

Article

Temporal Variability of Soil Respiration in Experimental Tree Plantations in Lowland Costa Rica

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Abstract: The principal objective of this study was to determine if there is consistent temporal variability in soil respiration from different forest plantations in a lowland tropical rainforest environment. Soil respiration was measured regularly over 2004 to 2010 in replicated plantations of 15- to 20-year-old evergreen tropical trees in lowland Costa Rica. Statistically significant but small differences in soil respiration were observed among hours of the day; daytime measurements were suitable for determining mean fluxes in this study. Fluxes varied more substantially among months, with the highest average emissions ($5.9 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) occurring in September and low emissions ($3.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) occurring in January. Three of the six tree species had significantly increasing rates of soil respiration across 2004–2010, with fluxes increasing at an average of $0.09 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ per year: the three other species had no long-term trends. It was hypothesized that there would be a tradeoff between carbon allocation aboveground, to produce new leaves, and belowground, to sustain roots and mycorrhizae, but the relationship between canopy leaf fall—a surrogate for canopy leaf flushing—and soil respiration was significantly positive. The similarities observed among temporal trends across plantation types, and significant relationships between soil respiration, soil water content and soil temperature, suggest that the physical environment largely controlled the temporal variability of soil respiration, but differences in flux magnitude among tree species were substantial and consistent across years.

Keywords: climate change; climate warming; forest carbon cycle; plant-soil system; soil carbon cycle; tropical forest; tropical forest phenology; tropical rainforest

1. Introduction

The tropical forest biome covers only about 12% of Earth's land surface [1,2], yet it harbors much of the world's biological diversity [3–6] and disproportionally influences global biogeochemistry. Tropical forests are responsible for one-third of the world's terrestrial plant productivity [1,2,7], one-third of the world's terrestrial respiration [8] and one-third of terrestrial evapotranspiration [9]. Although they vary greatly in composition and structure, tropical rainforests often contain substantial living biomass, and large stocks of detrital carbon and organic nitrogen [10–13] that sustain high rates of microbial activity. In brief, the warm, moist conditions that prevail year-round in tropical forests support abundant life and rapid land-atmosphere exchanges of energy, water and carbon. Both warmer temperatures and an accelerated hydrologic cycle are expected in tropical forest regions in future years [14]. Those changes will alter tropical forests and soils and, thus, land-atmosphere exchanges of carbon, energy and water. We do not fully envision what the resulting impacts will be.

Large stocks of detritus, warm temperatures, and humid conditions together create a strong potential for warming (without drying) to stimulate decomposer activity and the mineralization of detritus to CO_2 and other trace gases. That could generate a positive feedback to global warming,

because CO₂ is an important greenhouse gas [15–17]. The likelihood that this particular feedback will emerge has been extensively discussed [18–23] but has not been ruled out [24–29]. As a result, despite decades of discussion and debate, the question persists. Although greater warming is expected in northern latitudes than in the tropics [14], CO₂ fluxes from humid tropical forests are already large, and small changes in large fluxes can be important. For example, a 3% increase in a tropical soil respiration of 1500 g·C·m^{−2}·year^{−1} is greater than a 20% increase in a tundra soil-respiration rate of 200 g·C·m^{−2}·year^{−1}. Based on studies of moist tropical forests, it has been proposed that decomposition rates increase faster at warmer temperatures than does net primary productivity (NPP) [30]. That would be consistent with a positive-feedback scenario for tropical forest soil respiration. A variety of evidence suggests that the tropics already influence interannual variations in atmospheric CO₂ concentrations [31]. Measurements of soil respiration are insufficient, by themselves, to address this debate, but tropical forests play an important role in the earth’s carbon cycle; they will be impacted by climatic changes; they are likely to influence future atmospheric changes; and they remain understudied in relation to their potential to cause change.

Objectives

The over-riding objective of this study was to determine if there is consistent temporal variability in soil respiration (*R_{soil}*) from evergreen forest plantations in a lowland tropical rainforest environment. To do so, *R_{soil}* was measured over diel, monthly and multi-annual time frames. Second, I sought to identify the environmental variables underlying observed temporal variations in *R_{soil}*, to inform the process-based understanding of tropical forest carbon dynamics that is needed to improve predictive modeling [32]. Despite an increasing body of empirical data from tropical forests, there is a lack of agreement on several issues. For instance, diel variations in *R_{soil}* have been observed in some evergreen tropical forests, but not in others [33–38]. That issue underlies an important concern: most measurements of tropical forest *R_{soil}* are made only in the daytime, especially in remote locations. If fluxes are significantly different at night than during daylight hours, then we have a poor grasp of what average tropical forest *R_{soil}* truly is [35]. Additionally, daytime photosynthesis by a productive tree canopy may drive diel variations in *R_{soil}*, via temporally variable canopy-to-root carbon translocation [39–41]. Over longer time frames, most studies indicate that temporal variability in tropical forest *R_{soil}* is attributable to variations in soil moisture content or temperature [37,38,42], indicating that climatic variability is important. However, plant phenology may independently influence the temporal dynamics of *R_{soil}*, via seasonally variable rates of aboveground litter production or root growth or turnover [43]. Furthermore, if *R_{soil}* is limited by carbon (C) fluxes to roots, then trade-offs between aboveground and belowground C allocation may also cause seasonal variability in *R_{soil}*. For instance, belowground fluxes may be lower at times when forest canopies are producing a new crop of leaves. If so, that might suggest that root-shoot allocation patterns vary seasonally within a forest, and that carbon limitation influences the magnitude of *R_{soil}*, at least during some months.

I tested the following hypotheses, based on the measurements collected. First, Hypothesis 1: soil respiration varies on a diel basis. Such temporal variations in *R_{soil}* have important implications for interpretation of daytime-only measurements, and might result from a variety of processes. For instance, lowland, humid tropical forests have a unique climatic feature: diel variations in temperature often exceed the variations in mean monthly temperatures. Warmer daytime temperatures may drive faster daytime CO₂ production in, and diffusion from, soils. Also, observed night-time warming is greater than observed daytime warming in the tropics, probably due to increased cloud cover [44–47], yet most data available on soil CO₂ emissions from tropical rainforests are derived from daytime measurements. In tropical forests, soil temperatures typically exceed air temperatures at night, and that could promote movement of CO₂-rich soil air into the atmosphere. I also tested Hypothesis 2, that *R_{soil}* varies among months of the year. Even within relatively aseasonal wet tropical forests, there is climatic variability and there are phenological differences among tree species [48] that likely influence the magnitudes of aboveground and belowground C fluxes. However, seasonal patterns in belowground

carbon fluxes in evergreen tropical forests are very poorly understood. To further evaluate seasonal variability, I also tested Hypothesis 3, that R_{soil} and canopy leaf flushing are negatively correlated with one another. This hypothesis is based on the supposition that there is a trade-off between plant carbon use aboveground, to produce a new crop of canopy leaves, and belowground, to support root systems. Leaf flushing by tropical evergreen broad-leaved trees represents an important and seasonally variable investment of available carbon in a new crop of leaves. As new leaves expand out of their buds, old leaves are dropped. Thus, leaf flushing appears as seasonality of leaf fall by canopy trees. Finally, I tested Hypothesis 4, that R_{soil} increases with forest age in developing forest stands, as suggested by [49]. This hypothesis is put forth to determine if there is a multi-annual trajectory in R_{soil} , either positive or negative, in the 15- to 20-year old experimental tree plantations that were the focus of this research. It is widely accepted that forest productivity increases with age in young forests, to a point, but does not continue to increase continuously, and very often decreases as forests mature [50–52]. Such non-linear trends may be difficult to disprove, but tropical tree plantations can grow rapidly [53]; quantifying belowground dynamics in a variety of different forest types as they mature and age, within a single rainforest location, can provide valuable insights into the temporal dynamics of belowground processes, about which we know very little.

2. Materials and Methods

2.1. Study Site

This research was undertaken at the La Selva Biological Station of the Organization for Tropical Studies, in the Caribbean lowlands of northeastern Costa Rica (10°26' N, 84°03' W). Over 1997–2009, annual precipitation averaged 4537 mm and mean air temperature was 25.1 °C [54]. The driest season at La Selva generally extends from February through April, but rainfall averages > 150 mm·mol^{−1} in every month. Forest evapotranspiration averages > 2000 mm·year^{−1} [55]. The native vegetation at this site is species-rich broad-leaved evergreen rainforest that has a high abundance of *Pentaclethra macroloba* (Willd.) Kuntze (Fabaceae, Mimosoideae) trees, and many subcanopy palms. In primary forest on rolling terrain, there are an average of 528 trees·ha^{−1} having a basal area of 23 m²·ha^{−1} [56]. Long-term studies of old-growth forest at La Selva show that litterfall averages 9.1 Mg·ha^{−1}·year^{−1}, 78% of which is leaves [54]. Tree growth averages half that and their sum, aboveground net primary productivity (ANPP), averages 13.7 Mg·ha^{−1}·year^{−1} [54]. More information about the physical and biological features of La Selva is provided in [57].

