Foliar respiration and its temperature sensitivity in trees and lianas: in situ measurements in the upper canopy of a tropical forest

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Received November 19, 2012; accepted March 21, 2013; published online April 16, 2013; handling Editor Ülo Niinemets

Leaf dark respiration (R) and its temperature sensitivity are essential for efforts to model carbon fluxes in tropical forests under current and future temperature regimes, but insufficient data exist to generalize patterns of R in species-rich tropical forests. Here, we tested the hypothesis that R and its temperature sensitivity (expressed as Q10, the proportional increase in R with a 10 °C rise in temperature) vary in relation to leaf functional traits, and among plant functional types (PFTs). We conducted in situ measurements of R of 461 leaves of 26 species of tree and liana in the upper canopy of a tropical forest in Panama. A construction crane allowed repeated non-destructive access to measure leaves kept in the dark since the previous night and equilibrated to the ambient temperature of 23–31 °C in the morning. R at 25 °C (R25) varied among species (mean 1.11 µmol m−2 s−1; range 0.72–1.79 µmol m−2 s−1) but did not differ significantly among PFTs. R25 correlated positively with photosynthetic capacity, leaf mass per unit area, concentrations of nitrogen and phosphorus, and negatively with leaf lifespan. Q10 estimated for each species was on average higher than the 2.0 often assumed in coupled climate–vegetation models (mean 2.19; range 1.24–3.66). Early-successional tree species had higher Q10 values than other functional types, but interspecific variation in Q10 values was not correlated with other leaf traits. Similarity in respiration characteristics across PFTs, and relatively strong correlations of R with other leaf functional traits offer potential for trait-based vegetation modeling in species-rich tropical forests.

Keywords: canopy crane, carbon balance, climate change, lianas, Panama, respiration, Q10, temperature response of respiration, tropical forest.

Introduction

Tropical forests account for more than one-third of global terrestrial net primary productivity (NPP) (Malhi and Grace 2000; Saugier et al. 2001), but lack of empirical data on leaf dark respiration (R) hinders efforts to reliably model carbon fluxes in tropical forests under current and future temperature regimes (Malhi et al. 2009). R increases with leaf temperature, and increases in R will reduce NPP if gross photosynthetic productivity remains constant or decreases. Global rise of temperature, especially during night-time (Easterling et al. 1997), may thus have major impacts on the NPP of tropical forests (Galbraith et al. 2010). This mechanism is implicated in studies that found a negative correlation between tree diameter growth and annual means of daily minimum temperature (Clark et al. 2003, 2010). These results suggest that a temperature-driven increase in night-time respiratory carbon loss reduced the net daily carbon gain available for tree growth.

To model plant respiratory carbon efflux from tropical forest trees in response to climate warming, both respiration at a set temperature (e.g., R at 25 °C) and the temperature sensitivity of R need to be known. The latter is commonly described by the Q10: the proportional increase in R with a
10 °C temperature rise. Many coupled climate–vegetation models assume a constant value of 2.0 for $Q_{10}$, i.e., $R$ doubles as temperature increases by 10 °C (e.g., Cramer et al. 2001, Cox et al. 2004, Wang et al. 2011). However, $Q_{10}$ is not constant over a wide range of temperature. Rather, $Q_{10}$ is lower when measured at higher temperature ranges (Tjoelker et al. 2001, Atkin et al. 2005). Available data from tropical forests suggest that $R$ and $Q_{10}$ differ widely among tree species (Meir et al. 2001) and growth forms (Cavaleri et al. 2008). Unfortunately, reliable species-level measurements of $R$ and $Q_{10}$ are extremely scarce in tropical forests, hindering efforts to generalize patterns of $R$ and its temperature sensitivity for tropical trees and lianas.

Species-level data on $R$ and $Q_{10}$ will be valuable both to parameterize carbon flux models, and to identify their relationships with other leaf functional traits. If $R$ and $Q_{10}$ correlate strongly with commonly measured traits, such as photosynthetic capacity, leaf mass per unit area (LMA), nitrogen or phosphorus content and leaf lifespan, these relationships may be used to predict $R$ and $Q_{10}$ in species-rich tropical forests. Global analyses show that $R$ per unit leaf mass at 25 °C ($R_{25}$) correlates positively with leaf nitrogen content and with photosynthetic capacity (Reich et al. 1998, Wright et al. 2004a), but it remains unknown whether $Q_{10}$ correlates with leaf functional traits and also whether $R$ correlates with functional traits within the limited range of trait values observed in tropical forests. Identification of leaf traits that correlate with respiration characteristics would facilitate scaling up from leaf to ecosystem and biome-level processes, and may enable trait-based vegetation modeling in which traits rather than species identity are the starting point of the analysis (Van Bodegom et al. 2012).

Generalizable differences in $R$ among plant functional types (PFTs) provide another means to upscale carbon flux estimates from individual leaves to the canopy in species-rich tropical forests. Plant functional types in tropical forests, such as lianas or tree species of different successional status, can be identified with remote sensing techniques (e.g., Lefsky et al. 2002, Kalacska et al. 2007, Alvarez-Añorve et al. 2012). If generalizable patterns of $R$ and $Q_{10}$ exist among PFTs, estimation of carbon fluxes of a given tropical forest could be facilitated when the relative abundance of different PFTs is known. Leaf traits of tree species differ among PFTs defined by their successional status, from the trait syndrome associated with high metabolic activity in fast-growing early-successional trees, to the syndrome associated with a conservative growth strategy of late successional trees (Reich et al. 1995, Kitajima and Poorter 2008).

