

Short-term photosynthetic responses of selected kerangas species in Northwest Borneo to changes in leaf temperature and CO₂ concentration

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ABSTRACT

Climate change, which includes rising temperatures and elevated atmospheric CO₂ concentrations, has a significant effect on photosynthesis and plant adaptation. This study examines how four native species from Kerangas forests respond to changes in temperature and CO₂ levels through photosynthesis under climate change stress. The species are *Buchanania arborescens*, *Dillenia suffruticosa*, *Calophyllum inophyllum*, and *Ploiarium alternifolium*. Photosynthetic parameters, including Amax, Aqe, LCP, Vcmax, and J, were measured to assess carbon assimilation efficiency and physiological performance under controlled temperature and CO₂ conditions. The results showed substantial differences between the species. For example, among the four species, *C. inophyllum* and *P. alternifolium* demonstrated higher maximum photosynthetic capacity (Amax) and electron transport potential (J) compared to *B. arborescens* and *D. suffruticosa*, indicating greater potential for carbon assimilation under the tested chamber conditions. Higher CO₂ levels generally increased photosynthetic rates. The results highlight the importance of species-specific approaches for managing and protecting forests, particularly to enhance the resilience of tropical heath forests to climate change. Promoting native species with strong adaptive traits can support reforestation and help maintain ecosystem balance.

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1. INTRODUCTION

The ability of plant species, particularly those indigenous to nutrient-deficient and acidic soils such as the Kerangas (Anirudh et al., 2025), to adapt photosynthetically is essential for understanding how these species endure environmental pressures. The Kerangas woodlands, known as "land where rice cannot grow" in the local Dayak language, possess distinctive ecological characteristics that challenge plant growth due to their sandy, acidic, and nutrient-deficient soils (Din et al., 2015). Despite these challenging conditions, these woodlands support a diverse range of plant species that have evolved specific adaptations to ensure their survival (Suhaili et al., 2016).

Kerangas (tropical heath) forests occur on nutrient-poor, acidic, sandy soils and are characterised by specialised plant communities adapted to low fertility and stressful

microclimates (Din et al., 2015; Rahayu et al., 2018). Research has shown that kerangas forests harbour distinct vegetation types, including stunted trees, shrubs, and various epiphytes (Nisaa, 2023). These forests are typically found on podzolised siliceous sands, where organic matter decomposes gradually on the soil surface (Kamoona et al., 2023). Kerangas forests are known for their high conservation value, hosting endemic plant species and unique flora such as carnivorous plants and myrmecophytes (Tuah et al., 2020). Studies have highlighted the importance of identifying the bioactivity of tree species in kerangas forests to determine their economic value (Oktavia et al., 2022).

Plant photosynthesis is strongly influenced by short-term changes in leaf temperature and CO₂ availability, which affect carbon assimilation capacity and related biochemical limitations (Slot & Winter, 2017). Previous studies have shown that warming can alter photosynthetic rates through effects on

enzymatic activity and stomatal regulation, while elevated atmospheric CO₂ can modify carboxylation efficiency and electron transport demand (Lin et al., 2015). However, most physiological evidence comes from non-heath systems, and comparable measurements for many Kerangas tree species remain limited. This restricts our understanding of how these specialised species may perform under near-future temperature and CO₂ scenarios. Photosynthetic responses vary across species because physiological traits and resource-use strategies differ. These differences are especially important in Kerangas environments, where nutrient limitation can constrain carbon assimilation and growth. A study by Ibrahim et al. (2021) has shown that plant species living in nutrient-poor environments, such as Kerangas species, often make certain adaptations to increase their photosynthetic efficiency.

These adaptations may involve modifications in leaf morphology, increased efficacy of photosynthetic enzymes, and changes in stomatal conductance (Masoni et al., 1996). However, there is a lack of data on the precise physiological responses of indigenous Kerangas species to different climatic conditions, particularly regarding their gas exchange characteristics. This study provides a detailed examination of the photosynthetic and respiratory efficiency of four selected species in their natural habitat. *Buchanania arborescens*, *Dillenia suffruticosa*, *Calophyllum inophyllum*, and *Ploiarium alternifolium* were chosen for their prevalence in Kerangas forests and their distinct ecological roles. By comparing their gas exchange parameters, we can infer the relative efficiency and adaptive capacity of each species to cope with the challenging conditions of their natural environment.