Field studies for this research were conducted in replicated experimental tree plantations that were established on formerly grazed pastures, to test the influence of tree species identity on soil properties after reforestation [58,59]. The pastures were established from mature forest in the mid-1950s, and trees were planted, after removal of the cattle, in the winter of 1988–1989 [53,58,60]. This study began 15 years later. The study plots were at 10°26' N, 83°59' W, on hilly terrain with elevations of 44 to 89 m. They were approximately 3.3 km from the biological station and weather station. The soils were Oxisols derived from volcanic parent materials, and belong to the Matabuey consociation [61]. In brief, they are deep, acidic, highly permeable clays with low base saturation and relatively high soil organic matter contents [61–63]. Surface-soil pH (in water) was <4.5 in all plots [63]. The available data indicate that total soil C and nitrogen (N) stocks were lower in the plantations than in nearby, undisturbed forest, on average; and that soil organic C mineralization rates (gCO₂-C gSoil^{−1}·day^{−1}) were lower in plantation soils than in mature forest soils [8,53,63]. Nevertheless, rates of N cycling in the plantations were very high [64]. Fine-root biomass was concentrated in the surface 15 cm of mineral soil, and declined rapidly with increasing soil depth to 1 m [65]. The forest floors were comprised primarily of leaves and particulate debris that decomposed rapidly: forest floor turnover rates among the plantations we studied ranged from 1.5 to 2.3 year^{−1} [66]. The diversity and abundance of litter-dwelling organisms were high.

The experimental design included four randomized blocks composed of twelve 50 m × 50 m plots, each of which originally contained a single tree species planted at 3 m × 3 m spacing, except that the control plots were not planted or otherwise managed in any way [58,67]. Each block was centered across a single hill and thus encompassed a range of slope and aspect positions. Plantations of the fastest growing species were thinned three years after planting, and additional thinning was done three years later [67,68]. Each of four replicate plots of six plantation types, a total 24 plots, were included in this study. These included plantations of *Pinus patula* subsp. *tecunumanii* (Eguiluz and J. P. Perry) Styles; *Hieronyma alchorneoides* Allemao; *Pentaclethra macroloba* (Willd.) Kuntze; *Virola koschnyi* Warb.; *Vochysia ferruginea* Mart.; and *Vochysia guatemalensis* Donn. Sm. *Pentaclethra* is a Mimosoid legume with occasionally nodulated roots; *Pinus patula* was the only conifer and the only non-native species included in this study. Site management included understory clearing over the first four years, and thinning, generally to 50% of the standing basal area (i.e., every other tree), but the timing of thinning varied among species [67]. *Hieronyma* and *Vochysia* spp. coppiced after being thinned, and *Pentaclethra* apparently was never thinned. In 2004, when this study began, these plantations had an average of 405 trees·ha^{−1} with a total basal area of 23 m²·ha^{−1} and average tree heights that ranged from 14 to 26 m (Table 1). Over the course of this study, there was a decline in tree stem densities whereas overstory basal areas and tree heights increased, as is typical in growing forests. The exceptions were plantations of *Pinus patula* and *Vochysia ferruginea*, which lost basal area as a result, apparently, of fungal attacks. The understories of the experimental plantations developed dense and diverse understories [67,68] that continued to grow throughout this study.

Table 1. Characteristics of the experimental tree plantations in 2004, fifteen years after planting, and in 2010, at the end of this study. Values are means ± 1 S.E. based on measurements of all trees in four replicates of each plantation type.

Tree Species	Year of Measurement	Density (stems·ha ^{−1})	Basal Area (m ² ·ha ^{−1})	Height ¹ (m)	Diameter ² (cm)
<i>Hieronyma alchorneoides</i>	2004	349 ± 13	15.2 ± 0.9	31.1 ± 1.1	23.6 ± 1.0
	2010	307 ± 8	17.4 ± 1.0	32.0 ± 0.6	26.9 ± 1.1
<i>Pentaclethra macroloba</i>	2004	611 ± 87	21.2 ± 4.4	21.6 ± 1.7	21.2 ± 2.9
	2010	548 ± 50	25.3 ± 5.9	23.3 ± 1.7	24.0 ± 3.3
<i>Pinus patula</i>	2004	289 ± 9	19.8 ± 1.0	28.9 ± 0.8	29.6 ± 1.2
	2010	155 ± 18	14.0 ± 2.2	30.9 ± 2.0	33.8 ± 1.2
<i>Virola koschnyi</i>	2004	455 ± 48	19.8 ± 3.6	26.7 ± 1.4	23.1 ± 1.7
	2010	432 ± 50	22.2 ± 4.2	27.1 ± 1.4	25.1 ± 1.8
<i>Vochysia ferruginea</i>	2004	206 ± 44	20.3 ± 2.3	31.3 ± 0.7	36.4 ± 2.2
	2010	156 ± 45	19.1 ± 3.7	31.7 ± 0.7	41.0 ± 3.4
<i>Vochysia guatemalensis</i>	2004	519 ± 30	40.2 ± 3.6	33.9 ± 1.7	31.4 ± 1.3
	2010	476 ± 31	43.6 ± 1.7	36.2 ± 1.3	34.3 ± 1.5

¹ The mean of the tallest tree in each plot (N = 4); ² the diameter at breast height of an average-sized tree (i.e., the quadratic mean diameter).

2.2. Measurements of Soil Respiration

Measurements of soil respiration were initiated in September 2004 in each of the four replicate plots of six plantation types and continued until February 2010 in four of the plantation types. All studies were based on LI-COR[®] automated soil gas flux instruments (LI-COR Biosciences, NE, USA) that were returned to the factory for cleaning and recalibration annually. The specific measurement chambers utilized varied, but they provided fully comparable measurements of in situ soil respiration, *R_{soil}*. I herein report the results of two principal studies: diel study and survey measurements. The diel study characterized variations in *R_{soil}* each hour across 2-day and longer periods, based on automated sampling with a single instrument that was moved to sample each of the 24 study plots at least twice. The Survey study involved sampling each of the experimental plots at one time, during daytime hours, so that the effects of the experimental treatments could be cleanly compared. It sometimes took two days to sample all the chambers in all plots. Measurements were conducted through time so that

seasonal variations in *R_{soil}* could be quantified. Summary results of the first two years of this study were reported earlier [53,65], but data from 2008 to 2010 have not been previously reported, nor have data from plantations of *Vochysia ferruginea* or from the diel study. Based on the data collected during both studies, I also tested for longer-term trends in fluxes in the maturing plantations (Hypothesis 4), which were 16 years old in 2004 and 21 years old in 2009. Thus, hourly, monthly, and inter-annual variations in *R_{soil}* were assessed for this article.

2.2.1. Diel Measurements

Soil CO₂ emissions were measured every hour over a total of 52 continuous periods of >2 days between November 2004 and February 2010, with a single chamber in one plot at a time, to investigate diel variations in *R_{soil}*. Measurements were made with a LI-COR 8100 soil CO₂ flux system attached to an 8100-101 long-term chamber (LI-COR® Environmental, Lincoln, NE, USA) and powered by a deep-charge marine battery, all of which were back-packed into an experimental plot and then left in place for the duration of measurements. The battery allowed for measurements to be collected every hour over 2–3 day periods. A day before measurements began, a single 20-cm diameter, 12-cm tall polyvinyl chloride collar was inserted approximately 2 cm deep into the surface soil of a plot by carefully cutting through the forest floor with a sharp knife. All measurements were at randomly located positions without regard to tree positions. On the measurement date, the automatic chamber was carefully situated such that it closed firmly on top of the collar, and lifted freely after each measurement. During measurements, the chamber remained tightly closed for 2 min, and within-chamber CO₂ concentrations were monitored as the chamber headspace was circulated through the IRGA (Infrared Gas Analyzer, total system volume averaged 7 L). The first 30 s of measurements were ignored to allow for internal mixing to complete. Over the remaining 90 s, the concentration of CO₂ within the chamber was measured every second, and the rate of change in headspace CO₂ concentrations was used to quantify *R_{soil}*. The resulting time-series data were analyzed using LI-COR's embedded FV8100 file viewer software. In most cases, exponential fits were utilized because the rate at which within-chamber CO₂ concentrations increased typically declined through time. The R^2 values of curve fits averaged 0.99 ($N = 2650$) and the minimum R^2 was 0.75. The first hourly measurement collected at a new location was discarded because of consistently high ambient CO₂ concentrations that were attributable to human respiration. A summary of the 52 measurement periods is provided in Table S1. Due to time commitments to other studies, no diel measurements were made from May through September.

