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Differences in leaf temperature between lianas and trees in the Neotropical canopy

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Abstract

Leaf temperature (T_{leaf}) influences photosynthesis and respiration. Currently, there is a growing interest on including lianas in productivity models due to their increasing abundance, and their detrimental effects on net primary productivity in tropical environments. Therefore, understanding the differences of T_{leaf} between lianas and trees is important for future of forest on whole ecosystem productivity. Here we determined the displayed leaf temperature ($T_{\mathrm{d}}= T_{\mathrm{leaf}} -$ ambient temperature) of several species of lianas and their host trees during ENSO and non-ENSO years to evaluate if the presence of lianas affects the T_{d} of their host trees, and if leaves of lianas and their host trees exhibit differences in T_{d}. Our results suggest that close to midday, the presence of lianas does not affect the T_{d} of their host trees; however, lianas tend to have higher values of T_{d} than their hosts across seasons, in both ENSO and non-ENSO years. Although lianas and trees tend to have similar physiological-temperature responses, differences in T_{d} could lead to significant differences in rates of photosynthesis and respiration based temperature response curves. Future models should thus consider differences in leaf temperature between these life forms to achieve robust predictions of productivity.

Key words: gas exchange, leaf canopy temperature, life forms, thermography, woody vines.

1 Introduction

Variations in leaf temperature (T_{leaf}) have been considered a factor that can affect the net primary productivity of the biosphere. Most Terrestrial Biosphere Models (TBMs) use kinetic constants of T_{leaf} dependence to evaluate the response of photosynthesis and respiration in a given ecosystem [1]. However, the increasing effects of global warming and the high diversity of

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species and ecological strategies pose a challenge to determining with accuracy the T_{leaf} of different individuals and plant communities. In tree communities of temperate regions, Leuzinger & Körner [2] have found that the presence or absence of certain tree species in the canopy can play a significant role in the control of the forest surface temperature. This control depends in large part on the spatial arrangement and leaf functional traits of such species, such as the stomatal conductance and the capacity of leaf cooling associated with water transpiration [3–5]. Currently, there is no concrete evidence how the spatial arrangement of species can affect the forest surface temperature of tropical forest; nevertheless, it could be expected that high diversity of species, life forms, and functional traits produce a highly dynamic surface temperature that could reduce our ability to predict different ecological processes.

Studies have shown several implications of the increasing temperature on ecological processes at different levels. For example, at the leaf level, increases in temperature above the photosynthesis optimum are associated with the decline of CO_2 assimilation rates [6,7], stomatal conductance [8], and increases in respiration [9]; trends that can vary widely among species and life forms [7,9,10]. Likewise, at the ecosystem level in tropical forests, climate warming are associated with long-term increases in biomass [11] and dominance of plants such as lianas [12].

Associated with this later life form, since 2002 studies have reported a notable increase in liana abundance in tropical and temperate environments [13–17]. Likewise, other studies have shown significant detrimental effects of lianas presence on the tree recruitment, growth, survival, and carbon stock [18–20]. Together, these trends have cast doubt the accuracy of TBMs that predict the carbon cycle [21]; highlighting the need to incorporate lianas a future factor in such models for a better understanding of the ecosystem dynamics. Currently, most of the temperature–response studies that have compared the physiological performance of lianas and

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trees at the leaf-level suggest that there is no need to make a distinction between the physiological behavior of these life forms in future models [7,9,10,22]. However, the higher interception of light by lianas [23] and the greater competitive advantage of lianas in water use [24] suggests that their T_{leaf} may differ from that of their host trees, and might also affect T_{leaf} of their hosts; such differences in T_{leaf} between these life forms could reduce our ability to predict carbon fluxes in tropical forest canopies accurately.

In this study, we analyze the intra- and inter-specific trends in T_{leaf} for full-sun exposed leaves of several liana species and four host trees of a neotropical seasonal forest in Panama. We achieved this by using thermography and addressed two hypotheses at the canopy level: i) the presence of lianas affects the leaf temperature of their host trees (intra-specific trends), and ii) leaves of lianas and their host trees exhibit differences in leaf temperature (inter-specific trends). These hypotheses were addressed by observing temporal variations during the wet and dry seasons in contrasting El Niño (2015-2016) and La Niña years (2016-2017). Our hypotheses were analyzed using the displayed leaf temperature (T_{d}) as the difference of T_{leaf} obtained from the thermal images less the ambient air temperature (T_{a}). The T_{d} was estimated as a proxy of T_{leaf} in order to reduce the effect of the variation of the surrounding T_{a} during each measurement and perform temporal comparisons.

