Growth responses of light demanding and shade tolerant peat swamp forest saplings to elevated CO₂

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Abstract

Aim: To determine the growth responses of two peat swamp forest species, *Shorea platycarpa*, a shade-tolerant slow-growing species and *Macaranga pruinosa*, a light-demanding fast-growing species under elevated atmospheric CO₂ concentration.

Methodology: The saplings of both species were grown in a shade house at ambient (400±50 µmol mol⁻¹) and in an open roof ventilation greenhouse at elevated atmospheric CO₂ concentration 800±50 µmol mol⁻¹ for seven months. The temperature in both environments ranged between 25–33°C with 55–60% sunlight transmittance and the saplings were thoroughly watered twice a day. Plants growth measurements were estimated at frequent intervals. Saplings biomass characteristics were examined using destructive methods after seven months of treatment and non-destructive method was used for determination of leaf area.

Results: Elevated CO₂ enhanced all the growth characteristics in *M. pruinosa* with a significant increase was observed particularly on both height and diameter relative growth rate and biomass characteristics. The height relative growth rate and leaf area were significantly reduced under elevated CO₂ in *S. platycarpa* but did not affect the shoot or root diameter and biomass significantly. A positive correlation ($r=0.77$, $p>0.05$) between stem biomass and basal diameter for plants under elevated CO₂ was recorded for *M. pruinosa*, but not in *S. platycarpa*. Both species showed negative correlation (*S. platycarpa*; $r = -0.53$, *M. pruinosa*; $r = -0.46$, $p>0.05$) between stem growth and stem biomass at elevated CO₂.

Interpretation: These results unveiled profound effects of elevated CO₂ on the growth of light-demanding species *M. pruinosa*, while shade-tolerant species *S. platycarpa* was not relatively affected by elevated CO₂. This underscored the necessity to analyse different species performance to elevated CO₂, thereby improving the ability to predict tropical swamp forest ecosystem responses to rising CO₂.

Key words: Carbon-di-oxide, Growth responses, *Macaranga pruinosa*, Peat swamp species, *Shorea platycarpa*

Growth responses of two peat swamp forest species under ambient CO₂ (400±50 ppm) and elevated CO₂ (800±50 ppm) for seven months monitored through six morphological parameters.

Effect of elevated [CO₂] on relative growth rate and biomass compared to ambient [CO₂]

H = ↓	BG = —
D = —	AG = —
LA = ↓	TB = —

H = ↑	BG = ↑
D = ↑	AG = ↑
LA = —	TB = ↑

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Introduction

Climate change is a global issue that arise due to unprecedented increase in greenhouse gas emissions from anthropogenic sources. Carbon dioxide (CO₂) concentration has dramatically increased since pre-industrial period from 280 to 412 $\mu\text{mol}^{-1} \text{mol}^{-1}$ (NOAA, 2019). The projections for the end of 21st century based on RCP8.5 scenario showed that CO₂ concentration may reach up to 936 ppm leading to elevation in air temperature by 2.6–4.8°C relative to 1986–2005 (IPCC, 2013). Plants have been directly affected by rising atmospheric CO₂ concentration because they are the first molecular link between the atmosphere and biosphere. Plant species vary in their response to CO₂. The differing responses of shade-tolerant and light-demanding plant group species to various levels of CO₂ are likely to change their competitiveness. Liang et al. (2001) reported that elevated CO₂ suppressed photosynthesis of *Pongamia pinnata*, a shade tolerant species at both low and high light condition. Difference in plants identity can alter plant-CO₂ interaction, for instance, there are some reports that the fast-growing plant species are more responsive to changes in CO₂ concentration than slow-growing species (Singh et al., 2019). Light-demanding species are likely to become a problem in shade-tolerant species distribution, while light-demanding plants may get an advantage over shade-tolerant plants in terms of rapid growth. Global climate change also influence vegetation transformation by modifying the growth and competitiveness of different vegetation types and distribution of vegetation is connected both to direct effects of climate on growth, and to indirect effects from climate-induced disturbances (Chen et al., 2019). Some studies have reported that climate change can trigger the replacement of several species from some biomes with those better adapted to extreme weather conditions (Menezes-Silva et al., 2019).

