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Photosynthetic responses of tropical fruit plants to different temperatures and CO₂ concentrations

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Abstract

Climate change leads to a deterioration of environmental conditions that negatively affect yield, growth rates, photosynthesis, transpiration rates and moisture availability. Therefore, this study aims to assess the effect of climate change such as elevated temperature and CO₂ concentration on the photosynthetic performance of tropical fruit plants. The leaves of five tropical fruit plants, namely Durian (*Durio zibethinus*), Mangosteen (*Garcinia mangostana*), Kristal (*Pometia pinnata*), Dabai (*Canarium odontophyllum*), Engkalak (*Litsea garciae*) were sampled at Kuching, Kota Samarahan and Siburan, Sarawak. Leaves were collected from each mature trees and the effects of photosynthetic responses at different temperatures (25 and 30 °C), as well as CO₂ concentrations (400 and 700 ppm) were measured using a portable photosynthesis system (LI-6400 XT). At 1800 μmol m⁻² s⁻¹, highest net photosynthetic assimilation rate (A) showed by *D. zibethinus* (46.12 μmol CO₂ m⁻² s⁻¹), *G. mangostana* (42.38 μmol CO₂ m⁻² s⁻¹) *L. garciae* (41.23 μmol CO₂ m⁻² s⁻¹), and *P. pinnata* (45.15 μmol CO₂ m⁻² s⁻¹). Meanwhile, for instantaneous gas-exchange performance, *C. odontophyllum*, *G. mangostana* and *P. pinnata* have a greater advantage to an increase in temperature and CO₂ concentration. In conclusion, these results suggest that *G. mangostana* and *P. pinnata* are more suitable for cultivation as they are more heat tolerant and adapt well to climate change. These results provide information which could be beneficial for farmers to prepare with the best management strategies, especially for tropical fruit plants, which are an important source for the agricultural sector in tropical region.

Keywords Climate change, Photosynthetic performance, Tropical fruit plants, Elevated temperature, Increase CO₂ concentrations

1 Introduction

Climate change leads to environmental degradation, which adversely affects germination, growth and biodiversity of plants. Environmental degradation is further deteriorated due to burning of fossil fuels, flooding, mining and eutrophication over the last 20 years. Climate change affected agriculture such as changes in food quality and quantity [38], shorter or longer growing seasons [57], soil erosion [16], and flood [3] due to



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fluctuations in rainfall, elevated temperature and changes in carbon dioxide levels [65]. Climate change also affects yield [46], growth rates [42], photosynthesis [10], transpiration rates [35] and moisture availability [50], especially when the temperatures are above a critical threshold for an extended period [67].

Increased atmospheric CO₂ often accelerates photosynthesis, but photosynthetic activity will decrease over time due to biochemical, structural or resource limitations [25]. Increased CO₂ concentrations elevate photosynthesis temporarily as the intercellular CO₂ (C_i) rises by reducing several processes of diffusion limitations. Plants are able to redirect resources away from CO₂ fixation even if other processes (light, harvest, carbohydrate export, nitrogen uptake) that regulate plant growth are thrown out of balance. For example, increasing photosynthesis generates additional carbohydrates, whereupon photosynthetic activity is reduced through feedback inhibition mechanisms [25]. A study over 11 years on grassland using the free-air CO₂ enrichment (FACE) showed that plants growing under an increase of CO₂ levels reduces stomatal conductance, leaf nitrogen and assimilation for grasses, sedges, forbs, and legumes [31].

On the other hand, elevated temperature also affects plant biological processes, such as cambial activity, membrane lipid content and fluidity, and morphogenesis [4, 44]. Higher temperature causes various impacts on other metabolic processes including influencing carbon metabolism and increase the enzyme activity rates [2], describing the majority of the direct temperature impacts on carbon fluxes in leaves at optimum temperatures such as 5–40 °C for most of the C3 species.

Temperature has a direct effect on enzyme function; hence plant respiration rises with higher leaf temperature ranges between 48 to 60 °C (maximum temperature) [17, 58]. Net photosynthesis rate (A_{net}) thermal response curves for some photosynthetic species, including C3 species, peak between 25 and 30 °C, however some can withstand high A_{net} temperatures of up to 45 °C [27, 61]. According to Yamori and Von Caemmerern [62], photosynthesis diminishes above the thermal optimum of A_{net} for two reasons: losses in electron transport and Rubisco activase heat lability. Rubisco is the principal enzyme in photosynthesis which remains stable at high temperature but decreases as the ATPase activity decreases due to heat sensitivity. Leading to decrease of photosynthesis rate under heat stress conditions [59].

Agriculture is important to millions of people, especially those with low incomes or living in developing countries as it provides livelihoods and job opportunities [41]. However, lately, the agriculture sector has been facing difficulties in terms of food production, livelihoods and the overall economy of countries due to climate change [56]. One of the reasons is due to unmanaged human activities such as livestock grazing [13], logging [52] and fire [43]. With significant regional differences, the average global surface temperature has risen by 0.74 °C since the late nineteenth century and is expected to increase 1.4–5.8 °C more by 2100 AD [22]. Meanwhile, in January 2016, the atmospheric concentration of CO₂ rose from 280 ppm in the pre-industrial era to approximately 403 ppm [40] and by the end of the twenty-first century it is expected to reach 750 ppm [21]. The amount of CO₂ concentration in the atmosphere has been rising continuously over the last 50 years, and this trend is predicted to continue for the next 30 years. Global warming has resulted from this, as the earth's temperature has generally increased [34].

Fruit has an estimated RM5, 243.40 million in market potential, making it one of the main sources in the agriculture industry [12]. To expand the agricultural sector, fruits

are identified as one of the most important sources due to the low commodity price. Fruits are important as food source for animals and local communities due to its high nutritive values. Fruits also contain medicinal benefits and are used by the local communities in their traditional medicines since ancient times [24]. Malaysia is a country with a huge range of widely grown tropical fruits including banana, durian, jackfruit, mango-steen, papaya, pineapple, pomelo, rambutan, and watermelon [24]. The reason for this is the favourable tropical climate for the production of various exotic fruits, as Malaysia is rarely hit by cyclones or droughts, which has an impact on tropical fruit exports.

It is estimated that no less than 135,000 smallholders grow fruit on an area of around 375,000 hectares (5.4%) in Malaysia [64]. Malaysia exported about RM269.07 million worth of fruits to Singapore, Thailand, Hong Kong and Indonesia [9]. Some of these fruits are identified by the National Agricultural Policy 3 (1998–2010) and the National Agrofood Policy (2011–2020) as potential fruits to be developed for Malaysia's export markets. Local tropical fruits were also in high demand and predicted to increase to 2.7 million metric tonnes due to customers preference towards healthy eating habits [39]. These unexploited fruits could make a great economic potential and are suitable for research and commercialisation. They have a wide range of flavour and colour with potential health benefits [8]. Therefore, because of the nutritional and commercial benefits of fruits, researchers, growers, and consumers in developing nations are now paying more attention to unexploited fruits. Thus, this study will look into the effect of different temperatures and CO₂ concentrations, on the photosynthetic responses of tropical fruit plants.