During diel measurements, near-surface air temperatures, relative humidity, atmospheric pressure, and CO₂ concentrations were monitored continuously as the measurement chamber closed and then within the closed chamber. Mineral-soil temperature at 10 cm depth was monitored with a soil thermistor probe (LI-COR 8150-203). Surface-soil volumetric moisture content was assessed at four locations surrounding the chamber, at the beginning and end of each measurement period, using a CS620 Hydrosense system with 12-cm rods (Campbell Scientific, Inc., Logan, UT, USA). Following successful completion of one measurement period (i.e., one continuous sequence of hourly measurements at one plot, typically lasting >50 h), the equipment was disassembled and relocated to a different plot. All 24 plots were measured twice between January 2008 and February 2010, to capture both dry and wet periods (Supplementary Table S1). Additional measurements collected in 2004, before sensor malfunctions halted measurements, are included in the analyses (Table S1).

Weather data encompassing 2008 through 2010 were obtained from the La Selva meteorological station, which was approximately 3.3 km from the experimental plots. These data included half-hourly air temperature (°C), relative humidity (RH, %), rainfall (mm), mean wind speed (m·s^{−1}), solar radiation (W·m^{−2}) and photosynthetic photon flux density (PPFD, μmol·m^{−2}·s^{−1}). To meld data into a single file for analyses of flux- \times -environment relationships, measurements were matched to the nearest half-hourly meteorological data. I also assigned each measurement to its nearest hour so that

‘hour-of-day’ could be used as a categorical variable for statistical analyses. Detailed weather data were not available for 2004.

2.2.2. Across-Site Surveys of Soil Respiration

The study site was on hilly terrain, and measurements were conducted with backpacked instruments and were limited to daytime hours. Altogether, 99.5% of the measurements were collected between 07:30 and 16:30 sunrise and sunset were at approximately 06:00 and 18:00 daily. The survey measurements were undertaken to test for significant influences of plantation type (tree species) on the magnitude of R_{soil} . These data are utilized herein for three purposes: (a) to quantify monthly variability in R_{soil} (Hypothesis 2); (b) to test Hypothesis 3, which posits a temporal offset between aboveground and belowground C fluxes; and (c) to identify longer-term (2004–2010) trends in R_{soil} (Hypothesis 4). The survey measurements undertaken for this study are summarized in Table S2.

Soil respiration within the plantations was measured 66 times between August 2004 and March 2010 using a LI-COR® 8100 soil CO₂ flux system. From 2004 through 2008, measurements were made with an 8100-102 chamber placed on top of a 10-cm diameter, 5-cm tall plastic collar that was carefully inserted by cutting with a sharp knife through the forest floor and about 1 cm deep into the mineral soil. There were 3–4 collars per plot (12–16 collars per species each date), and they were moved to new, randomly selected locations every year or whenever they were disturbed. At each collar on each measurement date, soil CO₂ fluxes were monitored every second for 90 s. Fluxes were calculated over the final 70 s of chamber closure, using the embedded LI-COR file viewer software, with the first 20 s being excluded to allow for full mixing of the within-chamber atmosphere. The mean flux from the final 70 s was based on an exponential fit of the CO₂ concentration over time relationship. Initial measurements included six species, in one plot per block of each. Measurements in *Vochysia ferruginea* were discontinued after May 2006 because entire trees began falling as a result of butt rot, which seemed to spread among adjacent trees via root grafts. Measurements were discontinued in *Pinus palustris* after March 2008 because trees dropped all their needles and disintegrated. From February 2009 through February 2010 an 8100-103 (20-cm diameter) chamber was utilized, with four 20-cm diameter collars in each of the four plots of each of the remaining four tree species (Supplementary Table S2). Within-chamber CO₂ concentrations were monitored every second for four minutes, with the first 40 s being allowed for full mixing of the air within the chamber, and the subsequent 200 s being used to calculate CO₂ emissions. It was sometimes possible to collect data from all soil collars within all four blocks in one day, but it often took two. Each measurement cycle began at a randomly selected block to minimize the potential for temporal bias to influence comparisons among blocks and species.

At the time of soil respiration measurements, a thermistor probe (LI-COR 8100-201) was inserted 5 cm into the mineral soil approximately 20 cm distant from the measurement collar at three locations, to measure soil temperature. In 2009, we started measuring soil temperature (T_{soil}) at 10 cm depth. After chamber closure, we measured surface-soil water content with a hand-held electronic soil moisture sensor that was inserted into three locations around but >20 cm from the chamber. Early measurements were made with an ECH₂O Dielectric Aquameter (Model EC-10, Decagon Devices, Inc., Pullman, WA, USA; LI-COR part 8100-202). In 2005, that instrument was replaced with a Campbell 620 Hydrosense system with 12-cm long probes (Campbell Scientific, Inc., Logan, UT, USA), and it proved more durable under the site conditions. We cross-calibrated the two water-content sensors such that they provided the similar readings across the breadth of observed soil moisture contents. Local weather data were obtained from the La Selva Biological Station, which was 3.3 km from the closest study plots.

2.3. Canopy Leaf Fall

Total fine litterfall was measured with four traps per plot that were emptied at the middle and end of each month. Traps had wooden frames that had 1.3 × 0.4 m internal dimensions and 2-mm

mesh screen bottoms. They were supported about 30 cm above the soil on steel legs. The collected materials, which included branches ≤ 1 cm in diameter and all non-woody materials, were combined within months to generate a single sample per plot that was sorted into four fractions: branches and bark; canopy leaves; other leaves; and miscellaneous materials [65,66]. Traps were removed, repaired and repositioned annually. More than four years of litterfall measurements were made from October 2003 to December 2009. They are used herein to test for temporal offsets between leaf fall and soil respiration (i.e., Hypothesis 3).

2.4. Statistical Analyses

Statistical analyses were conducted using JMP[®] 11.2.0 (SAS Institute, Inc., Cary, NC, USA). The underlying experimental design was a randomized complete-block with four blocks and six plantation types, which are referred to by the single tree species that was planted into each plot. A combination of parametric and non-parametric statistical analyses was applied to test for significant differences among the test variable, typically time (hour or month or year); tree species; and their interaction. Tests of hourly and monthly data were based on binned values, 24 h of day and 12 months of year, rather than the continuous time variables that were collected. Several features characterize the datasets. First, the hypotheses were designed to test for landscape-level patterns but, commonly, results varied among the plantation types. Also, sample sizes differed among treatments. Therefore, hypotheses typically were tested at both the all-plot (landscape) and treatment (tree species) levels. Homogeneity of variances was specifically tested with the Brown-Forsythe and Levene tests and was very frequently rejected. In those cases, Welch's test was applied. In cases where data were not normally distributed, transformations were applied prior to statistical analysis. For instance, measurements of daytime *R_{soil}* ($N = 4962$) were not normally distributed and included occasional very high fluxes (maximum = $46 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Natural-log transformation of the data reduced kurtosis from 54.7 to 0.8, reduced skewness from 3.6 to -0.13 , and changed the median-to-mean ratio from 0.94 to 1.01. Statistical tests of *R_{soil}* therefore were based on $\ln(R_{\text{soil}})$, but results typically are presented as actual values to facilitate understanding. In all cases of comparisons among groups, a non-parametric Kruskal–Wallis test was applied to validate the results of parametric analyses of variance; reported results represent the more conservative result (i.e., lowest P value). Differences among factors were considered significant at $P = 0.05$.