We hypothesized that leaves of trees with lianas would experience higher values of T_{d} than leaves of trees without lianas. This is based on the negative effects of lianas on trees associated with the ability of lianas to reduce the water availability of around their host trees [25]; a process that could affect the transpirational cooling of leaves of host trees [26]. Likewise, we expect that leaves of lianas would show lower T_{d} in comparison with host tree leaves; due to their ability to grow in drought environments [16] and their greater competitive advantage on the

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acquisition, regulation, and efficient use of water in comparison with trees [24,27–29]. To address our hypotheses, we first had to estimate the emissivity of leaves for each life form to calculate the T_{leaf}. To show the impact of the differences in T_{d}, and consequently T_{leaf}, on carbon fluxes between these life forms, we calculated rates of photosynthesis (P) and respiration (R) using equations of temperature-response previously published by Slot *et al.* [9] and Slot & Winter [7], and our estimations of T_{leaf}. Our results highlight the fact that lianas are an important biotic factor at the canopy level, that in turn can affect forest temperature. Therefore, their differential expression in T_{leaf} should be considered for future predictions of forest productivity; that could become a part of the challenges of including lianas in future global vegetation models [30].

2 Materials and Methods

2.1 Study site

This study was conducted in Parque Natural Metropolitano (PNM, 8° 59’ 39.95’’ N, 79° 32’ 34.68’’ W, 150 m a.s.l.) that is located west in Panama City on the Pacific coast of the Republic of Panama. This site presents a tropical dry forest with a mean annual temperature of 26.5 °C and annual rainfall average of 1740 mm. In general, the region is characterized by two contrasting seasons: a wet season between May and December when most of the rainfall occurs, and a dry season between January and March (Fig S1). The PNM contains 265 ha of natural forest reserve with an old secondary forest of 80-150 years with tree heights of up to 40 m. This site has a 42 m standing crane with a 51 m long jib with a suspended cage that was used to access the top of the canopy. The crane covers approximately 8,000 m^2 of forest in which 65 and 20 species of trees and lianas can be found, respectively [31]. Using this crane, we conducted

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four data collection campaigns: November 2015, February 2016, October 2016, and February 2017 (two in wet and two in dry seasons). The first two campaigns were conducted during a strong El Niño year (2015-2016), while the last two campaigns occur during a starting La Niña year (2016-2017).

2.2 Species selection and field design

At the top of the canopy we selected four of the most abundant tree species that were fully exposed to the sun: *Anacardium excelsum* (Bertero & Balb. ex Kunth), a late-successional species; *Annona spraguei* (Saff.), a mid-successional species; *Castilla elastica* (Liebm.), a mid-successional species; and *Luehea seemannii* (Triana & Planch), an early-successional species. We took between four and six fusion images (RGB and thermal) over two or three individuals of each species with lianas and without lianas using a thermal infrared camera (FLIR T400, Oregon, USA). This camera has a wavelength range between 7.3 and 13 µm, a standard calibration range from -20 to 650 °C, an image of 320 x 240 pixels, and a temperature error of 2% (*e.g.*, 2% of 30 °C = ±0.6 °C). The thermal imagery was acquired between 10:00 am and 12:00 pm (Fig S2) at 1.8 m to the leaves leading to a nominal spatial resolution of ~26.37 mm per pixel.

2.3 Estimation of the leaf temperature

From each thermal image acquired with the FLIR T410, we estimated the T_{leaf} for the upper-middle region of the leaf blade from five leaves of trees and lianas (in trees with liana infestation). Selected leaves did not have apparent mechanical damage or had herbivore attacks. The estimation of T_{leaf} from the thermal images was performed using the FLIR Tools 5.12 software (http://www.flir.com/instruments/display/?id=51975). To compute the T_{leaf}, we used the

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mean relative air humidity and air temperature (T_a) recorded every 15 min by a meteorological station located at the crane's structure. These meteorological station data sets were provided by the Physical Monitoring Program of the Smithsonian Tropical Research Institute. Likewise, we used the same value of T_a as a reflected temperature (or commonly known as background radiance) to compute the T_{leaf}; due to high emissivity and closed objects allow accurate temperature measurements in almost any background radiance conditions [32]. In addition, to compute T_{leaf}, the emissivity of leaves for the four tree species and seven liana morpho-species was estimated in February 2017. The calculation of the T_{leaf} for lianas was performed using the mean value of emissivity (0.983) estimated for this life form, while the calculation for leaves of trees was conducted using the mean value of emissivity determined for each species. The estimation of the leaf emissivity is described in the next section.

