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First Approach of Abiotic Drivers of Soil CO_2 Efflux in Barro Colorado Island, Panama

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ABSTRACT: Soil CO_2 fluxes from tropical forests into the atmosphere are expected to increase due to global warming. Studies of environmental conditions that contribute to carbon flux are now an important focus for climate change research. However, carbon flux in tropical areas such as Panama has received less attention. In Panama, water sources, rainforests, and soil conditions are vital natural resources, particularly within the Panama Canal watershed. Mature and secondary forests represent around 60% of Panama land cover. Secondary forests are considered potential carbon sinks and they are of economic interest as a means of mitigating increasing anthropogenic CO_2 emissions; however, the dynamics of carbon fluxes in the soil of secondary forests remain poorly understood. This research investigated which environmental factors influence soil CO_2 efflux. We used a closed chamber method to measure soil CO_2 in the tropical forest of Barro Colorado Island, Panama. During 2016 to 2017, humidity had a significant effect on CO_2 flux (average: 4.36 μmol/m²s), which was substantially lower than expected for this type of tropical forest. These findings will contribute to a better understanding of the complex and dynamic interrelationships between the water and carbon cycle, as well as abiotic drivers of soil CO_2 fluxes. Our use of soil respiration chambers and infrared gas analyzer systems represents an innovative contribution to the water-carbon nexus of Panama and potentially of other countries.

KEYWORDS: Barro Colorado Island, closed soil respiration chamber, efflux, soil CO_2, flux, soil respiration

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Introduction

CO_2 represents 60% of total global greenhouse gas (GHG) emissions[1]; its increased levels in the atmosphere are mainly related to human activity. Soils act as sources and sinks for GHGs such as methane, CO_2, and nitrous oxide.[2] Although CO_2 storage may be an effective method for mitigating its effects on climate, exact quantification of CO_2 emissions is required to determine appropriate strategies to address-related land-use management and global climate change issues.[3]

The mitigation of CO_2 emissions is essential for decreasing the impact of climate change in the coming decades.[4,5] In particular, developing countries with extensive green areas have been encouraged to contribute to climate change mitigation efforts through conservation, management, and forest expansion.[6] Deforestation is the second leading source of anthropogenic CO_2 emissions, after fossil fuel combustion.[7] Fossil fuels represent 6% to 17% of global anthropogenic CO_2 emissions into the atmosphere.[8,9] Panama is among the countries with the greatest natural diversity in the world. Varied evergreen and deciduous forests dominate the Panamanian landscape and are broken up by mangrove swamps, grasslands, crops, and scrub. From 1950 to 2000, Panama lost 30% of its forest cover due to settlement expansion and growth of the national transportation network. In the past 20 years, the deforestation rate has slowed due to the implementation of environmental regulations, respect for indigenous areas, and reforestation in uninhibited agricultural plots.[10]

Carbon stocks in tropical forests include aerial and subterranean biomass.[11] The natural release of CO_2 into the atmosphere from tropical forests occurs through respiration in aerial and underground biomass.[12] Heterotrophic respiration occurs via macro- and microinvertebrates in the soil.[13] When forest areas are cleared, carbon stored above- and belowground in leaves, branches, stems, and roots is released in various ways such as combustion, vegetable matter decomposition, and soil carbon accumulation,[14] thus contributing to greenhouse gas emissions.[15]

The assessment of CO_2 stocks and net CO_2 capture is of crucial importance for determining whether a forest acts as a carbon sink or source. This knowledge is important for establishing a link between carbon sequestration and carbon neutrality, a frequent goal for energy policy.[16] Reclaimed mine soils can be used to sequester carbon. The CO_2 sequestration potential of an 11-year-old reclaimed mine afforested with fast-growing trees was compared with that of the Sal forest as a reference; the results showed that annual soil CO_2 flux was higher in forest soil (53.7 t CO_2 ha^{-1} y^{-1}) than in reclaimed soil (33.3 t CO_2 ha^{-1} y^{-1}), demonstrating that forest reclamation of postmining land increases its potential as a terrestrial C sink and reduces CO_2 levels.[17] Currently, manufacturing, transportation, and local industry produce nearly 10 Gt of carbon to the atmosphere annually, with no expectation of a substantial imminent decrease in these emission rates. Therefore, the sequestration of atmospheric CO_2 as organic carbon in the

biosphere is a topic of interest to stem the rate of GHG increase and associated changes to our climate.[18]