2 Methodology

2.1 Study site and species

Three study locations in Sarawak, Malaysia, namely Kuching (N 01°23.1832, E 110°16.9970), Siburan (N 01°22.715, E 110°19.1693), and Kota Samarahan (N 01°27.34, E 110°29.56), were selected for this study (Fig. 1). These locations were chosen due to their comparable climatic conditions, with mean annual temperatures ranging from 32.9

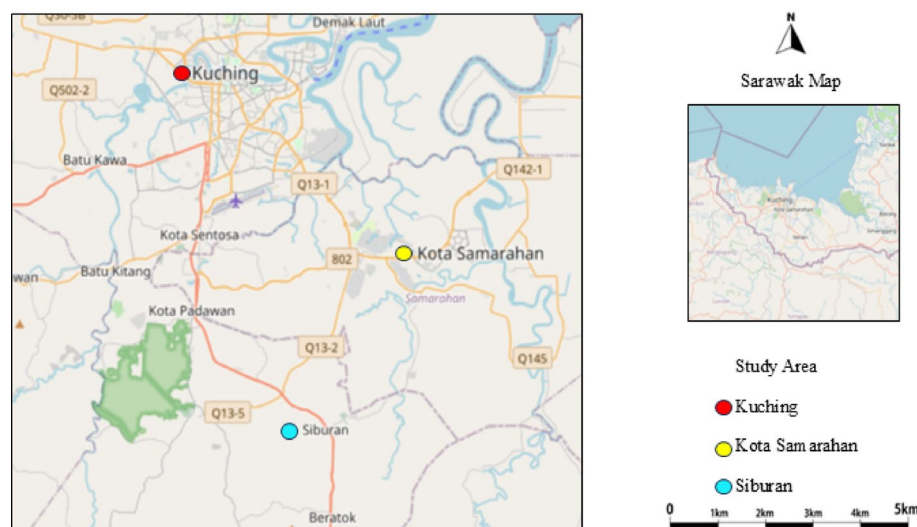


Fig. 1 The location of study area, Kampung Begu (Siburan), Kampung Malaban (Kota Samarahan) and Kampung Betong (Kuching)

to 33.9 °C and relative humidity between 60.8 and 64.6%. Each location was treated as a replicate to minimise climatic variability across study sites. Five tropical fruit plant species commonly found across all three locations were selected: Durian (*Durio zibethinus*), Mangosteen (*Garcinia mangostana*), Dabai (*Canarium odontophyllum*), Kristal (*Pometia pinnata*), and Engkalak (*Litsea garciae*). These species represent a combination of commercially important tropical fruit crops and indigenous species that are sensitive to climatic conditions. Plant materials were sampled directly from mature, healthy trees (age between 5 and 10 years old) naturally growing in situ at each study location. No commercial seeds or nursery-propagated planting materials were used. For each species, samples were collected from trees within the respective study areas in Kuching, Siburan, and Kota Samarahan, with geographic coordinates recorded for all sites to ensure traceability and reproducibility.

2.2 Photosynthesis determination

2.2.1 Twig sampling

Two twigs of approximately 30 cm in length and 22 cm width (about 2 cm diameter range) were collected from each species from three mature and healthy individual trees ($n=3$), with two twigs sampled per tree. The additional twig from each tree served as a backup to ensure availability of healthy, fully expanded, sun-exposed leaves for gas-exchange measurements. For the actual analysis, one fully expanded leaf from each tree was measured, giving a total of three biological replicates per species. The cut ends of the twigs were wrapped with a wet towel to maintain hydration, sealed with a rubber band, placed in plastic zip-lock bags, and transported immediately to the laboratory for same-day measurement using the LI-6400XT system [19].

2.2.2 Photosynthetic measurement

Photosynthetic light response (A–Li) curves were measured under controlled conditions in the leaf gas-exchange chamber, where irradiance (Li) was set by the instrument light source rather than ambient conditions. PPFD was stepped through 10, 40, 60, 120, 250, 500, 1000, 1500, and 1800 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$, while relative humidity was maintained at 50–60%, CO_2 concentration at 400 and 700 ppm, and leaf temperature at 25 and 30 °C.

2.2.3 Photosynthetic determination

The instantaneous leaf gas-exchange parameters, including net CO_2 assimilation rate (A; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$), transpiration rate (E; $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$), and stomatal conductance (Gs; $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), were obtained directly using a portable gas-exchange system. Water-use efficiency (WUE; $\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{H}_2\text{O}$) was calculated as A/E. Measurements were conducted under controlled conditions inside the leaf gas-exchange chamber (relative humidity: 50–60%), with irradiance supplied by the instrument light source and maintained at 1800 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$. To evaluate responses to CO_2 and temperature, the chamber reference CO_2 concentration was set to 400 ppm (baseline/ambient level) and 700 ppm (elevated CO_2 treatment), while leaf temperature was set to 25 °C and 30 °C using the chamber temperature control. Leaves were allowed to equilibrate at each CO_2 –temperature setting before logging stable readings.

2.3 Statistical analysis

The interactions between species and temperature or internal CO₂ concentration on the variables of instantaneous gas exchange parameters (A, E, Gs and WUE) were evaluated using two-way analysis of variance (ANOVA). Tukey's tests were used to analyse the significance difference between the parameters. Unpaired t-test was used to analyse significance differences between temperatures (25 and 30 °C) and internal CO₂ concentrations (400 and 700 ppm). Triplicates of each species were used for all tests. All statistical analyses were analysed using the Statistical Analysis System version 9.2 (SAS. Corp 2009).

3 Results

3.1 Photosynthetic assimilation response under different temperatures and carbon dioxide concentrations of tropical fruit plants

Figure 2 shows A measurement using A-Li curves of tropical fruit plants under constant intercellular CO₂ concentration of 400 ppm and leaf temperature at 25 °C. *L. garciae* showed the highest net photosynthesis value until it reaches 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, then *D. zibethinus* started to increase to the highest value of 46.12 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ at 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$. *P. pinnata* increases constantly as the light increases (31.88 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) at the highest PPFD value. On the other hand, for *G. mangostana*, it showed the lowest value of all species till it reaches high light of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (28.66 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), the value increases higher than *C. odontophyllum*, (25.96 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$).

Figure 3 shows A measurement using A-Li curves of tropical fruit plants under constant intercellular CO₂ concentration of 400 ppm and leaf temperature at 30 °C. The highest A value was showed by *G. mangostana* (42.38 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), followed by *P. pinnata* (40.68 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), *C. odontophyllum* (37.07 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), and *L.*

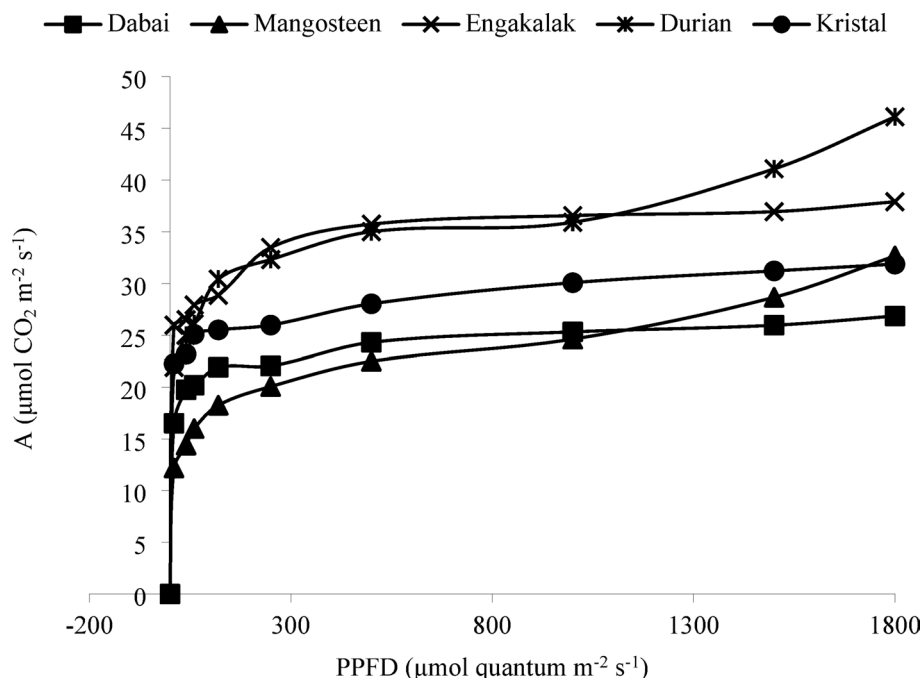


Fig. 2 A-Li curves showing CO₂ assimilation rate at different photon flux densities of five tropical fruit plants (n = 3 leaves per species), Durian (*Durio zibethinus*), Mangosteen (*Garcinia mangostana*), Kristal (*Pometia pinnata*), Dabai (*Canarium odontophyllum*), Engkalak (*Litsea garciae*) measured at a constant intercellular CO₂ concentration of 400 ppm and leaf temperature at 25 °C

