Dry-Heat Tolerance of Common Tree Species in a Central Chinese City: Responses to Heterogeneous Habitat Characteristics

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Article

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Abstract

Global warming has intensified the occurrence of dry heatwaves, and the heterogeneous urban habitats can influence trees' tolerance to dry-heat conditions, however the specific mechanisms remain unclear. This research investigated the dry-heat tolerance of nine common trees in Wuhan, a central Chinese city facing persistent heatwave threats, and explored the multifactorial influence of urban habitat variations on trees' dry-heat tolerance. Diverse habitat sites with the sample plots in various spatial scales were established for each tree species. Dry-heat tolerance was evaluated through visual assessment, measuring the degree of leaf damage during a historic dry heatwave event. A significant interspecific difference was observed in trees' dry-heat tolerance, with *Pittosporum tobira* exhibiting the highest dry-heat tolerance, while *Prunus × yedoensis* displayed the lowest, in relevance to the life forms and provenances of species. And the dry-heat tolerance of trees in a specific species varied across various habitats, influenced by surrounding building enclosure and land cover composition. The Degree of Building Enclosure was the most prominent habitat factor, followed by the Percentage of Canopy Coverage and the Percentage of Grove Area, all of which positively affected tree tolerance, in contrast with the Percentage of Impermeable Surface showing a negative effect. In addition, the scale effect was evident, that the 50m and 100m range were identified as the most effective spatial scale of campus habitats affecting trees' dry-heat tolerance, especially for the species with weaker tolerance. The findings can support the selection of tree species and optimization of artificial habitats to enhance the heatwave resilience of urban vegetation in central Chinese cities.

Introduction

The introduction should not include subheadings. Urban trees have garnered considerable attention for their ecological benefits in carbon sequestration and microclimate moderation [1–3], which contribute to the migitation of climate risks in urban settlements[4]. However, the exacerbation of global warming has intensified the occurrence of extreme climate events, particularly heatwaves and droughts, posing unprecedented threats to the growth and adaptation of urban trees [5, 6].

In recent years, heatwaves have often been accompanied by lower relative humidity, a phenomenon termed "dry heatwaves" [7, 8]. Compared to the period before the 1970s, the frequency of simultaneous occurrence of summer heatwaves and droughts in China has increased tenfold in the 21st century [9]. And the historic dry heatwaves attacking the middle and lower reaches of the Yangtze River during the summer of 2022 has led to extensive forest mortality in Central China [10], which is anticipated to suffer even more from dry heatwaves in the future[11]. When trees experience heatwaves in conjection with drought conditions, additional challenges arise [12]. Dry heatwaves can exacerbate trees' energy load and water deficienty, rendering them more susceptible to environmental stresses [13, 14].

Urban trees exhibit substantial interspecific variability in their tolerance to dry heatwaves, referred to as "dry-heat tolerance" in abbreviation [15]. With the increasing prevalence of dry heatwave occurrences, the idenification of tree species possessing high dry-heat tolerance is crucial for enhancing the climate resilience of urban vegetation. Methods for assessing the responsive dry-heat tolerance of trees primarily involved physiological indicator measurement and visual tree assessment. Physiological measurement evaluates the dry-heat tolerance of tree individuals mainly based on parameters indicating photosynthetic and water use efficiency, conducted in controlled experiments or field investiations [16–19]. Visual tree assessment (VTA) evaluates tree vitality under climate stress by visually assessing the degree of morphological damage or abnormality for tree individuals, with higher vitality indicating greater tree tolerance [20–24]. Crown and leaf damage are considered important indicators for visual tree assessment, given that leaf damage is one of the most sensitive symptoms of plants in response to environmental hydrothermal stresses [25, 26]. By scoring the percentage of leaf wiltering, scorch, discoloration, and defoliation, the morphorlogical tolerance of various urban tree species to heatwave or drought threats has been evaluated in Japan [27], China [28], Australia [19, 29], and Central Europe [25]. Based on the long-term monitoring of crown dynamics in size, density, and epicormic growth, Callow evaluated the response characteristics of Holly Oak trees (*Quercus ilex*) to prolonged drought [26]. In addition to crown damage, damage symptoms on branches, stems, and other parts of the tree were also utilized in the tolerance assessment [30–32]. Visual tree assessment, as a straightforward and efficient method to evaluate trees' health condition and morphological response to environmental stresses, can reflect the direct impacts of climate threats on the landscape of urban forests.

Urban habitats act as predisposing factors influencing tree responses to climate change [23]. The adverse conditions prevalent in urban settings, such as shading, limited growing spaces, and conflicts with surrounding artificial infrastructure, can diminish tree vitality and further exacerbate the vulnerability of urban trees to climate change [33–36]. On the other hand, specific aspects of urban habitats may also provide refuge for certain tree species, potentially mitigating the adverse effects of climate change [37], and even offering essential resources for the conservation of threatened species [38].

Previous studies have examined the impacts of specific habitat charactersitics on the growth and adaptability of urban trees. Notable investigations have focused on variables such as the type of urban green spaces [39–41], as well as the impermeability of underlying surfaces Some scholars further explored how urban habitats influence trees' responses to extreme climates [42]. For instance, Savi illustrated the correlation between the drought tolerance of Holm oak trees (*Quercus ilex*) and the proportion of impermeable surface at planting sites [43].

Rahman observed divergent transpiration water loss in small-leaved Lime trees (*Tilia cordata*) growing in different types of squares with varying degree of building enclosure under the summer heat stress in Munich, Germany [44].

The aforementioned studies mainly explored the impact of the variation in single habitat factor on the growth and acclimation of urban trees, however, the comprehensive impact mechanism of multiple habitat factors as a integrity remains unclear for typical urban settlements. And furthre investigation into the multifaceted comprehensive influence is imperative for illustrating how heterogeneous urban environment is shaping trees' tolerance to climate threats. Among the diverse habitat types in urban built-up areas, campus habitats are distinguished by the integration of fragmented green-blue spaces, impervious surfaces and buildings, reflecting the typical characteristics of high-density habitat types such as residential and commercial areas [45]. Therefore, campus environments can offer ideal settings for exploring the influence of habiat features on tree heat tolerance in densely pupulated and constructed urban settlements.

This study was conducted in a university campus green space in Wuhan, where heat risks are prevalent and escalating. Employing visual tree assessment method, we quantitatively measured the dry-heat tolerance of common urban tree species in response to a recent historic dry heatwave event, and explored the multifactorial impact mechanism of habitat characteristics on tree heat tolerance. Our objective is to elucidate the varying degrees of dry-heat tolerance among different tree species, reveal the key habitat factors influencing the dry-heat tolerance, and identify the spatial scales of habitat with the most prominent effects. The findings are expected to provide strategic insights for enhancing the climate resilience of urban vegetation in central Chinese cities.

