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Variations in the temperature response of photosynthesis among nine common tree species planted in Singapore

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Tree planting is regarded as one of the most cost-effective ways to mitigate climate change impacts. As part of the global tree planting movement, the tropical city-state of Singapore initiated a project to plant one million trees in 10 years. However, the environmental impacts (e.g., carbon sequestration, urban cooling) of this tree planting effort are challenging to assess, as historically, we lack an understanding of key plant traits (i.e., photosynthetic capacity, or V_{cmax}) for species in tropical Asia. Here, a survey was conducted to assess key photosynthetic traits of the nine most popular tree species planted in Singapore and their short-term temperature response. We found a threefold interspecific variation in their photosynthetic capacities (e.g., V_{cmax} ranges from 20 to 60 μmol m^{-2} s^{-1}) as well as a large discrepancy in their temperature response. Photosynthesis in some species (e.g., *Cyrtophyllum fragrans* and *Terminalia catappa*) is more sensitive to rising temperature than others (e.g., *Rhizophora apiculata* and *Barringtonia asiatica*), while a commonly used photosynthesis model consistently overestimates photosynthesis but underestimates many species' temperature sensitivities. Species with lower temperature sensitivity of photosynthesis are likely to have a stronger ability to adjust leaf temperature. This study provides critical information on the temperature response of photosynthesis of tree species in tropical Asia, which can be used to guide tree planting in Singapore and broadly in Southeast Asia.

KEYWORDS
carboxylation, climate change, CO_2 response curves, electron transport, leaf temperature, stomatal conductance, tree planting

1 Introduction

Tree planting is considered the most cost-effective way to mitigate the impacts of climate change (Griscom et al., 2017; Lewis et al., 2019), as trees remove CO_2 from the atmosphere through photosynthesis and store carbon in biomass. Many initiatives, such as the global One Billion Tree Project (Goymer, 2018) and the One Million Trees movement in Singapore (NParks, 2024), are utilizing the carbon uptake of trees to offset part of the anthropogenic CO_2 emissions. However, the photosynthetic capacities of tree species

are known to vary with rising temperatures (Berry and Bjorkman, 1980), consequently influencing the potential carbon uptake of trees under future climates. Previous studies have indicated that the impacts of temperature variability on photosynthesis contribute considerably to the uncertainty in the terrestrial carbon cycle (Booth et al., 2013; Mercado et al., 2018) and climate change prediction (Friedlingstein et al., 2006). Therefore, advancing the understanding of the temperature response of photosynthesis is essential to constrain the uncertainty in vegetation carbon uptake, and thus important for evaluating the effectiveness of tree planting efforts for mitigating climate change.

Previous studies have explored the temperature response of key photosynthetic traits (i.e., the maximum carboxylation rate, V_{cmax}, and the maximum electron transport rate, J_{max}) for species across the globe (Ainsworth and Long, 2005; Slot and Winter, 2017). While some were able to develop a unified function that describes the temperature response across species (Medlyn et al., 2002a,b), other studies found significant interspecific variation in the magnitude and shape of the temperature response (Way and Oren, 2010). Given that V_{cmax} and J_{max} determine plant photosynthetic capacity in the photosynthesis simulation modules in Dynamic Global Vegetation Models (DGVMs) or Earth System Models (ESMs), their dependence on temperature will further influence the temperature response of the carbon cycle over large scales (Mercado et al., 2018). However, these previous studies greatly lack observations in tropical Asia (Crous et al., 2022). Tropical Asia hosts some of the most carbon-dense (Saatchi et al., 2011) and diverse ecosystems (Slik et al., 2015) in the world. Currently, the temperature response of V_{cmax} and J_{max} for species in tropical Asia is extrapolated from either other parts of the tropics (e.g., French Guiana, Coste et al., 2005) or the high-temperature scenarios for extra-tropics species (Slot and Winter, 2017). Such extrapolations may introduce substantial uncertainty in model estimates of photosynthesis and carbon uptake for this region. A recent study demonstrated that Southeast Asia has the most considerable uncertainty in GPP across models (Bastos et al., 2020), further emphasizing the lack of observational constraints for the temperature response of photosynthesis in tropical Asia.

Therefore, in this study, we aimed to investigate the temperature response of photosynthesis for nine commonly planted tree species in Singapore, a city-state in tropical Asia. Our research objectives are to: (1) quantify the V_{cmax} and J_{max} across tree species in tropical Asia; (2) determine how V_{cmax} and J_{max} respond to temperature for the tree species, and (3) explore the physiological mechanism for the interspecific variation in the temperature response of photosynthesis for these species.

2 Materials and methods

2.1 Study site and tree species

We conducted our fieldwork from July 2023 to October 2023 across various locations in Singapore (1.283°N, 103.833°E). Singapore is located near the equator and under the influence of the intertropical convergence zone, with annual temperatures of 27–30°C, and a daily mean maximum of 30–31°C (Meteorological Service Singapore, 2024). These temperatures have increased by 0.25°C per decade from 1948 to 2023 (Marzin et al., 2015). The annual total precipitation is approximately 2,800 mm yr^{-1}, with an average relative humidity at about 80% (Acero et al., 2024).

