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Effects of Elevated Atmospheric CO_2 on Photosynthesis, Growth and Biomass in *Shorea platycarpa* F. Heim (Meranti Paya)

(Kesan Peningkatan CO_2 dalam Atmosfera Terhadap Fotosintesis, Pertumbuhan dan Biojisim *Shorea platycarpa* F. Heim (Meranti Paya))

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ABSTRACT

Elevated atmospheric CO_2 is widely reported to stimulate the plant growth and affect plant physiological processes. However, studies on the respond of tropical plant species to elevated CO_2 are quite limited and remain largely unknown. The objective of this study was to investigate the effects of elevated atmospheric CO_2 treatments on the photosynthetic characteristics, growth and biomass in Shorea platycarpa. *Saplings of* S. platycarpa *were grown for seven months in the open roof gas chamber supplied with elevated CO_2 (800±50 µmol mol^{-1}) and in the shade house with ambient CO_2 (400±50 µmol mol^{-1}). Measurements of* S. platycarpa *growth and photosynthetic characteristics were made at frequent intervals. Biomass characteristics were determined using destructive methods after seven months of treatment and nondestructive method was used for leaf area index (LAI) determination. Photosynthetic rate (A) of* S. platycarpa *was not significantly affected by elevated CO_2. Increased water use efficiency (WUE) of* S. platycarpa *grown in elevated CO_2 was due to the reduced stomatal conductance (g_s) and transpiration rate (E). The CO_2 elevation had no significant effect on the* S. platycarpa *relative growth rates (RGR) and biomass but significantly reduced the leaf area. A weak correlation was found between photosynthetic rate (A) and relative growth rate (RGR). The results clearly showed that photosynthesis, growth rate and biomass of* S. platycarpa *were not significantly enhanced by elevated CO_2. The findings indicated that elevated CO_2 did not affect a relatively slow growing and a late successional peat swamp tree species.*

Keywords: Biomass; elevated CO_2; growth rate; photosynthesis; Shorea platycarpa

ABSTRAK

Peningkatan CO_2 dalam atmosfera telah dilaporkan secara meluas kerana dapat meningkatkan pertumbuhan pokok dan memberi kesan kepada proses fisiologi pokok. Namun begitu, kajian ke atas tindak balas spesies pokok tropika terhadap peningkatan CO_2 agak terhad dan sebahagian besarnya tidak diketahui. Objektif kajian ini ialah untuk mengkaji kesan rawatan peningkatan CO_2 dalam atmosfera ke atas ciri fotosintesis, pertumbuhan dan biojisim Shorea platycarpa. *Anak pokok* S. platycarpa *telah ditanam selama tujuh bulan di dalam bilik gas dengan bumbung terbuka dan dibekalkan dengan peningkatan CO_2 (800±50 µmol mol^{-1}) dan di dalam rumah teduh dengan ambien CO_2 (400±50 µmol mol^{-1}). Pengukuran secara selang berulang ke atas pertumbuhan* S. platycarpa *dan ciri fotosintesis telah dibuat. Selepas tujuh bulan rawatan, ciri biojisim telah ditentukan dengan menggunakan kaedah musnah dan tanpa musnah untuk indeks luas daun (LAI). Kadar fotosintesis (A)* S. platycarpa *tidak dipengaruhi secara signifikan oleh peningkatan CO_2. Peningkatan kecekapan penggunaan air (WUE)* S. platycarpa *yang hidup di CO_2 berganda disebabkan oleh pengurangan stomata konduktans (g_s) dan kadar transpirasi (E). Peningkatan CO_2 tidak memberi kesan signifikan ke atas kadar pertumbuhan relatif (RGR) dan biojisim tetapi mengurangkan luas daun secara signifikan. Korelasi lemah wujud antara kadar fotosintesis (A) dengan kadar pertumbuhan relatif (RGR). Hasil jelas menunjukkan bahawa fotosintesis, kadar pertumbuhan dan biojisim* S. platycarpa *tidak meningkat secara signifikan dengan peningkatan CO_2. Penemuan tersebut memberi indikasi bahawa peningkatan CO_2 tidak memberi kesan kepada spesies pokok paya gambut dengan ciri pertumbuhan perlahan secara relatif dan lewat sesaran.*

Kata kunci: Biojisim; fotosintesis; kadar pertumbuhan; peningkatan CO_2; Shorea platycarpa

