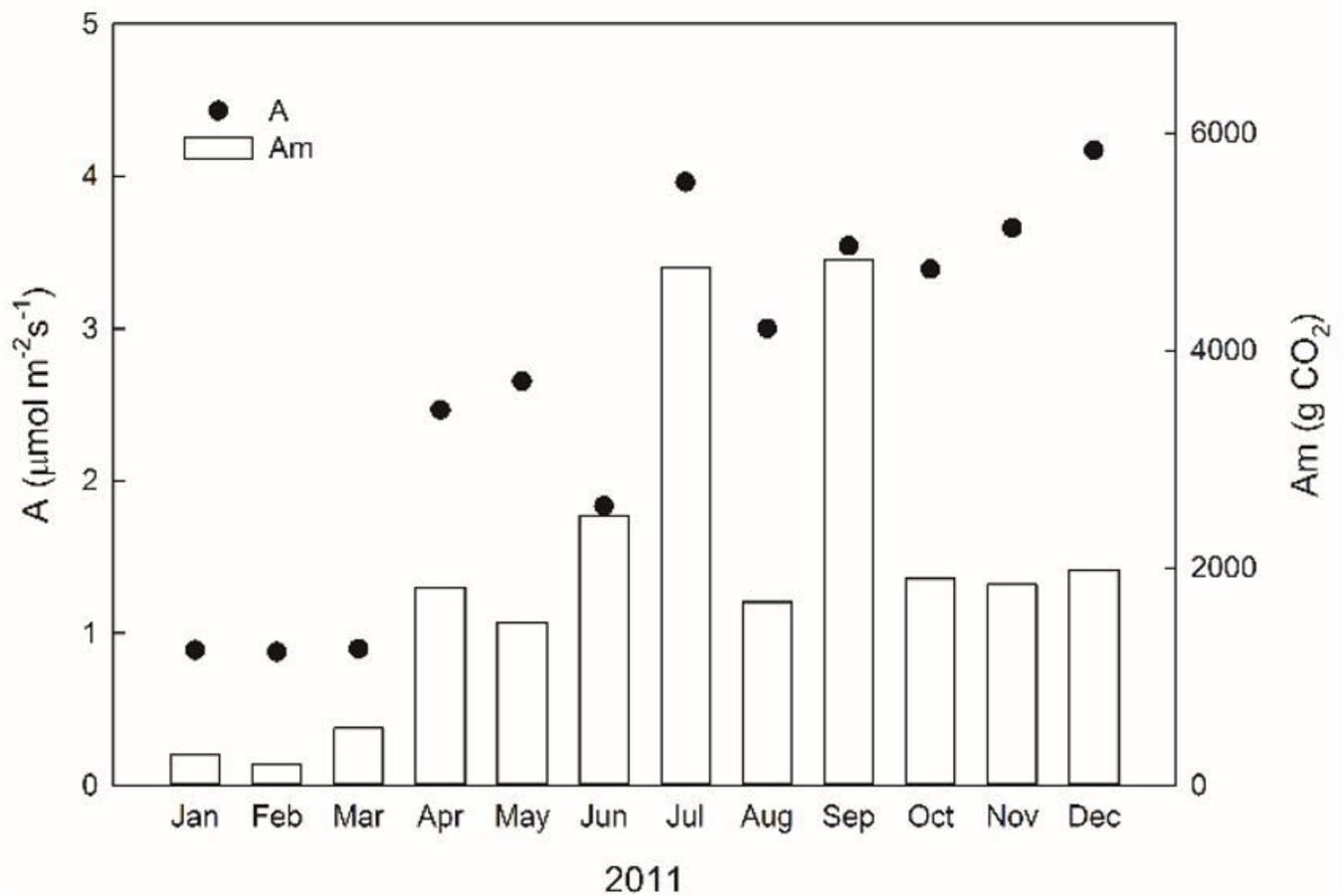


Figure 5

The monthly leaf assimilation rate (A) and monthly CO₂ assimilation (Am) of *Zelkova serrata*

