

JGR Biogeosciences

RESEARCH ARTICLE

10.1029/2019JG005353

Key Points:

- Hourly soil respiration in a tropical moist forest varied significantly with a monthly diel amplitude from 1 to $7 \ \mu mol \ CO_2 \ m^{-2} \ s^{-1}$
- The diel pattern of soil respiration had a morning and afternoon peak, with a midday decline occurring during the warmest months
- Decoupling between soil respiration and soil temperature suggests both aboveground and belowground processes may be driving diel variation of soil respiration

Supporting Information:

- Supporting Information S1
- Data Set S1
- Data Set S2

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Citation:

Gutiérrez del Arroyo, O., & Wood, T. E. (2020). Significant diel variation of soil respiration suggests aboveground and belowground controls in a tropical moist forest in Puerto Rico. Journal of Geophysical Research: Biogeosciences, 125, e2019JG005353. https://doi.org/ 10.1029/2019JG005353

Received 2 JUL 2019 Accepted 22 JAN 2020 Accepted article online 5 MAR 2020

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Significant Diel Variation of Soil Respiration Suggests Aboveground and Belowground Controls in a Tropical Moist Forest in Puerto Rico

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Abstract Soil respiration in tropical forests represents a major source of carbon dioxide (CO_2) to the atmosphere. The magnitude of this large flux is projected to change in response to climate change, with global implications due to the disproportionate role of tropical forests in the carbon cycle. Evaluating diel patterns of soil respiration concomitantly with biophysical drivers is a valuable approach for elucidating the mechanisms controlling soil respiration. We measured hourly soil respiration rates in a tropical moist forest in Puerto Rico over a 3-year period using automated chambers, as well as soil temperature/moisture, air temperature, relative humidity, and photosynthetically active radiation. Hourly soil respiration exhibited as much as threefold variation on diel time scales (monthly diel amplitude ranged from 1 to 7 μ mol CO₂ m⁻² s⁻¹), and both the magnitude and shape of diel patterns changed significantly from month to month. Soil respiration peaked in the morning and late afternoon with a midday decline that was evident during the warmest summer months. The relationship between soil respiration and soil temperature differed during daytime versus the night, with a nonlinear relationship in the daytime but a significant positive linear relationship at night. These findings suggest factors other than/in addition to temperature could be controlling soil respiration during the day; however, soil respiration did not correlate with any of the other measured biophysical variables. Overall, our results highlight the potential role of aboveground processes as drivers of soil respiration at diel time scales, especially in closed canopy tropical forests with low diel variation in soil temperature/moisture.

Plain Language Summary Tropical moist forests have soils that produce large amounts of carbon dioxide being released to the atmosphere. Although this is a natural process, it is important to study how carbon dioxide production in the soil changes with time because it is one of the main greenhouse gases causing climate change. To study this process, we measured carbon dioxide production from the soil in a tropical moist forest in Puerto Rico over a 3-year period. As expected, we found large amounts of carbon dioxide being produced, especially during the afternoon hours. An important finding of our study was that the amount of carbon dioxide produced varied throughout the day, which was unexpected due to the constant warm temperatures of soils in tropical moist forests. Overall, our findings suggest that the processes involved in producing carbon dioxide in the soil are more dynamic than expected and respond to changing environmental conditions throughout 24 hr periods.

Plain Language Summary Translation Los bosques tropicales húmedos tienen suelos que producen grandes cantidades de dióxido de carbono que se liberan a la atmósfera. Aunque este es un proceso natural, es importante estudiar los cambios de la producción de dióxido de carbono en el suelo con el tiempo, pues este es uno de los principales gases invernaderos causando el cambio climático. Para estudiar este proceso, medimos la producción de dióxido de carbono en el suelo de un bosque tropical húmedo durante un periodo de 3 años. Como esperábamos, encontramos grandes cantidades de dióxido de carbono siendo producidas, especialmente durante las horas de la tarde. Un hallazgo importante de nuestro estudio fue que la cantidad de dióxido de carbono que se produce varía durante el día, lo que fue inesperado dada la temperatura poco cambiante de los suelos en bosques tropicales húmedos. Nuestros resultados sugieren que los procesos envueltos en la producción de dióxido de carbono en el suelo en este bosque tropical húmedo son más dinámicos de los esperado, y que responden a los cambios de condiciones ambientales durante periodos de 24 horas.