Lianas represent another important PFT in tropical forest canopies, and their abundance has increased in several tropical forests over recent decades (Phillips et al. 2002, Wright et al. 2004b, Ingwell et al. 2010, Schnitzer and Bongers 2011). Many lianas grow fast, because they invest proportionally less in structural support and more in metabolism than trees. Indeed, in a Costa Rican rainforest, Cavaleri et al. (2008) found that lianas had on average higher $R$ per unit leaf area at a given temperature than trees. Their data also showed that lianas had a marginally lower $Q_{10}$ than trees, suggesting that lianas may have the competitive advantage of lower respiratory carbon loss at higher temperatures. However, these differences between trees and lianas are yet to be confirmed in another tropical forest or with species-level measurements.

The main objective of this study was to quantify in situ leaf respiration rates of trees and lianas in the upper canopy of a tropical forest, in relation to leaf temperature and leaf functional traits, and to determine whether PFTs differ in respiration characteristics. More specifically, the following hypotheses were tested: (i) Leaf respiration rates and $Q_{10}$ values vary considerably among 26 species of tree and liana, showing significant differences among PFTs. (ii) Species differences in $R$ and $Q_{10}$ are associated with differences in other leaf functional traits. We hypothesized that early-successional species would have higher $R$ than later successional species, in accordance with general leaf trait syndromes associated with the species’ successional status, and that lianas would have higher $R$ than trees, in accordance with Cavaleri et al. (2008). We further hypothesized that $R$ would correlate with leaf traits according to the predictions of the leaf economic spectrum (Wright et al. 2004a). Species differences in $Q_{10}$ may be caused by differences among species in factors controlling the rate of $R$ at different temperatures (Atkin and Tjoelker 2003), such that fast-growing species with high demand for respiratory products (energy and carbon skeletons) are likely to exhibit a greater increase in $R$ with temperature than slow-growing species with lower respiratory demand. We thus expected $Q_{10}$ to vary among PFTs and correlate with leaf traits associated with growth and metabolism, such as $R$ and photosynthetic capacity.

We developed a new protocol to conduct in situ measurements of $R$ of intact and pre-darkened leaves equilibrated with ambient temperature in the upper canopy. Leaf respiration of tropical canopy trees is frequently measured on cut-off branches taken to the laboratory (e.g., Cavaleri et al. 2008, Metcalfe et al. 2010, Van de Weg et al. 2012). Many such studies appear to have confirmed the adequacy of laboratory measurements with cut branches with a pilot study, but the magnitudes of potential artifacts have not been reported in the literature. Furthermore, many large tropical leaves cannot be enclosed entirely in a gas exchange chamber of a typical size, and warming only the portion of the leaf enclosed in the chamber may cause artifacts. The in situ measurement protocol used in the study avoided these problems, and allowed rapid sampling of a large number of leaves in ambient conditions of temperature and humidity.
Materials and methods

Study site and species

The study was conducted in Parque Natural Metropolitano (PNM, 8°59'N, 79°33'W, 100 m a.s.l.), a seasonally dry tropical forest on the Pacific coast of the Republic of Panama, near Panama City. Annual rainfall at the site averages 1740 mm, most of which falls during the rainy season from May through December. The park is a 256-hectare natural reserve consisting of 80–150-year-old secondary forest with tree heights up to 40 m. A 42-m-tall construction crane with a 51-m-long jib (Parker et al. 1992) allows repeated non-destructive measurements of upper canopy leaves (Kitajima et al. 2005). Tree and liana species were selected to represent a variety of functional types defined in terms of growth form (trees and lianas) and successional status (early-, mid- and late-successional tree species) (Pérez and Condit 2012). Thirteen tree species and 13 liana species were selected from the upper forest canopy (Table 1). Additional leaf trait data had been collected previously at the same site for most of these species (S. J. Wright, unpublished data). Together these 26 species cover >70% of the canopy area in reach of the crane (Avalos and Mulkey 1999, M. Slot, personal observation).

Field measurements of leaf respiration rates

All measurements were made in the late wet season of 2010 (between late September and late November) when all study species had mature and non-senescenting leaves. For each species, two to five sun-exposed terminal shoots were selected on one to three individuals. Prior to sunset (6.00 p.m.) on the day before respiration measurements, 10–34 recently matured leaves were covered with thin aluminum foil, so that they would not be exposed to sunlight till the measurements. The abaxial side was not completely covered to allow free gas exchange during the night. The following morning each leaf was measured once between 5.45 and 11.00 a.m. at ambient temperature. Before each gas exchange measurement, we measured the leaf and ambient temperature with a thermocouple. The air temperature in the upper canopy rose from 23–24 °C pre-dawn to 28–31 °C at 11.00 a.m., and the temperature of leaves that were kept covered with aluminum foil closely followed the ambient air temperature. Because the leaves were covered overnight our measurements avoided the effects of light-enhanced dark respiration (Atkin et al. 1998), and light-induced metabolites and respiratory gene expression (Florez-Sarasa et al. 2012) on respiration. Thus, our measurements attempted to estimate nighttime dark respiration so as to minimize the effects of respiration associated with carbohydrate exports and temporal variation in substrate availability during the night (Noguchi 2005).