Material and Methods

Research site

The research site is located in Wuhan, China (29°58'N-31°22'N, 113°41'E-115°05'E), situated in the central region of the country on the plain of the middle reaches of the Yangtze River. The local forests are primarily constituted with evergreen and deciduous broad-leaved tree species, interspersed with some coniferous ones. Wuhan's climate falls under the realm of the North Subtropical Monsoon Climate, characterized by chilly winters and scorching summers. According to the meteorology data from the Wuhan National Meteorological Observatory, the number of scorching days and the average temperature during the summer of 2022 in Wuhan were significantly higher than the long-term average, breaking the previous high-temperature records since 1961. A typical dry heatwave occurred from August 1st to August 23rd, with daily maximum temperatures consistently exceeding 35°C and extreme peaks reaching 40°C, accompanied by no rainfall.

The research was conducted in the educational and residential districts of Huazhong Agricultural University (HZAU), covering a flat terrain spanning 265 km^2. As shown in Fig. 1, the heterogeneous underlying surface composed of green-blue spaces, impervious surfaces and buildings, provides diverse habitats for tree growth. The campus hosts a diverse array of tree species, representative of common species in Wuhan. Many mature trees were planted 20–30 years ago, exhibiting consistent size and sourcing of seedling, as well as a robust state of health. These trees have endured harsh onslaught from the heatwave event in 2022 with less artificial intervention until responsive irrigation measures were implemented at the later phase of the heatwave stress.

Research objects

The research objects selected nine most common urban tree species in Wuhan, widely distributed across diverse habitats within the campus. These species include *Pittosporum tobira* (Japanese Cheesewood), *Cercis chinensis* (Chinese Redbud), *Magnolia grandiflora* (Southern Magnolia), *Camphora officinarum* (Camphor Tree), *Prunus × yedoensis* (Tokyo Cherry), *Ginkgo biloba* (Ginkgo), *Platanus acerifolia* (London Plane), *Koelreuteria bipinnata* (Chinese Flame Tree), and *Metasequoia glyptostroboides* (Dawn Redwood), as detailed in Table 1. At least 5 sample trees were selected from each habitat site for every species, adhering to the following criteria: i) Mature individuals of similar ages, characterized with relatively consistent diameter at breast height and tree height. ii) Robust individuals without evident crown bias or damage, free from diseases and pests.

Table 1
Information of the studied tree species

Latin name	abbreviation	Life form		Origin	Areal-types of genera
Pittosporum tobira	*Pto.*	Shrub	Evergreen	Native	Old World Tropical
Cercis chinensis	*Cch.*	Shrub	Deciduous	Exotic	North Temperate
Magnolia grandiflora	*Mgr.*	Arbor	Evergreen	Exotic	East. Asia & North. American Disjuncted
Camphora officinarum	*Cof.*	Arbor	Evergreen	Native	Tropical Asia & Trop. Australasia
Prunus × yedoensis	*Pve.*	Arbor	Deciduous	Exotic	North Temperate
Ginkgo biloba	*Gbi.*	Arbor	Deciduous	Native	North Temperate
Platanus acerifolia	*Pac.*	Arbor	Deciduous	Exotic	North Temperate
Koelreuteria bipinnata	*Kbi.*	Arbor	Deciduous	Native	East. Asia
Metasequoia glyptostroboides	*Mgl.*	Arbor	Deciduous	Native	North Temperate

"Origin" refers to the original natural distribution range of trees. Tree species are classified as indigenous species or exotic species based on whether they originate from China [46]. "Areal-type of genera" refers to the distinct geographical patterns of genera distribution, reflecting the ecological and evolutionary processes that influence where genera are found. The information of areal-types of genera for the studied species was derived from Wu [47].

Setting of Sample Plots

For each tree species, eight habitat sites were selected, varying in the composition and structure of underlying surface. Sample plots with ranges of 50m, 100m, 150m, and 200m were established at each habitat site, as illustrated in Fig. 2. The scale setting of the sample plots took reference from the revealed spatial scale of urban habitat in affecting microclimate [48–50], along with the characteristics of the sites' underlying surface.

Evaluation of Tree Dry-Heat Tolerance

The dry-heat tolerance of sample trees was evaluated using visual tree assessment, based on the degree of crown leaf damage or abnormality at the end of the 2022 heatwave event (before effective irrigation measures were implemented). This evaluation involved three symptom indicators: leaf discoloration, leaf wilting and leaf fall. Each indicator was scored from 0 to 10, with scoring criteria shown in Table 2. Considering the varying severity of tree damage reflected by the three indicators — specifically, leaf fall > leaf discoloration > leaf wilting— they are weighted with 0.5, 0.3, and 0.2 respectively. And the weighted average score represents the dry-heat tolerance of each sample tree.

Table 2
Indicator scoring criteria for evaluating the dry-heat tolerance of trees

Indicators	Score range	Symptoms of tree leaf damage
Leaf wilting	8 ~ 10	0 ~ 20% of the leaves are wilting, with slight curling at the edges.
	6 ~ 8	20% ~ 40% of the leaves are wilting, with slight drooping at the edges, which can recover in the short term.
	4 ~ 6	40% ~ 60% of the leaves are wilting and drooping, irreversibly.
	2 ~ 4	60% ~ 80% of the leaves are wilting and drooping, irreversibly.
	0 ~ 2	More than 80% of the leaves are wilting and drooping, irreversibly.
Leaf discoloration	8 ~ 10	0 ~ 20% of the leaves turn yellowing, with overall normal appearance.
	6 ~ 8	20% ~ 40% of the leaves turn yellow, with discoloration appearing along leaf tips and margins, accompanied by occasional scorched points.
	4 ~ 6	40% ~ 60% of the leaves turn yellow, with intensified discoloration along leaf tips and margins, accompanied by marginal scorching.
	2 ~ 4	60% ~ 80% of the leaves turn yellow, showing patchy scorching.
	0 ~ 2	More than 80% of the leaves turn yellow, with extensive browning and desiccation.
Leaf fall	8 ~ 10	0 ~ 20% of the leaves have fallen.
	6 ~ 8	20% ~ 40% of the leaves have fallen.
	4 ~ 6	40% ~ 60% of the leaves have fallen, exposing some small branches.
	2 ~ 4	60% ~ 80% of the leaves have dropped, resulting in sparse canopy.
	0 ~ 2	More than 80% of the leaves have fallen, leaving the branches completely bare.

Evaluation of Habitat Characteristics

Two categories of structural indicators, including land cover composition and spatial enclosure, were selected to quantify the characteristics of campus habitats. To evaluate the land cover composition, we categorized the underlying surface of campus habitats into different land cover types, and calculated the proportional area of each type in the sample plots. This enables us to derive seven habitat factors: percentage of canopy coverage (PerCC), percentage of grove area (PerGA), percentage of canopy-covered impervious surface area (PerCS), percentage of lawn area (PerLA), percentage of building area (PerBA), percentage of impervious surface area (PerIS), and percentage of water area (PerWA). Each factor is detailed in Table 3.

Table 3
The habitat factors indicating land cover composition

Habitat Factors	Abbreviation	Definition
Percentage of Canopy Coverage	PerCC	The percentage of the total area covered by vertical projection of tree crowns.
Percentage of Grove Area	PerGA	The percentage of the total area of groves or forestland.
Percentage of Canopy-Covered Impervious Surface Area	PerCS	The percentage of the total area of impervious surface covered with tree canopy.
Percentage of Lawn Area	PerLA	The percentage of the total area of open lawn without canopy cover.
Percentage of Building Area	PerBA	The percentage of the building footprint area.
Percentage of Impervious Surface Area	PerIS	The percentage of the total area of impervious artificial surfaces, including roads and paved squares, without canopy cover.
Percentage of Water Area	PerWA	The percentage of the total area of water bodies, such as lakes.