1. Introduction

Although tropical forests account for less than 15% of Earth's land surface, they have a disproportionately large effect on the global C cycle with the highest measured rates of soil respiration globally (Asner et al., 2009; Bond-Lamberty & Thomson, 2010a; Pan et al., 2013; Raich & Schlesinger, 1992; Singh & Gupta, 1977). There is evidence that soil respiration in tropical forests may be sensitive to changes in environmental conditions, such as soil moisture and temperature (Schwendenmann et al., 2003; Sotta et al., 2007; *Vargas et al.*, 2010; Wood & Silver, 2012). Considering the large magnitude of the tropical flux, an improved mechanistic understanding of the biophysical controls on soil respiration in tropical forested ecosystems is essential for reducing uncertainty in model predictions of the C cycle at a global scale and remains a high priority for the scientific community (Bahn et al., 2010; Bond-Lamberty & Thomson, 2010b; Cavaleri et al., 2015; DOE US, 2012; Schimel et al., 2015).

Historically, the temporal variation of soil respiration in tropical moist forests has been largely explained by seasonal changes in soil moisture, which is an important driver of biological activity in soils and litterfall inputs, especially in forests with a pronounced dry season (Davidson et al., 2000; Medina & Zelwer, 1972; Schwendenmann et al., 2003; Sotta et al., 2004; Valentini et al., 2008). However, despite the low intra-annual variation and consistently warm temperatures throughout the year, temperature can also play an important role in influencing temporal variation of soil respiration in tropical moist forests (Raich et al., 2006; Wood et al., 2013). Given the low seasonality of temperature in the tropics, particularly that of soil temperature, the effects of temperature on soil respiration can be difficult to detect. This ability to detect temperature effects is further confounded by the tendency of temperature and moisture to covary (Meir et al., 1996; Schwendenmann et al., 2003; Schwendenmann & Veldkamp, 2006; Valentini et al., 2008). In addition, temperature can also affect soil respiration indirectly through its influence on ecophysiological processes in the canopy (i.e., photosynthesis, transpiration) and on gas-mixing processes (i.e., diffusion rates, air mass movement) in the soil and understory environment (Medina & Zelwer, 1972; Phillips et al., 2011; Tang et al., 2005; Vargas & Allen, 2008a). Although moisture and temperature are clearly key drivers of soil respiration, the diversity and complexity of sources of soil CO₂ production in the soil, other biophysical drivers, such as photosynthetically active radiation (PAR) and relative humidity (RH), which may play important roles via the regulation of substrate supply belowground should also be considered (Vargas & Allen, 2008b; Vargas et al., 2010b; Zhang et al., 2018).

In all forests there is a consistent diel (i.e., hourly changes over a 24-hr period) pattern of light availability that drives changes in temperature. Due to the high volumetric heat capacity of soil relative to air, soil temperature usually lags air temperature and has a smaller diel and seasonal range. Changes in light availability and temperature throughout the day also drive marked diel patterns of plant photosynthetic activity, which can be highly sensitive to even slight changes in RH (Davidson & Holbrook, 2009; Goulden et al., 2004). Concurrent with warming as the day proceeds, RH also varies in the forest canopy, usually reaching a minimum near midday coincident with the warmest air temperatures, potentially causing partial stomatal closure in response to high vapor pressure deficits (Huc et al., 1994; Pons & Welschen, 2003; Zotz et al., 1995). The complex effects of these hourly changes in PAR, temperature, and RH on canopy photosynthesis may strongly regulate photosynthate supply belowground, which is a critical source of C for root-rhizospheric respiration and may also play a role in regulating soil nutrient availability (Davidson & Holbrook, 2009; Medina, 1969; Medina et al., 1980; Medina & Zelwer, 1972; Mencuccini & Holtta, 2010; Odum & Jordan, 1970; Vandecar et al., 2009; Zhang et al., 2018). Given that root-rhizospheric respiration can amount to more than 40% of soil respiration in tropical forest ecosystems (Subke et al., 2006), and that diel variation of soil temperature is usually small in closed canopy forests (~1 to 2 °C), it is likely that processes regulating belowground substrate supply (i.e., photosynthesis, phloem transport) can affect diel variation of soil respiration (Ekblad & Högberg, 2001; Gaumont-Guay et al., 2008; Högberg et al., 2008; Hopkins et al., 2013; Medina, 1969; Medina et al., 1980; Trumbore et al., 2006).