Ecosystem CO_2 emissions are mainly produced through respiration; therefore, this process influences the net productivity of the ecosystem.[19,20] On a global scale, the total mass of carbon stored in soil is 1576 Pg, of which 32% is found in the tropics. Carbon storage is lost mainly through changes in land use. With increased deforestation, carbon loss is expected to increase[21]; therefore, soil carbon is considered to be more important than carbon stored in aerial biomass.[22] In Panama, soil carbon is not linked with common predictors used in models, such as plant biomass or litter production; one fundamental equation model including base cations, soil clay content, and rainfall as exogenous factors and root biomass as an endogenous factor has been used to predict nearly 50% of the variation in tropical soil carbon stocks, indicating a robust indirect effects of base cation accessibility on tropical soil carbon storage.[23]

Organic carbon in soil varies temporally and spatially; however, data are scarce and unrepresentative of tropical areas.[24] Soil is a complicated medium consisting of organic and mineral aggregate particles containing microorganisms that perform a diversity of physiological processes.[25] Soil properties vary spatially and temporally in all directions.[26] Soil erosion processes other than surface runoff and sediment transport have significant effects on soil organic carbon transport and loss along slopes.[27] Soil organic carbon variation across a landscape can determine differences in soil fertility and plant vigor.

CO_2 flux is the result of several processes including underground biomass respiration by macro- and microorganisms, and CO_2 production and transportation through soil.[28] CO_2 flux is also influenced by environmental factors such as temperature, moisture, and soil properties.[29] In arid Patagonian ecosystems, seasonal differences in soil respiration are affected mainly by the interaction between soil temperature and water content.[30] In response to soil warming, manure application, and soil salinity, CO_2 flux values were higher at high soil temperatures than at low soil temperature.[31] The transport of soil CO_2 to the surface has been found to be affected by diffusion, convection, and mass flow in the gaseous and liquid states.[32] Diffusion is thought to be the most important process influencing CO_2 flux in the gas phase, controlled by the CO_2 concentration gradient[33] in a manner similar to that of mass flow by pressure fluctuations in surface soil.[34,35]

In forest soils, CO_2 is produced from respiration by autotrophic roots and heterotrophic microbes, related rhizosphere bacteria, and fungi living in organic and mineral soil, and also by soil faunal activity.[36] The activity of soil heterotrophic organisms is comparable with the decay of soil carbon, and CO_2 exuded from roots and the rhizosphere is linked to that produced by aboveground plant tissues.[37] The contribution of CO_2 from the soil to the atmosphere in a tropical forest can be quantified by surface soil CO_2 flux measurements.

Rainforest soils are important natural resources in Panama, particularly in the Panama Canal watershed. Mature and secondary forests represent around 60% of the land cover of Panama. Secondary forests, which are considered potential carbon sinks, are of great economic interest due to their low inversion and large potential contribution to mitigating increasing anthropogenic CO_2 emissions. Therefore, in this study, we examined the influence of environmental factors on soil CO_2 efflux on Barro Colorado Island using a closed chamber soil CO_2 measurement method.

Materials and Methods

Study site

This study was conducted on a 1 ha plot within the Ava research area (Figure 1), which was named for its Barro Colorado Island soil class, on Barro Colorado Island, Panama (9°9′N, 79°51′W). Barro Colorado Island is a unique ecosystem within an international waterway that was formed as a result of construction of the Panama Canal. Its forests are mainly secondary and primary forest. The soil at the study site mainly consists of Luvic, Alumic, Lixic, and Acric soils.[38] The island extends over an area of 1500 ha and has an altitude of about 137 m above Gatun Lake.[39]

Soil is a complex medium that varies spatially. The soils on the island are generally less than 50 cm deep and rich in clay,[40] with soils deeper than 1 m on flat peaks. The island contains 2 formations of fossiliferous sedimentary rock, the Bohío and Caimito formations.[40] The soils of Barro Colorado Island differ from those of other wet tropical forests in that they develop on kanditic clay minerals through intermediate smectites, rather than via allophane and halloysite.[40] These widely distributed aluminum-saturated smectitic soils are theoretically unbalanced and make Barro Colorado Island soils distinct. Although texturally uniform, these soils are physically mutable in terms of water source, root ventilation, and site stability. Stoichiometric differences in soils among Asian tropical forests have shown that Barro Colorado Island soils are moderately rich in Ca and Mg, but not in K.[41] Figure 2A to C shows our research site on the island and the equipment used for the study.

