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RESEARCH ARTICLE

Contrasting heat tolerance of evergreen and deciduous urban woody species during heat waves

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Abstract

1. The increasing frequency and intensity of heat waves caused significant damages to urban woody species, and the different leaf structures between evergreen and deciduous species may be closely related to leaf heat tolerance. However, whether the different leaf structural traits of evergreen and deciduous plants contribute to their different responses under heat waves is still unclear.
2. During the record-breaking and long-lasting 2022 summer heat waves in China, we investigated the relationships between leaf thermal indices and leaf structural traits of 36 urban woody species in four cities along the Yangtze River.
3. We found that all the four thermal indices were significantly but weakly related with leaf damage status. The critical temperature that causes the initial 15% damage to photosystem II (Tcrit) may serve as a sensitive measure of heat tolerance. Evergreen species suffered less leaf damage during the heat waves and exhibited higher leaf heat tolerance, thicker leaves than deciduous species. Tcrit was significantly correlated with leaf mass per area, leaf thickness and thickness of spongy tissue.
4. *Synthesis*. Urban woody species with higher Tcrit, leaf mass per area and leaf thickness tend to be more tolerant to heat stress. This study provides insights for predicting leaf heat tolerance of urban woody plants in subtropical China and their physiological and ecological responses to severe heat waves.

KEYWORDS
leaf damage ratio, leaf economic spectrum, leaf habit, leaf mass per area, leaf photosynthetic heat tolerance, stomatal density

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1 | INTRODUCTION

With global warming, heat waves have increased in intensity, frequency and duration (Perkins-Kirkpatrick & Lewis, 2020), which exhibit extreme high temperatures (commonly refer to the daily maximum temperature exceeding 35°C) and last for several consecutive days (Shi et al., 2021). Especially in cities, the extreme temperatures during heat waves contribute to dry atmospheric conditions with high vapour pressure deficits (Czaja et al., 2020; Teskey et al., 2015), which directly affect plant physiology. Heat waves have been shown to reduce leaf photosynthetic rates (Duarte et al., 2016) and harm photosystem II (PSII; Guha et al., 2018). This can culminate in major effects such as extensive leaf loss (Sanusi & Livesley, 2020), dieback of trees (Marchin, Esperon-Rodriguez, et al., 2022) and tree mortality (Chaste et al., 2019), which influence urban greening and microclimate. Therefore, there is an urgent need to understand physiological and ecological tolerance of urban trees under such extreme conditions.

Leaf photosynthetic heat tolerance is the ability of plants to survive under high temperatures (Kitudom et al., 2022). Photosynthesis and PSII are sensitive to thermal changes, so a commonly used method to quantify leaf heat tolerance is to assess changes in Fv/Fm (the maximum quantum efficiency of the photosystem II) when leaves are exposed to different temperatures (Baker, 2008). The temperature that causes the initial damage (15%) to photosystem II (critical temperature, Tcrit) and the temperature that causes 50% damage to photosystem II (T50) (Drake et al., 2018) are two indices that indicate the loss of function leading to leaf necrosis (O'sullivan et al., 2017). When leaf temperature exceeds Tcrit or T50, the growth and physiological processes of plants will be affected. However, Tcrit and T50 are not sufficient to evaluate the safety of plants under heat stress (Kitudom et al., 2022), because species with low leaf heat tolerance might be able to control leaf temperature well below their thermal limit through physical and physiological cooling mechanisms (Lin et al., 2017), while species with high leaf heat tolerance can still suffer severe damage following rising leaf temperature. Meanwhile, thermal safety margin (TSM, the difference between leaf temperature and Tcrit or T50) was suggested to evaluate the thermal safety of the photosystem II better than Tcrit or T50 (Ahrens et al., 2021; Gunderson & Stillman, 2015). TSM differs among species in different forest types, mainly due to the variation of leaf temperature caused by fluctuant air temperature (Kitudom et al., 2022). Even in the same habitat, different leaf structural traits and physiological processes also contribute to different leaf temperatures and TSMs across species (Tserej & Feeley, 2021). However, TSM has mostly been calculated based on air temperature rather than leaf temperature in previous studies (Curtis et al., 2012; Duarte et al., 2016; O'sullivan et al., 2017; Sastry & Barua, 2017), resulting in quite inaccurate TSM values (Defraeye et al., 2013; Scheffers et al., 2017). Thus more efforts are needed to evaluate leaf thermal risks through comparing different thermal indices.

Leaf habit, mainly evergreen and deciduous species, reflects the ecological adaptability of plants (Eamus, 1999; Ribeiro et al., 2022). Along the leaf economic spectrum, normally the higher construction costs of evergreen than deciduous leaves result in different leaf structures (Kröber et al., 2015) and probably higher heat tolerance (Sastry et al., 2018; Slot et al., 2021; Teskey et al., 2015). However, previous studies have indicated that the relationships between leaf structural traits and heat tolerance were controversial. For example, as a classic trait reflecting different construction costs between evergreen and deciduous leaves (Wang, Colin Prentice, et al., 2023), leaf mass per area (LMA) is expected to be positively linked with T50, such as for species in tropical mountain lowland forests (Slot et al., 2021), but LMA and T50 were not correlated for plants in highland areas (Slot et al., 2021) and for Asian mangrove trees in hot wet habitats (Li et al., 2022). LMA was even negatively correlated with leaf heat tolerance for Mediterranean species (Godoy et al., 2011). On the one hand, leaf morphological traits can indirectly influence photosynthetic heat tolerance through leaf heat exchange rates (Jones, 2013; Tserej & Feeley, 2021). For instance, large leaves have a high leaf-air temperature difference due to slow heat exchange between leaves and surrounding air, while smaller leaves respond quickly to changes in air temperature, making them more adaptable to high temperatures in hot and dry habitats than larger leaves, but the relationship between leaf area (LA) and T50 is still inconsistent (Li et al., 2022; Wright et al., 2017). On the other hand, leaf anatomical traits can also influence photosynthetic heat tolerance, including leaf thickness (LT) and stomatal traits through leaf temperature regulation (Kitudom et al., 2022; Lin et al., 2017; Tserej & Feeley, 2021). Thicker leaves have higher heat tolerance (Leigh et al., 2012), thus thickness-related traits are also assumed to be related to heat tolerance. For example, palisade and sponge tissues play a certain role in scattering the incident light and storing water to regulate heat exchange and maintain physiological processes, which may affect heat tolerance (Leigh et al., 2017; Teskey et al., 2015). Meanwhile, high stomatal density and large stomata can increase transpiration, leading to a chilling effect on leaves (Lin et al., 2017). Therefore, it is necessary to systematically investigate how leaf structural traits contribute to different leaf heat tolerance across leaf habits, which is essential for predicting plant responses to increasing heat waves.

In the summer of 2022, air temperatures in 1680 out of the total 2424 weather stations in China frequently exceeded 35°C, 262 of which even reached historical extremes (the daily maximum temperature broke the daily maximum temperature recorded for over 60 years in the same weather station) (Figure S1) (CMA Climate Change Centre, 2022). The extreme heat stress led to the worst declines of photosynthesis and the gross primary productivity of vegetation by 7.46% since 2000 in the Yangtze River basin (Wang, Yan, et al., 2023) and provided a good opportunity to monitor the status of leaf damage and plant physiological responses under heat waves. Thus, we conducted experiments in four cities along the Yangtze River that experienced 23–49 days of heat waves from June to August 2022 (Figure 1; Table 1). We measured the ratio of leaf damage and a set of leaf heat tolerance and structural traits of the most common and typical tree species (five evergreen and five deciduous