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, 2003). This species is generally found in deep peat swamp forest and the wood is commonly used for joinery and furniture (Choo et al., 1998). Dipterocarp species vary greatly in growth rates, some, are usually tolerant to low light intensities, show rapid growth rate and reach mature habit within 60 years under forest conditions, others, usually shade tolerant grow very slowly (Ashton, 1982). *Macaranga pruinosa* (Euphorbiaceae) is a large early successional tree of lowland peat swamp forest; commonly distributed in Peninsular Thailand, Malay Peninsula, Sumatra, Borneo (Central Kalimantan, East Kalimantan, Sarawak) and often form huge monospecific stands in degraded areas (Van Welzen et al., 2009). There is a lack of experimental research on the effect of CO₂ enrichment on peat swamp trees and as this forest type is rapidly vanishing, it is necessarily important to investigate the response of these two fundamental species in the

peat swamp ecosystem. Moreover, tropical peat lands are becoming more responsive to climate change and anthropogenic influences (Leng et al., 2019), and it is critical to quantify the climate feedback potentials from peat swamp forests (Cooper et al., 2019). The present study aimed to determine the growth response of peat swamp light-demanding species, *Macaranga pruinosa* and shade-tolerant species, *Shorea platycarpa* grown under elevated CO₂. It is hypothesized that young light demanding, *M. pruinosa* would show a positive growth response to elevated CO₂ than young shade tolerant, *S. platycarpa*. Understanding how species with different functional strategies respond to elevated CO₂ would offer us a useful basis to predict their competitive ability in resources utilization and it is a critical process, as it can largely determine the dynamic of peat swamp forest ecosystem regeneration and therefore, the ability of these species to coexist. The differential competitive potentials among co-occurring species can exacerbate the survivability of young plants that cannot prevail over its competitors and thereby induced community shift in a peat swamp forest ecosystem.

Materials and Methods

Plant material, growth condition and experimental design:

The experiment was conducted at the Universiti Kebangsaan Malaysia (UKM) from March to October 2015 in both ambient ($400 \pm 50 \mu\text{mol mol}^{-1}$) and elevated ($800 \pm 50 \mu\text{mol mol}^{-1}$) atmospheric CO₂ concentration. A total of 20 saplings each of *S. platycarpa* (n=10) and *M. pruinosa* (n=10) were grown at elevated CO₂ (open roof chamber) and 16 saplings each of *S. platycarpa* (n=8) and *M. pruinosa* (n=8) were grown at ambient CO₂ concentration (shade house). The saplings height of both species ranged from 70–100 cm. The elevated concentration of CO₂ ($800 \pm 50 \mu\text{mol mol}^{-1}$) was selected to match with the predicted concentration at the end of the century from a global climate model under WGIII scenario of IPCC (2014). Humidity and temperature were monitored and controlled using a smart control panel ventilation system. The temperature and humidity recorded for both environments within seven months of treatment ranged between 25–33°C and 78–86%, respectively. The saplings received 55–60% sunlight transmittance. The daily automatic continuous injection of pure CO₂ in the open roof chamber was fixed from 9.00 am - 11.00 am till it reached the desired concentration ($800 \pm 50 \mu\text{mol mol}^{-1}$). The CO₂ concentration inside and outside the room were substantially same after 2 hrs of CO₂ injection. It was estimated that photosynthesis in plants was maximum during the selected time. Daily maximum values of carbon assimilation (A) and stomatal conductance (g_s) were generally observed in the morning, followed by decrease in midday (Siddiq et al., 2019). CO₂ was supplied through an open roof air supply system from the CO₂ cylinder that was connected to air blower, and the concentration was controlled by diluting the airflow generated by the blower. The CO₂ concentration in the room was monitored and administered using CO₂ analyzer. The

saplings were planted in perforated polybags (25 cm diameter x 30 cm depth) containing $\pm$ 10 kg of prepared growing medium. The growing medium used was topsoil of podzolic type that was mixed with organic fertilizer in 4:1 ratio. To avoid specific bias in the experiment, the filled polybags laid out in rows at a distance of 30 cm were relocated randomly every two month. NPK was applied (15:15:15) at a low dose of 5 g/polybag/month. The polybags were watered twice a day, early in the morning and late in the afternoon to sustain soil moisture.