The climate of the island is typical of a tropical lowland forest, with an average temperature of 27°C; the rainy season extends from May to December and the dry season from mid-December to April. The average annual rainfall is 2642 (±566) mm.[42] The island is enclosed by a semi-deciduous, mixed-age rain forest, mainly comprising 2 abundant free-standing fig species (*Ficus insipida* and *Ficus yoponensis*) as a result of past settlement.[43]

Barro Colorado Island was an agricultural site for at least 6000 to 7000 years,[44,45] and most areas have been deforested at some point during the past 1000 years. In the 1920s, agriculture on the island was abandoned and it was made a natural reserve, with a field station was established for tropical studies.[46,47] Currently, the island supports about 100 people including staff scientists, administrative personal, and visitors.

CO_2 flux in soil

In April 2016, an automated gas flux system (LI-8100A; LI-COR Biosciences, Lincoln, NE, USA) was installed on Barro

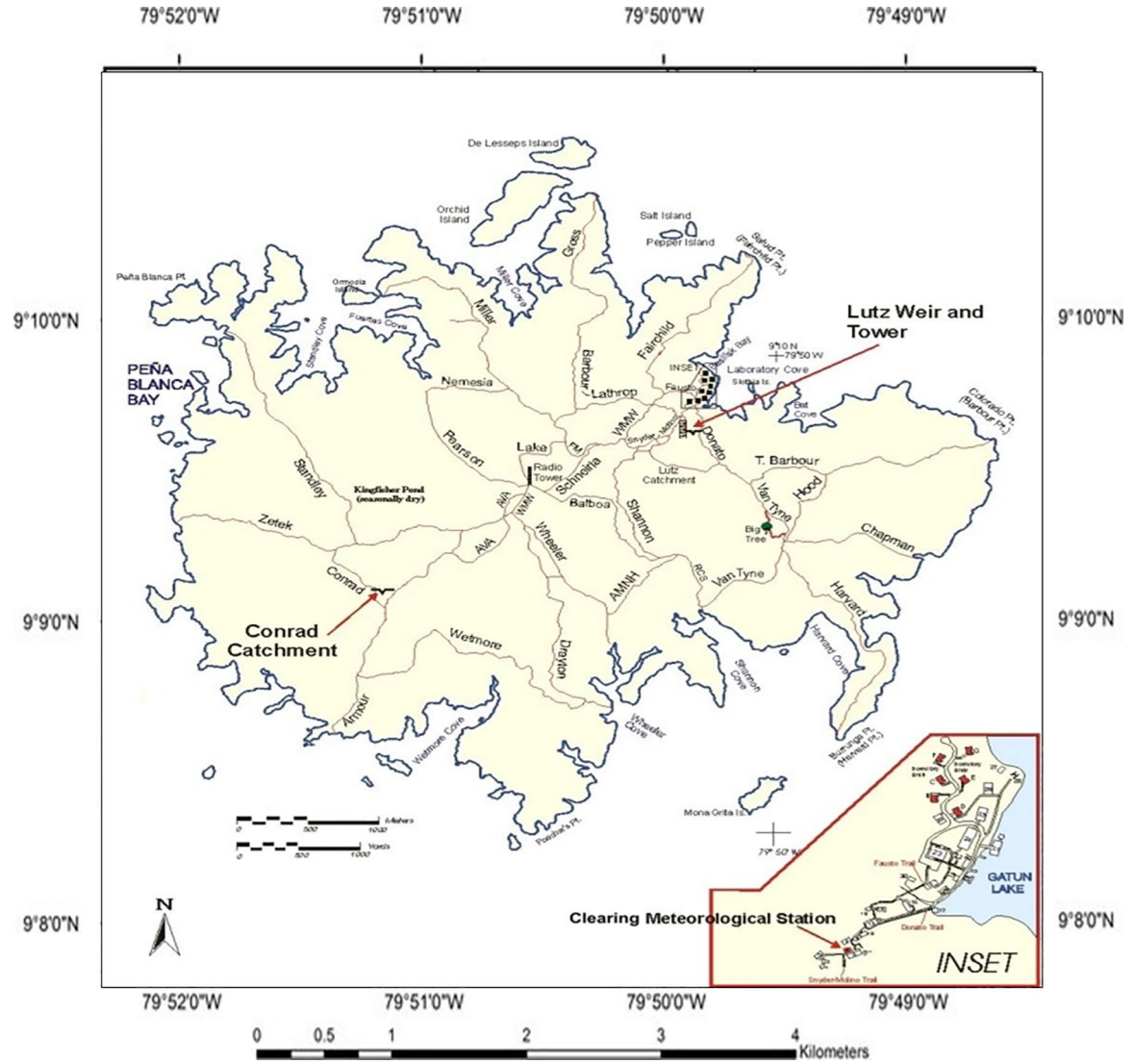

Figure 1. Map of Barro Colorado Island located within Gatun Lake. Trails and research sites are indicated. The Ava research site is a 6 ha plot used the Smithsonian Tropical Research Institute (STRI) for carbon quantification research projects.
Source: STRI website (https://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado).