Following the estimation of T_{leaf}, we compute the displayed leaf temperature (T_d) for each leaf as the difference of T_{leaf} - T_a. For its nature, T_d can show positive and negative values, where positive values describe hottest leaves and negative values cooler leaves according to the surrounding environment. This calculation was conducted as a parameter that can allow us to reduce the temporal variation of the ambient temperature between seasons and years. These values of T_d were used later to perform the statistical comparisons below.

2.4 Estimations of photosynthesis and leaf respiration

We calculated the leaf photosynthesis (P, µmol CO_2 m^{-2} s^{-1}) and leaf dark respiration (R, µmol CO_2 m^{-2} s^{-1}) to show that despite the similar physiological–temperature behavior of these life forms [7], differences in leaf temperature combined with the physiological performance can produce different estimations of productivity for these functional groups at the leaf level. These

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gas exchange traits were estimated using the equations and parameters published by Slot & Winter [7] (See Equ. 1) and derived from Slot *et al.* [9] (See Equ. 2) for the species of trees and lianas of this study:

$$P = P_{opt} \times e^{-\left(\frac{T_{leaf}-T_{opt}}{\Omega}\right)^2} \qquad (1)$$

$$R = R_{25} \times Q_{10}^{(T_{leaf}-25)/10} \qquad (2)$$

where P_{opt} is the maximum rate of photosynthesis at an optimum temperature (T_{opt}), Ω represent the difference in temperature between T_{opt} and the temperature in which P drops to e^{-1} (37%) of its value at T_{opt}, R_{25} is the leaf respiration at 25 ºC, Q_{10} is the proportional increase in R with a 10 ºC temperature rise, and T_{leaf} is our actual measurements of leaf temperature using thermography. Because we do not make an identification of lianas species, we estimate the gas exchange traits using the mean values reported by [7] and [9] as a functional group. Likewise, for the case of *A. excelsum,* we estimated P by the published values for Parque Nacional San Lorenzo, Panama. Using the selected leaves for our second hypothesis, we solved these equations assuming that the kinetic leaf temperature is equal to our estimation of T_{leaf}. This aims to simulate the productivity at leaf level based on the surface canopy temperature that it is commonly used by most of the TBMs.

Although studies have reported a significant variation in photosynthesis and respiration performance of lianas and trees between seasons [28], we conduct these calculations assuming a lack of seasonal variation in the physiological behavior. From the values of P and R extracted above, we calculate the normalized differences based on each species of host tree following:

$$\text{Normalized P or R} = \frac{P\ or\ R\ value - P\ or\ R\ mean}{P\ or\ R\ standar\ deviaion} \qquad (3)$$

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This latter calculation was implemented to reduce the temporal variation of leaf temperature which can produce erroneous interpretations from the comparisons of P and R across seasons and ENSO years. The resulted values from this normalization are unitless, and the magnitude of their variation can be compared between life forms, seasons, and ENSO years.

2.5 Data analysis

To address our hypotheses, we used linear mixed-effect models to compare the variability of the T_d according to the season, ENSO year and: i) the presence of lianas on the T_d of trees, or ii) differences between leaf type (liana and tree) on the T_d. On average, more than 240 samples were used in each analysis (Table S1 and Table S2). Due to the hierarchical nature of our design, linear mixed-effect models that combine fixed and random components [33] were used to reduce the “random” factors that we cannot control in the field such as micro-climatic variations on leaves or the health of the individuals. Specifically, our model can be described by the following equation:

$$T_d = \alpha + \beta_{1ij} + Season_{ij} + ENSO_{ij} + \beta_{1ij} \times Season_{ij} + \beta_{1ij} \times ENSO_{ij} + Season_{ij} \times ENSO_{ij} + \beta_{1ij} \times Season_{ij} \times ENSO_{ij} + a_{i|j} + e_{ij} \qquad (4)$$

where α represents the intercept, β_1 the presence of lianas for our first hypothesis and the leaf type for our second hypothesis, e the unexplained error, and a the random factor which is affected by each thermal image (i) nested within each individual (j). Likewise, we applied this same analysis to compare the variations of the normalized differences of P and R using these parameters as response variables and β_1 as leaf type. These analyses were performed using the *nlme* package [34] under the open-source statistical software R version 3.3.1 [35]. Box-Cox transformations were performed when the normality of the data was not reached.

