Spatial and seasonal variation in leaf temperature within the canopy of a tropical forest

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ABSTRACT: Understanding leaf temperature (T_{leaf}) variation in the canopy of tropical forests is critical for accurately calculating net primary productivity because plant respiration and net photosynthesis are highly sensitive to temperature. The objectives of this study were to (1) quantify the spatiotemporal variation of T_{leaf} in a semi-deciduous tropical forest in Panama and (2) create a season-specific empirical model to predict T_{leaf} in the canopy. To achieve this, we used a 42 m tall construction crane for canopy access and monitored the microenvironment within the canopy of mature, 20–35 m tall trees of 5 tropical tree species during the wet and the dry season. T_{leaf} was correlated to photosynthetic photon flux density (PPFD) in the wet season but not in the dry season, possibly due to seasonal differences in wind speed, physiology, and canopy phenology. A structural equation model showed that T_{leaf} is best explained by air temperature (T_{air}) and PPFD in the wet season, whereas in the dry season, T_{air} alone predicted most of the variation in T_{leaf}. These results suggest the utility of an empirical approach to estimate T_{leaf} variability where simple meteorological data are available. This approach can be incorporated in future models of vegetation–atmosphere carbon and water exchange models of mature tropical forests with similar seasonality.

KEY WORDS: Leaf temperature · Tropical forest · Canopy research · Carbon modeling

1. INTRODUCTION

Tropical forests account for more than one-third of global terrestrial net primary productivity (NPP; abbreviations used in the article given in Box 1) (Malhi & Grace 2000), but their potential to take up and store carbon in the coming decades can be reduced as temperatures rise to levels that are thought to be close to the thermal maximum of plants (Doughty & Goulden 2008). Plant respiration has a characteristic exponential response to temperature, whereas net photosynthesis declines steeply above a narrow optimal temperature (Berry & Björkman 1980). In addition, frequent occurrence of high temperatures in tropical forest leaves (Krause et al. 2010) can cause down-regulation of net photosynthesis, especially in combination with stomatal closures (e.g. midday and afternoon depression) (Gamon et al. 2005, Kosugi et al. 2008). T_{air} from standard meteorological station (SMSs) are often used to incorporate temperature in models of photosynthetic productivity of forest canopies (Cramer et al. 1999, Blum et al. 2013). This adds a significant source of error, not only because the temperature from SMS differs substan-

tially from the temperature of the canopy (Helliker & Richter 2008, Blum et al. 2013, De Frenne & Verheyen 2016), but also because SMS T_{air} values cannot account for within-canopy T_{air} variation.

Even though many models of carbon and water fluxes assume that there is no spatial variation in T_{leaf} in the canopy, large spatial variation in T_{leaf} may occur vertically within the canopy (Bauerle et al. 2009) and horizontally among tree crowns (Leuzinger & Körner 2007). Hence, understanding T_{leaf} variability in the canopy is necessary with regards to our ability to accurately estimate NPP under current and future climate scenarios, particularly in tropical forest canopies where substantial variation in leaf energy budgets may be found due to the high diversity of species and leaf display patterns (Kitajima et al. 2005). At a given moment, T_{air} in the upper canopy can be very different from the lower canopy. Although there are few data of within-canopy T_{air} in tropical forests (Doughty & Goulden 2008), it has been reported for temperate forests that T_{air} may vary up to 5°C in the canopy of *Picea abies* L. (Zweifel et al. 2002), and 12°C in a mature *Acer rubium* L. canopy (Bauerle et al. 2007). The spatial variability of temperature in the canopy is expected to be even higher when individual leaves instead of the air are measured. This variability should not be ignored, because deviations of T_{leaf} from T_{air} potentially explain the discrepancies between expected and observed climate–NPP relationships across the globe (Michaletz et al. 2014).

In theory, a biophysical model of energy balance can predict the spatial variability of T_{leaf} in forest canopies from radiation, T_{air}, and 3-dimensional data of wind speed, if certain assumptions are met. T_{leaf} is the result of the balance between inputs and outputs of energy. Leaves absorb solar and thermal radiation and return this energy to the environment as longwave radiation, conductive and convective heat losses, and latent heat loss, with negligible effects of heat storage and metabolic heat production at a given moment (Campbell & Norman 1998). Wind speed, canopy drag, and internal attenuation of wind can be adequately modeled in a forest canopy (e.g. Baldocchi & Meyers 1988), but the energy balance experienced by individual leaves also depends on evapotranspiration, which reflects physiology (stomatal regulation) and complex boundary layer structure associated with leaf display and branch architecture. This is particularly true for tropical forests, where high diversity of leaf form and function brings high variability in the boundary layer of leaves (Gates 1968) and in leaf stomatal control among spe-

Box 1. Abbreviations used in the article

A_{net}	Net photosynthetic assimilation
LAI	Leaf area index
N	Number of days
n	Number of observations
NPP	Net primary productivity
PDF	Probability density function
PPFD	Instantaneous photosynthetic photon flux density incident on a leaf (μmol m^{-2} s^{-1})
$PPFD_{daily}$	Averaged daily PPFD incident on a leaf (mol m^{-2} s^{-1})
RH	Relative humidity (%)
$RPPFD_{daily}$	Averaged daily PPFD incident on a horizontal plane (mol m^{-2} s^{-1})
RPPFD	Instantaneous PPFD incident on a horizontal plane above the canopy
RT_{air}	Instantaneous reference air temperature (crane meteorological station) (°C)
$\overline{RT_{air}}$	Mean daytime air temperature measured at the crane meteorological station for the time a tree species was monitored (°C)
SEM	Structural equation model
SMS	Standard meteorological station
T_{air}	Instantaneous air temperature in the canopy (°C)
T_{diff}	Instantaneous difference between leaf and air temperature in the canopy (°C)
$\overline{T_{diff}}$	Mean daytime difference between leaf and air temperature for the time a tree species was monitored (°C)
TOD	Time of day
T_{leaf}	Instantaneous leaf temperature (°C)
$\overline{T_{leaf}}$	Mean daytime leaf temperature for a monitored leaf (°C)
$\overline{\overline{T_{leaf}}}$	Mean daytime leaf temperature of all leaves in a species for the time the tree species was monitored (°C)
T_{range}	Maximum difference between the coolest and hottest leaf in the canopy (°C)
VP	Vapor pressure (KPa)
VPD	Vapor pressure deficit (KPa)

cies (Meinzer et al. 1993) and among shade and sun leaves within an individual (Vogel 1968).

Here, we seek empirical correlative rules that describe how temperature experienced by individual leaves in a canopy can be related to easy-to-access meteorological data. If available, such rules may allow us to create simplified models of canopy respiration and net photosynthesis without wind speed and transpiration rates experienced by individual leaves. Similar efforts have been successful for estimation of soil temperature under the forest from T_{air} measurements (Bond-Lamberty et al. 2005) or to predict stomatal conductance in response to changes in PPFD, VPD, or T_{air} (Collatz et al. 1991, Leuning 1995). These approaches place mechanistic details in a

black box (e.g. ignoring wind speed), but they have been widely used in certain ecosystem process models, e.g. Biome-BGC (Running & Coughlan 1988) or SiB2 (Sellers et al. 1996). Such empirical 'black box' approaches may avoid unwarranted assumptions necessary for applications of theoretical wind models to a complex forest canopy, which exhibits spatial and temporal variations that reflect biological strategies of trees for leaf display and physiology.

The first objective of this study was to quantify the spatiotemporal variation of T_{leaf} and other environmental variables within the canopy of a seasonal tropical forest. In this semi-deciduous forest, only evergreen species maintain leaves during the dry season, whereas during the wet season, the fully-foliated canopy creates a steep vertical gradient of light within the canopy (Kitajima et al. 2005). Thus, our overall hypothesis was that T_{air} and T_{leaf} exhibit contrasting daily patterns between the wet and dry seasons. More specifically, we hypothesized that clouds and frequent rain moderate T_{air} in the wet season, resulting in a stronger effect of solar radiation load on T_{leaf} than T_{air}. In contrast, we expected that higher T_{air} and wind speeds in the dry season result in greater coupling of T_{air} with evergreen leaves. Such coupling of leaf and T_{air} indicates the importance of conductive heat loss for the evergreen upper canopy leaves for avoiding lethal temperatures under the sunny and water-limited conditions of the dry season. Our second objective was to develop a season-specific empirical model to estimate T_{leaf} variation within the canopy from simple meteorological data. Such a model has the potential to be incorporated in estimations of net carbon flux in the forest.