The spatial enclosure characteristics of campus habitats was quantified by the degree of building enclosure (DegBE). Serving as a morphological indicator of external spaces, DegBE refers to the extent of all-directions enclosure primarily created by buildings surrounding trees within a specific spatial range. It is derived from aspect ratio (H/W) and plan enclosure rate (L/C) that are commonly utilized to evaluate the spatial enclosure of typical urban open spaces like street canyons [51], and calculated using formula (1).

$$DegBE = \sum_{i=1}^{n} \frac{H_i}{D_i} * \frac{\alpha_i}{360} (1)$$

where H_i respectively refers to the height of Building i (m), D_i refers to the minimum horizontal distance between the sample tree and the facade of Building i (m), α_i refers to the horizontal enclosed angle between the sample tree and the facade of Building i (°), i refers to the number of buildings surrounding sample trees, as illustrated as Fig. 3. The data for these parameters were obtained through field measurement and visual interpretation of drone aerial images.

Statistical analysis

The interspecific difference in dry-heat tolerance among urban tree species was investigated through one-way analysis of variance (ANOVA) and multiple comparisons. Linear regression analysis was employed to explore the influence of habitat characteristics on the dry-heat tolerance of sample trees for specific tree species. Univariate correlation analysis was conducted to identify key habitat factors posing significant impacts on the dry-heat tolerance, and multiple regression analysis was performed to elucidate the multifactorial impact mechanism of campus habitat. The optimal regression equation between habitat factors and tree tolerance was selected for each tree species at every spatial scale, based on the significance (p) and goodness of fit (R^2) of the equation, which indicates the overall sensitivity of tree dry-heat tolerance to habitat variation. Higher sensitivity was identified when the equation was significant ($p < 0.05$) with a higher R^2 value.

Results

Interspecific difference in the dry-heat tolerance of urban tree species

A significant interspecific difference in dry-heat tolerance was observed among various tree species. Based on their dry-heat tolerance, the nine tree species can be classified into three groups. Group 1 includes *P. tobira* and *M. grandiflora*, exhibiting the highest dry-heat tolerance with mean values above 7; Group 2 consists of *K. bipinnata*, *P. acerifolia*, and *C. officinarum*, showing moderate dry-heat tolerance with mean values of 5–6; Group 3 consists of *C. chinensis*, *M. glyptostroboides*, *G. biloba*, and *P. yedoensis*, displaying lower dry-heat tolerance with mean values of 3–5, with *G. biloba* and *P. yedoensis* exhibiting the lowest. The dry-heat tolerance of species in Group 1 is significantly higher than that of Group 3, as depicted in Fig. 4. Detailed values of dry-heat tolerance for different tree species in every habitat site are presented in Table 4.

The dry-heat tolerance of tree species was found to be correlated with their life forms and geographical provenance. Evergreen species exhibited significantly higher dry-heat tolerance than deciduous species ($p < 0.05$), indicating distinct adaptive strategies. While shrub species generally displayed higher dry-heat tolerance than arbor species, this difference did not reach statistical significance. Regarding geographical provenance, native tree species exhibited insignificantly higher dry-heat tolerance compared to exotic species. Further evidence of geographical influence was seen in the tolerance variations observed among species with different areal-types of genera. Specifically, the dry-heat tolerance of tree species with genera originating from North Temperate region was notably lower compared to those from Old World Tropical region, East. Asia & North. American Disjuncted and Tropical Asia & Trop. Australasia region ($p < 0.05$). This suggests that species with genera from tropical origins tend to demonstrate superior resilience in coping with heatwave stress.

Table 4
Dry-heat tolerance of various tree species.

Species	Habitat code	Dry-heat tolerance	Mean Value	Species	Habitat code	Dry-heat tolerance	Mean Value	Species	Habitat code	Dry-heat tolerance	Mean Value
G. biloba	1	7.33	3.74 ± 3.80	*P. tobira*	1	9.67	7.23 ± 2.20	*M. glyptostroboides*	1	8.67	4.02 ± 3.10
	2	10.00			2	9.33			2	4.18	
	3	3.00			3	9.20			3	3.00	
	4	0.00			4	9.00			4	3.67	
	5	0.19			5	6.33			5	2.00	
	6	0.00			6	5.33			6	3.33	
	7	4.67			7	4.67			7	0.00	
	8	4.76			8	4.33			8	7.33	
K. bipinnata	1	9.67	5.90 ± 2.53	*C. chinensis*	1	6.33	4.57 ± 2.40	*C. officinarum*	1	7.73	5.47 ± 2.34
	2	6.33			2	6.00			2	2.00	
	3	4.75			3	5.33			3	3.74	
	4	3.09			4	5.00			4	7.41	
	5	8.67			5	5.00			5	7.33	
	6	2.67			6	3.33			6	4.67	
	7	5.33			7	1.00			7	6.67	
	8	6.67			—	—			8	4.20	
P. yedoensis	1	7.33	3.28 ± 2.81	*P. acerifolia*	1	8.00	5.80 ± 2.64	*M. Grandiflora*	1	8.33	7.14 ± 1.80
	2	2.60			2	6.67			2	8.00	
	3	3.67			3	2.67			3	6.33	
	4	2.86			4	7.83			4	9.67	
	5	4.67			5	7.33			5	7.67	
	6	2.78			6	7.84			6	6.00	
	7	2.33			7	4.72			7	4.00	
	8	0.00			8	1.33			—	—	

"—" indicates data loss due to the absence of available habitat sites.

Response of trees' dry-heat tolerance to habitat variation

The intra-specific variation in the dry-heat tolerance of sample trees was clearly evident across different habitats, with the variation being most pronounced for *G. biloba* and least apparent for *M. grandiflora*. To unveil the mechanism underlying the spatial variation, we explored the influence of habitat characteristics on the dry-heat tolerance of trees using linear regression analysis.

(1) Key habitat factors and their combined effects on trees' dry-heat tolerance

The correlation between trees' dry-heat tolerance and various habitat factors was analyzed for specific tree species. Among these factors, DegBE (Degree of Building Enclosure) showed a significant positive impact on the dry-heat tolerance of trees for most species, especially within the 50m and 100m scales. Other influential factors include PerGA (Percentage of Grove Area), PerCC (percentage of Canopy Coverage), and PerIS (Percentage of Impervious Surface Area), as illustrated in Fig. 5. DegBE, PerGA and PerCC showed positive effects, indicating their roles in mitigating dry-heat stress and enhancing the climate adaptation of trees. Conversely, PerIS exhibited a negative correlation with trees' dry-heat tolerance, suggesting that impervious surfaces are detrimental for trees in coping with dry-heat stress.

"—" indicates no significant correlation, "●" indicates a significant positive correlation at the 0.05 level, "●●" indicates a significant positive correlation at the 0.01 level, "●" indicates a significant negative correlation at the 0.05 level, and "●●" indicates a significant negative correlation at the 0.01 level.