The results of this study will have significant implications for forest management and nature conservation. Identifying species with higher photosynthetic efficiency and adaptability may help prioritise these species in reforestation and conservation efforts. Such species are likely to be more resilient to environmental change and thus enhance the stability and productivity of Kerangas forests. Furthermore, understanding native species with high photosynthetic capacity under elevated CO₂ conditions is crucial for developing effective control measures.

In addition to providing insights into species-specific adaptations, this research contributes to a broader understanding of how tropical heath forests may respond to future climate scenarios. With rising global temperatures and CO₂ concentrations, the ability of native species to adapt to these changes will be crucial for the survival of Kerangas forests. This study demonstrates the importance of maintaining genetic and species diversity in these ecosystems to ensure their resilience to environmental stressors.

This study examined the short-term photosynthetic responses of four Kerangas species under controlled chamber conditions by comparing leaf gas exchange at two leaf temperatures (25°C and 30°C) and two CO₂ concentrations (400 and 700 ppm), as well as across CO₂/Ci response curves. The two leaf temperatures (25°C and 30°C) were chosen to represent an ecologically realistic range for Kerangas foliage under current conditions and modest near-future warming. A leaf temperature of 25°C was used as a baseline, reflecting typical daytime conditions for shaded to moderately exposed leaves, while 30°C represents warmer leaf temperatures during hot periods. The CO₂ concentrations were set at 400 ppm to represent present-day ambient conditions and 700 ppm as an elevated level commonly used to assess short-term CO₂ responsiveness under plausible future scenarios. We quantified key photosynthetic parameters (e.g., Amax, Aqe, LCP, Vcmax, and J) to compare species-level physiological performance and infer differences in potential carbon assimilation capacity under the tested conditions.

2. MATERIALS AND METHODS

2.1 Study site and species

This study was conducted in secondary coastal heath forests (Kerangas) (4°57.388'N, 114°52.194'E; elevation 60 m asl) near Universiti Brunei Darussalam in Brunei Darussalam, Northwest Borneo, from June to August 2015. The average annual temperature in 2015 was 28.8°C, and total annual precipitation was 3714 mm, recorded at Brunei International Airport, located approximately 14 km from the study site (Brunei Darussalam Meteorological Department, unpublished data). Bornean heath forest, a unique type of lowland seasonal rainforest, develops mainly on podsolised, highly acidic sandy soils with low macronutrient content (Ibrahim 2023; Jaafar et al. 2016). Four native plant species were selected for this study: *Buchanania arborescens* (Blume) Blume, *Dillenia suffruticosa* (Griff.) Martelli, *Calophyllum inophyllum* L., and *Ploiarium alternifolium* (Vahl) Melch. These species were chosen based on their prevalence and co-occurrence at the study sites and in other disturbed coastal heath forests in Brunei Darussalam (Tuah et al., 2020).

2.2 Leaf gas exchange measurements

Leaf gas exchange was measured ex situ using freshly excised, sun-exposed branches collected from the study site. Branches were cut with clean secateurs and immediately recut under water to minimise xylem cavitation, then transported to the measurement area in sealed plastic bags with moist tissue to reduce dehydration. Measurements

were initiated within 1 hour of collection. Before data logging, leaves were clamped in the LI-6400XT chamber and allowed to stabilise under the set cuvette conditions until net assimilation (A) and stomatal conductance (gs) reached a steady state (typically 10–20 min). Two branches from each of three mature individuals ($n = 6$ samples) of *B. arborescens*, *C. inophyllum*, *D. suffruticosa* and *P. alternifolium* were selected and collected for measurements (Ibrahim et al., 2021).

2.3 Photosynthetic light and CO₂ response curves

Photosynthetic light response curves (A–Li curves) were generated under a range of photosynthetic photon flux density (PPFD) values: 1800, 1500, 1000, 500, 250, 120, 60, 40, and 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at a relative humidity of 50–60% and an intercellular CO₂ concentration of 400 ppm in the chamber. For the A–Ci curves, CO₂ was applied in a stepwise sequence, and at each reference CO₂ level, leaves were allowed to equilibrate until gas-exchange variables stabilised before values were recorded (typically about 30 minutes per step, or longer if required to reach steady state). The leaf temperature in the chamber was maintained at either 25°C or 30°C. Photosynthetic CO₂ response curves (A–Ci curves) were developed under a range of intercellular CO₂ concentration values: 1250, 950, 700, 500, 380, 250, 150, 100, and 50 ppm at a relative humidity of 50–60%, a PPFD of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and a leaf temperature of 25°C.