2. MATERIALS AND METHODS

2.1. Study site

The study was conducted in Parque Natural Metropolitano, a 265 ha tropical forest reserve in Panama City, Panama (08° 59′ 39.95″ N, 79° 32′ 34.68″ W, 30 m above sea level). This reserve protects an 80–150 yr old semi-deciduous forest with tree heights up to 40 m. The annual precipitation averages 1764 mm, most of which falls in the rainy season that occurs between mid-May and mid-December. Average T_{air} is 25.7°C as registered in the 17 yr record of a meteorological station located at mid-height in the canopy. For the time of our study, which occurred between November and December 2011 (wet season) and February and March 2013 (dry season), the average

T_{air} was 24.4 and 29.6°C, respectively. Wind speed was significantly higher in the dry season (3.22 m s^{-1}) than in the wet season (2.11 m s^{-1}) (t-test, p < 0.001). The wet season of 2011 experienced a weak La Niña event, whereas the dry season of 2013 was neither an El Niño nor a La Niña year. Thus, the data reported in our study are indicative of typical contrast between the 2 seasons even though they are not consecutive.

The upper forest canopy was accessed via a 42 m free-standing construction crane with a 52 m long jib (Parker et al. 1992). We selected 5 of the most representative tree species of the area: *Luehea seemannii* Triana & Planch; *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels; *Castilla elastica* var. *costaricana* (Liebm.) C.C. Berg; *Pittoniotis trichantha* Griseb, and *Ficus insipida* Willd (hereafter referred to by their genera). The approximate height of the canopy of the selected trees ranges between 16.5 m in *Castilla* and 29 m in *Anacardium* and the leaf area index (LAI) ranges between 2.4 and 7.5 for the same species, respectively (Kitajima et al. 2005). Despite variations in height, all selected individuals were fully exposed to the sun at the top of the canopy. In the wet season, we measured 1 vertical gradient in the crown of 1 individual of each of the 5 species. In the dry season, only 2 evergreen species, *Anacardium* and *Luehea*, were monitored. We had no replication within species due to logistical limitations, but our main intention was to sample broadly from the multi-species forest canopy within the reach of the crane.

2.2. Measurement of environmental variables

We measured PPFD incident on the adaxial surface of several leaves within the canopy distributed among species and different light gradients. To ensure sampling of a large enough PPFD gradient, the crown of each tree was classified *a priori* to 3 light levels for the wet season (upper canopy or 'sun' leaves, intermediate, and shade) and to 2 levels for the dry season (sun and shade; Fig. 1); we selected 3 or 4 mature, fully-expanded leaves at each light level. The leaves within each light level were grouped in clusters 2 to 5 m wide but were far enough from each other to avoid interference with the readings of other leaves. PPFD was measured with gallium-arsenide photodiodes (G1118, Hamamatsu) that were individually calibrated against an LI-190SA quantum sensor (Li-Cor). T_{leaf} on the same leaves was measured using copper-constantan Type T thermocouples (Omega) with a thin tip attached to the abaxial surface of the leaf with porous adhesive tape that allows transpira-

Wet season

Dry season

3-4 Leaves with PPFD sensors, Thermocouples and air temperature sensor: I-buttons
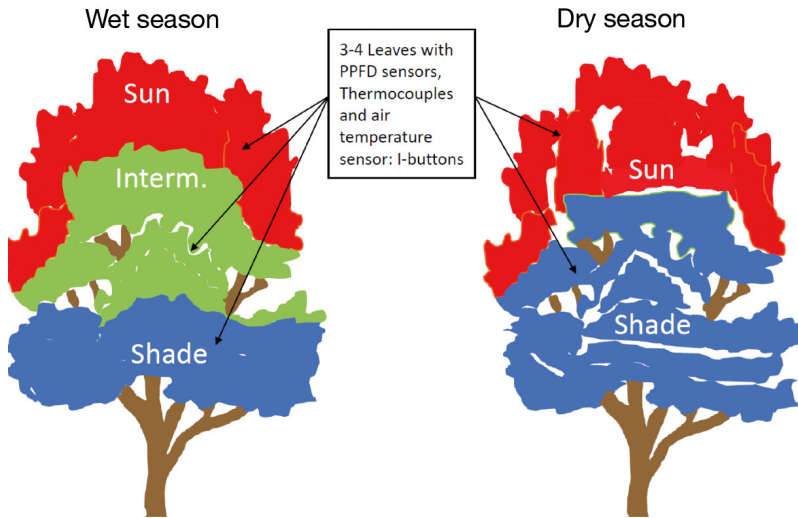
Fig. 1. Schematic representation of classifying portions of each tree crown to 2 to 3 light levels, using *Anacardium* sp. as an example tree. Three to 4 leaves were chosen at each light level and each leaf was monitored with a thermocouple for leaf temperature, a photodiode for photosynthetic photon flux density (PPFD), and an i-button for air temperature. We chose to classify to 2 light levels in the dry season, when the forest canopy was semi-deciduous, and evergreen tree crowns had lower leaf density due to phenological balance of leaf production and loss

tion in the contact zone (Transpore 3M). In total, 51 leaves were successfully monitored; for the wet season 18 leaves in shade, 8 in intermediate, and 13 in well-exposed sunny conditions, and for the dry season 6 leaves in the shade and 6 in well-exposed sunny conditions. The sensors were carefully installed to minimize changes in the natural leaf angle. T_{leaf} and PPFD were measured at similar positions on the leaves and were recorded every 2 min with a Campbell 21X datalogger (Campbell Scientific) for 2 to 10 consecutive days for each species (Table 1). RPPFD was monitored every 15 min with a LI-190SA Quan-

tum sensor connected to a CR1000 datalogger (Campbell Scientific).

T_{air} and RH within the canopy were measured using i-button sensors (Maxim Integrated). The i-buttons were placed within 1 m of a subset of the same leaves used to measure T_{leaf} and PPFD, and shielded from direct radiation with a shade frame made of inverted 50 ml plastic cups covered with aluminum foil to reflect light. VP and VPD at different positions in the canopy were calculated using the Tetens formula (Buck 1981). RT_{air} at the study site was obtained from a meteorological station located on the crane tower 25 m above ground. This station provided 15 min averages of T_{air}, RH, precipitation, and global solar radiation and has been in operation since 1995 (http://biogeodb.stri.si.edu/physical_monitoring/research/metpark).

Because T_{air} data from SMSs at 1.2 m above the ground are often used to inform ecosystem carbon balance models, we wanted to verify the extent of the discrepancy of T_{air} and RT_{air} data to T_{air} collected at 2 SMSs managed by the Panama Canal Authority. The Balboa station (08° 58′ 08″ N, 79° 32′ 58″ W) is located 2.95 km south of the study site, and the Corozal station (08° 58′ 51″ N, 79° 34′ 29″ W) is located 3.84 km west of the study site. Besides T_{air}, we also used wind speed data from these stations to compare differences among seasons. We used data from 2010, which were the most recently available at the time of the study, and compared these data to T_{air} data from our study site for the same year.