The diel study comprised 52 independent observational studies that were designed to determine the effect of time-of-day on *R_{soil}*. Each study included automated measurements of *R_{soil}* that were made every hour over more than two continuous days, at one location in one plantation type. Measurements were made a minimum of two times in each plantation type in each block, at different times of year (Table S1). Thus, the measurements incorporated variability attributable to tree species, hour-of-day, and season-of-year, all of which were found to significantly affect fluxes, at least sometimes. Therefore, to quantify the hour-of-day effect, each of the 39 to 70 hourly measurements made during each of the 52 measurement periods was normalized to a measurement-period mean value of precisely 1.0. Within an individual measurement period, then, fluxes varied through time but had an overall average normalized flux rate of one. As a result, all measurement periods had fully comparable fluxes that varied only with time of day. The normalized data then were combined for statistical analyses. The resulting dataset had a sample size of 2650, a median = 0.99, a range of 0.025–1.798, a CV (coefficient of variation) of 0.14, a skewness of -0.12 , and a kurtosis of 6.5. To test for diel variations in *R_{soil}* (Hypothesis 1), data were assigned to hourly bins (categorical variable, hour 14 = 13:30–14:29).

The survey study similarly comprised individual observational comparative studies during which *R_{soil}* was measured within plantations within all four blocks. This study included 66 such measurement periods: the species being measured varied through time (Table S2). To test for seasonal differences (Hypothesis 2), measurements were assigned to monthly bins. Block was treated as a random effect. Tree species and their interaction significantly influenced *R_{soil}* (least squares ANOVA, $N = 4858$), so comparisons among months were done on a per-species basis. In most cases, variances among months

were not homogeneous, so the results of Welch's test are reported. In cases where variables were not normally distributed, the non-parametric ranked-sum Kruskal–Wallis Test was applied.

To compare the seasonality of leaf flushing with that of R_{soil} , to test Hypothesis 3, mean monthly soil respiration data were paired with mean monthly canopy leaf fall data from the same species and time frame. Pearson product–moment correlations were calculated on a single dataset including all months and species, i.e., mean monthly canopy leaf fall and mean monthly R_{soil} for each month and species ($N = 72$).

To assess whether there were long-term trends in R_{soil} over the duration of the study (Hypothesis 4), data from both the diel and survey studies were combined into a single dataset, and the hypothesis was tested independently for each species. Least-squares linear regression modeling was applied with $\ln(R_{soil})$ as the dependent variable. Results from simple correlations, non-linear models, or multiple linear models having additional time-related variables (e.g., time^2) added no meaningful information, and are not reported.

3. Results

This study ran from October 2003 through February 2010, during which largely normal weather patterns prevailed at La Selva. Rainfall averaged $4420 \text{ mm} \cdot \text{year}^{-1}$ and temperatures averaged 25.1°C ; both are similar to longer-term means (Table S3). Dry-season precipitation (January through April) was below average in 2007 and 2008, but exceeded 65 mm in every month. Overall, both the diel and survey measurements included a broad range of the weather conditions that typify the climate of La Selva, including brief rain-free periods.

3.1. Diel Variability in R_{soil} and the Environment

Soil respiration varied widely within and among days, without obvious regularity (Figure 1). Nevertheless, normalized fluxes did vary significantly among hours of the day (Kruskal–Wallis test, $df = 23$, $\chi^2 < 0.0001$). This finding supports Hypothesis 1, that R_{soil} varies on a diel basis. However, the R^2 was low (0.02) and variability within hours was high. Overall, R_{soil} was lowest between 06:30 and 10:30, when it averaged $4.03 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Figure 2a). There was no equivalent identifiable period of maximum emissions; all other hours of the day had statistically equivalent fluxes.

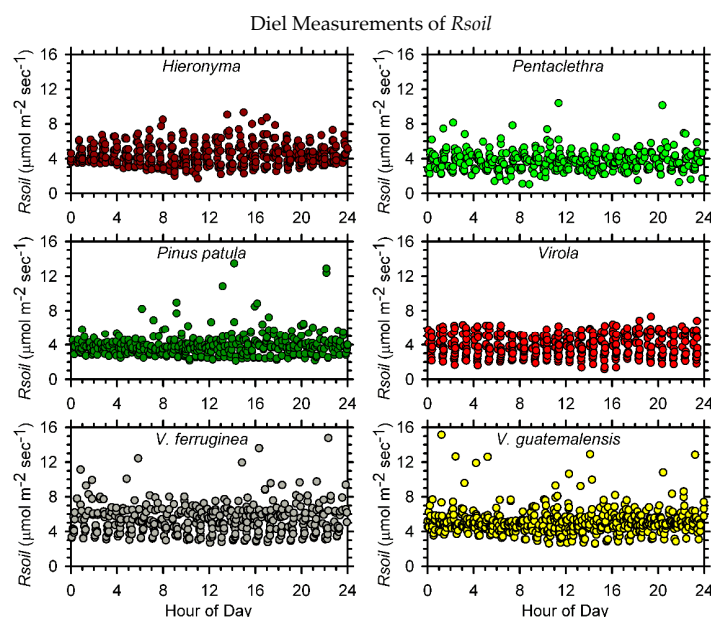


Figure 1. Soil respiration was highly variable at all hours of the day and night, within all plantation types. This figure includes all data collected during diel measurement periods ($N = 2650$).

Several meteorological variables that potentially influenced emissions also varied through time (Figure 2) and, thus, potentially provide insight into environmental controls over within-soil CO₂ production and its rate of escape into the atmosphere. Note that data in Figure 2 represent averages calculated from hours during which *R_{soil}* was measured. Across all measurement dates, soil temperature (*T_{soil}*) at 10-cm depth averaged <24.2 °C from 07:30–12:30 but >24.5 between 16:30 and 23:30 (Figure 2c). Air temperatures increased from an average daybreak minimum of 21.6 °C to a post-noon maximum of 27.3 °C (Figure 2d). The temperature difference between the soil and atmosphere varied more widely (Figure 2b), ranging from −3.1 °C at 13:00 to 2.7 °C at 06:00. Atmospheric relative humidities were quite high, on average (Figure 2e), but they too varied across the day: they averaged >93% between 02:30 and 08:30 but <83% between 11:30 and 16:30. Among those variables, *R_{soil}* most closely paralleled changes in soil temperature, and increased with *T_{soil}* at 10 cm depth with a Q₁₀ of 3.3 (Least-squares linear regression, *N* = 2432, *R*² = 0.07, *P* < 0.0001, temperature exponent = 0.1204 ± 0.0086 per °C).

Ambient CO₂ concentrations above the forest floor varied significantly with hour-of-day in plantations of each of the study species (GLM (General Linear Modeling procedure), *N* = 398 to 539, χ^2 < 0.0001) and across all species combined (*N* = 2650, χ^2 < 0.0001). Carbon dioxide, presumably from the soil, accumulated on-site when wind speeds (measured in the open) averaged <1 m·s^{−1}, and atmospheric CO₂ typically exceeded 500 μmol·mol^{−1} during the nighttime (Figure 2g). Ambient CO₂ and wind speed (Figure 2h) were strongly negatively correlated (*N* = 2492, *r* = −0.61, *P* < 0.0001), based on wind-speed measurements at the La Selva Biological Station, about 3.5 km from the field plots. Also measured at that weather station, over 2008 through 2010, were solar irradiance and photosynthetic photon flux density (PPFD). During diel measurements of *R_{soil}*, irradiance averaged 551 W·m^{−2} at noon and had a slightly skewed distribution, with slightly more sunlight in the morning than afternoon (Figure 2f). Based on parallel measurements at the same location, photosynthetic photon flux density (PPFD, not shown) was linearly correlated with irradiance according to

$$\text{PPFD } (\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}) = 7.88 + 2.49 \times \text{Irradiance } (\text{W}\cdot\text{m}^{-2}) \quad (1)$$

(Least-squares linear regression, *N* = 1889, *R*² = 0.99, *P* < 0.0001). This suggests that either variable would be equally suitable for predictive modeling. In the current study, stepwise linear regression indicated that the normalized soil CO₂ efflux was negatively related to incident sunlight received two days earlier, and positively related to sunlight received 5.5 days previously:

$$\text{Normalized}[\ln(R_{\text{soil}})] = 1.00 - 0.0000204 \times \text{PPFD}(-2.0 \text{ days}) + 0.0000209 \times \text{PPFD}(-5.5 \text{ days}) \quad (2)$$

(stepwise linear regression, selected for minimum BIC (Bayesian Information Criterion), *N* = 1889, *R*² = 0.02, *P* < 0.0001). The three parameters in this equation were significant at *P* < 0.0001, 0.0015 and 0.0025, respectively. The predictive utility of this relationship is virtually nil, but a 5.5-day lag between photosynthesis and soil-CO₂ emissions is consistent with a 4 to 5 day lag for forest trees [41].