INTRODUCTION

For the 1000 years prior to the Industrial Revolution CO_2 was stable at about 270 µmol mol^{-1}; today CO_2 is approximately 38% higher at 372 µmol mol^{-1} and by the middle of this century it is predicted to reach 550 µmol mol^{-1} and to surpass 700 µmol mol^{-1} by the end of the century (Long et al. 2004). Extensive botanical investigations have been done to comprehend the potential effect of elevated atmospheric CO_2 concentration, e.g. studies on *Populus tremuloides*, *Betula papyrifera*, *Pinus taeda* and *Quercus ilex* (Karnosky 2003). However, not all plant species respond the same way to elevated CO_2. There is a considerable variation in the direction and magnitude of growth responses to elevated CO_2, partly depending on the duration of the exposure, plant development, species (e.g. species that differ in inherent growth rate or type of photosynthetic pathway) and the availability of primary resources (Poorter & Pérez-Soba 2001). Even though growth of *Ochroma lagopus*, a pioneer species and *Pentaclethra macroloba*, a climax species increased significantly in elevated CO_2, *O. lagopus* responded more to elevated CO_2 compared to *P. macroloba* (Oberbauer et al. 1985). In addition, Liang et al. (2001) reported that elevated CO_2 did suppresses photosynthesis of *Pongamia pinnata*, a shade tolerant species in both low and high light condition. Nonetheless, more than half of the recognized angiosperm families have not had a single species evaluated for CO_2 response in a field environment and there are large gaps in knowledge for a number of keystone species and genera, including those in the Dipterocarpaceae family (Leakey et al. 2012).

Shorea platycarpa also known as Meranti paya is a timber tree, belonging to Dipterocarpaceae family and is considered as endangered species due to forest conversion (Ashton et al. 1988). This species is generally found in deep peat swamp forest and the wood is commonly used for joinery and furniture (Choo et al. 1998). Compared to temperate regions and crop plants, the studies on elevated CO_2 on peat swamp trees is relatively limited. Peatland represent a major store of soil carbon and sink for carbon dioxide. Plants play an important roles in sequestering carbon through photosynthesis process and the amount and composition of carbon forms that plants sequester can be related to plant trait (De Deyn et al. 2008). Hence, the investigation on the responses of such important species in the peat swamp ecosystem to elevated CO_2 is timely. The present study describes the growth and physiological responses of a dominant, late successional (Hamzah et al. 2009), tropical tree species of a peat swamp forest i.e. *Shorea platycarpa* grown under elevated CO_2 with main focus on photosynthetic leaf gas exchange, relative growth rate and biomass allocation.

MATERIALS AND METHODS

PLANT MATERIAL, GROWTH CONDITION AND EXPERIMENTAL DESIGN

The experiments were conducted from March to October 2015 in an open roof chamber with elevated CO_2 that of 800±50 μmol mol^{-1} and in the shade house with ambient CO_2 that of 400±50 μmol mol^{-1} at the Universiti Kebangsaan Malaysia (UKM). The elevated concentration of CO_2 (800 ± 50 μmol mol^{-1}) were selected to match with the predicted concentration at the end of the century from a global climate models under WGIII scenario of IPCC (2014). Eighteen months old saplings of *S. platycarpa* were collected from Forest Research Institute Malaysia (FRIM). Seeds of this species are not readily available due to the non-mast years. For several species of dipterocarps, mast years occur unpredictably at intervals of 2-10 years (Ashton et al. 1988). Saplings growth responses can be measured easily compared to adult trees. Hence, they are more amenable to experimentation by short term research projects. Seedling growth and survival may also be more responsive to environmental than that of large trees (Zagt & Werger 1998). Microclimatic measurements were taken within and outside the chamber (shade house) at different time intervals. Humidity and temperature were monitored and controlled using ventilation system. Temperature and relative humidity were 0.1-0.2°C and 2-4% respectively, relatively higher in the chamber compared to shade house. The light intensity in the chamber was 94-95% of the shade house/ambient level. Treatment of CO_2 (800±50 μmol mol^{-1}) was done by daily automated continuous injection of pure CO_2 for 2 h starting from 9 until 11 am until the desired concentration (800±50 μmol mol^{-1}) was reached. CO_2 was supplied through CO_2 cylinder which was connected to air delivery system of the open roof chamber and air blower, and the concentration was regulated by dilution with air stream generated by the blower. CO_2 concentration in the chamber was monitored and administered using CO_2 analyzer. After two hours of CO_2 injection, the CO_2 levels inside the chamber and the ambient CO_2 was virtually the same. Growing medium used was ground parts topsoil podzolic types that were mixed with organic fertilizer with a ratio of 4:1. The saplings were planted in polybags (25 cm diameter × 30 cm depth). NPK was applied (15:15:15) with a low dose of 5 g/polybag/month. The pots were watered periodically to sustain soil moisture.