Table 1. Summary of light and daytime temperature of canopy leaves by species and season during the period corresponding to measurements of each species. Abbreviations are defined in Box 1; Max T_{diff}: maximum instantaneous difference between leaf and air temperature and Max T_{range}: maximum range of temperatures within the canopy. Standard deviations are also shown for $\overline{RT_{air}}$ (measured every 15 min), $\overline{\overline{T_{leaf}}}$, and $\overline{\overline{T_{diff}}}$ (measured every 2 min)

Season	Species	RPPFD$_{daily}$ (mol m^{-2} s^{-1})	N	$\overline{RT_{air}}$ (°C)	$\overline{\overline{T_{leaf}}}$ (°C)	$\overline{\overline{T_{diff}}}$ (°C)	Max T_{diff} (°C)	Max T_{range} (°C)
Wet	*Luehea*	23.0	2	25.8 ± 1.7	26.3 ± 2.2	1.0 ± 1.1	8.7	7.7
Wet	*Anacardium*	17.0	2	25.1 ± 2.1	25.7 ± 3.1	0.9 ± 1.5	10.4	13.1
Wet	*Castilla*	32.8	3	26.5 ± 2.4	26.3 ± 2.4	0.0 ± 1.1	6.4	9.2
Wet	*Pittoniotis*	22.1	2	25.3 ± 3.0	25.9 ± 3.5	0.6 ± 1.5	9.3	15.7
Wet	*Ficus*	22.1	3	26.1 ± 2.2	27.1 ± 3.6	1.2 ± 2.3	9.9	17.5
Dry	*Anacardium*	39.4	10	29.7 ± 2.6	29.7 ± 2.8	−0.7 ± 0.8	5.3	7.6
Dry	*Luehea*	37.9	5	29.4 ± 2.5	29.3 ± 2.7	−0.8 ± 0.7	1.6	3.2

2.3. Data analysis

Because our analysis focused on the effect of PPFD on temperature, we analyzed daytime and nighttime separately, except for the analysis of T_{air}. Sunrise, solar noon, and sunset times were calculated with Sun-Earth orbit geometry equations for the latitude of the site (Campbell & Norman 1998). Nighttime for Day of Year *j* corresponded to the time from sunset to midnight of Day *j* plus the time from midnight to sunrise of Day *j* + 1. We only used leaves that had uninterrupted temperature and radiation data for 2 to 3 consecutive days for the wet season and 5 to 10 for the dry season (Table 1).

We calculated species means for $RPPFD_{daily}$, $\overline{RT_{air}}$, $\overline{T_{leaf}}$, and $\overline{T_{diff}}$. Also summarized was the maximum values for T_{diff}, as well as T_{range} of each species (Table 1).

T_{air} in the canopy was compared to the T_{air} of the reference meteorological station in the forest (RT_{air}, a covariate) with analysis of covariance to test for differences between slopes among the light levels. To evaluate T_{leaf} and its relationship to PPFD, mean T_{leaf} of each measured leaf was regressed against integrated daily PPFD incident on the leaf ($PPFD_{daily}$). Finally, we used an analysis of variance to compare nighttime temperatures relative to RT_{air} among species and canopy light levels.

We fitted frequency distributions of the temperature of individual leaves separately for daytime and nighttime. Because most daytime frequency distributions were bimodal, we fitted them to a di-gamma PDF (see Appendix 1 for more information). All of the above data analyses were done using R version 3.0.0 (R Development Core Team 2012).

To create an empirical model for predicting the instantaneous response of T_{leaf} to environmental variables, we used an SEM that was run through AMOS (Arbuckle 2006). We constructed different models for expected causal relationships between T_{leaf} and relevant environmental variables: RPPFD, PPFD, RT_{air}, T_{air}, VP, VPD, and TOD. TOD is a unitless variable running from approximately 6 (06:00 h) to 18 (18:00 h), and it had a non-linear relationship with the other variables. Thus, in order to guarantee linearity between all relationships, TOD was transformed using a second-order polynomial function, whereas all other variables were transformed to their natural logarithm. For the SEM, we used measurements taken every 15 min and calculated 15 min averages from the leaf data. We selected the model with the best fit using maximum likelihood chi-squared and Akaike's information criterion (AIC).

3. RESULTS

3.1. T_{air} within the forest canopy

T_{air} values from the SMSs, ca. 3 to 4 km away, were significantly higher than the temperatures at the forest meteorological station (RT_{air}) (1-way ANOVA, p < 0.005) in both seasons (Fig. 2) by 1.41 ±_0.98 (mean ± 1 SD for hourly data of 2010) and 1.28 ± 0.96°C at Balboa and Corozal stations, respectively. T_{air} in different canopy positions was linearly correlated with RT_{air} (Fig. 2). In the wet season, the slope of the relationship between T_{air} and RT_{air} was significantly greater for sun leaves than for intermediate (ANCOVA, p < 0.001) and shade leaves (ANCOVA, p < 0.001) (Fig. 2). Although the differences in the dry season were also significant (ANCOVA, p < 0.001), sun and shade leaves were more similar than in the wet season (Fig. 2). The shade and intermediate locations exhibited slopes significantly <1 in the wet season (ANCOVA, p < 0.001), whereas the sun locations in the wet season and both shade and sun locations in the dry season had slopes >1 (ANCOVA, p < 0.001), in both seasons.
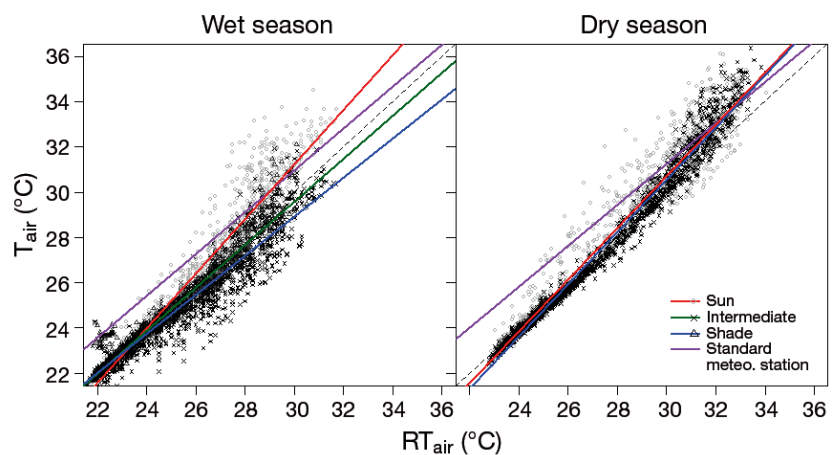

Fig. 2. Air temperature (T_{air}) for fully exposed sun, intermediate, and shade positions within the canopy, in the wet and dry season. Data from within-canopy T_{air} of all species and times of day were plotted in relation to the T_{air} from the meteorological station located on the crane tower at 25 m above the ground (RT_{air}). The slope of the relationship between the temperatures at the standard meteorological stations and RT_{air} is also shown. The dashed line shows the 1-to-1 relationship

3.2. Seasonal differences of T_{leaf} and incident radiation

The reference photosynthetic photon flux density (RPPFD) was significantly higher in the dry season than in the wet season (1-way ANOVA, p < 0.005). Average T_{air} was also higher in the dry season by 3.8°C (1-way ANOVA, p < 0.005). Within each season, $RPPFD_{daily}$ and T_{air} did not differ significantly among the periods used for different species, except for *Castilla* that exhibited significantly higher $RPPFD_{daily}$ values (but similar RT_{air}) than other species (Tukey-HSD, p < 0.05; Table 1).

The overall temperature for all leaves was 3.3°C higher in the dry season than in the wet season (*t*-test, p < 0.001). $\overline{T_{diff}}$ was positive in the wet season and negative in the dry season (Table 1), i.e. leaves were significantly warmer than the air in the wet season (*t*-test, p < 0.001) and significantly cooler than the air in the dry season (*t*-test, p < 0.001). $\overline{T_{diff}}$ varied considerably among tree crowns in the wet season, ranging from near 0 recorded from a *Castilla* crown to 1.2°C recorded from a *Ficus* crown (Table 1). There were brief periods of large differences between T_{leaf} and T_{air} especially in the wet season, with the maximum instantaneous difference between T_{leaf} and T_{air} being as high as 10.4°C in *Anacardium*, and 9.9°C in *Ficus* (Table 1). Similarly, T_{range} values were high in the wet season, reaching maximum values of up to 17.5°C (Table 1).