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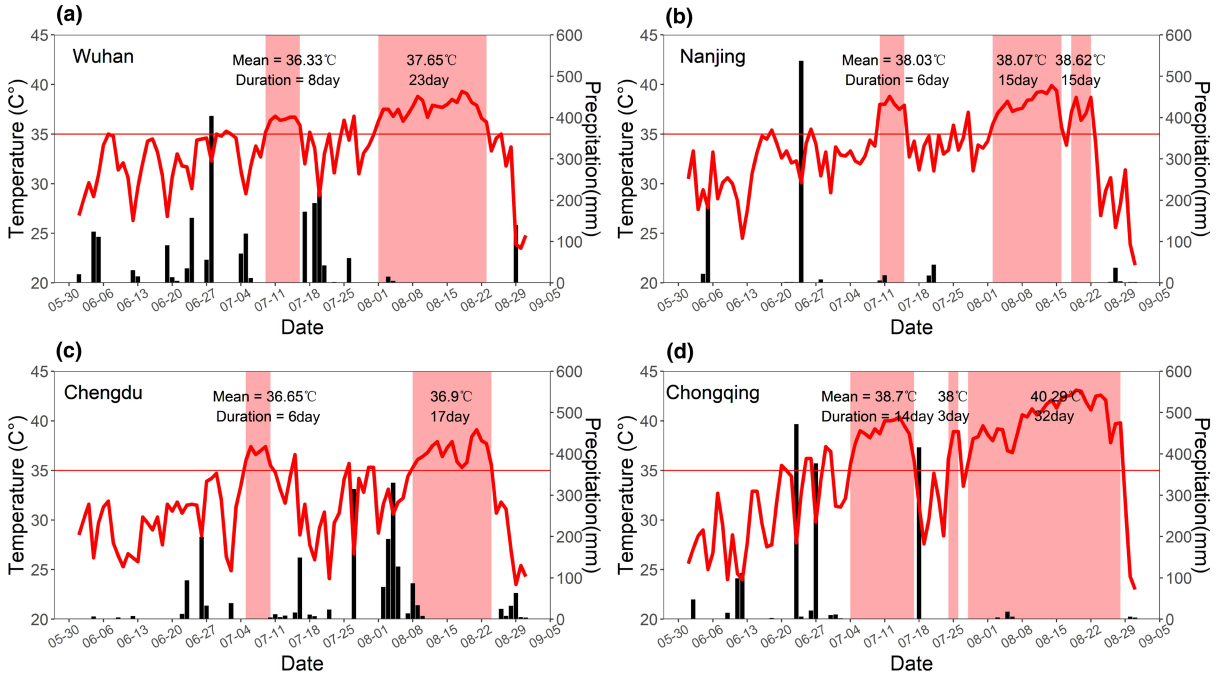

FIGURE 1 Daily maximum temperature and daily precipitation during the summer of 2022 (1 June to 30 August) in Wuhan (a), Nanjing (b), Chengdu (c) and Chongqing (d) along the Yangtze River, China. Heat waves are highlighted as red zones, temperature is shown as red curves with the 35°C-threshold marked by red horizontal lines, and precipitation is shown as black bars.

TABLE 1 Coordinates of sampling sites and weather stations, historical climate, excess heat factor (EHF) and heat wave data for the four cities.

City	Sampling location	Weather station location	MAT (°C)	MAP (mm)	EHF	Heat wave days	July		August	
							History (°C)	2022 (°C)	History (°C)	2022 (°C)
Wuhan	30°32′ N 114°25′ E	30°37′ N 114°12′ E	17.00	1256	8.59	31	28.70	30.50	28.50	31.65
Nanjing	32°06′ N 118°29′ E	31°45′ N 118°52′ E	15.70	1047	12.99	26	28.20	30.47	27.90	31.15
Chengdu	30°46′ N 104°08′ E	30°35′ N 104°04′ E	16.50	1078	18.31	23	26.00	27.69	25.80	28.90
Chongqing	30°49′ N 108°22′ E	30°48′ N 108°26′ E	18.80	1077	32.48	49	28.30	31.18	28.60	35.35

Note: History: Monthly average temperature during 1960–2018; 2022: Monthly average temperature in 2022. MAT, MAP and History data are extracted from WorldClim version 2.1 (Fick & Hijmans, 2017); 2022 data and heat wave days are from daily reports of each weather station; EHF values are calculated in this study.

Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature.

species in each city, 17 deciduous species and 19 evergreen species in total). We aimed to explore two questions: (1) how leaf damage status relates to the intensity of heat waves and leaf thermal indices, with the hypothesis that leaf damage ratio (LDR) may be positively related with the intensity of heat waves and could be more effectively assessed by TSM than Tcrit and T50 (Kitudom et al., 2022); and (2) how leaf habit differs in leaf structural traits, thermal tolerance, safety and damages across species, with the hypothesis that evergreen species characterized by higher leaf construction cost may exhibit higher heat tolerance and lower leaf damage than deciduous species, and most structural traits especially LMA should be positively related with leaf heat tolerance (Curtis et al., 2012; Sastry & Barua, 2017).

2 | MATERIALS AND METHODS

2.1 | Study sites and species sampling

In this study, we focused on four cities along the Yangtze River with similar latitude: Wuhan, Nanjing, Chengdu and Chongqing, which experienced multiple heat waves in the summer of 2022 (Table 1;

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Figure 1). Four cities are located in the subtropical monsoon climatic zone, with similarly strong seasonality: 75%–90% precipitation occurs during the wet season (April–October) along with the hottest weather. To quantify the intensity of heat waves in each city, we calculated the excess heat factor (EHF) of each heat wave event. First, historical climate data (2001–2021) was accessed from the National Centers for Environmental Information (NCEI) (https://www.ncei.noaa.gov/data/global-summary-of-the-day/archive/) to calculate the daily average temperature of each city over the past 20 years. For June, July and August in 2022, the average and maximum daily temperatures were obtained from weather stations located approximately 10–40 km away from each sampling site (Table 1). EHF is calculated from two excess heat indices (EHIs) (Nairn & Fawcett, 2014):

$$\mathrm{EHI}_{sig} = \frac{\left(T_i + T_{i-1} + T_{i-2} + \ \dots \ + T_{i-n-1}\right)}{n} - T_{95},$$

$$\mathrm{EHI}_{accl} = \frac{\left(T_i + T_{i-1} + T_{i-2} + \ \dots \ + T_{i-n-1}\right)}{n} - \frac{\left(T_{i-n} + T_{i-n+1} + \ \dots \ + T_{i-n+30}\right)}{30},$$

$$\mathrm{EHF} = \mathrm{EHI}_{sig} \times \mathrm{EHI}_{accl}.$$

First of all, we counted the number of days (n) of each heat wave period (the daily maximum temperature exceeding 35°C more than three consecutive days) (Shi et al., 2021) and defined the last day of the heat wave period as day i; then, Ti is the average temperature of the location on day i. $\frac{(T_i + T_{i-1} + T_{i-2} + \dots + T_{i-n-1})}{n}$ is the daily average temperature during the n days of heat wave period. T95 is the 95th percentile for the historical daily mean temperature (2001–2021) at each location. Thus, a positive EHI_{sig} means that the period is warmer than the local annual climate of previous 20 years. $\frac{(T_{i-n} + T_{i-n+1} + \dots + T_{i-n+30})}{30}$ is the average temperature during the 30 days before the start of the heat wave, thus a positive EHI_{accl} means that the period is warmer than the recent past 30 days. The EHF of each heat wave event occurred in each city from 1 June 2022 to 31 August 2022 was calculated separately, and the overall intensity of heat wave of each city was expressed as the day-weighted averaged EHF (day-weighted EHF), which weighted each heat wave by the number of days it lasted.

After nearly two-month heat stress, we conducted plant damage survey and leaf sampling from 21 to 29 August 2022. We collected samples from common tree species, five evergreen and five deciduous species identified by local researchers and gardeners in each city (Table S1; 36 species in total, we did not need permission for fieldwork). To minimize environmental disturbances, we only sampled species from large semi-natural parks with minimal human management such as irrigation. We randomly sampled leaves from sun-exposed canopy of 3–5 trees (fully established in the park) for each species and collected 50–60 leaves from each tree. Leaves were put into sealed plastic bags with moist tissues, and quickly brought back to the hotel in an ice box, where the maximum quantum efficiency (Fv/Fm) of the leaf photosystem II was measured. Other leaf samples were sent back to the laboratory (South China Botanical Garden, 113.33° E, 23.17° N) by fresh logistic and stored in the refrigerator at 4°C. After receiving the express, people in the laboratory started to measure leaf heat tolerance immediately, normally completed the 10 species in each city within a week, and the anatomical experiment was completed within a month. All the traits measured are listed in Table 2.

