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Seasonal Variations in the Leaf Temperature of Four Common Tropical Woody Plants

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Abstract: Leaf temperature (T_{leaf}) is a critical factor influencing plant ecophysiological processes and ecosystem responses to environmental changes. In this study, we investigated the seasonal T_{leaf} variations among different growth forms (shrubs and trees) of four common tropical woody species in South China and identified the dominant drivers of T_{leaf}. We hypothesized that T_{leaf} patterns between shrubs and trees would differ significantly between dry and rainy seasons and that leaf traits and environmental temperature would predominantly affect T_{leaf} among species. From December 2022 to October 2023, we measured T_{leaf}, leaf traits, and environmental conditions. The results revealed that T_{leaf} was consistently greater than air temperature (T_{air}) across all species, growth forms, and seasons. The regression line slopes between T_{air} and T_{leaf} indicated limited homeothermy, with significant differences observed between seasons. Trees had higher T_{leaf} values than shrubs across dry and rainy seasons, possibly due to their distinct microclimatic adaptations. Leaf chlorophyll content (LCC) and leaf mass per area (LMA) were significant predictors of T_{leaf}. Furthermore, while soil temperature (T_{soil}) positively influenced T_{leaf}, T_{air} had a negative effect on T_{leaf}. Our findings suggest that T_{leaf} is intricately linked to leaf traits and environmental conditions, with implications for plant performance and ecosystem dynamics.

Keywords: leaf temperature; tropical species; chlorophyll content; leaf mass per area; soil and air temperature

1. Introduction

Leaf temperature (T_{leaf}) plays a pivotal role in the microenvironment of plants [1], significantly influencing their ecophysiological processes, such as photosynthesis and respiration, which determine the carbon assimilation rate [2,3]. It also governs the transpiration rate through stomatal conductance [4]. Beyond the individual plant level, T_{leaf} is a crucial factor in ecosystems and regional water, carbon, and energy budgets [5,6]. Its role is prominently recognized within the frameworks of dynamic global vegetation models [7,8]. This underscores the importance of understanding and accurately modeling T_{leaf} in predicting and managing ecosystem responses to environmental changes.

T_{leaf} can significantly differ from air temperature (T_{air}), leading to substantial impacts on carbon and water fluxes [9]. Different studies have shown that the difference between T_{leaf} and T_{air} can reach 20°C and that this thermal decoupling varies greatly across species and environments [1,10]. In certain environments, such as alpine regions and humid tropics, T_{leaf} can be as much as 20°C higher than T_{air}, whereas in warm deserts, it can be 15–20°C lower [2,9]. These deviations highlight the complex relationships between T_{leaf} and T_{air} and their ecological implications.

The thermal response of a leaf to changes in air temperature is crucial for its physiological function, and this response is characterized by the slope of the regression line between T_{leaf} and T_{air} [11,12]. A slope less than 1 indicates limited homeothermy, where leaves remain cooler than the air, which is especially useful for carbon uptake at higher T_{air} [3,13]. A slope equal to 1 represents poikilothermy, where T_{leaf} closely follows T_{air}, showing little to no thermal regulation [7]. Conversely, a slope greater than 1 suggests megathermy, where leaves heat up more than the air does, potentially leading to thermal stress [14]. The implications of these responses for plant performance are significant but not fully explored, and the mechanisms behind each type of response require further investigation.

Trees and shrubs may have different physiological and morphological adaptations to their environment, which can affect how their leaves respond to temperature changes. Previous studies have reported that shrubs have exhibited greater sensitivity to climate warming than trees have in recent decades [15,16]. However, Gazol and Camarero [17] reported that shrub species might actually be less affected by temperature fluctuations than trees are, as they are more significantly influenced by microclimatic conditions, topography, and soil temperature. This microclimatic connection allows shrubs to grow at sites that are more sheltered from regional atmospheric temperatures, potentially increasing their survival in areas with more extreme climate conditions [18].

Previous studies have shown that increases in T_{leaf} are associated with decreased transpiration rates [3,19], which are a consequence of stomatal closure in response to environmental stressors, such as water scarcity [20]. In the rainy season, when soil moisture is plentiful, plants reach their zenith in terms of liquid photosynthesis, stomatal conductance, transpiration, and leaf water potential [21]. This optimal physiological state effectively shields plants from high-temperature damage [22], facilitating normal growth. In contrast, during the dry season, leaf stomata are predominantly impacted by drought conditions [23,24]. A reduction in stomatal density and the closure of stomata lead to a significant decline in photosynthesis and an increase in T_{leaf} [25].