3 Results

3.1 Leaf temperature of trees with and without lianas

The intra-specific comparison of T_d in each of our four tree species between leaves of trees with and without lianas suggest that the presence of lianas does not affect the T_d of host trees across seasons or ENSO years during our measurement times (Table 1). In general, tree species with and without lianas showed values of T_d in a range of -4.11 ºC and 9.91 ºC with mean values close to 1.48 ± 2.99 ºC (sd) (Fig. 1). Regardless of the tree species, season, or ENSO year, trees without lianas showed values of T_d of 1.39 ºC on average (sd ± 2.84), while trees with lianas showed values of T_d of 1.57 ºC (sd ± 3.14). As such trees with lianas were 12.94% hotter than trees without lianas based on the average value, but this difference was not significant. At the species level, the lowest values of T_d (-2.81 ± 0.58 ºC) was observed for *L. seemanni* trees measured in the dry season of an El Niño year, while trees of *C. elastica* with lianas showed the highest values of T_d (7.10 ± 1.54 ºC) in the wet season of La Niña year. Across seasons and ENSO years, *A. excelsum* trees without lianas tended to have slightly higher values of T_d than trees of the same species with lianas. Conversely, during an El Niño year trees without lianas of *A. spraguei* had marginally lower values of T_d than trees with lianas; however, both trends are not significant. Trees of *L. seemanni* and *A. excelsum* with and without lianas showed the most contrasting—albeit non-significant—trends between years, with leaves during El Niño year showing lower values of T_d than during La Niña year.

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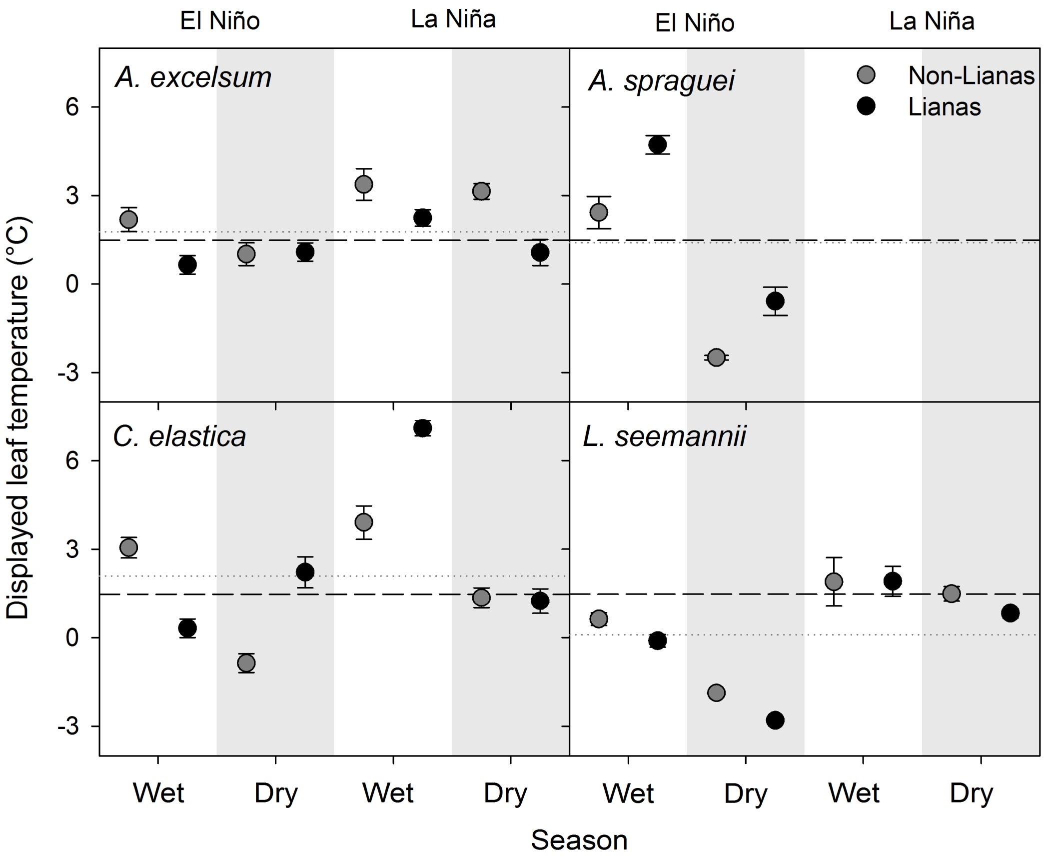

Figure 1. Displayed leaf temperature of tropical tree leaves with and without lianas during wet and dry season in contrasting ENSO years at the canopy of Parque Natural Metropolitano, Panama. Each point represents the mean (±SE). Dotted lines represent the mean of displayed leaf temperature per tree, while dashed lines represent the mean of all samples.

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Table 1. Effect of the liana presence, season, ENSO year, and their interaction on the displayed leaf temperature of tropical trees. Values represent *F-ratios* and values in parentheses describe the degree of freedoms; no statistical significance was found.