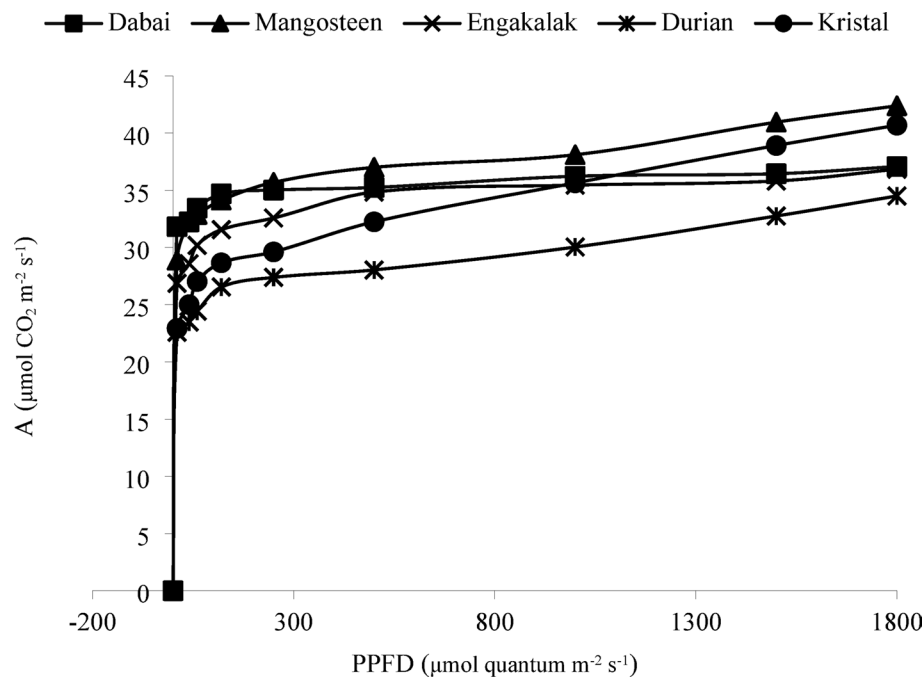


Fig. 3 A-Li showing CO₂ assimilation rate at different photon flux densities curves of five tropical fruit plants (n=3 leaves per species), Durian (*Durio zibethinus*), Mangosteen (*Garcinia mangostana*), Kristal (*Pometia pinnata*), Dabai (*Canarium odontophyllum*), Engkalak (*Litsea garciae*) measured at a constant intercellular CO₂ concentration of 400 ppm and leaf temperature at 30 °C

garciae (36.83 μmol CO₂ m⁻² s⁻¹) at 1800 μmol m⁻² s⁻¹. *D. zibethinus* exhibited the lowest A value of all five species with 34.49 μmol CO₂ m⁻² s⁻¹ at the highest light intensity.

Figure 4 shows A measurement using A-Li curves of tropical fruit plants under constant intercellular CO₂ concentration of 700 ppm and leaf temperature at 25 °C. *L. garciae* showed the highest A value of 41.23 μmol CO₂ m⁻² s⁻¹ at increased carbon dioxide concentration. *G. mangostana* showed a constant increase of assimilation rate until the highest PPFD value (37.91 μmol CO₂ m⁻² s⁻¹) followed by *D. zibethinus* (37.88 μmol CO₂ m⁻² s⁻¹). The A value of *P. pinnata* progressively increased to 36.85 μmol CO₂ m⁻² s⁻¹ at the highest PPFD value. Assimilation rate value of *C. odontophyllum* increased to 34.04 μmol CO₂ m⁻² s⁻¹ at 1000 μmol m⁻² s⁻¹ before decreasing slightly to 33.58 μmol CO₂ m⁻² s⁻¹ at 1500 μmol m⁻² s⁻¹, then peaked again to 36.66 μmol CO₂ m⁻² s⁻¹ at the highest PPFD value.

Figure 5 shows A measurement using A-Li curves of tropical fruit plants under constant intercellular CO₂ concentration of 700 ppm and leaf temperature at 30 °C. The highest A value (45.15 μmol CO₂ m⁻² s⁻¹) is shown by *P. pinnata* at increased CO₂ concentration and temperature. *D. zibethinus* showed highest assimilation rate with increasing photosynthetic photon flux density (PPFD) and then decreases from 28.58 to 27.24 μmol CO₂ m⁻² s⁻¹ at 120 μmol m⁻² s⁻¹, before rising again to 40.60 μmol CO₂ m⁻² s⁻¹ at 1800 μmol m⁻² s⁻¹. For *G. mangostana*, A value increases steadily and improves performance at 60 μmol m⁻² s⁻¹ (29.15 μmol CO₂ m⁻² s⁻¹) until reaches high PPFD (44.25 μmol CO₂ m⁻² s⁻¹). *L. garciae* showed a constant increase of A value (35.25 μmol CO₂ m⁻² s⁻¹) followed by *C. odontophyllum* (30.10 μmol CO₂ m⁻² s⁻¹) at 1800 μmol m⁻² s⁻¹.

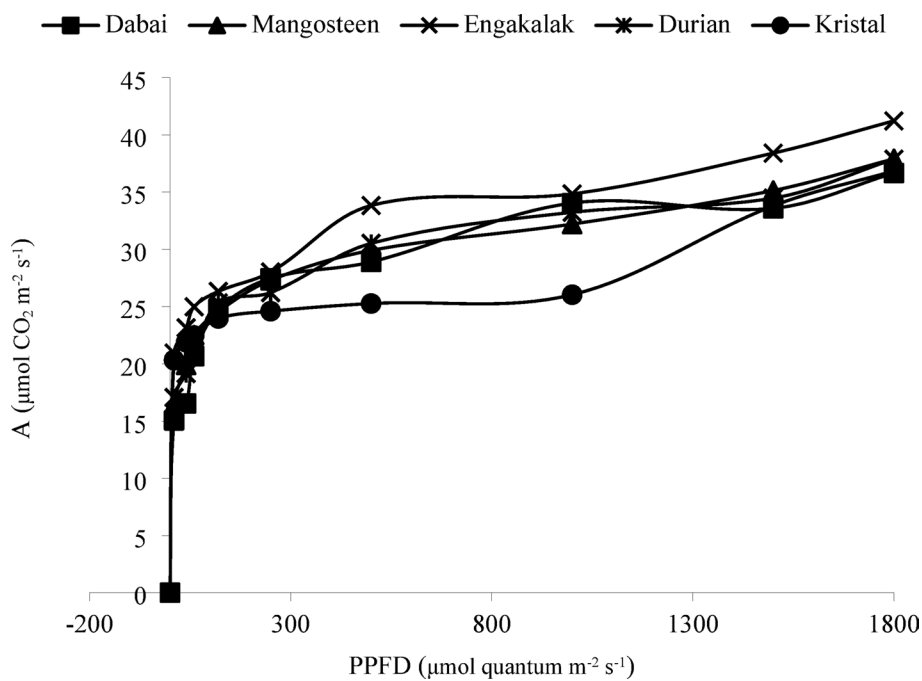


Fig. 4 A-Li curves showing CO₂ assimilation rate at different photon flux densities of five tropical fruit plants (n=3 leaves per species), Durian (*Durio zibethinus*), Mangosteen (*Garcinia mangostana*), Kristal (*Pometia pinnata*), Dabai (*Canarium odontophyllum*), Engkalak (*Litsea garciae*) measured at a constant intercellular CO₂ concentration of 700 ppm and leaf temperature at 25 °C