We sampled the nine most common tree species planted in Singapore (Figure 1 and Supplementary Table S1): Rain Tree (*Samanea saman*), Tembusu (*Cyrtophyllum fragrans*), Sea Almond (*Terminalia catappa*), Pink Poui (*Tabebuia rosea*), Sea Hibiscus (*Hibiscus tiliaceus*), African Mahogany (*Khaya senegalensis*), Tall-stilt Mangrove (*Rhizophora apiculata*), Fish Poison (*Barringtonia asiatica*), and Cannonball Tree (*Couroupita guianensis*). We selected these tree species based on the records from Singapore's tree planting initiatives, such as the One Million Tree Movement and the Garden City Campaign. These tree species are native to either Singapore or Southeast Asia or have been introduced to Singapore for more than a century. Therefore, they are among the most widely planted and abundant urban trees in Singapore and represent a range of common tropical tree taxa used in urban greening programs. The specific sampling locations are as follows: *S. saman*, *C. fragrans*, *B. asiatica*, and *H. tiliaceus* at Bishan-Ang Mo Kio Park (1.3634 °N, 103.8436°E), *C. guianensis* at Singapore Botanic Gardens (1.3138°N, 103.8159°E), *T. rosea* and *K. senegalensis* at Jurong Lake Gardens (1.3359°N, 103.7262°E), *T. catappa* at East Coast Park (1.3008°N, 103.9122°E), *R. apiculata* at Pasir Ris Mangrove Boardwalk (1.3715°N, 103.9524°E). All the sampled trees grow in well-drained soils in open green spaces, except for *R. apiculata* in Pasir Ris Mangrove Boardwalk, which is a coastal swamp forest. All the locations share similar climatic conditions (Meteorological Service Singapore, 2024).

2.2 Gas exchange measurements and curve fitting

In this study, we sampled three leaves from a single mature tree per species and measured the photosynthesis of sunlit mature leaves from the outer canopy to ensure consistency in their light exposure. All these measurements were conducted on sunny days from approximately 08:00 to 16:00 during the drier season, minimizing the influence of rainfall seasonality on our results. We used the LICOR-6800 Portable Gas Exchange System (Li-Cor Inc., 2019) to measure the CO_2 response of leaf photosynthesis (A-C_i curve) under an air temperature gradient from 30 to 34°C. We selected the temperature range of 30–34°C as it aligns with Singapore's current mean temperature (~30°C) and the projected worst-case warming scenario of an increase of 4.4°C by 2,100 according to the IPCC AR6 report (Calvin et al., 2023). This range allowed us to explore interspecific variation in photosynthetic performance under future climates. For each species, three healthy and mature sunlit leaves per species were selected and acclimated to 30°C for at least 20 min, with five A-C_i curves recorded for each leaf at every 1°C interval from 30 to 34°C. Leaf temperature was simultaneously recorded by the thermocouple within the leaf chamber. We calculated the mean difference between leaf and air temperature. The CO_2 concentrations in the reference chamber for the A-C_i curves were set in a sequence of 400, 300, 200, 100, 50, 0, 400, 400, 600, 800, 1,000, 1,200, and 1,600 μmol mol^{-1}. We set a saturating light intensity at 1,600 μmol m^{-2} s^{-1} and kept the relative humidity in the leaf chamber greater than 30% and less than 80%. For each CO_2 concentration, measurements were recorded only after steady-state



FIGURE 1
Images of the sampled tree species: **(A)** *Samanea saman*, **(B)** *Cyrtophyllum fragrans*, **(C)** *Terminalia catappa*, **(D)** *Tabebuia rosea*, **(E)** *Hibiscus tiliaceus*, **(F)** *Khaya senegalensis*, **(G)** *Rhizophora apiculata*, **(H)** *Barringtonia asiatica*, **(I)** *Couroupita guianensis*.

conditions were reached, as determined using the instrument's default thresholds for the slope and standard deviation of CO_2 and water vapor within the chamber. The initial measurement at 400 μmol mol^{-1} in each A–C_i curve was used to stabilize the leaf flux and to provide a visual check of the range of net photosynthetic rate (A_n). Only A_n and stomatal conductance (G_s) measured at the latter two steps of 400 μmol mol^{-1} were used for analysis and visualization. We then fitted the A-C_i curves using the "*fitaci*" function from the R package "*plantecophys*" (Duursma, 2015) with the bilinear fitting method and extracted V_{cmax} and J_{max}. This package employs the Farquhar, von Caemmerer, and Berry (FvCB) photosynthesis model (Farquhar et al., 1980).

2.3 Examination of additional plant functional traits using data from the TRY database and statistical analysis

To provide an ecological explanation for the interspecific variations in photosynthetic capacity, we examined the life strategies of tree species with the functional spectrum (fast growth vs. long longevity) using additional trait observations from the TRY database (Kattge et al., 2020). We accessed four plant functional traits archived in the TRY database, namely leaf nitrogen per dry mass (N_{mass}), specific leaf area (SLA), stem density (SD), and seed dry mass (SDM), which are key elements in the plant function spectrum (Díaz et al., 2016). A plant is considered fast-growing if it exhibits high N_{mass} and SLA but low SD and SDM, whereas a slow-growing plant shows the opposite traits. There is no record of these traits for *S. saman* and *C. fragrans* from the TRY database.