The myriad ecological processes that control soil respiration in forest ecosystems operate at multiple time scales, ranging from seconds (i.e., root exudation) to millennia (i.e., landscape evolution; Kuzyakov, 2006; Ryan & Law, 2005). Consequently, disentangling the responses of soil respiration to environmental variation has been difficult, as biophysical drivers such as light, temperature, and moisture tend to covary both in space and time (Davidson & Holbrook, 2009; Kuzyakov & Gavrichkova, 2010; Savage et al., 2009; Zhang





Figure 1. Study site at El Tallonal Natural Reserve in Arecibo, Puerto Rico (figure by Jessica Fonseca da Silva and Olga Ramos).

et al., 2018). A promising approach for identifying the most important biophysical drivers of soil respiration in tropical moist forests are automated chambers measuring at high temporal frequency, with concomitant measurements of biophysical variables in the soil and canopy environment (Carbone & Vargas, 2008; Courtois et al., 2019; Rubio & Detto, 2017; Savage et al., 2009; Savage et al., 2014; Vargas & Allen, 2008a; Wood et al., 2013). In tropical moist forests, these data are especially valuable, as hourly measurements of soil respiration with seasonal resolution are scarce (but see Raich, 2017; Rubio & Detto, 2017; Zanchi et al., 2014). Insights gained by using this approach could facilitate further development of mechanistic hypotheses that address the role of aboveground and belowground linkages in regulating soil respiration across forest ecosystems (Carbone & Vargas, 2008; Savage et al., 2009; Savage et al., 2013). Considering the high magnitude of soil respiration in tropical moist forests, as well as its disproportionate contribution to the global C cycle, an improved understanding of the links between carbon fixed by the canopy and its subsequent consumption belowground is essential for determining the carbon sink strength of these forests (Bahn et al., 2010; Collalti et al., 2019; Phillips et al., 2017; Vargas et al., 2010). In this study, we focus on diel patterns of soil respiration in a tropical moist forest in Puerto Rico and investigate the potential biophysical variables (air and soil temperature, soil moisture, RH, and PAR) driving these patterns over a 3-year period.

2. Materials and Methods

2.1. Site Description

Our study was conducted in El Tallonal, a private natural reserve located in the limestone hills of northern Puerto Rico, in the municipality of Arecibo (Figure 1; 114 ha; 100 m.a.sl.; 18°24′27″N 66°43′53″W). The site is classified as a subtropical moist forest according to the Holdridge life zone system, and currently sustains a 60-year old secondary forest (~30 m in height; Ewel & Whitmore, 1973; Holdridge, 1967). Mean annual temperature is 23 °C, with a 4 °C seasonal range of monthly means, usually peaking during July or August and reaching a minimum in January (Daly et al., 2003). Mean annual precipitation from 1999 to 2013 was ~2,000 mm, with a short dry season typically occurring between December and March, when total monthly precipitation can be less than 100 mm (A. Vale, unpublished data). Throughout the study period, we observed no variation in the seasonal pattern of rainfall at our site.



Soils are classified as undeveloped humid Oxisols (termed blanket sands), which are derived from the accumulation of volcanic-derived sediment over limestone bedrock (Beinroth et al., 2003). Accordingly, surface soils (0 cm to 10 cm) are slightly acidic (pH in KCl = 5.7, pH in $H_2O = 6.5$), with high aluminum (Al) and iron (Fe) content (Gutiérrez del Arroyo, 2014; Martínez et al., 2008). Surface soils (0 cm to 10 cm) have soil C and nitrogen (N) contents of 4.38% and 0.43%, respectively, while soil particle composition (i.e., soil texture) is 39%, 26%, and 35% sand, silt, and clay, respectively (Gutiérrez del Arroyo, 2014).

2.2. Measurements and Data Processing

We measured hourly soil respiration from March 2011 to April 2014 using a Li-Cor LI-8100 infrared gas analyzer, along with an 8150 multiplexer system connected to six automated chambers (Long-Term Chamber 8100–104, Li-Cor Biosciences, Lincoln NE, USA). One month prior to starting our measurements, the six chamber collars (20 cm diameter) were permanently inserted 2 to 4 cm into the soil at a mean distance of ~5 m in a semicircular shape within a ~600-m² forested area. We were careful to maintain the litter layer in place during chamber installation and made sure the affected area continued receiving normal inputs of litterfall throughout our study period (i.e., chambers remained open while not measuring). Although relatively uncommon, seedlings that sprouted within the chambers were clipped at the base of their stem to prevent the confounding effects of foliar photosynthesis and respiration.

Hourly soil respiration values for each chamber were calculated by the Li-Cor FluxPro software based on the linear or exponential increase in CO_2 concentrations during a 1.5-min period. Occasionally, branches or snails (*Caracolus caracolla* (L.), which are highly abundant in the forest understory) impeded proper closure of soil respiration chambers during the measurement period, resulting in erroneous rates of soil respiration (i.e., negative and zero fluxes). We identified these data points using field notes and by visual examination of the data and excluded them from subsequent statistical analyses. We also excluded from our analyses all soil respiration values <0 μ mol CO_2 m⁻² s⁻¹. From April 2013 to June 2013, soil respiration was not measured due to necessary maintenance of the LI-8100 infrared gas analyzer (light sensor replacement and recalibration).