2.4 Instantaneous leaf gas exchange parameters

The instantaneous leaf gas exchange parameters were measured at a PPFD of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, an air CO₂ concentration of 400 ppm and leaf temperatures of 25°C and 30°C. The PPFD response sequence was applied from high to low to ensure leaves were fully light-induced at the beginning of the light-response curve and to reduce artefacts associated with delayed stomatal opening and induction at low irradiance. At each PPFD step, leaves were allowed to acclimate until gas-exchange variables stabilised before recording (typically ~2–3 min per step, or longer if required to reach steady state). The net CO₂ assimilation rate [A; $\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$], the transpiration rate [E; $\text{mmol}(\text{H}_2\text{O}) \text{m}^{-2} \text{s}^{-1}$], the stomatal conductance [Gs; $\text{mol}(\text{H}_2\text{O}) \text{m}^{-2} \text{s}^{-1}$] and water utilisation efficiency [WUE; $\mu\text{mol}(\text{CO}_2) \text{mmol}(\text{H}_2\text{O})^{-1}$], calculated from the A/E ratio (Farquhar & Sharkey 1982; Le et al. 2016).

Maximum photosynthesis [A_{max}; $\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$], apparent quantum yield [A_{qe}; $\mu\text{mol}^{-1} \text{quantum}$], light compensation point [LCP; $\mu\text{mol}^{-1} \text{quantum} \text{m}^{-2} \text{s}^{-1}$], maximum carboxylation rate of Rubisco [V_{cmax}; $\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$] and the potential electron transport rate for the regeneration of ribulose-1,5-bisphosphate [J; $\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$] were calculated using the following formulae from Aleric

& Kirkman (2005) and Sharkey et al. (2007). A nonlinear mixed modelling procedure in SAS version 9 (SAS, 2009) to fit the photosynthetic data curves for each plant species. Then estimated ,A-max., ,V-cmax ., and J using the PROC NONLIN parameter estimation analysis.

2.5 Data analysis

The collected data were analysed to evaluate the effects of species, temperature, and CO₂ concentration on photosynthetic parameters and gas exchange performance. Differences among species were tested using one-way ANOVA for key parameters, including maximum photosynthetic capacity (A_{max}), apparent quantum yield (A_{qe}), light compensation point (LCP), maximum carboxylation rate (V_{cmax}), and potential electron transport rate for ribulose-1,5-bisphosphate regeneration (J). Where significant effects were detected, Tukey's HSD post hoc test was applied to identify pairwise differences between species. Within each species, paired-samples t-tests were used to compare photosynthetic rates between the two measurement temperatures (25°C and 30°C) and between the two CO₂ concentrations (400 ppm and 700 ppm), using measurements from the same samples under both conditions. All analyses were conducted using SAS version 9.2 (SAS Corp., 2009). Statistical significance was set at $p < 0.05$, and data are presented as mean $\pm$ standard error (SE).

3. RESULTS

3.1 Comparison in photosynthetic light response curves and photosynthetic performances at leaf temperatures of 25 °C and 30°C

All species exhibited higher photosynthetic rates at 30°C compared to 25°C. The photosynthetic light-response curves of the four native species (*B. arborescens*, *D. suffruticosa*, *C. inophyllum*, and *P. alternifolium*) were analysed at the two temperatures (Figure 1). For *B. arborescens* and *D. suffruticosa*, photosynthetic rate increased with light intensity up to approximately 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, after which the response plateaued. A similar pattern was observed for *C. inophyllum* and *P. alternifolium*, but with a steeper rise and higher maximum photosynthetic rates.

Variation in photosynthetic parameters CO₂ assimilation rate (A), transpiration rate (E), stomatal conductance (Gs), and water-use efficiency (WUE) was assessed for four native species (*B. arborescens*, *D. suffruticosa*, *C. inophyllum*, and *P. alternifolium*) at 25°C and 30°C. Measurements were conducted at a photosynthetic photon flux density (PPFD) of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and an ambient CO₂ concentration of 400 ppm. *B. arborescens* and *C. inophyllum* exhibited the highest CO₂ assimilation rates,

and these increased significantly at 30°C (Figure 2), whereas *D. suffruticosa* and *P. alternifolium* showed lower assimilation rates with no significant temperature-related variation.