Factors	Species			
	A. excelsum	*A. spraguei*	*C. elastica*	*L. seemannii*
Presence	0.90 (1, 14)	2.27 (1, 13)	0.01 (1, 13)	1.88 (1, 7)
Season	0.01 (1, 14)	9.07 (1, 13)	2.11 (1, 13)	2.13 (1, 7)
ENSO	1.56 (1, 14)	---	4.47 (1, 13)	5.37 (1, 7)
Presence*Season	0.01 (1, 14)	0.02 (1, 13)	0.60 (1, 13)	0.01 (1, 7)
Presence*ENSO	0.02 (1, 14)	---	0.09 (1, 13)	0.01 (1, 7)
Season*ENSO	0.02 (1, 14)	---	1.14 (1, 13)	2.45 (1, 7)
Presence*Season*ENSO	0.25 (1, 14)	---	3.55 (1, 13)	0.12 (1, 7)

3.2 Leaf temperature of lianas and their host trees

The inter-specific comparisons of T_d suggest that liana leaves present higher values of T_d than leaves of their host trees (Table 2, Fig. 2). In general, liana leaves showed T_d values in a range of -4.11 ºC and 15.45 ºC with mean values close to 2.69 ± 3.99 ºC; these values are 93.52% higher than those reported above for tree leaves based on mean values. This expression of the T_d between life forms is significantly affected by the season, where lianas tend to have higher values of T_d in the wet season in comparison with the dry season. The difference associated with each host tree suggest that for *L. seemannii* leaves of lianas and their host have a significant interaction with ENSO, where leaves of both life forms during La Niña showed higher and contrasting values of T_d with respect to an El Niño year. The effect of season, ENSO, and leaf type (tree or liana) was also observed in the host tree of *C. elastica* (Table 2).

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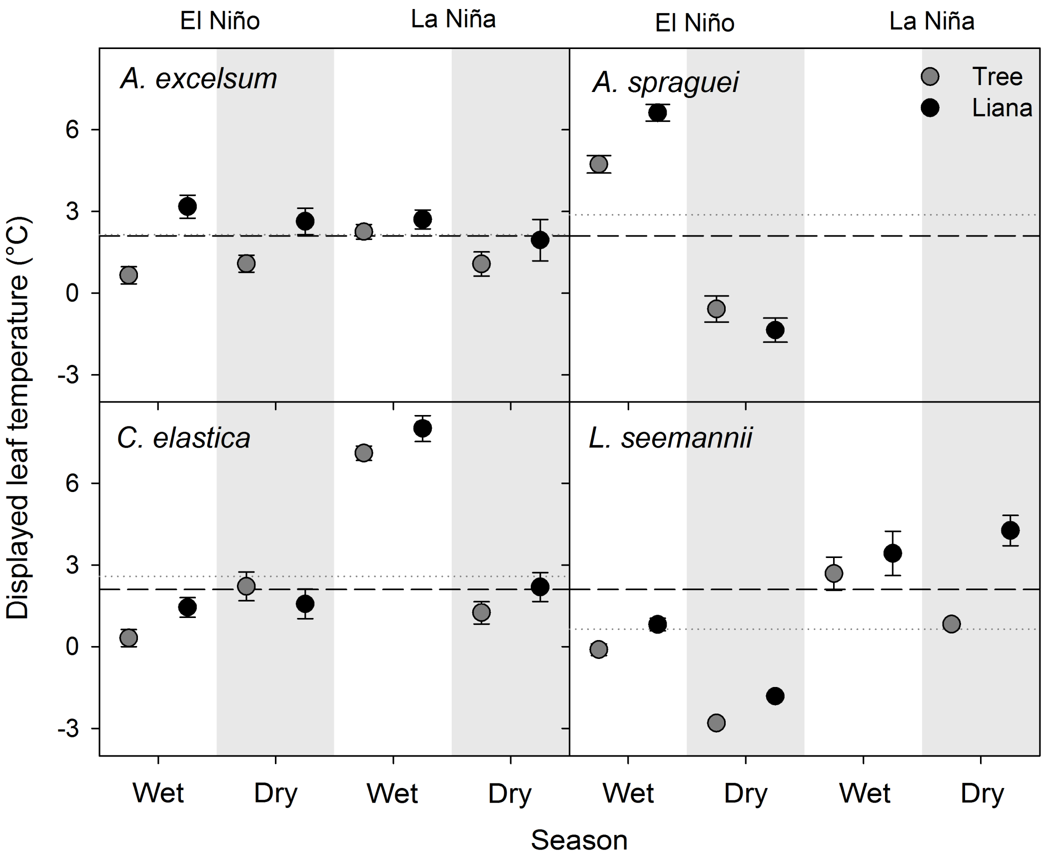

Figure 2. Displayed leaf temperature of lianas and their host tree in four tree species during wet and dry season in contrasting ENSO years at the canopy of Parque Natural Metropolitano, Panama. Each point represents the mean (±SE). Dotted lines represent the mean of displayed leaf temperature per host tree, while dashed lines represent the mean of all samples.