3.3. Mean T_{leaf} in relation to light variation

$\overline{T_{leaf}}$ values differed more among individual leaves in the wet season (24.5 to 28.7°C) than in the dry season (29.0 and 29.6°C; Fig. 3), both within and among species (e.g. 25.8–27.7°C for *Luehea* and 25.3–28.7°C for *Ficus*). $PPFD_{daily}$ varied widely among days and canopy positions, ranging from 0.1 to 26.7 mol m^{-2} d^{-1} in the wet season and from 3.9 to 27.4 mol m^{-2} d^{-1} in the dry season (Fig. 3). $PPFD_{daily}$ explained a large proportion of the variation of $\overline{T_{leaf}}$ during the wet season (r^2 = 0.683, p < 0.005: Fig. 3a) but not during the dry season (r^2 = 0.13, p > 0.05; Fig. 3b).

3.4. T_{leaf} variation in relation to incident light

In contrast to the relationship between daily average T_{leaf} and total daily PPFD, instantaneous (measured every 2 min) T_{leaf} was related to instantaneous PPFD in a hyperbolic manner (Fig. 4). At low PPFD, there was a rapid increase in T_{leaf} but the relationship became asymptotic at high PPFD. In addition, the relationships between T_{leaf} and PPFD varied with time of the day (morning or afternoon; Fig. 4). At low to intermediate PPFD, T_{leaf} was lower in the morning than in the afternoon regardless of the position within the canopy. The highest values of PPFD and T_{leaf} occurred in the morning in the wet season, whereas in the dry season high values of PPFD and T_{leaf} were observed both in the morning and in the afternoon (Fig. 4).
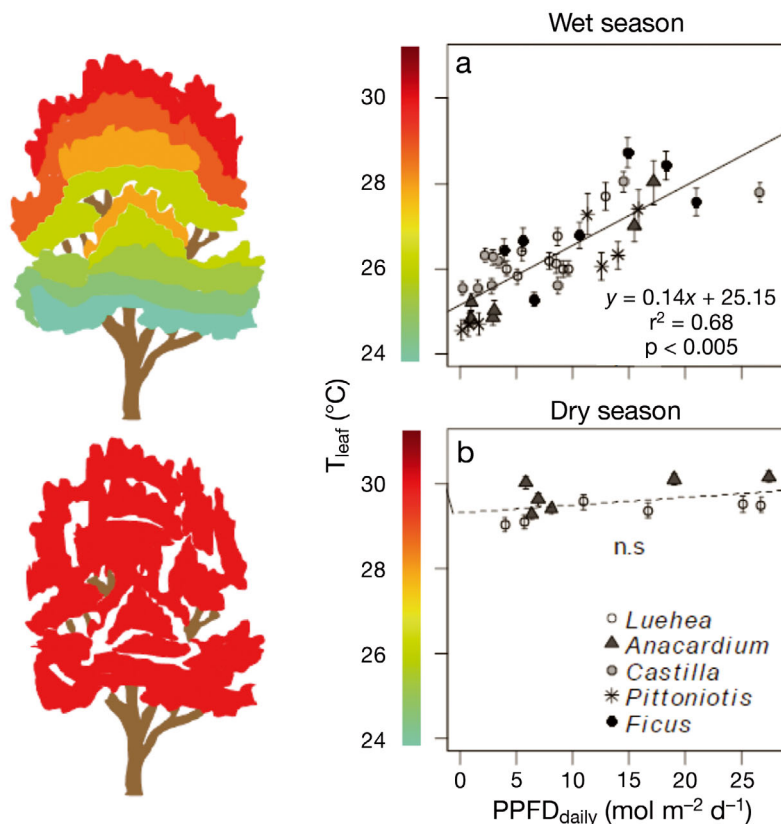

Fig. 3. Daytime mean leaf temperature (T_{leaf}) in response to the vertical gradient of daily photosynthetic photon flux density ($PPFD_{daily}$) for (a) the wet season and (b) the dry season (not significant). Each point in the plot corresponds to the average of a leaf measured for N days (Table 1) at 2 min (wet season) and 5 min (dry season) intervals. Error bars indicate 1 SE of the mean. The diagrams on the left show a schematic representation of the temperature gradient in each season for an *Anacardium* tree
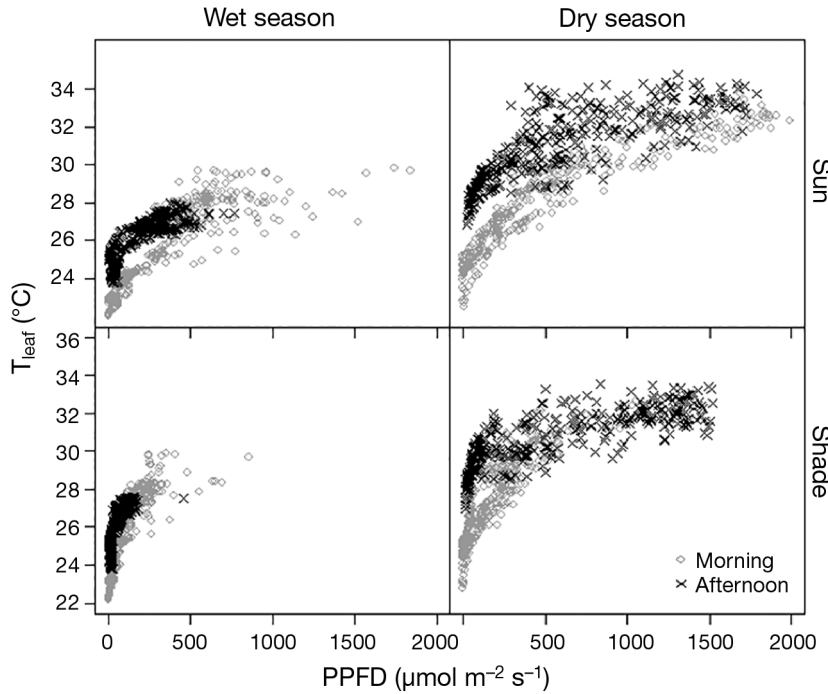
Fig. 4. Example of the instantaneous leaf temperature (T_{leaf}) variation in response to photosynthetic photon flux density (PPFD) for a leaf of *Luehea* in the morning and afternoon periods. Each plot corresponds to a representative sun and shade leaf in the wet season (left panels) and in the dry season (right panels)

3.5. Nighttime T_{leaf}

Mean nighttime T_{leaf} did not vary much between positions in the canopy in either season (data not shown). Leaves were slightly warmer and cooler than the reference T_{air} in wet and dry seasons, respectively. Fig. 5 shows this result by computing the ratio of T_{leaf} to T_{air} (T_{leaf}:RT_{air}) at different positions within
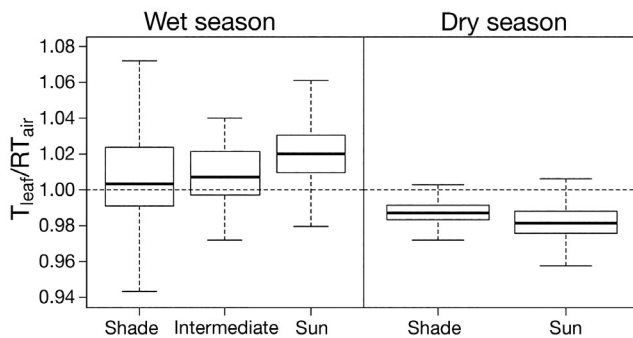

Fig. 5. Ratio of nighttime leaf temperature to air temperature (T_{leaf}: RT_{air}) in sun, intermediate, and shade leaves for the wet and dry seasons. RT_{air} was measured at the canopy meteorological station. Box plots indicate the median and 25th and 75th percentiles. Whiskers extend to 1.5 times the interquartile range. The horizontal dotted line marks the point where RT_{air} is equal to T_{leaf}

the canopy. Ratios >1 mean that leaves were warmer than the air and ratios <1 mean that the leaves were cooler than the air. Sun leaves had higher T_{leaf}:RT_{air} ratios than shade leaves in the wet season and lower ratios in the dry season (p < 0.005 for both seasons; Fig. 5). This supports the idea that during the nights of the dry season, sun-exposed leaves are subjected to more radiative cooling compared to more shaded leaves.