2.2 | Leaf damage measurement

We used two methods to measure leaf damage status:

1. Leaf damage ratio. To quantify physical leaf tissue damage caused by heat waves, we visually assessed and recorded the percentage of damaged leaves in the entire plant canopy as LDR following Esperon-Rodriguez et al. (2021). Specifically, burned areas on the leaf surface associated with a colour change from green to light brown with dark brown margins were considered as leaf damage. Two fixed people scored the LDR of each tree, and if their results were similar (within 10% difference), the average value was taken. If the results differed greatly, a third evaluator was asked to provide more information to achieve a more accurate value. We evaluated five replicates per species, and the final average was taken to represent the LDR.
2. The maximum quantum efficiency (Fv/Fm) of the leaf photosystem II. We sampled 3–5 individuals per species, collected over 20 leaves for each individual (totally 60–100 leaves per species), and put them into sealed plastic bags with moist tissues. After a 2 h 25°C dark treatment of the leaf samples, we measured Fv/Fm of the leaf photosystem II with PAM 2500 fluorometer (Walz, Effeltrich, Germany).

2.3 | Leaf photosynthetic heat tolerance

We set up 9 water baths to measure leaf heat tolerance, the control bath was set at 26°C and the experimental water baths were set at 36, 41, 46, 50, 52, 54, 56 and 60°C, respectively. Leaf samples were kept in the dark for at least 2 h in plastic bags with moist paper tissues. For each species, leaves were cut into many 4 cm^2 pieces and 6–8 pieces were placed into a sealed plastic bag (nine plastic bags for nine temperature gradients) in water bath for 15 min, followed by 24 h of dark adaptation. Fv/Fm was recorded to detect leaf irreversible damage caused by temperature treatments. Tcrit and T50 of each species were derived using a Weibull function fitted to Fv/Fm versus treatment temperature using the R package *fitplc* (Drake et al., 2018), showing the critical temperature (Tcrit) that causes the initial damage (15%) and the temperature (T50) that causes 50% damage to photosystem II.

As there are different definitions of Tcrit, we also calculated and compared four types of Tcrit calculated from different models. Besides the Tcrit we introduced above, Perez and Feeley (2020) calculated Tcrit by 'finding the temperature where the slope of the Fv/Fm versus temperature relationship reached 15% of its most negative value', Tiwari et al. (2021) used the temperature at which Fv/Fm has decreased by 5% relative to its maximum (we named it T5

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TABLE 2 Abbreviations and descriptions of all the traits measured in this study.

Abbreviation	Description	Unit
LDR	Leaf damage ratio	%
Fv/Fm	The maximum quantum efficiency of the leaf photosystem II	Unit less
Tleafmax	The maximum temperature of leaf during the day	°C
Tcrit	The critical temperature causes the initial damage (15%) to Fv/Fm	°C
T50	The temperature causes 50% damage to Fv/Fm	°C
TSMcrit	The difference between thermal tolerance (Tcrit) and Tleafmax	°C
TSM50	The difference between thermal tolerance (T50) and Tleafmax	°C
LMA	Leaf mass per area	g/m^2
LA	Individual leaf area	cm^2
LT	Leaf thickness	μm
Tup	Thickness of upper epidermis	μm
Tlow	Thickness of lower epidermis	μm
Tp	Thickness of palisade tissue	μm
Ts	Thickness of spongy tissue	μm
P/S	The ratio of thickness of palisade tissue to spongy tissue	Unit less
GCL	Guard cell length	μm
SD	Stomatal density	mm^{-2}
SPI	Stomatal pore index	Unit less

here), and Slot et al. (2021) calculated Tcrit as 'as the temperature at which a line describing the slope of the Fv/Fm decline at T50 intersected with a horizontal line indicating its maximum' (Table S2). We found that the four indices showed similar patterns, Tcrit defined by Slot et al. (2021) and Perez and Feeley (2020) had significant negative correlations with LDR, while T5 (Tiwari et al., 2021) also had a negative trend with LDR with a marginal significance (Figure S2). Therefore, we only used the Tcrit calculated from the R package *fitplc* in the following analyses.

To determine the TSM, we measured the maximum leaf temperature (Tleafmax) of each species (3–5 individuals) during 12:00–14:00 (Marchin, Esperon-Rodriguez, et al., 2022) in the same day in each city with an infrared thermal camera (FLIR, America). Although leaf temperature fluctuates, and capturing the maximum leaf temperature is challenging, we tried our best to ensure that leaf temperatures of fully sun-exposed leaves are comparable across species in each city within a short period, as reported in previous studies (Blasini et al., 2022; Lin et al., 2017). Moreover, the maximum leaf temperature recorded for each species in each city on a given day can be measured accurately to calculate TSM. TSM is the difference between T50 or Tcrit and Tleafmax (i.e. TSMcrit = Tcrit − Tleafmax), following the method described by Kitudom et al. (2022). This metric provides a good prediction of leaf heat vulnerability, with the threshold of leaf temperature reached when Tleafmax equals Tcrit or T50.

2.4 | Leaf morphological traits

For each species (3–5 replicates), 10 leaves from each replicate were scanned using a flatbed scanner (HP Deskjet 1050). Leaf area (cm^2) was analysed using Image J (National Institutes of Health, Bethesda, USA) based on the scanned image. Then leaves were dried (65°C for 72 h) and their masses were determined. LMA (g/cm^2) was calculated by the ratio of leaf dry weight to LA.

2.5 | Leaf anatomical traits

We made cross sections of leaves using the freehand sectioning method. We measured LT (μm) and thickness of upper and lower epidermis (Tup, Tlow), palisade mesophyll (Tp), and spongy mesophyll (Ts). All cross sections were photographed with a microscope (YS100, Nikon, Tokyo, Japan) at 40× magnification, and analysed by Image J software. Three images were captured from each of four leaves per species.

To measure the stomatal traits, epidermal peels from both leaf surfaces of four leaves per species were used to determine stomatal traits (guard cell length (GCL), stomatal pore length (SL) and stomatal density (SD)). We used a layer of transparent nail polish to fix the stomata of the leaves. The nail polish layer was then glued to a piece of transparent tape cut into 1.0 cm × 1.0 cm and flattened on a microscope slide before being covered with a coverslip for imaging. All images were captured using a microscope (YS100, Nikon, Tokyo, Japan), and analysed using Image J software. Three images of epidermal peels were captured from each of four leaves per species. At 400× magnification, we scored guard cell length (GCL, μm) and stomatal pore length (SL, μm). At 100× magnification, we counted stomata in a 0.25 mm^2 field of view to determine stomatal density (SD, mm^{-2}), calculating stomatal pore index ($SPI = SD \times SL^2$).

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2.6 | Statistical analyses

All the analyses were performed in R 4.3.1 (R Core Team, 2023). First, mean values of all the traits measured from multiple leaves within one tree were calculated, and these mean values were replicates (3–5 individuals) of each species used in the following analyses. Then all data were tested for normality using the Shapiro and Wilk test. Levene's method was used to test for homogeneity of variance, and unsatisfactory data were log transformed to meet the requirements of the basic parameter test, here only LDR was log transformed. To verify whether TSM is more effective to assess leaf damage status (the first hypothesis), the relationships between LDR and four thermal indices were examined by fitting linear models. To test if evergreen species showed higher leaf heat tolerance and other traits (the second hypothesis), traits between evergreen and deciduous leaves were compared using the *t*-test (with the *t.test* function in R) and Principal component analysis (PCA) (with the *prcomp* function in R). Two-way ANOVA was used to determine the effects of the day-weighted average of the excess heat factor (day-weighted EHF), leaf habit and their interaction on LDR, heat tolerance and structural traits. Pearson correlation between leaf heat tolerance and structural traits was calculated using the *ltm* function in R to identify the most important structural traits affecting leaf heat tolerance.