After obtaining the data, we first obtained the standardized values of each trait and excluded the values from seedlings or potentially with errors. We then applied a Kruskal-Wallis test and multiple comparisons of the means among species using a pairwise Wilcoxon test with *p*-value adjustment using the Benjamini-Hochberg method. These non-parametric tests were used because the data did not fully meet the assumptions of normality and homogeneity of variance.

2.4 Estimation of leaf photosynthesis along a warming gradient

To compare the temperature response of photosynthesis of these common species against the temperature response prescribed in Earth System Models, we estimated the temperature response of photosynthesis using the model from Medlyn et al. (2002a) and Kattge and Knorr (2007), which has been adopted in Earth System Models (e.g., the CABLE model, Haverd et al., 2018) and the CLM model, Smith et al. (2017). We first employed the global map of V_{cmax} at 25°C (Luo et al., 2021, spatial resolution: 0.5° × 0.5°). We then extracted Singapore's V_{cmax} at 25°C using its longitude and latitude. After that, we estimated the V_{cmax} from 30 to 34°C using a peaked Equation 1 as follows:

$$V_{\mathrm{cmax}}(T_{\mathrm{k}}) = V_{\mathrm{cmax},25}\exp\left[\frac{E_{\mathrm{a}}(T_{\mathrm{k}}-298)}{298RT_{\mathrm{k}}}\right]\frac{1+\exp\left[\frac{298\Delta S-H_{\mathrm{d}}}{298R}\right]}{1+\exp\left[\frac{T_{\mathrm{k}}\Delta S-H_{\mathrm{d}}}{T_{\mathrm{k}}R}\right]} \quad (1)$$

in which $V_{cmax}(T_k)$ denotes V_{cmax} at a certain temperature (T_k, in K), $V_{cmax,25}$ is the value of V_{cmax} or J_{max} at 25°C, E_a and H_d represent the exponential rate of the increase and decrease of the function, R is the universal gas constant (8.314 J mol^{-1} K^{-1}), and ΔS is an entropy factor (650 J mol^{-1} K^{-1}). Since none of the sampled species have any observations of E_a and H_d,

we adopted their values from Medlyn et al. (2002b), 71,500 and 20,000 J mol^{-1} for E_a and H_d, respectively and assumed their interspecies variation is negligible. We then estimated J_{max} using its empirical relationship to V_{cmax} under varying temperatures (T, in °C) according to Equation 2 from Leuning (2002):

$$J_{max} = V_{cmax}(0.0017T^2 - 0.1378T + 4.384) \quad (2)$$

We then input the estimated values of V_{cmax} and J_{max} into the FvCB model and estimated A_n using the "*Photosyn*" function from the "*plantecophy*" package. Here we assumed that atmospheric CO_2 concentration is 400 μmol mol^{-1}, vapor pressure deficit is 0.75 kPa, and light intensity is 1,200 μmol m^{-2} s^{-1}.

3 Results

3.1 Species-specific temperature response of V_{cmax} and J_{max}

We found that V_{cmax} and J_{max} across species vary substantially in magnitude as well as in their temperature response (Figure 2 and Table 1). Among the nine species, *H. tiliaceus* had the largest V_{cmax} (56 μmol m^{-2} s^{-1}), followed by *S. saman*, *T. catappa*, and *K. senegalensis* (from 40 to 50 μmol m^{-2} s^{-1}), while the remaining species (*C. guianensis*, *B. asiatica*, *T. rosea*, *R. apiculata*, and *C. fragrans*) had lower V_{cmax} of approximately 20–30 μmol m^{-2} s^{-1}. *T. catappa* also had the largest J_{max} of 110 μmol m^{-2} s^{-1}, followed by *S. saman* and *H. tiliaceus* (100–120 μmol m^{-2} s^{-1}), while J_{max} of the other species varied from 40 to 80 μmol m^{-2} s^{-1}.

Furthermore, we generally observed a decline in V_{cmax} with rising temperature (six out of the nine species). The effect of temperature and species was statistically significant (both $p < 0.001$) (Table 1). The most significant declines were observed for *K. senegalensis* and *C. fragrans* (nearly 50%) (Figures 2A,I) over the 5°C gradient from 30 to 34 °C. *S. saman* and *T. catappa* demonstrate an optimal temperature of around 31–32°C. In contrast, we found that V_{cmax} of *C. guianensis*, *B. asiatica*, *H. tiliaceus*, and *R. apiculata* are not sensitive to temperature.

We observed slightly different patterns of J_{max} change with rising temperature. Overall, J_{max} differed significantly among species ($p < 0.001$), whereas the effect of temperature was not statistically significant (Table 1). Five out of the nine species demonstrated an increase of J_{max} with certain temperature ranges, with the most significant increase observed for *R. apiculata* and *T. catappa* (20–30% from 30 to 32°C). *C. fragrans* is the only species showing a decrease of J_{max} with rising temperature. *K. senegalensis*, *S. saman*, and *T. catappa* demonstrated an optimal temperature of around 31–32°C. The J_{max} of *C. guianensis*, *T. rosea*, and *H. tiliaceus* was not sensitive to temperature (Figures 2B,D,G).