3.6. Frequency distributions of T_{leaf}

The frequency distribution of T_{leaf} during the night was unimodal, with a narrow range of variation that fitted a simple gamma distribution (data not shown). In contrast, daytime distributions were bimodal (Fig. 6) and were parameterized well with the digamma probability function (Appendix 1). The bimodal distribution, similar to those shown in Fig. 6, was found in 49 of the 51 leaves monitored as shown, regardless of the seasons and positions within the canopy. The highest temperatures occurred during the morning in the wet season, and during both morning and the afternoon in the dry season (Fig. 6), similar to the pattern shown in Fig. 4. The parameters of the di-gamma distribution differed significantly between the 2 seasons (1-way ANOVA, p < 0.05). In the dry season, the frequency distributions were similar and there were no significant differences between the 2 species (1-way ANOVA, p > 0.05). In the wet season, however, the parameters of the digamma distributions were significantly different among species (1-way ANOVA, p < 0.05). In general, all species except *Luehea* had a large left-hand mode in the leaf temperature histogram in shade leaves, while a second and relatively small right-hand mode was present in sun leaves (e.g. Fig. 6a,b).

3.7. Structural equation model

The SEM that best explains T_{leaf} variations is shown in Fig. 7. Other models that included alternative paths and other variables such as VP, VPD, or T_{air} at the canopy microsites were rejected ($\chi^2 > 15$, p < 0.05). To improve normality and linearity of the data,
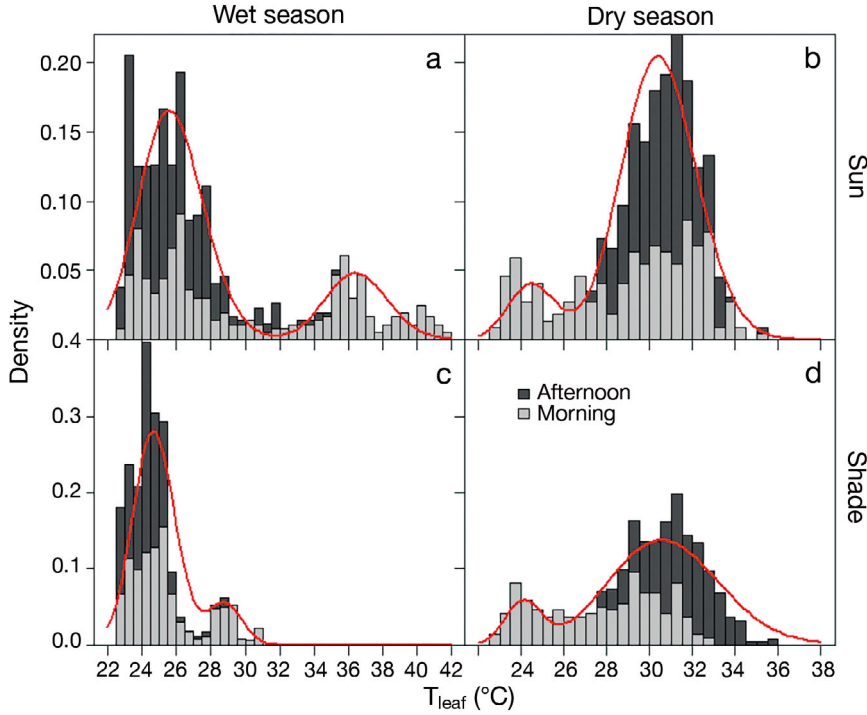
Fig. 6. Example of frequency histograms (bars) and fitted di-gamma probability density functions (red lines) for leaves of *Anacardium* in the wet and the dry season as well as for sun and shade leaves. T_{leaf}: leaf temperature
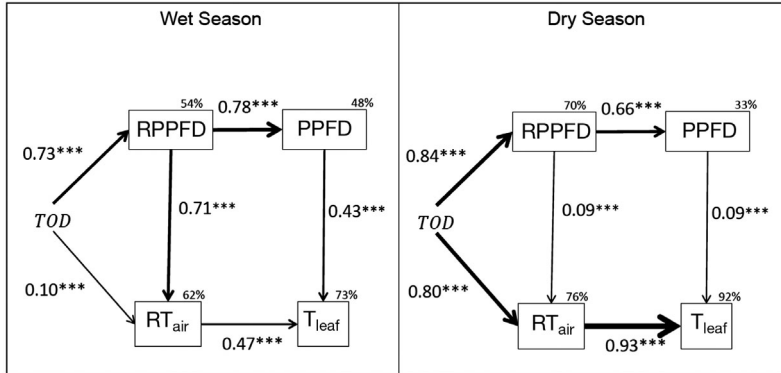

Fig. 7. Structural equation model showing the interactive effects of environmental variables on leaf temperature in the wet and the dry season. Each arrow represents a causal relationship between 2 variables. Variables within boxes are endogenous variables (dependent on other variables) and variables outside boxes are exogenous (independent). The width of the arrow represents the path coefficient (β) whose magnitude is shown next to it, with its level of statistical significance (*p < 0.05, **p < 0.005, ***p < 0.001). β indicates the strength of the relationship and varies between 0 and 1. The percentage of the variance that is explained by each variable is shown above each box on the right-hand side. Abbreviations are given in Box 1

we transformed all variables to their natural logarithm. Henceforth, however, the variables will be referred as the non-transformed form. This model was run for the wet season (5 species) and the dry season (2 species), as well as for each species individually. Fig. 7 shows the result of the SEM using all daytime

measurements for all species combined by season. TOD had a strong relationship with RPPFD in both seasons. The TOD relationship with RT_{air} was weak in the wet season (β = 0.1) and strong in the dry season (β = 0.80). RPPFD was a good predictor of RT_{air} in the wet season but not in the dry season (β = 0.71 and 0.09, respectively). RPPFD had a strong relationship with PPFD incident on leaves in both seasons but stronger in the wet than in the dry season (β = 0.78 and 0.66, respectively). RT_{air} was a stronger predictor of T_{leaf} in the dry season (β = 0.93) than in the wet season (β = 0.47). PPFD was a good predictor of T_{leaf} in the wet season but not in the dry season (β = 0.43 and 0.09, respectively). Overall, these models explained a greater proportion of T_{leaf} variance in the dry season (92%) than in the wet season (73%). Unlike these SEM models analyzing data pooled for all species, models run at the species level were not significant, except for *Anacardium* (see Appendix 2).

3.8. Performance of the model

Multiple regression equations of the SEM were calculated for the wet season and the dry season (Eqs. 1 & 2, respectively):

$$T_{leaf}(wet) = e^{1.354} \times PPFD^{0.026} \times RT_{air}^{0.554} \quad (1)$$

$$T_{leaf}(dry) = e^{-0.074} \times PPFD^{0.005} \times RT_{air}^{1.015} \quad (2)$$

We chose RT_{air} in the model over T_{air} because only the former is typically available in most forest research sites, and because our intention is to develop a predictive tool of individual T_{leaf} variation in tropical forest canopies of similar composition and with a distinct dry and wet season.

When evaluating the performance of these equations by plotting observed values against the predicted values (Fig. 8), T_{leaf} variation was well predicted in the dry season, when T_{air} and T_{leaf} were
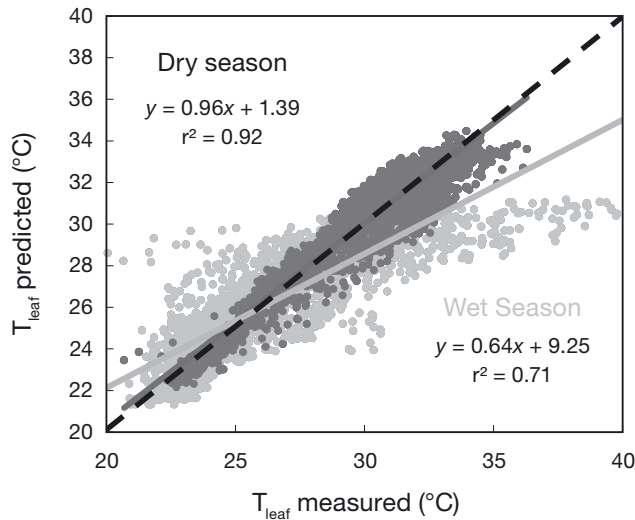
Fig. 8. Measured leaf temperature compared to the prediction from the equations of the structural equation model for the wet and the dry season (Eqs. 1 & 2). The dashed line is the 1:1 relationship. The light (dark) gray dots show the wet (dry) season

better coupled. At the same time, Fig. 8 shows that the model was unable to accurately predict high temperature episodes (above 35°C), which were more common in the morning under high PPFD during the wet season (Figs. 4 & 6).

