Comparison and environmental controls of soil respiration in primary and secondary dry dipterocarp forests in Thailand

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Soil respiration (Rs) in forest ecosystems is an important process in the global carbon cycle. The unbalanced use of forest natural resources and deforestation in the past have resulted in changes in forest structure, tree growth, and the release of carbon dioxide (CO_2) emissions from Rs. Understanding Rs in both primary and secondary forests plays a crucial role in the global carbon cycle. Therefore, the purpose of this study was to estimate and compare Rs in primary dry dipterocarp forests (PDDF) and secondary dry dipterocarp forests (SDDF) in Thailand, in relation to diurnal and seasonal variations in environmental variables (air and soil temperatures, and soil moisture). CO_2 flux was measured continuously from March 2019 to February 2020 in the PDDF and SDDF sites in the Nakhon Ratchasima and Ratchaburi provinces of Thailand. Using the soil gradient method, CO_2 probes were employed to measure average CO_2 concentrations from Rs every minute in the both sites. Additionally, air and soil temperatures and soil moisture were measured continuously to analyze the correlation between Rs and environmental variables. The average annual soil respiration rate in PDDF and SDDF were 8.16 and 8.83 tons C ha^{-1} yr^{-1}, respectively. The diurnal variation of Rs in both sites changed according to air and soil temperatures. The monthly variation of the average Rs was lower in the PDDF site than in the SDDF site. Soil moisture and soil temperature were significantly correlated with the monthly variation of Rs in both sites. Rs in the PDDF and SDDF sites exhibited high emissions during the wet season, accounting for ~61 and 56% of the total annual emissions, respectively. The results indicated that soil and air temperatures were the main drivers of diurnal variation, while the combination of soil moisture and soil and air temperatures determined the seasonal variations. Additionally, litterfall production was the main carbon substrate promoting soil respiration in the SDDF site, as litterfall production was significantly lower in the PDDF site (5.32 tons dry matter ha^{-1} yr^{-1}) than in the SDDF site (10.49 tons dry matter ha^{-1} yr^{-1}).

KEYWORDS

soil respiration, litterfall production, air and soil temperatures, soil moisture, primary and secondary forests, dry dipterocarp forest

Introduction

Soil respiration (R_s) is a critical component of the global carbon cycle, as it represents a major pathway for the release of carbon dioxide (CO_2) from terrestrial ecosystems to the atmosphere (Bond-Lamberty et al., 2024). It is the second largest carbon flux in forest ecosystems, contributing 50–90% of the total ecosystem respiration (Janssens et al., 2001; Chambers et al., 2004; Hanpattanakit et al., 2015), and also is a key process in the global carbon cycle that supplies nutrients to forest ecosystems (Hanpattanakit, 2014). R_s is a combination of autotrophic root respiration and heterotrophic microbial respiration, consists of microbial activity and the respiration of aboveground and belowground litter (Hanpattanakit et al., 2015). Tropical forest ecosystems, which cover approximately 7% of the Earth's land surface, are responsible for a significant portion of global R_s (Hashimoto et al., 2004) and global carbon cycle by storing 45% of global terrestrial carbon stores in vegetation (IPCC, 2007). Plants serve as carbon sinks by accumulating carbon through photosynthesis. Some organic carbon compounds are used to develop biomass, while others are broken down during respiration to supply plants with energy. During this process, CO_2 is released into the atmosphere from ecosystem respiration, deforestation, and animal respiration (Hanpattanakit et al., 2015). Understanding the environmental controls and the spatial and temporal variations of R_s in different forest types is essential for accurately estimating the carbon balance of these important ecosystems and predicting the effects of environmental changes on carbon dynamics (Mavrovic et al., 2023; Shao et al., 2024).

Generally, compared to boreal and temperate forests, tropical forests exhibit higher rates and greater variations in R_s (Raich and Schlesinger, 1992). A study in a temperate coniferous-deciduous forest in Belgium measured the R_s rate of 2.24 kg CO_2 m^{-2} yr^{-1} (Curiel Yuste et al., 2004). The R_s rate was measured at 4.62 kg CO_2 m^{-2} yr^{-1} in dry evergreen forest in Chachoengsao province, Thailand (Wiriyatangsakul et al., 2006) and 3.83 kg CO_2 m^{-2} yr^{-1} in dry dipterocarp forest in Nakhon Ratchasima province, Thailand (Dorji, 2010). By comparing R_s between forest types, previous study of Panuthai et al. (2005) found that the average soil CO_2 emission rate was 4.29 kg CO_2 m^{-2} yr^{-1} in the Sakaerat dry evergreen forest in the Nakhon Ratchasima province of Thailand, compared to 5.07 kg CO_2 m^{-2} yr^{-1} in the Maeklong mixed deciduous forest in the Kanchanaburi province of Thailand. For the primary and secondary forest, Adachi et al. (2006) found R_s rate of tropical primary and secondary forest ecosystems in Pasoh Forest Reserve on the Malaysian Peninsula were 831 ± 480 and 838 ± 143 mg CO_2 m^{-2} h^{-1}. Jiang et al. (2017) reported that the annual total soil C efflux was significantly higher in the tropical primary mountain rain forest (1,567 ± 205 g C m^{-2} yr^{-1}) than that in the secondary forest (1,300 ± 70 g C m^{-2} yr^{-1}, $p < 0.05$). Compared with the primary forest, the secondary forest has a lower biomass, lower soil C storage, lower litter production, and a simpler community structure (Bréchet et al., 2009; Zhou et al., 2013). This indicates that the primary forest has a higher concentration of substrate and higher microbial activity, which leads to a higher R_s rate (Wang et al., 2003). In contrasts, the studied of Wang (2006) in tropical rainforest in Bukit Timah Nature Reserve, Singapore reported that

the R_s rates observed in the secondary forest was higher than that of the primary forest. However, none of the tested factors (soil temperature, soil moisture, diameter of trees at breast height, and canopy cover) were significantly influencing R_s rates. Other factors such as soil organic carbon content and species composition are more important factors influencing spatial variation of R_s between primary and secondary tropical forests (Wang, 2006).

While significant progress has been made in research on R_s in primary and secondary forests few studies have directly compared these two forest types, particularly in the context of tropical dry dipterocarp forests. Which the tropical dry dipterocarp forests are a dominant forest type in mainland Southeast Asia, including Thailand, and are characterized by a pronounced dry season and distinctive tree species composition (Hanpattanakit et al., 2009, 2015). According to the government report, the total coverage area of dry dipterocarp forests in Thailand is estimated at 15,865,260 ha (Royal Forest Department: Ministry of Natural Resources Environment, 2009). The dry dipterocarp forest is the most extensive forest type in Thailand, covering around 13.91% of the total land area of the country (Eiadthong, 2008). These forests play a crucial role in the regional and global carbon cycle, with soil respiration being a significant component of the overall carbon flux (Wangluk et al., 2013). The differences in forest structure, composition, and successional stage can lead to distinct belowground carbon dynamics, potentially resulting in divergent patterns of R_s between primary and secondary forests (Intanil et al., 2018; Raczka et al., 2023).

This study aims to estimate and compare CO_2 emissions from R_s in the primary dry dipterocarp forest (PDDF) and secondary dry dipterocarp forest (SDDF) sites in Thailand, in relation to diurnal and seasonal variations in environmental variables (air and soil temperatures, and soil moisture). We anticipate significant diurnal and seasonal variations in environmental variables, which we expect will influence the rate of CO_2 emissions from soil respiration (Rs). Additionally, we predict that CO_2 emissions will correlate with soil temperature and moisture levels across both forest types. By comparing Rs between primary and secondary dry dipterocarp forests and investigating the influence of environmental factors, we aim to enhance our understanding of the drivers of belowground carbon dynamics in these crucial tropical ecosystems. The findings may also have implications for the management and restoration of the dry dipterocarp forests, which face threats from various anthropogenic disturbances and climate change impact.