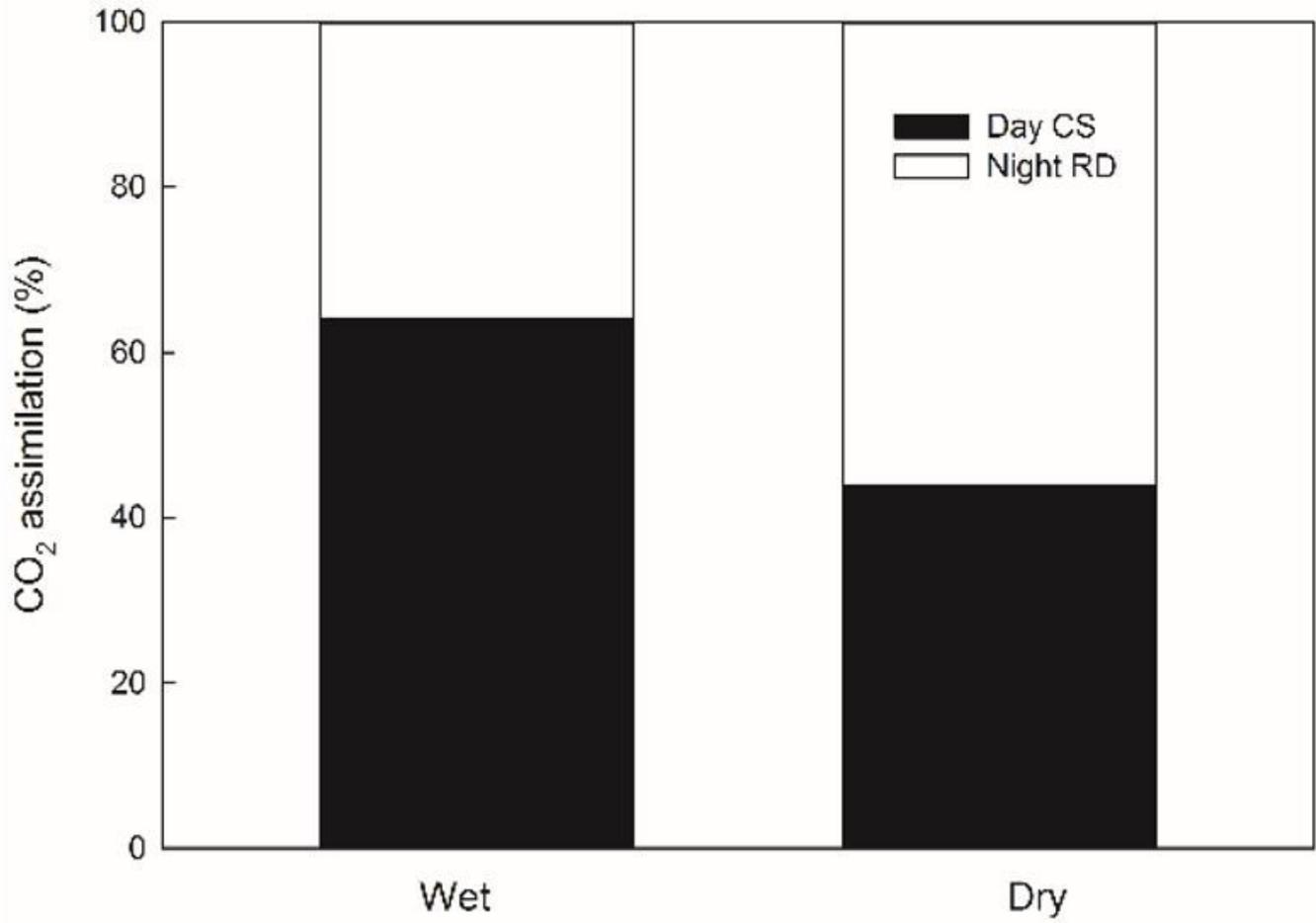


Figure 6

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