PLANT GROWTH

Plant growth (n=18) was assessed by regular, nondestructive measurements. Plants height, stem diameter and number of leaf were measured weekly for seven months. Plant height (cm) was measured vertically from the soil surface to the tip of youngest leaf (at the top of the plant) using a measuring tape. In addition, the main stem diameter (mm) was measured at a consistent point (5 cm above the base of the stem) using callipers. Relative height growth rate (RHGR), stem basal diameter growth rate (SDGR) and number of leaf growth rate (NLGR) were calculated every month according to Jach and Ceulemans (1999).

$RGR = (\ln l_2 - \ln l_1)/(t_2 - t_1)$ where l_1 = the height / diameter at time t_1 and l_2 = the height /diameter at t_2.

BIOMASS DETERMINATION

At the end of the experiment, the plants were cut at the base and divided into above ground and below ground parts. The roots were carefully washed in water to remove all soil particles and then both components were oven dried at 65°C for seven days. For growth analysis, the dry weight (DW) of the average above ground biomass (AGB), average below ground biomass (BGB) and below ground: above ground ratio (BG: AG) were calculated. The (BG: AG) was determined as below ground dry matter divided by the sum of above ground dry matter.

LEAF AREA INDEX DETERMINATION

A simple nondestructive method was used to estimate the leaf area index (LAI) using digital image taken *in situ* and public domain software ImageJ. Samples were taken after three months of treatment (first phase) and after seven months of treatment (second phase). To record the image of a leaf, a 30 cm ruler was placed on board with white paper where the leaf was positioned. Then, a photograph of each young, and fully expanded leaf (*n*=160 leaves originating from 8 plants) was taken using digital camera. The digital images were then processed in ImageJ for leaf area index (LAI) estimation.

PHOTOSYNTHETIC LEAF GAS EXCHANGE MEASUREMENTS

The measurements of the photosynthetic rate (A), stomatal conductance (g_s), transpiration rate (E) and water use efficiency (WUE) was made at frequent intervals throughout seven months treatment with the LI-6400 Portable Photosynthesis System (Li-cor, Lincoln, NE, USA). The levels of A, g_s, E, and WUE were measured at ambient CO_2 concentration (400 µmol mol^{-1}), air temperature (28-29°C), relative humidity (about 65%) and photosynthetic photon flux density (PPFD, 1000 µmol mol^{-1}) in the leaf chamber. For each treatment; ambient (400±50 µmol mol^{-1}) and elevated CO_2 (800±50 µmol mol^{-1}) concentration, measurements were made on randomly selected fully expanded leaf from each plant (*n*=18) from 9 am to 12 pm.

STATISTICAL ANALYSIS

An analysis of variance was conducted to evaluate the effects of elevated CO_2 on several growth characteristics using one way ANOVA of MINITAB version 16.0 software package. Growth characteristics, biomass characteristics, photosynthetic characteristics and leaf area index were included in the analysis of variance (ANOVA). The data were tested for normality using Anderson-Darling's test and where necessary raw data were transformed logarithmically to meet assumptions of normality. Statistical significance of the mean data was assessed by Tukey's multiple range test ($p \leq 0.05$). Relationship between gas exchange and growth parameters were analyzed by correlations and regression analysis using MINITAB version 16.0.

RESULTS

Elevated CO_2 did not enhanced the RHGR (Figure 1(a)), SDGR (Figure 1(b)) and NLGR (Figure 1(c)) of the plants. The highest peak of RHGR for ambient CO_2 and elevated CO_2 was 0.0043 and 0.0036 cm cm^{-1} day^{-1}, respectively. However, only at month five there was a significant difference ($p<0.05$) in RHGR between these two treatments. This was probably being influenced by the variability of individual growth performance. The highest peak of SDGR for ambient CO_2 and elevated CO_2 was 0.0048 and 0.0054 cm cm^{-1} day^{-1}, respectively. The SDGR in plants between ambient CO_2 and elevated CO_2 did not show significant