3 | RESULTS

3.1 | Relationship between leaf damage and leaf thermal indices

Heat waves occurred repeatedly at all the study sites, with Chongqing experiencing the longest heat wave of 32 days and the highest daily maximum temperature of 43.1°C during the heat waves. According to the intensity of the heat waves, that is, the day-weighted average of the excess heat factor (day-weighted EHF), the four cities were ranked in ascending order as Wuhan, Nanjing, Chengdu, and Chongqing (Table 1). LDR ranges from 0% to 80% (average 26.25%) across all species, and LDR was not significantly related with day-weighted EHF (Figure S3). Day-weighted EHF had significant effects on Tleafmax, Tcrit, T50, TSMcrit and TSM50, but not on leaf structural traits (Table S3).

Leaf Tcrit, T50, TSMcrit and TSM50 all had significant negative correlations with LDR, with Tcrit having the highest R^2 value ($p<0.05$; Figure 2), thus all the subsequent correlation analyses used Tcrit to represent heat tolerance. However, these correlations were not found within evergreen or deciduous species (Figure S4). TSMcrit of 10 deciduous tree species was negative (TSMcrit = 1.01 ± 6.10°C), that is Tleafmax was higher than Tcrit (Table 3; Figure 2).

3.2 | Leaf heat tolerance and traits difference between evergreen and deciduous species

Compared with evergreen species, deciduous species exhibited a significantly higher LDR and a lower maximum quantum efficiency of the photosystem II (Fv/Fm) during heat waves ($p<0.05$; Table 3). Normally Fv/Fm is 0.8, and a 15% decrease in Fv/Fm marks the onset of photosystem damage II (Fv/Fm = 0.68). The Fv/Fm of 6 deciduous tree species reached this critical point, indicating that their photosystem II was damaged. The maximum leaf temperature did not differ significantly ($p=0.61$; Table 3), but evergreen species had higher Tcrit, T50, TSM50, and TSMcrit, being 5.41, 3.20, 4.90 and 7.15°C higher than those of deciduous species, respectively ($p<0.05$; Table 3).

Evergreen species showed significant higher values than deciduous species in LMA and LT traits, including LT, Tup, Tlow, Tp, and Ts ($p<0.05$; Table 3). However, no significant difference in the palisade to spongy mesophyll thickness ratio (P/S) was found between the two types of plants ($p=0.37$; Table 3). In addition, there were no significant differences in stomatal traits, including guard cell length (GCL), stomatal density (SD), and stomatal pore index (SPI) ($p>0.05$; Table 3).

According to the PCA results, evergreen and deciduous plants were separated in the space defined by the first two principal components (PCs). PC1 and PC2 explained 31.5% and 17.3% of the total variation, respectively (Figure 3). Four leaf thermal indices clustered together on the negative side of PC1, whereas LDR loaded on the positive side of PC1. Most of leaf structural traits located on the negative side of PC2, leading by LT, Tp, SD and LMA. Overall, PC1 represents a leaf economic spectrum, showing that heat-tolerant species were mainly evergreen species at the slow end of the leaf economic spectrum with a conservative strategy.

3.3 | Tcrit in relation to leaf morphological and anatomical traits

Tcrit exhibited positive correlations with LMA and LT, but not with LA (Figure 4). Furthermore, Tcrit showed a positive correlation with the thickness of the spongy mesophyll (Ts), but not with the thickness of the upper epidermis (Tup), lower epidermis (Tlow), palisade mesophyll (Tp) and palisade to spongy mesophyll thickness ratio (P/S) (Figure S6). However, the anatomical traits of stomata, such as stomatal density (SD), stomatal pore index (SPI), and guard cell length (GCL), did not exhibit any correlations with Tcrit (Figure S7). No correlations between Tcrit and leaf structural traits existed within evergreen or deciduous trees, except for a positive correlation between LA and Tcrit in deciduous species (Figures S5–S7).

4 | DISCUSSION

One notable point of our study was that it captured the *in situ* responses of urban woody species under long-term heat waves. We found that four leaf thermal indices were all weakly related with leaf damage status under heat waves, and Tcrit may be a sensitive indicator for the selection of heat-tolerant woody plants (Esperon-Rodriguez et al., 2021). We also analysed the contrasting leaf heat tolerance between evergreen and deciduous species with leaf

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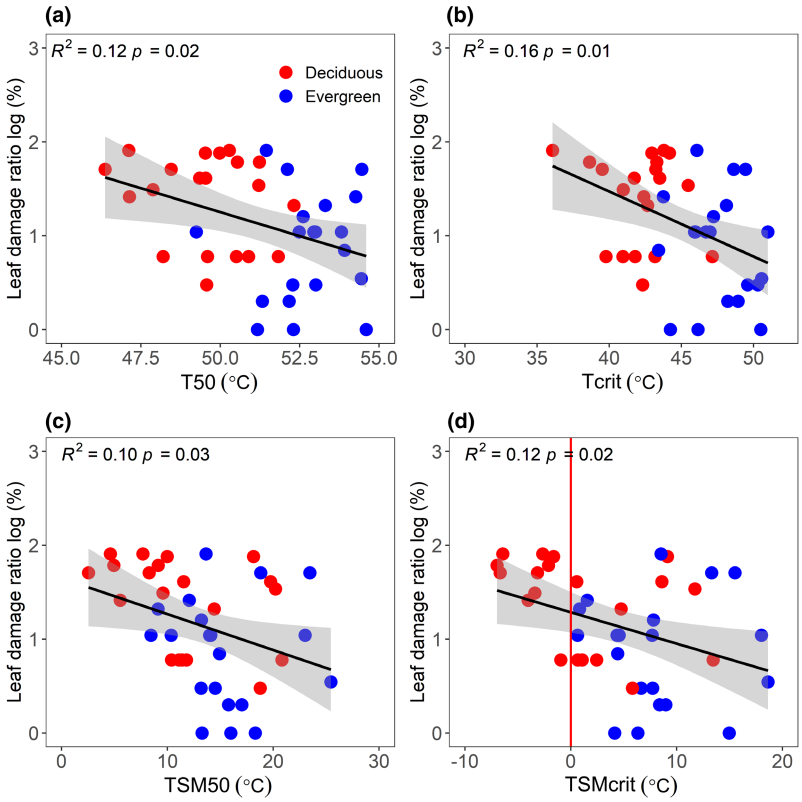

FIGURE 2 The relationships between leaf damage ratio and T50 (a), Tcrit (b), TSM50 (c) and TSMcrit (d). Deciduous species are shown in red, and evergreen species in blue. Statistically significant relationships ($p < 0.05$) are shown in solid lines with shaded areas representing the 95% confidence interval. In (d), TSMcrit <0 (vertical red line) means leaf temperature passed Tcrit. [Correction added on 24 June 2024, after first online publication: The colour of the dots in Figure 2b has been corrected.]

TABLE 3 Results of *t*-tests on traits between evergreen and deciduous species.

Traits	Deciduous ($n = 20$)	Evergreen ($n = 20$)	t	p
LDR(%)	37.27 ± 6.25	15.23 ± 4.75	2.81	0.01*
Fv/Fm	0.70 ± 0.01	0.75 ± 0.01	−2.66	0.01*
Tleafmax (°C)	38.05 ± 1.11	37.32 ± 0.91	0.51	0.61
Tcrit (°C)	42.17 ± 0.55	47.58 ± 0.52	−7.18	<0.01**
T50 (°C)	49.57 ± 0.36	52.74 ± 0.30	−6.71	<0.01**
TSMcrit (°C)	1.01 ± 6.10	8.16 ± 5.39	−3.17	<0.01**
TSM50 (°C)	11.53 ± 1.24	15.43 ± 1.02	−2.43	0.02
LMA (g/m^2)	64.37 ± 3.16	123.02 ± 8.54	−6.44	<0.01
LA (cm^2)	82.24 ± 20.55	46.34 ± 8.80	1.61	0.12
LT (μm)	186.62 ± 9.57	294.87 ± 21.18	−4.66	<0.01**
Tup (μm)	22.38 ± 1.85	32.97 ± 4.04	−2.38	0.02*
Tlow (μm)	17.43 ± 1.28	27.09 ± 3.30	−2.73	0.01*
Tp (μm)	78.67 ± 5.86	115.16 ± 8.21	−3.62	<0.01**
Ts (μm)	76.65 ± 4.21	130.22 ± 11.29	−4.44	<0.01**
P/S	1.08 ± 0.08	0.98 ± 0.08	0.90	0.37
GCL (μm)	21.92 ± 1.93	20.20 ± 1.44	0.72	0.48
SD (mm^{-2})	383.56 ± 52.39	426.38 ± 50.47	−0.59	0.56
SPI	0.37 ± 0.15	0.77 ± 0.60	−0.66	0.52

Note: Data are mean ± SE, sample sizes (n) are given in brackets. * and ** indicates $p < 0.05$ and < 0.01, respectively.