Relative plant growth: Plant growth (n=36) was weekly assessed for seven months by regular, non-destructive measurements. Destructive measurements are generally not preferred due to increased labor requirement and loss of plants and therefore, it was highly desirable to develop affordable techniques that could non-destructively measure plant growth characteristics and were highly sensitive to identify small growth differences in plants (Li *et al.*, 2020). Plant height (cm) was measured from the collar to the apical meristem using a standard measuring tape, while stem diameter (mm) was measured with digital callipers 5 cm from the collar of the saplings. Relative height growth rate (RHGR) and stem basal diameter growth rate (SDGR) were calculated every month according to Jach and Ceulemans (1999). Relative Growth Rate (RGR) was calculated by the following formula:

$$(\ln I_2 - \ln I_1) / (t_2 - t_1)$$

Where, I_1 is the height / diameter at time t_1 and I_2 is the height / diameter at t_2 .

Estimation of biomass: After seven months of treatment, dry matter accumulation was determined through destructive harvesting of saplings. The harvested plant materials were cut at the base and separated into above and below ground parts. The roots were carefully washed with water to remove all soil particles. The above and below ground parts were oven dried separately at 65°C for seven days and then weighed using digital balance. For growth analysis, the dry weight of average above ground dry biomass (AGDB), average below ground dry biomass (BGDB), total dry biomass (TDB) and below-ground: above-ground ratio and (BG:AG) were calculated. The BG:AG ratio was calculated by dividing the below ground dry matter by above ground dry matter.

Estimation of leaf area: Leaf area was measured after seven months of treatment. A simple non-destructive method was used to estimate the leaf area using digital image taken *in-situ* and public domain software Image J. This software is commonly used to analyze and determine macro- and microscopic images of different plant species and is widely used for imaging studies in plants such as plant phenotyping, fractal analysis, foliar surface analysis and leaf dimensional elements (Drienovsky *et al.*, 2017). To record the image of a leaf, a 30 cm ruler was placed on a white paper board where the leaf was placed. The image of each young,

and fully expanded leaf (n=200 leaves) was taken with a digital camera. The digital images were processed using the software ImageJ for measuring the leaf area.

Statistical analysis: Analysis of variance (ANOVA) at $p \leq 0.05$ was used to consider significant differences in growth and biomass characteristics for the saplings grown in ambient and elevated CO₂ conditions. ANOVA was performed using Minitab version 16.0. Differences between means $\pm$ standard error of each parameter were examined by Tukey's Studentized Range Test at $p \leq 0.05$.

Results and Discussion

Peat swamp tree growth parameter responses to elevated CO₂:

Both *S. platycarpa* and *M. pruinosa* exhibited widely contrasting responses to elevated CO₂. The saplings of *M. pruinosa* exhibited the maximum height and diameter increments under elevated CO₂ as compared to *S. platycarpa*. At the end of treatment, the height of *S. platycarpa* was 140.84 cm at elevated CO₂, 2% lower as compared to ambient CO₂. However, the height of *M. pruinosa* was 186.20 cm, 68% higher at elevated CO₂ as compared to ambient CO₂ (Fig. 1A). The basal stem diameter of *S. platycarpa* was 19.98 mm and *M. pruinosa* was 22.54 mm, which were 15% and 101%, larger as compared to ambient CO₂ grown plants (Fig. 1B). The Height Relative Growth Rate (HRGR) of *S. platycarpa* exhibited a significant difference between elevated CO₂ and ambient CO₂ ($p < 0.001$) after seven months of treatment, but the highest growth rate recorded for *S. platycarpa* saplings grown under elevated CO₂ was lower (0.35 cm cm⁻¹ d⁻¹) as compared to ambient CO₂ (0.55 cm cm⁻¹ d⁻¹) (Fig. 1C). In contrast, the HRGR of *M. pruinosa* was significantly higher (0.94 cm cm⁻¹ d⁻¹) under elevated CO₂ ($p < 0.001$) (Table 1) as compared to ambient CO₂ (0.73 cm cm⁻¹ d⁻¹) (Fig. 1C). Diameter Relative Growth Rate (DRGR) of *S. platycarpa* was not significantly different ($p > 0.05$) to CO₂ treatment as compared to HRGR (Table 1). The highest recorded DRGR of *S. platycarpa* was 0.07 mm mm⁻¹ d⁻¹ and 0.08 mm mm⁻¹ d⁻¹ under elevated CO₂ and ambient CO₂, respectively (Fig. 1D). On the other hand, the elevated CO₂ showed a significant effect on DRGR of *M. pruinosa* ($p < 0.001$). The highest DRGR of *M. pruinosa* at elevated CO₂ treatment was 0.1 mm mm⁻¹ d⁻¹ and in ambient CO₂ was 0.08 mm mm⁻¹ d⁻¹ (Fig. 1D). Significant decrease in leaf area of *S. platycarpa* ($p < 0.001$) was observed under elevated CO₂ as compared to ambient CO₂, however, no significant changes were observed for the leaf area of *M. pruinosa* (Table 1).