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Table 2. Effect of the leaf type (tree or liana leaf), season, ENSO, and their interaction on the displayed temperature of leaves of/on host tropical trees. Bold values represent significant effects. Values represent *F-ratios*, values in parentheses describe the degree of freedoms, and the asterisks represent the significance: * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$.

Factors	Species			
	A. excelsum	*A. spraguei*	*C. elastica*	*L. seemannii*
Type	**22.22***** (1, 301)	**12.96***** (1, 209)	**10.04**** (1, 300)	**192.32***** (1, 173)
Season	0.02 (1, 8)	9.06 (1, 2)	0.40 (1, 6)	1.12 (1, 3)
ENSO	0.15 (1, 8)	---	2.46 (1, 6)	1.87 (1, 3)
Type*Season	**13.60***** (1, 301)	**32.49***** (1, 129)	**5.92*** (1, 300)	**16.22***** (1, 173)
Type*ENSO	0.69 (1, 301)	---	2.40 (1, 300)	**7.32**** (1, 173)
Season*ENSO	0.01 (1, 8)	---	2.46 (1, 6)	2.40 (1, 3)
Type*Season*ENSO	1.09 (1, 301)	---	**11.88***** (1, 300)	0.44 (1, 173)

3.3 Comparisons of photosynthesis and leaf respiration between life forms

From the predictions of P and R using our estimations of T_{leaf} we compute the normalized difference for each host tree in order to conduct temporal comparison based on life forms, seasons, and ENSO years. Our results suggest that the differences in the expression of T_{leaf} in combination with the physiological performance of these life forms can produce different estimations of P and R between life forms in all host species, which can be affected (in some cases) by seasons and the ENSO (Table 3, Fig. 3). These differences are more pronounced for P than R, for which leaves of lianas exhibit lower rates per unit leaf area than leaves of trees.

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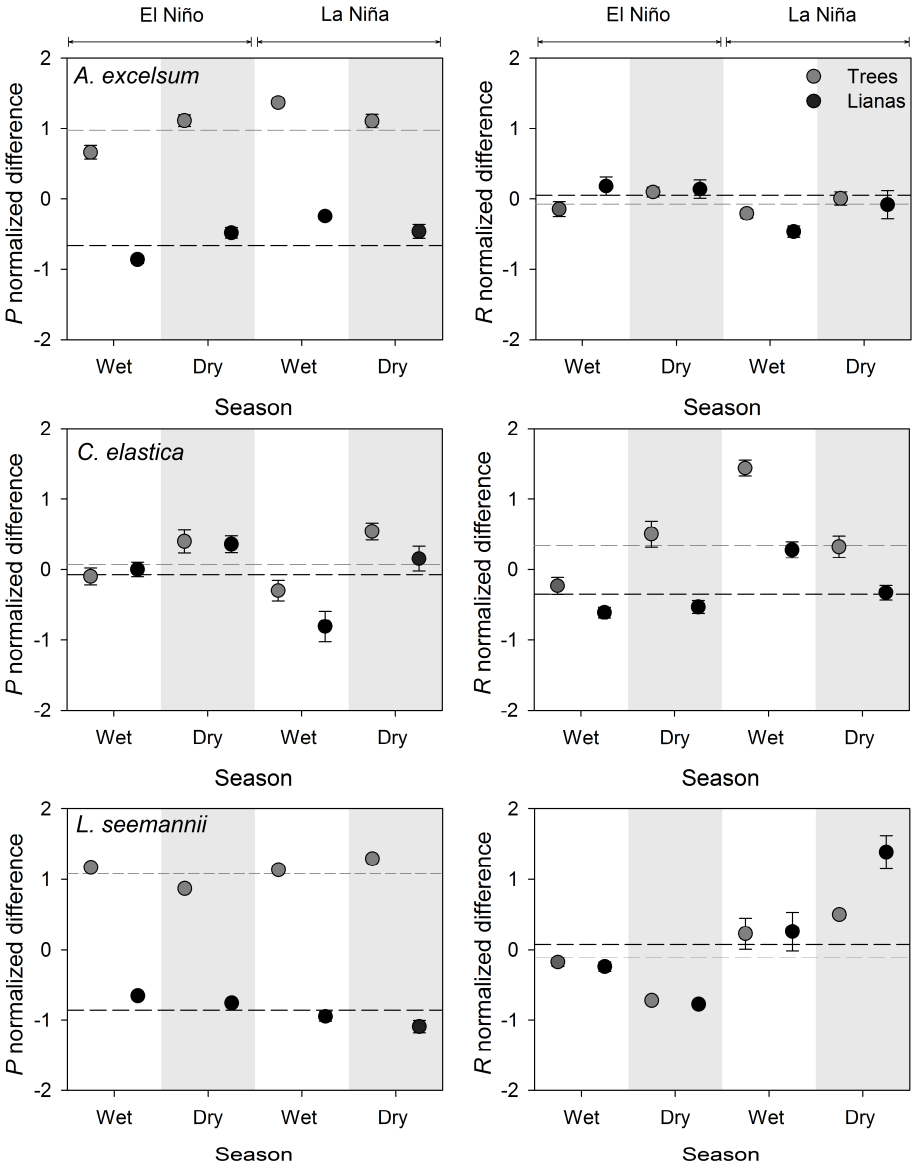