Materials and methods

Site description

The primary dry dipterocarp forest (PDDF) in this study was located within the Sakaerat Environmental Research Station, Nakhon Ratchasima province, northeastern Thailand (latitude: 14° 30ı 29.80ıʹ N, longitude: 101° 56ı 58.50ıʹ E, elevation 390 m; Figure 1A). This area is part of the Sakaerat Biosphere Reserve, with a total area of 79.61 km^2 and a the PDDF area of 11.80 km^2 (1,180 ha), accounting for 14.8% of the total area. The average annual precipitation and air temperature over 4-year period (2013–2016)

were 1,260 mm and 20.44°C, respectively (Sakaerat Environmental Research Station, 2018). The average minimum and maximum air temperatures are 21.18 and 30.39°C, respectively. The soil at this site is a sandy loam (Sonkanha et al., 2012). There are approximately 185 tree species and 49 families in this study area. The main tree species are *Shorea obtuse*, *Xylia xylocarpa* var. *Kerrii*, *Pterocarpus macrocarpus*, *Lannea coromandelica*, and *Quercus kerrii* (Kachina, 2018). The main ground cover plant species are *Arundinaria pusilia*, *Arundinaria cililta*, and *Cycas siamensis* Miq. (Sakaerat Environmental Research Station, 2018). The average tree height and circumference were 11.01 m and 39.19 cm, respectively. The tree basal area and density were 16.43 m^2 ha^{-1} and 325 trees ha^{-1}, respectively (Tammadid, 2019).

The secondary dry dipterocarp forest (SDDF) was located within *King Mongkut's University of Technology Thonburi*, Ratchaburi campus, Ratchaburi province, western Thailand (latitude: 13° 35ı 13.3ı' N, longitude: 99° 30ı 3.9ı' E, elevation 110 m; Figure 1B). The SDDF site has a total area of 187.2 ha, which has been preserved since 2005 after the forest was utilized by surrounding communities for energy (wood and charcoal), and building structures (menagerie and hut). As a result, most of the trees are in the recovery phase (Hanpattanakit et al., 2015). From 2011 to 2015, the average annual precipitation was 1,029 mm and the air temperature was 28.46°C. The average minimum and maximum air temperatures are 22.82 and 34.18°C, respectively (Statistical Office of Ratchaburi Province, 2017). The soil texture for the top 100 cm depth at this site is loamy sand soil, with average sand, silt and clay particle contents of 75.79, 20.86, and 3.35% respectively (Hanpattanakit, 2008). Of the ~77 tree species, the main tree species are *Dipterocarpus intricatus*, *Dipterocarpus obtusifolius*, *Dipterocarpus tuberculatus*, *Shorea obtuse*, and *Shorea siamensis*. The main ground cover plant species is *Polyalthia debilis* (Pierre) Finet and Gagnep (Phianchroen et al., 2008). The average tree height and circumference were 8.11 m and 20.48 cm, respectively. The tree basal area and density were 34.32 m^2 ha^{-1} and 2,538 trees ha^{-1}, respectively (Tammadid, 2019). Most plants regenerated after deforestation.

Instrumentation and CO_2 flux calculations

CO_2 flux from R_s was measured using a CO_2 probe (GMP343: Vaisala Inc., Finland) with the soil gradient method. Two CO_2 probes were buried vertically at depths of 5 and 20 cm. The average CO_2 concentrations from the R_s were recorded every minute by a data logger (CR1000: Campbell Scientific, Logan, Utah, USA; Figure 2). The soil CO_2 concentration from R_s in the site was continuously measured from March 2019 to February 2020. The CO_2 concentrations (μmol mol^{-1} or μmol m^{-3}) with environmental variables (air and soil temperatures and soil moisture) were used to calculate the CO_2 flux (μmol m^{-2} s^{-1} or mg CO_2 m^{-2} hr^{-1}) via Equations (1–5) (Tang et al., 2003; Maier and Schack-Kirchner, 2014; Bulsathaporn et al., 2018).

$$F = -D_s \frac{dC}{dZ} \tag{1}$$

where F is the soil CO_2 flux (mg CO_2 m^{-2} hr^{-1}), D_s is the CO_2 diffusion coefficient in the soil (m^2 s^{-1}), $\frac{dC}{dZ}$ is the vertical soil CO_2

gradient, C is the CO_2 concentration (μmol mol^{-1} or μmol m^{-3}), and Z is the soil depth (m).

$$Ds = \xi D_a \tag{2}$$

where D_a is the CO_2 diffusion coefficient in free air (m^2 s^{-1}) and ξ is the gas tortuosity factor.

$$D_a = D_{a0} \left(\frac{T}{293.15} \right)^{1.75} \left(\frac{P}{101.3} \right) \tag{3}$$

where D_{a0} is the reference value of D_a at 20°C (293.15 K) and 101.3 kPa, given as 14.7×10^{-3} m^2 s^{-1}, T is the air temperature (K), and P is the air pressure (kPa). There are several empirical models for computing ξ (Tang et al., 2003) as

$$\xi = \alpha^{10/3}/\varphi^2 \tag{4}$$

where α is the volumetric air content and ϕ is the porosity.

$$\varphi = \alpha + \theta = 1 - \frac{\rho_b}{\rho_m} \tag{5}$$

where θ is the volumetric soil water content, ρ_b is the bulk density (g cm^{-3}) and ρ_m is the particle density of the mineral soil (g cm^{-3}). The bulk density in the PDDF and SDDF sites for calculations were 0.59 and 1.04 g cm^{-3}, respectively. These was measured in January 2019. The particle density in the PDDF site for calculation was 2.73 g cm^{-3}, it measured concurrently with bulk density (Tammadid, 2019). The particle density in the SDDF site was 2.68 g cm^{-3} reference from Bulsathaporn et al. (2018).
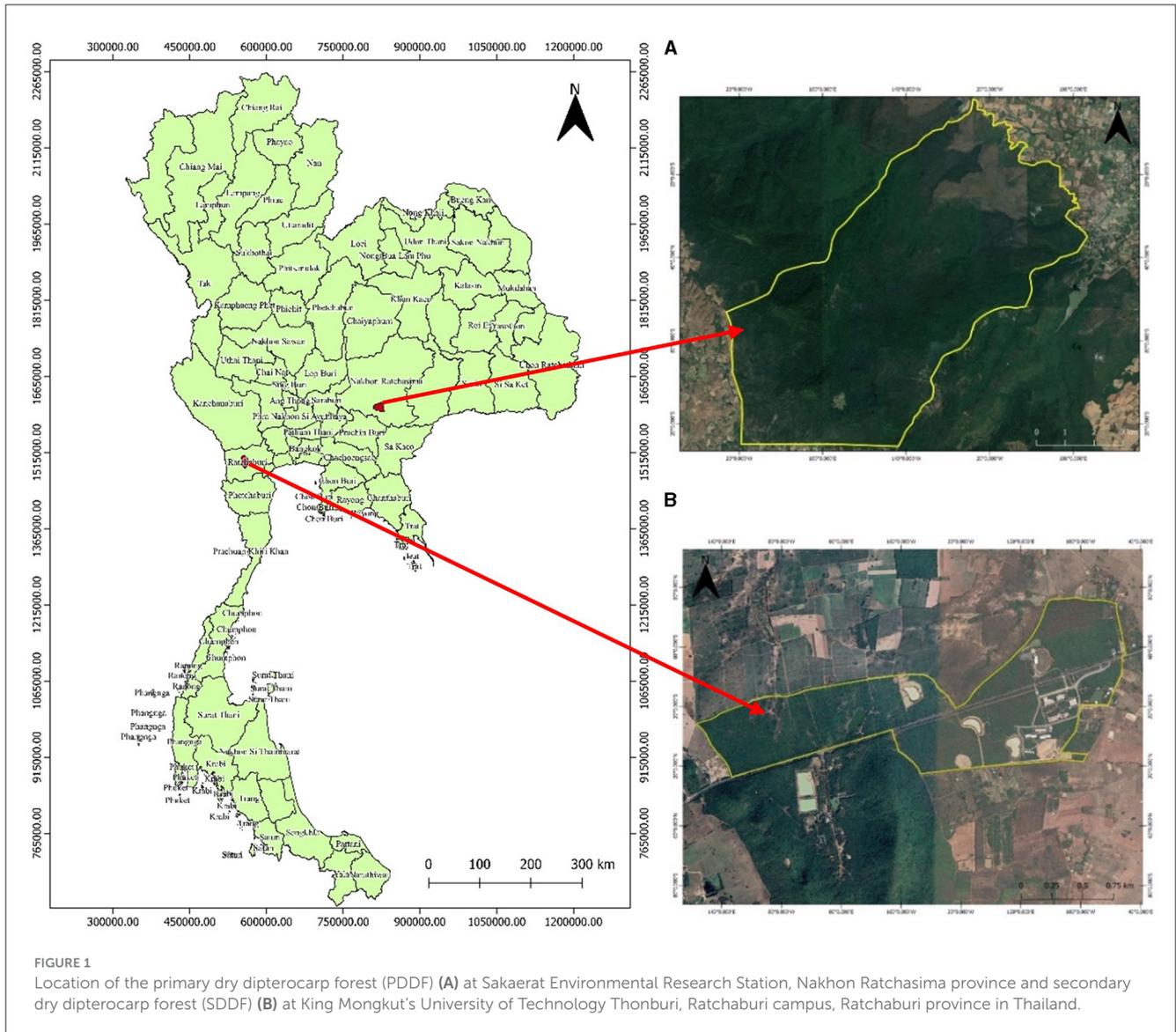
Air and soil temperatures, and soil moisture were measured continuously to analyze the correlation between R_s and environmental variables. Soil temperature and moisture were measured at a depth of 5 cm. Air and soil temperatures were measured using two thermocouple probes per each factor (TCAV, Campbell Scientific, Inc., USA) and soil moisture was measured using two water content reflectometers (CS615, Campbell Scientific, Inc).