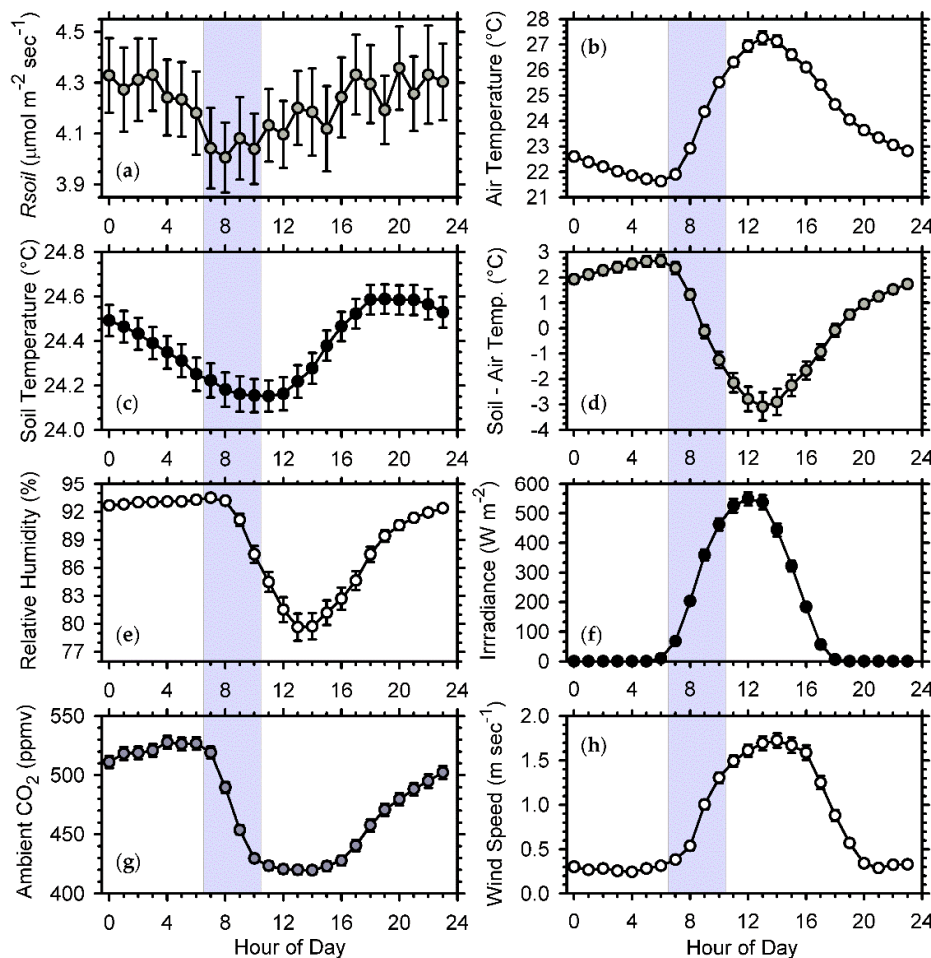
Diel variability in *R_{soil}* and environment

Figure 2. Observed diel variability in (a) soil respiration (*R_{soil}*) was significant, but inconsistent ($R^2 = 0.02$), whereas the variability in potentially controlling environmental variables was pronounced. The shaded hours highlight the period between 06:30 and 10:30 when *R_{soil}* was lowest on average; (b) Mean surface air temperatures; (c) soil temperatures at 10-cm depth; (d) the difference between air and soil temperatures; (e) atmospheric relative humidity and (g) ambient atmospheric CO_2 concentration were all measured in situ, with *R_{soil}*. Shown are means (\pm S.E.) of each variable, based on all diel measurement dates and times; (f) Solar irradiance and (h) mean wind speeds were measured at the La Selva weather station, about 3.5 km from the field sites; the data included here were temporally synchronized with the diel measurements.

3.2. Seasonal Variability in *R_{soil}* and Environment

Soil respiration during across-site surveys ranged from 0.85 to 46.1 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ($N = 4858$). Fluxes varied significantly among species (Kruskal–Wallis $\chi^2 < 0.0001$, Welch's $P < 0.0001$): they were lowest in plantations of *Pinus*, at 3.8 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; and highest in plantations of *Vochysia* spp., at 5.3 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Table 2). Fluxes varied significantly among months in all six plantation types ($N = 274\text{--}1040$, Welch's $P < 0.0001$), consistent with Hypothesis 2. In all six plantation types, *R_{soil}* was highest in either August or September, and lowest in January or February (Table 3, Table S4). That is, there were remarkably consistent seasonal patterns of soil respiration across the six different plantation types.

Table 2. Annual average (± 1 S.E.) rates of daytime soil respiration (R_{soil}) and litterfall in experimental plantations of evergreen trees at La Selva, Costa Rica during this study. Means are weighted by days per month; and standard errors reflect variation among months. Both fluxes varied significantly among the plantation types.

Tree Species	R_{soil} (2004–2010) ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Litterfall (2003–2009) ($\text{g}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)
<i>Hieronyma alchorneoides</i>	4.91 ± 0.64	2.88 ± 0.21
<i>Pentaclethra macroloba</i>	4.15 ± 0.42	2.65 ± 0.17
<i>Pinus patula</i>	3.81 ± 0.84	2.63 ± 0.14
<i>Virola koschnyi</i>	4.08 ± 0.40	2.13 ± 0.09
<i>Vochysia ferruginea</i>	5.26 ± 0.97	3.12 ± 0.17
<i>Vochysia guatemalensis</i>	5.26 ± 0.54	2.69 ± 0.09

Soils were wettest, on average, in November, when 53% of the total soil volume was water, and driest (28%) in April, at the end of La Selva's drier season (Table 3). Soil moisture content varied significantly among months within all six plantation types (Welch's tests, $P < 0.0001$), and the correlation between mean monthly R_{soil} and mean monthly soil moisture content was significantly negative ($N = 72$, Pearson's $r = -0.44$, $P < 0.0001$). Soil temperature also varied significantly among months, based on measurements at both 5-cm and 10-cm depth (Welch's tests, $P < 0.0001$). Soil temperatures were coolest in January or February, and were warmest in August or September, depending upon the depth of measurement. Thus, the seasonality observed in T_{soil} matched that observed in R_{soil} , and soil temperature and R_{soil} correlated positively for most species (Table S6). Incident solar radiation is bimodally distributed at the study site, peaking in April and September each year, with a wintertime minimum (Table 3). Such seasonal variations in climate and microclimate potentially drive seasonal variability in R_{soil} .

Table 3. Mean monthly soil respiration (R_{soil}), soil temperatures (T_{soil}), soil water contents, canopy leaf fall and incident solar radiation across 24 monodominant plantations of six tree species in the Atlantic lowlands of Costa Rica. Not all species were measured over the duration of the study; the mean values for each month were determined from the mean monthly values determined for each species. Soil temperatures refer to 2008–2010, when they were measured at 10 cm depth. Error intervals are ± 1 S.E.

Month	R_{soil} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	T_{soil} ¹ ($^{\circ}\text{C}$)	Soil H_2O ($\text{cm}\cdot\text{m}^{-1}$)	Canopy Leaf Fall ($\text{g}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)	Mean Daily Irradiance ² ($\text{W}\cdot\text{m}^{-2}$)
January	3.67 ± 0.18	21.6 ± 0.04	51.0 ± 1.8	1.41 ± 0.14	177 ± 43
February	3.80 ± 0.27	24.0 ± 0.09	52.0 ± 1.7	1.61 ± 0.17	154 ± 24
March	4.50 ± 0.30	22.8 ± 0.04	38.1 ± 1.0	2.01 ± 0.39	214 ± 24
April	4.73 ± 0.29	24.7 ± 0.04	31.2 ± 2.6	1.24 ± 0.19	272 ± 23
May	4.84 ± 0.30	25.2 ± 0.04	36.3 ± 1.8	1.24 ± 0.15	232 ± 15
June	4.68 ± 0.31	25.4 ± 0.05	38.8 ± 1.6	1.27 ± 0.15	178 ± 16
July	4.31 ± 0.32	25.4 ± 0.03	44.8 ± 2.0	1.29 ± 0.17	187 ± 22
August	4.58 ± 0.49	25.5 ± 0.03	47.6 ± 1.6	1.21 ± 0.15	236 ± 29
September	5.85 ± 0.33	26.1 ± 0.03	38.6 ± 0.9	1.60 ± 0.23	214 ± 26
October	4.97 ± 0.38	25.3 ± 0.03	50.6 ± 1.4	1.78 ± 0.25	193 ± 22
November	4.12 ± 0.33	24.3 ± 0.03	53.5 ± 1.0	1.34 ± 0.22	176 ± 43
December	4.25 ± 0.31	24.0 ± 0.05	52.4 ± 2.3	1.02 ± 0.12	159 ± 22

¹ January 2008 through February 2010; ² on dates of R_{soil} measurements; data courtesy of La Selva Biological Station.