Leaf $R$ was measured as CO$_2$ release rates with a portable infrared gas analyzer (LI-6400, LI-COR, Lincoln, NE, USA), at ambient humidity (70–90%) and a set CO$_2$ concentration of 400 ppm maintained with the built-in CO$_2$ mixer. The block temperature of the LI-6400 was set to equal the ambient leaf temperature just before the measurement. Thus, during the respiration measurements, the leaf portion inside the gas exchange cuvette had the same temperature as the whole leaf, avoiding the potential measurement artifacts associated with warming a single leaf or leaf portion as opposed to warming of the whole plant (Atkin et al. 2000) or stand (Griffin et al. 2002). After the measurement at a single temperature, each leaf was harvested and brought back to the lab for additional trait measurements.

Functional trait data

Photosynthetic capacity ($A_{\text{max}}$) was measured on a separate set of 3–6 leaves per species, similar in sun exposure and apparent leaf age, between 9.00 and 10.00 a.m. at a saturating irradiance of 1200 µmol photons m$^{-2}$ s$^{-1}$ and 400 ppm CO$_2$ at ambient temperature (range 26–29 °C). After measurement of the leaf area with a LI-3000 leaf area meter (LI-COR), each leaf was dried ≥96 h at 60 °C for determination of dry mass and LMA. Five randomly selected leaves per species on which respiration was measured were ground for analysis of nitrogen (N) concentration with an elemental analyzer (Costech Analytical, Los Angeles, CA, USA).

We report $R$ on an area basis ($R_{\text{area}}$) unless otherwise specified, but we also calculated respiration per unit leaf mass ($R_{\text{mass}}$) by dividing $R$ by LMA of each leaf. The median leaf lifespan and mean leaf phosphorus concentrations had been collected independently at the species level from the same site (S. J. Wright, unpublished data). The species means for $A_{\text{max}}$, N and LMA in this independent data set match well with the species means determined in the current study ($R^2 > 0.65$ for each trait comparison).

Data analysis

In our protocol, each leaf was measured only once at one specific temperature, and we estimated temperature dependence ($Q_{10}$) and respiration at a standardized temperature of 25 °C at the species level by pooling all measurements from each species. The temperature dependence of $R$ was evaluated for each species from least square regression of natural-log transformed $R$ on leaf temperature:

$$\text{ln}(R) = a + bT_{\text{leaf}}$$

(1)

In Eq. (1), $a$ (the intercept) and $b$ (slope) are species-specific constants, used to estimate species-specific $Q_{10}$ as

$$Q_{10} = e^{10b}$$

(2)

We report $Q_{10}$ values calculated from the temperature response of $R_{\text{area}}$, but also calculated $Q_{10}$ of $R_{\text{mass}}$ (Table S1 available as
Table 1. Species used in the study, their PFT (ES, early-successional; MS, mid-successional; LS, late successional; L, liana) and their trait values. Respiration (R) at 25 °C (R25) and Q10 was determined from the CI of the slope of the temperature response curves (Figure 1). Cs of R25 were determined assuming normal distribution, as mean R25 ± 1.96 × (standard deviation of R25). Also reported are photosynthetic capacity (Amax) measured on 3–6 leaves per species, leaf mass per unit leaf area (mean of n leaves) (LMA), % leaf nitrogen (N) determined for 5 leaves per species. Phosphorus (P) and leaf lifespan data were obtained from S. J. Wright (unpublished data).

