Abstract: As one of the important factors affecting plant productivity and plant distribution, temperature also affects the physiological and ecological characteristics of plants to a large extent. We report canopy leaf temperature distribution over a 36 m tall primary tropical rain forest and samplings of 28 tree species in SW China by means of two high resolution thermal cameras (P25, Flir systems, Wilsonville, OR, USA). The leaf temperature of dominant tree Species *Pometia tomentosa* was the highest (31.8 °C), 10.2 °C higher than that of tree species *Mezzettipsis creaghii* (21.6 °C). The mean leaf to air temperature difference ($T_c$–$T_a$) of *Pometia tomentosa* was the highest (6.4 K), the second highest was *Barringtonia pendula* (6.1 K), and *Mezzettipsis creaghii* had the lowest ($T_c$–$T_a$) (1.9K). ($T_c$–$T_a$) of tree species with smaller leaves and larger stomatal conductance was lowly sensitive to climate factors. Leaf size and stomatal conductance together decided the effect of climate change to ($T_c$–$T_a$) of the different tree species. We have shown that the composition of tree species in tropical rain forest areas is important to the climate through our research.

Keywords: leaf temperature; infrared thermography; thermal imagery; tropical rain forest

1. Introduction

There are many factors that affect plant productivity and plant distribution, such as climate, topography, water, soil, microorganisms, and so on. However, as one of the important factors affecting plant productivity and plant distribution, temperature also affects the physiological and ecological characteristics of plants to a large extent. Temperature influences rates of plant photosynthesis and respiration, litter decomposition and microbial activity [1], and other biological processes will affect the fixation and release of carbon dioxide [2]. On the other hand, leaf temperature is also affected by stomatal control of transpiration [3] and traits affecting heat exchange [4]. For example, leaf size, leaf shape, petiole length, and other traits can affect leaf temperature [5–7]. As a result, global warming is expected to affect carbon pools on land, increasing the amount of carbon dioxide in the atmosphere [8,9]. The rate of ecosystem respiration will increase with increasing temperature. At the same time, rising temperatures may lead to plant stomata closing, thus reducing the primary productivity of tropical rainforest ecosystems.
With the global biodiversity crisis becoming increasingly serious, research on plant diversity and its role in ecosystem function is becoming increasingly important in ecology. Due to the good combination of precipitation and temperature in the tropical rain forest area, the plant types in the tropical rain forest area are also very rich. Moist rainforests cover about 6~7% of the earth’s surface, but they are home to more than half of all life on earth [10]. According to research, the tropical rainforest contains the largest collection of living plant species in the world [9]. They contain 40% of the world’s forest biomass [10] and soil carbon [11]. Especially on a small scale, dominant tree species in a tropical rain forest community have a great influence on forest carbon sequestration [12].

Due to the incomplete development of technology, the early research mostly focused on the microhabitat temperature measurement of single tree species. Recently, new digital technologies in combination with thermal (IR) transmission lenses have been developed to accurately measure actual temperature regimes in canopies. For example, Kumar et al. conducted field experiments on farms in central and southern India (18°9′ N, 74°28′ E). They used thermal imaging to assess the canopy temperature differences among different genotypes of soybeans to further differentiate the soybean’s ability to withstand water stress [13]. Padhi et al. used infrared thermal imaging technology to measure the canopy temperature of cotton fields at Kingsthorpe Research Station (27°30′44″ S,151°46′55″ E), thus providing a basis for assessing crop water deficit pressure using stomatal conductance index [14]. Daniel and Körner assessed, by using a combination of IR imagery, both surface and root zone temperatures on a landscape scale in the Swiss Alps [13]. In Switzerland, leaf surface temperatures vary widely between species in mixed deciduous forests and urban environments [14,15]. Stomatal conductance, the key factor controlling leaf temperature, varies greatly in ten tropical forests [3]. Thus, we can see that different plants have different canopy temperatures. Moreover, the temperature of the crown is closely related to the stomatal conductance and water content of the leaves. Canopy temperatures have a series of uncertainties in their variations, and controlling environmental factors [3,4]. Therefore, we hypothesized that canopy temperatures of broadleaved trees in primordial tropical forests may differ significantly among species. According to the 2007 report by the Intergovernmental Panel on Climate Change (IPCC), global temperatures are expected to rise from 2.4 to 5.5 °C as carbon dioxide levels in the atmosphere increase [16]. This global warming may be related to changes in solar radiation, precipitation, and other micrometeorological factors on a regional or ecosystem scale. Studying the responses of different tree species to these climatic stress factors is helpful to understand the dynamics of vegetation in the context of global warming [14,15].

