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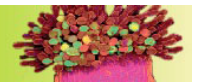


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## RESEARCH ARTICLE

# Correlations between photosynthetic heat tolerance and leaf anatomy and climatic niche in Asian mangrove trees

X. Li<sup>1</sup> , Y. Wen<sup>2</sup> , X. Chen<sup>1</sup>, Y. Qie<sup>1</sup> , K.-F. Cao<sup>1</sup>  & A. K. S. Wee<sup>1,3</sup> 

<sup>1</sup> Guangxi Key Laboratory of Forest Ecology and Conservation, College of Forestry, Guangxi University, Nanning, Guangxi, China

<sup>2</sup> Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China

<sup>3</sup> School of Environmental and Geographical Sciences, University of Nottingham Malaysia, Jalan Broga, Semenyih, Malaysia

## Keywords

heat stress; heat tolerance; mangroves; photosynthesis;  $T_{50}$ .

## Correspondence

A. K. S. Wee, School of Environmental and Geographical Sciences, University of Nottingham Malaysia, Jalan Broga, Semenyih, 43500 Malaysia.

E-mail: kimshan.wee@nottingham.edu.my

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## ABSTRACT

- Photosynthetic heat tolerance ( $P_{HT}$ ) is a key predictor of plant response to climate change. Mangroves are an ecologically and economically important coastal plant community comprised of trees growing at their physiological limits. Mangroves are currently impacted by global warming, yet the  $P_{HT}$  of mangrove trees is poorly understood.
- In this study, we provide the first assessment of  $P_{HT}$  in 13 Asian mangrove species, based on the critical temperature that causes the initial damage ( $T_{Crib}$ ) and the temperature that causes 50% damage ( $T_{50}$ ) to photosystem II. We tested the hypotheses that the  $P_{HT}$  in mangroves is: (i) correlated with climatic niche and leaf traits, and (ii) higher than in plants from other tropical ecosystems.
- Our results demonstrated correlations between  $P_{HT}$  and multiple key climate variables, the palisade to spongy mesophyll ratio and the leaf area. The two most heat-sensitive species were *Kandelia obovata* and *Avicennia marina*. Our study also revealed that mangrove trees show high heat tolerance compared to plants from other tropical ecosystems.
- The high  $P_{HT}$  of mangroves thus demonstrated a conservative evolutionary strategy in heat tolerance, and highlights the need for integrative and comparative studies on thermoregulatory traits and climatic niche in order to understand the physiological response of mangrove trees to climate change-driven heatwaves and rising global temperatures.

## INTRODUCTION

Climate change-driven heatwaves and rising global temperatures have led to large-scale metabolic disorders and reduced biomass accumulation in plant communities worldwide (Ameye *et al.* 2012; Teskey *et al.* 2015). Photosynthetic heat tolerance ( $P_{HT}$ ), which assesses damage to photosystem II (PSII) from exposure to heat stress, is a useful indicator of plant physiological responses to climate change (Feeley *et al.* 2020a; Geange *et al.* 2021). Heat tolerance is commonly defined as the threshold temperature beyond which basic plant functions cannot be maintained, with symptoms of irreversible damage to PSII and cell death (Porch & Hall 2013). Quantification of  $P_{HT}$  typically uses two diagnostics of the loss of PSII function (Slot *et al.* 2019):  $T_{Crib}$ , the critical temperature that causes the initial damage; and  $T_{50}$ , the temperature at which  $F_v/F_m$  is reduced by 50%. These two diagnostics provide common ground for comparison of plant lineages and communities to explore the upper thermal limit of physiological mechanisms.

Recent studies have shown that heat tolerance decreases with increased elevation across forest stands, and that warm-climate plants generally exhibit higher heat tolerance than those from cooler climates (Zhu *et al.* 2018; Feeley *et al.* 2020a; Slot *et al.* 2021). However,  $P_{HT}$  variation is higher within as