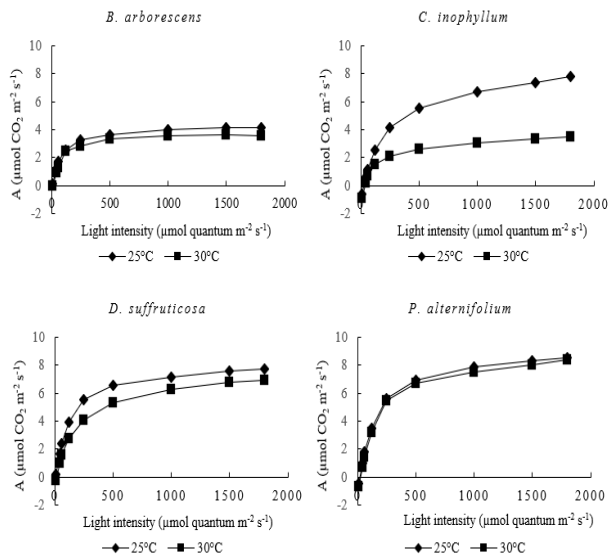


Figure 1: Photosynthetic light response curves of four native species (*B. arborescens*, *D. suffruticosa*, *C. inophyllum* and *P. alternifolium*) in sites of the coastal heath forests (n = 6 trees).

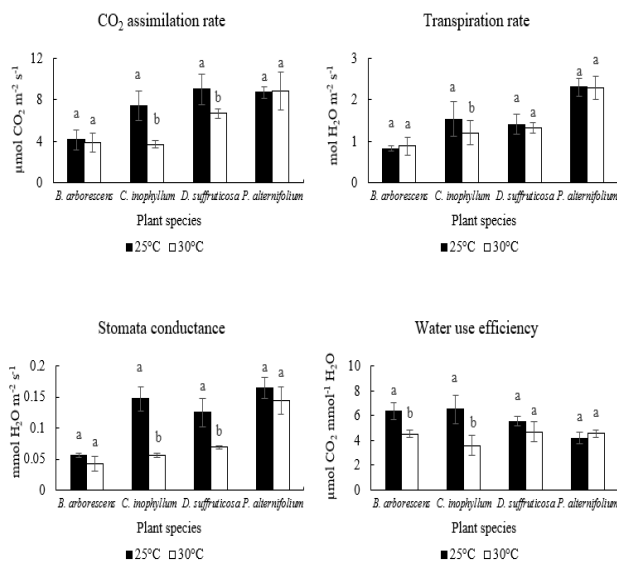


Figure 2: Variation in photosynthetic parameters (CO_2 assimilation rate or A , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; transpiration rate or E , $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$; stomatal conductance or G_s , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ and water use efficiency or WUE , $\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$) of four native species (*B. arborescens*, *D. suffruticosa*, *C. inophyllum* and *P. alternifolium*) in sites of the coastal heath forests. Measurements were made at photosynthetic photon flux density (PPFD) of $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and air CO_2 concentration of 400 ppm. The data were expressed as means $\pm$ SE (n = 6). Different letters indicated differences in means between temperatures conducted using Paired t-test.

Transpiration rates were generally higher in all species at 30°C, with *C. inophyllum* showing the greatest increase. Stomatal conductance showed the same temperature trend, increasing at 30°C for *B. arborescens*, *C. inophyllum*, and *P. alternifolium*, while *D. suffruticosa* did not

show an increase. The rise in stomatal conductance was most pronounced in *C. inophyllum*. Water utilization efficiency varied by species and temperature. *B. arborescens* and *C. inophyllum* had higher WUE at 25°C, which decreased at 30°C, whereas *D. suffruticosa* and *P. alternifolium* showed no significant (paired t-test, $p > 0.05$) WUE changes between temperatures.

3.2 Comparison in CO_2 response curves and photosynthetic performances at internal CO_2 (C_i) 400 ppm and 700 ppm

The study investigated the photosynthetic CO_2 response curves (A - C_i curves) of four tropical heath species (Kerangas), including the early secondary plant species *B. arborescens* and *D. suffruticosa* and the secondary plant species *C. inophyllum* and *P. alternifolium*. The measurements were carried out at a constant photosynthetic photon flux density of $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and a leaf temperature of 25°C. The results showed that the native species *B. arborescens* and *C. inophyllum* showed an increase in photosynthetic rates with increasing CO_2 levels. *D. suffruticosa* and *P. alternifolium* also increased CO_2 assimilation as internal CO_2 rose from ~ 400 to $\sim 700 \mu\text{mol CO}_2 \text{ mol}^{-1}$, with A increasing by approximately $+1.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ($\sim 18\%$) and $+2.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ($\sim 17\%$), respectively; however, their absolute rates remained lower than *B. arborescens* and *C. inophyllum* (Figure 3).