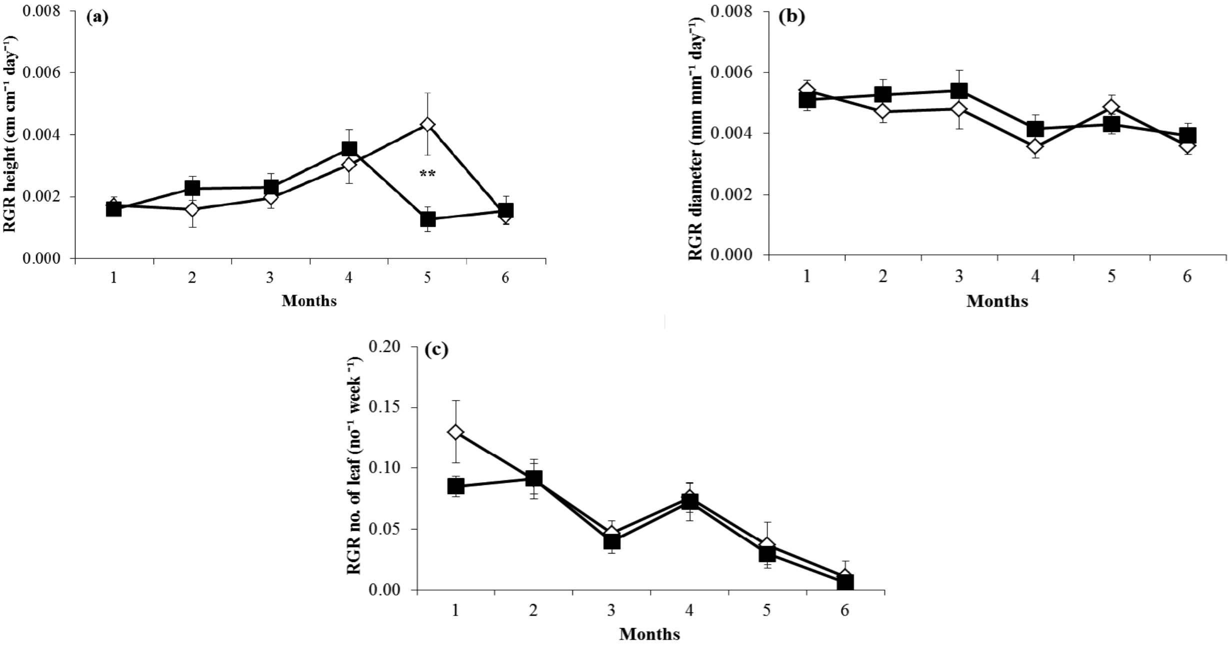

FIGURE 1. Time course of monthly relative growth rate (RGR) for height (a), diameter (b) and number of leaf (c) of *Shorea platycarpa* during seven months of treatment (Mac - October 2015) under ambient CO_2 and elevated CO_2. An ◇= 400±50 µmol mol^{-1}, ■ = 800±50 µmol mol^{-1}. Values represent means ± SE; n=18. The statistical significance is based on one-way ANOVA ($p \leq 0.05$). An asterisk (**) in (a) indicates a significant difference ($p<0.01$) between the ambient and elevated CO_2 treatment

($p<0.05$) variations in seven months of treatment. The NLGR from month one to month seven for both ambient CO_2 and elevated CO_2 treatment was continuously decreasing from 0.13 to 0.011 no.$^{-1}$ week^{-1} and 0.085 to 0.006 no.$^{-1}$ week^{-1}, respectively. Overall, there were no significant differences ($p<0.05$) in the mean relative growth rate (RGR) of height, diameter and number of leaf of *S. platycarpa* after seven months treatment in elevated CO_2 (Table 1).

There was no significant difference in the mean dry weight biomass of *S. platycarpa* grown in the two CO_2 conditions at ($p<0.05$) (Table 1). Though, a decreased biomass yield was observed for plant grown in elevated CO_2. Total dry weight biomass was 56.26 g higher in ambient CO_2 compared to elevated CO_2, which 48.12 g of it was from the above ground biomass. The below ground biomass was 8.14 g higher in ambient CO_2 compared to elevated CO_2. There was no significant ($p<0.05$) CO_2 effect on BG: AG, even though the ratios were slightly higher in elevated CO_2. On the other hand, leaf area index (LAI) (Table 1) shows significant difference ($p<0.05$) after seven months of treatment compared to after three months of treatment, indicating that duration of treatment under elevated CO_2 did give significant effect on the LAI of *S. platycarpa*. The LAI of *S. platycarpa* increased by 159.7% and 3.6% by the end of seven months treatment in the ambient and elevated CO_2, respectively.