From November 2012 to April 2014, we collected hourly data from six soil temperature sensors at 5 cm depth and six volumetric soil moisture sensors from 0 to 10 cm depth, each within 0.5 m distance of each soil respiration chamber (TMC-50HD; S-SMD-M005; Onset Computer Corporation, Bourne, MA, USA). Due to sensor and datalogger malfunction, the volumetric soil moisture data set last from December 2012 to December 2013. Additionally, from January 2013 to April 2014, two 25-m scaffolding towers on site were equipped with sensors measuring hourly canopy air temperature, RH, and PAR (S-THB-M002; S-LIA-M003; Onset Computer Corporation, Bourne, MA, USA). Finally, as part of an independent long-term monitoring effort, precipitation and other microclimate variables (air temperature, RH, PAR, volumetric soil moisture) were also measured at 15-min intervals on a land-based meteorological station located <1 km from our site (S-THB-M002; S-SMD-M005; S-LIA-M003; Onset Computer Corporation, Bourne, MA, USA). To match the measurement frequency of the soil and forest canopy microclimate data, these data were aggregated to hourly intervals. In summary, our observational data set comprises approximately 3 years of hourly soil respiration data, as well as concurrent approximately 1-year measurements of soil and canopy microclimate data.

2.3. Statistical Analyses

A General Linear Mixed Model for Repeated Measures was used to determine if there was a significant change in soil respiration over a 24-hr period (Proc Mixed Repeated in SAS; SAS for Windows V8.0, 2002, SAS Institute;). In this model, we evaluated between subject effects (i.e., does the magnitude of soil respiration differ among chambers?) as well as within subject effects (i.e., did soil respiration change significantly over a 24-hr period? where hour was repeated, and was there a chamber and time interaction?), which was our primary objective. Our null hypothesis was that soil respiration does not change significantly over a 24-hr period and that there would be no time and chamber interaction. Soil respiration data were evaluated for homogeneity of variance, and when assumptions were not met, data were log-transformed. Linear regression analyses were used to determine the relationships between hourly soil respiration, soil temperature, and air temperature from months with >15 days of data available (JMP 12.0.1, SAS Institute Inc.). We calculated the wavelet power spectrum for soil temperature and soil respiration during a 1-year period from



Figure 2. Mean hourly canopy (a) photosynthetically active radiation (PAR), (b) air temperature, (c) relative humidity (RH), and (d) vapor pressure deficit (VPD) for monthly periods from March 2013 to February 2014. Error bars denote ± 1 standard error (n = 6 to 31).

August 2013 to July 2014 (Wavelet Comp, R Package). We also calculated the cross-wavelet spectra to identify the periods of maximum coherence between time series (i.e., diel and seasonal).

3. Results

3.1. Biophysical Factors (Air and Soil Temperature, PAR, RH, and Soil Moisture)

Mean monthly air temperature (from March 2013 to March 2014) ranged from 21.9 ± 0.8 to 24.9 ± 0.6 °C, in January and August, respectively, while mean monthly precipitation (from 2005 to 2014) ranged from 75 ± 19 to 231 ± 42 mm in February and May, respectively. In this Caribbean climate, temperature and precipitation covary across seasons, resulting in an approximately 4-month period with cool temperatures and reduced precipitation toward the beginning of the year (typically <100 mm of total monthly precipitation from December to March). The remaining months tend to have warmer temperatures, as well as higher total monthly precipitation (>150 mm), with warm/wet climatic conditions dominating during the late summer (Figure 2).

Mean hourly air temperature in the canopy (from March 2013 to March 2014) ranged from 19.9 ± 0.5 to 28.1 ± 0.3 °C, reaching a minimum during sunrise (between 6 and 7 a.m.) and peaking at midday (around 1 p.m.; Figures 2 and 3). Although the diel pattern of air temperature was conserved throughout the year, showing a steep increase in the morning hours followed by a gradual decrease during the afternoon and into the night, the diel amplitude (maximum minus minimum hourly mean) of air temperature showed seasonal variation, ranging from 7 °C in July 2013 to 10.7 °C in March 2014 (Figures 2 and 3). In contrast to air temperature, mean hourly soil temperature at 5 cm showed a narrow diel amplitude of ~1 °C (Figure 4). The attenuated diel pattern of soil temperature tracked air temperature with a lag of several hours (~3.5 hr) and reflected the volumetric heat capacity of soils, being slightly cooler in the morning and warmest in





Figure 3. Hourly time series of (a) soil respiration (black) and air temperature (gray), and (b) relative humidity (dashed black), photosynthetically active radiation (PAR) above the canopy (black) from Julian Days 213 to 243 of 2013.

the late afternoon. However, the diel amplitude of soil temperatures also showed significant month-to-month variation, ranging from 0.8 to 1.7 °C in December 2013 and March 2014, respectively. The wavelet spectral analysis of soil temperature confirmed the significant diel periodicity (red area of high power centered at period = 24), which was maintained throughout the year (Figure 6a).