3.3. Litterfall and Leaf Fall

Total fine litterfall over the course of this study ranged from an average of $2.13 \pm 0.09 \text{ g}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in plantations of *Virola* to $3.12 \pm 0.17 \text{ g}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in plantations of *V. ferruginea*. Across all plantation types and years, both total and canopy leaf litter production varied by species, by month, and with a significant species \times month interaction (GLM, $N = 1072$, $\chi^2 < 0.0001$). Canopy leaf fall varied significantly through the year in all species except *Vochysia ferruginea*. Canopy leaves made up an

average of 53% of the total fine litterfall and largely defined the seasonality of leaf fall; other litterfall components were not strongly seasonal. Across all species and plots, canopy leaf fall had a bimodal distribution that enveloped the vernal and autumnal equinoxes (Table 3, Table S7). Contrary to Hypothesis 3, which posited that canopy leaf fall and R_{soil} would be negatively correlated, mean monthly canopy leaf fall and mean monthly R_{soil} were positively correlated (Figure 3, $N = 72$, Pearson's $r = 0.42$, $P < 0.001$).

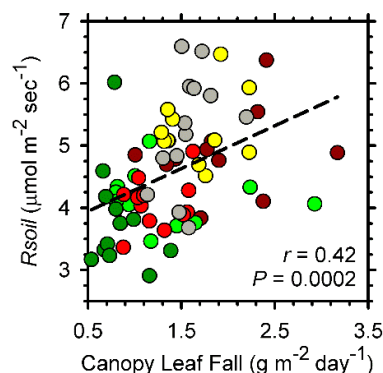


Figure 3. Mean monthly canopy leaf fall and soil respiration (R_{soil}) correlated positively across all plantations studied ($N = 72$, $P = 0.0002$, $r = 0.42$). Symbol colors are as in Figure 1. Each symbol is the mean of all measurements from a particular plantation type and month, from 2004 to 2010.

3.4. Longer-Term Trends in R_{soil}

Soil respiration in plantations of *Heironyma* ($N = 1486$, $\chi^2 < 0.0001$), *Pinus* ($N = 846$, $\chi^2 < 0.001$) and *Virola* ($N = 1493$, $\chi^2 < 0.0004$) increased significantly over the five-year duration of this study, with slopes (\pm SE) of 0.13 ± 0.026 , 0.079 ± 0.028 and $0.054 \pm 0.031 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{year}^{-1}$, respectively (Figure 4). There were no discernible influences of time, across years, on R_{soil} in any of the other plantation types.

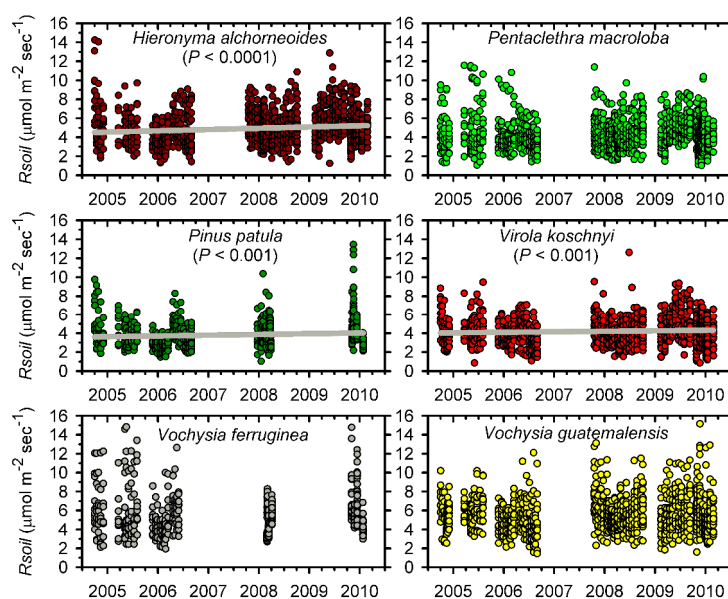


Figure 4. From late 2004 to early 2010, soil respiration (R_{soil}) increased significantly in plantations of *Hieronyma*, *Pinus* and *Virola*, but not in other plantation types. Lines show the least-square regressions of significant relationships; among those three species the rate of increase averaged $0.09 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{year}^{-1}$.

4. Discussion

The spatial variability of *R_{soil}* at the study site was high: coefficients of variation (CV) among fluxes gathered over individual across-site surveys averaged 37% and, in some cases, exceeded 100% (Table S2). Previous studies at this site demonstrated differences in *R_{soil}* among tree species. Those differences have persisted through time. For instance, over 2004–2010, *R_{soil}* in plantations of *Vochysia* spp. averaged 30% greater than emissions in *Virola* plantations (Table 2), as they did after years one [65] and two [53]. Thus, some of the spatial variability encountered during this study resulted directly from the experimental treatment. Temporal variability was significant but somewhat less important quantitatively: CVs of flux measurements from individual chambers that were sequentially monitored every hour at a single location averaged 18% (Table S1). It was apparent in the field, while measurements were being collected, that the activities of fauna, particularly ants, also generated substantial spatial flux variability, as demonstrated elsewhere [69]. Despite this variability, demonstrable differences were apparent.

The principal objective of this study was to characterize temporal variability in *R_{soil}* within evergreen tree plantations in a lowland tropical rainforest environment. Soil respiration varied significantly on diel, monthly and, in three of six species, multi-annual time frames (Figure 2, Table 3 and Figure 4, respectively). Temporal variations in soil respiration have been documented at other sites [38,49,70–72]. They commonly are attributed to temporal variations in plant productivity, or to environmental characteristics such as prevailing temperatures and water availability.

4.1. Diel Variability

The diel variability of *R_{soil}* in this study was not pronounced (Figure 1), but significant differences among hours of the day were observed ($\chi^2 < 0.0001$). Specifically, lower fluxes were observed between 06:30 and 10:30, with sunrise occurring at about 06:00. One important reason for measuring hourly variations in *R_{soil}* is to determine if daytime-only measurements cause bias in the estimation of annual fluxes. In this study, more than 99% of the across-site survey measurements of *R_{soil}* were made between 07:30 and 16:30, over which *R_{soil}* averaged $4.12 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. That value is 2% greater than the morning minima, and 2% lower than the 24-h average flux of $4.21 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, based on hourly measurements. In short, there was no evidence that daytime measurements of soil respiration generated biased estimates of monthly or seasonal soil respiration from the plantations studied, as a result of diel flux variability.

The notable differences between daytime and nighttime ambient conditions in tropical rainforest environments (e.g., Figure 2) provide the opportunity to apply diel measurements to identify environmental controls over *R_{soil}*. In this study, hourly variations in *R_{soil}* correlated with hourly variations in soil temperatures (Figure 5a, $N = 24$, Pearson's $r = 0.82$, $P < 0.0001$), with high probability ($\chi^2 < 0.0001$) but low predictability ($R^2 = 0.02$). This also was true at the monthly scale (Figure 5b, $N = 72$, $r = 0.50$, $P < 0.0001$). Warmer soils had greater *R_{soil}*. This is consistent with our understanding that rates of metabolism and gas diffusion both increase with temperature. Soil respiration also varied with soil water content (Table S5). However, soil moisture content was not monitored continuously during the diel studies, so sample sizes were too low to evaluate meaningfully. Other considered factors did not correlate with *R_{soil}*, including concurrent atmospheric humidity, ambient CO₂ concentrations, the temperature difference between the air and soil, or solar radiation, all of which varied consistently across days (Figure 2).