T_{leaf} is intricately linked to the leaf's energy balance, which is influenced by a suite of leaf traits that modulate the absorption and dissipation of energy [7,26]. Specific leaf characteristics, such as the leaf chlorophyll content (LCC) [27], leaf area (LA) [9], leaf thickness (LT) [28], leaf mass per area (LMA) [29], and leaf water content (LWC) [1], play pivotal roles in this context. As the LA increases, the size of the leaf's boundary layer also correspondingly increases [30]. This increase in boundary layer thickness leads to a decrease in the rate of sensible heat exchange between the leaf and its surrounding air [31]. Consequently, larger leaves typically exhibit higher maximum surface temperatures than smaller leaves do [32,33], assuming that all other factors are equal. When T_{leaf} increases, the activity of chlorophyll synthesis enzymes increases, leading to increased chlorophyll content [29]. However, once a certain T_{leaf} (>30°C) is reached, the enzyme activity rapidly decreases, and the chlorophyll content also rapidly decreases [34]. A higher LWC results in greater thermal inertia due to the high specific heat capacity of water. This allows leaves to absorb more heat with less significant temperature increases, thus protecting them from rapid temperature fluctuations and potential damage [35]. Thicker leaves can accumulate more energy and maintain a higher thermal mass [28], which helps stabilize T_{leaf} with minimal fluctuations. This is facilitated by the positive correlation between LT, LMA, and the content of heat-retaining substances within the leaf, such as water and macromolecules [30]. Consequently, an increase in LT and LMA not only enhances the leaf's water retention capacity but also slows the rate at which T_{leaf} increases. Despite the acknowledged influence of leaf traits on T_{leaf}, the primary determinants that drive T_{leaf} remain elusive.

In this study, we selected four common tropical woody species in South China on a university campus and examined the seasonal variations (rainy and dry seasons) in T_{leaf} between different growth forms (shrubs and trees) and their dominant drivers. We hypothesized that (1) T_{leaf} consistently exceeded T_{air}, suggesting limited homeothermy; (2) the pattern of T_{leaf} between shrubs and trees would be significantly different between the dry and rainy seasons; and (3) leaf traits and environmental temperature could strongly affect T_{leaf} among species.

2. Materials and Methods

2.1. Site Description

The study area was located at Hainan Normal University Longkun South Campus in Haikou, Hainan Province, China (19.59°N, 110.20°E). The area has an annual average sunshine duration of 1752 hours and an average annual temperature of 23.8°C. The climate is characterized by a tropical maritime monsoon with an average annual rainfall of 1724.5 mm, which is highly unevenly distributed. The year is divided into two seasons: the rainy season, which spans from May to October, and the dry season, which spans from November to April of the following year. The rainfall during the rainy season accounts for approximately 80% of the annual total [36]. The average annual evaporation is 1834 mm, with an average relative humidity of 85%. The area is predominantly influenced by northeast and east winds, with an average annual wind speed of 3.4 m s^{-1}.

2.2. Measurement of Leaf Temperature

We selected four common woody plants on the campus for experimentation, including two tree species, *Bauhinia blakeana* and *Fagraea ceilanica*, and two shrubs, *Ligustrum × vicaryi Rehder* and *Hibiscum rosa-sinensis* Linn. From December 2022 to October 2023, leaf temperature (T_{leaf}) measurements were conducted on clear days in the middle of each month. Between 12:00 and 14:00 under full sunlight conditions, the leaf canopy temperature was measured remotely via an infrared thermometer gun (Fluke-MT4, Fluke Corporation, Everett, USA) [37]. Canopies emit longwave infrared radiation as a function of their temperature. The infrared thermometer senses this radiation and converts it to an electrical signal, which is displayed as temperature [38]. For each tree species, three individuals were selected for replication, and for each individual, eight random leaves were repeatedly measured, and the average value was taken.

2.3. Leaf Trait Measurements

From each of the three individual plants, twenty fully mature and robust green leaves were collected at random from the sunlit central portion of the canopy. The leaf chlorophyll content (LCC, SPAD) was measured via a chlorophyll meter (SPAD-502, Konica Minolta Holdings, Tokyo, Japan). The fresh leaf mass (LFM, g) was then measured via an analytical balance with a precision of one part in ten thousand. The leaves were subsequently placed into a portable leaf area scanner (LI-3000C, LI-COR, Nebraska, USA) to scan and determine the single leaf area (LA, cm^2) [39]. Finally, the leaves were placed in envelopes and dried in a 60°C oven for 48 hours until they reached a constant weight, after which they were weighed again, and the leaf dry mass (LDM, g) was recorded. The leaf mass per area (LMA, g cm^{-2}) and leaf water content (LWC, %) were calculated as follows:

$$\mathrm{LMA}\ (\mathrm{g\ cm^{-2}}) = \mathrm{LDM}/\mathrm{LA}$$

$$\mathrm{LWC} = (\mathrm{LFM} - \mathrm{LDM})/\mathrm{LDM} \times 100\%$$

2.4. Environmental Conditions Measurement

Infrared radiation thermometers were used to measure the temperature of the cloudless open sky near each target plant (T_{air}). Portable soil moisture and temperature meters (TDR 350, Spectrum Technologies Inc., Aurora, USA) were employed to determine the soil temperature (T_{soil}) and soil water content (SWC). For each tree species, three individuals were selected for replication, with measurements taken in a circular pattern three times around each plant, and the average value was then calculated [40].