3.2 Differing temperature responses of net photosynthetic rate

We then compared the observed net photosynthetic rate (A_n) of nine species over a 5°C temperature gradient with those estimated using the FvCB model. *S. saman* and *H. tiliaceus* showed generally higher A_n than that of *T. catappa*, *C. fragrans*, *T. rosea*, and *K. senegalensis*, while *C. guianensis*, *R. apiculata*, and *B. asiatica* showed the lowest A_n (Figure 3). Despite the differing levels of A_n across species, we also found that the patterns of temperature responses of A_n considerably varied across species. *S. saman*, *T. catappa*, and *C. fragrans* exhibited a maximum A_n under 31–32°C (Figure 3). A_n of *T. rosea* and *K. senegalensis* declined with temperature, while A_n of *H. tiliaceus*, *C. guianensis*, *R. apiculata*, and *B. asiatica* did not show clear changes with temperature. Furthermore, we estimated the theoretical A_n under Singapore's climate using the local V_{cmax} at 25°C provided by Luo et al. (2021) and the models provided by Medlyn et al. (2002a) and Leuning (2002). We found that the average A_n observed at the local species level was significantly lower ($p < 0.05$) (Figure 3 and Table 2) than the estimated A_n (Figure 3) (black triangles) from the global datasets and models, though we noted that some measurements of A_n for *S. saman* and *H. tiliaceus* could be above the estimated A_n due to these species' high average A_n and large inter-leaf variations in A_n.

3.3 Leaf thermal regulation coordinates with the temperature sensitivity of V_{cmax} and J_{max}

We further explored the interspecific variations in the temperature response of V_{cmax} and J_{max} and examined their relationship with leaf thermal regulation. The temperature response of V_{cmax} and J_{max} was indicated by the coefficient of variation (CV) for V_{cmax} and J_{max} under different temperatures—a greater CV indicates greater temperature sensitivity. We found the CV of V_{cmax} varies substantially across species, from less than 10% (e.g., *H. tiliaceus*, *S. saman*, and *R. apiculata*) to above 30% (e.g., *C. fragrans*) (Figure 4). The CV of V_{cmax} was generally greater than that of J_{max} except for *C. fragrans* (Figure 4). We then calculated the difference of leaf temperature to air temperature (T_{diff}), as an indicator of leaf thermal regulation. Since in the tropical daytime, leaf temperature is often higher than the air temperature, a smaller T_{diff} indicates greater capacity for leaf thermal regulation. We found that all species show a positive T_{diff}, and the species with a small T_{diff} tend to exhibit a low CV of V_{cmax} and J_{max} (e.g., *H. tiliaceus*) and *vice versa* (e.g., *C. fragrans*). The correlations between CV and T_{diff} have Pearson's correlation coefficient (r) of 0.48 ($p = 0.20$) for V_{cmax} and 0.58 ($p = 0.10$) for J_{max}, respectively.

3.4 Life strategy of tree species suggested by plant functional traits

We also compared four plant functional traits (N_{mass}, SLA, SD, and SDM) of the studied tree species (Supplementary Figure S1), leveraging records from the TRY database. We found that *C. guianensis* had significantly higher SLA than *H. tiliaceus* and *R. apiculata* (Supplementary Figure S1A) ($p < 0.05$). Although differences in N_{mass} were not statistically significant, *C. guianensis* showed a ~60% higher mean value compared to *R. apiculata* and *T. catappa* (Supplementary Figure S1B). *R. apiculata* showed a significantly higher SD than any other species