Colorado Island. The system continuously measures long-term CO_2 flux in soil; it consists of closed dynamic automated chambers, a multiplexer, and a closed-loop infrared gas analyzer.[42]

Four polyvinyl chloride collars were buried at a shallow depth at selected measurement sites. Chambers with an external diameter of 20 cm were installed on the collars at the vertices of a 20 m × 20 m square centered radially to a microclimatic tower linked to an electrical network. CO_2 flux measurements are taken every second for 2 minutes after the chamber was closed. A pre-purge of 30 seconds and post-purge of 45 seconds were performed to ensure that the system was cleaned between measurements.[34,42]

During each measurement, a small portion of the air in the chamber was pumped to the infrared gas analyzer to determine the CO_2 concentration. The system software calculated the CO_2 flux results according to the rate of change in gas concentration over time within the chamber, as well as other parameters. We performed regression analyses and based on R^2, adjusted the values using an exponential or linear equation.[34] All recorded data were included except for those collected by chamber 4 because it was impacted by a fallen branch, rendering it unusable.

Soil temperature and humidity

Soil temperature and humidity data were recorded by the Smithsonian Tropical Research Institute (STRI; https://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado) at the Ava study site near the microclimatic tower for the period from January 2016 to November 2017, using procedures described in detail below.

Temperature. In January 2016, 2 floor thermistors 10.4 cm long (Model 107; Campbell Scientific, Logan, UT, USA) were permanently installed, and data were recorded using a datalogger (CR1000; Campbell Scientific) in 5-minute intervals. Soil