The photosynthetic rate (*A*) was averagely increased by 82% and 85% by the end of seven months treatment in the ambient and elevated CO_2, respectively. Photosynthetic rate (*A*) of plant grown in elevated CO_2 did increase in the second month of treatment, but then it was getting lower than (*A*) for plants grown in ambient CO_2 (Figure 2(a)). Decreased stomatal conductance (g_s) (Figure 2(b)) and transpiration rate (E) (Figure 2(c)) in *S. platycarpa* under elevated CO_2 were recorded. After seven month of treatments, the value of stomatal conductance (g_s) and transpiration rate (E) of plants kept at elevated CO_2, compared with that of their counterparts grown in ambient CO_2, was 0.4% and 51.9% lower, respectively. As expected, transpiration rates (E) were significantly lower ($p<0.05$) at elevated CO_2 than at ambient CO_2 from early treatment until end of treatment. Transpiration was reduced due to a lower stomatal conductance (g_s). The water loss transpiration then will correspond to water use efficiency (WUE). Therefore, because of lower transpiration rate (E), plants grown under elevated CO_2 showed an average increase in water use efficiency (WUE) by 88% than their respective controls.

The correlation analysis between photosynthetic rates (*A*) and relative growth rate (RGR) after seven-month treatment showed a non-significant weak correlation ($r=0.4$, $p<0.05$)) for both RHGR (Figure 3(a)) and (SDGR) (Figure 3(b)), indicating that the photosynthetic rate (*A*) is not a primary influence for RHGR and SDGR of *S. platycarpa* under elevated CO_2.

DISCUSSION

EFFECTS OF ELEVATED CO_2 ON GROWTH

Growth increments of *S. platycarpa* were not profoundly influenced by elevated CO_2 despite (*A*) were increased in both condition. In many cases (e.g. Rasineni et al. 2011), high CO_2 usually increases the photosynthetic rate and thereby the growth rate. However, in the present study and some other experiments (Novriyanti et al. 2012), there were no positive effects of elevated CO_2 on growth of *S. platycarpa*. Nevertheless, in particular, the mean SDGR was higher under elevated CO_2 condition compared to ambient CO_2, whereas mean RHGR in elevated CO_2 was equivalent to the ambient CO_2 condition. Stem diameter was more responsive to CO_2 treatment compared to plant height. Many studies reported that elevated CO_2 resulted in the formation of wider tree rings in conifers (*Pinus radiata*

TABLE 1. Effects of atmospheric CO_2 (ambient; 400±50 µmol mol^{-1} and elevated 800±50 µmol mol^{-1}) on relative growth rate (RGR), biomass and leaf area index (LAI) in *Shorea platycarpa* after seven months of treatment (Mac - October 2015)

Characters	Ambient CO_2	Elevated CO_2	*P* level
Plant growth (RGR)			
RGR height (cm cm^{-1} day^{-1})	0.002 ± 0.00	0.002 ± 0.00	0.46 ns
RGR diameter (mm mm^{-1} day^{-1})	0.004 ± 0.00	0.005 ± 0.00	0.46 ns
RGR no. of leaf (no^{-1} week^{-1})	0.07 ± 0.00	0.05 ± 0.00	0.28 ns
Biomass (g DW plant^{-1})			
Below ground	41.51 ± 4.61	33.37 ± 6.23	0.32 ns
Above ground	137.71 ± 15.44	89.59 ± 21.83	0.11 ns
Total biomass	179.22 ± 18.51	122.96 ± 27.45	0.13 ns
BG:AG ratio	0.31 ± 0.02	0.40 ± 0.04	0.12 ns
Leaf area index (cm^2 plant^{-1})			
LAI (3 months of treatment)	2.24 ± 0.04	2.18 ± 0.03	0.10 ns
LAI (7 months of treatment)	4.50 ± 0.06	3.84 ± 0.08	0.00 ***

Values represent means ± SE; $n=18$. The calculation of statistical significance is based on one-way ANOVA ($p=0.05$). The symbol used ***$p<0.001$; **$p<0.01$; *$p<0.05$; not significant (ns) $p>0.05$.