Little is known about how species-scale variation in leaf temperature influences community-scale variation in canopy temperature [14]. Our study has two main purposes (1) to study the spatial and temporal distribution of species under specific canopy temperature, (2) to discuss the possible influence of future climate change on canopy temperature difference (CTD). Through this study, we want to explore the significance of forest tree species’ composition on canopy heat accumulation.

2. Materials and Methods

2.1. Site Description and Studied Species

Our experiment was conducted in a tropical rain forest in Xishuangbanna, southwestern China (21°55′39″ N, 101°15′ 55″ E, elevation 750 m). Xishuangbanna Nature Reserve Authority is mainly responsible for protecting the reserve forest sites. Our institute workers were approved by Xishuangbanna Nature Reserve Authority to conduct experiments in the site. There were no specific permissions required for the activities. The height of the rainforest canopy is about 36 m. The stand has a stem density of 964 trees ha⁻¹ (diameter ≥ 5 cm) and a total basal area of 32.28 m² ha⁻¹; the number of tree species in the plot was 179 in 2007 [17].
2.2. Dominant Mature Tree Species

The important value of the five tree species ranked in the top five over the whole tree species [17]. So, we selected the top five canopy mature tree species in this rainforest which is dominated by *Pometia tomentosa*, *Barringtonia macrostachya*, *Gironniera subaequalis*, *Ardisia tenera*, and *Mezzettiopsis creaghi*, respectively [18]. The canopy temperature characteristics of the five tree species are shown in Table 1. The sites did not involve endangered or protected species.

2.3. Saplings of 28 Tree Species

We also selected samplings of 28 tree species in the lower layer of the forest that could be adequately replicated. Five tree samples of each tree species were measured.

2.4. Thermal Imaging of the Canopy Dominant Tree Species

A 70 m tower was established at the center of the plot. In this study, two thermal imaging cameras (P25, Flir systems, Wilsonville, OR, USA) with a resolution of 320 × 420 pixels were used to determine the canopy temperature of the dominant tree species. Two thermal imaging cameras (P25, Flir systems, Wilsonville, OR, USA) were mounted 3 to 5 m above the canopy. In addition, exposed and certain sized canopies were selected to measure the average canopy surface temperature. The camera (P25, Flir systems, Wilsonville, OR, USA) software was used to analyze the canopy surface temperature of the measured images. This provided us with 76,800 temperature data with a resolution of 0.1K under sunny conditions. We only cut three leaves in a tree to analyze the leaf stomatal conductance.

2.5. Thermal Imaging and Stomatal Conductance of 28 Tree Species Samplings

By measuring the temperature of the leaves and the temperature of the air, we calculated the difference between the two average temperatures. In addition, we measured the leaf stomatal conductance of samplings of 28 tree species. All measurements were conducted on 13–15 June 2018, three meteorologically similar days (from 09:30 to 13:00). We also used two thermal cameras (P25, Flir systems, Wilsonville, OR, USA) to measure the leaf temperature. Then, the leaf stomatal conductance was measured with a portable photosynthesis system (LI-6400, Li-COR, Lincoln, NE, USA).

2.6. Environmental Data and Soil Moisture

In the corresponding period, wind speed (A100R, Vector, UK), air temperature and humidity (HMP45C, Vaisala, Vantaa, Finland), photosynthetically active radiation (LI-190SB, Li-COR, Lincoln, NE, USA), net radiation (CNR-1, Kipp & Zonen, The Netherlands), soil temperature (TCAV, Scientific Inc., Logan, UT, USA), and soil moisture (CS616, Campbell Scientific Inc., Logan, UT, USA) were measured simultaneously. All these factors were sampled at 0.5 Hz and the data were stored in the data logger. The 30 min average was also calculated and stored by the data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA).

The canopy temperature difference was calculated by using the canopy surface temperature and air temperature at the same time.