Litterfall production

Litterfall production was measured from March 2019 to February 2020 using litter traps. Litter traps consisted of nylon netting and a PVC frame, each 1 m wide x 1 m long, randomly installed 1 m above ground with 12 traps per area in the PDDF and SDDF sites. Litterfall was collected every month and oven-dried at 50°C for 48 h. or until constant weight. The carbon content was calculated using dry biomass multiplied by the carbon content in the biomass analyzed via a CHN analyzer (628 series, LECO Corporation, St Joseph, Michigan, USA).

Soil properties analysis

The soil pH, soil bulk density, soil carbon and nitrogen contents, and soil organic carbon (SOC) were measured. Soil samples were collected from four soil depth levels (0–5, 5–10,

FIGURE 1
Location of the primary dry dipterocarp forest (PDDF) **(A)** at Sakaerat Environmental Research Station, Nakhon Ratchasima province and secondary dry dipterocarp forest (SDDF) **(B)** at King Mongkut's University of Technology Thonburi, Ratchaburi campus, Ratchaburi province in Thailand.

10–15, and 15–20 cm) using a soil core with a 5 cm diameter. The soil pH was analyzed with a pH meter (HI-3220, Hanna Instrument, Inc., USA) with a soil to water ratio of 1:1 (w w^{-1}; Land Development Department, 2004). The soil was oven-dried at 105°C for 48 h and weighed to calculate the bulk density using Equation (6) (Hanpattanakit, 2013). The soil carbon and nitrogen contents were analyzed using a CHN analyzer (628 series, LECO Corporation, St Joseph, Michigan, USA) and the SOC was calculated using Equation (7) (Li et al., 2017).
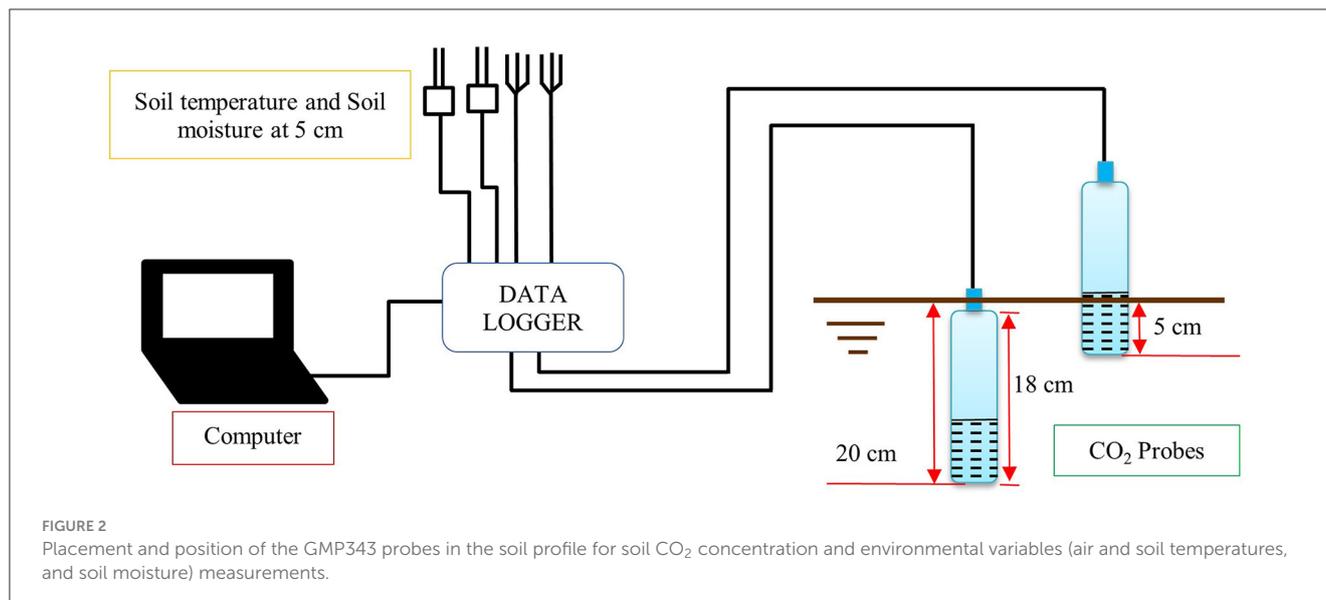
$$Soil\ bulk\ density = \frac{Dry\ weight\ of\ soil\ (g)}{Total\ volume\ of\ soil\ (cm^3)} \qquad (6)$$

$$SOC = C \times BD \times D \qquad (7)$$

where SOC is the soil organic carbon (g cm^{-2}), C is the soil carbon content (%), BD is the soil bulk density (g cm^{-3}), and D is the soil depth (cm).

Data analysis

CO$_2$ emissions from R$_s$, litterfall production, soil properties, air and soil temperatures, and soil moisture in the PDDF and SDDF sites were statistically compared via one-way analysis of variance (ANOVA), facilitating the evaluation of mean differences among the various groups. This statistical approach served to ascertain the presence of significant disparities in CO$_2$ emissions between the season and forest sites. The seasonal variation of R$_s$ in the PDDF and SDDF sites was divided into changes during the dry season (November to April) and the wet season (May to October). In the dry season, the seasonal variation in daily R$_s$ averaged from 136 and 169 days in the PDDF and SDDF sites, respectively. Then in the wet season, the seasonal variation in daily R$_s$ averaged from 170 and 184 days in the PDDF and SDDF sites, respectively. The relationships between diurnal and daily variation in the R$_s$ and, air and soil temperatures, and soil moisture, and the relationships between monthly variation in the R$_s$ and litterfall production, air and soil temperatures, and soil moisture in both sites were determined via

FIGURE 2
Placement and position of the GMP343 probes in the soil profile for soil CO_2 concentration and environmental variables (air and soil temperatures, and soil moisture) measurements.

TABLE 1 Soil properties in primary dry dipterocarp forest (PDDF) and secondary dry dipterocarp forest (SDDF).