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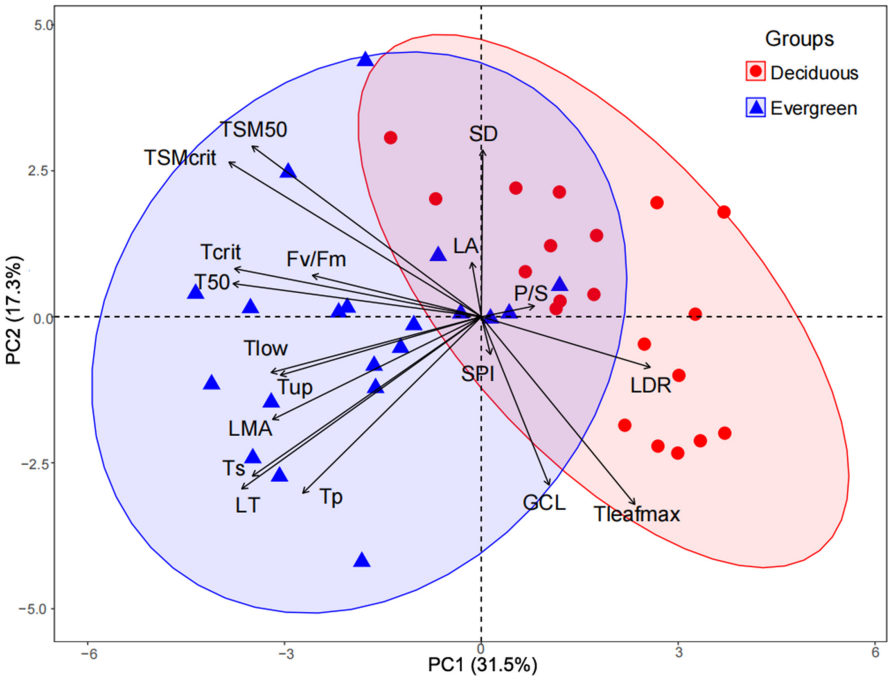

FIGURE 3 Principal component analysis of evergreen and deciduous urban woody species based on 18 leaf functional traits in this study. Deciduous species are shown in red, evergreen species are shown in blue.

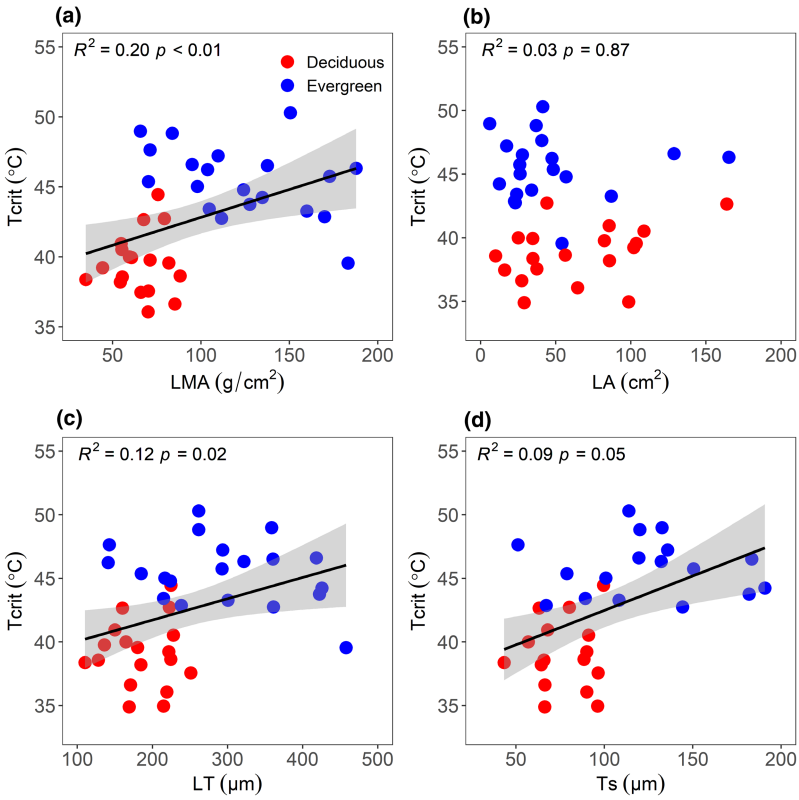

FIGURE 4 The relationships between Tcrit and leaf mass per area (LMA) (a), leaf area (LA) (b), leaf thickness (LT) (c), thickness of spongy tissue (Ts) (d). Deciduous species are shown in red; evergreen species in blue. Only statistically significant relationships ($p < 0.05$) are shown as solid lines with shaded areas representing the 95% confidence interval.

economic traits, finding that evergreen leaves were more heat tolerant than deciduous leaves, with LMA, LT and thickness of spongy tissue (Ts) relating tighter with Tcrit than other traits (Drake et al., 2018; Marchin, Backes, et al., 2022; Slot et al., 2021). Our results could provide insights in understating variation in heat tolerance between leaf habits and improve our ability to predict the vulnerability of tree species to future heat stress.

4.1 | Tcrit can reflect leaf heat tolerance and damage status

Leaf Tcrit, T50, TSMcrit, and TSM50 can all reflect leaf damage status during the natural heat waves, with Tcrit more related to LDR ($R^2 = 0.16$) but not TSMs as we expected in our first hypothesis (Figure 2). Thus, Tcrit may serve as a sensitive measure of leaf heat

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tolerance than the commonly used T50. First, air and leaf temperatures (around 38°C) were normally lower than T50 (46–55°C here), but can easily pass the wide-ranged Tcrit (34–50°C here), which provided early warning for plants under heat stress. Second, compared with T5 (5% decline of Fv/Fm) and Tcrit defined in other studies (Perez & Feeley, 2020; Slot et al., 2021), our Tcrit is associated tighter with visual damage of leaves under heat waves (Figure 2; Figure S2). Third, damage to PSII may be irreversible at temperatures above 40°C in tree species (Yordanov., 1992), suggesting that Tcrit could represent leaf damage status better than the relatively high and stable T50. In recent studies, Tcrit has already been used as a key indicator of heat tolerance (Doughty et al., 2023; Grossman, 2023), and is negatively associated with visible tissue damage in a warming experiment (Marchin, Esperon-Rodriguez, et al., 2022).

In addition, the low explanatory power of LDR by the four thermal indices may be explained by leaf acclimation after several heat waves (Ahrens et al., 2021), just as the two-month hot weather in this study. Attributing to the physiological plasticity in response to the recurrent heat waves (Daas et al., 2008; Niinemets, 2010), leaf heat tolerance such as Tcrit and T50 may increase, leading to the larger TSMs (Ahrens et al., 2021). Therefore, different degrees of variation in the four thermal indices across species after the heat waves may weaken their powers in predicting LDR, such as species with lower heat tolerance have lower plasticity and greater leaf damages (Ahrens et al., 2021; Kullberg & Feeley, 2022). Moreover, although parks in our study have minimal human management especially irrigation, there may still be micro-environmental heterogeneity, such as soil water availability and root depth differences, all of which could weaken the relationships between leaf thermal indices and LDR.