2.5. Data Analysis

We calculated the slope of the regression line between T_{air} and T_{leaf} for different growth types (shrub vs. tree), seasons (rainy vs. dry), and species. Analyses of covariance (ANCOVAs) were performed to test whether the slopes among those regression lines were significantly different [41].

To examine the effects of growth type and season on leaf traits, we used linear mixed effect models with sampling date as a random effect to account for temporal autocorrelation.

To estimate the relative importance of the predictor variables, we performed multimodel inference via Akaike's information criterion (AIC). The relative importance value, regarded as the overall support for each predictor across all models, was estimated as the sum of the Akaike weights for the models in which the predictor appeared. A cutoff relative importance value of 0.8 was set to differentiate between the important and unimportant predictors. Partial regression plots were created for each important predictor to illustrate its relationship with T_{leaf} while holding all the other variables constant. All the statistical analyses were performed via the R statistical software package (ver. 4.3.0). All the statistical tests were considered significant at $P < 0.05$.

3. Results

3.1. Leaf Temperature Across Different Groups

T_{leaf} was consistently greater than T_{air} with respect to growth type, season, and species (Table 1). In general, T_{leaf} increased with T_{air} across the different groups (Figure 1). Across the species, the slope of the regression line between T_{air} and T_{leaf} was 0.45 (< 1), indicating limited homeothermy (Table 1 and Figure 1). For different growth types and species, the slopes were lower than one and did not differ among them (Table 1 and Figure 1). During different seasons, the slopes significantly differed (Table 1). The plants in the dry season displayed megathermy (slope >1), whereas the plants in the rainy season presented a slope < 0, suggesting a negative relationship between T_{leaf} and T_{air} (Figure 1).

Table 1. Summary of the linear regressions between leaf temperature (T_{leaf}) and air temperature (T_{air}) and the statistics (mean ± standard error) of T_{leaf} and T_{air} in plants of different growth types, seasons, and species. Different lowercase letters represent significant differences at $P < 0.05$ for different growth types, seasons, and species.

Groups	Slope (95% CI)	R^2	P	T_{leaf} (°C)	T_{air} (°C)
All	0.45 (0.21, 0.70)	0.13	<0.001	33.01±0.55	24.83±0.43
Growth type					
Shrub	0.54 (0.18. 0.90)a	0.16	0.004	32.62±5.31	24.09±3.98
Tree	0.38 (0.03, 0.73)a	0.09	0.035	33.39±5.40	25.57±4.32
Season					
Dry	1.40 (0.88, 1.92)a	0.59	<0.001	27.66±5.60	20.77±3.07
Rainy	−0.25 (−0.50, −0.004)b	0.06	0.047	34.79±3.89	26.18±3.63
Species					
Hibiscus rosa-sinensis	0.73 (0.22, 1.25)a	0.28	0.008	33.39±5.82	25.22±4.21
Bauhinia blakeana	0.57 (0.07, 1.07)a	0.21	0.026	32.96±5.33	26.46±4.23
Ligustrum × vicaryi Rehder	0.21 (−0.39, 0.81)a	0.02	>0.05	31.86±4.74	22.95±3.46
Fagraea ceilanica	0.27 (−0.28, 0.83)a	0.05	>0.05	33.82±5.55	24.68±4.32