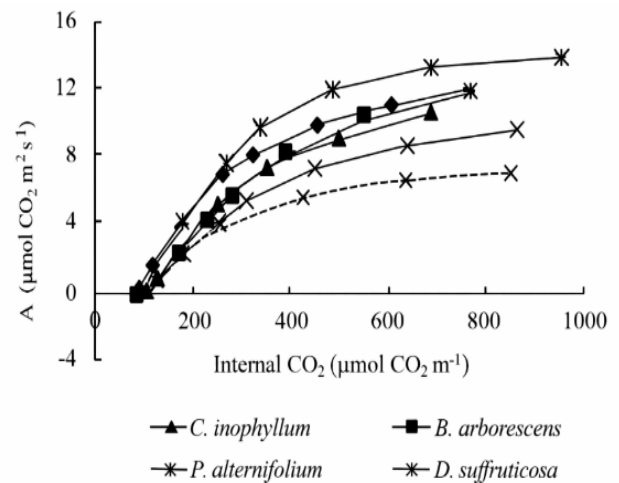


Figure 3: Photosynthetic CO_2 response curves (A - C_i curves) of four tropical heath (Kerangas) species (early secondary plant species: *B. arborescens* and *D. suffruticosa*, and secondary plant species: *C. inophyllum* and *P. alternifolium*), measured at constant photosynthetic photon flux density of $1500 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$ and leaf temperature of 25°C. The data are expressed as mean values (n = 6 trees).

At low C_i , all species had similar photosynthetic rates, but as C_i increased, *C. inophyllum* diverged significantly, with the highest rates. The study investigated the variation of photosynthetic parameters CO_2 assimilation rate (A), transpiration rate (E), stomatal conductance (G_s) and

water-use efficiency (WUE) of four native species (*B. arborescens*, *D. suffruticosa*, *C. inophyllum*, and *P. alternifolium*) under two atmospheric CO₂ concentrations (400 ppm and 700 ppm). Measurements were conducted at a leaf temperature of 25°C and a photosynthetic photon flux density (PPFD) of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with CO₂ concentration controlled at the specified treatment level.

The results showed that CO₂ assimilation rates were significantly higher for all species at 700 ppm CO₂. *Buchanania arborescens* and *C. inophyllum* showed the highest assimilation rates at elevated CO₂ levels, indicating a strong response to increased CO₂ availability (Figure 4). *Dillenia suffruticosa* and *Ploiarium alternifolium* also showed increased assimilation rates, but these were comparatively lower. Transpiration rates decreased at 700 ppm CO₂ across all species (Figure 4). The largest absolute reductions were observed in *P. alternifolium* (around 2.3 to 1.1 mol H₂O m⁻² s⁻¹) and *C. inophyllum* (1.5 to 0.6 mol H₂O m⁻² s⁻¹), whereas changes were smaller in *D. suffruticosa* (1.4 to 1.0 mol H₂O m⁻² s⁻¹) and *B. arborescens* (0.8 to 0.7 mol H₂O m⁻² s⁻¹). Stomatal conductance, a measure of gas exchange through the stomata of the leaves, increased significantly at 700 ppm CO₂ in *B. arborescens* and *C. inophyllum*, indicating more open stomata that allow greater CO₂ uptake. *D. suffruticosa* and *P. alternifolium* also showed increased conductance, although the changes were less pronounced.