The diel pattern of PAR atop the forest canopy did not exhibit strong seasonality, always peaking between 11 a.m. to 1 p.m., depending on the month (Figures 2 and 3). However, day length, as well as the magnitude of peak PAR values experienced at midday, varied throughout the year, showing a trend of higher values during the warm and wet summer relative to the cool and dry months (Figure 2). RH in the forest canopy showed a sharp decrease from 100% around 9 a.m., reaching a minimum at midday (~80%), followed by a



Figure 4. Hourly time series of soil temperature at 5 cm (long-dash), volumetric soil moisture at 10 cm (fine dash), and soil respiration (continuous) from Julian Days 335 to 365 of 2012. The magnitude of significant precipitation events (>5 mm) that caused significant increases and decreases in soil moisture and soil respiration, respectively, are labeled above the figure. Note that left axis corresponds to both soil temperature and soil respiration.

Figure 5. Hourly mean soil respiration ± 1 standard error (n = 12 to 31) for monthly periods in years (a) 2011, (b) 2012, (c) 2013, and (d) 2014.

gradual increase back to 100% during the evening hours (Figures 2 and 3). Although the shape of the diel pattern in RH was conserved throughout the year, the magnitude of the midday decrease varied among months, with warm and/or dry months causing stronger depressions of RH at midday (i.e., 80% vs. 90%; Figure 2).

Mean volumetric soil moisture throughout our study period was $0.359 \pm 0.001 \text{ m}^3 \text{ m}^{-3}$, suggesting ample soil water availability in this forest (Meir et al., 2015), which may be due to the high clay content, as well as a shallow water table (Martínez et al., 2008). The diel pattern of soil moisture showed a narrow amplitude, with mean hourly soil moisture ranging from 0.357 ± 0.003 to $0.359 \pm 0.003 \text{ m}^3 \text{ m}^{-3}$, at midday and during the night, respectively. However, significant changes in soil moisture at diel time scales occurred following large precipitation events (>3 mm), which cause a sudden peak in soil moisture that limits diffusion, effectively decreasing soil-atmosphere gas exchange (Figure 4).

3.2. Soil Respiration

Throughout our study period, from April 2011 to March 2014, we observed significant variation in hourly soil respiration (df = 23, n = 4254, F = 66.06, p < 0.0001), with diel patterns of soil respiration changing considerably in magnitude and shape from month to month (Figures 5 and 8). The mean diel amplitudes of soil respiration (averaged by month) ranged from 1 to 7 µmol CO₂ m⁻² s⁻¹ (Figure 5). Soil respiration during warm/wet months (i.e., April through September) demonstrated two peaks; one in the morning ~10 a.m., and another in the afternoon ~6 p.m., where maximum fluxes consistently occurred (Figure 5). The diel pattern was also characterized by a midday depression of soil respiration (declines of up to 50% of mean soil respiration), which was most evident during the warmer months (i.e., July through October), and became negligible as temperatures decreased throughout the year. During dry/cool months (i.e., December through March) soil respiration showed small diel amplitudes (1 to 2 µmol CO₂ m⁻² s⁻¹), but still conserving the afternoon peak of soil respiration (Figure 5). Altogether, soil respiration fluctuates significantly at diel time scales in this tropical moist forest and diel patterns are highly dynamic, changing in magnitude and shape throughout the year.

The wavelet spectral analyses also revealed periods of significant diel variation of soil respiration (red area centered around period = 24, indicating high spectral power at diel time scales), although temporal variation

Figure 6. Wavelet power spectrum for a 1-year time series of (a) soil temperature and (b) soil respiration from August 2013 to July 2014 reveals the significant diel variation of both variables (warm colors centered at period = 24 h). White contours delineate areas of high significance at p < 0.10.

at longer time scales (i.e., driven by seasonal changes in climate) also seems to be significant during the late summer period (Figure 6b).

3.3. Relationships Between Soil Respiration and Biophysical Factors

We found a parabolic relationship between soil moisture and soil respiration at daily and monthly time scales, but not at diel time scales. However, precipitation-induced spikes in soil moisture preceded or coincided with sudden drops in soil respiration, altering the usual diel pattern of soil biophysical factors (both

Figure 8. Diel hysteresis between mean hourly soil temperature and soil respiration for three periods throughout the year. (warm/wet: June, July, August; wet: April, May, September, October, November; dry/cool: December, January, February, March; all hysteresis loops follow the same direction as indicated by the arrows).

soil temperature and moisture) as well as soil respiration (Figure 4). We found that precipitation events greater than 3 mm led to soil moisture increases of at least 10%.