Soil depth (cm)	PDDF				SDDF			
	pH	Bulk density (g m^{-3})	Carbon content (%)	Nitrogen content (%)	pH	Bulk density (g m^{-3})	Carbon content (%)	Nitrogen content (%)
0–5	4.46[A]	0.55[A]	1.56[A]	0.13[A]	5.53[B]	1.05[B]	0.38[B]	0.05[B]
5–10	4.73[A]	0.58[A]	1.33[A]	0.12[A]	4.78[B]	0.95[B]	0.27[B]	0.03[B]
10–15	4.44[A]	0.60[A]	1.34[A]	0.10[A]	5.38[B]	1.03[B]	0.24[B]	0.03[B]
15–20	4.52[A]	0.63[A]	1.17[A]	0.10[A]	4.89[B]	1.12[B]	0.21[B]	0.03[B]
Average	4.54[A]	0.59[A]	1.35[A]	0.11[A]	5.15[B]	1.04[B]	0.27[B]	0.03[B]

Means with different letters are significantly different (p < 0.05) between the PDDF and SDDF sites within the soil depth.

Pearson's correlation analysis and simple linear regression analysis (R^2-value). In addition, the multiple relationships between daily variation in the R_s with air and soil temperature, and soil moisture were determined via the multiple linear regression analysis. The statistical analyses were conducted Statistical Package for the Social Sciences (SPSS) program version 17.0 for Windows (IBM Crop., Armonk, N.Y. USA), at a confidence level 95 and 99% ($p < 0.05$ and $p < 0.01$).

Results

Soil properties, environmental variables and litterfall production

In the PDDF site, the soil was acidic, with a pH range of 4.44–4.73 and an average of 4.54. The soil bulk density ranged from 0.55 to 0.63 g cm^{-3}, with an average of 0.59 g cm^{-3}. The carbon content range about 1.17–1.56%, an average around 1.35% and nitrogen content 0.10–0.13%, an average about 0.11% (Table 1). Soil organic carbon (SOC) ranged 3.70–4.29 tons C ha^{-1}, an average and total organic carbon in the soil were 3.98–15.91 tons C ha^{-1}

TABLE 2 Soil organic carbon content in primary dry dipterocarp forest (PDDF) and secondary dry dipterocarp forest (SDDF).

Soil depth (cm)	PDDF (tons C ha^{-1})	SDDF (tons C ha^{-1})
0–5	4.29 (±0.10)[A]	1.99 (±0.07)[B]
5–10	3.89 (±0.12)[A]	1.29 (±0.07)[B]
10–15	4.03 (±0.26)[A]	1.24 (±0.00)[B]
15–20	3.70 (±0.27)[A]	1.15 (±0.04)[B]
Average	3.98 (±0.19)[A]	1.42 (±0.05)[B]
Total	15.91[A]	5.67[B]

Means with different letters are significantly different (p < 0.05) between the PDDF and SDDF sites with in the soil depth.

at the 4 soil depth levels in the PDDF site (Table 2). The range of the air temperatures was ∼20.96–30.40 and soil temperatures range was ∼20.86–29.72°C, between March-2019 to February-2020. The average annual air temperatures were 28.48°C. The maximum average was 31.38°C in March-2019 and minimum in December-2019 was 24.03°C. The average annual soil temperatures

were 26.08°C. The maximum average was 28.27°C in March-2019 and minimum in December-2019 was 22.82°C. The soil moisture contain range was ∼38.48–53.65% water-filled pore space (WFPS) The average annual soil moisture was 43.02% WFPS. The maximum average was 48.62% in September-2019 and minimum in February-2020 was 39.24% WFPS at the PDDF site (Figure 3A). The litterfall production was highest in January 2020 and lowest in December 2019. The total litterfall production averaged 5.32 tons dry matter ha^{-1} yr^{-1}, the most of which was leaves with an average of 2.98 tons dry matter ha^{-1} yr^{-1}, followed by other parts and branches with averages of 1.23–1.11 tons dry matter ha^{-1} yr^{-1} at the PDDF site (Figure 4).

While in the SDDF site, the soil was slightly less acidic, with a pH ranged of 4.78–5.53 and an average of 5.15. Soil bulk density ranged from 0.95 to 1.12 g cm^{-3}, with an average of 1.04 g cm^{-3}. The carbon content range about 0.21–0.38%, an average around 0.27%, and nitrogen content 0.03–0.05%, an average about 0.03% (Table 1). The soil organic carbon (SOC) ranged from 1.15 to 1.99 tons C ha^{-1}, with average and total organic carbon of 1.42–5.67 tons C ha^{-1} at the 4 soil depth levels (Table 2). The range of the air temperatures was around 24.00–42.17 and the soil temperatures range was about 21.57–31.53°C, between March-2019 to February-2020. The average annual air temperatures were 32.80°C. The monthly maximum average was 38.38°C in April-2019 and minimum in December-2019 was 28.67°C. The average annual soil temperatures were 27.39°C. The monthly maximum average was 29.83°C in April-2019 and minimum in December-2019 was 24.62°C. The soil moisture contain range was ∼24.08–31.82% WFPS. The average annual soil moisture was 26.09% WFPS. The monthly maximum average was 28.72% in October-2019 and minimum in March-2019 was 24.16% WFPS at the SDDF site (Figure 3B). The litterfall production was highest in January 2020 and lowest in November 2019. The total litterfall production averaged 10.49 tons dry matter ha^{-1} yr^{-1}, the most of which was leaves with an average of 7.89 tons dry matter ha^{-1} yr^{-1}, followed by branches and other parts, with averages of 1.75 and 0.85 tons dry matter ha^{-1} yr^{-1} in the SDDF site (Figure 4).

Moreover, the SOC decreased with increasing soil depth and was significantly greater in the PDDF site than in SDDF site ($p<0.05$). The air and soil temperatures were significantly lower in the PDDF site than in the SDDF site and soil moisture was significantly greater in the PDDF site than in the SDDF site ($p < 0.05$). Litterfall production was significantly lower in the PDDF site than in the SDDF site ($p < 0.05$).

Soil respiration

Diurnal variation

The diurnal variation of the CO_2 flux from R_s in both the PDDF and SDDF sites were measured and compared between the dry (March 2019) and wet (May 2019) seasons from an average of 5 consecutive days. The diurnal variation of R_s clearly changed according to the air and soil temperatures, but soil moisture was relatively stable during all days. The diurnal average R_s in the dry season in the PDDF site was 315.57 mg CO_2 m^{-2} hr^{-1}, with a maximum was 350.03 mg CO_2 m^{-2} hr^{-1} (0.00 hour), and a

minimum was 265.49 mg CO_2 m^{-2} hr^{-1} (23.00 h; Figure 5A). In the wet season, the diurnal average R_s at the PDDF site was 449.04 mg CO_2 m^{-2} hr^{-1}, with a maximum was 471.65 mg CO_2 m^{-2} hr^{-1} (14.00 h), and a minimum was 422.93 mg CO_2 m^{-2} hr^{-1} (9.00 h; Figure 5B). At the SDDF site, the diurnal average R_s in the dry season was 217.36 mg CO_2 m^{-2} hr^{-1}, with a maximum was 244.11 mg CO_2 m^{-2} hr^{-1} (22.00 h), and a minimum was 162.64 mg CO_2 m^{-2} hr^{-1} (14.00 h; Figure 5C). The diurnal average R_s in the wet season was 475.98 mg CO_2 m^{-2} hr^{-1}, with a maximum was 501.98 mg CO_2 m^{-2} hr^{-1} (2.00 h), and a minimum was 454.35 mg CO_2 m^{-2} hr^{-1} (11.00 h; Figure 5D).

The diurnal CO_2 flux from R_s in the PDDF and SDDF sites was significantly lower in the dry season than in the wet season ($p < 0.05$). The diurnal variations of R_s in the PDDF site in the dry season exhibited significant positive correlations with air ($R^2 = 0.6114$) and soil temperatures ($R^2 = 0.6299$), and soil moisture ($R^2 = 0.6239$; $p < 0.05$; Figures 6A–C). In the wet season, R_s was significantly positively correlated with air ($R^2 = 0.7714$) and soil temperatures ($R^2 = 0.7088$; $p < 0.05$; Figures 6D–F). The diurnal variations of R_s in the SDDF site in the dry season showed a significant negative correlation with air ($R^2 = 0.7995$) and soil temperatures ($R^2 = 0.8075$), and a significant positive correlation with soil moisture ($R^2 = 0.5651$; $p < 0.05$; Figures 6A–C). In the wet season, R_s was significantly negatively correlated with soil temperature ($R^2 = 0.6452$; $p < 0.05$; Figures 6D–F).