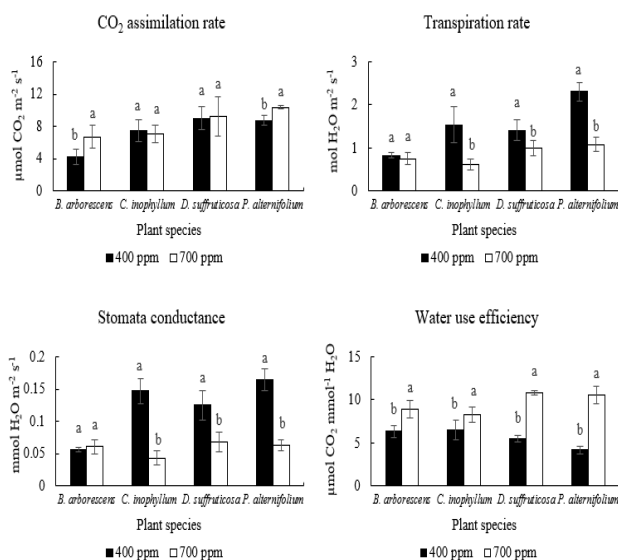


Figure 4: Variation in photosynthetic parameters (CO₂ assimilation rate or A, $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$; transpiration rate or E, $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$; stomatal conductance or Gs, $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ and water use efficiency or WUE, $\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$) of four native species (*B. arborescens*, *D. suffruticosa*, *C. inophyllum* and *P. alternifolium*) in sites of the coastal heath forests. Measurements were made at leaf temperature of 25°C and photosynthetic photon flux density (PPFD) of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The data were expressed as means $\pm$ SE (n = 6). Different letters indicated differences in means between temperatures conducted using Paired t-test.

Water-use efficiency (WUE) increased under elevated CO₂ (700 ppm) for all four species (Figure 4). *B. arborescens* showed a significant rise ($p < 0.05$) in WUE at 700 ppm compared to 400 ppm. *C. inophyllum* showed a smaller increase in the difference between CO₂ treatments. In contrast, *D. suffruticosa* and *P. alternifolium* exhibited the higher differences (50 % differences), with WUE increasing markedly at 700 ppm relative to 400 ppm.

3.3 Comparison in efficiency and performance of photosynthesis and respiration in Native Coastal Heath Forest Species

The study also investigated the instantaneous gas exchange performance of four native species namely *B. arborescens*, *D. suffruticosa*, *C. inophyllum*, and *P. alternifolium* at uninfected sites in coastal heath forests. The parameters measured included photosynthetic capacity (Amax), apparent quantum yield (Aqe), light compensation point (LCP), maximum carboxylation rate (Vcmax) and potential electron transport rate (J) (Table 1). *B. arborescens* showed an Amax of $9.39 \pm 1.79 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, Aqe of $0.0037 \pm 0.0003 \mu\text{mol}^{-1} \text{quantum}$, LCP of $92.58 \pm 9.75 \mu\text{mol}^{-1} \text{quantum m}^{-2} \text{s}^{-1}$, Vcmax of $17.91 \pm 2.51 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, and J of $70.40 \pm 9.60 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$. *C. inophyllum* had the highest Amax at $11.52 \pm 1.73 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ and a notable Aqe of $0.0031 \pm 0.0010 \mu\text{mol}^{-1} \text{quantum}$ (Table 1). Its LCP was $110.63 \pm 12.13 \mu\text{mol quantum m}^{-2} \text{s}^{-1}$, with Vcmax of $28.87 \pm 6.82 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ and J of $86.69 \pm 9.81 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$.

D. suffruticosa showed an Amax of $10.57 \pm 2.07 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, Aqe of $0.0039 \pm 0.0006 \mu\text{mol}^{-1} \text{quantum}$, LCP of $85.29 \pm 5.95 \mu\text{mol quantum m}^{-2} \text{s}^{-1}$, Vcmax of $27.77 \pm 3.98 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, and J of $100.56 \pm 12.81 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$. *P. alternifolium* showed comparatively high carboxylation capacity, with Vcmax of $29.60 \pm 0.78 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, alongside Amax of $11.18 \pm 0.53 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ and J of $104.65 \pm 1.90 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (Table 1). One-way ANOVA followed by Tukey's HSD (Section 2.5) indicated significant species effects on key photosynthetic parameters. *C. inophyllum* and *P. alternifolium* had higher Amax and J values, indicating higher photosynthetic efficiency and greater potential for carbon assimilation. *D. suffruticosa* and *B. arborescens* showed moderate performance but had comparatively lower values. These differences emphasise the differed in their dominant carbon-gain strategy and adaptability of these species in the coastal heath forest environment.

Table 1: Instantaneous leaf gas exchange performances (Photosynthetic capacity or light saturated photosynthesis, $A_{\max}$; apparent quantum yield, A_{qe} ; light compensation point, LCP; maximum carboxylation rate, $V_{c\max}$ and potential electron transport rate for Ribulose 1.5 biphosphate regeneration, J) of four native species (*B. arborescens*, *D. suffruticosa*, *C. inophyllum* and *P. alternifolium*) in the coastal heath forests.