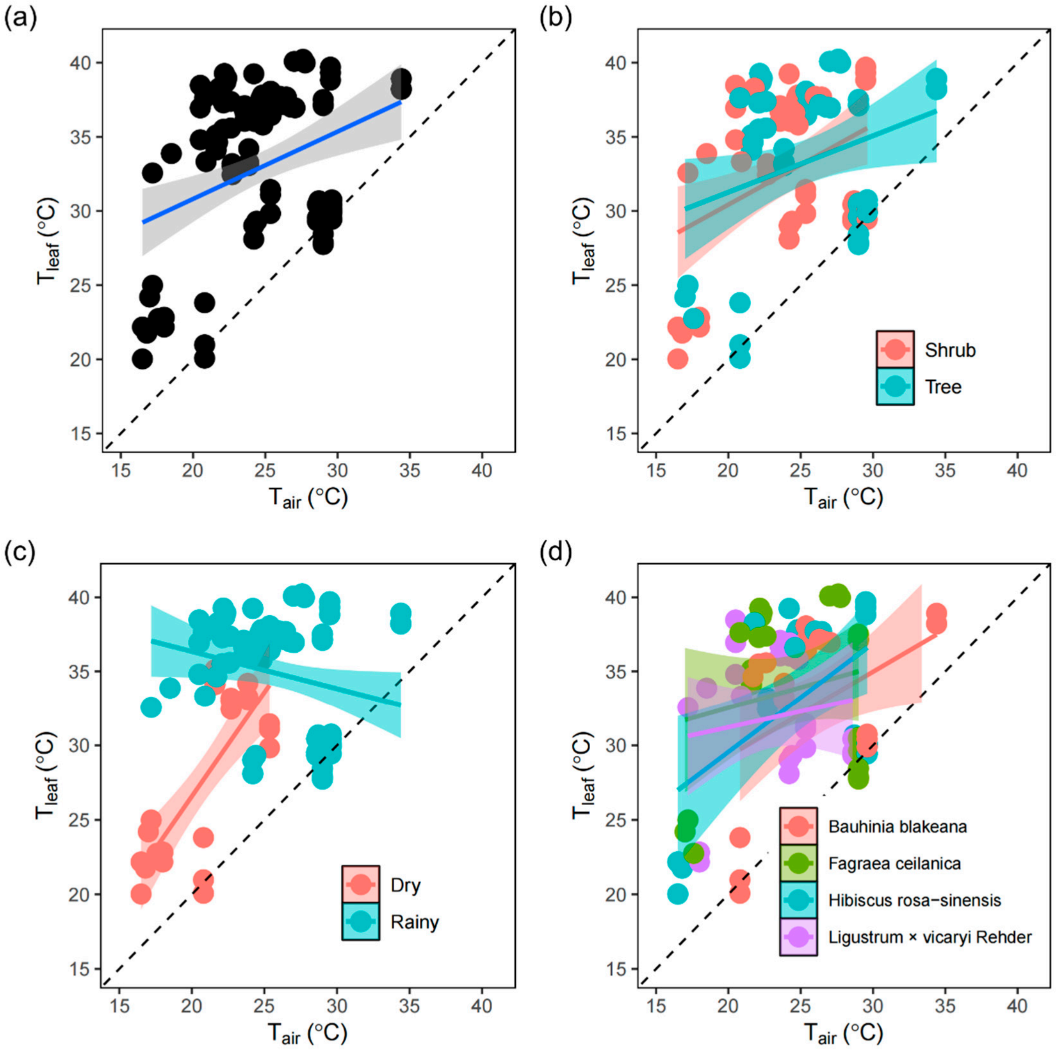

Figure 1. Linear regression between leaf temperature (T_{leaf}) and air temperature (T_{air}) in plants. (a) All species pooled together, (b) plants classified by growth form, (c) plants classified by season, and (d) plants classified by species. The slope of the dashed line is 1.

3.2. Leaf Traits According to Growth Type and Season

The LCC was significantly greater in the rainy season than in the dry season ($P < 0.05$, Figure 2). However, no significant differences between seasons were found for LA, LDM, T_{leaf}, LMA, or LWC ($P > 0.05$, Figure 2). Compared with shrubs, trees had greater LCC, LA, LDM, T_{leaf}, and LMA ($P < 0.05$), whereas growth form had no significant effect on LWC ($P > 0.05$, Figure 2). We found no significant interactive effects between season and growth form on any of the traits ($P > 0.05$, Figure 2).