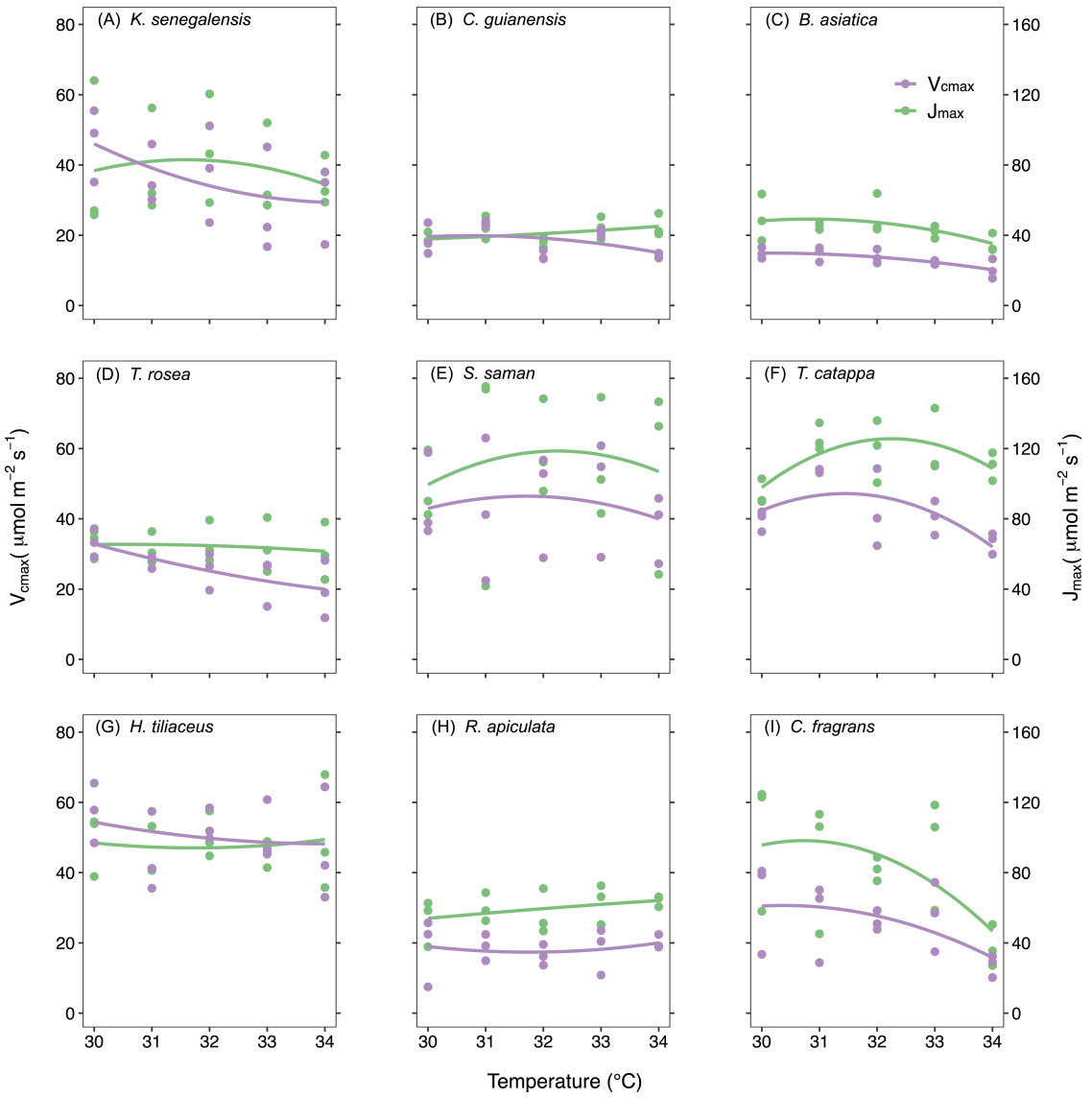


FIGURE 2
The temperature response of maximum carboxylation rate (V_{cmax}) and maximum electron transport rate (J_{max}) of the nine common tree species: **(A)** *S. saman*, **(B)** *C. fragrans*, **(C)** *T. catappa*, **(D)** *T. rosea*, **(E)** *H. tiliaceus*, **(F)** *K. senegalensis*, **(G)** *R. apiculata*, **(H)** *B. asiatica*, **(I)** *C. guianensis*. We show the empirical quadratic temperature responses of V_{cmax} (purple) and J_{max} (green) fitted using observations under 30–34°C.

(Supplementary Figure S1C), which may be partly attributable to its growth in poorly drained soil conditions, while *T. catappa* showed the highest SDM (Supplementary Figure S1D).

4 Discussion

In this study, we found substantial variations (i.e., greater than threefold) in photosynthetic capacity (V_{cmax} and J_{max}) among nine common tree species in the tropical state of Singapore. There was a large discrepancy in their temperature response, where we found the photosynthesis of *C. guianensis*, *B. asiatica*, *H. tiliaceus*, and *R. apiculata* is relatively insensitive to rising temperature. Species that better adjust leaf temperature according to air temperature (with a small T_{diff}) tend to exhibit low temperature response of their photosynthetic capacity, suggesting that the capacity of leaf thermal regulation contributes to photosynthetic thermal variability. These results provide valuable information on the photosynthesis dynamics of understudied tree species in tropical Southeast Asia.

4.1 Interspecific variation in photosynthetic capacity

In this study, we found considerable variations in the temperature response of photosynthesis among the common tree species. We could not explain these variations by the origin of the species, leaf lifespan, or tree height (Supplementary Table S1). For instance, *S. saman* and *C. guianensis* share similar leaf

TABLE 1 Summary of a two-way analysis of variance (ANOVA) on the responses of V_{cmax}, J_{max}, and A_n to a temperature gradient across species.

Predictor	df	Sum of squares	Mean square	*F*-value	*p*-value
V_{cmax}					
Temperature	1	870.29	870.29	13.49	< 0.001
Species	9	25270.11	2807.79	43.52	< 0.001
Temperature: Species	9	759.44	84.38	1.31	0.24
Residuals	130	8387.35	64.52		
J_{max}					
Temperature	1	157.82	157.82	0.39	0.53
Species	9	106875.19	11875.02	29.14	< 0.001
Temperature: Species	9	5490.61	610.07	1.50	0.16
Residuals	130	52976.34	407.51		
A_n					
Temperature	1	94.3	94.3	12.1	< 0.001
Species	9	8322	925	118	< 0.001
Temperature:Species	9	91.7	10.2	1.3	0.24
Residuals	130	1993	7.82		