compared to across plant communities (O'Sullivan *et al.* 2017; Feeley *et al.* 2020a). When diverse plant lineages grown in a common garden were examined, both phylogeny and climate niche were weak predictors of  $P_{HT}$ , pointing to the potential role of microenvironment, thermoregulatory traits and leaf temperatures in determining heat tolerance (Perez & Feeley 2021). In general, wider leaves and a larger leaf area are connected to higher leaf temperatures (Tserej & Feeley 2021) due to reduced transpirational cooling (Fauset *et al.* 2018), which, in turn, scale with heat tolerance (Perez & Feeley 2020). Also, both leaf mass per unit area and leaf thickness are correlated with leaf water content and, hence, predict the maximum leaf temperature (Tserej & Feeley 2021). Leaf traits not only determine the temperature tolerance of plants, but also the growth strategies. For example, tropical trees have a lower palisade to spongy mesophyll thickness ratio than their temperate counterparts, which reduces photosynthetic capacity in exchange for a longer leaf lifespan (He *et al.* 2018). As diverse thermoregulatory strategies can be found across plant lineages and communities, empirical data from poorly studied plant groups is crucial to reconcile the relative roles of macroclimate, microhabitat and thermoregulatory traits in heat tolerance.

Data for  $P_{HT}$  of mangrove trees are surprisingly sparse, despite them being a key coastal plant community and prime example of trees growing in harsh environments (*e.g.*

hypersaline, frequent inundation, anaerobic, high heat, high light; Tomlinson 2016). Mangroves comprise diverse plant lineages that convergently adapt to (sub)tropical intertidal environments, hence, could offer substantial insights on the predictors of heat tolerance. Present research on the responses of mangroves to temperature extremes mainly focuses on cold-tolerant species and their climate-driven poleward expansion (Chen *et al.* 2020; Ximenes *et al.* 2021). However, growing evidence suggests that mangroves are increasingly exposed to heat stress that is aggravated by extreme weather events and variations in sea level (Duke *et al.* 2017; Lovelock *et al.* 2017). Notably, the 2016 large-scale heat- and drought-induced mangrove tree mortality in northern Australia demonstrated the devastating effects of an intense El Niño Southern Oscillation on mangroves (Duke *et al.* 2017; Lovelock *et al.* 2017). A global dataset showed that rising temperatures would cause minimal increases in abundance of thermophilic mangrove species, possibly due to niche truncation and extreme environmental conditions that prevent new species establishment (Feeley *et al.* 2020b). Furthermore, a broad comparison of various forest types showed that the red mangrove (*Rhizophora mangle*) in the Neotropics had the highest  $T_{50}$  among 147 tree species (Slot *et al.* 2021). However, heat tolerance data are absent for Asian mangrove species; hence, there is an urgent need to assess the thermal adaptation and vulnerability of mangrove lineages at their centre of diversity.

In this study, we provide the first assessment of  $P_{HT}$  in 13 Asian mangrove species and test the hypotheses that  $P_{HT}$  of mangroves is: (i) correlated with climate niche and leaf traits, and (ii) higher than in plants from other ecosystems. Specifically, we quantified  $P_{HT}$  as heat-induced changes in  $F_v/F_m$  and computed  $T_{50}$  and  $T_{Crit}$ . We then used this novel dataset to test correlations between  $P_{HT}$ , climatic variables and leaf traits to examine the relative effects of macroclimate and thermoregulatory traits on plant thermal limits. To further understand how the thermal limits differ across environments, we compared thermotolerance of Asian mangrove species with published data for trees from other tropical ecosystems.

## MATERIAL AND METHODS

### Study species and sites

The 13 commonly occurring Asian mangrove tree species examined in this study range from predominantly tropical (*e.g.* *Rhizophora apiculata*) to predominantly subtropical (*e.g.* *Kandelia obovata*) (Table 1). All are true mangroves (*i.e.* complete fidelity to the mangrove habitat) and major components of the mangrove community (Tomlinson 2016). Sampling was conducted in two adjacent mangrove nature reserves in Hainan Province in southern China: Dongzhaigang National Nature Reserve (19.9556°N, 110.5794°E) and Qinglan Port Provincial Mangrove Nature Reserve (19.6292°N, 110.8361°E).

### Photosynthetic heat tolerance ( $P_{HT}$ )

A total of five mature, healthy, naturally occurring individuals of similar age per species were sampled in May–June 2021. Healthy, mature, sun-facing leaves were collected before 08:00 h on a clear day, inserted in water and brought to a nearby laboratory within 1 h for the heat treatment.