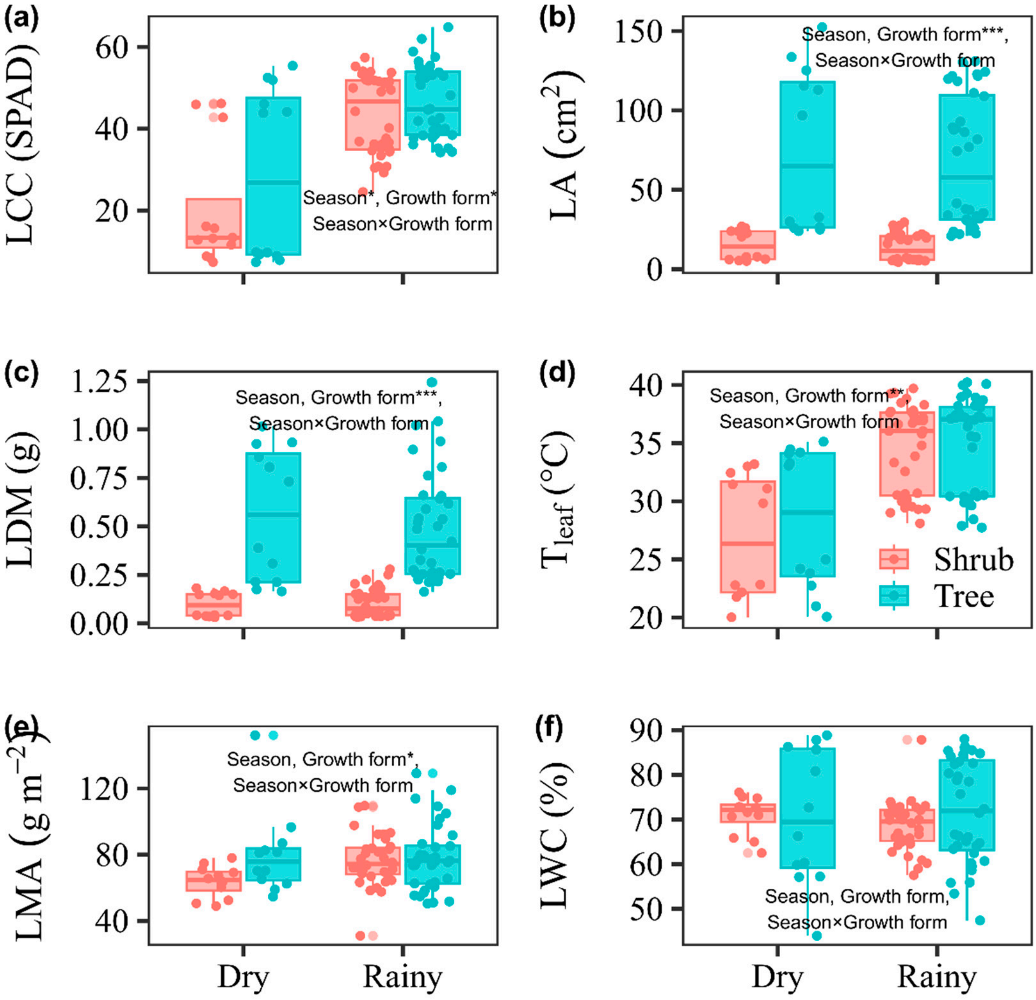

Figure 2. Leaf traits between growth forms (shrub and tree) within dry and rainy seasons. *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$. Leaf chlorophyll content (SPAD, LCC), leaf area (cm^2, LA), leaf dry mass (g, LDM), leaf temperature (°C, T_{leaf}), leaf mass per area ($g\ m^{-2}$, LMA), and leaf water content (%, LWC) were measured.

3.3. The Impact of Environmental Conditions and Leaf Traits

Model selection analysis showed that the best model describing T_{leaf} included LCC, T_{soil}, LMA, and T_{air} as important predictors (Figure 3). Partial regression analysis indicated that T_{leaf} increased significantly with increasing LCC and T_{soil} but decreased with increasing LMA and T_{air} ($P < 0.05$, Figure 4).