Mean hourly soil respiration and soil temperature were significantly, positively related in some months, but not in others (Table 2). This significant relationship at diel time scales was also evident in the cross-wavelet power spectrum, which suggests the time series of both of these variables are in phase (Figure 7; note arrows pointing right). However, across all months, mean hourly soil respiration and soil temperature demonstrated diel hysteresis patterns, resulting in one or two loops when plotted together (Figure 8). The shape of the hysteresis varied considerably among months and across seasons, due primarily to changes in the shape of the diel pattern of soil respiration rather than that of soil temperature, as the shape of the diel pattern of soil temperature was consistent across months. For example, months that had large afternoon peaks of soil respiration (i.e., summer months during the warm/wet season) had a hysteresis pattern consisting of one large loop with a tall and narrow peak that corresponded with the afternoon peak of soil respiration (Figure 8). During most of the remaining months there was a diel pattern of soil respiration with two peaks, resulting in one or two hysteresis loops when related with soil tem-

perature (Figure 8). The hysteresis pattern tracked seasonal changes in the magnitude of both soil respiration and soil temperature, with months having cooler soil temperatures corresponding with periods of reduced soil respiration rates (Figure 8). Moreover, diel hysteresis between soil respiration and soil temperature was evident even during months that showed the lowest diel amplitude of soil respiration.

In order to evaluate the potential effects of photosynthesis on soil respiration, we analyzed relationships between soil respiration and both air and soil temperature for hours with daylight versus those without (Figure 9 and Tables 1 and 2). Hourly soil temperature and soil respiration showed different relationships during the day and in the evening, exhibiting a stronger relationship at night during, relative to daytime periods (Figure 9 and Table 2). Nighttime air temperature explained between 82% to 98% of the variation in evening soil respiration across months, showing a similar but often stronger positive relationship than with soil temperature (Table 1). In contrast, during the day none of the linear regressions were significant between hourly air temperature and soil respiration (Table 1).

Day-time Regressions (7 am to 6 pm)

Figure 9. Diel regressions between hourly soil temperature and soil respiration for a daytime (7 a.m. to 6 p.m.) and (b) nighttime (7 p.m. to 6 a.m.) periods by month (see Table 2 for regression results).

Table 1

Linear Regressions of Mean Hourly Air Temperature and Soil Respiration During Monthly Periods From March 2013 to March 2014, Considering Full 24-hr Periods, Daytime Hours (7 a.m. to 6 p.m.), or Nighttime Hours (7 p.m. to 6 a.m.; *p Value <0.05)

	Full 24-hr period		Daytime (7 a.m. to 6 p.m.)		Nighttime (7 p.m. to 6 a.m.)	
Month	R^2	<i>p</i> value	R^2	<i>p</i> value	R^2	<i>p</i> value
March 2013	0.05	0.2833	0.00	0.9363	0.82	< 0.0001*
July 2013	0.17	0.0429*	0.28	0.0777	0.92	< 0.0001*
August 2013	0.08	0.1865	0.25	0.0962	0.92	< 0.0001*
September 2013	0.25	0.0125*	0.01	0.7105	0.86	< 0.0001*
October 2013	0.66	< 0.0001*	0.30	0.0628	0.88	< 0.0001*
November 2013	0.53	< 0.0001*	0.24	0.1099	0.94	< 0.0001*
December 2013	0.46	0.0003*	0.28	0.0757	0.96	< 0.0001*
January 2014	0.21	0.0228*	0.08	0.3759	0.95	< 0.0001*
February 2014	0.21	0.0244*	0.09	0.3362	0.97	< 0.0001*
March 2014	0.06	0.2354	0.00	0.9742	0.98	< 0.0001*

4. Discussion

Our high frequency measurements using automated chambers revealed significant diel variation of soil respiration in this tropical moist forest throughout a 3-year period. Results from prior studies investigating soil respiration on this time scale in other tropical forests have been mixed, with some studies reporting significant diel variation of soil respiration (Lugo et al., 2008; Medina, 1969; Medina et al., 1980; Meir et al., 1996; Raich, 2017 ; Rubio & Detto, 2017; Vargas & Allen, 2008a; Zanchi et al., 2014), and others reporting relatively consistent soil respiration values throughout the day (Davidson et al., 2000; Doughty & Goulden, 2008; Giardina & Ryan, 2002; Goulden et al., 2004; Litton et al., 2011; Salimon et al., 2004; Schwendenmann et al., 2003; Trumbore et al., 1995; Wood et al., 2013). The lack of significant variation of soil respiration at diel time scales in tropical forests could be a consequence of insufficient sampling frequency-a common limitation of soil respiration studies conducted in the tropics. Alternatively, the primary controls on soil respiration at this time scale may differ among tropical forests