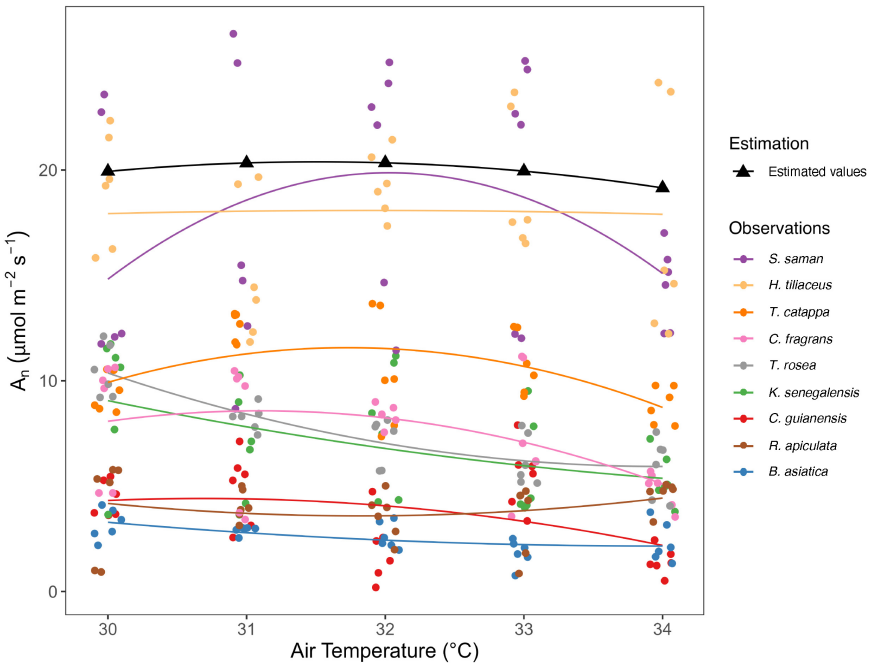


FIGURE 3
The responses in net photosynthetic rate (A_n) to a range of air temperatures (30–34°C). Each dot indicates one observation of A_n, and the palette shows observations from different species. The black dots denote the estimated theoretical A_n under the climate of Singapore (see Methods). Solid quadratic curves were fitted using observations under 30–34°C.

lifespan and tree height; however, they differed considerably in their photosynthetic rates and CV of V_{cmax}. Moreover, studies have found that coexisting species under similar climate exhibit significant variations in photosynthetic traits (e.g., A_{max} and leaf mass per area), suggesting distinctly different functional modulations among species irrespective of biomes or climate (Wright et al., 2004; Wang et al., 2022). Therefore, our study emphasizes that enhanced observations of photosynthetic traits of more representative species are necessary for constraining the uncertainty in carbon modeling of tropical Asia.

In this study, we could not determine the exact age of the trees that we sampled. However, we noticed that tree species mostly planted in the Garden City Initiative (launched in 1967), such as *S. saman*, *H. tiliaceus*, *T. catappa*, and *C. fragrans*, had higher A_n than those planted in the more recent One Million Tree Movement (launched in 2020), such as *B. asiatica* and *R. apiculata*. Furthermore, high SD and SDM but low SLA and N_{mass} of

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TABLE 2 Summary of the 95% confidence interval of the responses of A_n to a temperature gradient across species and the modelled temperature response.

Species/model	Air temperature (°C)				
	30	31	32	33	34
K. senegalensis	[6.056, 12.725]	[4.099, 9.546]	[4.584, 10.938]	[3.152, 8.181]	[4.086, 6.635]
C. guianensis	[3.514, 5.277]	[3.101, 6.736]	[0.363, 3.716]	[3.857, 7.156]	[0.761, 2.105]
B. asiatica	[2.430, 3.949]	[2.718, 3.105]	[1.981, 3.291]	[1.189, 2.481]	[1.328, 3.306]
T. rosea	[9.138, 11.737]	[7.626, 8.848]	[5.986, 8.334]	[4.955, 7.464]	[4.424, 7.387]
S. saman	[9.205, 21.767]	[9.741, 24.606]	[14.173, 25.977]	[13.442, 26.224]	[12.483, 16.509]
T. catappa	[8.479, 10.396]	[11.905, 13.320]	[7.593, 13.265]	[9.290, 12.340]	[7.940, 9.763]
H. tiliaceus	[16.337, 21.928]	[11.630, 18.843]	[17.729, 20.906]	[15.779, 22.612]	[11.442, 22.781]
R. apiculata	[1.516, 6.473]	[3.331, 4.830]	[2.475, 4.690]	[1.702, 5.255]	[3.927, 5.301]
C. fragrans	[5.341, 11.393]	[4.384, 11.503]	[7.846, 8.889]	[4.369, 10.701]	[3.965, 5.740]
Model	19.917	20.340	20.306	19.950	19.122