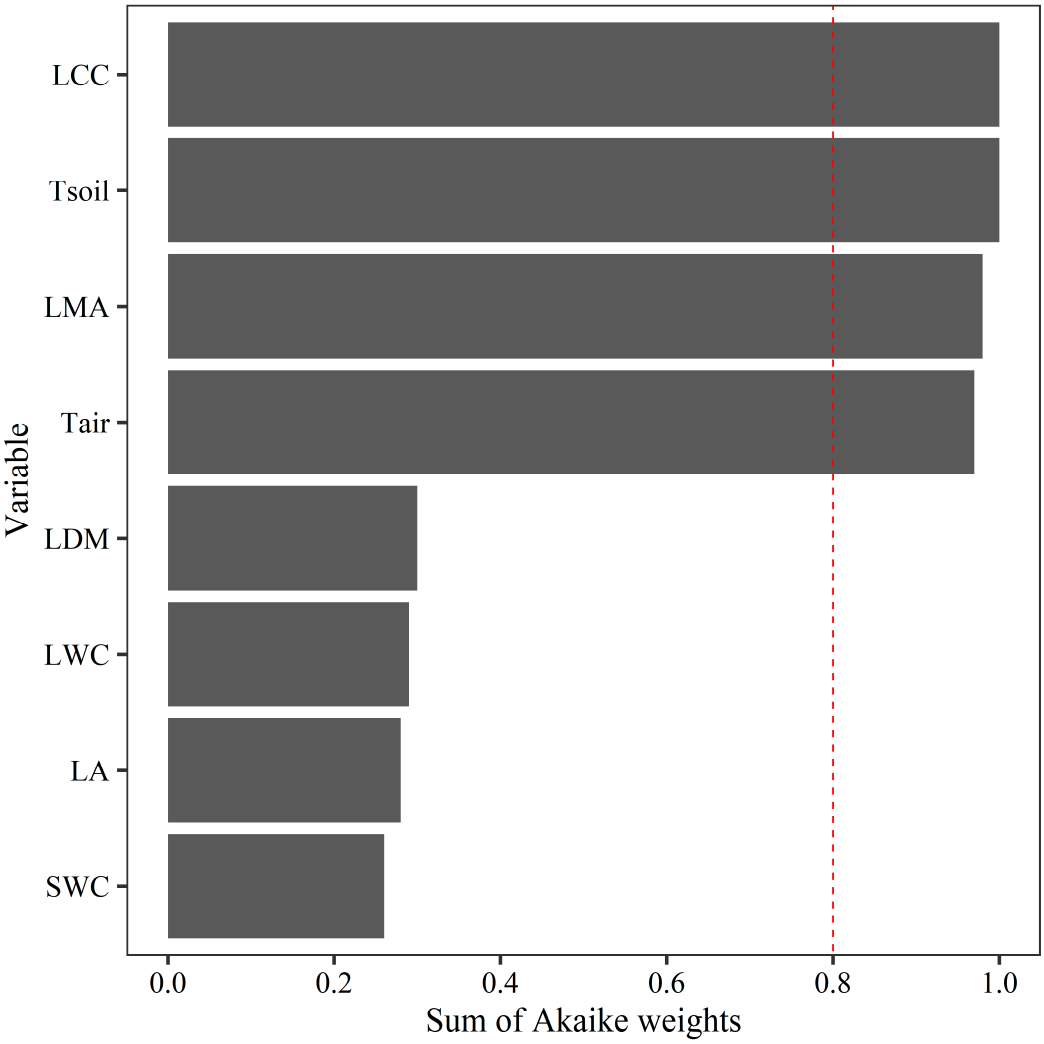

Figure 3. Model-averaged importance of the predictors of leaf temperature (°C, T_{leaf}). The importance value is based on the sum of the Akaike weights derived from model selection via the corrected Akaike information criterion. The cutoff is set at 0.8 to differentiate among the most important predictors. Leaf chlorophyll content (SPAD, LCC), soil temperature (°C, T_{soil}), leaf mass per area (g m^{-2}, LMA), air temperature (°C, T_{air}), leaf dry mass (g, LDM), leaf water content (%, LWC), leaf area (cm^2, LA), and soil water content (%, SWC) were measured.

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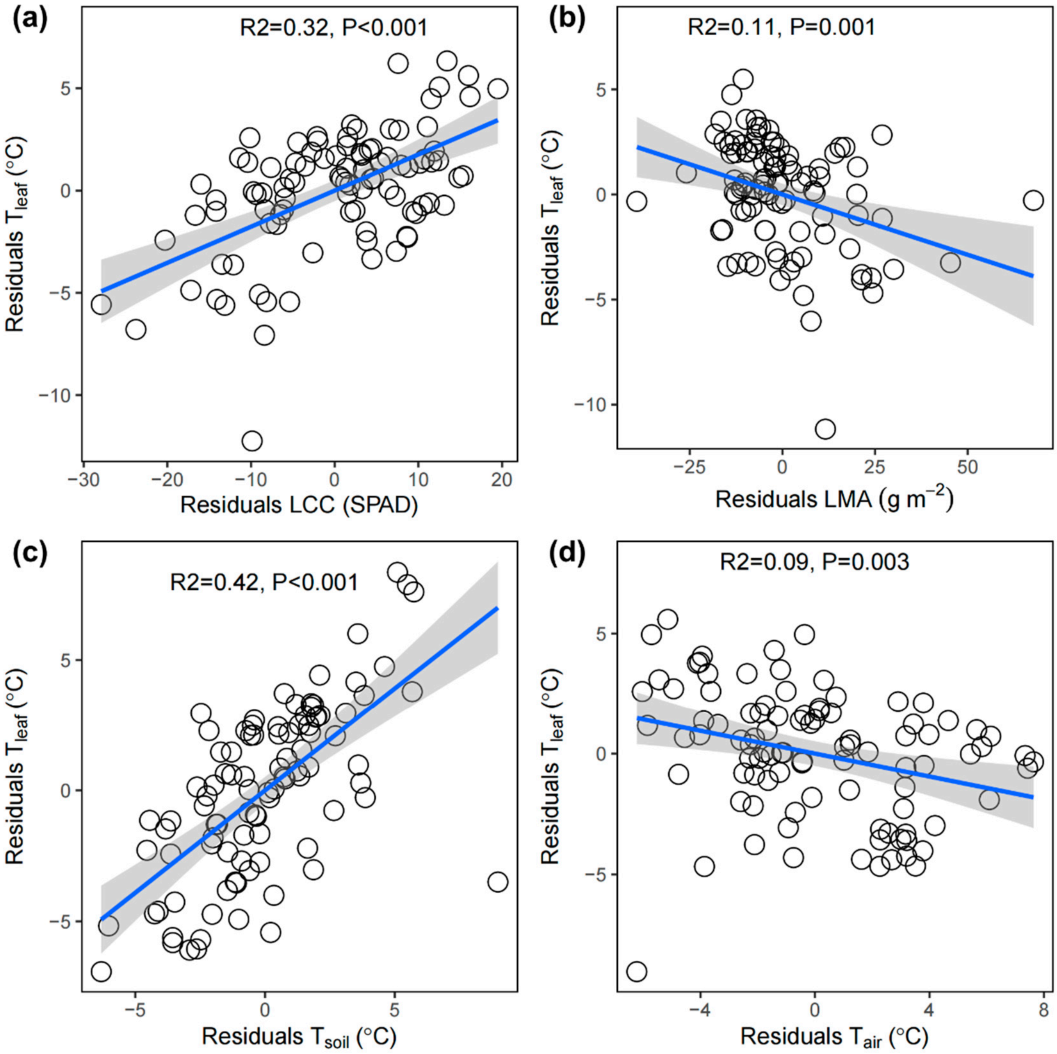

Figure 4. Partial regression plots of the leaf chlorophyll content (SPAD, LCC), leaf mass per area (g m^{-2}, LMA), soil temperature (°C, T_{soil}), and air temperature (°C, T_{air}) in relation to the leaf temperature (°C, T_{leaf}) from multiple linear regression models once all other variables in the model were statistically controlled.