2.7. Evaluate the Canopy Temperature Change

In order to explore the possible influence of future climate change on the canopy temperature difference (CTD), we used Function (1) to evaluate the canopy temperature change [19].

\[
T_c - T_a = \frac{P_a(R_n - G) - g_c A VPD + (g_c / g_H)P_a(R_n - G)]}{g_c C_p + g_H C_p VPD}
\]

where \( P_a \) is atmospheric pressure (kPa), \( R_n \) is net radiation (W m\(^{-2}\)), \( G \) is soil heat flux (W m\(^{-2}\)), \( g_c \) is canopy stomatal conductance (mmol m\(^{-2}\) s\(^{-1}\)), \( g_H \) is boundary layer heat conductance (mmol m\(^{-2}\) s\(^{-1}\)),
Cₚ is the specific heat of air at constant pressure (J mol⁻¹ K⁻¹), λ is latent heat of vaporization (J mol⁻¹), VPD is the vapor pressure deficit (kPa), and Pₐ is atmospheric pressure (kPa).

2.8. Statistical and Analytical Methods

All data processing and statistical analyses were conducted using the Statistical Analysis System (SPSS 26.0 Software, IBM, Armonk, NY, USA). Significant differences between means were tested using one-way analysis of variance (ANOVA). Significant effects of the main meteorological elements on the canopy temperature difference rates were determined by multiple linear regressions.

3. Results

3.1. Environmental Conditions

Figure 1 showed diurnal variations in the main meteorological elements during the observational period. The maximum air temperature was 27.6 °C. The maximum photosynthetic active radiation (PAR) was 1380 μmol m⁻² s⁻¹. Wind speed was very low in this site.

Soil moisture has a strong influence on the plant surface temperature. During the measurement, the soil moisture content at 5 cm depth was 12.5%. This is an area with very low soil moisture throughout the year, which means trees can tolerate drought.

3.2. Spatial and Temporal Temperature Distribution of the Dominant Mature Tree Species

Canopies were scanned on 4 February, 2018 from 13:55 to 14:05 true local time. Figure 2 shows the pattern of the mean temperature of the three layers at 14:00. The mean leaf temperature of Pometia tomentosa in upper layer was the highest (31.8 °C), 10.2 °C higher than that of the tree species Mezzettipsis creaghii (21.6 °C) in the lower layer.
We measured the mean \((T_c - T_a)\) on 4 February, 2018. The mean \((T_c - T_a)\) consisted with the photo flux density patterns (Figures 3 and 4). The five species of the three layers monitored on that day showed significant differences in \((T_c - T_a)\). 

- \textit{Pometia tomentosa} had the highest \((T_c - T_a)\) (6.4 K), the second highest was \textit{Barringtonia pendula} (6.1 K), and \textit{Mezzettiopsis creaghii} had the lowest \((T_c - T_a)\) (1.9 K) (Figure 4).

We found that the temperature change within the canopies was very significant \((p < 0.01)\) (Figure 4).

The canopy temperature difference of \textit{Pometia tomentosa} and \textit{Barringtonia macrostachya} reached the highest at about 13:00. However, the canopy temperature difference of \textit{Gironniera subaequalis} reached its maximum two hours later (at about 15:00) (Figure 4).

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{false_color_thermal_image.png}
\caption{The false color thermal image of part of the canopy of five tree species taken at 14:00 on 4 February 2018, shows the canopy surface temperature of five different tree species. The squares show some selected frames that have been used (Table 1 and Figure 5).}
\end{figure}