Multiple regression analysis was conducted to explore the multifactorial impacts of habitat features on trees' dry-heat tolerance. Optimal regression equations for each species at various spatial scales were identified and presented in Table 5. The findings revealed that the variation in dry-heat tolerance among different habitats can be mainly explained by the combined effects of 24 habitat factors about building enclosure and surrounding green spaces, with varying magnitudes of effect for different habitat factors. At the 50m scale, PerCC emerged as the primary factor for *P. tobira*, *C. chinensis*, and *M. glyptostroboides*, with DegBE, PerIS, and PerGA playing a critical role for other species. At the 100m, 150m and 200m scales, however, the factor of DegBE was dominant for most species, exerting the highest explanatory power for trees' dry-heat tolerance, and other habitat factors acted as supplementary ones.

Table 5
Multivariate regression equations of trees' dry-heat tolerance against habitat factors for various tree species

Species	Spatial scale of sample plot	Optimal multiple regression equation	R^2	p
P. tobira	50m	Y = 0.77 PerCC* + 0.26 PerLA	0.676	0.026*
	100m	Y = 0.59 DegBE* + 0.48 PerCC − 0.27 PerCS	0.855	0.013*
	150m	Y = 0.87 DegBE* − 0.40 PerTS	0.717	0.018*
	200m	Y = 0.83 DegBE* − 0.15 PerIS	0.733	0.016*
C. chinensis	50m	Y = 0.92 PerCC** + 0.13 DegBE	0.956	0.001**
	100m	—	—	> 0.050
	150m	Y = 0.70 PerCS* − 0.37 PerGA	0.648	0.050*
	200m	—	—	> 0.050
G. biloba	50m	Y = 0.72 DegBE** + 0.56 PerCC* + 0.29 PerIS	0.832	0.017*
	100m	Y = 0.94 DegBE** + 0.24 PerGA	0.785	0.009**
	150m	Y = 0.71 DegBE* − 0.31PerGA	0.779	0.010**
	200m	Y = 0.79 DegBE** + 0.31 PerGA + 0.25 PerIS	0.872	0.010**
K. bipinnata	50m	Y = 0.85 PerGA* -0.36 PerCS	0.772	0.011*
	100m	Y = 0.73 DegBE** − 1.03 PerIS** − 0.63 PerLA*	0.925	0.003**
	150m	Y = 0.65 DegBE* − 0.37 PerIS	0.575	0.050*
	200m	—	—	> 0.050
M.Glyptostrob	50m	Y = 0.69 PerCC** + 0.85 DegBE* − 0.75 PerBA*	0.950	0.002**
-oides	100m	Y = 3.20 PerCC* − 0.76 PerBA* − 1.42 PerCS- 2.17 PerGA	0.825	0.049*
	150m	Y = 5.19 PerCC* − 2.91 PerCS* − 3.41 PerGA*- 0.63 PerLA	0.794	0.050*
	200m	—	—	> 0.050
P. yedoensis	50m	Y = − 0.76 PerIS* − 0.22 DegBE	0.803	0.007**
	100m	Y = 0.59 DegBE* + 0.48 PerCC − 0.27 PerCS	0.855	0.013*
	150m	Y = 0.69 DegBE* + 0.32 PerCC	0.796	0.008**
	200m	Y = 0.83 DegBE** − 0.15 PerIS	0.733	0.016*
P. acerifolia	50m	Y = − 0.90 PerIS** − 0.35 PerCS*	0.876	0.002**
	100m	Y = 0.72 DegBE* + 0.60 PerLA + 0.56 PerBA	0.801	0.023*
	150m	Y = 0.75 DegBE* − 0.57 PerCS	0.710	0.050*
	200m	Y = 0.67 PerCC* − 0.37 PerLA	0.712	0.019*
C. officinarum	50m	Y = 0.93 DegBE** + 0.48 PerGA	0.738	0.015*
	100m	Y = 0.88 DegBE* + 0.34 PerGA	0.743	0.034*
	150m	Y = − 0.99 PerIS* − 0.56 PerBA	0.609	0.041*
	200m	Y = 0.88 PerCS* − 0.49 PerLA − 0.46 PerGA	0.723	0.044*
M. grandiflora	50m	—	—	> 0.050
	100m	Y = 0.91 PerCS* + 0.54 PerIS	0.760	0.050*
	150m	—	—	> 0.050
	200m	—	—	> 0.050

"**" denotes a significant correlation at the 0.01 level, "*" denotes a significant correlation at 0.05 level "—" indicates that no significant regression equations were available at the spatial scale.

(2) Scale effects and interspecific difference in the sensitivity of dry-heat tolerance to habitat variation

The significance and goodness of fit (R^2) of the optimal regression equations were used to evaluate the overall sensitivity of a specific species' dry-heat tolerance to habitat variation at specific spatial scales. This sensitivity varied across different spatial scales. The R^2 values of multiple species at the 50m and 100m scales were observed to be higher compared to the 200m scale ($p > 0.05$) and 150m scale ($p < 0.05$), indicating that overall, the dry-heat tolerance of trees is most sensitive to the habitat variation at the 50m and 100m scales, a pivotal spatial scale for campus habitat in affecting trees' climate adaptation.

Significant interspecific differences existed in the sensitivity of trees' dry-heat tolerance in response to habitat variations. *G. biloba*, *P. yedoensis*, *P. acerifolia*, *C. officinarum*, and *P. tobira* all showed sensitive responses to habitat characteristics across four spatial scales, with average R^2 values of 0.82 ± 0.04, 0.80 ± 0.04, 0.77 ± 0.07, 0.75 ± 0.07, and 0.70 ± 0.05, respectively. *M. glyptostroboides* exhibited sensitivity to habitat characteristics at three spatial scales, with average R^2 value of 0.86 ± 0.06. Additionally, *C. chinensis* and *K. bipinnata* exhibited sensitivity to habitat characteristics at two spatial scales, with average R^2 values of 0.80 ± 0.15, and 0.76 ± 0.14, respectively. And *M. grandiflora* only showed sensitivity to habitat characteristics at the 150m spatial scale, with an R^2 value of 0.76. This suggests that the sensitivity of *G. biloba*, *P. yedoensis*, and *M. glyptostroboides*, which exhibit weaker dry-heat tolerance, to habitat variation is more pronounced, while *M. grandiflora* with the prominently higher dry-heat tolerance displayed the lowest sensitivity. Furthermore, the aforementioned sensitivity of a certain specie was found to be linked with its life form. The dry-heat tolerance of deciduous tree species exhibited higher sensitivity to habitat variations compared to evergreen tree species, especially with a significant difference at the 50m scale ($p < 0.05$).

Discussion

Interspecific difference in the dry-heat tolerance of urban tree species

This study elucidated the significant interspecies variability in the dry-heat tolerance of common urban tree species in Wuhan. Notably, *P. tobira* showed the highest dry-heat tolerance, whereas *G. biloba* and *P. yedoensis* exhibited the lowest, and the observed low tolerance of *G. biloba* to dry heatwaves aligns with the findings of Okubo [27]. Moreover, our investigation revealed that the dry-heat tolerance of tree species correlates with their life forms and geographical distribution.