Biomass allocation pattern: Elevated CO₂ had a significant effect on total dry biomass of *M. pruinosa* ($p < 0.01$), which was 96% higher as compared to total dry biomass of plants grown in ambient CO₂ (Fig. 2C). However, the total dry biomass of *S. platycarpa* at elevated CO₂ was 31% lower as compared to ambient CO₂ (Fig. 2C), but were insignificantly different ($p > 0.05$). Above-ground dry biomass (AGDB) (Fig. 2A) and below-ground

Fig. 1 : Time course of monthly plant height (A) basal stem diameter (B), height relative growth rate (HRGR) (cm cm⁻¹ day⁻¹) (C) and stem diameter relative growth rate (DRGR) (mm mm⁻¹ day⁻¹) (D) during seven months of treatment (March - October 2015) of *S. platycarpa* and *M. pruinosa* under ambient CO₂ (400±50 µmol mol⁻¹) and elevated CO₂ (800±50 µmol mol⁻¹). SP Ambient = *S. platycarpa* in ambient CO₂, SP Elevated = *S. platycarpa* in elevated CO₂, MP Ambient = *M. pruinosa* in ambient CO₂ and MP Elevated = *M. pruinosa* in elevated CO₂. Values represent means ± SE; n=36. (Mean ± SE) HRGR (C) of *S. platycarpa* and *M. pruinosa* were statistically different (p<0.001). (Mean ± SE) DRGR (D) of *S. platycarpa* was not statistically different (p>0.05) but DRGR (D) of *M. pruinosa* was statistically different (p<0.001).

Table 1 : Effects of atmospheric CO₂ (ambient; 400±50 µmol mol⁻¹ and elevated 800±50 µmol mol⁻¹) on relative growth rate (RGR), biomass and leaf area in *Shorea platycarpa* and *Macaranga pruinosa* after seven months of treatment (March - October 2015)

Characters	<i>Shorea platycarpa</i>		<i>Macaranga pruinosa</i>	
	Ambient CO ₂ (400±50 µmol mol ⁻¹)	Elevated CO ₂ (800±50 µmol mol ⁻¹)	Ambient CO ₂ (400±50 µmol mol ⁻¹)	Elevated CO ₂ (800±50 µmol mol ⁻¹)
Plant growth (RGR)				
Height RGR (cm cm ⁻¹ day ⁻¹)	0.24 ± 0.03	0.21 ± 0.02***	0.42 ± 0.04	0.63 ± 0.04***
Diameter RGR (mm mm ⁻¹ day ⁻¹)	0.05 ± 0.00	0.06 ± 0.00 n.s	0.05 ± 0.00	0.08 ± 0.00***
Dry biomass (g)				
Belowground	41.51 ± 4.61	33.37 ± 6.23 n.s	51.68 ± 8.66	121.89 ± 24.83**
Aboveground	137.71 ± 15.44	89.59 ± 21.83 n.s	147.76 ± 27.03	268.81 ± 36.36**
Total biomass	179.22 ± 18.51	122.96 ± 27.45 n.s	199.44 ± 35.56	390.69 ± 56.29**
Leaf area (cm ²)	104.95 ± 7.12	65.23 ± 5.95***	221.93 ± 9.89	240.64 ± 11.75 n.s