\begin{table}[h]
\centering
\begin{tabular}{llllll}
\hline
Species & \(T_c - T_a\) & \text{Range} & \text{Min} & \text{Max} & n \\
\hline
\textit{Pometia tomentosa} & 6.4 \(^a\) & 14.5 \(\pm\) 1.51 & 24.3 \(\pm\) 0.37 & 38.8 \(\pm\) 1.14 & 9 \\
\textit{Barringtonia pendula} & 6.1 \(^b\) & 11.7 \(\pm\) 2.04 & 23.8 \(\pm\) 0.61 & 35.5 \(\pm\) 1.43 & 9 \\
\textit{Gironniera subaequalis} & 4.7 \(^c\) & 8.7 \(\pm\) 1.26 & 25.6 \(\pm\) 0.25 & 34.3 \(\pm\) 1.01 & 9 \\
\textit{Ardisia tenera} & 4.4 \(^d\) & 13.8 \(\pm\) 1.05 & 19.4 \(\pm\) 0.18 & 33.2 \(\pm\) 0.87 & 9 \\
\textit{Mezzettiopsis creaghii} & 1.9 \(^e\) & 10.9 \(\pm\) 1.07 & 16.8 \(\pm\) 0.26 & 27.7 \(\pm\) 0.81 & 9 \\
\hline
\end{tabular}
\caption{The average canopy temperature repeat number \(n\), canopy temperature difference (CTD), temperature range, minimum and maximum values of the five rainforest tree species selected in the study (letter \(a\)–\(e\) represents the difference from high to low at the significant level of 0.05 \((p < 0.05)\)).}
\end{table}
The maximum stomatal conductance of the five species ranged from 93~120 mmol m\(^{-2}\) s\(^{-1}\) (Figure 3), and there were significant differences between the five species. The leaf size of the five species ranged from 14~173 cm\(^2\) (Figure 3). With the increase in temperature, the relative frequency of *Gironniera subaequalis* changed most obviously, and reached the maximum at 28 °C. The change of the other four trees was relatively gentle (Figure 3).

![Figure 3. Leaf temperature distributions of the five tree species showed (photos). Maximum \(g_s\) and leaf size values are inserted.](image)

We measured the mean \((T_c-T_a)\) on 4 February, 2018. The mean \((T_c-T_a)\) consisted with the photo flux density patterns (Figures 3 and 4). The five species of the three layers monitored on that day showed significant differences in \((T_c-T_a)\). *Pometia tomentosa* had the highest \((T_c-T_a)\) (6.4 K), the second highest was *Barringtonia pendula* (6.1 K), and *Mezzettipsis creaghii* had the lowest \((T_c-T_a)\) (1.9K) (Figure 4). We found that the temperature change within the canopies was very significant \((p < 0.01)\) (Figure 4). The canopy temperature difference of *Pometia tomentosa* and *Barringtonia macrostachya* reached the highest at about 13:00. However, the canopy temperature difference of *Gironniera subaequalis* reached its maximum two hours later (at about 15:00) (Figure 4).
3.3. \((T_c-T_a)\) Variations in a Changing Climate

\((T_c-T_a)\) ranged from nearly 0 K (\textit{Barringtonia racemosa} (L.) \textit{Spreng.}) to 3 K (\textit{Swietenia mahagoni} (L.) \textit{Jacq.}), showing that the mean leaf temperatures of 28 tree species had a highly species-specific manner (Table 2). The mean leaf temperature cannot be fully or solely explained by stomatal conductance or leaf area. This is because of the complex feedback effect between leaf temperature and climatic conditions or leaf function [20].

**Table 2.** Leaf-to-air temperature \((T_c-T_a)\), leaf area, and maximum stomatal conductance \((\dot{g}_{s\text{\text{\text{\text{\text{\text{\text{\text{max}}}}}}}}})\) of 28 tree species.