**Table 1.** The 13 mangrove tree species used in the present study.

species	family	clade
<i>Aegiceras corniculatum</i> (L.) Blanco	Mysinaceae	Asterids
<i>Avicennia marina</i> (Forsk.) Vierh	Verbenaceae	Asterids
<i>Scyphiphora hydrophyllacea</i> C.F.Gaertn	Rubiaceae	Asterids
<i>Bruguiera gymnorhiza</i> (L.) Lamk	Rhizophoraceae	Fabids
<i>Bruguiera sexangula</i> (Lour.) Poir	Rhizophoraceae	Fabids
<i>Ceriops tagal</i> (Perr.) C. B. Rob	Rhizophoraceae	Fabids
<i>Kandelia obovata</i> (S., L.) Yong	Rhizophoraceae	Fabids
<i>Rhizophora apiculata</i> Blume	Rhizophoraceae	Fabids
<i>Rhizophora stylosa</i> Griff	Rhizophoraceae	Fabids
<i>Lumnitzera littorea</i> (Jack) Voigt	Combretaceae	Malvids
<i>Xylocarpus granatum</i> J.Koenig	Meliaceae	Malvids
<i>Sonneratia alba</i> Sm	Lythraceae	Malvids
<i>Sonneratia caseolaris</i> (L.) Engl	Lythraceae	Malvids

Experimental protocol for  $P_{HT}$  was adapted from Krause *et al.* (2010, 2015) and is described in the Supplementary material. The  $F_v/F_m$  was measured using a PAM-2500 chlorophyll fluorometer (Walz, Effeltrich, Germany). The two diagnostic parameters,  $T_{50}$  and  $T_{Crit}$ , were determined using the 'nls' function in the 'stats' package of the R statistics platform (R Core Team 2021) using the formula and R script of Perez *et al.* (2021).  $T_{Crit}$  and  $T_{50}$  were defined as the temperatures having 15% and 50% reduction from the initial  $F_v/F_m$ , respectively (Perez *et al.* 2021).

### Leaf traits

Six leaf traits were measured – leaf area (LA), leaf dry mass per area (LMA), (whole) leaf thickness ( $\mu\text{m}$ ), palisade mesophyll thickness (PT,  $\mu\text{m}$ ), spongy mesophyll thickness (ST,  $\mu\text{m}$ ) and upper cuticle thickness (UCu,  $\mu\text{m}$ ) – on all 13 studied species except *Scyphiphora hydrophyllacea* C.F.Gaertn., *Sonneratia alba* Sm. and *S. caseolaris* (L.) Engl. For the latter two species, leaf trait data were extracted from Tian *et al.* (2016) for the same sites, with the exception of LA and UCu. The palisade to spongy mesophyll thickness ratio (P/S) was also estimated from PT and ST measurements. The experimental protocol for leaf trait measurements is provided in Appendix S1. A Pearson's correlation was computed using the 'car' function in R to examine the relationship between each leaf trait and  $P_{HT}$ .

### Climatic niche

The climatic niche for each species was determined using species occurrence data available through the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>) using the 'dismo' package implemented in R. Occurrence records were screened and records with obvious geo-referencing errors or duplicate entries were excluded from the dataset. All 19 bioclimatic variables were extracted from the WorldClim database (30' resolution) at every occurrence location (Hijmans *et al.* 2005), and the mean value for each variable calculated. To minimize the influence of outliers potentially caused by geo-referencing or taxonomic errors, all occurrence records outside of the 90% quantile for BIO1 and BIO5 were excluded, and the new mean values referred to as upper BIO1 and upper BIO5. A Pearson's correlation was computed using the 'car'

function in R to examine the relationship between each bioclimatic variable and  $P_{HT}$ .