Figure 3. Normalized differences of predictions of photosynthesis (*P*) and leaf dark respiration (*R*) of leaves of trees and lianas on four host species during the wet and dry season in contrasting ENSO years. Each point represents the mean (±SE). Grey dashed lines represent the mean for trees, while black dashed lines represent the mean for lianas.

Table 3. Effect of the leaf type (tree or liana leaf), season, ENSO, and their interaction on the normalized difference of photosynthesis and leaf respiration of the values predicted. Bold values represent significant effects. Values represent *F-ratios*, values in parentheses describe the degree of freedoms, and the asterisks represent the significance: * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$.

Factors	Species or host tree					
	Photosynthesis			Respiration		
	A. excelsum	*C. elastica*	*L. seemannii*	*A. excelsum*	*C. elastica*	*L.a seemannii*
Type	**1133.01***** (1, 301)	**11.42***** (1, 300)	**3432.71***** (1, 173)	**18.45***** (1, 301)	**420.99***** (1, 300)	**4.56*** (1, 173)
Season	0.49 (1, 8)	1.03 (1, 6)	2.49 (1, 3)	0.05 (1, 8)	0.01 (1, 6)	0.02 (1, 3)
ENSO	0.97 (1, 8)	0.37 (1, 6)	3.39 (1, 3)	0.09 (1, 8)	1.51 (1, 6)	0.19 (1, 3)
Type*Season	**12.33***** (1, 301)	0.19 (1, 300)	0.03 (1, 173)	**13.85***** (1, 301)	**5.43*** (1, 300)	0.15 (1, 173)
Type*ENSO	**5.86*** (1, 301)	**3.87*** (1, 300)	**86.23***** (1, 173)	0.57 (1, 301)	0.99 (1, 300)	**39.76***** (1, 173)
Season*ENSO	1.69 (1, 8)	0.41 (1, 6)	0.34 (1, 3)	0.17 (1, 8)	1.29 (1, 6)	2.71 (1, 3)
Type*Season*ENSO	**4.97*** (1, 301)	0.01 (1, 300)	**10.61**** (1, 173)	0.87 (1, 301)	**20.99***** (1, 300)	0.17 (1, 173)

4 Discussion

4.1 Leaf temperature of trees with and without lianas

We hypothesized differences in T_{d} between trees with and without lianas due to the lianas presence could diminish the transpirational cooling of leaves of host trees for water competition. However, we found that the presence of lianas on trees does not seem to affect the temperature of tree leaves. This unexpected observation could either be due to: i) the lack of direct competition for water that may not reduce the surrounding water availability for trees (possibly because the site is evergreen without not a full deciduous season) [24], or ii) the possible compensation of more assignation of water to fully exposed leaves than leaves covered by lianas for transpiration cooling. It is important to note here that this result is based on four tree species which may not

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cover the whole spectrum of liana-trees relationship. For example, Visser *et al.* [37] suggest that liana infestation can have negative effects on tree population growth rates; however, this effect is more harmful to fast-growing species than slow-growing species. Therefore, we can not exclude the possibility that lianas could have an effect on leaf temperature on trees of others life history groups, or even other sites. Likewise, it is important to note that in our study we use the presence and absence of lianas on trees; that is why we consider that the density and extent of lianas on tree crowns may influence that host tree performance and should be examined in the future.