<table>
<thead>
<tr>
<th>Species</th>
<th>PFT</th>
<th>n</th>
<th>R25 Area (95% CI)</th>
<th>R25 Harea (95% CI)</th>
<th>Q10 Area (95% CI)</th>
<th>Amax (95% CI)</th>
<th>LMA</th>
<th>N (%)</th>
<th>P (%)</th>
<th>Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annona spraguei Saff.</td>
<td>ES</td>
<td>11</td>
<td>0.95 (0.89–1.01)</td>
<td>10.7 (10.2–11.2)</td>
<td>2.79 (1.96–3.98)</td>
<td>13.5</td>
<td>89</td>
<td>2.8</td>
<td>0.17</td>
<td>216</td>
</tr>
<tr>
<td>Cecropia peltata L.</td>
<td>ES</td>
<td>12</td>
<td>1.19 (1.07–1.31)</td>
<td>17.5 (15.6–19.3)</td>
<td>2.58 (1.58–4.20)</td>
<td>13.5</td>
<td>68</td>
<td>2.3</td>
<td>0.14</td>
<td>180</td>
</tr>
<tr>
<td>Castilla elastica var. costaricana (Liebm.) C.C. Berg</td>
<td>MS</td>
<td>22</td>
<td>1.15 (1.10–1.19)</td>
<td>11.0 (10.5–11.5)</td>
<td>2.84 (2.23–3.63)</td>
<td>19.5</td>
<td>104</td>
<td>2.8</td>
<td>0.17</td>
<td>180</td>
</tr>
<tr>
<td>Ficus insipida Wild.</td>
<td>MS</td>
<td>13</td>
<td>1.45 (1.35–1.55)</td>
<td>9.9 (9.2–10.6)</td>
<td>1.70 (1.03–2.80)</td>
<td>23.4</td>
<td>147</td>
<td>2.3</td>
<td>0.17</td>
<td>92</td>
</tr>
<tr>
<td>Luehea seemannii Triana &amp; Planch.</td>
<td>MS</td>
<td>34</td>
<td>1.14 (1.10–1.19)</td>
<td>10.9 (10.5–11.3)</td>
<td>2.12 (1.61–2.80)</td>
<td>19.8</td>
<td>105</td>
<td>2.4</td>
<td>0.15</td>
<td>186</td>
</tr>
<tr>
<td>Pseudobombax septumatum (Jacq.) Dugand</td>
<td>MS</td>
<td>22</td>
<td>1.17 (1.09–1.25)</td>
<td>11.5 (10.7–12.1)</td>
<td>1.51 (1.07–2.13)</td>
<td>16.3</td>
<td>102</td>
<td>2.3</td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>Spondias mombin L.</td>
<td>MS</td>
<td>16</td>
<td>1.48 (1.40–1.55)</td>
<td>14.5 (13.8–15.0)</td>
<td>1.73 (1.31–2.27)</td>
<td>16.5</td>
<td>102</td>
<td>2.7</td>
<td>0.13</td>
<td>173</td>
</tr>
<tr>
<td>Zuelania guidonia (Sw.) Britt. &amp; Millsp.</td>
<td>MS</td>
<td>13</td>
<td>1.36 (1.27–1.45)</td>
<td>11.0 (10.1–11.8)</td>
<td>2.42 (1.50–3.91)</td>
<td>17.3</td>
<td>124</td>
<td>2.0</td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>Anacardium excelsum (Bertero &amp; Balb. ex Kunth) Skeels</td>
<td>LS</td>
<td>23</td>
<td>1.22 (1.18–1.26)</td>
<td>11.2 (10.8–11.5)</td>
<td>1.99 (1.73–2.30)</td>
<td>13.8</td>
<td>109</td>
<td>1.4</td>
<td>0.14</td>
<td>280</td>
</tr>
<tr>
<td>Chrysophyllum cainito L.</td>
<td>LS</td>
<td>25</td>
<td>0.81 (0.77–0.85)</td>
<td>7.0 (6.7–7.3)</td>
<td>1.94 (1.61–2.34)</td>
<td>14.1</td>
<td>116</td>
<td>1.8</td>
<td>0.10</td>
<td>153</td>
</tr>
<tr>
<td>Amphilophium paniculatum (I) kunth</td>
<td>L</td>
<td>23</td>
<td>0.84 (0.80–0.88)</td>
<td>12.8 (12.0–13.4)</td>
<td>1.75 (1.33–2.31)</td>
<td>10.9</td>
<td>66</td>
<td>2.8</td>
<td>0.17</td>
<td>122</td>
</tr>
<tr>
<td>Aristolochia tondzi O.C. Schmidt</td>
<td>L</td>
<td>20</td>
<td>1.02 (0.98–1.07)</td>
<td>12.6 (11.9–13.4)</td>
<td>2.19 (1.65–2.90)</td>
<td>12.1</td>
<td>81</td>
<td>3.1</td>
<td>0.15</td>
<td>173</td>
</tr>
<tr>
<td>Bonamia trichantha Hallier f.</td>
<td>L</td>
<td>18</td>
<td>0.80 (0.76–0.89)</td>
<td>11.7 (10.8–12.6)</td>
<td>1.82 (1.09–3.06)</td>
<td>10.4</td>
<td>69</td>
<td>3.2</td>
<td>0.18</td>
<td>179</td>
</tr>
<tr>
<td>Gissus eosa Rich.</td>
<td>L</td>
<td>13</td>
<td>1.30 (1.22–1.37)</td>
<td>22.7 (20.4–24.8)</td>
<td>2.45 (1.57–3.83)</td>
<td>17.2</td>
<td>57</td>
<td>3.2</td>
<td>nd</td>
<td>89</td>
</tr>
<tr>
<td>Combretum fruticosum (Loefl.) Stuntz</td>
<td>L</td>
<td>13</td>
<td>1.09 (1.03–1.15)</td>
<td>14.5 (10.3–14.3)</td>
<td>2.19 (1.20–3.98)</td>
<td>17.7</td>
<td>75</td>
<td>2.3</td>
<td>0.16</td>
<td>154</td>
</tr>
<tr>
<td>Forsteronia myriantha Donn. Sm.</td>
<td>L</td>
<td>11</td>
<td>0.99 (0.89–1.08)</td>
<td>14.8 (13.4–16.2)</td>
<td>2.46 (1.19–5.14)</td>
<td>17.5</td>
<td>67</td>
<td>2.9</td>
<td>0.16</td>
<td>107</td>
</tr>
<tr>
<td>Govaiana isupoides (L.) Urb.</td>
<td>L</td>
<td>22</td>
<td>0.90 (0.83–0.98)</td>
<td>18.9 (16.7–21.7)</td>
<td>1.49 (0.97–2.31)</td>
<td>12.7</td>
<td>48</td>
<td>4.0</td>
<td>0.18</td>
<td>92</td>
</tr>
<tr>
<td>Mikania leiotricha Benth.</td>
<td>L</td>
<td>10</td>
<td>0.72 (0.63–0.81)</td>
<td>12.4 (10.8–13.9)</td>
<td>2.58 (1.09–6.12)</td>
<td>9.8</td>
<td>59</td>
<td>2.4</td>
<td>0.13</td>
<td>213</td>
</tr>
<tr>
<td>Phryganocarya corymbosa (Vent.) Bureau ex K. Schum.</td>
<td>L</td>
<td>17</td>
<td>1.79 (1.62–1.96)</td>
<td>18.3 (16.7–19.5)</td>
<td>1.69 (1.10–2.59)</td>
<td>12.2</td>
<td>98</td>
<td>3.7</td>
<td>0.15</td>
<td>89</td>
</tr>
<tr>
<td>Serjania mexicana (I) wild.</td>
<td>L</td>
<td>11</td>
<td>1.01 (0.90–1.12)</td>
<td>10.9 (9.8–11.9)</td>
<td>2.52 (1.35–4.71)</td>
<td>12.9</td>
<td>93</td>
<td>2.4</td>
<td>0.15</td>
<td>nd</td>
</tr>
<tr>
<td>Stigmaphyllon lindenianum A. Juss.</td>
<td>L</td>
<td>12</td>
<td>1.05 (1.01–1.10)</td>
<td>13.2 (12.5–14.0)</td>
<td>1.62 (1.32–2.00)</td>
<td>16.3</td>
<td>80</td>
<td>2.7</td>
<td>0.14</td>
<td>150</td>
</tr>
<tr>
<td>Trichostigma octandrum (L.) H. Walt.</td>
<td>L</td>
<td>23</td>
<td>1.15 (1.07–1.23)</td>
<td>20.1 (18.6–21.5)</td>
<td>2.13 (1.25–3.63)</td>
<td>15.1</td>
<td>57</td>
<td>4.1</td>
<td>0.32</td>
<td>57</td>
</tr>
<tr>
<td>Vitis triplorhinon Humb. &amp; Bonpl. ex Roem. &amp; Schult.</td>
<td>L</td>
<td>17</td>
<td>0.94 (0.86–1.03)</td>
<td>14.3 (12.9–15.7)</td>
<td>2.34 (0.99–5.54)</td>
<td>13.0</td>
<td>66</td>
<td>2.1</td>
<td>0.13</td>
<td>66</td>
</tr>
</tbody>
</table>