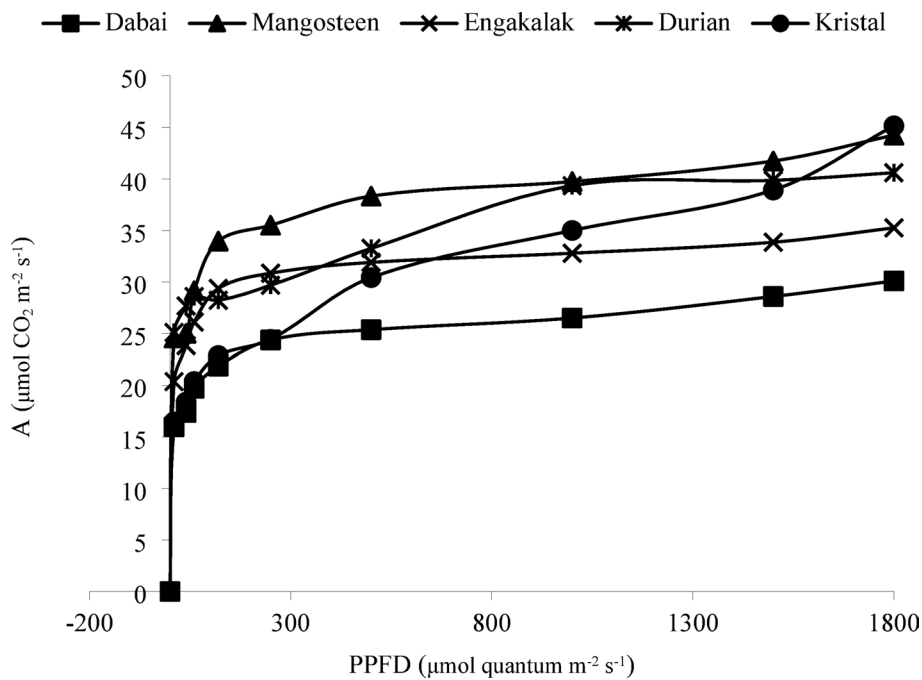


Fig. 5 A-Li curves showing CO₂ assimilation rate at different photon flux densities of five tropical fruit plants (n=3 leaves per species), Durian (*Durio zibethinus*), Mangosteen (*Garcinia mangostana*), Kristal (*Pometia pinnata*), Dabai (*Canarium odontophyllum*), Engkalak (*Litsea garciae*) measured at a constant intercellular CO₂ concentration of 700 ppm and leaf temperature at 30 °C

3.2 A-Li curve showing photosynthetic gas exchange of tropical fruit plants at different carbon dioxide concentrations and temperatures

Table 1 shows the comparison between 400 and 700 ppm at 25 °C, where A, E, G_s and WUE was significantly affected by species, carbon dioxide concentration and their interactions (all $p < 0.001$). For A, at 400 ppm, *C. odontophyllum*, *L. garciae* and *D. zibethinus* showed significance between species. However, at 700 ppm, only *L. garciae* showed significance difference between species. *C. odontophyllum* (36.49%), *L. garciae* (6.99%), *G. mangostana* (16.08%), and *P. pinnata* (15.60%) showed increase in A value as the CO₂ concentration increases at 25 °C except for *D. zibethinus* (-17.87%). Transpiration rate showed significance difference between species for *L. garciae* and *G. mangostana* at 400 ppm while at 700 ppm, it was showed by *L. garciae*, *D. zibethinus* and *P. pinnata*. *C. odontophyllum*, *D. zibethinus* and *G. mangostana* thrived better in increased CO₂ concentration as the E value increases from 400 to 700 ppm, except for *L. garciae* (-91.52%) and *P. pinnata* (-52.34%).

For G_s, *L. garciae* and *P. pinnata* showed a decrease in value as CO₂ concentration increased, with values reaching near-zero levels (0.00 ± 0.00 and 0.01 ± 0.00 mmol H₂O

Table 1 Instantaneous gas-exchange performance of five tropical tree species at 25 °C under PPFD 1800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and two internal CO₂ levels (400 and 700 ppm). Values are means $\pm$ SE (n = 3 trees per species, with one leaf from each tree). Mean separation used Tukey Test ($\alpha = 0.05$). Lowercase letters within a row show differences between CO₂ levels; uppercase letters within a column show differences among species. A = net CO₂ assimilation rate ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$); E = transpiration rate ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$); G_s = stomatal conductance ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$); WUE = water-use efficiency ($\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$)

A-Li curve at 25 °C (400 & 700 ppm)					
Species	CO ₂ (ppm)		F-value		
	400	700	Species	CO ₂	Species*CO ₂
Net CO ₂ assimilation rate (A) ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)					
<i>C. odontophyllum</i>	26.86 $\pm$ 0.36 ^{b,D}	36.66 $\pm$ 0.45 ^{a,B}	133.31***	84.03***	91.44***
<i>L. garciae</i>	37.91 $\pm$ 0.33 ^{b,B}	40.56 $\pm$ 0.55 ^{a,A}			
<i>D. zibethinus</i>	46.12 $\pm$ 0.55 ^{a,A}	37.88 $\pm$ 0.37 ^{b,B}			
<i>G. mangostana</i>	32.66 $\pm$ 0.38 ^{b,C}	37.91 $\pm$ 0.37 ^{a,B}			
<i>P. pinnata</i>	31.88 $\pm$ 0.77 ^{b,C}	36.85 $\pm$ 0.66 ^{a,B}			
Transpiration rate (E) ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$)					
<i>C. odontophyllum</i>	1.44 $\pm$ 0.02 ^{a,B}	1.74 $\pm$ 0.05 ^{a,B}	70.71***	66.10***	243.24***
<i>L. garciae</i>	4.48 $\pm$ 0.29 ^{a,A}	0.38 $\pm$ 0.03 ^{a,D}			
<i>D. zibethinus</i>	1.06 $\pm$ 0.05 ^{a,B,C}	1.99 $\pm$ 0.02 ^{a,A}			
<i>G. mangostana</i>	0.59 $\pm$ 0.01 ^{a,C}	1.66 $\pm$ 0.01 ^{a,B}			
<i>P. pinnata</i>	1.28 $\pm$ 0.05 ^{a,B}	0.61 $\pm$ 0.04 ^{a,C}			
Stomatal conductance (G _s) ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$)					
<i>C. odontophyllum</i>	0.03 $\pm$ 0.00 ^{a,B}	0.03 $\pm$ 0.00 ^{a,A}	46.50***	141.55***	155.81***
<i>L. garciae</i>	0.05 $\pm$ 0.00 ^{a,A}	0.00 $\pm$ 0.00 ^{b,D}			
<i>D. zibethinus</i>	0.01 $\pm$ 0.00 ^{b,C}	0.02 $\pm$ 0.00 ^{a,B}			
<i>G. mangostana</i>	0.00 $\pm$ 0.00 ^{b,C}	0.02 $\pm$ 0.00 ^{a,C}			
<i>P. pinnata</i>	0.03 $\pm$ 0.00 ^{a,B}	0.01 $\pm$ 0.00 ^{b,D}			
Water use efficiency (WUE) ($\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$)					
<i>C. odontophyllum</i>	26.42 $\pm$ 0.29 ^{b,C}	30.56 $\pm$ 0.10 ^{a,D}	15,761.7***	49,989.1***	36,652.6***
<i>L. garciae</i>	8.40 $\pm$ 0.27 ^{b,D}	206.69 $\pm$ 0.67 ^{a,A}			
<i>D. zibethinus</i>	49.16 $\pm$ 0.24 ^{a,B}	33.18 $\pm$ 0.39 ^{b,C}			
<i>G. mangostana</i>	65.85 $\pm$ 0.62 ^{a,A}	28.77 $\pm$ 0.12 ^{b,E}			
<i>P. pinnata</i>	27.18 $\pm$ 0.29 ^{b,C}	138.00 $\pm$ 0.23 ^{a,B}			