Values represent means ± SE; n=36. 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 (n.s.) p > 0.05

dry biomass (BGDB) (Fig. 2B) of *M. pruinosa* significantly increased (p<0.01) at elevated CO₂ by 82% and 136%, as compared to ambient CO₂ grown plants. On the other hand, the final biomass of *S. platycarpa* plants grown at elevated CO₂ showed 35% reduction in AGDB (Fig. 2A) and 20% reduction in

BGDB (Fig. 2B) (p>0.05) as compared to final biomass of plants at ambient CO₂ level. The below ground and above ground ratio (BG:AG) of both species increased by 0.09 under elevated CO₂ level as compared to ambient CO₂ level, but were insignificantly different (p>0.05) (Fig. 2D).

Regression analysis and correlation were established between DRGR versus AGDB and stem basal diameter to understand the relationship between the stem growth rates and stem biomass of *S. platycarpa* and *M. pruinosa* under ambient and elevated CO₂ conditions (Fig. 3). A negative correlation between DHGR and AGDB was recorded for *S. platycarpa* ($r = -0.53$) grown at elevated CO₂, however, a weak positive correlation ($r = 0.32$, $p > 0.05$) was observed for plants grown in ambient CO₂ (Fig. 3A). Similar results were observed in *M. pruinosa*, whereby the coefficient correlation value of plants grown under elevated CO₂ and ambient CO₂ was -0.46 and 0.17 ($p > 0.05$), respectively (Fig. 3B). However, there was a strong positive correlation between stem basal diameter and AGDB of *S. platycarpa* grown in ambient CO₂ ($r = 0.86$) as compared to elevated CO₂ grown plants ($r = 0.36$) ($p > 0.05$) (Fig. 3C). Conversely, the relationship between stem basal diameter and AGDB of *M. pruinosa* plants grown at elevated CO₂ showed a strong positive correlation ($r = 0.77$) but weak correlation for plants grown under ambient CO₂ level ($r = 0.37$, $p > 0.05$) (Fig. 3D).

The study demonstrated that early successional, light demanding species, *M. pruinosa* showed a positive growth response to elevated CO₂ throughout the experimentation compared to late successional, shade-tolerant species, *S. platycarpa*. Giertych et al. (2015) reported that the higher ratios of increased stem height and stem radial to seedling mass in light-demanding species indicate that these species invest proportionally more of their carbon into growth as compared to shade-tolerant species. *M. pruinosa* plants were 68% taller with 101% thicker stems after seven months of elevated CO₂ treatment when compared to ambient CO₂. *M. pruinosa* had significantly high relative growth rates for both HRGR and DRGR in response to elevated CO₂. Elevated CO₂ had maximum influence on the growth of *Elaeis guineensis* by significantly increasing the plant height, number of frond per plant, basal diameter, leaf area per seedling, root biomass, total dry matter, net assimilation rate (NAR) and relative growth rate (RGR) (Ibrahim et al., 2018). *S. platycarpa* on the other hand, showed 2% decrease in saplings height and 15% increase in stem basal diameter under elevated CO₂ treatment, which resulted in a significant reduction of HRGR, but a non-significant in DRGR. The maximum enhancement of *M. pruinosa* growth response to elevated CO₂ is highly regulated by its source-sink interaction. The capability of this fast-growing species to acquire carbon resources from the external environment and assimilate it into plant parts leads to shoot and root expansion at faster rate. Elevated CO₂ increases the potential of carbon source activity of plant by stimulating photosynthesis, generally leading to increased growth, and studies comparing species or cultivars with different sink sizes reveal that growth is faster when sinks are larger (Angela et al., 2016). Major and Mosseler, (2019) reported that faster-growing species have greater absolute and relative growth responses to elevated CO₂ than inherently slower-