nd: no data available.
Supplementary Data at *Tree Physiology* Online). Confidence intervals for the $Q_{10}$ estimates were calculated from the confidence intervals associated with the parameter $b$ in Eq. (1). Subsequently, $R_{25}$ of each leaf was calculated as

$$R_{25} = \frac{R}{Q_{10}^{[10-25]}}$$

(3)

where $R$ and $T$ were the actual measurements for each leaf. The sample size varied from 10 to 34 leaves per species (Table 1), with larger sample size associated with species that could be sampled from multiple trees under the crane. For 4 out of 26 species the temperature range of $R$ measurements did not include 25 °C (with minimum measurement temperature between 25 and 27 °C). Thus, we also calculated $R_{25}$ in a similar manner as $R_{27}$, because 27 °C fell within the temperature range for all species (Table S1 available as Supplementary Data at *Tree Physiology* Online). But, we report only $R_{25}$ values, because they are widely reported in the literature, and because trait correlations and comparisons among PFTs were similar for $R_{27}$ and $R_{25}$.

Trait correlations were analyzed with standardized major axis regression using the SMATR package (Warton et al. 2012) in R (R Development Core Team 2011). Slopes of trait correlations were compared between trees and lianas, but because no differences were found, all species were pooled. Not enough data were available for comparison of trait correlations among PFTs. Comparisons among species, PFTs and growth forms were made using one-way analyses of variance (ANOVAs) and Tukey’s honestly significant difference post hoc tests, or Student’s $t$-tests. Data were transformed to improve normality and homogeneity of variance where necessary. All statistical analyses were performed in R version 2.14.1 (R Development Core Team 2011).

**Results**

Respiration increased significantly with temperature for 22 of the 26 species (Figure 1). The four species for which $R$ did not increase significantly with temperature were included in the analyses to avoid biasing against low $Q_{10}$ values. Both the elevation and the steepness of the slopes of the temperature response curves of ln $R$ varied across species, resulting in considerable variation in $R_{25}$ and $Q_{10}$ (Table 1). The average $R_{25}$ per unit leaf area ($R_{25, \text{Area}}$) did not differ significantly among PFTs (Figure 2a). $R_{25}$ expressed on a mass basis ($R_{25, \text{Mass}}$) was higher in lianas than in trees (Table 2), but differences among early-, mid- and late-successional tree species were not significant (Figure 2b).

The $Q_{10}$ varied widely among species (range 1.24–3.66, mean 2.19; Table 1), exhibiting similar patterns across PFTs for $Q_{10}$ derived from area- and mass-based $R$. $Q_{10}$ did not differ significantly between trees and lianas (Table 2), but $Q_{10}$ values were higher for early-successional trees than for each of the other PFTs (Figure 2c). The mean $Q_{10}$ for all 26 species was marginally $>2.0$ ($Q_{10, \text{Area}} = 2.18$, $P = 0.09$; $Q_{10, \text{Mass}} = 2.26$, $P = 0.03$, $t$-test), although the 95% confidence intervals of the $Q_{10}$ of individual species included 2.0 for 25 of 26 species.

$R_{25, \text{Area}}$ correlated positively with photosynthetic capacity ($A_{\text{max}}$), LMA and concentrations of N and P ($P < 0.01$ for all) (Figure 3a–e; Table S1 available as Supplementary Data at *Tree Physiology* Online). $R_{25, \text{Mass}}$ showed positive correlations with $A_{\text{max}}$, N and P, and negative correlations with LMA and leaf lifespan (Figure 3f–j; Table S1 available as Supplementary Data at *Tree Physiology* Online). When analyzed separately the slopes of these correlations were the same for trees and lianas ($P > 0.1$ for all comparisons of slopes).