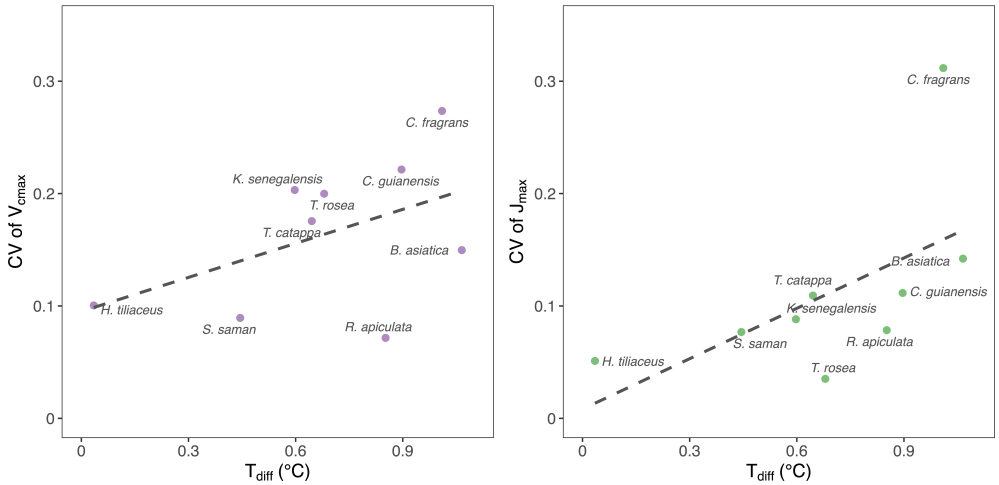


FIGURE 4
The coordination between the thermal variability of photosynthetic capacity [coefficient of variations, or CV of V_{cmax} and J_{max}] and the difference between leaf temperature and air temperature (T_{diff}). CV was calculated using values of V_{cmax} and J_{max} under five air temperatures (30–34°C). T_{diff} was calculated as T_{leaf}-T_{air}. The dashed line indicates the correlation between CV and T_{diff}.

R. apiculata (Supplementary Figure S1) suggest this species is slow-growing but with a long lifespan. This is opposite to the pattern of high N_{mass} but low SD of *H. tiliaceus* and *C. guianensis*. This suggests that the tree species planted in the Garden City Initiative were likely to be fast-growing species, and those in the One Million Tree Movement were likely to be selected for their ecological importance and not necessarily fast-growing. This analysis also indicates that plant photosynthetic performance and associated functional traits provide useful ecological guidance on the future tree-planting movements in Singapore. In addition, we note that the tree age may play a role in the interspecific variations in photosynthetic capacity. There is an ongoing debate on the influences of tree age on leaf photosynthesis (Bond, 2000; Steppe et al., 2011), with equivalent amounts of reports on increased, decreased, or unchanged photosynthetic capacity along with tree ages. It is likely that the age effect is species-dependent and could contribute to the interspecific variation in photosynthetic capacity we observed, though we do not have the stand age data to analyze the impact.

Leaf-level knowledge on the empirical temperature response of A_n or V_{cmax} has been extensively incorporated in models simulating ecosystem carbon cycles. Our result suggests that a commonly used process-based photosynthesis model overestimated A_n compared to the observed A_n for most species, and underestimated the temperature variability of A_n from some species (i.e., *S. saman* and *T. catappa*) in our sites (Figure 3). This could be attributed to the fact that values of the parameters for temperature response were mostly extrapolated from temperate or boreal plant species (e.g., *Nicotiana tabacum* and *Abies alba*), thus not reflecting the temperature sensitivity of photosynthesis for tropical tree species. Moreover, temperature regulates stomatal conductance, and reductions in stomatal conductance directly limit photosynthesis by restricting CO_2 diffusion into the leaf. In addition, stomatal closure can indirectly affect photosynthesis by altering leaf energy balance and reducing transpirational cooling, thereby increasing leaf temperature and the risk of photoinhibition (Slot and Winter, 2017). Such indirect effects—particularly heat-induced photoinhibition associated with

reduced stomatal conductance—are not explicitly represented in the FvCB biochemical model, which does not account for photoinhibition processes (Bambach et al., 2020). Therefore, a better understanding of linking the role of physiological acclimation to stomatal dynamics is needed for improved predictions of carbon assimilation under a warming climate.

4.2 Interspecific variation in temperature response of photosynthesis and its coordination with leaf thermal adjustment

In this study, the correlation between the CV of photosynthetic capacity (V_{cmax} and J_{max}) and the T_{diff} potentially indicates the role of leaf thermal regulation capacity in the interspecific variation of leaf photosynthetic temperature response. The large spread in CV and T_{diff} suggests divergent strategies of plants to coordinate thermal regulation and photosynthetic variability. In particular, species with a smaller T_{diff} (i.e., a stronger capacity for transpiration and leaf cooling) tend to have low CV of V_{cmax} and J_{max}. The capacity to maintain a small CV is related to the plasticity of stomatal conductance (G_s) under different temperatures, as *H. tiliaceus* had a much larger plasticity of G_s than *C. fragrans* and *C. guianensis* (Figure 5). Although the inter- or intra-species variations of photosynthetic thermal response have been explored in previous studies (Zaka et al., 2016; Vico et al., 2019), our work related these variations to the stomatal behavior and the capacity of the leaf to regulate its temperature.

4.3 Implication for guiding tree planting initiatives

Our study provides the critical information to select suitable tree species for tree-planting initiatives aimed at climate change mitigation. This is especially relevant to Singapore due to its land scarcity and profound urban heat island effect (Grace Wong, 2004; Chow and Roth, 2006). Therefore, selecting tree species that have maximized and sustained photosynthesis under higher temperatures will help ensure the effectiveness of tree planting initiatives in the future. We found that *H. tiliaceus* and *S. saman* tend to have high A_n, but only *H. tiliaceus* has low thermal variability under future rising temperatures. *T. rosea* and *K. senegalensis* show clear declines in A_n when the temperature rises. *T. catappa* and *C. fragrans*, along with *S. saman*, have an optimal temperature of photosynthesis around 32°C, beyond which their photosynthesis would decline. *C. guianensis*, *B. asiatica*, and *R. apiculata* show a high degree of temperature resistance in their photosynthesis, though their photosynthesis rate is lower than other major tree species. Overall, *H. tiliaceus* seems to be the only species that has great and sustained carbon sequestration potential under future climate compared to other species. This could be explained by its high N_{mass} but low SD and SDM as an acquisitive species. A recent study (Augusto et al., 2025) found a widespread advantage in the growth of acquisitive species over conservative species in tropical regions with moist and mild climates. Therefore, we suspect these acquisitive species will continue their potential advantage in achieving photosynthetic potentials under future warmer climates in Singapore and Southeast Asia.