growing species. Kerstiens (2001), however, showed an opposite result to this study, where high shade-tolerant species (*Acer pensylvanicum*, *A. saccharum*, *Fagus grandifolia*, *F. sylvatica*, *Tsuga canadensis*) showed growth stimulation at elevated CO₂ that was almost three times as strong as that of low shade-tolerance species (*Betula papyrifera*, *B. populifolia*, *P. tremuloides*, *Prunus serotina*). In many cases, high CO₂ usually increases the photosynthetic rate and thereby the growth rate, but some environmental limitations may retard the growth and photosynthesis, thus, assimilates were allocated to other priorities than plant growth for example defense system or food reserve or lignin content and leaf mass area (Novriyanti et al., 2012). It should be noted that there is CO₂ concentration threshold for each plant species and thus, exceeding their growth CO₂ concentration threshold may adversely affect the growth of higher plants (Zheng et al., 2017). The effects of elevated CO₂ on the growth of plant species, is often time dependent. Long term exposure to elevated CO₂ may result in photosynthetic acclimation due to greater stomatal resistance, higher carbohydrate accumulation, diluted chlorophyll concentrations, feedback inhibition or physical damage at chloroplast level, eventually reducing the photosynthetic capacity (Ravi et al., 2019). This is consistent with the result of RGR shown by *M. pruinosa* that was highly stimulated in the first 3 months of treatment and later decreased. The stimulation in growth rate of shade-intolerant, fast growing plants due to high CO₂ environment can be offset after a certain period due to increased size of high CO₂ plants and concomitantly lower RGR (Poorter, 1993). Such transient growth stimulation by elevated CO₂ has also been reported in certain herbaceous species such as *Rumex crispus* and *Lolium multiflorum* (Rasineni et al., 2011; Thomas et al., 1999).

Coherently, the high growth rate of *M. pruinosa* grown under elevated CO₂, indicated sustained increase in biomass yields. Response of *M. pruinosa* to elevated CO₂ was remarkable, as it had the greatest response as compared to *S. platycarpa*, with almost twice total biomass response to elevated CO₂. Remarkably, the total dry biomass of *S. platycarpa* was 31% lower at elevated CO₂ as compared to ambient CO₂. The production of biomass is one of many paths along which carbon is metabolized and there is also strong evidence that plant biomass production under elevated CO₂ is mostly higher than in ambient air, although some studies have shown insignificant increase (De Souza et al., 2008), or even a decrease (Tamara et al., 2014) of biomass production under elevated CO₂ (Lottiomran et al., 2016). Singh et al. (2019) reported that elevated CO₂ significantly increased plant height, stem and shoot weight, and total plant biomass of fast-growing species *Tectona grandis*, but these plant traits did not considerably differed between elevated CO₂ and ambient CO₂ treatments of slow-growing species *Butea monosperma*. Shade-intolerant trees are generally fast-growing than shade-tolerant species and gain high biomass than their more shade-tolerant

Fig. 2 : Analysis of biomass characteristics of *S. platycarpa* and *M. pruinosa* after seven months of treatment (March - October 2015) under ambient CO₂ (400±50 µmol mol⁻¹) and elevated CO₂ (800±50 µmol mol⁻¹). Above ground dry biomass (AGDB) (A), below ground dry biomass (BGDB) (B), total dry biomass (TDB) (C) and above ground:below ground ratio (AG:BG) (D). SP Ambient = *S. platycarpa* in ambient CO₂, SP Elevated = *S. platycarpa* in elevated CO₂, MP Ambient = *M. pruinosa* in ambient CO₂ and MP Elevated = *M. pruinosa* in elevated CO₂. (Mean ± SE) AGDB (A), BGDB (B) and TDB (C) of *S. platycarpa* were not statistically different ($p > 0.05$). (Mean ± SE) AGDB (A), BGDB (B) and TDB (C) of *M. pruinosa* were statistically different ($p < 0.01$). (Mean ± SE) BG:AG of both species were not statistically different ($p > 0.05$).

counterparts (Kerstiens, 2001). Winter and Lovelock (1999) reported that shade-intolerant pioneer species show increased biomass enhancement responses (BER) than shade-tolerant climax species. It has been documented that the increase in aboveground plant biomass under elevated CO₂ is higher with the fast-growing species than adjacent slow growing and it is likely attributed to better nutrient use efficiency of fast-growing species (Singh *et al.*, 2019). Elevated CO₂ stimulated above-ground biomass by an average of 20% increment in C3 species (Ainsworth and Long, 2005), 33% in grassland (Reich *et al.*, 2014) and 60% in *Senna alata*, a pioneer species (Saraiva *et al.*, 2018). Elevated CO₂ concentrations often results in greater allocation of resources to non-photosynthetic structure (stems and roots). The two test species, *M. pruinosa* and *S. platycarpa* had a similar allocation pattern in response to elevated CO₂. Most notably, both species allocated relatively more biomass in roots as compared to stem. The increase in biomass production may be attributed to enhanced rate of photosynthesis and higher fixation of carbon and its allocation to plant components (Bhatt *et al.*, 2010). It has been proposed that higher biomass of root under elevated CO₂ is to cope with nutrient stress, and to maintain the consistent supply of nutrients for CO₂ induced growth in plant productivity (Ellsworth *et al.*, 2017). This can be observed by