The observed higher dry-heat tolerance of evergreen tree species compared to deciduous species concurs with the conclusion drawn by Okubo [27]. This variation can be ascribed to the inherent capacity of evergreen species to sustain photosynthetic stability under hydrothermal stresses, especially heat threat [52]. This research further revealed the superior dry-heat tolerance of species with tropical-origin genera like *P. tobira*, compared to those with temperate-origin genera such as *G. biloba* and *P. yedoensis*. Previous studies have also unveiled a correlation between the heat tolerance of tree species and the climate attributes of their natural distribution areas, suggesting that the species originating from warmer regions had stronger adaptation to heat stress [29, 53, 54]. In terms of the difference in tolerance between native and exotic species, we found that native tree species exhibited higher dry-heat tolerance compared to exotic counterparts, although the difference was not significant, consistent with the findings of Esperon-Rodriguez [19]. However, different viewpoints from other studies indicated that native species may possess markedly superior adaptability to extreme climates compared to exotic ones [55–57], or vice versa [58, 59]. Such divergent outcomes highlight the need for further exploration of the differences between indigenous and alien species in their climate adaptation against the backdrop of climate change.

Influence of habitat factors on trees' dry-heat tolerance

The dry-heat tolerance of trees in urban habitats is influenced not only by inherent species characteristics, but also by the enclosure structure of open spaces and land cover composition of underlying surface. This study found that the degree of building enclosure (DegBE) posed a significant positive impact on trees' dry-heat tolerance for most investigated species, consistent with the findings of Rahman [44]. They observed that *Tilia cordata* growing on a plaza with a circular enclosure by buildings showed lower transpiration water loss in response to summer heatwaves compared to those growing on a counterpart plaza enclosed on two sides, indicating a stronger heat resilience. This correlation is closely associated with the impact of spatial enclosure characteristics on wind environments. Decreasing spatial enclosure, i.e., increasing openness, leads to higher local wind speeds and vapor pressure deficit (VPD) [60, 61], resulting in an increased transpiration rates of trees during hot weather conditions [62, 63], which is unfavorable for the physiological stability of plants under heat stress. Moreover, given that the influence of building enclosure on local climates depends not only on its degree but also on its orientation [64], investigating how the direction of building enclosure affects the climate adaptation of urban trees could be a promising avenue for future research.

In addition to DegBE, indicators of land cover composition, including the percentage of green space area such as grove area (PerGA) and canopy coverage (PerCC), as well as the percentage of impervious surface area (PerIS), were also found to significantly influence the dry-heat tolerance of trees in this research. PerGA and PerCC were proven to be significantly positively correlated with the heat tolerance of plants, primarily because urban tree canopies can effectively reduce ambient temperatures through transpiration and shading effects, thereby alleviating extreme heat stress [16, 65]. In contrast, the correlation between PerIS and dry-heat tolerance was revealed to be negative, aligning with the findings of Savi, Dale, McClung & Ibanez, and Zhao & Wang [43, 66–68]. The extensive hardening of underlying surface can impede rainwater infiltration and soil moisture replenishment, exacerbating water stress and hindering tree growth under the threat of heatwaves [39]. Besides, the low albedo of impervious surfaces during hot periods enhances heat absorption, causing a rapid rise in surface and near-ground air temperature [69, 70], increasing canopy transpiration and exacerbating the climatic vulnerability of trees [66].

Targeting the influence of heterogeneous and fragmented urban habitats, previous studies mainly focused on the impact of single habitat factor on the climate adaptation of urban trees [39, 43, 44], while the comprehensive multifactorial effects have been less explored. This research revealed that trees' dry-heat tolerance in a specific habitat can be largely explained by the combined effects of 2–4 key habitat factors, particularly DegBE and PerCC for most tree species, with PerCC having a more pronounced impact at the 50m scale, while DegBE is more prominent at the 100, 150m and 200m scales. The findings indicate that a habitat with building enclosure and extensive canopy coverage surrounding trees can potentially enhance their adaptation to dry heatwaves.

Scale effects in the sensitivity of trees' dry-heat tolerance to habitat variation

Our research revealed that the sensitivity of trees' dry-heat tolerance in response to habitat characteristics varied across different spatial scales, with most trees exhibiting the highest sensitivity to habitat variation at the spatial scale of 50 and 100 meters. Although some studies have illustrated the scale effects of urban habitat on influencing microclimates [50, 71], very few have directly addressed the critical spatial scales at which habitat features can effectively impact tree climate adaptation. Given that habitat characteristics influence tree climate adaptation by affecting microclimates [72, 73], the revealed scale effects of habitats in affecting microclimate can provide insights to their scale effects in shaping trees' climatic adaptation. The optimal spatial range of habitat for effectively influencing microclimate varies across different habitat types, ranging from a radius of 20m in high-density urban residential areas [50] to a radius of approximately 150m for low-density suburban settlements [48]. This indicates potential habitat-type specificity in the critical spatial scale for affecting tree acclimation. This study specifically investigated the scale effects of campus habitats, and further exploration of other urban habitat types is warranted in future work.

Limitations and Prospects

Considering that the morphological characteristics of urban trees can intuitively reflect their response to extreme climates, this study utilized a visual tree assessment method to evaluate the dry-heat tolerance of urban trees based on the severity of leaf damage. While this approach facilitates efficient evaluation of trees' adaptation to heatwave threats, it has certain limitations. During periods of extreme climate, trees initially undergo physiological changes, with morphological abnormality, such as leaf chlorosis and shedding, twig or branch die-back, and reduction in crown canopy, manifesting only after a certain tolerance threshold is exceeded [29, 74, 75]. Therefore, leaf damage symptoms may exhibit a delayed effect in detecting tree response to climate threats [76]. To decipher the timely responses of trees to hydrothermal threats throughout the entire stress period, it is essential to supplement visual assessment with physiological measurements, such as changes in photosynthesis and water potential, which presents the direction for future research.

In addition, the structure and characteristics of urban habitats varied across different habitat types. Our investigation focused on the specific type of campus habitats, characterized by the integration of buildings, impervious surfaces, and green spaces, which are representative for the densely populated habitat types, such as residential and commercial areas. However, further exploration is needed to understand the influence of other urban habitat types, such as urban parks with their greenspace-dominated composition distinct from highly artificial environments, on the climate adaptation of urban trees.

The frequency of heatwaves worldwide is projected to increase by 5–10 times over the next 40 years [77]. While artificial irrigation and shading can temporarily ease the heat and drought threat on urban trees, relying solely on high-density maintenance is insufficient and impractical for addressing long-term climate challenges, especially considering the sustainability of urban green spaces. Selecting climate-resilient tree species and optimizing tree habitats can offer sustainable approaches for improving the climate adaptation of urban vegetation. This study identified the varying dry-heat tolerance of common tree species in Wuhan, providing evidence for species selection to enhance the heatwave adaptation of urban species composition. We also elucidated the impact mechanism of typical artificial habitat factors, such as building enclosure and land cover composition, on the dry-heat tolerance of urban trees. This insight can inform the creation and optimization of climate-resilient habitats for local urban trees, especially the vulnerable ones, thereby enhancing their ability to withstand heatwaves and other climatic challenges.