4.4 Limitations of the study

While we have revealed a significant variation in the temperature responses of photosynthesis across species in Singapore, we acknowledge that there are a few points for improvement in future studies to upscale the observations. First, in this study, we collected the samples for each species from one tree, while there is also a possibility for the inter-individual variation within a species. Second, although the study area in Singapore is small and climatic variation is expected to be limited, we did not have the resources to quantify the effects of soil conditions on which the trees are planted. Nevertheless, soil conditions are unlikely to vary greatly across the island. Despite these points, we would like to emphasize that the sampled species are commonly planted in Singapore and Southeast Asia, yet they have few observations in global databases or the literature. Though the current field observations are not comprehensive, our observations and analysis are a key step to fill the knowledge gap that limits predictions of photosynthesis in Southeast Asia under future climate and their potential to mitigate climate change impacts.

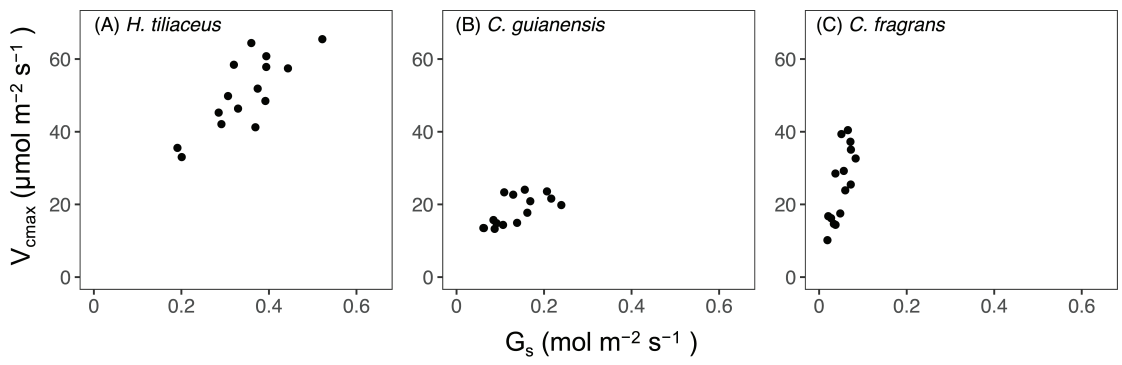


FIGURE 5
The correlation between V_{cmax} and stomatal conductance (G_s) of species differing in the plasticity of G_s: **(A)** *H. tiliaceus*, **(B)** *C. guianensis*, and **(C)** *C. fragrans*.

We would also like to acknowledge that our reported temperature responses are short-term responses. Over the long term, photosynthetic acclimation to temperature (Medlyn et al., 2002b; Kattge and Knorr, 2007) may impact the interspecific variation that we observed. Nevertheless, our result provides a much-needed set of observations on the photosynthesis of common species in tropical Asia and will guide the tree planting efforts in Singapore and Southeast Asia.

Finally, tree selection for urban forestry and climate adaptation requires comprehensive considerations, not only the physiological properties related to photosynthesis, but also the ecosystem functions and services that the trees can provide (Bodnaruk et al., 2017). In addition, carbon sequestration is more directly linked to tree growth and biomass accumulation than to photosynthetic capacity alone, and the relationship between photosynthesis and growth is not always straightforward. Trees with higher photosynthesis under warming do not necessarily provide greater carbon sequestration or other ecosystem services, such as biodiversity conservation and aesthetic values, highlighting potential trade-offs in tree planting strategies. Therefore, further studies that integrate physiological traits, growth performance, and multiple ecosystem services will help to better inform the management of urban forest systems.

5 Conclusion

In summary, our study revealed substantial variations in the temperature responses of photosynthesis among nine tree species commonly planted in Singapore's tree planting initiatives. Our study underscores the need for a strategic approach to tree selection in these initiatives, considering the temperature response of photosynthesis, to optimize the carbon sequestration potential of urban forests and mitigate climate change. Our study also demonstrates that interspecific difference in the temperature response of photosynthesis is likely linked to the capacity of leaf thermal regulation of each species. This finding deepens our understanding of the physiological mechanisms underlying photosynthetic temperature response and facilitates the identification of tree species that are resilient to future climate.

Data availability statement

The data collected and presented in the study are openly available at https://zenodo.org/records/19327962.

Author contributions

LT: Writing – original draft, Formal analysis, Methodology, Investigation, Data curation, Visualization, Writing – review & editing. LY: Writing – original draft, Visualization, Formal analysis, Methodology, Writing – review & editing, Investigation. XL: Methodology, Conceptualization, Resources, Funding acquisition, Writing – review & editing, Project administration, Supervision.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The author(s) declared that generative AI was not used in the creation of this manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2026.1738900/full#supplementary-material

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