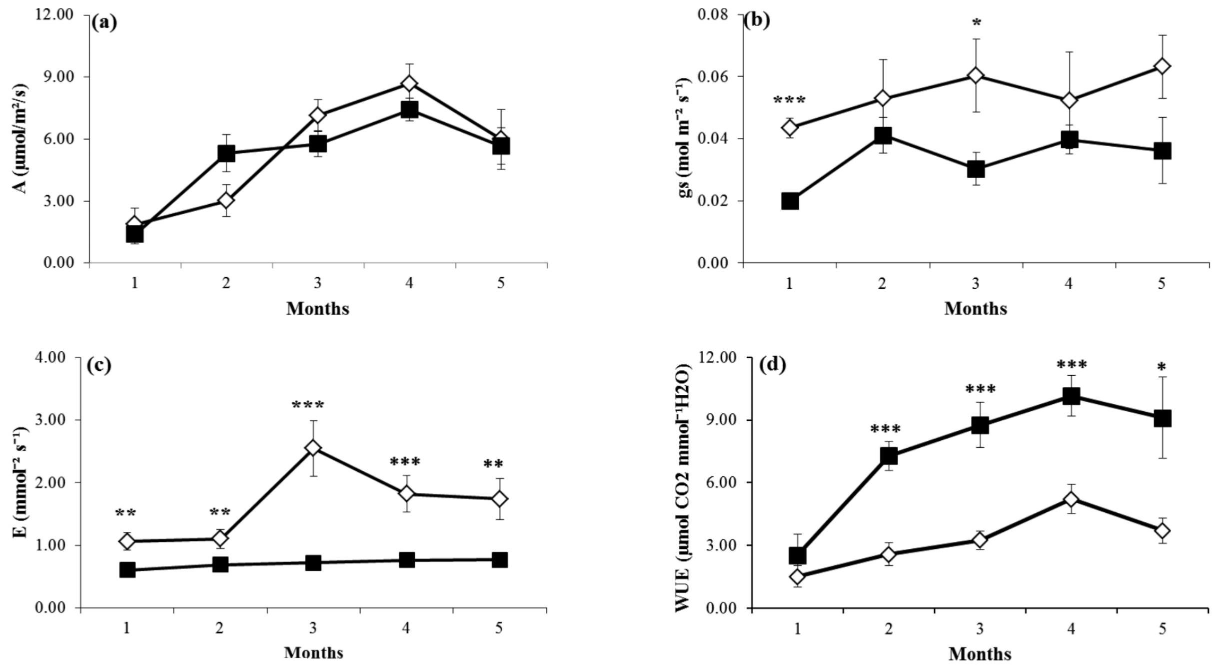

FIGURE 2. The effect of different CO$_2$ (400±50 μmol mol^{-1}and 800±50 μmol mol^{-1}) on photosynthetic rate (a), stomatal conductance (b), transpiration rate (c), and water use efficiency (d) of *Shorea platycarpa* in five months of treatment. An ◇ = 400 ± 50 μmol mol^{-1}; ■ = 800±50 μmol mol^{-1}. Values represent means ± SE; *n*=18. The statistical significance is based on one-way ANOVA ($p<0.05$). The symbol used indicates *** $p<0.001$; ** $p<0.01$ and * $p<0.05$

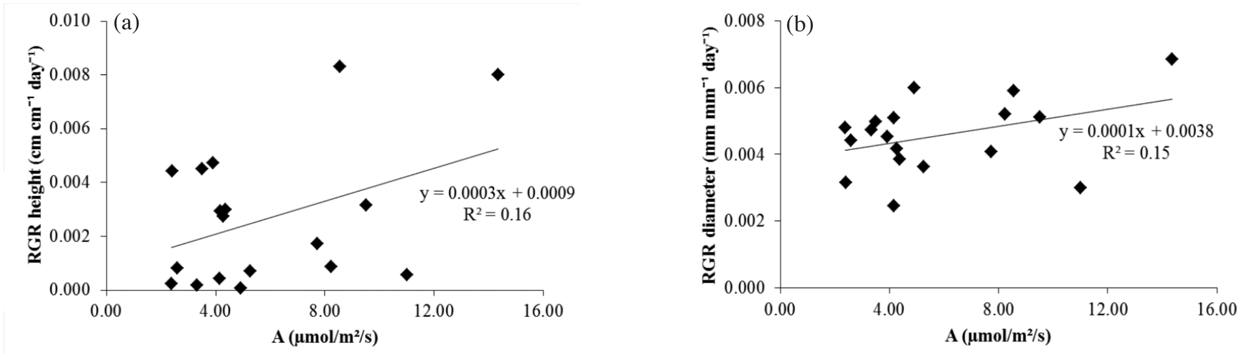

FIGURE 3. Correlation between photosynthetic rate (*A*) to relative growth rate (RGR) of height (a), ($r = 0.4$, $p = 0.10$) and RGR of stem diameter (b), ($r = 0.4$, $p = 0.11$) of *Shorea platycarpa* in ambient CO$_2$ and elevated CO$_2$. Relationship between *A* and RGR of height and diameter was not significant at ($p<0.05$)