F-tests for species, CO₂, and Species $\times$ CO₂ are reported; *, **, *** denote $p < 0.05$, $p < 0.01$, $p < 0.001$; ns = not significant

$\text{m}^{-2} \text{s}^{-1}$, respectively), indicating that transpiration was negligible or below the instrument detection limit under these measurement conditions. Conversely, *C. odontophyllum* did not show any changes but the G_s value for *D. zibethinus* ($0.02 \pm 0.00 \text{ mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) and *G. mangostana* ($0.02 \pm 0.00 \text{ mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) increases slightly with increase of CO_2 concentration. Most of the species showed significance difference between species at both CO_2 concentration except for *C. odontophyllum* and *P. pinnata* at 400 ppm for WUE. *D. zibethinus* and *G. mangostana* were more sensitive with the change of CO_2 concentration compared to *C. odontophyllum*, *L. garciae* and *P. pinnata* as the WUE value decreases drastically, 32.51% and 56.29% respectively.

Table 2 shows the comparison between 400 and 700 ppm at 30 °C, where species, carbon dioxide concentration and their interactions (all $p < 0.001$) were highly significant. For A, *C. odontophyllum* and *L. garciae* performed better at 400 ppm compared to *D. zibethinus* (17.72%), *G. mangostana* (4.41%) and *P. pinnata* (10.99%) as the value increased at 700 ppm. *D. zibethinus* was significantly different between species at both CO_2 concentrations. At lower CO_2 concentration, E was uniformly high for all species ($1.46\text{--}4.29 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$) except *C. odontophyllum* that showed a higher value at

Table 2 Instantaneous gas-exchange performance of five tropical tree species at 30 °C under PPFD 1800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and two internal CO_2 levels (400 and 700 ppm). Values are means $\pm$ SE ($n = 3$ trees per species, with one leaf from each tree). Mean separation used Tukey Test ($\alpha = 0.05$). Lowercase letters within a row show differences between CO_2 levels; uppercase letters within a column show differences among species. A = net CO_2 assimilation rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$); E = transpiration rate ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$); G_s = stomatal conductance ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$); WUE = water-use efficiency ($\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{H}_2\text{O}$)

A-Li curve at 30 °C (400 & 700 ppm)					
Species	CO ₂ (ppm)		F-value		
	400	700	Species	CO ₂	Species*CO ₂
Net CO ₂ assimilation rate (A) (μmol CO ₂ m ⁻² s ⁻¹)					
<i>C. odontophyllum</i>	37.07 ± 0.26 ^{a,C}	30.10 ± 0.43 ^{b,D}	253.11***	10.52***	93.52***
<i>L. garciae</i>	36.83 ± 0.41 ^{a,C}	35.25 ± 0.14 ^{b,C}			
<i>D. zibethinus</i>	34.49 ± 0.30 ^{b,D}	40.60 ± 0.60 ^{a,B}			
<i>G. mangostana</i>	42.38 ± 0.33 ^{a,A}	44.25 ± 0.42 ^{a,A}			
<i>P. pinnata</i>	40.68 ± 0.42 ^{b,B}	45.15 ± 0.31 ^{a,A}			
Transpiration rate (E) (mol H ₂ O m ⁻² s ⁻¹)					
<i>C. odontophyllum</i>	2.39 ± 0.02 ^{b,B}	3.44 ± 0.01 ^{a,A}	506.15***	551.82***	835.28***
<i>L. garciae</i>	4.29 ± 0.07 ^{a,A}	0.84 ± 0.01 ^{b,E}			
<i>D. zibethinus</i>	2.41 ± 0.35 ^{a,B}	2.02 ± 0.08 ^{a,B}			
<i>G. mangostana</i>	1.61 ± 0.02 ^{a,C}	1.56 ± 0.02 ^{a,C}			
<i>P. pinnata</i>	1.46 ± 0.05 ^{a,C}	1.24 ± 0.03 ^{a,D}			
Stomatal conductance (Gs) (mmol H ₂ O m ⁻² s ⁻¹)					
<i>C. odontophyllum</i>	0.03 ± 0.00 ^{b,B}	0.04 ± 0.00 ^{a,A}	959.49***	957.82***	816.02***
<i>L. garciae</i>	0.06 ± 0.00 ^{a,A}	0.01 ± 0.00 ^{b,D}			
<i>D. zibethinus</i>	0.03 ± 0.00 ^{a,C}	0.02 ± 0.00 ^{b,B}			
<i>G. mangostana</i>	0.02 ± 0.00 ^{a,D}	0.02 ± 0.00 ^{a,C}			
<i>P. pinnata</i>	0.02 ± 0.00 ^{a,D}	0.01 ± 0.00 ^{b,CD}			
Water use efficiency (WUE) (μmol CO ₂ mmol ⁻¹ H ₂ O)					
<i>C. odontophyllum</i>	18.00 ± 0.54 ^{a,B}	9.07 ± 0.46 ^{b,E}	3358.93***	6717.99***	4964.65***
<i>L. garciae</i>	8.89 ± 0.49 ^{b,D}	129.82 ± 0.88 ^{a,A}			
<i>D. zibethinus</i>	15.00 ± 0.39 ^{b,C}	23.58 ± 0.62 ^{a,D}			
<i>G. mangostana</i>	29.41 ± 0.53 ^{b,A}	33.49 ± 0.24 ^{a,C}			
<i>P. pinnata</i>	27.80 ± 0.12 ^{b,A}	40.66 ± 0.62 ^{a,B}			

F-tests for species, CO_2 , and Species $\times$ CO_2 are reported; *, **, *** denote $p < 0.05$, $p < 0.01$, $p < 0.001$; ns = not significant

700 ppm (43.93%). All the species showed significance difference between each other at 700 ppm. Stomatal conductance achieved higher value at 400 ppm but this advantage decreased at 700 ppm except for *C. odontophyllum* that showed a slightly higher value as the CO₂ concentration increases (33.33%). Only *G. mangostana* did not show significance difference between CO₂ concentrations and the significance difference between species were shown by *C. odontophyllum*, *L. garciae*, and *D. zibethinus*. In contrast, the result was different for WUE value as the values were higher at 700 ppm than 400 ppm except for *C. odontophyllum*. All the species showed significance difference between CO₂ concentration (400 and 700 ppm) and species (700 ppm).