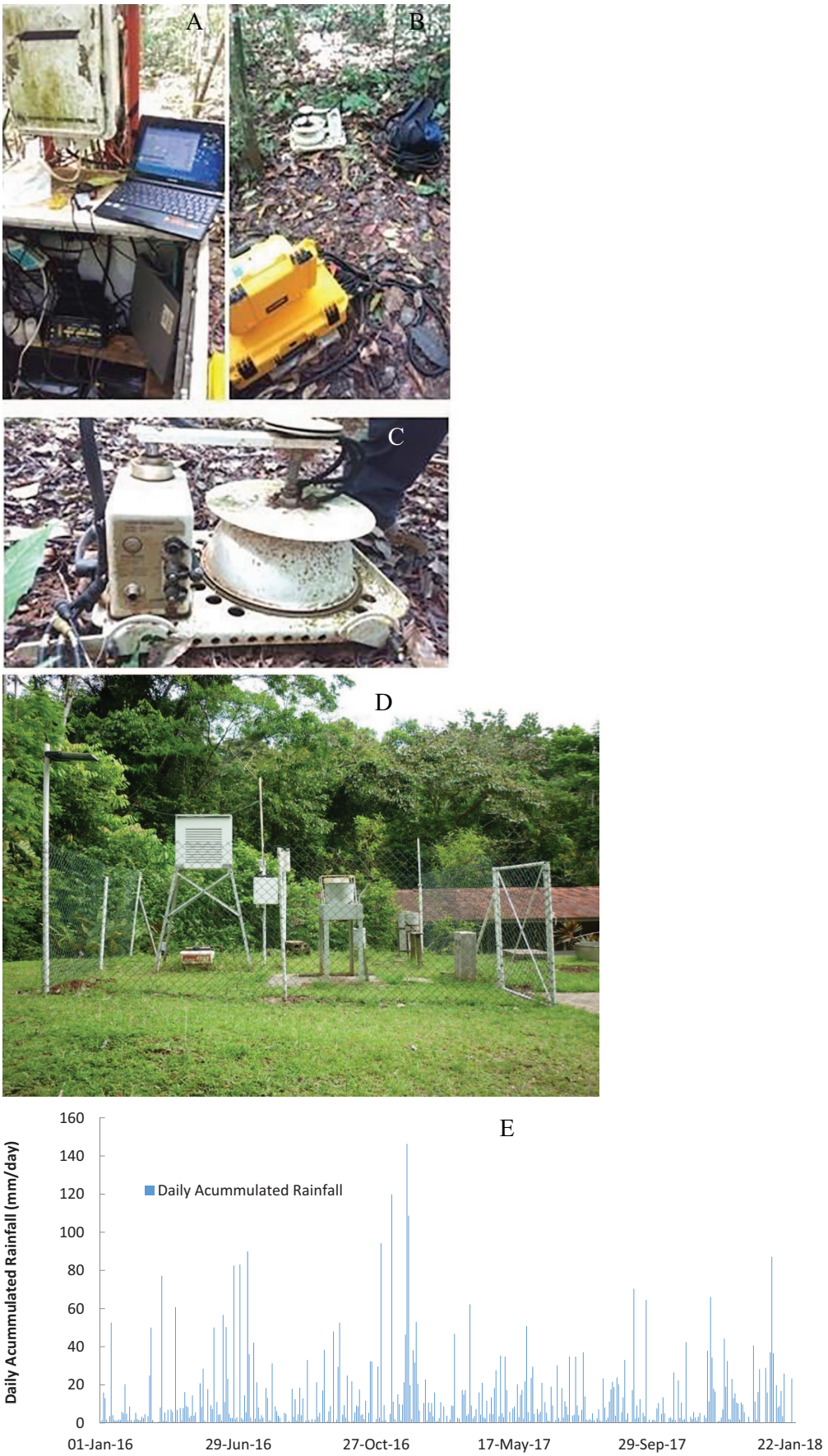

Figure 2. Research site in a 1 ha plot: (A) main eddy tower, (B) equipment used in this study, (C) soil gas flux chamber, (D) meteorological station called at El Claro, and (E) daily accumulated rainfall (mm) from January 2016 to January 2018. The rainy and dry seasons are evident from patterns in the data.

Table 1. CO_2 flux data collection period for each of the 4 measurement chambers. ×: Data not recorded. ✓: Data recorded.

CHAMBER	MAY-AUGUST 2016	SEPTEMBER 2016	OCTOBER 2016	JANUARY-MAY 2017	AUGUST 2017	JANUARY 2018
1	×	✓	✓	✓	✓	✓
2	×	✓	×	✓	✓	✓
3	×	✓	×	✓	✓	✓
4	×	✓	×	×	×	×

temperatures were measured continuously near the chambers using 4 thermistors 6 cm long (model 8150–203; LI-COR) that functioned in combination with the chambers.

Humidity. Soil moisture was monitored using 3 time-domain reflectometers (TDRs; CS616; Campbell Scientific) vertically inserted into the soil near the chamber system.[42] Soil moisture measurements were taken continuously throughout the study period.

Rainfall

Rainfall was recorded in the El Claro region of Barro Colorado Island (Figure 2C, D). The measurement area was surrounded by trees above 20 m in height. Rainfall was recorded using a tipping rain gauge (model TB3; Hydrological Services) that collected data every 5 minutes throughout the study period. The duration and peaks of the rainy seasons in 2016 and 2017 are shown in Figure 2B.

Statistical analysis

We analyzed variation in soil temperature, humidity, precipitation, and CO_2 flux using the coefficient of variation and standard deviation (SD). Linear regression was performed to examine the relationships among abiotic factors and CO_2 flux during the dry and rainy seasons of 2016 and 2017, using Pearson product correlation coefficient (r) as an index of the covariation between 2 known linearly related quantitative variables.[48,49] We calculated r as follows:

$$r = \frac{\sum (x-\bar{x})(y-\bar{y})}{\sqrt{\sum (x-\bar{x})^2 \sum (y-\bar{y})^2}} \quad (1)$$

where $\bar{x}$ is the arithmetic mean of x and $\bar{y}$ is that of y.[48] We normalized r dividing the covariance by the SD of each variable. We further used the determination coefficient (R^2) to evaluate the amount of variation in one variable that is shared by another variable.[48]

We tested the normality of the CO_2 flux data using the Kolmogorov-Smirnov (K-S) test,[50] which does not require pooling of the data and works for small samples. For a random sample of size n from the distribution of random variable x, divided into k classes, the K-S statistic D_n was calculated as follows:

$$D_n = \max_x \left| S_n(x) - F_0(x) \right| \quad (2)$$

$$S_n(x) = \begin{cases} 0 & x < x_{(1)} \\ \frac{k}{n} & x_k \le x < x_{(x+1)} \\ 1 & x \ge x_n \end{cases} \quad (3)$$

where S_n is the proportion of sample values that are equal to or less than x.