Species	$A_{\max}$	A_{qe}	ACI component		
			LCP	$V_{c\max}$	J
<i>B. arborescens</i>	9.39 ± 1.79^b	0.0037 ± 0.0003^b	92.58 ± 9.57^{ab}	17.91 ± 2.51^b	70.40 ± 9.60^c
<i>C. inophyllum</i>	11.52 ± 1.73^a	0.0031 ± 0.0010^b	110.63 ± 12.13^a	28.87 ± 6.82^a	86.69 ± 9.81^b
<i>D. suffruticosa</i>	10.57 ± 2.07^{ab}	0.0039 ± 0.0006^b	85.29 ± 5.95^b	27.77 ± 3.98^a	100.56 ± 12.81^{ab}
<i>P. alternifolium</i>	11.18 ± 0.53^a	0.0054 ± 0.0004^a	98.55 ± 6.14^{ab}	29.60 ± 0.78^a	104.65 ± 1.90^a

The data were expressed as means $\pm$ SE ($n = 6$). Note: Paired t-test were conducted for differences in means between sites indicated by ns: non-significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

4. DISCUSSION

4.1 Photosynthetic response to temperature variations

Our analysis revealed the photosynthetic light response curves of four native species: *B. arborescens*, *D. suffruticosa*, *C. inophyllum*, and *P. alternifolium* at leaf temperatures of 25°C and 30°C. The results showed a higher photosynthetic rate at 30°C for all species, indicating a positive temperature response within this range. In particular, *B. arborescens* and *D. suffruticosa* exhibited a significant increase in photosynthetic rate with increasing light intensity up to about 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, after which the rate stagnated. *C. inophyllum* and *P. alternifolium* followed a similar trend but reached higher maximum photosynthetic rates, indicating greater maximum photosynthetic capacity ($A_{\max}$) under saturating light. Similar patterns have been reported for many tropical trees when warming is modest and remains below heat-damage thresholds (Carter et al., 2024).

Temperature can increase the photosynthetic rate by enhancing enzymatic activity and accelerating electron transport up to a species-specific optimum (T_{opt}). Many tropical species also exhibit thermal acclimation. T_{opt} can shift upward after exposure to warmer growth conditions (Wu et al., 2025). This helps explain why assimilation remained higher at 30°C in the chamber. Species differed in their maximum rates under saturating light. *C. inophyllum* and *P. alternifolium* achieved higher $A_{\max}$ than *B. arborescens* and *D. suffruticosa*. This suggests greater biochemical capacity under high irradiance. Kerangas forests are nutrient-poor and acidic. Species often adopt contrasting resource-use strategies under these conditions (Ikbal et al., 2023). *B. arborescens* and *D. suffruticosa* showed a clear increase in A with rising PPFD until around 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, after which the curve levelled off. This plateau is common when biochemical capacity becomes limited rather than light supply. It can also reflect limits to CO_2 delivery through stomata under the measurement settings.

4.2 Photosynthetic performance under varying CO_2 concentrations

The study also examined photosynthetic CO_2 response curves at internal CO_2 concentrations of 400 and 700 ppm. Among the four species studied, *B. arborescens* and *C. inophyllum* showed a marked increase in net CO_2 assimilation as CO_2 increased, indicating a robust capacity to capitalise on elevated CO_2 under the chamber conditions. This response is expected for C_3 plants, as higher CO_2 increases carboxylation and reduces photorespiration in the short term (Xu et al., 2025). In a nutrient-poor Kerangas ecosystem, this CO_2 responsiveness may provide an advantage by enabling greater carbon gain per unit time, supporting growth and maintenance costs when resources constrain productivity. Such an advantage could translate into improved performance during favourable periods (e.g. high light) and potentially better resilience under future conditions with higher atmospheric CO_2 , although field outcomes will still depend on nutrient and water availability.

Transpiration rates were generally higher at 700 ppm CO_2 , with *C. inophyllum* showing the most pronounced increase. This tends to increase intrinsic water-use efficiency when assimilation rises simultaneously (Mndela et al., 2022). Stomatal conductance, a measure of gas exchange, also increased significantly at higher CO_2 levels, particularly in *B. arborescens* and *C. inophyllum*. This indicates that, under the same chamber conditions (including vapour pressure deficit), higher stomatal conductance reflects greater stomatal opening, which increases the potential for CO_2 diffusion into the leaf. It can also occur when gas exchange is partly decoupled from transpiration by boundary-layer effects and vapour pressure conditions. Recent synthesis work shows that gs responses can vary by taxon and experimental setting (Gardner et al., 2023).