and *Pinus sylvestris*) and hardwoods (*Quercus ilex* and *Liquidambar styraciflua*) though some studies found no difference in growth ring width (*Picea abies* and *Larix kaempferi*) (Yazaki et al. 2005). Cambial activities, is the frequency of cell division, affects the radial growth of plants. Stem expansion could indicate that elevated CO$_2$ affects the apical meristem and cambium differently or has different effects on cell division and cell expansion, or both. Elevated CO$_2$ may affect plant development not only by altering photosynthetic activity, but also by altering apical cell development (Yazaki et al. 2001).

The total number of leaves for *S. platycarpa* in both ambient and elevated CO$_2$ was increased, however the growth rate was continually decreased. Low nutrient level could generally limit the NLGR of plants to CO$_2$ enrichment. Some environmental limitations may slow down growth than photosynthesis. Thus, supposedly, assimilates were not allocated more to growth of those species, but shifted to other allocation, instead (defense system or food reserve) (Novriyanti et al. 2012). It also appears that response could also be related to experimental duration. This climax species was known as slow growing species. Therefore, the stimulation developed very slowly. By prolonging the experimental duration, this species will probably enter a phase during which a significant above ground effect becomes measureable.

EFFECTS OF ELEVATED CO_2 ON BIOMASS

Elevated CO_2 has the potential to yield significant increase of biomass accumulation and this have been observed in many plants. Effects of elevated CO_2 on tree seedlings or juvenile trees generally showed an increase in above ground and below ground biomass (*Gmelina arborea)* (Rasineni et al. 2011). However, in this experiment there were no detectable increase in the above ground and below ground biomass of *S. platycarpa* grown in elevated CO_2. Variation in biomass responses to elevated CO_2 has been attributed to a large number of confounding factors, such as the length of study, plant functional group and species morphological physiology. Dijkstra et al. (2002) reported that elevated CO_2 did significantly increase the above ground biomass of dominant species, *Quercus myrtifolia*, tended to increase the above ground biomass of *Q. chapmanii*, but has no effect on above ground biomass of the subdominant species, *Q. geminata*. Some environmental limitations such as water stress and nutrient deficiency (N, P and K^+) may retard the biomass allocation. In response to environmental cues, plants re-adjust partitioning of photosynthates to maintain a functional equilibrium between shoot and root growth, since they are interdependent (Mooney & Winner 1991). Increased C supply from elevated atmospheric CO_2 can preferentially induce the distribution of photosynthate below ground because plants tend to allocate photosynthate to tissues needed to acquire the most limiting resource, whereas, when CO_2 is elevated, the most limiting resource becomes water or nutrients (Prior et al. 2011). The production of new leaf or leaf loss and the nutrient availability during treatments might give an added effect on the LAI result. Oikawa et al. (2013) reported that elevated CO_2 did stimulate the LAI in the soybeans cultivars but the LAI was also being regulated by the leaf production rate and leaf loss. The effects of (CO_2) on LAI are probably modified by N availability, which strongly controls leaf area growth (Anten et al. 2003). The LAI of plants in elevated CO_2 might be affected by the insufficiency of N uptake. The elevated CO_2 affect the ability of soil-root system to supply N. In addition, low dosage of N supplied during the experiment might also contribute to this interactive effect of CO_2 and N. Subsequently, this will decrease the acquisition of N in the plants and yet the demand for N is increasing. Kim et al. (2001) found LAI for a given N uptake to be greater for plants under elevated CO_2, but only when N uptake itself was high, and not when it was low.

EFFECTS OF ELEVATED CO_2 ON PHOTOSYNTHESIS

The present study demonstrates the responses of *S. platycarpa* with significant variation in photosynthetic performance to increasing atmospheric CO_2. Elevated CO_2 did not significantly ($p<0.05$) increase (*A*) in *S. platycarpa* leaves (Table 2), however it did induce significant ($p<0.05$) changes in (g_s), (E) and (WUE) (Table 2). Though the leaf photosynthetic rates (*A*) give non-significant effects, it is believed that by prolonging the treatments it will significantly changes the outcomes. The photosynthetic rate (*A*) can be reduced during long term elevated CO_2 exposure, often referred as photosynthetic acclimation or down-regulation. However, tree species have a wide range of responses that are correlated with their successional status. Down-regulation of photosynthesis in *P. macroloba*, a late successional slow growing climax species was decreased after long periods of exposure to elevated CO_2 (Oberbauer et al. 1985) but this effect was not reduced over time in *Luehea seemannii*, a fast growing canopy tree (Lovelock et al. 1999).