Seasonal variation

The seasonal variation of CO_2 flux from R_s changed according to soil moisture. R_s gradually increased from the beginning of the wet season to the end of the wet season and gradually decreased from the end of the wet season to the dry season. The daily average R_s in the dry and wet seasons at the PDDF site were 309.39 and 391.92 mg CO_2 m^{-2} hr^{-1}, respectively, accounting for 39% of the total R_s in the dry season and 61% of the total R_s in the wet season. At the SDDF site, the daily average R_s in the dry and wet seasons were 338.84 and 402.92 mg CO_2 m^{-2} hr^{-1}, respectively, accounting for 44% of the total R_s in the dry season and 56% of the total R_s in the wet season (Figure 7). The monthly average R_s in the dry and wet seasons at the PDDF site were 307.26 and 389.20 mg CO_2 m^{-2} hr^{-1}, respectively, while at the SDDF site, they were 337.73 and 402.91 mg CO_2 m^{-2} hr^{-1}, respectively. R_s was significantly lower in the dry season than in the wet season at both the PDDF and SDDF sites ($p < 0.05$). Additionally, R_s in the dry season was significantly lower at the PDDF site compared to the SDDF site ($p < 0.05$).

The correlation between the seasonal variation of R_s and three factors—air temperature (AT), soil temperature (ST), and soil moisture (SM)—at the PDDF and SDDF sites was analyzed using multiple linear regression analysis. The results found that R_s in the dry season at both the PDDF and SDDF sites was significantly positively correlated with soil moisture and soil temperature, and significantly negatively correlated with air temperature ($R^2 = 0.50$ and 0.53; $p < 0.01$). The multiple linear regression equations were as follows: R_s in the dry season (PDDF) $= -1.3(AT) + 5.66(ST) + 16.14(SM) - 463.98$, and R_s in the dry season (SDDF) $= -4.94(AT) + 3(ST) + 19.49(SM) - 66.44$, respectively. In the wet
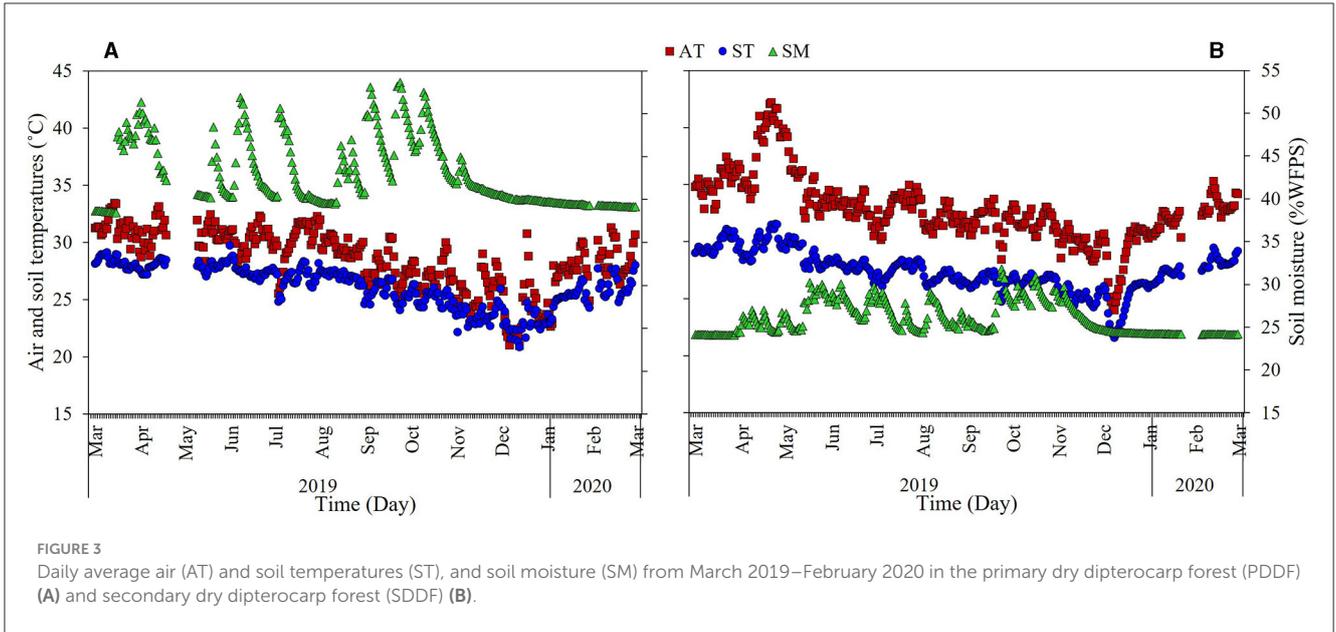
FIGURE 3
Daily average air (AT) and soil temperatures (ST), and soil moisture (SM) from March 2019–February 2020 in the primary dry dipterocarp forest (PDDF) **(A)** and secondary dry dipterocarp forest (SDDF) **(B)**.
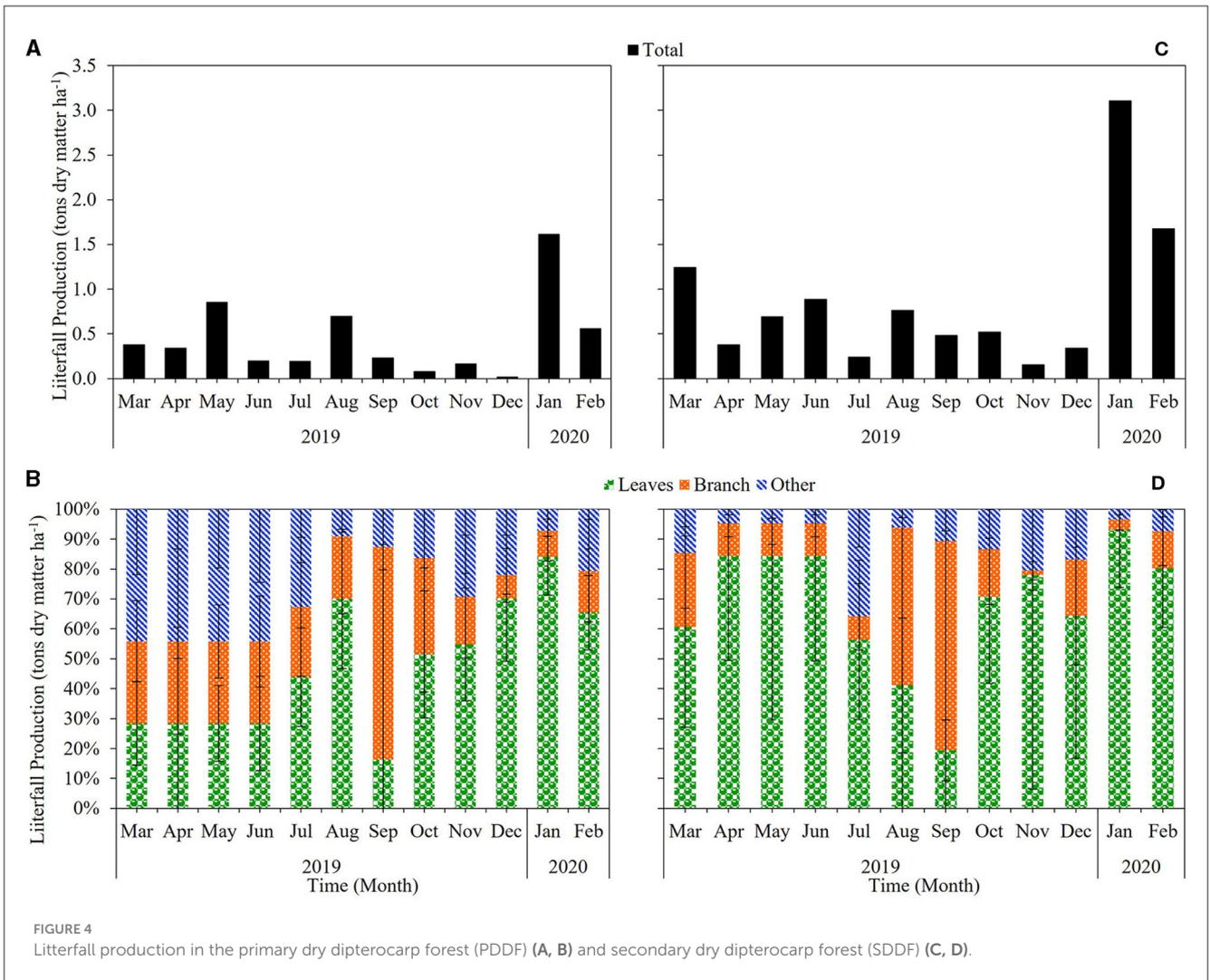