Water-use efficiency (WUE) varied between species, with *B. arborescens* and *C. inophyllum* showing higher WUE at 400 ppm CO_2 , which decreased slightly at 700 ppm CO_2 . In contrast, the WUE of *D. suffruticosa* and *P. alternifolium* remained relatively stable at both CO_2 concentrations.

Previous studies have shown that photosynthetic up-regulation under elevated CO₂ can occur, particularly when nutrient availability is high, with reported increases in parameters such as A, V_cmax, and J_{max} (Zhang & Dang, 2006). This supports the view that the effects of CO₂ on photosynthetic performance can be strongly influenced by resource conditions. The increased photosynthetic rates at elevated CO₂ concentrations indicate that these species could benefit from future increases in atmospheric CO₂. However, the corresponding increases in transpiration and stomatal conductance suggest that water availability may become a critical factor in determining the overall benefit of elevated CO₂ on photosynthesis.

4.3 Efficiency and performance of photosynthesis and respiration in native Coastal Heath forest species

C. inophyllum and *P. alternifolium* exhibited higher A_{max} and J values, indicating greater light-saturated photosynthetic capacity and higher electron transport potential under the measurement conditions compared with *D. suffruticosa* and *B. arborescens* (Table 1). Higher J reflects a stronger capacity for RuBP regeneration and electron transport, which can support higher assimilation when photosynthesis is limited by the light reactions rather than by photon supply (Ye et al., 2020; Buckley & Diaz-Espejo, 2015).

In contrast, *B. arborescens* and *D. suffruticosa* exhibited a more moderate capacity, consistent with a comparatively conservative carbon-gain strategy that may be favoured in nutrient-poor heath forest environments, where investment in high photosynthetic machinery can be constrained by soil fertility (Ibrahim et al., 2023). Apparent quantum yield (A_q/AQY) also differed among species, with *P. alternifolium* displaying the highest light-use efficiency at low irradiance (Table 1). As A_q represents the initial slope of the light-response curve, higher values indicate more efficient conversion of low photon flux into net CO₂ assimilation, which can be advantageous under patchy or fluctuating canopy light (Pignon et al., 2017).

Taken together, these trait differences suggest contrasting functional strategies among the Kerangas species. *C. inophyllum* and *P. alternifolium* appear better positioned to capitalise on high-light periods through higher capacity (A_{max}, J), while *P. alternifolium* also maintains efficient carbon gain at low light (higher A_q). In resource-limited coastal heath forests, these patterns likely reflect different ways of maximising assimilation opportunities under strong soil constraints, rather than implying that one species is uniformly “more efficient” across all physiological processes (Din et al., 2015).

4.4 Implications for forest management and conservation

The results of the study have important implications for forest management and conservation strategies in tropical heath forests. The differential responses of native species to temperature and CO₂ fluctuations suggest that species-specific management practices may be necessary to optimise forest productivity and resilience. For example, promoting species such as *C. inophyllum* and *P. alternifolium*, which have higher photosynthetic efficiency, could enhance ecosystem carbon uptake potential. However, carbon sequestration at the forest scale depends on additional factors (such as growth, biomass allocation, mortality, and nutrient limitation) that were not assessed in this study. Therefore, our findings should be interpreted as leaf-level physiological evidence that may inform future field-based evaluations of carbon storage.

5. CONCLUSION

Our results show clear species-level contrasts in leaf gas exchange performance under natural conditions, highlighting the contrasting adaptive strategies among species in response to the unique challenges of Kerangas forests. *B. arborescens* and *D. suffruticosa* exhibited significantly higher photosynthetic rates at higher temperatures, reflecting their adaptability to warmer climatic conditions. However, *B. arborescens* and *D. suffruticosa* consistently showed lower maximum photosynthetic capacity and carboxylation potential than *C. inophyllum* and *P. alternifolium*, which exhibited higher A_{max} and V_cmax, and therefore greater potential for carbon assimilation under the measurement conditions. Collectively, these findings highlight the importance of selecting species with robust adaptive traits for reforestation and conservation projects. By favouring native species that demonstrate resilience and efficiency, forest management practices can better support the stability and ecological function of Kerangas forests in the face of environmental stressors and climate change.

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