Because the data did not follow a normal distribution, we compared means using the nonparametric Mann-Whitney U test,[50] where U was calculated as follows for a random variable R_1 and of the sample sizes n_1 and n_2:

$$U = n_1 n_2 + \frac{n_1(n_1+1)}{2} - R_1 \quad (4)$$

Results

In the first quarter of 2016, Panama was experiencing a strong El Niño phenomenon that had begun in 2014. Rainfall frequency and intensity was lower on Barro Colorado Island during this period, which ended in May 2016.[51] In 2017, the island experienced a neutral El Niño year, which was accompanied by increased rainfall throughout the Central Caribbean region.[52]

CO_2 soil flux

Between April 2016 and January 2018, the minimum and maximum CO_2 flux values were 1.11 and 8.40 µmol/m²s, respectively (average ± SD = 4.36 ± 1.62 µmol/m²s), with a coefficient of variation of 37.1% (Table 1 and Figure 3). Measuring chamber 1 measured lower CO_2 flux values than chambers 2 and 3. There was less variability between chambers 2 and 3 (SD = 1.42). Spatial variability between chambers may have been due to the composition and structure of the forest floor and the distribution of tree roots near the chambers. We observed no pattern among the average CO_2 flux values of the chambers, despite an apparent decrease within each chamber as the rainy season progressed (Figures 4 and 5). CO_2 flux differed between the dry (4.62 µmol/m²s) and rainy (5.15 µmol/m²s) seasons during

Figure 3. Photographs of the soil gas flux chambers used in this study: (A) infrared gas analyzer (IRGA) multiplexer device with chambers 1 and 2, (B) chambers 2 and 3, and (C) chamber 4.

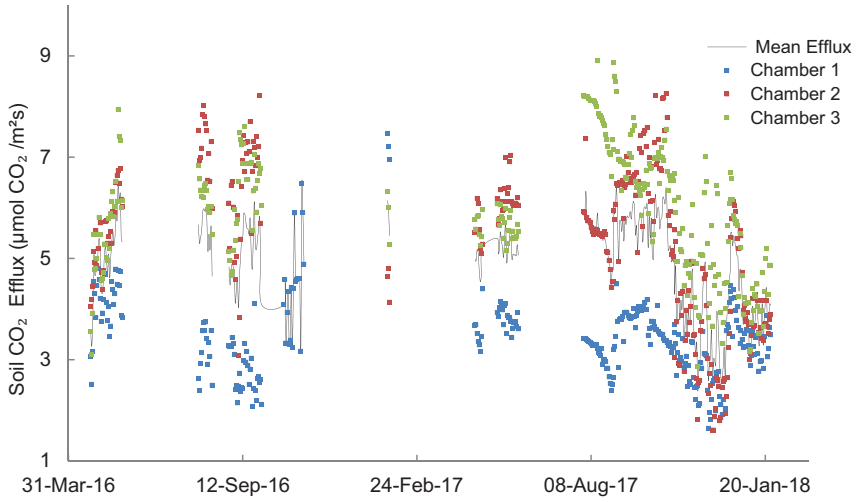

Figure 4. Soil CO_2 efflux data (µmol/m²s) collected by chambers 1, 2, and 3 at the Ava site from April 2016 to January 2018.

2016 to 2018 (Mann-Whitney *U* test, n = 63 for each season, $P < .0005$).

We performed separate linear regressions to examine the relationships between CO_2 flux and 3 environmental factors: soil temperature, soil moisture, and rainfall. The R^2 values are listed in Table 2. Then, we performed multiple regression analyses of the same factors in the dry and rainy seasons of 2016 and 2017 (Table 3). In 2017, the relationships between CO_2 flux and the environmental factors were positive in both seasons. Temperature had the strongest relationship with CO_2 flux during the dry season ($R^2 = .33$). Soil moisture was the most significant environmental factor during the rainy season ($R^2 = .46$). However, none of the R^2 values were greater than .5.

Soil temperature

Soil temperature was measured using a single thermistor from January 21, 2016 to November 18, 2017. The maximum and

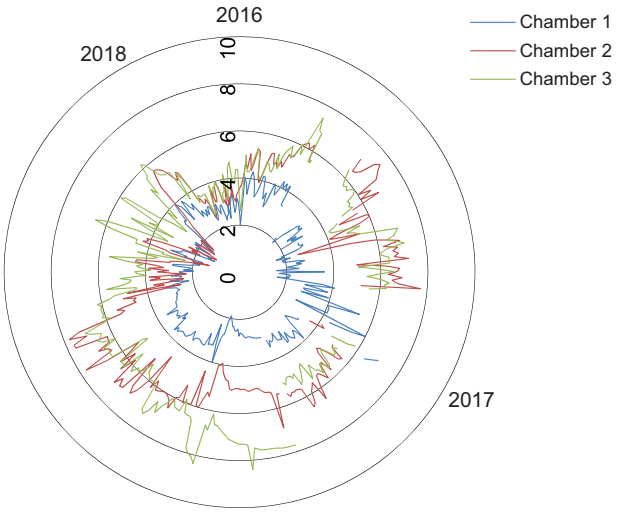

Figure 5. Soil CO_2 efflux data (µmol/m²s) collected by chambers 1, 2, and 3 at the Ava site from April 2016 to January 2018.