### The $P_{HT}$ across ecosystems

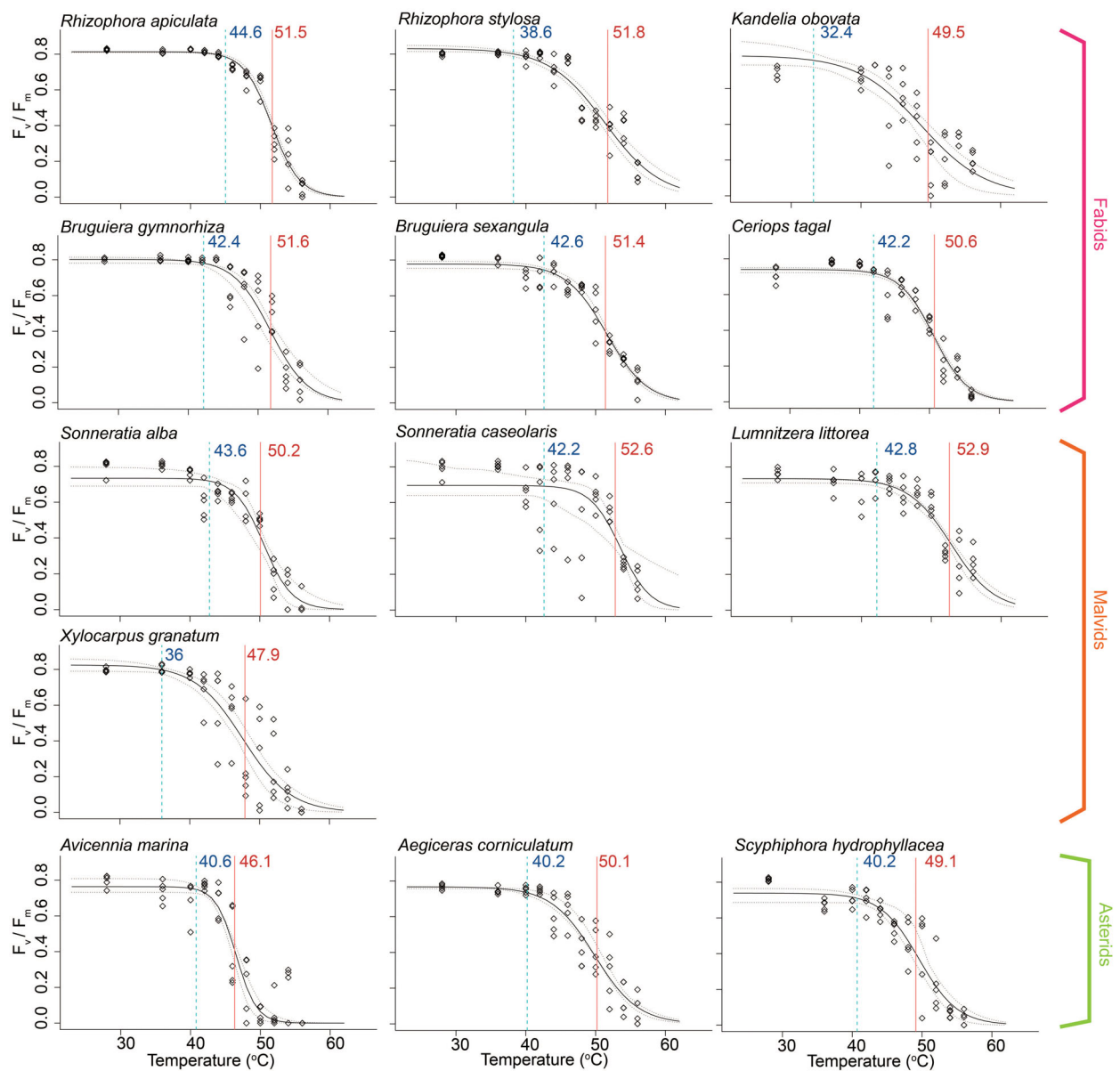
The  $T_{50}$  data of the 13 mangrove species were compared to published  $T_{50}$  data for trees distributed in the lowland (sub) tropics (generally defined as <200 m a.s.l., <35° latitude). Seedling and greenhouse studies, and those with fundamentally different definition of  $T_{50}$  (as defined in Perez *et al.* 2021) were excluded. The ecosystem of the data points was determined by comparing each coordinate to the ecoregion dataset (Dinerstein *et al.* 2017); ten tropical ecosystems were included in the final dataset. A least significant difference (LSD) test was

conducted using the ‘agricolae’ package implemented in R to compare the mean values of  $T_{50}$  across all ecosystems, with a Bonferroni correction of the  $P$ -value at 0.05.