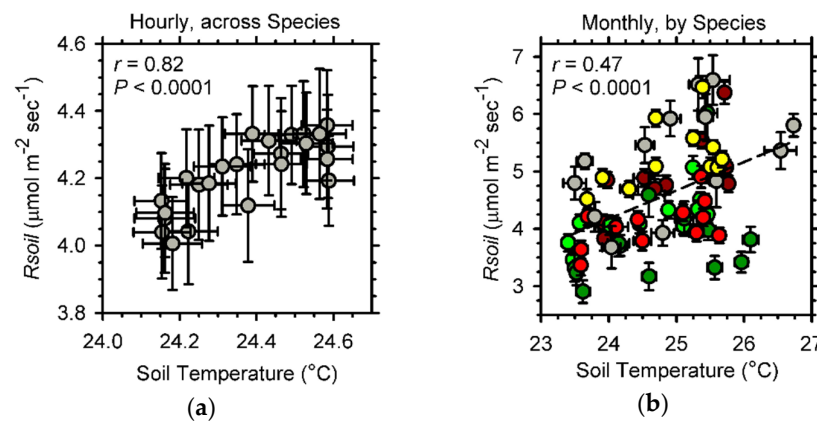


Figure 5. (a) Mean hourly soil respiration (R_{soil}) in relation to mean hourly soil temperature over the course of the diel study ($N = 24$, Pearson $r = 0.82$). (b) Mean monthly soil respiration (R_{soil}) in relation to mean monthly daytime soil temperature for all six species over the course of the across-site survey study ($N = 72$, Pearson's $r = 0.50$). Symbol colors follow Figure 1; error bars show ± 1 S.E.

In contrast to the relatively predictable diel dynamics of many physical factors (Figure 2), precipitation at La Selva occurs at all hours of the day and night (Figure 6). That simple observation may explain the great within-hour variability in CO_2 emissions that was observed (Figure 1). Rainfall during this study averaged $4420 \text{ mm} \cdot \text{year}^{-1}$. Annual canopy interception of rain may be as high as 710 mm [55], and transpiration is perhaps 1500 mm. Every time that 1 cm of rain falls, 442 times a year, about 8 mm of water enters the soil, where it advectively displaces 8 liters per m^{-2} of CO_2 -rich soil atmosphere. The soil atmosphere, in other words, is awash with rainwater, more frequently than it is connected by air-filled pores through which soil gases might continuously diffuse. Every time that 1 cm of soil water is taken up by vegetation and transpired, 150 times each year, 10 liters of atmosphere are pulled into each m^2 of soil, refreshing it with oxygen. Water movement into and out of the soil at La Selva occurs all all hours of the day and, I submit, obfuscates the temperature- and CO_2 -concentration gradient-driven processes that typically control gas diffusion from soils. Carbon dioxide still escapes from the soil, at a very high rate, but likely through advection as frequently as diffusion, and when it can rather than when it is produced. Animal tunnels offer routes of escape.

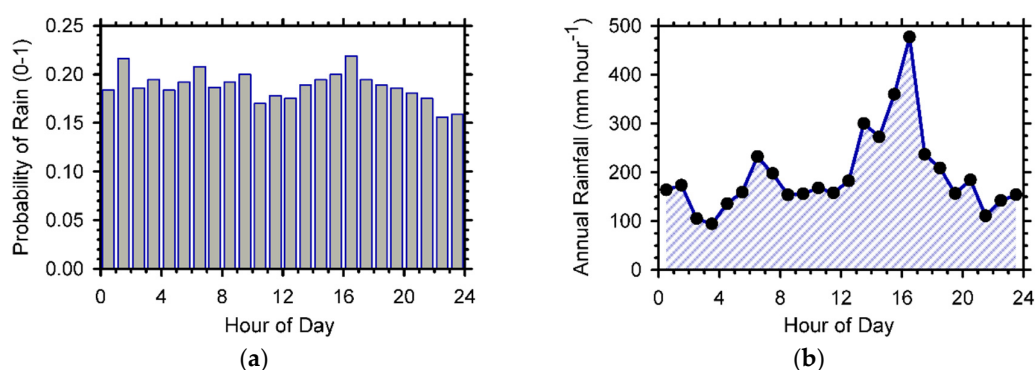


Figure 6. (a) The likelihood that rain will occur within any given hour at La Selva is quite uniform across the day. (b) The amount of rain that falls each hour of the day at La Selva is variable: afternoon showers bring more rain. These figures are based on 2009, a relatively typical year.

Data from the diel study contained evidence of a time lag between PPFD and R_{soil} (Equation (2)). Such a lag is expected [73], if PPFD is a meaningful surrogate for canopy photosynthesis. The estimated time lag between canopy fixation of CO_2 and CO_2 release from soils is 4–5 days for forest trees [41],

but there are few data from tropical forests. Additional studies are required to verify that this result was not a Type 1 statistical error: the model included 30 different time lags for selection; two were found to be highly significant, and of opposite direction.

The time series that emerged from each diel measurement period further provide insight into processes. Across days without rain (Figure 7a,b) there are distinct diel variations in soil temperature that are not necessarily associated with parallel changes in R_{soil} . Figure 7a shows the best example of what predictable diel variability in R_{soil} would look like: peak emissions were offset from peak soil temperatures by about 13 h, and were either 4 h before or 20 h after mid-day. This pattern was not again observed, however. Moderate diel variations in soil temperature in *Pentaclethra* (Figure 7b) did not apparently influence R_{soil} on 28 March. A sharp decline in emissions at 14:00 that coincided with a rainstorm was observed in the time series retrieved from *Virola* (Figure 7c). The time series from *Vochysia guatemalensis* (Figure 7d) shows a typically rainy day. Rain seems to temporarily seal the soil surface with a skin of wet soil, impeding the outward diffusion of CO_2 , but when the rain stops, emissions slowly increase, as the water penetrates the soil. A rainforest is defined by rain and, it seems, so are its soil- CO_2 emission rates.

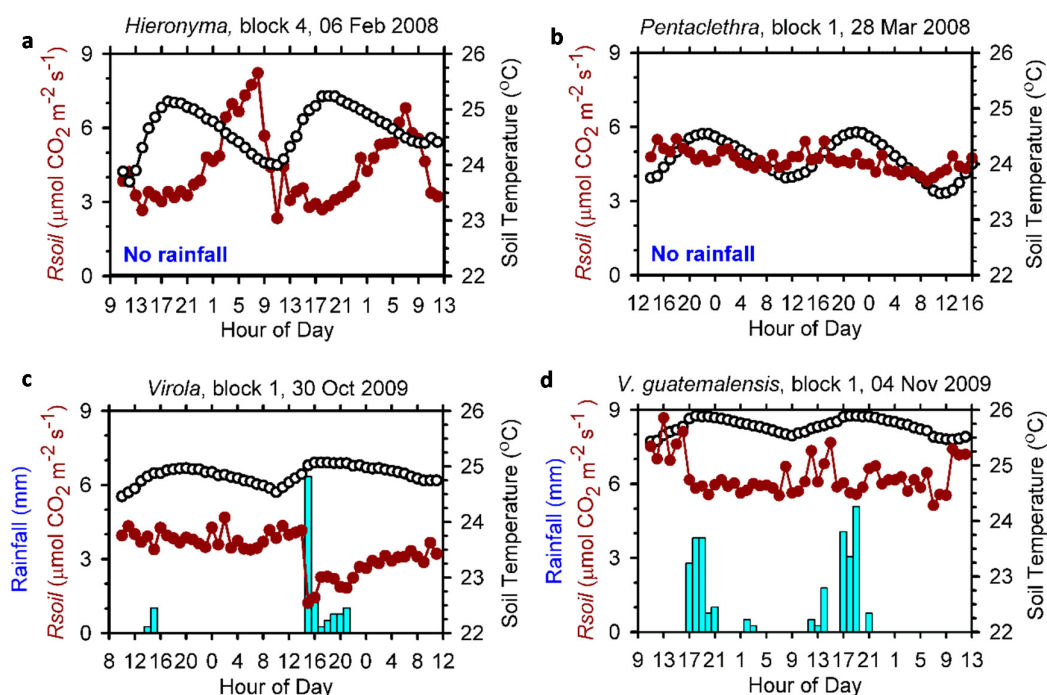


Figure 7. Soil temperatures at 10-cm depth (open symbols), soil respiration (R_{soil} , dark red symbols and lines) and hourly rainfall (blue bars) over 52 continuous hours on different dates in plantations of four different tree species at La Selva. Dates refer to the beginning of the measurement period. (a) *Hieronyma alchorneoides*, in this case, exhibited increasing rates of R_{soil} to morning peaks that were distinctly offset from maximum soil temperatures, on two consecutive rain-free days; (b) *Pentaclethra macroloba* showed no obvious trends in R_{soil} across two consecutive rain-free days, despite obvious variations in soil temperatures; (c) A rainstorm in the early afternoon on day two resulted in a dramatic decline in R_{soil} in a plantation of *Virola koschnyi*. Emissions slowly increased following the rain; (d) A typical day in a plantation of *Vochysia guatemalensis*: rainfall impedes CO_2 escape from the soil, and emissions increase after the rain stops.