All A, E, Gs, and WUE value of both 25 and 30 °C at 400 ppm between five species are presented in Table 3, with statistical significance assessed between temperatures and species. *L. garciae* and *D. zibethinus* achieved higher value of A at 25 °C, however this advantage decreased as the temperature increases to 30 °C. The results are different for *C. odontophyllum*, *G. mangostana* and *P. pinnata* that showed that showed higher A value at 30 °C. Only *G. mangostana* showed significance difference between temperatures. *C. odontophyllum*, *D. zibethinus*, *G. mangostana*, and *P. pinnata* showed higher or

Table 3 Instantaneous gas-exchange performance of five tropical tree species at 400 ppm under PPFD 1800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and two leaf temperatures (25 and 30 °C). Values are means $\pm$ SE (n = 3 trees per species, with one leaf from each tree). Mean separation used Tukey Test ($\alpha = 0.05$). Lowercase letters within a row show differences between °C levels; uppercase letters within a column show differences among species. A = net CO₂ assimilation rate ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$); E = transpiration rate ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$); Gs = stomatal conductance ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$); WUE = water-use efficiency ($\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$)

A-Li curve at 400 ppm (25 & 30 °C)A-Li CURVE at 400PPM (25°C, 30°C)					
Species	Temperature (°C)		F-value		
	25 °C	30 °C	Species	Temperature	Species*Temperature
Net CO ₂ assimilation rate (A) ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)					
<i>C. odontophyllum</i>	26.86 $\pm$ 0.36 ^{a,D}	37.07 $\pm$ 0.26 ^{a,C}	97.50***	136.25***	239.49***
<i>L. garciae</i>	37.91 $\pm$ 0.33 ^{a,B}	36.83 $\pm$ 0.41 ^{a,C}			
<i>D. zibethinus</i>	46.12 $\pm$ 0.55 ^{a,A}	34.49 $\pm$ 0.30 ^{a,D}			
<i>G. mangostana</i>	32.66 $\pm$ 0.38 ^{b,C}	42.38 $\pm$ 0.33 ^{a,A}			
<i>P. pinnata</i>	31.88 $\pm$ 0.77 ^{a,C}	40.68 $\pm$ 0.42 ^{a,B}			
Transpiration rate (E) ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$)					
<i>C. odontophyllum</i>	1.44 $\pm$ 0.02 ^{b,B}	2.39 $\pm$ 0.02 ^{a,B}	362.89***	115.05***	21.51***
<i>L. garciae</i>	4.48 $\pm$ 0.29 ^{a,A}	4.29 $\pm$ 0.07 ^{a,A}			
<i>D. zibethinus</i>	1.06 $\pm$ 0.05 ^{b,B,C}	2.41 $\pm$ 0.35 ^{a,B}			
<i>G. mangostana</i>	0.59 $\pm$ 0.01 ^{b,C}	1.61 $\pm$ 0.02 ^{a,C}			
<i>P. pinnata</i>	1.28 $\pm$ 0.05 ^{a,B}	1.46 $\pm$ 0.05 ^{a,C}			
Stomatal conductance (Gs) ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$)					
<i>C. odontophyllum</i>	0.03 $\pm$ 0.00 ^{a,B}	0.03 $\pm$ 0.00 ^{b,B}	358.21***	81.08***	50.11***
<i>L. garciae</i>	0.05 $\pm$ 0.00 ^{a,A}	0.06 $\pm$ 0.00 ^{a,A}			
<i>D. zibethinus</i>	0.01 $\pm$ 0.00 ^{b,C}	0.03 $\pm$ 0.00 ^{a,C}			
<i>G. mangostana</i>	0.00 $\pm$ 0.00 ^{b,C}	0.02 $\pm$ 0.00 ^{a,D}			
<i>P. pinnata</i>	0.03 $\pm$ 0.00 ^{a,B}	0.02 $\pm$ 0.00 ^{b,D}			
Water use efficiency (WUE) ($\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$)					
<i>C. odontophyllum</i>	26.42 $\pm$ 0.29 ^{a,C}	18.00 $\pm$ 0.54 ^{b,B}	2440.45***	3656.89***	1019.11***
<i>L. garciae</i>	8.40 $\pm$ 0.27 ^{a,D}	8.89 $\pm$ 0.49 ^{a,D}			
<i>D. zibethinus</i>	49.16 $\pm$ 0.24 ^{a,B}	15.00 $\pm$ 0.39 ^{b,C}			
<i>G. mangostana</i>	65.85 $\pm$ 0.62 ^{a,A}	29.41 $\pm$ 0.53 ^{b,A}			
<i>P. pinnata</i>	27.18 $\pm$ 0.29 ^{a,C}	27.80 $\pm$ 0.12 ^{a,A}			

F-tests for species, CO₂, and Species $\times$ CO₂ are reported; *, **, *** denote $p < 0.05$, $p < 0.01$, $p < 0.001$; ns = not significant

Table 4 Instantaneous gas-exchange performance of five tropical tree species at 700 ppm under PPFD 1800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and two leaf temperatures (25 and 30 °C). Values are means $\pm$ SE ($n = 3$ trees per species, with one leaf from each tree). Mean separation used Tukey Test ($\alpha = 0.05$). Lowercase letters within a row show differences between °C levels; uppercase letters within a column show differences among species. A = net CO_2 assimilation rate ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$); E = transpiration rate ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$); Gs = stomatal conductance ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$); WUE = water-use efficiency ($\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$)

A-Li curve at 700 ppm (25 & 30 °C)					
Species	Temperature (°C)		F-value		
	25 °C	30 °C	Species	Temperature	Species*Temperature
Net CO_2 assimilation rate (A) ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)					
<i>C. odontophyllum</i>	36.66 $\pm$ 0.45 ^{a,B}	30.10 $\pm$ 0.43 ^{b,D}	0.62 ns	0.07 ns	0.75 ns
<i>L. garciae</i>	40.56 $\pm$ 0.55 ^{a,A}	35.25 $\pm$ 0.14 ^{b,C}			
<i>D. zibethinus</i>	37.88 $\pm$ 0.37 ^{a,B}	40.60 $\pm$ 0.60 ^{a,B}			
<i>G. mangostana</i>	37.91 $\pm$ 0.37 ^{b,B}	44.25 $\pm$ 0.42 ^{a,A}			
<i>P. pinnata</i>	36.85 $\pm$ 0.66 ^{b,B}	45.15 $\pm$ 0.31 ^{a,A}			
Transpiration rate (E) ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$)					
<i>C. odontophyllum</i>	1.74 $\pm$ 0.05 ^{b,B}	3.44 $\pm$ 0.01 ^{a,A}	4.80**	2.78 ns	0.95 ns
<i>L. garciae</i>	0.38 $\pm$ 0.03 ^{b,D}	0.84 $\pm$ 0.01 ^{a,E}			
<i>D. zibethinus</i>	1.99 $\pm$ 0.02 ^{a,A}	2.02 $\pm$ 0.08 ^{a,B}			
<i>G. mangostana</i>	1.66 $\pm$ 0.01 ^{a,B}	1.56 $\pm$ 0.02 ^{a,C}			
<i>P. pinnata</i>	0.61 $\pm$ 0.04 ^{b,C}	1.24 $\pm$ 0.03 ^{a,D}			
Stomatal conductance (Gs) ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$)					
<i>C. odontophyllum</i>	0.03 $\pm$ 0.00 ^{b,A}	0.04 $\pm$ 0.00 ^{a,A}	4.82**	2.37 ns	0.46 ns
<i>L. garciae</i>	0.00 $\pm$ 0.00 ^{b,D}	0.01 $\pm$ 0.00 ^{a,D}			
<i>D. zibethinus</i>	0.02 $\pm$ 0.00 ^{a,B}	0.02 $\pm$ 0.00 ^{a,B}			
<i>G. mangostana</i>	0.02 $\pm$ 0.00 ^{a,C}	0.02 $\pm$ 0.00 ^{a,C}			
<i>P. pinnata</i>	0.01 $\pm$ 0.00 ^{a,D}	0.01 $\pm$ 0.00 ^{a,CD}			
Water use efficiency (WUE) ($\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$)					
<i>C. odontophyllum</i>	30.56 $\pm$ 0.10 ^{a,D}	9.07 $\pm$ 0.46 ^{b,E}	2.95*	1.64 ns	0.37 ns
<i>L. garciae</i>	206.69 $\pm$ 0.67 ^{a,A}	129.82 $\pm$ 0.88 ^{b,A}			
<i>D. zibethinus</i>	33.18 $\pm$ 0.39 ^{a,C}	23.58 $\pm$ 0.62 ^{b,D}			
<i>G. mangostana</i>	28.77 $\pm$ 0.12 ^{b,E}	33.49 $\pm$ 0.24 ^{a,C}			
<i>P. pinnata</i>	138.00 $\pm$ 0.23 ^{a,B}	40.66 $\pm$ 0.62 ^{b,B}			