Conclusions

This study investigated the dry-heat tolerance of common tree species and their responses to habitat variations in Wuhan. Significant interspecific differences were observed in the dry-heat tolerance, with *P. yedoensis* and *G. biloba* exhibiting the highest tolerance, while *P. tobira and M. grandiflora* displayed the lowest. The dry-heat tolerance of investigated species was associated with their life forms, with evergreen species showing significantly higher tolerance than deciduous species, and shrub species exhibiting higher tolerance than arbors, albeit with no significant difference. Additionally, the dry-heat tolerance of species was correlated with the climate attributes of their geographical provenance, with species originating from temperate regions exhibiting lower tolerance than those from tropical regions. While native tree species tended to show higher tolerance than exotic species, the difference was not statistically significant in our study. Besides species-specific traits, dry-heat tolerance was significantly influenced by building enclosure and land cover composition in urban habitats. Among habitat factors, the degree of buildings enclosure (DegBE) displayed the most pronounced positive impact, followed by percentage of grove area (PerGA) and canopy coverage (PerCC) with a positive effect, as well as impervious surface area (PerIS) with a negative effect. And the factors varied in their effect magnitudes when combinedly affecting trees' dry-heat tolerance, with green space factors such as PerCC being the primary ones at the 50m scale and DegBE acting as the dominant factor at the 100m-200m scales for most species. The sensitivity of trees' dry-heat tolerance to habitat variations varied across diverse spatial scales and different species, with the most prominent sensitivity observed at spatial scales of 100m and 50m, for species with weaker dry-heat tolerance such as *P. yedoensis* and *G. biloba*. These findings provide evidence supporting the selection of tree species and optimization of artificial habitats to enhance the heatwave resilience of urban vegetation in Wuhan and other cities in Central China.

Declarations

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Data Availability: All data generated or analysed during this study are included in this published article.

Code availability: No custom code was utilized in the analysis for this study.

Author contributions: All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by WZ, XX and LZ. The first draft of the manuscript was written by LZ and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Figures

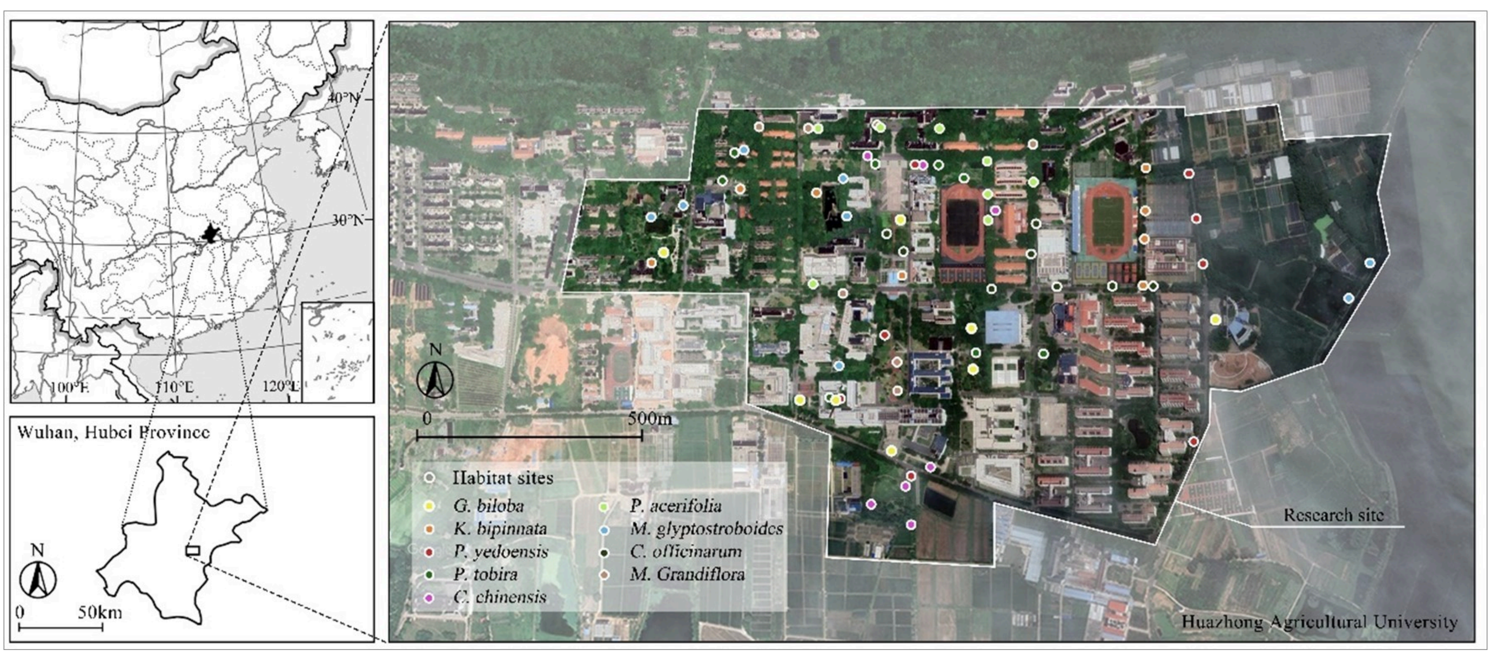

Figure 1

Location of research site (source: Google Map)