4.2. Monthly Variability

Monthly variability in R_{soil} was pronounced: mean soil respiration in September was 60% greater than it was in January (Table 3). Mean monthly fluxes correlated negatively with mean monthly soil moisture content ($N = 71$, Pearson's $r = -0.45$, $P < 0.0001$), demonstrating that R_{soil} was greater in

drier months. Emissions correlated positively with both mean monthly soil temperature (Figure 5b $N = 72$, $r = 0.50$, $P < 0.0001$) and irradiance ($\text{W}\cdot\text{m}^{-2}$) ($N = 72$, $r = 0.29$, $P < 0.02$). Those findings indicate that monthly weather data could be usefully applied to estimate monthly R_{soil} at this site. They do not, however, include any direct information about plant-to-soil carbon fluxes, which fundamentally control the amount of carbon available for respiration.

A specific objective of this study was to seek a plant-growth variable that would provide insight into aboveground–belowground interactions. Hypothesis 3 posited that R_{soil} and canopy leaf flushing would be negatively correlated, if carbon allocation aboveground, for the production of a new crop of leaves, was temporally offset from carbon allocation belowground, to produce fine roots and mycorrhizae. The fall of canopy tree leaves is an indirect measure of the timing of leaf flushing. Across all six plantation types, maximum canopy leaf fall occurred in March, in the dry season, before the coming of more dependable rains in May (Table 3 and Table S7). They also shared a secondary peak of canopy leaf fall in October, before the colder, darker, and wetter winter months set in. Over this study, including all species and blocks, canopy leaf fall and soil respiration were not offset from one another, they paralleled one another ($N = 72$, Pearson's $r = 0.42$, $P = 0.0002$). Fortunately, the phenological characteristics of La Selva's forest trees have been monitored. The number of tree species flushing many new leaves is maximum in February and March, with a secondary peak in September; and the number of species producing mature fruits is maximum in September [74]. Those observations support the inference that March and September are periods of high allocation of carbon to aboveground processes. They are also months having high soil respiration. Thus, the evidence gathered in this study strongly suggests that above- and belowground C use covaried temporally at this site, opposite of the a priori conjecture of Hypothesis 3. More evidence addressing this topic is warranted, but the alternative hypothesis, i.e., that roots and leaves are not competing with one another for photosynthate but, rather, together depend upon recently produced photosynthates, is reasonable and consistent with the data. Covariance between litterfall and soil respiration was previously found in three forest types in subtropical China [49].

4.3. Physical and Biological Factors

Evidence for a significant time lag between irradiance and soil- CO_2 emissions was found (Equation 2), which suggests the possibility of a time lag between canopy photosynthesis and R_{soil} . This finding is uncertain because of the large number of independent variables included in the model, and so deserves to be investigated further. The hypothesis that there would be a trade-off in C use between aboveground and belowground C use was tested and rejected. Positive relationships between soil temperatures and R_{soil} were observed at diel and monthly time steps (Figure 5), and are evident in the entire dataset derived from across-site surveys (Figure 8a). A significantly negative relationship between soil moisture content and R_{soil} was observed at the monthly scale ($r = -0.44$, $P < 0.0001$), which indicates that R_{soil} was greater in drier months. Across all measurements, R_{soil} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) varied non-linearly with surface-soil moisture content (SoilH_2O , $\text{cm}\cdot\text{m}^{-1}$) based on a quadratic polynomial fit:

$$\ln(R_{\text{soil}}) = 2.036 - 0.01075 \times \text{SoilH}_2\text{O} - 0.00037758 \times (\text{SoilH}_2\text{O} - 44.12)^2 \quad (3)$$

(Figure 8b, $N = 4486$, $F_{2,4483} = 415$, $R^2 = 0.16$) with all three parameters being significant at $P < 0.0001$. Relationships between R_{soil} and soil water content were observed for each of the six species, and were non-linear in all cases except for *V. ferruginea* (Table S5). At La Selva, soil respiration was limited by a lack of drier soils. Overall, these data support the conclusion that physical variables—soil moisture content, temperatures, solar radiation—can serve as useful inputs into models that are designed to evaluate the likely directional changes in R_{soil} that would accompany changing climatic conditions. The absolute magnitude of fluxes was species-dependent, however.

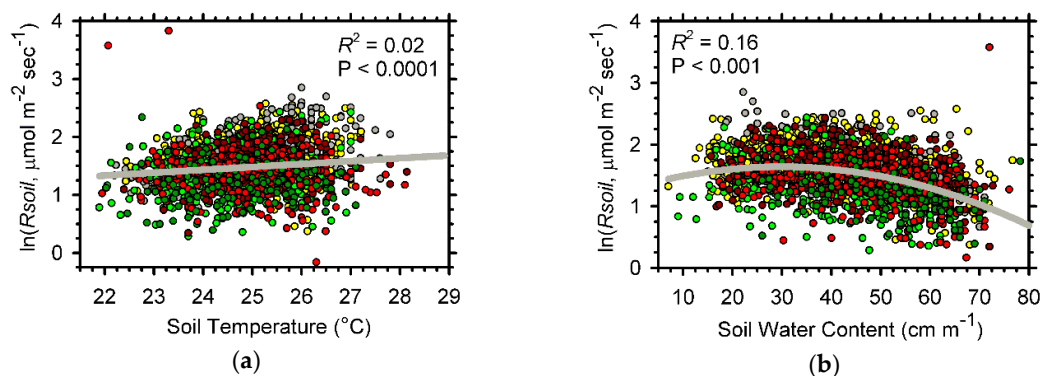


Figure 8. (a) The relationship between log (soil respiration), i.e., $\ln(R_{soil})$, and soil temperature at 5 cm depth was highly significant, signifying an exponential relationship between CO_2 emissions and temperature. Colors follow Figure 1; (b) The relationship between soil moisture content and soil respiration was non-linear (Equation (3)). Both figures include data from all across-site surveys; every other datum is shown to improve legibility.

5. Conclusions

In this study, the different tree plantations varied from 3.8 to 5.3 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in mean annual emissions, i.e., by 40% (Table 2) at one site, with all plots exposed to the same weather and on the same soils. It is frightening to consider the global ramifications. We need to improve our capacity to translate plant (and animal) species effects to broader spatial scales in a way that could inform physical climate models. This study did not provide new insights into that issue.

It is sometimes put forth that modeling R_{soil} is not particularly worthwhile (but see [75]), because R_{soil} derives from different processes that respond differently to environmental conditions [76], and often is considered to be the sum of soil heterotrophic and autotrophic respiration [77]. There is merit in modeling those components, and perhaps others, such as roots as distinct from mycorrhizae, and soil arthropods and annelids as distinct from microbes, but we require all the information we can muster, to broadly advance understanding. The value of soil respiration measurements and models is that they reflect an empirically measurable and important soil-to-atmosphere CO_2 flux. At a minimum, they provide useful information for testing models of subcomponents. The problem with R_{soil} measurements is that they reflect the composite emissions of multiple within-soil CO_2 -producing sources that are individually influenced by multiple environmental factors.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/8/2/40/s1, Table S1: Summary of diel measurements included in this study, Table S2: Summary of across-site survey measurements included in this study, Table S3: Annual climate data for the study site during this study, Table S4: Average soil respiration differed among months within species but in parallel among species, Table S5: Statistical relationships between observed R_{soil} and soil water content based on data from the across-site survey study, Table S6: Linear relationships between observed R_{soil} and soil temperature at 5 cm depth, Table S7: Mean monthly litterfall across 24 monodominant plantations of six tree species in the Atlantic lowlands of Costa Rica [78].

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Conflicts of Interest: The author declares no conflict of interest. The funding agency had no role in the design of the study; in the collection, analyses, or interpretation of data; or in the preparation of the manuscript.

Abbreviations

The following abbreviations are used in this manuscript:

ANOVA	analysis of variance
BIC	Bayesian Information Criterion
CV	coefficient of variation
GLM	general linear modeling statistical procedure
IRGA	infrared gas analyzer
PPFD	photosynthetic photon flux density
<i>R</i> _{soil}	soil respiration
<i>T</i> _{soil}	temperature of the soil

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