## RESULTS

### Photosynthetic heat tolerance, $P_{HT}$

The mean  $T_{Crit}$  for all 13 mangrove species was 40.7 °C, ranging from 32.4 °C in *K. obovata* to 44.6 °C in *R. apiculata*, while mean  $T_{50}$  was 49.1 °C, ranging from 46.1 °C in *Avicennia marina* to 52.9 °C in *Lumnitzera littorea* (Fig. 1). Overall,  $T_{Crit}$  was more variable across species (SD = 3.35) than  $T_{50}$  (SD = 1.91).  $T_{50}$  was, on average, 9.76 °C higher than  $T_{Crit}$ ; the distance



**Fig. 1.** The  $F_v/F_m$  response curve to temperature changes in 13 Asian mangrove species. Each circle represents the  $F_v/F_m$  reading for an individual leaf disc.  $T_{50}$  and  $T_{crit}$  are denoted by vertical red and blue lines, respectively. Dashed lines above and below the curve denote the 95% bootstrapped confidence interval for the fitted curve. The 13 species are arranged based on their plant clade.

between the two decreased as  $T_{\text{Crit}}$  increased ( $F = 23.4$ ,  $R^2 = 0.68$ ,  $P = 0.001$ ). There was no correlation between  $T_{\text{Crit}}$  and  $T_{50}$  ( $R^2 = 0.20$ ,  $P = 0.132$ ).

### Heat tolerance in relation to leaf traits

Among all seven measured leaf traits, a significant negative correlation was only observed between P/S and  $T_{50}$  (Fig. 2a). This was not statistically significant upon exclusion of *A. marina* that had an extremely high P/S ratio (Tables S1, S2). There was a positive correlation between  $T_{50}$  and LA upon exclusion of *L. littorea* (Fig. 2b). No other statistically significant correlation was negatively correlated between leaf traits and  $T_{50}$  or  $T_{\text{Crit}}$  (Figure S1, Table S2).

### Heat tolerance in relation to climate niche

There was a significant positive correlation between  $T_{50}$  and BIO10 (mean temperature of warmest quarter; Fig. 2c), BIO5, 8, 13, 16 and 18 (Figure S1). As the pattern of correlation was highly similar among these bioclimatic variables, only BIO10 is provided in Fig. 2.  $T_{\text{Crit}}$  was positively correlated with upper BIO1 (annual mean temperature) and BIO3 (isothermality), and negatively correlated with BIO4 (temperature seasonality) (Fig. 2d–f).

Similar to the correlation between P/S and LA (Fig. 2a,b), the significant correlations between heat tolerance and bioclimatic variables were largely driven by the two species with relatively weak heat tolerance and high P/S. The correlations between bioclimatic variables (upper BIO1, BIO3 and BIO4) and  $T_{\text{Crit}}$  were not significant upon removal of *K. obovata* (dark squares in Fig. 2), while the positive relationship between bioclimatic variables (BIO5, 8, 10, 13, 16 and 18) and  $T_{50}$  was no longer significant upon removal of *A. marina* (dark circles in Fig. 2).

### Comparison across ecosystems

Mangroves had one of the highest  $T_{50}$  across the ten tropical ecosystems examined (Fig. 2g); second only to xerophytes in the Tirari-Sturt Stony Desert. Mangroves had significantly higher heat tolerance than the Narmada Valley Dry Deciduous Forests and North-Western Ghats Montane Rain Forests.

## DISCUSSION

Our study provides novel empirical data on heat tolerance of 13 Asian mangrove species, showing that heat tolerance is correlated with mesophyll structure (*i.e.* P/S), LA and climate niche (eight out of 19 bioclimatic variables). When compared to other tropical ecosystems, mangrove trees display one of the highest heat tolerances. These much needed data allow us to understand the potential vulnerability of mangroves to climate anomalies and to predict their future distribution.