Whereas $R_{25}$ showed consistent and strong correlations with other leaf functional traits, $Q_{10}$ values did not correlate with $R$ or any of the other leaf traits (Figure S1 available as Supplementary Data at *Tree Physiology* Online). Weighted regression analysis, in which species were weighted by the goodness of fit of the respiration temperature response curves, improved the correlations, but did not produce significant results either (data not shown).

**Discussion**

In this study we determined in situ leaf dark respiration rates of tropical trees and lianas in the upper canopy of a seasonal tropical forest, using a new protocol to measure leaves darkened overnight, which allowed us to sample a large number of leaves per species. In our method, the whole leaf was equilibrated to the ambient temperature, and activation of photosynthetic metabolism was unlikely given continuous leaf darkening overnight till the measurement time. Our data fall within the range reported for tropical species in the global analysis of leaf $R$ of Wright et al. (2006).

On the other hand, species-level estimates of $R_{25}$ from our study are relatively high when compared with the available data of $R$ measured on upper-canopy leaves of other tropical trees (Table 3). Variations in ecosystem-characteristics and methods may have both contributed to the differences among studies. $R$ tends to be higher for trees on fertile soils than infertile soils when foliar N and P contents are accordingly high (Meir et al. 2001, Turnbull et al. 2005). The soil at PNM is less acidic and more fertile than many tropical rainforests ($\text{pH} = 7.01$; total exchangeable cations = 4.3 g kg$^{-1}$; available $P = 5.81$ mg kg$^{-1}$, B. L. Turner, personal communication). However, mean N content per unit leaf mass was comparable to that at most other tropical sites, with the exception of nitrogen-poor sites in Venezuela (Reich et al. 1998) and Australia (Pearcy 1987). Consequently, $R_{25}$ per unit leaf N was considerably higher at our site than at most other tropical sites (Table 3),
but comparable to the mean $R_{25}/N$ from the eight tree species in Venezuela (Reich et al. 1998).

Another explanation for the relatively high rates of $R$ we measured may be the large number of early- and mid-successional species that are fast growing and metabolically active. However, $R_{25}$ of early-successional species was not systematically higher than in late-successional species on a unit area basis (Figure 2a) and not significantly so on a unit mass basis (Figure 2b). It is also possible that measuring intact sun-exposed top canopy leaves contributed to the high rates of $R$ in our study, contrasting with studies that used detached branches, or that measured leaves from a tower with which the most sun-exposed position...
of the upper canopy may not have been accessible. Studies that use detached branches generally report that tests have been made to ensure that measurements of attached and detached leaves yield the same results (e.g., Cavaleri et al. 2008), but our measurements were also higher than in situ measured R (Table 3).

**Significant trait correlations with dark respiration over a small trait space**

\( R_{25} \) only varied by a factor of 2.5 in our study, but nevertheless we found trait correlations similar to those of the mass-based leaf economics spectrum (Wright et al. 2004a) in which \( R \) varied by more than an order of magnitude. Furthermore, these trait correlations also exist on a leaf area basis, with coefficients of correlation comparable to those found for leaf area based correlations reported in Wright et al. (2004a). \( R_{25} \) ranged from 0.7 to 1.8 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (Table 1) and this small interspecific variation correlated with other leaf traits that themselves cover a relatively small (2–4 fold) range of trait values (Tables S1 and S2 available as Supplementary Data at Tree Physiology Online). Although the percent of interspecific variation in \( R_{25} \) explained by other leaf traits was modest, the relationships were robust despite the small range of \( R_{25} \) among species, and variation among individual leaves. This result thus offers potential for a trait-based approach to vegetation modeling (Van Bodegom et al. 2012).

\( Q_{10} \) did not correlate with any of the other functional traits we determined. Previous observations in which the temperature sensitivity of \( R \) correlated with leaf traits were made within species across depths in the canopy (Griffin et al. 2002b, Turnbull et al. 2003). In both cases \( Q_{10} \) correlated positively with leaf N content, but while Griffin et al. (2002a, 2002b) found that lower canopy leaves of *Populus deltoides* Bartr. ex Marsh had higher \( Q_{10} \) values and higher N (per unit leaf mass), Turnbull et al. (2003) found for several species that \( Q_{10} \) values were higher in top canopy leaves, as was N (per unit leaf area). There is no clear mechanistic explanation for why the relationship between leaf N and respiratory temperature response exists. Similar to our study, Bolstad et al. (1999) found no correlation between \( Q_{10} \) and leaf N for 18 deciduous temperate tree species, despite considerable variation in shade tolerance and associated photosynthetic properties of the species.