4. Discussion

4.1. Thermal Regulation Capacity of Leaves

Consistent with our initial hypothesis, we found that T_{leaf} consistently surpassed T_{air}, which aligns with certain prior studies [1,42,43]. In numerous tropical studies, T_{leaf} can exceed ambient T_{air} by more than 10°C in sunlit leaves[44,45]. This temperature disparity is attributed to variations in microclimatic conditions [10,28]. For example, wind speeds below 0.5 m s^{-1} are common in nature [46], and even transient lulls can cause T_{leaf} to rise by more than 5°C within just a few seconds [47]. Furthermore, the leaf energy balance indicates that the leaf-to-air temperature difference is contingent upon the net energy provided (or lost) through radiation and the energy expended via transpiration [10]. Zhou et al. [1] reported that the effects of leaf physical warming are stronger than those of leaf transpirational cooling in hot environments. Consequently, the T_{leaf} of all the species was found to be greater than the ambient T_{air}.

The mechanistic relationship between T_{leaf} and T_{air} has received considerable attention in the literature [2,48]. Some studies have argued that leaves exhibit either limited homeothermy [11,49], poikilothermy [50], or megathermy [13,51]. In this study, the regression line slopes between T_{air} and T_{leaf} for the overall dataset, each different growth type, and each species were all less than one, indicating limited homeothermy. Energy balance theory suggests that limited homeothermy occurs under conditions of high stomatal conductance and low convective resistance, which implies that transpirational cooling outweighs physical warming [13]. However, our research did not observe a greater transpirational cooling effect over physical warming, as T_{leaf} consistently exceeded T_{air}. This unexpected result could be explained by the possibility that, under extremely hot conditions, plants may mitigate physical warming to alleviate heat stress. For example, Zhou et al. [1] reported that savanna woodland species possess the lowest absorptivity and the highest reflectivity, thereby reducing the radiation load and resulting in low levels of physical warming. Our findings indicate that the relationships between T_{air} and T_{leaf}, as well as the interactions between leaf physical traits and environmental parameters, are too intricate to be accurately simulated by a simplistic model.

Contrary to our initial hypothesis, plants during the dry season exhibited megathermy, characterized by a slope greater than 1, whereas those in the rainy season presented a slope less than 0, indicating a negative correlation between T_{leaf} and T_{air}. The capacity of plants to mitigate heat stress at the leaf level appears to decrease with increasing water stress [52,53]. In light of the anticipated rise in T_{air} due to global warming, the evaporative demand is projected to increase, resulting in the escalation of the air vapor pressure deficit (VPD) across many regions [54]. Prolonged exposure to elevated temperatures, in conjunction with high leaf-to-air VPD, is anticipated to elicit stomatal closure as a strategy to conserve water in hot-dry environments [43,55]. A reduction in stomatal aperture can lead to a faster increase in T_{leaf} than in T_{air} during the dry season, as diminished transpiration results in less cooling of the leaf surface [56]. Conversely, a negative relationship between T_{leaf} and T_{air} during the hot–wet season should increase overall carbon uptake by keeping leaves within optimal photosynthetic temperature ranges and below damaging temperatures [9].

4.2. Effects of Growth Form and Seasonal Variation on T_{leaf}

In this study, we found that the T_{leaf} of shrubs was significantly lower than that of trees, which may be interpreted in three ways. First, smaller leaves, as typically found on shrubs, have a thinner boundary layer [57], which allows for more efficient cooling through convection rather than evaporation of water [30,58]. Second, shrubs often have a relatively high surface area-to-volume ratio because of their relatively small stature and large number of small leaves [59]. This can lead to increased transpiration rates, which in turn can result in greater cooling of the leaf surface through the evaporation of water [60]. Finally, shrubs, which are closer to the ground, are more susceptible to the influence of soil temperature and moisture [61], which can significantly impact T_{leaf}. In contrast, trees, which are more exposed to atmospheric conditions, are less affected by ground-level microclimates. The soil temperatures and microclimates beneath shrubs can differ from those under trees, with shrubs often having denser canopies that shade the ground [62], potentially leading to lower soil temperatures and, consequently, reduced T_{leaf} [63]. As a result, the T_{leaf} of trees is generally greater than that of shrubs. This differential T_{leaf} response has implications for our understanding of plant thermal regulation and its ecological consequences for different growth forms.

Our findings revealed that there was no significant seasonal variation in leaf T_{leaf} across all the species studied. This outcome contradicts the results of a previous study by Rey-Sánchez et al.[45], which indicated that tree canopies in a tropical forest presented higher T_{leaf} values during the dry season than during the wet season. Additionally, Rey-Sánchez et al. [45] reported a correlation between T_{leaf} and photosynthetic photon flux density in the wet season, a relationship that was absent in the dry season. This discrepancy was hypothesized to be due to seasonal variations in wind speed, plant physiology, and canopy phenology [64,65]. In contrast, our study demonstrated a consistent T_{leaf} between the dry and wet seasons, which we attributed to the thermal regulation strategies employed by the plants. These strategies include transpirational cooling, physical warming, and species-specific adaptations that enable them to maintain optimal temperatures for photosynthesis and other physiological processes [1,66,67]. These adaptive mechanisms assist plants in buffering against extreme temperature fluctuations, thereby sustaining relatively stable T_{leaf} values irrespective of seasonal changes.