4. DISCUSSION

Concern over rising temperatures during the current century has drawn attention to the importance of understanding physiological responses of trees to temperature (Stocker et al. 2013) and their incorporation to climate models in various types of vegetation including tropical forests (Rowland et al. 2015). To predict the physiological responses of trees to expected changes in T_{air}, not only the dependency of physiological processes on T_{leaf} needs to be determined, but the relationship between T_{leaf} and T_{air} also needs to be understood. Leaf dark respiration rates at this study site respond to changes in T_{leaf} over the short term (minutes to hours: Slot et al. 2013) and over time scales that allow for physiological acclimation (days to weeks: Slot et al. 2014b). Using reference T_{air} data, Slot et al. (2014a) modeled stand-level respiratory carbon fluxes at the study site. In the current study, we used an empirical approach to assess how the relationship of T_{leaf} and T_{air} is influenced by PPFD, RH, and TOD for leaves in contrasting positions within a tropical forest canopy. We further assessed how T_{leaf} dependency on these environmental

variables may differ between seasons. Nighttime T_{leaf} did not deviate much from T_{air}, although some radiative cooling of leaves below T_{air} was observed on clear, dry season nights. Thus, overall respiration estimates from previous studies at the site will be minimally biased by an assumption of T_{leaf} equal to T_{air}. In contrast, daytime T_{leaf} values deviated significantly from T_{air}, making estimating physiological processes using T_{air} as a substitute for T_{leaf} prone to error.

4.1. T_{air} within the canopy differs from temperature at meteorological stations

T_{air} readings from nearby SMSs were 1.2°C (wet season) to 1.7°C (dry season) higher than readings from the meteorological station in the forest canopy (RT_{air}), probably as a result of shade and evaporative cooling within the forest (Leuzinger et al. 2010). The systematic overestimation of forest temperatures from SMSs may lead to erroneous estimations of forest carbon fluxes, and collecting T_{air} data in the forest (RT_{air}) should reduce these errors (De Frenne & Verheyen 2016). However, RT_{air} does not represent T_{air} throughout the canopy either, let alone T_{leaf}. When RT_{air} was high, the meteorological station in the forest overestimated T_{air} of the shaded layers of the canopy, and underestimated temperatures in the upper canopy where most photosynthesis occurs. This shows that a better method needs to be implemented to have a full representation of the heterogeneity of T_{air} within the canopy.

For all the species in the wet season, there was a mean difference of 0.4°C in T_{air} between the hottest (sun exposed) and the coolest (shaded) part of the canopy. However, at moments when temperatures were high and the sun warmed the upper canopy leaves, this difference rose to 7.8°C. This difference was greater than the 5°C difference found in the canopy of *Picea abies* (Zweifel et al. 2002). Perhaps the less dense and rougher canopy of the sub-alpine *Picea* forest allows for better air mixing throughout the canopy, with less shading occuring than for the tropical forest in this study.

4.2. T_{leaf} and T_{air} are systematically and predictably different

Daytime differences between T_{leaf} and T_{air} (T_{diff}) were on average 0.74°C, but as high as 10.4°C at a given measurement interval. These values are simi-

lar to published values (Ansari & Loomis 1959, Martin et al. 1999), but lower than the 14°C reported for *Ficus* at the same site when T_{leaf} reached extreme values of 48°C on sunny, wind-free periods (Krause et al. 2010).

One factor that is expected to influence T_{diff} is transpirational cooling, which is influenced by stomatal behavior, RH, and the coupling efficiency of leaves with the atmosphere (omega coefficient, Ω; Jarvis & McNaughton 1986). T_{diff} is high when leaves are not coupled ($\Omega = 1$), and when T_{diff} is close to 0, leaves are well coupled ($\Omega = 0$). We found that leaves are warmer than the air in the wet season but cooler than the air in the dry season. This is in accordance with observations by Meinzer at al. (1993, 1997) at the same study site, who found that *Anacardium* leaves were better coupled with the atmosphere in the dry season ($\Omega = 0.54$) than in the wet season ($\Omega = 0.75$). This result was attributed to lower boundary layer conductance due to lower wind speed in the wet season. In addition, Meinzer et al. (1997) found high Ω values (i.e. low coupling) for *Luehea* and *Ficus* in a prolonged wet season. The seasonal variation of Ω matches seasonal variation of wind speed, which suggests that the effect of wind on leaf and canopy boundary layer resistance may be crucial in explaining the seasonal differences of T_{diff}.

The fact that leaves were cooler than the air during the dry season suggests that transpiration is an important driver of T_{leaf} during this season, as transpiration represents a key mechanism by which leaves can cool down, especially when the wind speed is high. Previous research at the study site shows that transpiration is indeed high in the dry season (Meinzer et al. 1993; M. Slot & K. Winter unpubl. data), supporting this hypothesis.

4.3. Leaf-level incident irradiance as a driver of T_{leaf}

There was large spatial variation in T_{leaf}. The average difference between the warmest and the coolest leaf in the canopy was 3.8 and 1.5°C for the wet and dry season, respectively, and reached values of up to 17.5°C during the wet season. This last value is higher than the values obtained for a temperate mixed forest using thermal imagery (10–12°C; Leuzinger & Körner 2007). Whereas the results of Leuzinger & Körner (2007) were the product of horizontal differences in the upper canopy temperatures among species, our results were the product of vertical within-canopy temperature variation. The combination of species- and architectural diversity (Kita-

jima et al. 2005) and the multi-layered structure of tropical forest canopies (Kira 1975) generates potential for large deviations of T_{leaf} from T_{air} readings from meteorological stations.

Our analysis also suggests that solar radiation incident on the leaf surface (which shows a linear correlation with instantaneous PPFD) is key to explaining the deviations of T_{leaf} from T_{air} in the wet season (Figs. 3 & 7). There was a clear response of T_{leaf} to instantaneous PPFD (Fig. 3). This response, however, displayed hysteresis. The fact that a leaf in the afternoon was warmer than in the morning at the same irradiance can be related to 2 factors. First, during the afternoon, T_{air} is generally higher than in the morning, and therefore leaves are warmer in the afternoon even when they receive the same PPFD as in the morning. Second, although transpiration can be maintained even in the dry season, mid-day stomatal closure may still occur and restrict transpirational cooling (Gamon et al. 2005). It is likely that the higher T_{leaf} in the afternoon is caused by a combination of both factors, because higher T_{leaf} in the afternoon is observed in sun leaves, which are more likely to experience mid-day stomatal depression, as well as in shade leaves, whose temperature is controlled almost exclusively by T_{air} (data not shown).

The relationship between $\overline{T_{leaf}}$ and $PPFD_{daily}$ was strong in the wet season both within and across canopies (Fig. 2), but not in the dry season. Across all leaves, there was an increase of 0.14°C in the daytime average temperature for every mol m^{-2} d^{-1} increase of $PPFD_{daily}$ in the wet season. This means that on a given sunny day in the wet season (which may experience a $PPFD_{daily}$ of 30 mol m^{-2} d^{-1}), the variation in mean T_{leaf} can be up to 4.2°C based on irradiance differences alone. In the dry season, however, all leaves in the canopy had similar mean T_{leaf} and there was no effect of $PPFD_{daily}$ on mean T_{leaf}. Because T_{air} was higher in the dry season, shaded leaves could warm up without direct irradiance. The high transpirational demand and associated stronger potential cooling of sun-exposed leaves may have further moderated the irradiance-dependence of T_{leaf} in the dry season.