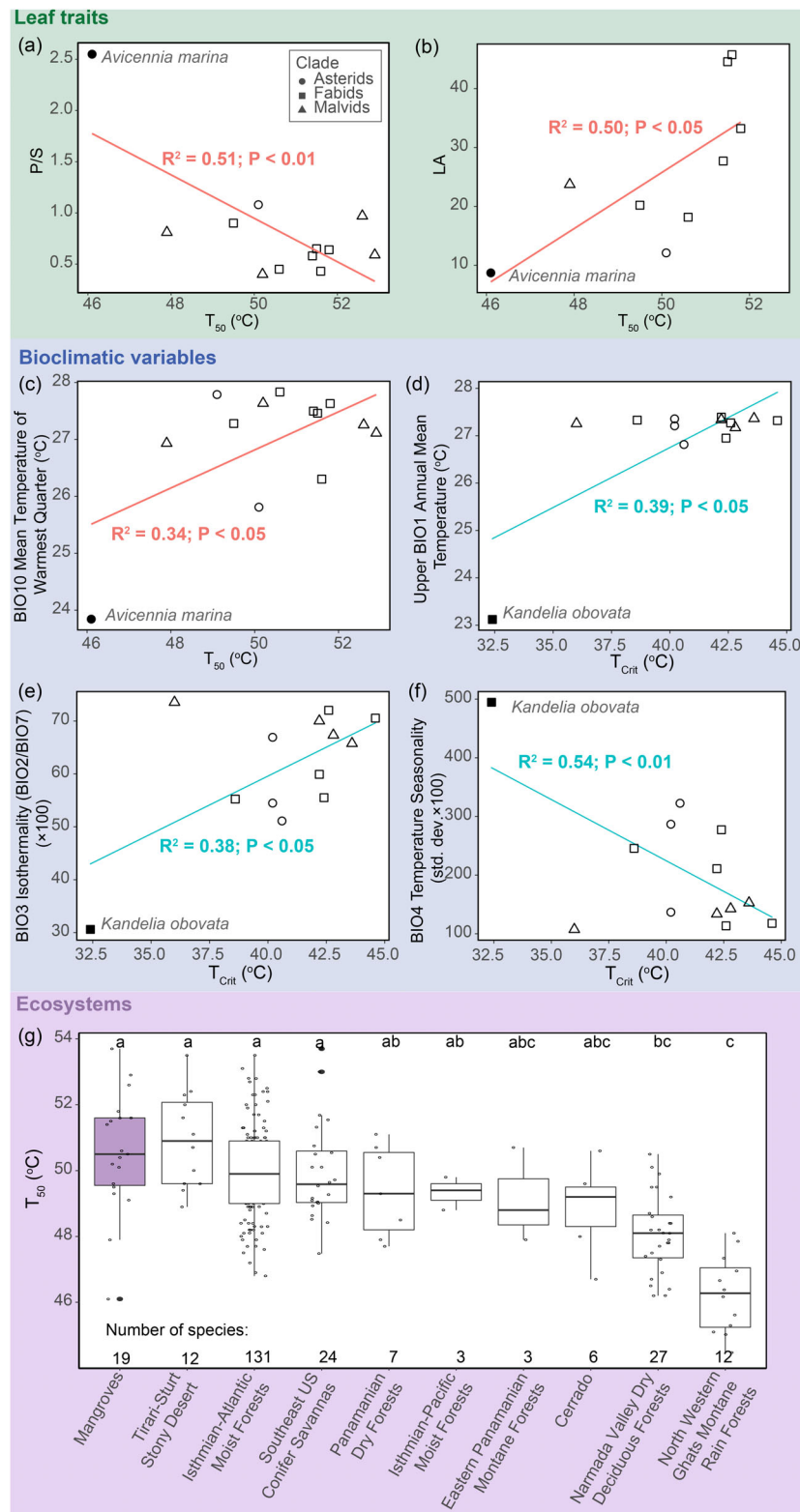
Mangroves are comprised of diverse lineages; hence, the considerable inter-species variations in  $P_{\text{HT}}$  in our study was expected and agrees with other studies on  $P_{\text{HT}}$  across divergent taxa in other ecosystems (Knight & Ackerly 2002; Curtis *et al.* 2016; Perez & Feeley 2020). The large range of  $T_{50}$  (6.8 °C) and  $T_{\text{Crit}}$  (12.2 °C) across species demonstrated that mangrove species vary in photosynthetic tolerance to high temperatures, with *R. apiculata*, *B. gymnorhiza*, *S. caseolaris* and *L. littorea* being

the most heat-tolerant. Interestingly, heat tolerance directly translates to cold sensitivity in most of our study species (Chen *et al.* 2017). The negative relationship between heat and cold tolerance indicates that mangroves are temperature-adapted and have a defined temperature envelope. The only exception to this inverse relationship between heat and cold tolerance was *B. gymnorhiza*, which had a high  $P_{\text{HT}}$  as well as a high cold tolerance (Chen *et al.* 2017). The large temperature envelope in *B. gymnorhiza* could be the reason for it being one of the most widely distributed mangrove species (see Figure S2). Understanding this temperature envelope is key to predicting future climate vulnerabilities. For example, *K. obovata* ( $T_{\text{Crit}}$ : 32.4 °C) regularly experiences critical temperatures in summer in Hainan, where the average temperature of the warmest quarter is 33 °C. As the current summer temperature in Hainan is already approaching the physiological limit of *K. obovata*, this species would be especially vulnerable to future extreme heat events. In essence, our data show that most mangrove species have a high  $P_{\text{HT}}$ ; and for those with a low  $P_{\text{HT}}$ , increasing summer temperatures could comprise a significant physiological stress.