FIGURE 4
Litterfall production in the primary dry dipterocarp forest (PDDF) **(A, B)** and secondary dry dipterocarp forest (SDDF) **(C, D)**.
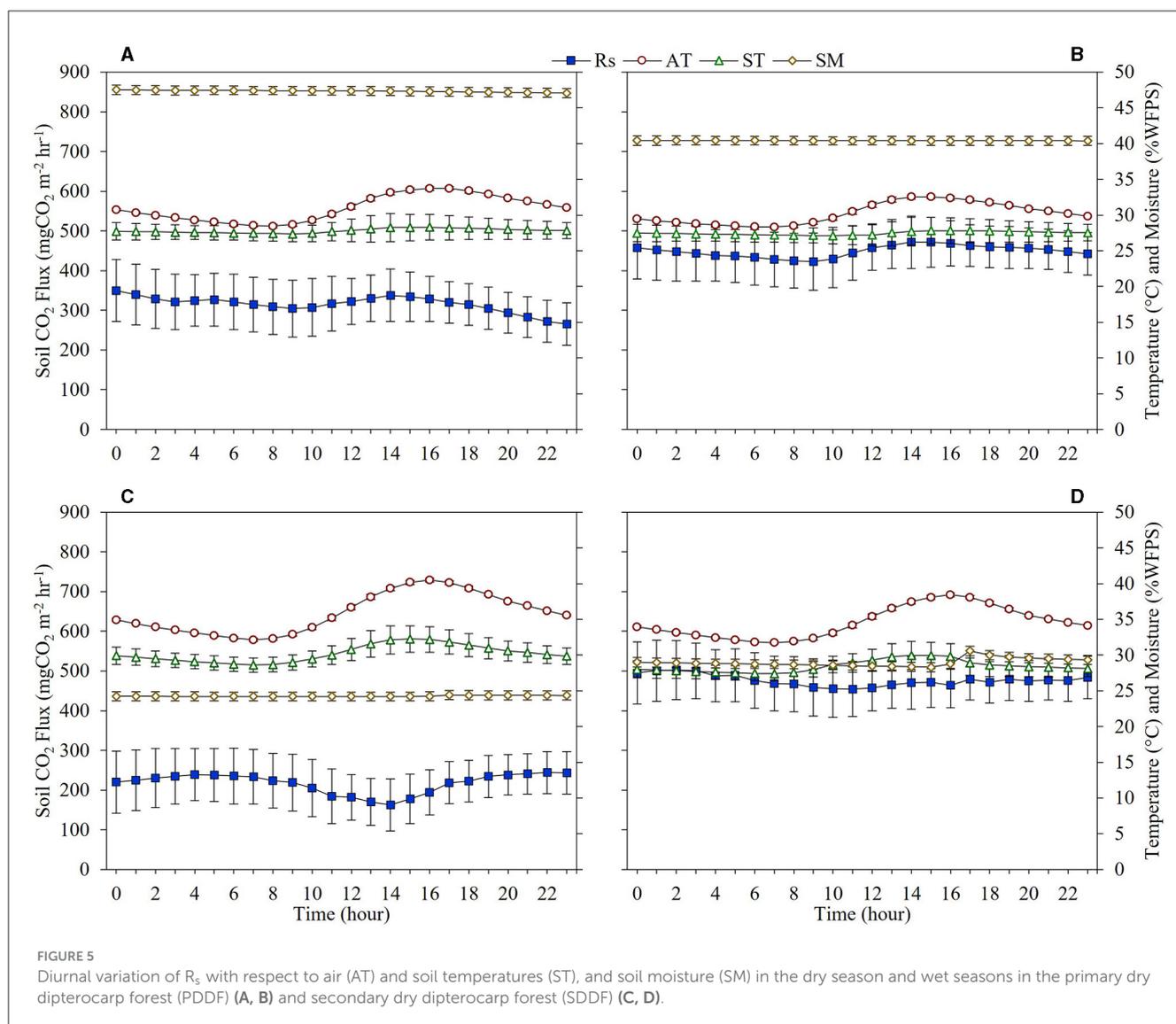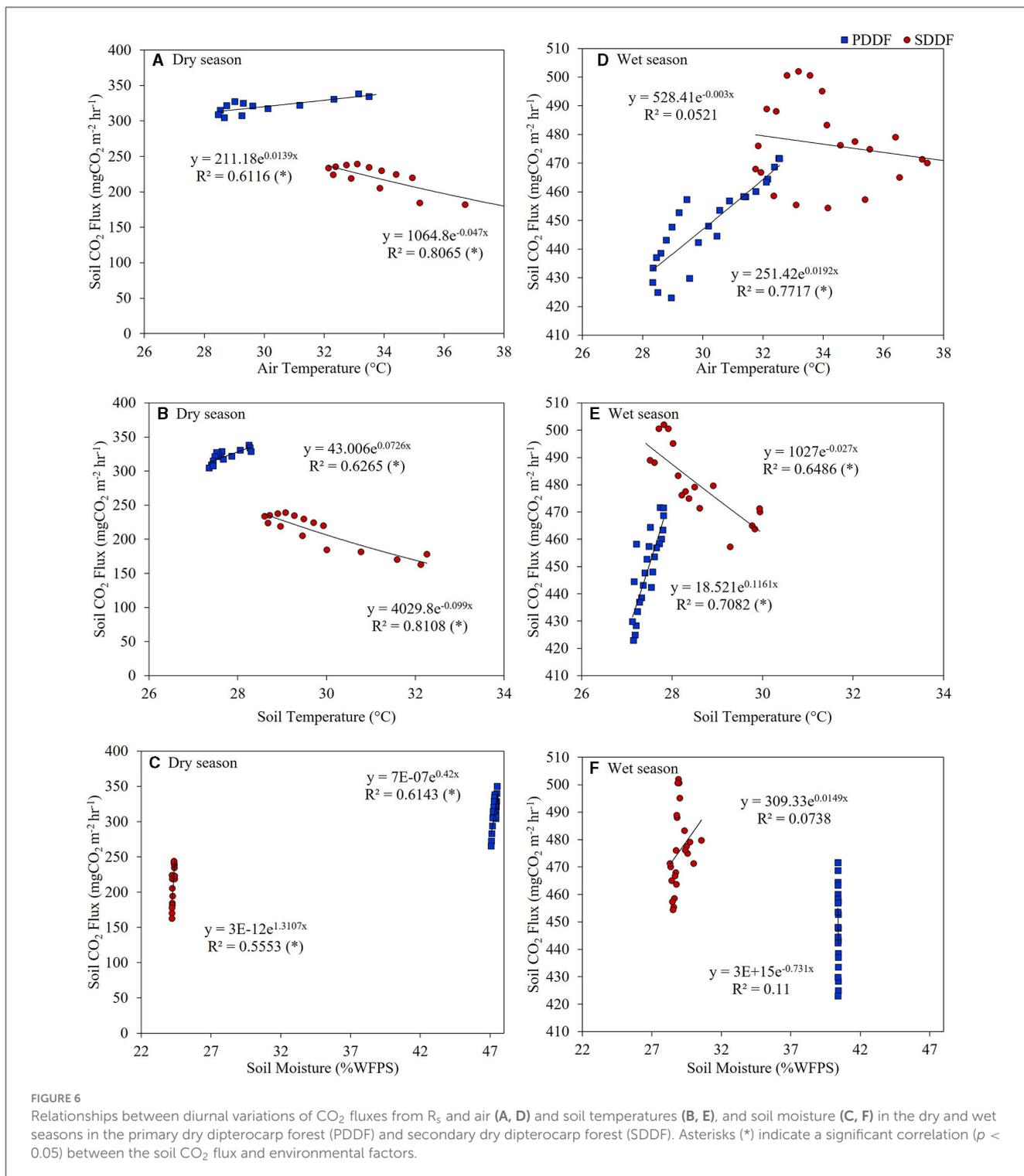
FIGURE 5
Diurnal variation of R_s with respect to air (AT) and soil temperatures (ST), and soil moisture (SM) in the dry season and wet seasons in the primary dry dipterocarp forest (PDDF) **(A, B)** and secondary dry dipterocarp forest (SDDF) **(C, D)**.