Table 2. Determination coefficients (R^2) for linear regressions of CO_2 flux with 3 environmental factors.

FACTOR	R^2				
	2016-2017	DRY SEASON 2016	RAINY SEASON 2016	DRY SEASON 2017	RAINY SEASON 2017
Soil temperature	.00	.01	.09	.33	.13
Soil humidity	.09	.65	.10	.00	.46
Rainfall	.03	.00	.04	.05	.05

Table 3. Determination coefficients (R^2) for multiple linear regressions of CO_2 flux with 3 environmental factors included and excluded (2016-2017).

FACTOR	R^2	
	INCLUDED	EXCLUDED
Soil temperature	.37	.03
Soil humidity	.41	.01
Rainfall	.06	.02

minimum temperatures were 27.5°C and 22.9°C (average = 25.4 ± 0.69°C), with a coefficient of variation of 2.7% (Figure 6). Soil temperatures decreased during the rainy season and increased during the dry season.

Soil humidity

Soil moisture was measured using a single TDR at a depth of 100 cm; measurements were adjusted using a polynomial equation. The maximum and minimum soil moisture values were 0.73 and 0.25 cm^3/cm^3 (average = 0.41 ± 0.9 cm^3/cm^3), with a coefficient of variation of 21.30% (Figure 7). Soil moisture increased during the rainy season and decreased during the dry season. Similar patterns were observed in both 2016 and 2017; humidity was generally higher in 2016.

Rainfall

Rainfall was measured from January 2016 to January 2018. The maximum and minimum cumulative daily rainfall values were 146.3 and 0.3 mm (average = 11.4 ± 18.1 mm), with a coefficient of variation of 155.15%. In 2016, soil moisture had the highest positive correlation with CO_2 flux in both the dry season (R^2 = .65) and the rainy season (R^2 = .10).

Discussion

Temperature and rainfall did not appear to directly influence the loss of carbon through soil CO_2 flux throughout the 2016 to 2018 study period; however, analyses of 2017 alone showed different results. A longer-term study is necessary to better identify seasonal and spatial variability in soil CO_2 flux in this region. Similarly, we did not detect conclusive patterns in soil CO_2 flux in relation to the factors examined in this study. It is necessary to analyze other soil physical variables to determine the role of these factors in soil CO_2 flux dynamics, as well as changes in rainfall and temperature patterns.

We found that variation in soil temperature had a positive relationship with that in soil CO_2 flux during the dry period in 2017. Increases in soil moisture do not always lead to an increase in soil CO_2 production or concentration.[53] In this study, soil moisture variation was more strongly positively correlated with CO_2 flux in the rainy season of 2017 than during the entire study period of 2016 to 2018. Thus, soil moisture appears to play a greater role in CO_2 flux variation than soil temperature.

Soil CO_2 flux was considerably lower during months with relatively high rainfall; however, during the transition from the dry season to the rainy season, it increased. This is consistent with previous findings that decreases in rainfall generally increase soil CO_2 flux.[54] It has been suggested that increased temperature and rainfall due to global climate change will increase soil CO_2 flux in the future.[55]

In a previous study, soil respiration was measured every 3 hours at each sample site for a period of 48 hours each on sunny days in the rainy and dry seasons, using an ultra-portable gas analyzer and soil gas flux systems; the results confirmed the need for long-term measurements.[56] In a sparse furrow-irrigated vineyard, an automatic CO_2 exchange system equipped with a transparent soil chamber and infrared gas analyzer was used to assess the spatiotemporal variability in soil respiration due to abiotic and biotic factors, which were found to depend on soil temperature via canopy structure, with irrigation-dependent soil moisture playing a secondary role in regulating soil respiration.[57]

A meta-analysis of the temperature sensitivity (Q_{10}) of soil respiration and potential controls of climate factors, soil properties, and vegetation characteristics across biomes at the global scale used a dataset including 658 groups of Q_{10} values and relevant environmental factors from 226 articles published before February 2018 and found that several environmental conditions affected these measurements under conditions similar to those of this study.[58]

In soil science studies, it is important to consider soil-specific parameters at different spatiotemporal scales.[59-61] In this study, certain factors were expected to greatly influence soil respiration, including abiotic factors such as weather and soil texture; however, longer-term measurements should be collected, over periods of at least 2 or 3 years.