| No. | Species Name                      | \(T_c-T_a\) °C | Leaf Area cm\(^2\) | \(\dot{g}_{s\text{\text{\text{\text{\text{\text{\text{\text{max}}}}}}}}\}\) mmol m\(^{-2}\) s\(^{-1}\) | n  |
|-----|-----------------------------------|----------------|---------------------|-------------------------------------------------|----|
| 1   | \textit{Mezzettiopsis creaghii}   | 0.99 ± 0.06    | 32.83 ± 6.47        | 173.29 ± 49.90                                  | 5  |
| 2   | \textit{Swietenia mahagoni} (L.) \textit{Jacq.} | 2.93 ± 2.00 | 44.32 ± 5.10        | 162.93 ± 27.76                                  | 5  |
| 3   | \textit{Dipterocarpus turbinatus} \textit{Gaertn. f.} | 1.80 ± 0.51 | 106.38 ± 7.44       | 222.04 ± 17.58                                  | 4  |
| 4   | \textit{Cleistanthus sumatranus} (Miq.) Muell. Arg. | 0.81 ± 0.11 | 15.98 ± 9.53        | 401.26 ± 29.47                                  | 5  |
| 5   | \textit{Dalbergia odorifera} T. Chen | 0.57 ± 0.48  | 14.51 ± 3.83        | 221.41 ± 57.08                                  | 5  |
| 6   | \textit{Pterocarpus indicus} \textit{Willd.} | 0.79 ± 0.15  | 70.93 ± 30.95       | 188.18 ± 65.16                                  | 5  |
| 7   | \textit{Artocarpus heterophyllus} \textit{Lam.} | 1.43 ± 1.92  | 97.80 ± 11.60       | 448.82 ± 44.31                                  | 5  |
| 8   | \textit{Hopea hainanensis} \textit{Merr. et Chun} | 0.83 ± 0.28  | 74.03 ± 12.96       | 480 ± 31.26                                    | 5  |
| 9   | \textit{Saraca dives} \textit{Pierre} | 1.27 ± 0.11  | 100.88 ± 30.05      | 166.59 ± 53.11                                  | 5  |
| 10  | \textit{Woodfordia fruticose} (Linn.) \textit{Kurz} | 1.15 ± 1.73  | 20.10 ± 3.70        | 548.88 ± 48.58                                  | 5  |
| 11  | \textit{Aquilaria agallocha} \textit{Roxb} | 0.31 ± 0.08  | 29.64 ± 4.88        | 217.26 ± 21.22                                  | 5  |
| 12  | \textit{Magnololia rostrata} \textit{W. W. Smith} | 0.59 ± 0.51  | 253.10 ± 116.03     | 170.23 ± 49.83                                  | 5  |
| 13  | \textit{Mesua ferrea} \textit{L.} | 0.63 ± 0.11  | 22.28 ± 7.27        | 127.65 ± 26.22                                  | 5  |
| 14  | \textit{Rauwolfia vominans} \textit{Tsang} | 0.23 ± 0.22  | 23.86 ± 4.01        | 88.26 ± 43.74                                  | 5  |
| 15  | \textit{Oxyclyium} \textit{indicum} | 0.50 ± 0.72  | 59.16 ± 23.86       | 355.58 ± 139.85                                 | 5  |
| 16  | \textit{Milletia rubiginosa} \textit{Wight et Arn.} | 1.68 ± 1.06  | 46.97 ± 16.90       | 235.17 ± 102.95                                 | 5  |
| 17  | \textit{Ficus curtipes} | 0.26 ± 0.38  | 70.38 ± 17.56       | 209.97 ± 78.20                                  | 5  |
| 18  | \textit{Buchinia} \textit{Liou} | 0.16 ± 0.17  | 65.65 ± 9.33        | 183.91 ± 53.83                                  | 5  |
| 19  | \textit{Mayodendron igneum} (\textit{Kurz}) \textit{Kurz} | 0.32 ± 0.22  | 41.82 ± 8.00        | 274.25 ± 77.56                                  | 6  |
| 20  | \textit{Dracaena cambodiensis} \textit{Pierre ex Gagnep.} | 0.93 ± 0.16  | 95.00 ± 21.43       | 80.78 ± 33.25                                  | 5  |
| 21  | \textit{Baccaraea ramiflora} \textit{Lour} | 0.67 ± 0.19  | 76.53 ± 8.38        | 121.56 ± 21.29                                  | 5  |
| 22  | \textit{Barringtonia racemosa} (L.) \textit{Spreng.} | 0.08 ± 0.24  | 178.54 ± 51.97      | 219.04 ± 79.81                                  | 5  |
| 23  | \textit{Moghania macrophyla} (\textit{Willd.}) \textit{O Ktze.} | 1.57 ± 0.46  | 115.02 ± 25.24      | 212.76 ± 70.90                                  | 5  |
| 24  | \textit{Pluknetia volubilis} \textit{Linneo} | 2.61 ± 1.69  | 94.54 ± 19.97       | 350.80 ± 93.84                                  | 5  |
| 25  | \textit{Terminalia bellirica} (\textit{Gaertn.}) \textit{Roxb.} | 0.38 ± 0.66  | 57.87 ± 11.24       | 269.73 ± 46.20                                  | 5  |
| 26  | \textit{Camptotheca acuminata} | 0.76 ± 0.23  | 144.90 ± 34.76      | 398.22 ± 93.55                                  | 5  |
| 27  | \textit{Cinnamomum japonicum} \textit{Sieb.} | 0.07 ± 0.42  | 23.21 ± 4.00        | 187.48 ± 28.19                                  | 5  |
| 28  | \textit{Clerodendrum bungii} \textit{Staud.} | 1.20 ± 0.12  | 171.80 ± 47.19      | 638.84 ± 43.46                                  | 5  |
It is estimated that global warming will strengthen the water cycle and increase the demand for evaporation in ecosystems. Under drought stress, stomatal conductance of plants decreases, thus reducing transpiration and increasing canopy temperature. Therefore, in order to explore the differences in canopy temperature among tree species in an expected changing climate, we assumed that the maximum gs value of each tree species decreased linearly to 50%. (Tc–Ta) was very sensitive to all simulated meteorological elements (Figure 5; p < 0.01) and increased linearly with the increase in direct radiation (DR) and relative humidity (RH) (Figure 5a,c). (Tc–Ta) decreased non-linearly with the increase in air temperature (Ta) and wind speed (Ws) (Figure 5b,d).