The relationship between heat tolerance and leaf traits was not as clear in our data as in the existing literature. In general,  $T_{50}$  in lowland tropical trees was positively correlated with LMA (Knight & Ackerly 2003; Sastry & Barua 2017; Slot *et al.* 2021), as heat tolerance increases with the increasing construction cost of leaves. Our data do not support this relationship, but instead, there was a positive correlation between  $T_{50}$  and LA. The relationship between  $T_{50}$  and LMA in mangroves could be obscured by the leaf sclerophylly that affects the mass per area ratio (Sereneski-de Lima *et al.* 2013). In addition, our data demonstrate that only P/S had a significant negative correlation with  $T_{50}$ . A high P/S ratio is typically found in xerophytes and can help to maintain high photosynthetic capacity in strongly irradiated environments (González-Paleo *et al.* 2018). However, our study showed a contradictory trend, indicating that mangroves have a similar P/S ratio to plants in high rainfall habitats, *e.g.* rainforests, as opposed to water-scarce environments, such as a hot dry valley (Lin *et al.* 2017). Leaf traits in mangroves could also be influenced by other stress factors, *e.g.* salinity and inundation (Xiao *et al.* 2009; Peel *et al.* 2017), and could result in complex response strategies to a coastal environment, instead of to heat alone. Specifically, mangroves in higher salinity environments have thinner palisade tissue, thinner leaf minor veins and a smaller leaf area (Cao *et al.* 2022). Furthermore, a suite of leaf traits affects thermal tolerance, and the interactions among them may be confounding (Lin *et al.* 2017). Therefore, more leaf traits, especially those related to hydraulic safety, need to be measured to further elucidate the relationship between leaf thermoregulation and  $P_{\text{HT}}$  in mangroves.

Our study also demonstrated that  $P_{\text{HT}}$  reflects the climatic niche and distribution range limits of mangrove species. All significant correlations between  $P_{\text{HT}}$  and bioclimate variables were driven by two heat-sensitive and cold-tolerant species: *K. obovata* (lowest  $T_{\text{Crit}}$ ) and *A. marina* (lowest  $T_{50}$ ). The former had the northern-most distribution, while the latter had the largest latitudinal distribution range among all mangrove species of the Indo-West Pacific region (Figure S2). Several key lines of evidence have demonstrated that heat tolerance is conserved across plant lineages (*i.e.* conservatism of upper thermal limits) and that cold tolerance tends to vary across species





**Fig. 2.** The relationship between (a)  $T_{50}$  (in red) and ratio of palisade to spongy mesophyll thickness, P/S; (b)  $T_{50}$  and leaf area, LA; (c)  $T_{50}$  and BIO10 mean temperature of warmest month; (d)  $T_{crit}$  (in blue) and upper 90 quantile of BIO1 annual mean temperature; (e)  $T_{crit}$  and BIO3 isothermality; (f)  $T_{crit}$  and BIO4 temperature seasonality. Only statistically significant relationships ( $P < 0.05$ ) are shown. The extreme points without which the statistical significance was absent are filled black: black circles denote *A. marina* and black squares denotes *K. obovata*. (g) Boxplots showing the comparison of  $T_{50}$  across ecosystems, with the lowercase letters in the panel denoting statistical significance at  $P < 0.01$ . The number of species in each ecosystem is listed at the bottom of the panel. Please see Appendix S1 for list of references used in the  $T_{50}$  comparison among ecoregions.

(Araujo *et al.* 2013). In trees, freezing temperatures define the evolutionary divergence between tropical and extratropical distribution, while seasonal water stress defines the divergence between distribution in moist or dry forests (Segovia *et al.* 2020). Therefore, cold tolerance could be a better predictor of species climatic distributions than heat tolerance (Perez & Feeley 2021). Our findings provide evidence that niche specialization/divergence in mangroves is mostly observed in heat-sensitive and cold-tolerant species. Hence, these species would be the most vulnerable to temperature extremes (both upper and lower), especially under climate change scenarios.