4.2 | Deciduous species have lower heat tolerance than evergreen species

Direct evidence of lower leaf heat tolerance of deciduous species was higher LDR compared with evergreens, and 10 deciduous plants showed negative TSMcrit. We noticed that the lower TSM50 and TSMcrit of deciduous species were caused by lower Tcrit and T50, because Tleafmax did not significantly differ between them. This pattern between leaf habit types was also supported by the lower Fv/Fm value of deciduous species, which indicated more severe photosystem II damage, suggesting that deciduous species are more susceptible to high temperature stress during the same heat wave (Sastry et al., 2018; Sastry & Barua, 2017). As for leaf structural traits, LMA and LT related traits (LT, Tup, Tlow, Tp, Ts) were lower in deciduous than in evergreen leaves, which is consistent with Kröber et al. (2015) who compared leaf structural traits of 40 evergreen and deciduous subtropical tree species. However, there were no significant differences between evergreen and deciduous species in LA, P/S ratio, and stomatal-related traits, which have been reported before that those traits are independent of leaf habit (Beerling & Kelly, 1996; Kröber et al., 2015).

All the leaf structural differences or similarity between deciduous and evergreen species reflect their different ecological strategies. Evergreen species have thicker, denser leaves at the slow end of the leaf economic spectrum, they tend to be exposed to a wider range of environmental extremes with longer life span, resulting in higher structural investment and greater tolerance to heat stress (Li et al., 2022; Sastry & Barua, 2017). In contrast, deciduous plants are at the fast end associated with high photosynthetic and respiration rates and other traits (Wright et al., 2004), leading to their lower heat tolerance than evergreen plants. However, because of the low leaf construction cost of deciduous plants, they may opt for shedding leaves during heat waves to avoid heat stress, a typical example was *Prunus lannesiana* in this study, which shed many leaves during the heat waves and grow 'cheap' (low LMA) new leaves after the events. Meanwhile, the carbon costs and benefits theory is more tightly with leaf dry matter and thickness, but not with LA and stomatal related traits, as has been demonstrated before (Kröber et al., 2015; Markesteijn et al., 2011), which may be linked with leaf heat tolerance in other ways.

4.3 | LMA and LT in relation to leaf heat tolerance of urban woody species

We found that LMA, LT and sponge tissue thickness were related with leaf heat tolerance (Figure 4), supporting our hypothesis that leaves with higher construction cost may exhibit higher heat tolerance. Although it is consistent with previous studies (Curtis et al., 2012; Drake et al., 2018; Sastry et al., 2018), we added new evidence that LMA was positively correlated Tcirt (Godoy et al., 2011; Slot et al., 2021). Generally, leaves with higher LMA are not only better to withstand and recover photosynthetic electron transport after heat stresses (Knight & Ackerly, 2003), but also have longer leaf life span (Wang, Colin Prentice, et al., 2023), which could promote nutrient retention and enhance long-term photosynthetic function, leading to high thermal tolerance than leaves with lower LMA (Sastry & Barua, 2017; Slot & Winter, 2017). In addition, many studies have found that LT is related to leaf temperature regulation (Curtis et al., 2012; Groom et al., 2004; Tserej & Feeley, 2021), but we did not find a correlation between Tleafmax and LT, indicating that besides temperature regulation, LT may have other linkages with thermal tolerance. For example, thick leaves tend to have high thermal buffer ability, that is heat up slowly (Leigh et al., 2012) to keep normal physiological processes (Leigh et al., 2017), and thus could maintain high heat tolerance, as found in Slot et al. (2021).

We did not find a significant relationship between LA and Tcrit, which is not consistent with a previous study that found a positive relationship (Li et al., 2022). However, the lack of relationship between LA and Tcrit was also commonly reported (Sastry et al., 2018; Slot et al., 2021). It is possible that LA may be more related to leaf temperature regulation because of different heat exchange rates between large and small leaves (Jones, 2013; Tserej & Feeley, 2021), thus LA might be not a decisive factor of heat tolerance. Meanwhile, Tup, Tlow,

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Tp and P/S ratio only showed trends but not significant correlations with Tcrit (Figure S6). Previous studies also found that leaf heat tolerance was not correlated with Tup and Tp, but had a negative correlation with P/S ratio across several mangrove species (Li et al., 2022). This may be due to the demand of thicker spongy tissues of mangroves to adapt to high salinity environment (Cao et al., 2023), but such an environmental pressure did not exist for our urban woody species.

Although stomatal regulation is important for leaf temperature regulation during heat waves (Blasini et al., 2022; Luján et al., 2009), Tcrit was not related with stomatal traits in our study (Figure S7). The reasons may include: first, similar stomatal traits between evergreen and deciduous plants may result in similar leaf temperatures among species (Table 3). Second, even plants keep transpiration at the beginning, they will soon close stomata to reduce water loss during heat waves (Esperon-Rodriguez et al., 2021), weakening leaf temperature differences. For example, many studies found that stomatal closure occurred as air temperature and vapour pressure deficit increased (Teskey et al., 2015), and stomatal conductance of some species became nearly zero at 42°C (Esperon-Rodriguez et al., 2021). In addition, Tleafmax in our study was influenced by heat wave intensity but not leaf habit (Table S3), suggesting that leaf temperature regulation probably failed during the severe heat waves and was influenced mainly by air temperature. However, it was noticeable that our Tleafmax of all the trees were measured in 1 day in each city, which may underestimate the true Tleafmax, indicating that more species may have negative TSMs and be threatened during the heat waves.

5 | CONCLUSIONS

This study connected leaf heat tolerance and TSMs to leaf damage status of urban woody species during natural heat waves, and found that Tcrit was related more with leaf damage status than other thermal indices. Evergreen species have higher leaf heat tolerance and less leaf damage, with higher LMA, LT and thickness of spongy tissue. Thus, leaf Tcrit, LMA and LT can serve as indicators in selecting heat-tolerant tree species. This study contributes to the prediction of leaf heat tolerance and the extension of ecological responses of urban woody species.

AUTHOR CONTRIBUTIONS

Haoping Zhang and Hui Liu conceived the ideas and designed methodology; Qiurui Ning, Qiang Li, Yi Jin, Yu Cao, Emily Patience Bakpa, Han Zhao, Jia Song, Pengcheng Ye, Yin Wen and Lingjie Song collected the data; Haoping Zhang and Qiurui Ning analysed the data; Haoping Zhang, Qiurui Ning, Emily Patience Bakpa and Hui Liu led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.7pvmcvf23.

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REFERENCES

Ahrens, C. W., Challis, A., Byrne, M., Leigh, A., Nicotra, A. B., Tissue, D., & Rymer, P. (2021). Repeated extreme heatwaves result in higher leaf thermal tolerances and greater safety margins. *New Phytologist*, *232*(3), 1212–1225. https://doi.org/10.1111/nph.17640

Baker, N. R. (2008). Chlorophyll fluorescence: A probe of photosynthesis in vivo. *Annual Review of Plant Biology*, *59*(1), 89–113. https://doi.org/10.1146/annurev.arplant.59.032607.092759

Beerling, D. J., & Kelly, C. K. (1996). Evolutionary comparative analyses of the relationship between leaf structure and function. *New Phytologist*, *134*(1), 35–51. https://doi.org/10.1111/j.1469-8137.1996.tb01144.x

Blasini, D. E., Koepke, D. F., Bush, S. E., Allan, G. J., Gehring, C. A., Whitham, T. G., Day, T. A., & Hultine, K. R. (2022). Tradeoffs between leaf cooling and hydraulic safety in a dominant arid land riparian tree species. *Plant, Cell and Environment*, *45*(6), 1664–1681. https://doi.org/10.1111/pce.14292

Cao, J.-J., Chen, J., Yang, Q.-P., Xiong, Y.-M., Ren, W.-Z., & Kong, D.-L. (2023). Leaf hydraulics coordinated with leaf economics and leaf size in mangrove species along a salinity gradient. *Plant Diversity*, *45*(3), 309–314. https://doi.org/10.1016/j.pld.2022.01.002

Chaste, E., Girardin, M. P., Kaplan, J. O., Bergeron, Y., & Hély, C. (2019). Increases in heat-induced tree mortality could drive reductions of biomass resources in Canada's managed boreal forest. *Landscape Ecology*, *34*(2), 403–426. https://doi.org/10.1007/s10980-019-00780-4

CMA Climate Change Centre. (2022). *Blue book on climate change in China (2022)*. Science Press.