With the increase in direct radiation (DR), the canopy temperature difference (CTD) of large-leaved trees increased more than that of small-leaved trees (Figure 5a). Species-specific differences in (Tc–Ta) became larger with the increasing DR.

The decrease amplitude of (Tc–Ta) with the increasing Ta of the tree species with the largest leaves (Magnolia rostrata W. W. Smith) was similar to the tree species with the smallest leaves (Woodfordia fruticose (Linn.) Kurz). (Tc–Ta) was negatively correlated with air temperature (Ta) and relative humidity (RH) (Figure 5b,c), indicating that (Tc–Ta) decreased with increasing water vapor pressure deficit (VPD). Species-specific differences in (Tc–Ta) became smaller with the increasing Ws (Figure 5d).

4. Discussion

Our results suggest that the species composition of trees has an important impact on the local climate of the primary tropical rain forest and are consistent with the study in a mixed deciduous forest [14]. The temperature changes found in this study may be critical in determining the diversity of canopy-dwelling plant communities. The patterns of temperature change identified by the study may be critical in determining canopy plant diversity [14].

The mean leaf temperatures of 28 tree species have a highly species-specific manner. Mean leaf temperature cannot be fully or solely explained by stomatal conductance or leaf area [21]. This is
because of the complex feedback effect between leaf temperature and climatic conditions or leaf function [22]. Variations in leaf temperature play a major role in determining rates of photosynthetic CO₂ uptake and transpiration [23]. On the other hand, changes in photosynthesis and transpiration resulting from changes in leaf temperature may have an impact on the efficiency of nutrient use [7,20].

On the other hand, the response of canopy temperature difference of 28 tree species to climate change was also diverse. (Tc-Ta) of tree species with smaller leaves and larger stomatal conductance was lowly sensitive to climate factors, such as Woodfordia fruticosa (Linn.) Kurz and Cleistanthus sumatranus (Miq.) Muell. Arg. In contrast, (Tc-Ta) of tree species (Dracaena cambodiana Pierre ex Gagnep.) with the smallest stomatal conductance was highly sensitive to climate factors. (Tc-Ta) of tree species (Magnolia rostrata W. W. Smith) with the largest leaves was also highly sensitive to climate factors, even if the stomatal conductance was not small. In other words, different tree species have their own strategies for climate change. With the maintenance of tree species diversity, the ability of ecosystems to resist climate change will be stronger. Conversely, loss of tree species diversity will make forests more vulnerable to climate change [24]. Climate change research for the future will involve a series of uncertainties, and it is still not sure what climate scenario will best reflect reality. What are the differences of short-term response and long-term adaptation of different tree species to climate change? [25]. Thus, tropical rainforest management for climate change has to deal with a range of uncertainties in the future.

5. Conclusions and Implications

Our study showed that the leaf size and stomatal conductance together decided the effect of climate change on (Tc-Ta) of the different tree species in the tropical rainforest. (Tc-Ta) of tree species with smaller leaves and larger stomatal conductance was lowly sensitive to climate factors. These results indicate species-specific functional traits which are needed to explicitly explore and model the interactions of individuals for improving the understanding and prediction of climate change impacts on vegetation.

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