4.2 Leaf temperature of trees and lianas

We hypothesized that leaves of lianas might have lower temperatures in comparison with their host tree due to their greater competitive advance on the acquisition, regulation, and efficient use of water as compared with trees. By contrast, our results suggest that liana leaves have considerably higher values of T_d than tree leaves. This result reinforces previous observations conducted on few leaves of three species of trees and two species of lianas using thermocouples [38]. Although the aim of this study was not to determinate which are the biotic drivers that can lead to differences in T_d between life forms, it is clear that several factors can influence T_{leaf}, such as leaf size [39], leaf inclination [40], anatomical traits [41], or the presence of photo-protection pigments. Although we do not have direct measurements of leaf inclination associated with our T_d estimations, perhaps the leaf angle distribution of liana leaves on the canopy facing the sun more directly may contribute to the highest T_d. As Rey-Sánchez *et al.* [42] pointed out, leaves that are facing the sun more directly have shown to have higher solar irradiation that strongly affects the T_{leaf}. On the other hand, the higher values of T_d of lianas could be related to the stomatal control. A recent study conducted in a botanical garden in China

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suggests that lianas tend to have earlier stomatal closure in comparison to trees to reduce the water transpiration close to noon [43]. If this pattern occurs at the forest canopy of the PNM, it is expected that lianas would present higher values of temperature associated with the physiological regulation, which could be detected using thermography [44]. Moreover, the differences T_d between life forms could be associated with the highest concentration of photo-protection pigments in trees in comparison with lianas [45]. Currently, there is strong evidence that the presence of pho-protection pigments is associated with the efficiency of thermal dissipation of the excess of energy from light stress environments such as the canopies [46,47]. Therefore, it could be expected that such differences in photo-protection pigments between life forms influence the efficiency of thermal dissipation and the T_d.

4.3 Effect of the temperature on photosynthesis and respiration of lianas and trees

Although lianas have a similar physiological–temperature response compared to trees [7,9,22], higher displayed temperatures of lianas would have significant implications for future TBMs. Specifically, in a future scenario of modelling in which there is a lack of seasonal variation in the physiological behavior of leaves and the differences in leaf temperature between these life forms are not taken into consideration, predictions of productivity of lianas could be underestimated in comparison to trees, mainly regarding photosynthesis. Although our calculations of gas exchange are based on T_{leaf} at noon, differences in T_{leaf} through the day could have a major role in diurnal courses of productivity between life forms. A daily course of T_{leaf} of leaves of lianas and trees has been reported by Sánchez-Azofeifa *et al.* [38] suggesting liana leaves had higher overall temperatures than tree leaves. The Sánchez-Azofeifa *et al.* [38] and our trends of T_{leaf} between life forms together with their physiological sensitivity to the temperature

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may lead to different expectations of productivity of lianas and trees. Therefore, future models should thus consider differences in leaf thermo-regulation between these life forms in order to achieve robust predictions of productivity.

4.4 Conclusion

Currently, there is a strong need to understand the variations of abiotic factors that can affect the forest productivity [1]. Like Slot & Winter [7] pointed out, in the absence of a solid understanding of the abiotic controls over physiological processes such as temperature, future predictions of productivity will remain speculative. We have shown that the presence of lianas may not affect the leaf temperature of their host trees; however, lianas leaves tend to have higher values of temperature than their host trees. Our results highlight these differences in the expression of the temperature of lianas as an important biotic factor at canopy levels that can influence the forest temperature; therefore, their differential expression may have a significant weight in future predictions of forest productivity. We consider that future studies should explore the spatial variability of liana leaf temperature between forest strata such as in trees [42], and consider the differential expression of leaf temperature between life forms in order to predict the productivity of ecosystems. Likewise, future studies should explore this differential expression of leaf temperature in other regions such as wet forest, where species present lower thermal optima of photosynthesis [7], in order to know if the magnitude and direction of this expression vary among environments.

Supplementary Materials

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Fig S1. Monthly total precipitation and average monthly temperature during wet and dry seasons in contrasting ENSO years at Parque Natural Metropolitano, Panama.

Fig. S2. Mean values of temperature (red lines) and relative humidity (blue lines) during the days of data collection according to the meteorological station on the crane at Parque Natural Metropolitano, Panama.

Table S1. Number of leaves measured to address the first hypothesis during the wet and dry season in contrasting ENSO years at the canopy of Parque Natural Metropolitano, Panama.

Table S2. Number of leaves measured to address the second hypothesis during the wet and dry season in contrasting ENSO years at the canopy of Parque Natural Metropolitano, Panama.

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Author Contributions

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A.S.A conceived and designed the field data collection at the crane. J.A.G. processed and analyzed the data and drafted the manuscript. A.S.A. and B.R. helped with the interpretation and revision of the manuscript. All authors read and approved the manuscript.

Conflicts of Interest

The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

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