F-tests for species, CO_2 , and Species $\times$ CO_2 are reported; *, **, *** denote $p < 0.05$, $p < 0.01$, $p < 0.001$; ns = not significant

no change in E value at 30 °C (2.39 ± 0.02 , 2.41 ± 0.35 , 1.61 ± 0.02 , and $1.46 \pm 0.05 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$ respectively) than at 25 °C. However, *L. garciae* showed lower E value (4.48 ± 0.29 at 25 °C, $4.29 \pm 0.07 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$ at 30 °C) as the temperature increases, indicating sensitivity to heat. Only *C. odontophyllum*, *D. zibethinus*, and *G. mangostana* showed significance difference between temperatures.

Most of the species except *P. pinnata* performed better at 30 °C for Gs. Other than *C. odontophyllum*, all species showed significance difference between 25 °C and 30 °C. At 30 °C, *C. odontophyllum*, *L. garciae*, and *D. zibethinus* showed significance difference between species. *C. odontophyllum*, *D. zibethinus* and *G. mangostana* achieved a higher WUE value at lower temperature (26.42 ± 0.29 , 49.16 ± 0.24 and $65.85 \pm 0.62 \mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$ respectively). However, this advantage decreased as the temperature increases except for *L. garciae*, and *P. pinnata*. Only *L. garciae* and *D. zibethinus* showed significance difference between species at both 25 and 30 °C.

Table 4 shows A, E, Gs, and WUE of tropical fruit plants at 700 ppm between different temperatures (25 °C, 30 °C). The net CO_2 assimilation rate has no significant difference for species, temperature and the interaction between species and temperature.

At 25 °C, *G. mangostana* and *L. garciae* had higher A (37.91–40.56 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) compared to *D. zibethinus*, *C. odontophyllum*, and *P. pinnata* (36.66–37.88 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). At 30 °C, however, *D. zibethinus* and *P. pinnata* showed higher A value while *G. mangostana* continuously increases with temperature (40.60–45.15 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Except for *D. zibethinus*, all the species showed significant difference between temperatures. The F value (temperature and species $\times$ temperature) for transpiration rate showed no significance difference except for species only ($F=4.80$, $p<0.01$). All the species constantly show higher E at 30 °C than 25 °C, except for *G. mangostana* (1.66 ± 0.01 to $1.56 \pm 0.02 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$).

Stomatal conductance varied significantly with species ($F=4.82$, $p<0.01$) while temperature ($F=2.37$, ns) and their interactions temperature $\times$ system ($F=0.46$, ns) showed no significance. At both temperatures, Gs remain constant or increase in value as the temperature increases for all species (0.00–0.04 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$). WUE was mainly influenced by the species ($F=2.95$, $p<0.05$) because temperature and their interactions (species $\times$ temperature) showed no significance. All species achieved a higher WUE at 25 °C (33.18–206.69 $\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$) except for *G. mangostana* than at 30 °C.

4 Discussion

4.1 Interactive effects of temperature and carbon dioxide concentration on photosynthetic light response in tropical fruit plants

The results show that at both 400 and 700 ppm, with increasing temperature (30 °C), *G. mangostana* and *P. pinnata* have the highest value for net photosynthesis. These results suggest that these two species are more suitable for cultivation and more resilient to climate change as the assimilation rate increases with increasing temperature and CO_2 concentration. According to Zhu et al. [68] and Leakey et al. [29], increased CO_2 concentration increases the rate of carboxylation via Rubisco and decreases photorespiration. This helps to increase the photosynthetic performance of C3 plants by reducing the competition between O_2 and CO_2 at the active sites of Rubisco leading to higher plant growth and yields [33, 51]. However, prolonged exposure of plants to CO_2 can reduce/inhibit the photosynthetic process [66]. At elevated temperature, electron transport rates limit photosynthesis by limiting the ATP/ADP ratio and stomatal homeostasis which varies depending on growth conditions and plant species. Most plants have a leaf net photosynthetic temperature that is between 25 and 30 °C, which is still below the optimal temperature for photosynthetic biochemistry [6, 47]. According to Hussain et al. [18], leaves are able to adapt photosynthesis or acclimatize to an elevated temperature in order to reach the maximum photosynthetic rate. This explains that the assimilation rate increases with increasing temperature or CO_2 concentration up to the optimal temperature and then decreases over a longer period of time.

Meanwhile, *C. odontophyllum* and *L. garciae* did not fare well under climate change especially with increased temperature and CO_2 concentration. This proves that these plants are more susceptible to changes in CO_2 concentration and temperature as the A value decreases drastically. The response of photosynthesis to the increase in temperature affects the uptake of excess energy and leads to an increase in the production of reactive oxygen species. This leads to damage to the photosynthetic machinery, especially PSII, due to disturbed electron chemistry. This is because PSII is very sensitive to light damage. Therefore, plants develop various coping mechanisms to protect PSII from

damage and activate its repair system. However, photosynthetic efficiency decreases when the rate of photo damage exceeds the rate of PSII recovery because photo inhibition takes place [36, 37]. Basically, an increase in CO₂ concentration leads to an increase in temperature, resulting in higher transpiration and lower water availability, which in turn leads to the decomposition of soil microbes and nutrients. As a result, photosynthesis decreases due to the reduced availability of nutrients for the plants. An increase in CO₂ concentration decreases Rubisco activation, electron transport and stomatal conductance responses, which could be associated with excessive carbohydrate aggregation or lower nitrogen content [51, 54].

4.2 Impact of temperature, and CO₂ concentration on instantaneous gas-exchange performance of tropical fruit plants

In this study, the light responses of A, E, Gs and WUE were measured, but with an interaction between leaf temperature and CO₂ concentration. It is known that an increase in CO₂ concentration increases photosynthetic performance in the short term [5, 48] and that low CO₂ concentration will limit photosynthesis. CO₂ exposures of 400 and 700 ppm were used to manipulate photosynthesis and to determine whether the acclimation potential of tropical fruit plants to temperature was increased or decreased at the different CO₂ concentrations.