Curtis, E. M., Leigh, A., & Rayburg, S. (2012). Relationships among leaf traits of Australian arid zone plants: Alternative modes of thermal protection. *Australian Journal of Botany*, *60*(6), 471–483. https://doi.org/10.1071/BT11284

Czaja, M., Kołton, A., & Muras, P. (2020). The complex issue of urban trees-stress factor accumulation and ecological service possibilities. *Forests*, *11*(9), 1–24. https://doi.org/10.3390/F11090932

Daas, C., Montpied, P., Hanchi, B., & Dreyer, E. (2008). Responses of photosynthesis to high temperatures in oak saplings assessed by chlorophyll-a fluorescence: Inter-specific diversity and temperature-induced plasticity. *Annals of Forest Science*, *65*(3), 305. https://doi.org/10.1051/forest:2008002

Defraeye, T., Verboven, P., Ho, Q. T., & Nicolai, B. (2013). Convective heat and mass exchange predictions at leaf surfaces: Applications, methods and perspectives. *Computers and Electronics in Agriculture*, *96*, 180–201. https://doi.org/10.1016/j.compag.2013.05.008

13652435, 2024, 7, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.14562 by Guangxi University, Wiley Online Library on [15/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Doughty, C. E., Keany, J., Rey-Sanchez, C., Carter, K. R., Cheesman, A. W., Goulden, M. L., da Rocha, H. R., Malhi, Y., Crous, K. Y., Fauset, S., Slot, M., Oliveras, I., Goldsmith, G. R., & Fisher, J. B. (2023). Tropical forests are approaching critical temperature thresholds. *Nature*, *621*(7977), 105–111. https://doi.org/10.1038/s41586-023-06391-z

Drake, J. E., Tjoelker, M. G., Vårhammar, A., Medlyn, B. E., Reich, P. B., Leigh, A., Pfautsch, S., Blackman, C. J., López, R., Aspinwall, M. J., Crous, K. Y., Duursma, R. A., Kumarathunge, D., De Kauwe, M. G., Jiang, M., Nicotra, A. B., Tissue, D. T., Choat, B., Atkin, O. K., & Barton, C. V. M. (2018). Trees tolerate an extreme heatwave via sustained transpirational cooling and increased leaf thermal tolerance. *Global Change Biology*, *24*(6), 2390–2402. https://doi.org/10.1111/gcb.14037

Duarte, A. G., Katata, G., Hoshika, Y., Hossain, M., Kreuzwieser, J., Arneth, A., & Ruehr, N. K. (2016). Immediate and potential long-term effects of consecutive heat waves on the photosynthetic performance and water balance in Douglas-fir. *Journal of Plant Physiology*, *205*, 57–66. https://doi.org/10.1016/j.jplph.2016.08.012

Eamus, D. (1999). Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology & Evolution*, *14*(1), 11–16. https://doi.org/10.1016/S0169-5347(98)01532-8

Esperon-Rodriguez, M., Power, S. A., Tjoelker, M. G., Marchin, R. M., & Rymer, P. D. (2021). Contrasting heat tolerance of urban trees to extreme temperatures during heatwaves. *Urban Forestry & Urban Greening*, *66*, 127387. https://doi.org/10.1016/j.ufug.2021.127387

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Godoy, O., de Lemos-Filho, J. P., & Valladares, F. (2011). Invasive species can handle higher leaf temperature under water stress than Mediterranean natives. *Environmental and Experimental Botany*, *71*(2), 207–214. https://doi.org/10.1016/j.envexpbot.2010.12.001

Groom, P. K., Lamont, B. B., Leighton, S., Leighton, P., & Burrows, C. (2004). Heat damage in sclerophylls is influenced by their leaf properties and plant environment. *Ecoscience*, *11*(1), 94–101. https://doi.org/10.1080/11956860.2004.11682813

Grossman, J. J. (2023). Phenological physiology: Seasonal patterns of plant stress tolerance in a changing climate. *New Phytologist*, *237*(5), 1508–1524. https://doi.org/10.1111/nph.18617

Guha, A., Han, J., Cummings, C., McLennan, D. A., & Warren, J. M. (2018). Differential ecophysiological responses and resilience to heat wave events in four co-occurring temperate tree species. *Environmental Research Letters*, *13*(6), 065008. https://doi.org/10.1088/1748-9326/aabcd8

Gunderson, A. R., & Stillman, J. H. (2015). Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1808), 20150401. https://doi.org/10.1098/rspb.2015.0401

Jones, H. G. (2013). *Plants and microclimate*. Cambridge University Press. https://doi.org/10.1017/CBO9780511845727

Kitudom, N., Fauset, S., Zhou, Y., Fan, Z., Li, M., He, M., Zhang, S., Xu, K., & Lin, H. (2022). Thermal safety margins of plant leaves across biomes under a heatwave. *Science of the Total Environment*, *806*, 150416. https://doi.org/10.1016/j.scitotenv.2021.150416

Knight, C. A., & Ackerly, D. D. (2003). Evolution and plasticity of photosynthetic thermal tolerance, specific leaf area and leaf size: Congeneric species from desert and coastal environments. *New Phytologist*, *160*(2), 337–347. https://doi.org/10.1046/j.1469-8137.2003.00880.x

Kröber, W., Heklau, H., & Bruelheide, H. (2015). Leaf morphology of 40 evergreen and deciduous broadleaved subtropical tree species and relationships to functional ecophysiological traits. *Plant Biology*, *17*(2), 373–383. https://doi.org/10.1111/plb.12250

Kullberg, A. T., & Feeley, K. J. (2022). Limited acclimation of leaf traits and leaf temperatures in a subtropical urban heat Island. *Tree Physiology*, *42*(11), 2266–2281. https://doi.org/10.1093/treephys/tpac066

Leigh, A., Sevanto, S., Ball, M. C., Close, J. D., Ellsworth, D. S., Knight, C. A., Nicotra, A. B., & Vogel, S. (2012). Do thick leaves avoid thermal damage in critically low wind speeds? *New Phytologist*, *194*(2), 477–487. https://doi.org/10.1111/j.1469-8137.2012.04058.x

Leigh, A., Sevanto, S., Close, J. D., & Nicotra, A. B. (2017). The influence of leaf size and shape on leaf thermal dynamics: Does theory hold up under natural conditions? *Plant, Cell and Environment*, *40*(2), 237–248. https://doi.org/10.1111/pce.12857

Li, X., Wen, Y., Chen, X., Qie, Y., Cao, K. F., & Wee, A. K. S. (2022). Correlations between photosynthetic heat tolerance and leaf anatomy and climatic niche in Asian mangrove trees. *Plant Biology*, *24*(6), 960–966. https://doi.org/10.1111/plb.13460

Lin, H., Chen, Y., Zhang, H., Fu, P., & Fan, Z. (2017). Stronger cooling effects of transpiration and leaf physical traits of plants from a hot dry habitat than from a hot wet habitat. *Functional Ecology*, *31*(12), 2202–2211. https://doi.org/10.1111/1365-2435.12923

Luján, R., LledÍas, F., MartÍnez, L. M., Barreto, R., Cassab, G. I., & Nieto-Sotelo, J. (2009). Small heat-shock proteins and leaf cooling capacity account for the unusual heat tolerance of the central spike leaves in *Agave tequilana* var. Weber. *Plant, Cell and Environment*, *32*(12), 1791–1803. https://doi.org/10.1111/j.1365-3040.2009.02035.x

Marchin, R. M., Backes, D., Ossola, A., Leishman, M. R., Tjoelker, M. G., & Ellsworth, D. S. (2022). Extreme heat increases stomatal conductance and drought-induced mortality risk in vulnerable plant species. *Global Change Biology*, *28*(3), 1133–1146. https://doi.org/10.1111/gcb.15976