with different rainfall regimes. For example, tropical moist forests, such as our site, might exhibit more frequent wetting and drying cycles as opposed to more seasonal tropical forests with marked dry seasons that result in prolonged periods of unfavorable conditions for biological activity in the soil. However, Rubio and Detto (2017) reported diel patterns were most evident during the dry season at their seasonal tropical wet forest suggesting the processes responsible for the diel variability remain active during dry periods. In addition, although small in magnitude, their observed diel patterns were apparently driven by fluctuations in soil moisture rather than temperature (Rubio & Detto, 2017). Other studies have found relationships with soil temperature similar to ours (Meir et al., 1996; Raich, 2017; Zanchi et al., 2014), although hysteresis was also evident suggesting other potential controls in addition to temperature on diel variation of soil respiration (Raich, 2017; Rubio & Detto, 2017; Vargas & Allen, 2008a; Zanchi et al., 2014).

The two primary characteristics of the diel patterns of soil respiration observed in this forest were midday depressions and afternoon pulses. Not only were patterns of soil respiration evident at diel time scales, but diel patterns also showed dynamic responses in magnitude and shape that appear to be related to seasonal variation in climate. Specifically, peak afternoon fluxes of soil respiration more than doubled during the

Table 2

Linear Regressions of Mean Hourly Soil Temperature and Soil Respiration During Monthly Periods From December 2012 to March 2014, Considering Full 24-hr Periods, Daytime Hours (7 a.m. to 6 p.m.), or Nighttime Hours (7 p.m. to 6 a.m.; *p Value <0.05)

	Full 24-hr period		Daytime (7 a.m. to 6 p.m.)		Nighttime (7 p.m. to 6 a.m.)	
Month	R^2	<i>p</i> value	R^2	<i>p</i> value	R^2	<i>p</i> value
December 2012	0.73	< 0.0001*	0.80	< 0.0001*	0.89	< 0.0001*
January 2013	0.68	< 0.0001*	0.56	0.0050*	0.92	< 0.0001*
February 2013	0.22	0.0206*	0.01	0.7705	0.94	< 0.0001*
March 2013	0.05	0.2797	0.00	0.8650	0.62	0.0023*
July 2013	0.05	0.2855	0.00	0.9643	0.76	0.0002*
August 2013	0.03	0.4225	0.00	0.9288	0.68	0.0009*
September 2013	0.37	0.0015*	0.51	0.0086*	0.67	0.0011*
October 2013	0.29	0.0070*	0.72	0.0005*	0.68	0.0009*
November 2013	0.43	0.0005*	0.79	0.0001*	0.74	0.0003*
December 2013	0.64	< 0.0001*	0.86	< 0.0001*	0.85	< 0.0001*
January 2014	0.50	0.0001*	0.57	0.0044*	0.80	< 0.0001*
February 2014	0.49	0.0001*	0.44	0.0183*	0.85	< 0.0001*
March 2014	0.14	0.0676	0.02	0.6778	0.84	< 0.0001*

summer months, when warm temperatures coincided with ample rainfall. Although the diel range of soil respiration tended to be higher during the summer months (>2 μ mol CO₂ m⁻² s⁻¹), we still observed significant diel variation during months when temperatures and rainfall are at an annual minimum. These results clearly demonstrate that significant diel variation in soil respiration occurs throughout the year, despite the relatively small seasonal variation in climate at our site.

We considered two key environmental variables—soil moisture and soil temperature—as potential drivers of the significant diel variation of soil respiration that we observed. The variation in soil moisture at the diel time scale was small (~0.002 m³ m⁻³), and we found no relationship between hourly soil respiration rates and soil moisture, apart from the rainfall-induced transient drops in soil respiration most likely caused by limited diffusion (Figure 4). In contrast, soil moisture did vary significantly over longer time scales (i.e., days to months) and demonstrated a significant parabolic relationship with soil respiration (Gutiérrez del Arroyo, 2014), which has been observed in other tropical forests (Meir et al., 2015; Wood et al., 2013). Despite the relatively narrow diel range of soil temperature (~1 °C), it explained between 22% and 73% of the variability in hourly soil respiration in most months, although not all (relationship was not significant for March, July, and August 2013 and March 2014). Nevertheless, considering the dynamic patterns of soil respiration observed at our site, and the narrow diel and seasonal ranges in soil temperature (~1 to 2 and 4 °C, respectively), these results would suggest that small changes in temperature could strongly influence soil respiration rates in this forest.