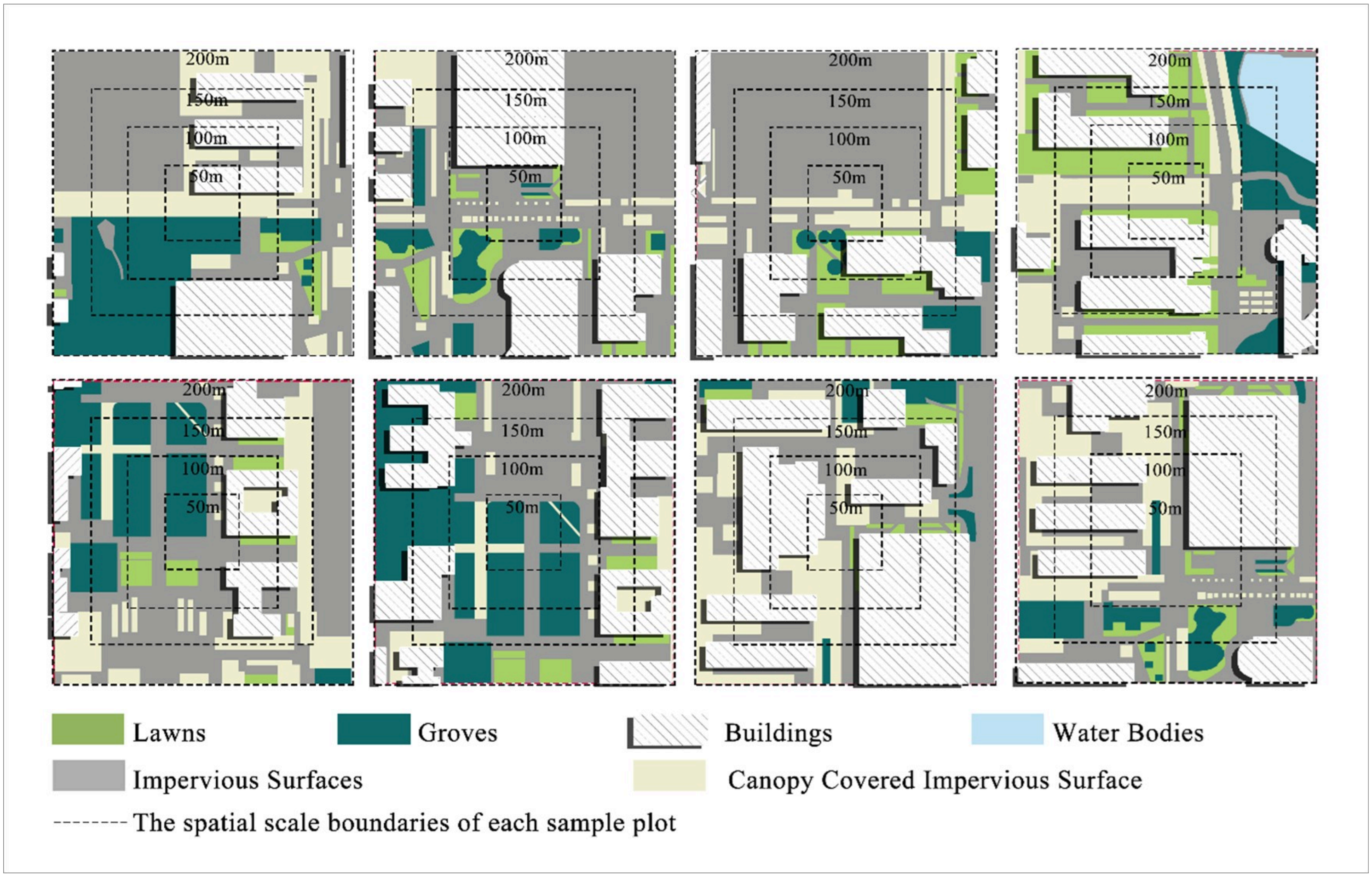

Figure 2

The land cover composition in the sample plots of eight habitats for *Cinnamomum officinarum*