season at the PDDF site, R_s was significantly positively correlated with soil moisture and soil temperature ($R^2 = 0.50$; $p < 0.01$), with the following equation: R_s in the wet season (PDDF) = 3.88(ST) + 16.18(SM) – 458.44. At the SDDF site in the wet season, R_s was significantly positively correlated with soil moisture, and significantly negatively correlated with air temperature and soil temperature ($R^2 = 0.27$; $p < 0.01$), with the following equation: R_s in the wet season (SDDF) = −0.18(AT) – 13.26(ST) + 13.91(SM) – 393.90 (Table 3).

The daily variation of R_s at the PDDF and SDDF sites ranged from 207.87 to 593.12 mg CO_2 m^{-2} hr^{-1} and 211.63 to 557.05 mg CO_2 m^{-2} hr^{-1}, respectively. The monthly average R_s at the PDDF site was 348.23 mg CO_2 m^{-2} hr^{-1}, with a monthly maximum in September (422.50 mg CO_2 m^{-2} hr^{-1}) and a minimum in February (241.36 mg CO_2 m^{-2} hr^{-1}). The monthly variations of R_s at the PDDF and SDDF sites were significantly positively correlated with soil moisture ($R^2 = 0.62$ and 0.84, respectively) and significantly negatively correlated with litterfall production ($R^2 = -0.59$ and -0.61, respectively; Table 4). These results indicate

that soil moisture and litterfall production drive CO_2 emissions in forest ecosystems and are the main factors influencing R_s in terms of the monthly variation of CO_2 flux at both the PDDF and SDDF sites. However, the yearly variation (January to December) of R_s at the PDDF site was significantly positively correlated with air temperature, soil temperature, and soil moisture ($R^2 = 0.62$; $p < 0.01$), as follows: Yearly R_s (PDDF) = 3.51(AT) + 9.84(ST) + 10.88(SM) – 473.98. At the SDDF site, the yearly variation of R_s was positively correlated with soil moisture and soil temperature, and significantly negatively correlated with air temperature ($R^2 = 0.62$; $p < 0.01$), as follows: Yearly R_s (SDDF) = −0.10(AT) – 4.28(ST) + 19.07(SM) – 5.03 (Table 3). These results indicate that air temperature, soil temperature, and soil moisture were the drivers of R_s at the PDDF and SDDF sites, with soil moisture having a particularly strong effect and being the main factor influencing R_s in terms of monthly, seasonal, and yearly variation of CO_2 flux at both sites.

Moreover, the CO_2 flux from R_s was lower at the PDDF site than at the SDDF site. In particular, the diurnal and daily CO_2

FIGURE 6
Relationships between diurnal variations of CO_2 fluxes from R_s and air **(A, D)** and soil temperatures **(B, E)**, and soil moisture **(C, F)** in the dry and wet seasons in the primary dry dipterocarp forest (PDDF) and secondary dry dipterocarp forest (SDDF). Asterisks (*) indicate a significant correlation ($p <$ 0.05) between the soil CO_2 flux and environmental factors.

fluxes from R_s at the PDDF site were significantly lower than those at the SDDF site ($p < 0.05$). The differences in R_s between the sites were driven by variations in air and soil temperatures, soil moisture, and litterfall production. Air and soil temperatures were significantly lower at the PDDF site than at the SDDF site, while soil moisture was significantly higher at the PDDF site than at the SDDF site ($p < 0.05$). Additionally, litterfall production was significantly lower at the PDDF site than at the SDDF site ($p < 0.05$). As a result, the cumulative annual CO_2 flux from R_s at the PDDF site (2.99 kg

CO_2 m^{-2} yr^{-1} or 8.16 tons C ha^{-1} yr^{-1}) was lower than at the SDDF site (3.24 kg CO_2 m^{-2} yr^{-1} or 8.83 tons C ha^{-1} yr^{-1}).

Discussion

The soil temperature is directly proportional to elevation and inversely proportional to precipitation and moisture (Zhang et al., 2022). The soil temperature decreases with increasing

FIGURE 7
Average daily of CO_2 flux from R_s in the primary dry dipterocarp forest (PDDF) and secondary dry dipterocarp forest (SDDF) during March 2019–February 2020.
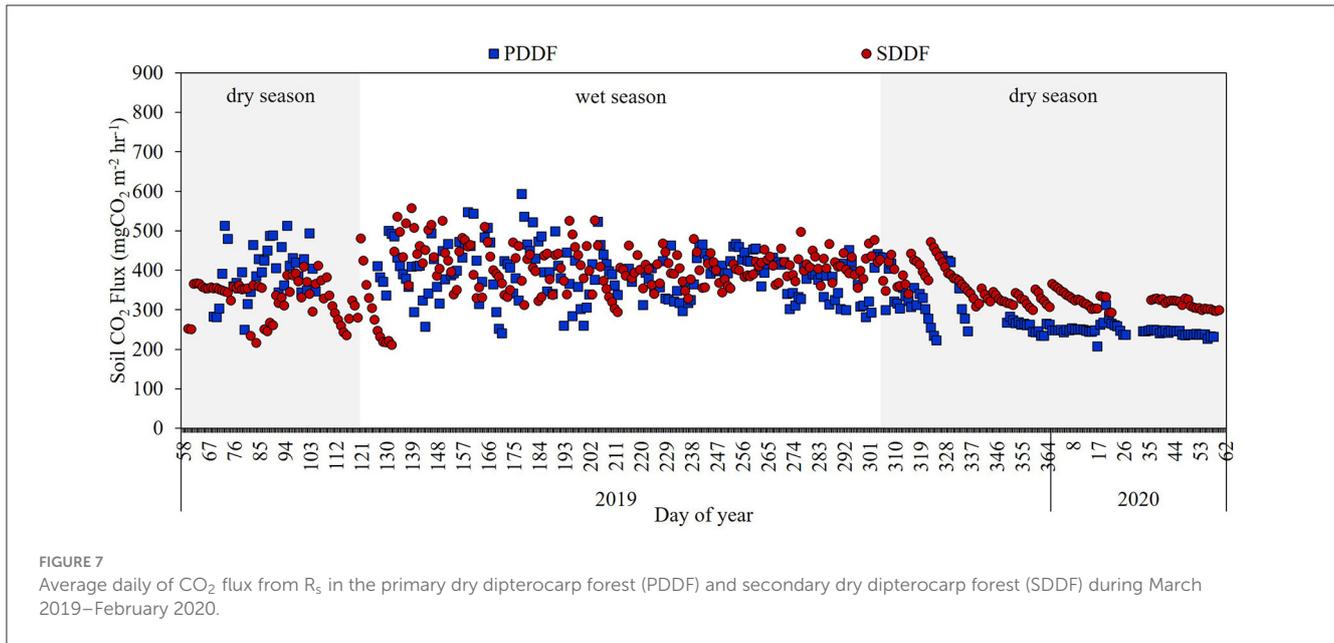
TABLE 3 The multiple regression in seasonal variation in primary dry dipterocarp forest (PDDF) and secondary dry dipterocarp forest (SDDF).