The observed relationship between temperature and soil respiration is complex. We found diel hysteresis (decoupling of time series at diel time scales) between soil respiration and soil temperature across all months, which is indicative of multiple controls on soil respiration in this forest (Phillips et al., 2011; Riveros-Iregui et al., 2007; Vargas & Allen, 2008a; Zhang et al., 2015). While the cross-wavelet power spectrum analysis suggests that soil respiration and temperature covary in phase, three important characteristics of the hysteresis patterns provide evidence for the decoupling of soil respiration and soil temperature: (1) soil respiration rates are often different for the same soil temperature occurring at a different time of day, (2) the afternoon pulse in soil respiration is independent of changes in soil temperature, and (3) the different relationship between temperature and soil respiration when separated by day and night. Combined, the hysteresis patterns suggest that the co-occurrence of maximum soil respiration and soil temperature that is observed in the late afternoon hours may not be linked mechanistically. Furthermore, the large fluctuations in soil respiration fluxes during midday depressions and afternoon pulses are independent of changes in soil temperature due to the short time period over which they occur (i.e., one to several hours). We hypothesize that the decoupling of the relationship between temperature and soil respiration could be the influence of aboveground processes influencing root-rhizosphere respiration during daylight hours (Kuzyakov & Gavrichkova, 2010; Mencuccini & Holtta, 2010), while temperature effects on biological activity of microbes may be a more predominant control on respiration rates in the evening.

Previous studies in tropical, temperate, and boreal forests have shown that recent photosynthates can serve as a major source of C for belowground respiration (Heinemeyer et al., 2012; Högberg et al., 2001; Litton et al., 2011; Medina et al., 1980; Tang et al., 2005; Vargas et al., 2010; Vargas & Allen, 2008b), and as such, the response of photosynthesis to changing environmental conditions could in turn influence the temporal dynamics of soil respiration. For example, the morning rise in PAR also corresponds with the morning peak in soil respiration, which could be an indication of photosynthetic activity influencing soil respiration. Further, midday decreases in RH roughly correspond to the midday depression of soil respiration, which could be a reflection of stomatal closure and reduced photosynthetic rates, especially when canopy temperatures are above optimum (>30 °C; Mau et al., 2018). During evening hours, when photosynthesis is not occurring, we observed a linear decline of soil respiration rates as temperatures cooled, which could reflect either a slowing of microbial activity in response to temperature, and/or a slowing of carbon supply to roots as photosynthesis stops. Given the observed diel hysteresis of soil respiration and temperature and the known importance of recently assimilated photosynthates as a substrate for root-rhizosphere respiration (Carbone & Trumbore, 2007; Högberg et al., 2001), future research should explore the potential linkages between aboveground and belowground processes in tropical moist forests with fast C cycling rates.

Overall, we find that soil respiration in this tropical moist forest is more dynamic at diel time scales than expected, especially given the low diel variation of the two main abiotic drivers in the soil, temperature and moisture. Our results suggest there may be a tight coupling between aboveground and belowground processes, which could explain the diel patterns observed (in the sense of Heinemeyer et al., 2012). Given the complexity of the processes fueling soil respiration in forest ecosystems, increased collaboration between plant and soil scientists will be indispensable for improving our projections of the response of the C cycle to ongoing climate change (Metcalfe et al., 2011; Raich & Tufekciogul, 2000; Richter & Billings, 2015; Wood et al., 2012). Coupling modeling and experimental research focused on understanding the links of the C cycle across the plant-soil-atmosphere continuum will yield invaluable insights on the potential effects of climate change on the C balance of tropical forested ecosystems.

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Acknowledgments

Thanks to Ciudadanos del Karso, Inc. and A. Vale for allowing us to conduct this study in their private reserve, to M. J. Sanchez, E. López, J. Olivencia, Y. Padilla, A. Dávila, J. Díaz, M. Alayón, and L. Sánchez at the International Institute of Tropical Forestry (IITF) for their commitment to the success of our research, as well as to the numerous volunteers who assisted with field work. Special thanks to A. E. Lugo, E. Medina, D. J. Lodge, T. M. Aide, and E. Cuevas, who provided invaluable support throughout the extent of this study, as well as constructive criticism that has substantially improved the quality of this manuscript. Finally, we gratefully acknowledge funding support from the Department of Biology at the University of Puerto Rico-Río Piedras, Puerto Rico Louis Stokes Alliance for Minority Participation, Sigma Xi Society, Puerto Rico NASA Space Grant Consortium, and IITF. Our data sets will be available in USDA Forest Service Research Data Archive (https://doi.org/10.2737/ RDS-2020-0011).

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