Interestingly, the average of the \( Q_{10} \) values across 26 species in our study was considerably higher than the 2.0 that is often used in coupled climate–vegetation models. Because the \( Q_{10} \) changes with the temperature interval over which it is measured, Atkin et al. (2005) described a temperature-dependent \( Q_{10} \): \( Q_{10} = 3.09 - 0.043 \times T \), where \( T \) is the measurement temperature. According to this relationship, a \( Q_{10} \) of

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**Table 2.** Comparison of means (±1 standard deviation) of physiological traits and LMA of trees (13 species) and lianas (13 species). Respiration at 25 °C (\( R_{25} \)), \( Q_{10} \) and photosynthetic capacity (\( A_{\text{max}} \)) are shown on a per unit area (subscript ‘Area’) and a per unit mass (subscript ‘Mass’) basis. The ratio of respiration over photosynthetic capacity is also shown.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Trees</th>
<th>Lianas</th>
</tr>
</thead>
<tbody>
<tr>
<td>( R_{25} ) Area</td>
<td>1.17 ± 0.22</td>
<td>1.05 ± 0.27</td>
</tr>
<tr>
<td>( R_{25} ) Mass</td>
<td>11.56 ± 2.63</td>
<td>15.17 ± 3.65</td>
</tr>
<tr>
<td>( Q_{10} ) Area</td>
<td>2.28 ± 0.67</td>
<td>2.10 ± 0.37</td>
</tr>
<tr>
<td>( Q_{10} ) Mass</td>
<td>2.36 ± 0.60</td>
<td>2.16 ± 0.55</td>
</tr>
<tr>
<td>( A_{\text{max}} ) Area</td>
<td>16.37 ± 3.43</td>
<td>13.36 ± 2.64</td>
</tr>
<tr>
<td>( A_{\text{max}} ) Mass</td>
<td>160.0 ± 26.3</td>
<td>197.0 ± 57.6</td>
</tr>
<tr>
<td>( R_{25}/A_{\text{max}} )</td>
<td>0.07 ± 0.01</td>
<td>0.08 ± 0.02</td>
</tr>
<tr>
<td>LMA ((\text{g m}^{-2}))</td>
<td>103.2 ± 19.3</td>
<td>70.4 ± 14.6</td>
</tr>
</tbody>
</table>

\( ^{1} \)Trees and lianas different (\( P < 0.05 \)).

\( ^{2} P < 0.01 \).
Figure 3. Correlations between respiration rates at 25 °C ($R_{25}$) and other leaf traits on a per unit leaf area basis (a–e) and on a leaf mass basis (f–j). All axes are on a natural-log scale. Each data point represents one species. $R_{25}$ is correlated with photosynthetic capacity ($A_{\text{max}}$, a and f), leaf mass per unit area (LMA, b and g), leaf nitrogen content (N, c and h), leaf phosphorus content (P, d and i) and leaf lifespan (e and j). Solid lines represent significant correlation of the traits (trees and lianas combined) ($P < 0.05$), as determined by standardized major axes regression. The dashed line in panel e indicates $P < 0.1$.

<table>
<thead>
<tr>
<th>Location</th>
<th>Growth form</th>
<th>n</th>
<th>$R_{25}$ (nmol g$^{-1}$ s$^{-1}$)</th>
<th>N (mg g$^{-1}$)</th>
<th>$R_{25}$/N (µmol CO$_2$ (g N)$^{-1}$ s$^{-1}$)</th>
<th>$Q_{10}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Panama$^1$ (PNM—this study)</td>
<td>Trees</td>
<td>13</td>
<td>11.6 ± 2.6</td>
<td>24.5 ± 5.2</td>
<td>0.49</td>
<td>2.28</td>
</tr>
<tr>
<td></td>
<td>Lianas</td>
<td>13</td>
<td>15.2 ± 3.7</td>
<td>29.9 ± 6.4</td>
<td>0.51</td>
<td>2.10</td>
</tr>
<tr>
<td>Costa Rica$^2$ (La Selva)</td>
<td>Trees</td>
<td>19</td>
<td>3.8</td>
<td>nd</td>
<td>0.32</td>
<td>2.34</td>
</tr>
<tr>
<td></td>
<td>Lianas</td>
<td>6</td>
<td>6.8</td>
<td>nd</td>
<td>2.14</td>
<td></td>
</tr>
<tr>
<td>Venezuela$^3$ (San Carlos)</td>
<td>Trees</td>
<td>8</td>
<td>8.6 ± 4.4</td>
<td>16.2 ± 4.3</td>
<td>0.53</td>
<td>nd</td>
</tr>
<tr>
<td></td>
<td>Lianas</td>
<td>6</td>
<td>6.8</td>
<td>nd</td>
<td>2.14</td>
<td></td>
</tr>
<tr>
<td>Brazil$^4$ (Jarau)</td>
<td>Trees</td>
<td>6</td>
<td>2.8</td>
<td>25.0</td>
<td>0.11</td>
<td>2.30</td>
</tr>
<tr>
<td></td>
<td>Lianas</td>
<td>8</td>
<td>4.6 ± 1.1</td>
<td>nd</td>
<td>nd</td>
<td></td>
</tr>
<tr>
<td>Brazil$^5$ (Caxiuana reserve)</td>
<td>Trees</td>
<td>6</td>
<td>7.4 ± 4.9</td>
<td>21.2 ± 6.4</td>
<td>0.35</td>
<td>nd</td>
</tr>
<tr>
<td></td>
<td>Lianas</td>
<td>6</td>
<td>7.2 ± 2.9</td>
<td>20.8 ± 3.2</td>
<td>0.35</td>
<td>nd</td>
</tr>
<tr>
<td>Cameroon$^6$ (Mbalmayo)</td>
<td>Trees</td>
<td>6</td>
<td>4.7</td>
<td>25.7</td>
<td>0.18</td>
<td>2.00</td>
</tr>
<tr>
<td>Australia$^7$ (Curtain Fig NP)</td>
<td>Trees</td>
<td>1</td>
<td>4.4 ± 1.6</td>
<td>16.7 ± 4.1</td>
<td>0.26</td>
<td>nd</td>
</tr>
<tr>
<td>Indonesia$^8$ (Bogor)</td>
<td>Trees</td>
<td>3</td>
<td>nd</td>
<td>nd</td>
<td>nd</td>
<td>2.00</td>
</tr>
</tbody>
</table>

Where necessary, $R$ values were converted into $R_{25}$ using a $Q_{10}$ of 2.0. nd, no data available.