On average, the stomatal conductance (g_s) of *S. platycarpa* only decreased by 0.1% in elevated CO_2 compared to their counterparts grown in ambient CO_2. Following the decrease in (g_s), it is expected that plants will use less water and become more efficient for water use. This data is consistent with the classic response of a decrease in stomatal conductance in plants grown in elevated CO_2. Similar result have been observed in climax species, *Pentaclethra macroloba* (Oberbauer et al. 1985), tropical canopy species, *Luehea seemanni* (Lovelock et al. 1999) and shade-tolerant species, *Pongamia pinnata* (Liang et al. 2001). Stomatal conductance (g_s) represents the abilities of stomata, which are the channels of CO_2 absorption and water loss transpiration in plants. As shown in Figure 2(d), (WUE) increased with CO_2, especially on the 2nd, 3rd and 4th months of treatment, suggesting that it is mainly due to significantly decreased of transpiration. The plant reacts to water deficit with a rapid closure of stomata to avoid further loss of water through transpiration. Under high CO_2 environment, reduced (g_s) and (E) resulting in substantial increase in (WUE) which contributed to increased water use efficiency (WUE) (Prior et al. 2011).

TABLE 2. Effects of atmospheric CO_2 (ambient; 400±50 μmol mol^{-1} and elevated 800±50 μmol mol^{-1}) on photosynthetic rate (*A*), stomatal conductance (g_s), transpiration rate (E) and water use efficiency (WUE) in *Shorea platycarpa*

Parameters	Ambient CO_2	Elevated CO_2	*P* level
Photosynthetic rate (*A*) (μmol/m^2/s)	5.35 ± 0.58	5.11 ± 0.42	0.74 ns
Stomatal conductance (g_s) (mol m^{-2} s^{-1})	0.22 ± 0.01	0.17 ± 0.00	0.002 **
Transpiration rate (E) ($mmol^{-2}$ s^{-1})	0.35 ± 0.09	-0.41 ± 0.05	0.000 ***
Water use efficiency (μmol CO_2 $mmol^{-1}H_2O$)	0.95 ± 0.12	1.78 ± 0.11	0.000 ***

Values represent means ± SE; $n=18$. The calculation of statistical significant is based on one-way ANOVA ($p=0.05$). The symbol used ***$p<0.001$; **$p<0.01$; *$p<0.05$; not significant (ns) $p>0.05$

In this study, *S. platycarpa* did not show any significant ($p<0.05$) correlation between growth rate and photosynthetic rate. However, according to Kenzo et al. (2011), high growth rate of *Dyera costulata* and *Dipterocarpus baudii* were observed under high light conditions may correspond to the high photosynthetic rate. A variety of hypotheses have been proposed that prolonged exposure to elevated CO_2 might decrease the photosynthetic rate (*A*) of plants. These responses were attributed to secondary responses related to either excess carbohydrate accumulation or decreased N content. Down-regulation or acclimation of photosynthesis is generally accompanied by a large increase in leaf carbohydrates (Cheng et al. 1998). Photosynthetic down regulation has been observed in hybrid larch F1 (*Larix gmelinii* var. *japonica×Larix kaempferi)* and *Quercus suber* seedlings. This response was not initiated by stomatal closure but mainly by the reduction in the assimilation capacity which increase the total soluble sugars and starch in leaves (Faria et al. 1996; Watanabe et al. 2011). Excess of carbohydrate remained in the leaf as sugars or starch made leaves heavier per unit area, thus, contributed to an ineffective transformation of photosynthetic carbon gain into new growth (Kirschbaum 2011). Enhanced storage of carbohydrates within the tree may lead to increased growth in the year following the elevated CO_2 treatment (Lovelock et al. 1999).

CONCLUSION

This study pointed out that elevated CO_2 did not give significant effect on the relative growth rate (RGR), photosynthetic rate (A) and biomass characteristics of *S. platycarpa*. *S. platycarpa* is a slow growing species. Possibly, the study indicated that elevated carbon concentration does not affect a relatively slow growing tree species and a late successional tree species. However, a longer-term exposure of elevated CO_2 on *S. platycarpa* would confirm the findings of this study. The study was conducted on the sapling. Perhaps, next study should look at different growth stages of *S. platycarpa* such as at seedling and juvenile/semi adult stages.

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