At 400 ppm, *C. odontophyllum*, *G. mangostana* and *P. pinnata* appeared to have a higher value of A, E and Gs at 30 °C than at 25 °C, except for WUE. Meanwhile, at 700 ppm, *G. mangostana* showed an increase in A, Gs and WUE at elevated temperature, except for transpiration rate. *C. odontophyllum*, *L. garciae*, *D. zibethinus* and *P. pinnata* showed higher transpiration rate and stomatal conductance at 30 °C. This is confirmed by Greer [15] as the optimum temperature for fruiting of Shiraz vines is between 30 and 35 °C. The increase in photosynthetic rate is higher than that of transpiration as stomatal conductance increases with increasing temperature. Under these extreme growing conditions, there may have been an increase in CO₂ assimilation capacity, suggesting that these tropical fruit plants are naturally tolerant to high temperatures. When the temperature exceeds the ideal temperature, the increase in temperature has a greater effect on transpiration than on photosynthesis, so that WUEs decrease again [1]. As CO₂ is rapidly converted to carbohydrates in the leaf, the gradient between the surrounding air and the intercellular spaces increases in the presence of light, benefiting A and WUEs. However, the kinetic model presented by Charles-Edwards [7] illustrates that there is a relationship between CO₂ uptake and water loss from a leaf.

In this study, at 25 °C, when CO₂ concentration increased to 700 ppm, *C. odontophyllum* definitely survived and showed high photosynthetic performance in all parameters, while *G. mangostana* only showed lower WUE at 700 ppm. On the other hand, *G. mangostana* showed high A, E and Gs values at 30 °C, except for WUE when CO₂ concentration increases. High CO₂ concentration in the atmosphere leads to heat accumulation at the earth's surface, resulting in an increase in temperature that affects fruit trees [5]. Although 14 to 32 °C is often the optimal temperature range for photosynthesis, photosystem II is typically damaged at higher temperatures [45, 60], while the respiration rate increases, which lowers the net photosynthetic rate [53]. In addition, warming also causes water stress in the form of moisture loss in the soil, leading to reduced photosynthesis and inhibition of nutrient uptake [11]. Elevated CO₂ promotes photosynthesis by

preventing photorespiration and increasing the carboxylation rate of Rubisco as the CO₂ concentration in the mesophyll cells increases [14, 49] until it reaches the CO₂ saturation point [26]. Increased CO₂ and temperature do lead to a higher photosynthetic rate, but a combination of both unfortunately reduces CO₂ accumulation, plant growth and development [30].

In *L. garciae* and *P. pinnata* at 400 ppm, it was found that an increase in temperature by 5 °C resulted in a decrease in A and WUE as well as E and Gs in *D. zibethinus*. In contrast, *C. odontophyllum* and *L. garciae* at 700 ppm showed lower E and Gs values when the temperature increased to 30 °C. The differences in photosynthetic capacity between tropical fruit plants could be related to the responses of stomatal mechanisms to changes in temperature and light conditions [20]. This is because the biochemical processes within the mesophyll are optimized under optimal temperature and light conditions as both enzymatic activity and electron transport chain (photosystems) increases [28]. On the other hand, Gs increases at 30 °C because the biochemical processes in the mesophyll layers of the phyllodes increase the CO₂ assimilation rate [63]. The Gs results at 700 ppm may explain why the A at 1800 μmol m⁻² s⁻¹ under 30 °C shows lower or no differences, except for *C. odontophyllum* and *L. garciae*.

Leaf size regulates leaf temperature through the thickness of the leaf boundary layer, as turbulent air outside the leaf is faster compared to heat transfer [23]. In general, smaller leaves are more favorable under hotter and drier conditions as the leaf temperature is expected to be lower than larger leaves to avoid overheating [32, 55]. This is because the heat transfer rate of a smaller leaf per unit area is higher than that of a large leaf, which has a thicker leaf boundary layer due to its larger leaf area [32]. However, the result is reversed when *D. zibethinus* and *L. garciae* have a higher A, suggesting that these plants may be more heat tolerant than other tropical fruit crops at elevated CO₂ concentrations. In general, it appears that *C. odontophyllum*, *G. mangostana* and *P. pinnata* have a greater advantage and are more resistant to an increase in temperature and CO₂ concentration. In contrast, *L. garciae* is more susceptible and has not fared well with climate change.

4.3 Management implication of the study

Our study shows that increased CO₂ concentration and temperature significantly improved photosynthetic efficiency in *G. mangostana* and *P. pinnata*. These results suggest that these tropical fruit trees may be prioritised in climate adaptation strategies, as they showed greater physiological resilience under the tested conditions compared to *D. zibethinus*, *L. garciae*, and *C. odontophyllum*. Plantation managers, agricultural sectors, and farmers may consider expanding the cultivation of *G. mangostana* and *P. pinnata* in areas expected to experience elevated CO₂ concentration and higher temperature. For *D. zibethinus*, *L. garciae*, and *C. odontophyllum*, implementing supplemental irrigation is suggested to ensure adequate water supply during dry periods, particularly when rainfall becomes irregular and less predictable under climate change. This may help sustain growth and yield and reduce the risk of crop failure for these more vulnerable species. However, these implications should be interpreted with caution because other environmental factors, such as soil fertility and pest pressure, were not examined in this study. Overall, aligning crop selection and management practices with plant physiological

responses may support more resilient tropical fruit production systems in Malaysia while safeguarding species that are more vulnerable to future climate conditions.

5 Conclusion

In this study, *G. mangostana* and *P. pinnata* were reported to have an advantage in photosynthetic response at higher temperature and CO₂ concentration. *D. zibethinus* thrived better in a lower temperature and CO₂ concentration while *L. garciae* and *C. odontophyllum* appear to either increase or remain unaffected. These results suggest that *G. mangostana* and *P. pinnata* are more suitable for cultivation at higher temperature and CO₂ concentrations as they are more heat tolerant and adapt well to climate change. Hence, this study is crucial to understand the adaptation of tropical fruit plants to climate change so that they can spread and grow well in tropical countries.

Acknowledgements

The authors acknowledge Universiti Malaysia Sarawak (UNIMAS) for supporting this project by VC High Impact Research Grant 2.0 (UNI/F07/VC-HIRG-2/86040/2023) and appreciation to the Siburan District Agriculture Department and Kuching District Agriculture Department for connecting us with the farmers. Special thanks to Mr. Apeng and Mr. Barry from Kampung Begu (Siburan), Kampung Malaban (Kota Samarahan) and Mr. Lee from Kampung Betong (Kuching) for their co-operation in data collection.

Author contributions

Conceptualization, data curation, material preparation, data collection and analysis, writing original draft were done by Vanishri Kaly Sitthan. Supervision, review and editing were performed by Hollena Nori and Freddy Yeo Kuok San. Supervision; data curation; formal analysis; writing—review and editing were performed by Mohamad Hilmi Ibrahim. All authors contributed to the study conception, design, commented on previous versions of the manuscript and approved the final manuscript.

Funding

Open Access funding provided by Universiti Malaysia Sarawak. This study is funded by VC High Impact Research Grant 2.0 (UNI/F07/VC-HIRG-2/86040/2023).

Data availability

For inquiries regarding data availability, please contact the author directly.

Declarations

Ethical approval

All plant materials were collected in accordance with relevant local and national guidelines in Malaysia. Sampling was conducted non-destructively from cultivated and naturally growing fruit trees in Kuching, Siburan, and Kota Samarahan, Sarawak, and involved species that are not protected or endangered. As the collection did not involve protected species or conservation areas, formal permits or licences were not required, and prior permission was obtained from landowners or site custodians.

Competing interests

The authors declare that they have no competing interests.

Received: 5 January 2026 / Accepted: 18 May 2026

Published online: 22 May 2026

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