4.4. Modeling T_{leaf}

4.4.1. Systematic bimodality of T_{leaf} distributions

The bimodality of the T_{leaf} frequency distributions was found in all species and in both seasons (Fig. 6), although the reasons why the bimodality occurred

differed between seasons. Bimodality in the wet season was mostly explained by distinct periods of low irradiance (early morning and following afternoon rain storms), and periods of relatively high intensity of light in the morning where T_{leaf} increased rapidly (Fig. 4). The transitions between these periods were sharp, with the arrival of full sun exposure in the morning, and the sudden onset of tropical rain or clouds in the afternoon. In contrast, bimodality in the dry season was mostly related to differences in temperatures in the morning and in the afternoon. In the dry season, both T_{air} and T_{leaf} decreased overnight to register the lowest values in the early morning due to radiative heat loss during the night. An increase in T_{leaf} did not happen until ca. 09:00 h, when temperatures rose rapidly and stayed high in the afternoon as no rainfall or clouds cooled the system (Figs. 4 & 6). This dry-season situation was similar to the bimodality of T_{leaf} frequency distributions reported for sun and shade leaves in the canopy of *Abies amabilis*, a subalpine forest tree (Martin et al. 1999), whose T_{leaf} distributions were directly associated with the bimodality of T_{air}.

4.4.2. T_{leaf} as a function of TOD, T_{air}, and irradiance: lessons from an SEM

Season-specific empirical correlative rules to predict T_{leaf} from the irradiance gradients within the canopy can be used to evaluate the significance of T_{leaf} variation in modeling carbon flux in the tropical forest canopy. The effects of wind speed and transpiration are empirically rolled into such a correlative approach, because wind speeds and transpiration rates are both highest in the sun-exposed canopy positions and lowest at the darkest end of the irradiance gradients. Distinct seasonal differences in wind speed are accounted for by presenting season-specific models.

The structural equation modeling approach explained 73% of the variance of T_{leaf} in the wet season and 92% in the dry season. The seasonal difference was related to cooler T_{air}, greater effects of PPFD on T_{leaf}, and the decoupling of leaves with the atmosphere in the wet season. In the dry season, the model was simpler, as the main driver of T_{leaf} was RT_{air} alone. It is interesting that PPFD had a much weaker effect on T_{leaf} in the dry season, because the total PPFD gradient was similar in the 2 seasons.

T_{leaf} of the 2 evergreen species, *Luehea* and *Anacardium*, were better explained by PPFD in the wet season and by $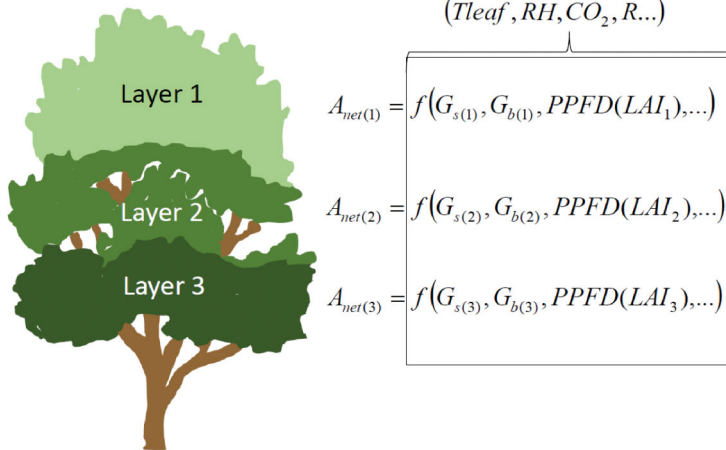RT_{air}$ in the dry season. *Luehea* leaves show pronounced paraheliotropic movements, and thus may change the radiative heat load they receive from direct irradiance during the day, whereas individual leaves of *Anacardium* rapidly close stomata in response to touch and sudden micrometeorological perturbation (A.C. Rey-Sanchez et al. pers. obs.), and as such may exert strong control over transpirational cooling rates. It is likely that these behaviors help maintain an optimum temperature for photosynthesis in both species. For example, the thermal optimum for photosynthesis of *Luehea* at this site is ca. 34°C (Graham et al. 2003); in the wet season, most leaves were well below this threshold, so a small temperature rise caused by PPFD could be advantageous, whereas in the dry season the T_{air} is close to the optimum and an increase in T_{leaf} with PPFD might be detrimental for photosynthesis. The convergence of T_{leaf} that allows plants to maximize photosynthesis has also been observed from subtropical to boreal ecosystems (Helliker & Richter 2008).

4.5. Potential application of the SEM in carbon flux models

One of the potential applications of the results of the SEM analysis is the improvement of multi-layered models of canopy assimilation. Multiple-layer models take into account the effects of canopy structure, and resolve for net photosynthetic assimilation (A_{net}) at different levels in the canopy and in response to drivers at each canopy level (Monson et al. 2014) (Fig. 9). We propose that one of these drivers should be the mean T_{leaf} in response to the vertical gradient of light. Similar to the approach of Leuning et al. (1995), where the effect on the canopy-integrated A_{net} of different levels of nitrogen at different canopy positions was evaluated, we can also evaluate the effect of mean T_{leaf} within the canopy on the integrated A_{net}.

Leuning et al. (1995) proposed an algorithm for T_{leaf} whose drivers were T_{air}, sensible heat, and the boundary layer conductance for heat. However, they assumed homogeneity of T_{air} and did not include the effect of radiation on T_{leaf}, which we showed has a strong relationship with T_{leaf} in the wet season. A model like the one developed by Leuning et al. (1995) is heavily parameterized and requires several assumptions about the homogeneity of the variables driving biophysical processes in the canopy. When it comes to T_{leaf}, we propose that an empirical approach is more advantageous and can be used to complement a biophysical model like the one developed by Leuning et al. (1995).

Common multi-layered model

$$(Tleaf, RH, CO_2, R...)$$

$$A_{net(1)} = f\left(G_{s(1)}, G_{b(1)}, PPFD(LAI_1),...\right)$$

$$A_{net(2)} = f\left(G_{s(2)}, G_{b(2)}, PPFD(LAI_2),...\right)$$

$$A_{net(3)} = f\left(G_{s(3)}, G_{b(3)}, PPFD(LAI_3),...\right)$$

Use of leaf temperature algorithm

$$(HR, CO_2, Tair...)$$

$$A_1 = f\left(G_{s(1)}, G_{b(1)}, PPFD(LAI_1), Tleaf_1...\right)$$
$$R_1 = f\left(Tleaf_1\right)$$
$$A_2 = f\left(G_{s(2)}, G_{b(2)}, PPFD(LAI_2), Tleaf_2...\right)$$
$$R_2 = f\left(Tleaf_2\right)$$
$$A_3 = f\left(G_{s(3)}, G_{b(3)}, PPFD(LAI_3), Tleaf_3...\right)$$
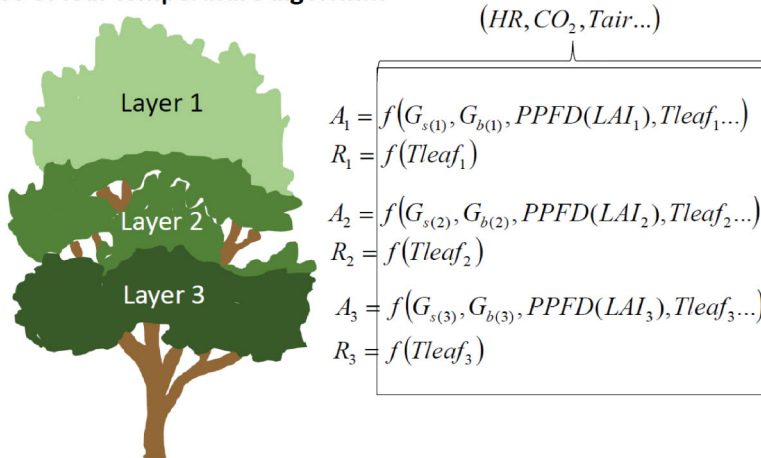$$R_3 = f\left(Tleaf_3\right)$$