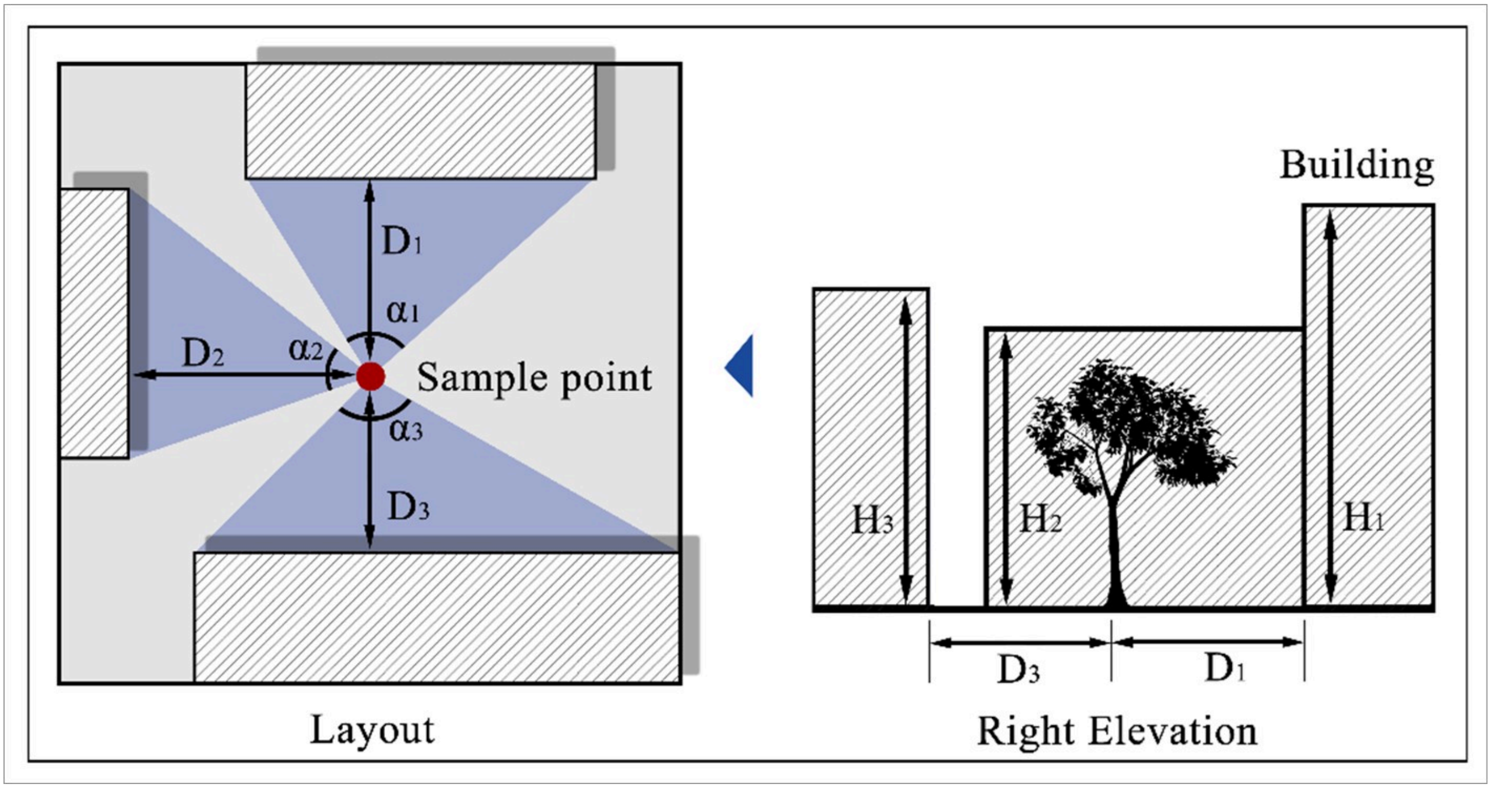

Figure 3

The illustration of parameters for the measurement of DegBE in a sample plot

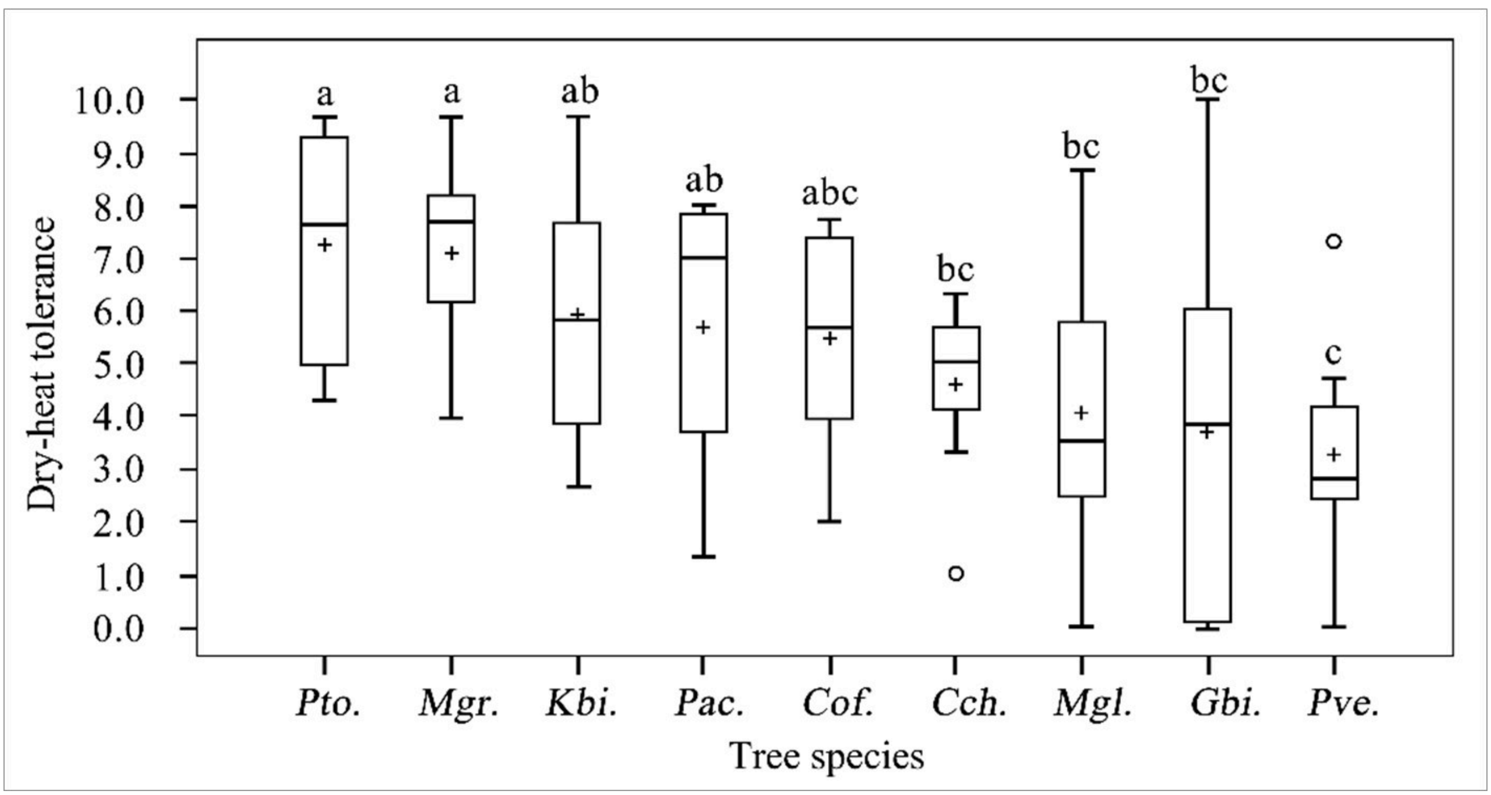

Figure 4

Variations in dry-heat tolerance among different tree species

Pto. = Pittosporum tobira, *Mgr. = Magnolia grandiflora*, *Kbi. = Koelreuteria bipinnata*, *Pac. = Platanus acerifolia*, *Cof. = Camphora officinarum*, *Cch. = Cercis chinensis*, *Mgl. = Magnolia grandiflora*, *Gbi. = Ginkgo biloba*, *Pve. = Prunus × yedoensis*. The letters above the boxes (abc) indicate the significance of interspecific differences. The absence of shared letters between two species signifies a significant difference in their dry-heat tolerance. ($p<0.05$). The symbol (+) marks the mean value.

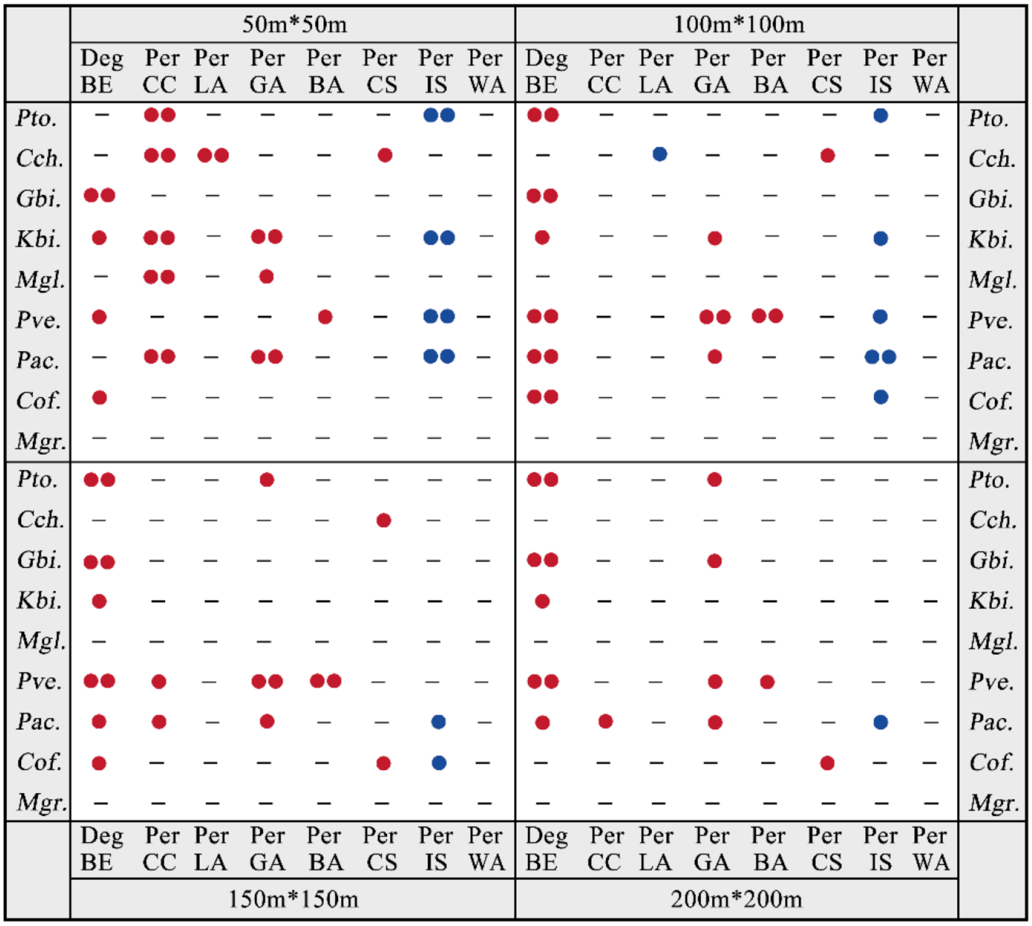

Figure 5 Univariate correlation analysis between the dry-heat tolerance of the trees and habitat factors
"—" indicates no significant correlation, "●" indicates a significant positive correlation at the 0.05 level, "●●" indicates a significant positive correlation at the 0.01 level, "●" indicates a significant negative correlation at the 0.05 level, and "●●" indicates a significant negative correlation at the 0.01 level.

Figure 5

See image above for figure legend