enhanced below-ground biomass in *M. pruinosa*, that was 54% higher as compared to above-ground biomass. Even though there was a reduction of biomass in above-ground biomass of *S. platycarpa*, but it was 15% lower than below-ground biomass. Increased carbon supply from elevated atmospheric CO₂ could 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 CO₂ is elevated, water or nutrients the becomes most limiting resource (Prior *et al.*, 2011). Studies have revealed that the increase in root biomass in agricultural and forest species takes the form of increased root length, enhanced root branching, and increased root diameter (Gray and Brady, 2016). The decrease in above ground biomass in *S. platycarpa* was consistent with significant decrease of leaf area for plants grown at elevated CO₂. The stimulation of above ground biomass by elevated CO₂ is associated with increased average leaf size in soybean and poplar (Dermody *et al.*, 2006; Taylor *et al.*, 2003). The ability of plant growth under elevated CO₂ not only depends on increased photosynthetic capacity but also on the ability of plants to possess or to develop greater sinks by increasing the plant height, number of branches, internodes and total plant biomass (Rasineni *et al.*, 2011). Studies on the effects of elevated CO₂ on plants showed

Fig. 3: Correlation analysis between above ground dry biomass (AGDB) to diameter relative growth rate (DRGR) of *S. platycarpa* (A), ($p > 0.05$), above ground dry biomass (AGDB) to diameter relative growth rate (DRGR) of *M. pruinosa* (B) ($p > 0.05$), stem basal diameter to above ground dry biomass (AGDB) of *S. platycarpa* (C) ($p > 0.05$) and stem basal diameter to above ground dry biomass (AGDB) *M. pruinosa* (D) ($p > 0.05$) in ambient CO₂ and elevated CO₂ (□, ambient; ●, elevated).

that increase in carbon availability for sink organs results in higher biomass yields (Hogy *et al.*, 2009; Lindroth *et al.*, 1993). Despite poor correlation between stem biomass and stem growth rate, at elevated CO₂ both species showed negative correlation instead of positive correlation with plants in ambient CO₂. Keeping in view that both species at elevated CO₂ invested more resources in roots, at the cost of stem component, in acquisition of mineral or water resources and also nutrients had directly affected the growth of stem basal diameter and subsequently its relative growth rate.

This study pointed out that elevated CO₂ atmosphere persistently enhanced all growth characteristics for the light demanding species, *M. pruinosa* contradictory to the growth responses of shade-tolerant species, *S. platycarpa*. The greater biomass allocation in *M. pruinosa* under elevated CO₂ also depicts its capability to store high amount of carbon into its plant part, thus suggesting that this species has high potential in carbon sequestration which could match the high sink demand. Nonetheless, the physiological or structural mechanism of differences in growth stimulation by elevated CO₂ remain uncertain. Consequently, there is a possibility that juvenile survivorship of late-successional, shade-tolerant species could be highly affected by the competitiveness of fast-growing, light demanding species under elevated CO₂ environment. If and how this effect would result in altering the species composition and

community structure of a tropical peat swamp forest ecosystem, remains to be investigated. Experiments to elucidate the growth responses and its underlying mechanisms of these two dominant tropical swamp tree species under interacting environmental factors under elevated CO₂ are urgently needed.

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Add-on Information

Authors' contribution: M.N.L. Wahidah: Carried out the experiment and wrote the manuscript with support and input from M.S; M.S. Nizam: Supervised the project and contributed to the final manuscript; C.M.Z. Che Radziah: Supervised the project and provided critical feedback; W.A. Wan Juliana: Supervised the project and contributed to the interpretation of the result.

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