Fig. 9. Schematic representation of the potential use of the leaf temperature algorithm in a multi-layered model for carbon flux. A and A_{net} are gross and net photosynthetic assimilation, respectively. G_s and G_b are the stomatal and boundary layer conductances, respectively. LAI: leaf area index, RH: relative humidity, R: respiration; other abbreviations as in Box 1. The variables above the boxes are variables that are assumed to be homogeneous within the canopy. Note that the common multi-layered models assume homogeneous leaf temperature, whereas our proposed approach includes leaf temperature at each of the layers of the canopy. Respiration is also resolved at each level according to its temperature response rather than assumed to be a constant proportion of assimilation

4.6. Implications for carbon flux modeling

It has been suggested that tropical forests exist close to their upper temperature threshold, as net ecosystem carbon uptake decreases on sunny days with $T_{air} > 29°C$ (Doughty & Goulden 2008), and further warming could move the tropics into a climate envelope not currently occupied by closed-canopy forest (Wright et al. 2009). While nighttime warming may result in acclimation of respiration (Slot et al. 2014a, Slot & Kitajima 2015), long-term daytime

warming of leaves of tropical forest trees appears to decrease net photosynthesis, without signs of thermal acclimation (Doughty 2011). This suggests that rising T_{leaf} may have a large impact on NPP of tropical forests and, consequently, the global carbon cycle. In addition to this, we found that neither the SMSs nor the forest station could capture the heterogeneity of temperatures in the canopy and in particular, the highest temperatures of the upper canopy during periods of high PPFD. In general, there is underestimation of temperatures in the upper canopy, and when these temperatures are above the thermal optimum of photosynthesis, net photosynthetic carbon uptake would be overestimated. High temperatures may cause stomatal closure when threshold levels of VPD are exceeded, so despite high irradiance, photosynthesis will likely be low. Midday stomatal closure leading to severe photosynthetic depression in *Ficus* leaves has been observed at this site (Slot et al. 2016), but much less so in *Luehea* leaves (M. Slot et al. unpubl. data), suggesting strong potential for species-specific effects of temperature change on physiology and performance (Zotz et al. 1995, Gamon et al. 2005).

To better understand climate change, it is essential to understand how temperature is changing inside the forests (De Frenne & Verheyen 2016). Our results show not only the importance of forest meteorological data but also the importance of within-canopy air and T_{leaf} variation. Tropical forests can maintain an LAI of ca. 6 m^2 m^{-2} (Clark et al. 2008), so there is a large amount of shaded leaf area that is cooler than the top most active layers, but that also contributes significantly to the tree carbon flux balance. A more accurate representation of T_{leaf} in the forest would have to include the variation of T_{leaf} from the upper to the lower canopy leaves in response to light availability, something that developments in LiDAR technology will make feasible in the coming years (e.g. Mascaro et al. 2014). Accounting for light extinction with cumulative LAI in the canopy would help in the study of irradiance incident

on shade leaves, as models of canopy photosynthesis have previously shown (Monsi & Saeki 2005).

We have shown the empirical relationship between T_{air} and T_{leaf} in a tropical forest canopy and determined the added predictive value of PPFD incident on the leaf. We have also shown how T_{air} from meteorological stations deviates from the temperature of the canopy, and in particular, how underestimating the temperature of the most photosynthetically active leaves can significantly compromise the accuracy of estimated carbon fluxes. Although the contribution of differently illuminated leaf layers to total canopy carbon uptake needs to be further quantified, we conclude that considering the relationship between T_{leaf} and light incident on leaves can improve carbon uptake models for tropical forests.

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APPENDICES

Appendix 1. Modeling the frequency distribution of leaf temperature (T_{leaf})

A gamma distribution uses the gamma function to explain the probability distribution of the variable *x*, according to the parameters shape (*k*) and scale (θ):

$$\Gamma(x, k, \theta) = \frac{1}{\theta^k} \frac{1}{\Gamma(k)} x^{k-1} e^{\frac{-x}{\theta}} \text{ for } k \text{ and } \theta > 0 \tag{A1}$$

For T_{leaf} modeling, this probability density function creates a bell-shaped curve, whose form can be explained with parameters *k* and θ. Normally parameter *k* explains the skewness of the distribution; however, when this parameter is higher than 10 (as in this study), the skewness is low and the distribution approaches a normal distribution. In such a case, the parameters explain the distribution as follows: higher values of *k* maintaining θ constant displace the curve to the right-hand side. Similarly, higher values of θ maintaining *k* constant displace the curve to the right-hand side. However, because the mean of the di-gamma distribution is equal to *k* × θ, the displacement of the curve to the right or to the left also comes with a change of the shape of the curve (height and width). For example, when we increase *k* maintaining θ constant, the curve not only displaces to the right but also becomes wider and shorter. If we want to displace the curve to the right by increasing *k*, but without altering the form of the curve, we must modify the parameter θ as well and make it lower. This last example illustrates the high coupling between these 2 parameters, and explains why they have an inverse relationship.

To account for the bimodality of the data we created a di-gamma probability density function (PDF) that consists of 2 gamma functions and a parameter '*p*' that varies between 0 and 1, and that indicates how much weight was given to each distribution:

$$diGamma(x) = p(Gamma(x, k_1, \theta_1)) + (1 - p)(Gamma(x, k_2, \theta_2)) \tag{A2}$$

The parameters k_1 and θ_1 corresponded to the first distribution (on the left-hand side) whereas the parameters k_2 and θ_2 were related to the second distribution (on the right-hand side). When *p* = 1, all the weight is given to the first distribution and when *p* = 0, all the weight is given to the second distribution. It is important to note that the product between k_1 and θ_1 gives the mean of the first distribution (E_1) whereas the product between k_2 and θ_2 gives the mean of the second distribution (E_2).

We used a genetic algorithm (GA) to find the best estimates of the 5 parameters of the di-gamma PDF (*p*, k_1, θ_1, k_2, θ_2) for each individual leaf. The GA is commonly used to find solutions to optimization problems, and was used to explore the search space of the parameters to find the minimum log-likelihood values. We used an R-based GA with floating point chromosome using the function *rbga* in the package *genalg* (Willighagen 2005). Based on preliminary runs, we selected limits for the optimization search space: *p* varied between 0.1 and 0.9, *k* between 200 and 1000, and θ between 0.05 and 0.3. We ran the algorithm for 1000 generations with a population size of 800, a mutation rate of 0.15, and an elitism of 25%.

LITERATURE CITED

Willighagen EL (2005) genalg — R based genetic algorithm. Version 3.0.0. http://CRAN.R-project.org/package=genalg

Appendix 2. Structural equation models by species

Table A1. Path coefficients and model fit of the structural equation model in Fig. 7 evaluated by species and season. The coefficients represent the strength of the relationship between a causal relationship between 2 variables (e.g. the effect of air temperature on leaf temperature: $T_{air} \rightarrow T_{leaf}$). χ^2 and p values show the statistical significance of the model

Season	Species	TOD $\rightarrow$RPPFD	TOD $\rightarrow T_{air}$	RPPFD $\rightarrow T_{air}$	RPPFD $\rightarrow$PPFD	T_{air} $\rightarrow T_{leaf}$	PPFD $\rightarrow T_{leaf}$	χ^2	p
Wet	*Luehea*	0.81	0.28	0.58	0.99	0.14	0.74	68.6	<0.01
Wet	*Anacardium*	0.63	0.18	0.71	0.73	0.41	0.52	8.1	0.02
Wet	*Castilla*	0.90	0.60	0.26	0.71	0.69	0.34	12.6	<0.01
Wet	*Pittoniotis*	0.63	-0.18	0.89	0.68	0.62	0.35	21.2	<0.01
Wet	*Ficus*	0.72	0.21	0.61	0.95	0.23	0.49	39.7	<0.01
	All wet	0.73	0.10	0.71	0.79	0.47	0.43	6.9	0.03
Dry	*Anacardium*	0.82	0.79	0.12	0.58	0.93	0.10	28.7	<0.01
Dry	*Luehea*	0.86	0.75	0.12	0.80	0.94	0.06	18.5	<0.01
	All dry	0.84	0.80	0.09	0.66	0.93	0.09	4.2	0.13