$^1$Current study.
$^2$Cavaleri et al. (2008). $R$ measured on detached leaves.
$^3$Reich et al. (1998).
$^4$Meir et al. (2001).
$^5$Metcalfe et al. (2010).
$^6$Domingues et al. (2007). $R$ obtained from photosynthetic light response curves.
$^8$Stocker (1935).
1.9 is predicted at 27 °C, the average mid-point of the temperature intervals over which we determined the $Q_{10}$. Our $Q_{10}$ data are comparable to $Q_{10}$ measured on other tropical forest canopy leaves (Table 3). Both the fixed $Q_{10}$ of 2.0 as used in many coupled climate–vegetation models and the prediction from the temperature-dependent $Q_{10}$ of Atkin et al. might thus be underestimating the $Q_{10}$ for tropical species.

**Similarity in respiration characteristics among PFTs**

We found limited patterns of $Q_{10}$ across 26 species of tree and liana. Similarly, Bolstad et al. (1999) found that interspecific variation in $Q_{10}$ among 18 temperate tree species was apparently independent of PFT. We did, however, find that early-successional trees exhibited higher $Q_{10}$ than later successional trees. There is no obvious mechanistic reason for this difference. Fast-growing, light-demanding species, such as the early-successional tree species in our study, have high demand for respiratory products, and they can achieve high $R$ when substrate is available (Noguchi and Terashima 1997). Conditions of high demand for respiratory products under non-limiting substrate supply can also result in high $Q_{10}$ values (Slot et al. 2008). However, $R_{25}$ was not significantly higher in early-successional species so it seems unlikely that the high $Q_{10}$ we observed was solely driven by differences in metabolic demands among PFTs. More research will be needed to establish the generality of the pattern we observed. $R$ measurements were made on a relatively large number of leaves per species, but because temperature dependence was not determined at the individual leaf level, wide 95% confidence intervals are associated with some of the $Q_{10}$ estimates (Table 1). Future work should include leaf-level measurements of $Q_{10}$ repeated within species so the intra-specific variation in $Q_{10}$ as well as of $R$ can be considered when analyzing patterns across large numbers of species and PFTs.

**Differences between trees and lianas**

$R_{25\text{Mass}}$ was higher, while $Q_{10}$ values were slightly lower in lianas than in trees, similar to the trend found by Cavalieri et al. (2008) in Costa Rica. The $Q_{10}$ differences were, however, small and not statistically significant (Table 2). Given that the global temperature has risen just about 0.2 °C per decade over the last 30 years (Hansen et al. 2006), the observed differences in respiration characteristics between trees and lianas were too small to suspect that temperature responses of respiration could have contributed to the increase in liana dominance in tropical forests over the last 30 years. Meanwhile, the similarity in area-normalized physiological traits of trees and lianas suggests that vegetation models could justifiably ignore growth form and consider all canopy leaves as equal, but use leaf traits to fine tune the model to account for underlying physiological differences among leaves of different species, PFTs and growth forms.

**Conclusion**

Given the species richness of tropical forests, the lack of species-level respiration data from tropical canopy species has been striking; indeed, the paucity of respiration data is a major source of uncertainty in modeling carbon fluxes in tropical forests (Malhi et al. 2009). The $R_{25}$ data generated from a total of 461 leaves measured in situ across 26 species of trees and lianas in the current study are a valuable addition. Furthermore, the results support that $R_{25}$ can be estimated from easy-to-measure ‘soft traits’ that are widely measured for tropical canopy trees, similar to the global trends (Wright et al. 2004a, 2004b). On the other hand, trees and lianas are similar in $R_{25}$ and in $R_{25}$-trait correlations and large variation in $R$ and leaf traits exists within each PFT. These results strongly support the notion that trait-based vegetation modeling is more promising than PFT-based modeling of ecosystem–atmosphere fluxes (Van Bodegom et al. 2012). Especially in diverse tropical forests, bypassing species as a working unit and instead using trait data to model ecosystem processes would greatly simplify data collection. The mean $Q_{10}$ across 26 species was $>2.0$, the value often assumed in coupled climate–vegetation models. This significantly higher $Q_{10}$ over the temperature range representative for current and near-future night-time in the tropics should be considered for modeling carbon fluxes in tropical forests under climate warming scenarios.

**Supplementary data**

Supplementary data for this article are available at Tree Physiology Online.

**Acknowledgments**

We gratefully acknowledge Edwin Andrade, Julio Piti and José Herrera for their skilled operation of the crane; Mirna Samaniego for logistical assistance; Danielle Palow and Grace Crummer for assistance in the lab; and two anonymous reviewers for thoughtful comments on an earlier version of the manuscript.

**Conflict of interest**

None declared.

**Funding**

M.S. was supported by a Smithsonian Tropical Research Institute (STRI) Short-term Fellowship.

**References**


Spinacia oleracea Alocasia odora