Marchin, R. M., Esperon-Rodriguez, M., Tjoelker, M. G., & Ellsworth, D. S. (2022). Crown dieback and mortality of urban trees linked to heatwaves during extreme drought. *Science of the Total Environment*, *850*, 157915. https://doi.org/10.1016/j.scitotenv.2022.157915

Markesteijn, L., Poorter, L., Paz, H., Sack, L., & Bongers, F. (2011). Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell and Environment*, *34*(1), 137–148. https://doi.org/10.1111/j.1365-3040.2010.02231.x

Nairn, J. R., & Fawcett, R. J. B. (2014). The excess heat factor: A metric for heatwave intensity and its use in classifying heatwave severity. *International Journal of Environmental Research and Public Health*, *12*(1), 227–253. https://doi.org/10.3390/ijerph120100227

Niinemets, Ü. (2010). Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management*, *260*(10), 1623–1639. https://doi.org/10.1016/j.foreco.2010.07.054

O'sullivan, O. S., Heskel, M. A., Reich, P. B., Tjoelker, M. G., Weerasinghe, L. K., Penillard, A., Zhu, L., Egerton, J. J. G., Bloomfield, K. J., Creek, D., Bahar, N. H. A., Griffin, K. L., Hurry, V., Meir, P., Turnbull, M. H., & Atkin, O. K. (2017). Thermal limits of leaf metabolism across biomes. *Global Change Biology*, *23*(1), 209–223. https://doi.org/10.1111/gcb.13477

Perez, T. M., & Feeley, K. J. (2020). Photosynthetic heat tolerances and extreme leaf temperatures. *Functional Ecology*, *34*(11), 2236–2245. https://doi.org/10.1111/1365-2435.13658

Perkins-Kirkpatrick, S. E., & Lewis, S. C. (2020). Increasing trends in regional heatwaves. *Nature Communications*, *11*(1), 1–8. https://doi.org/10.1038/s41467-020-16970-7

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Ribeiro, D. R., Silva, J. L. A., do Nascimento, M. T., & Vitória, A. P. (2022). Leaf habits and their relationship with leaf and wood traits in tropical dry forests. *Trees-Structure and Function*, *36*(1), 7–24. https://doi.org/10.1007/s00468-021-02200-0

13652435, 2024, 7, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.14562 by Guangxi University, Wiley Online Library on [15/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Sanusi, R., & Livesley, S. J. (2020). London plane trees (*Platanus × acerifolia*) before, during and after a heatwave: Losing leaves means less cooling benefit. *Urban Forestry & Urban Greening*, *54*, 126746. https://doi.org/10.1016/j.ufug.2020.126746

Sastry, A., & Barua, D. (2017). Leaf thermotolerance in tropical trees from a seasonally dry climate varies along the slow-fast resource acquisition spectrum. *Scientific Reports*, *7*(1), 11246. https://doi.org/10.1038/s41598-017-11343-5

Sastry, A., Guha, A., & Barua, D. (2018). Leaf thermotolerance in dry tropical forest tree species: Relationships with leaf traits and effects of drought. *AoB Plants*, *10*(1), 1–13. https://doi.org/10.1093/aobpla/plx070

Scheffers, B. R., Edwards, D. P., Macdonald, S. L., Senior, R. A., Andriamahohatra, L. R., Roslan, N., Rogers, A. M., Haugaasen, T., Wright, P., & Williams, S. E. (2017). Extreme thermal heterogeneity in structurally complex tropical rain forests. *Biotropica*, *49*(1), 35–44. https://doi.org/10.1111/btp.12355

Shi, Z., Jia, G., Zhou, Y., Xu, X., & Jiang, Y. (2021). Amplified intensity and duration of heatwaves by concurrent droughts in China. *Atmospheric Research*, *261*, 105743. https://doi.org/10.1016/j.atmosres.2021.105743

Slot, M., Cala, D., Aranda, J., Virgo, A., Michaletz, S. T., & Winter, K. (2021). Leaf heat tolerance of 147 tropical forest species varies with elevation and leaf functional traits, but not with phylogeny. *Plant, Cell and Environment*, *44*(7), 2414–2427. https://doi.org/10.1111/pce.14060

Slot, M., & Winter, K. (2017). *In situ* temperature response of photosynthesis of 42 tree and liana species in the canopy of two Panamanian lowland tropical forests with contrasting rainfall regimes. *New Phytologist*, *214*(3), 1103–1117. https://doi.org/10.1111/nph.14469

Teskey, R., Wertin, T., Bauweraerts, I., Ameye, M., McGuire, M. A., & Steppe, K. (2015). Responses of tree species to heat waves and extreme heat events. *Plant, Cell and Environment*, *38*(9), 1699–1712. https://doi.org/10.1111/pce.12417

Tiwari, R., Gloor, E., da Cruz, W. J. A., Schwantes Marimon, B., Marimon-Junior, B. H., Reis, S. M., de Souza, I. A., Krause, H. G., Slot, M., Winter, K., Ashley, D., Béu, R. G., Borges, C. S., Da Cunha, M., Fauset, S., Ferreira, L. D. S., Gonçalves, M. D. A., Lopes, T. T., Marques, E. Q., … Galbraith, D. (2021). Photosynthetic quantum efficiency in south-eastern Amazonian trees may be already affected by climate change. *Plant, Cell and Environment*, *44*(7), 2428–2439. https://doi.org/10.1111/pce.13770

Tserej, O., & Feeley, K. J. (2021). Variation in leaf temperatures of tropical and subtropical trees are related to leaf thermoregulatory traits and not geographic distributions. *Biotropica*, *53*(3), 868–878. https://doi.org/10.1111/btp.12919

Wang, H., Colin Prentice, I., Wright, I. J., Warton, D. I., Qiao, S., Xu, X., Zhou, J., Kikuzawa, K., & Stenseth, N. C. (2023). Leaf economics fundamentals explained by optimality principles. *Science Advances*, *9*(3), 1–11. https://doi.org/10.1126/sciadv.add5667

Wang, J., Yan, R., Wu, G., Liu, Y., Wang, M., Zeng, N., Jiang, F., Wang, H., He, W., Wu, M., Ju, W., & Chen, J. M. (2023). Unprecedented decline in photosynthesis caused by summer 2022 record-breaking compound drought-heatwave over Yangtze River basin. *Science Bulletin*, *68*(19), 2160–2163. https://doi.org/10.1016/j.scib.2023.08.011

Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Díaz, S., Gallagher, R. V., Jacobs, B. F., Kooyman, R., Law, E. A., Leishman, M. R., Niinemets, Ü., Reich, P. B., Sack, L., Villar, R., Wang, H., & Wilf, P. (2017). Global climatic drivers of leaf size. *Science*, *357*(6354), 917–921. https://doi.org/10.1126/science.aal4760

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. https://doi.org/10.1038/nature02403

Yordanov, I. (1992). Response of photosynthetic apparatus to temperature stress and molecular mechanisms of its adaptations. *Photosynthetica*, *26*, 517–531. https://api.semanticscholar.org/CorpusID:89103823

SUPPORTING INFORMATION

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

Figure S1: Distribution of extreme high temperature event in China from 1 June to 15 August 2022.

Figure S2: The relationships between leaf damage ratio and Tcrit from different definitions.

Figure S3: The relationship between day-weighted average of the excess heat factor and leaf damage ratio.

Figure S4: The relationships between leaf damage ratio and T50, Tcrit, TSM50 and TSMcrit.

Figure S5: The relationships between Tcrit and leaf mass per area, leaf area, leaf thickness, thickness of spongy tissue.

Figure S6: The relationships between Tcrit and thickness of upper epidermis, thickness of lower epidermis, thickness of palisade tissue and palisade to spongy mesophyll thickness ratio.

Figure S7: The relationships between Tcrit and guard cell length, stomata density and stomata pore area index.

Table S1: Species names, leaf habit and diameter at breast height (DBH) of the 36 species measured in this study.

Table S2: Different definitions to calculate Tcrit.

Table S3: Summary on ANOVA of the effects of the day-weighted average of the excess heat factor (day-weighted EHF), leaf habit and their interaction on leaf damage ratio, heat tolerance and structural traits.

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