In contrast to our second hypothesis, we found that trees presented significantly higher T_{leaf} values than shrubs did across the rainy and dry seasons. Trees and shrubs may have evolved different adaptive strategies to cope with environmental conditions [68,69]. Trees, as the dominant species in a forest canopy, may have adapted to maintain a relatively high T_{leaf} as a way to optimize photosynthesis and growth under full sunlight conditions [70]. Shrubs, on the other hand, may have adapted to lower light and temperature conditions characteristic of the understory, leading to lower T_{leaf} [71]. These factors combined can result in trees maintaining higher T_{leaf} values than shrubs do, regardless of the seasonal changes in rainfall.

4.3. T_{leaf} Regulated by LCC and LMA

In agreement with our third hypothesis, we found that T_{leaf} increased with increasing LCC. This finding aligns with the research of Winter and Koniger [27], who noted significant reductions in LCC and photosynthetic capacity in *Gossypium hirsutum* L. as T_{leaf} decreased from approximately 33°C to 27°C under high light conditions. The higher the LCC is, the greater the leaf's capacity to absorb light energy, leading to increased heat production and, consequently, an increase in T_{leaf} [72,73]. Conversely, Khan et al. [74] reported that the T_{leaf} of *Triticum aestivum* at temperatures ranging from 20°C to 35°C did not affect the LCC or nitrogen content per unit leaf area. Phylogenetic history can significantly influence plant traits, including LCC and T_{leaf} [34]. Our study indicates that different plant species have evolved distinct adaptive strategies to cope with environmental conditions, affecting their T_{leaf} and LCC.

In this study, we found a negative correlation between T_{leaf} and LMA, which is in line with several previous studies [75,76]. Owing to the significant positive correlation between LT and LMA with the substances contained within the leaf, such as water and macromolecules, an increase in LT and LMA not only enhances the water retention of the leaf but also slows the rate of increase in T_{leaf} [77].

4.4. T_{soil} and T_{air} Mediated T_{leaf}

In agreement with our third hypothesis, the multivariate analysis revealed that T_{leaf} was positively regulated by T_{soil} and negatively mediated by T_{air}.

Similar findings were also reported in several previous studies [76,78,79], which reported a positive correlation between T_{leaf} and T_{soil}. The relationship between epidermal cell area and stomatal density follows an inverse pattern, as noted by Rogiers et al. [80]. Consequently, an increase in T_{soil} can lead to a reduction in stomatal density, which may be attributed to the increase in epidermal cell size and leaf expansion influenced by T_{soil} [81]. This reduction in stomatal density, coupled with stomatal closure, could significantly curtail photosynthesis and consequently increase T_{leaf} [82]. Furthermore, the stresses induced by elevated T_{soil} led to a decrease in the relative water content of the leaves, which in turn resulted in increased Tleaf and cellular rupture [83].

Additionally, Manzi et al. [9] reported a positive correlation between the T_{leaf} of sun-exposed leaves and T_{air} across various species. In contrast, our study revealed an inverse relationship, which we attributed to the enhanced transpirational cooling effect under conditions of warming. Several mechanisms have been proposed to explain the stimulation of plant transpiration by elevated temperatures. First, elevated temperatures lead to increased expression of aquaporins in the mesophyll and heightened activity of potassium (K+) channels, which are crucial for stomatal opening, facilitating greater transpiration rates [84]. Second, warming enhances plant transpiration by increasing membrane fluidity, which is essential for water transport, and by reducing water viscosity, thereby lowering resistance to water flow within the plant [85]. Third, our research indicates that under warmer conditions, fine roots adapt by becoming thinner and growing deeper into the soil, which improves their capacity for water absorption [86]. These observations underscore the intricate and heterogeneous responses of diverse vegetation types to climate change, which has profound implications for the field of forest ecology and the formulation of adaptive management strategies.

5. Conclusions

Our study demonstrated that T_{leaf} consistently surpassed T_{air}, indicating limited homeothermy in tropical woody species. Trees have higher T_{leaf} values than shrubs do, potentially due to their distinct microclimatic adaptations. Notably, leaf traits, with a focus on LCC and LMA, substantially influence T_{leaf}. T_{soil} positively modulates T_{leaf}, whereas T_{air} exerts a negative regulatory effect. These insights highlight the complex interplay between leaf thermal dynamics and environmental factors. Future studies should broaden the species and climate ranges to obtain more generalizable findings. Examining additional environmental factors and their interactions with leaf traits will deepen our understanding of T_{leaf} dynamics. Long-term studies will also be crucial for tracking T_{leaf} responses to climate change, informing ecosystem management strategies.

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Conflicts of Interest: The authors declare no conflicts of interest.

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