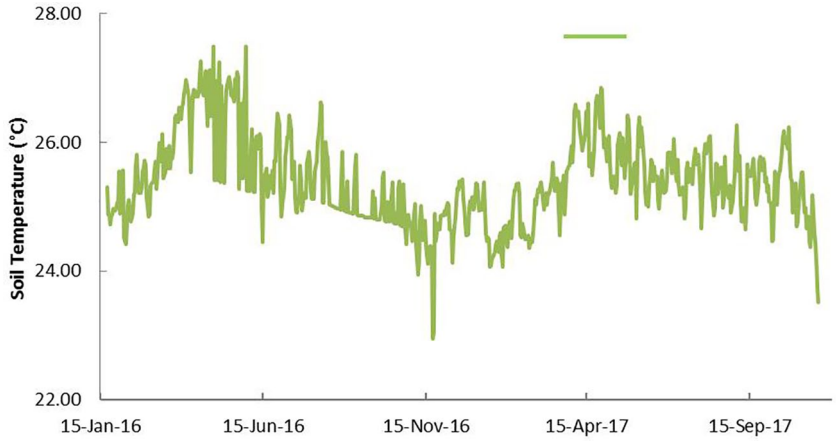

Figure 6. Soil temperature data (°C) collected from April 2016 to November 2017.

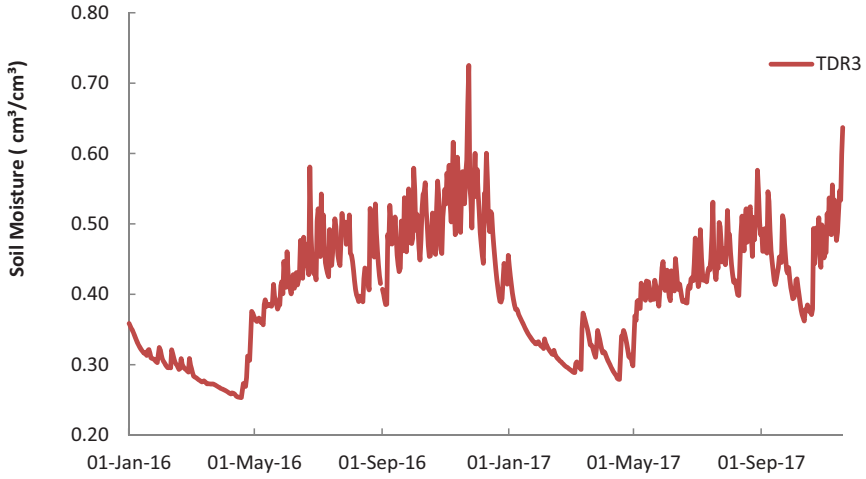

Figure 7. Soil moisture data (cm^3/cm^3) collected from January 2016 to November 2017.
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The contributions of urban land use to ambient air quality were examined in Bahir Dar and Hawassa cities of Ethiopia using data collected daily with a portable gas monitor with attached temperature and relative humidity sensor and a hand-held multigas detector; elevated levels of CO, CO_2, and volatile organic compounds were detected in the atmosphere and found to have a significant impact on the terrestrial ecosystem and global warming.[62]

Conclusions

During April 2016 to January 2018, we examined soil CO_2 flux on Isla Barro Colorado, Panama, using 4 closed soil gas flux chambers. The average CO_2 flux during the study period was 4.36 µmol/m^2s, which was surprisingly low for this type of tropical forest. We did not identify significant flux patterns in response to environmental factors during the dry and rainy seasons of 2017. Rain, soil moisture, and soil temperature were positively correlated with seasonal variation in CO_2 flux; the strongest relationships were with temperature overall, and soil moisture during the rainy season. We concluded that soil moisture played a more important role in soil CO_2 flux throughout the 2016 to 2018 study period. The results of this study show that CO_2 fluxes at ground level are an important source of atmospheric CO_2. A longer-term study is required to determine whether environmental factors play a significant role in seasonal CO_2 flux patterns over time.

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Author Contributions

LS and RP conceived and designed the experiments and performed and interpreted the data analyses. LS wrote the first draft of the manuscript and RP made critical revisions and contributed to the final manuscript. All authors reviewed and approved the final manuscript.

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