Compared to other biomes and ecosystems, mangroves show high heat tolerance, second only to plants from arid tropical habitats. As mangroves occur in hyper-saline environments and regularly experience physiological drought, their high  $P_{HT}$  reflects low water availability, similar to that found in desert plants (Cook *et al.* 2021). This further underscores the vulnerability of mangroves to climate change, since species at low latitudes may be at greater risk of heat stress due to the narrower thermal safety margins (Perez & Feeley 2020). Furthermore, the conservative evolutionary strategy in mangrove heat tolerance means that evolution to high temperature conditions is constrained by hard physiological boundaries that limit adaptation to current climate warming (Araujo *et al.* 2013). With the increase in extreme heat events, mangroves will experience increasing water scarcity and hyper-salinity, especially those growing in arid regions (Adame *et al.* 2021). Thus, minor changes in hydrology, climate or nutrient load could lead to a drastic reduction in forest cover and functionality of mangrove ecosystems (Sippo *et al.* 2018; Krauss & Osland 2020).

In conclusion, we show that the high  $P_{HT}$  in mangrove trees generally translates to cold sensitivity, indicating that each species has a defined temperature envelope. Heat tolerance is correlated with the palisade to spongy mesophyll thickness ratio and leaf area, which could be an adaptation to strong irradiation in coastal areas. No correlation with other leaf traits commonly attributed to thermoregulation was detected, likely due to the complex physiological response to multiple abiotic stressors in the intertidal environment. The correlation between  $P_{HT}$  and multiple bioclimatic variables (e.g. isothermality, precipitation of wettest month) demonstrates that the climate niche of mangrove species reflects its heat tolerance, and points towards the niche specialization of heat-sensitive and cold-tolerant species. We also show that mangrove trees have a high  $P_{HT}$  among tropical ecosystems, which further highlights the fact that mangroves are functioning at the physiological limits for tropical trees and could be especially vulnerable to heat stress. These findings advocate strongly for further integrative and comparative studies on mangrove thermoregulatory traits and climatic niche in order to understand the physiological response of mangrove trees to climate change-driven heatwaves and rising global temperatures.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

### Appendix S1. Extended experimental protocol.

**Figure S1.** The relationship between heat tolerance  $T_{50}$  (red) and  $T_{crit}$  (blue) and (a) Leaf dry mass per area (LMA), (b) BIO1 annual mean temperature, (c) BIO5 Max Temperature of Warmest Month, (d) BIO8 Mean Temperature of Wettest Quarter, (e) BIO13 Precipitation of Wettest Month, (f) BIO16 Precipitation of Wettest Quarter, (g) BIO18 Precipitation of Warmest Quarter; Statistically significant relationships ( $P < 0.05$ ) are denoted by solid lines, while not significant correlations are denoted by dash lines. Extreme data points (without which the statistical significance was absent) are filled black: black circles are data points for *A. marina* and black squares are data points for *K. obovata*.

**Figure S2.** Distribution maps of each mangrove species in this study. (a) The distribution of *Kandelia obovata* (blue) and *Avicennia marina* (red) as compared to the range of other mangrove species in the Indo-West Pacific region. (b) Distribution of other 11 mangrove species.

**Table S1.** Photosynthetic heat tolerance ( $T_{crit}$ ,  $T_{50}$ ) and estimates of the leaf traits for each species. LA: leaf area, LMA: leaf mass per area, LT: (whole) leaf thickness, PT: palisade mesophyll thickness, ST: spongy mesophyll thickness, P/S: palisade to spongy mesophyll thickness ratio, UCu: upper cuticle thickness.

**Table S2.** Pearson's correlation test between each leaf trait and photosynthetic heat tolerance ( $T_{crit}$ ,  $T_{50}$ ). LA: leaf area, LMA: leaf mass per area, LT: (whole) leaf thickness, PT: palisade mesophyll thickness, ST: spongy mesophyll thickness, P/S: palisade to spongy mesophyll thickness ratio, UCu: upper cuticle thickness.

**Table S3.** Estimates of the parameters for climatic niche for each species measured in this study.

**Table S4.** Pearson's correlation test between each bioclimatic variable and photosynthetic heat tolerance ( $T_{crit}$ ,  $T_{50}$ ).

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