Type of forest	Dry season	Wet season	Yearly variation
	November to April	May to October	January to December
PDDF	$R_s = -1.3(TA) + 5.66(TS) + 16.14(SM) - 463.98$	$R_s = 3.88(TS) + 16.18(SM) - 458.44$	$R_s = 3.51(TA) + 9.84(TS) + 10.88(SM) - 473.98$
	$R^2 = 0.50, p < 0.01$	$R^2 = 0.50, p < 0.01$	$R^2 = 0.62, p < 0.01$
SDDF	$R_s = -4.94(TA) + 3(TS) + 19.49(SM) - 66.44$	$R_s = -0.18(TA) - 13.26(TS) + 13.91(SM) - 393.90$	$R_s = -0.10(TA) - 4.28(TS) + 19.07(SM) - 5.03$
	$R^2 = 0.53, p < 0.01$	$R^2 = 0.27, p < 0.01$	$R^2 = 0.62, p < 0.01$

latitude (Edith and Charles, 1931). The average rate at which air temperature changes with increasing altitude or a rising parcel of air (environmental lapse rate) is a decreased of by ~6.5°C km^{-1}, but this rate varies in different regions, airstreams, and seasons (Storm, 2008). Air and soil temperatures were lower in the PDDF site compared to the SDDF site, and soil moisture was greater in the PDDF site than in the SDDF site, due to differences in latitude, elevation, and precipitation. The low air and soil temperatures and high soil moisture in the wet season stimulate the activity of microbes and plant roots in the soil to increase CO_2 flux from R_s (Broken et al., 1999). The diurnal CO_2 flux from R_s was significantly lower in the dry season than in the wet season due to greater air and soil temperatures and lower soil moisture in the dry season (Medina and Zelwer, 1972). The diurnal pattern of R_s consisted of a gradual increase in the morning and a gradual decrease at night (after midnight; Intanil, 2017). The CO_2 flux from R_s is greater in the wet season than in the dry season because the rapid increase in soil temperature in the wet season promotes root and microbial activities (Hanpattanakit et al., 2015; Hanpattanakita et al., 2021).

Soils in tropical forests are generally acidic (Suwanprapa, 2014). Topsoil (0–5 cm) has the lowest bulk density, which increases with depth due to the accumulation of organic matter from litterfall, minerals, and organic carbon in the topsoil (Kookkhunthod et al.,

2018). Subsoil has less organic matter, is more compacted, and has smaller pores, which increases the bulk density of the subsoil (Wongtangprasert, 2015). SOC was significantly greater in the PDDF site than in the SDDF site ($p < 0.05$). The soil structure and SOC can be changed by disturbance (e.g., land-use change, and deforestation), which could help explain the difference between the PDDF and SDDF sites (Wigginton et al., 2000). The PDDF site experienced less disturbance and land-use change than in the SDDF site, which would affect forest structure, resulting in SOC and nutrients that would remain stable or change slowly.

Litterfall production was positively correlated with soil temperature and negatively correlated with soil moisture (Hanpattanakit and Chidthaisong, 2012). Litterfall production was lower in the PDDF site compared to the SDDF site, due to the lower density of trees in the PDDF site than in the SDDF site (Wongtangprasert, 2015; Kookkhunthod et al., 2018; Zhang et al., 2022). The lower soil temperature and higher soil moisture in the PDDF site is resulted in lower litterfall production in the PDDF site than in the SDDF site (Hanpattanakit and Chidthaisong, 2012). R_s was determined by litterfall production in terms of the monthly variation in both the PDDF and SDDF sites. R_s was negatively related to litterfall production at both sites ($p < 0.05$; Table 4). Normally, foliage and litterfall in dry dipterocarp forest were

TABLE 4 Pearson's correlation matrix between the monthly average of R_s, litterfall production, air and soil temperatures, and soil moisture in primary dry dipterocarp forest (PDDF) and secondary dry dipterocarp forest (SDDF).

	R_s	AT	ST	SM	Litterfall production
PDDF					
R_s	1	0.25	0.25	0.62**	−0.59*
AT		1	0.98**	0.06	−0.02
ST			1	0.07	−0.01
SM				1	−0.41*
Litterfall production					1
SDDF					
R_s	1	−0.04	−0.07	0.84**	−0.61**
AT		1	0.91**	−0.0004	0.007
ST			1	−0.01	0.06
SM				1	−0.44*
Litterfall production					1

R_s, soil respiration; AT, air temperature; ST, soil temperature; SM, soil moisture.

*p < 0.05, significant correlation.

**p < 0.01, significant correlation.

concentrated during the cool and dry period (January–March). The foliage fall on the surface implies a decrease in aboveground respiration. The litterfall production is the substrate available for microbial activity in soil respiration processes (Hanpattanakit and Chidthaisong, 2012; Hanpattanakit et al., 2012).

The diurnal CO_2 flux from R_s was determined by air and soil temperatures. Low air and soil temperatures and high soil moisture in the wet season stimulate the activity of microbes and plant roots in the soil to increase CO_2 flux from R_s (Broken et al., 1999). R_s rate are greater at night than during the day in arid ecosystems due to increased relative humidity and decreased soil temperature at night (Medina and Zelwer, 1972). The diurnal variation of R_s gradually increased from morning to afternoon and gradually decreased from evening to night. These results are consistent with the results of Intanil (2017), who reported that the diurnal pattern of R_s consisted of a gradual increase in the morning and a gradual decrease at night (after midnight). According to Hanpattanakit et al. (2015) the CO_2 flux from R_s is greater in the wet season than in the dry season because the rapid increase in soil temperature in the wet season promotes root and microbial activities.

Seasonal patterns of R_s are largely determined by soil water availability (Davidson et al., 2000; Hanpattanakit et al., 2017). In tropical climate regimes with cold, wet winters and hot, dry summers, water usually constrains biological activity in the summer (Xu and Qi, 2001). R_s in both sites was limited during the dry season. R_s was positively correlated with soil moisture in the PDDF and SDDF sites (Figure 6C, Tables 3, 4). Soil moisture was the main factor limiting R_s in terms of daily and monthly variations of CO_2 flux in both the PDDF and SDDF sites. The relationship between soil respiration and temperature is well-established, and understanding how temperature affects soil respiration is necessary for predicting soil responses to changes in climate. Air temperature and seasonal and yearly variations of R_s were negatively correlated and soil temperature was negatively correlated with seasonal and

yearly variations of R_s (Tables 3, 4). Shown that, the R_s variation was concurrently influenced by air and soil temperatures, soil moisture. These similarly to the studies of Bowden et al. (1998), Fernandez et al. (1993), Hanpattanakit (2013), and Yi et al. (2007) that reported the multiple correlation between R_s and temperature and soil moisture. Air and soil temperatures were significantly lower in the PDDF site than in the SDDF site ($p < 0.05$) due to differences in topography, latitude, elevation, and forest characteristics between sites (Figures 3A, B). At both sites, a linear relationship was observed in which the lowest R_s coincided with the highest air and soil temperatures. However, a positive relationship was observed only when the soil temperature was <27°C and the air temperature was <30°C. R_s was positively correlated with low air and soil temperatures in the PDDF site and negatively correlated with high air and soil temperatures in the SDDF site.

The CO_2 flux from R_s was significantly lower in the PDDF site than in the SDDF site ($p < 0.05$), which can be attributed to differences in biotic and abiotic factors such as climate, soil properties, litterfall production, and forest structure. Air and soil temperatures were significantly lower in the PDDF site than in the SDDF site ($p < 0.05$). CO_2 fluxes from R_s and air and soil temperatures were positively correlated in the PDDF site and negatively correlated in the SDDF site. R_s increases linearly when air and soil temperatures are relatively low, but extreme air and soil temperatures effectively stop R_s (Intanil, 2017). In a previous study of dry dipterocarp forest, the air temperature ranged from 22.50 to 41.25°C and the soil temperature ranged from 23.75 to 33.75°C (Hanpattanakit et al., 2009). R_s was negatively correlated with soil temperature and the lowest R_s coincided with the highest soil temperature. If there had been data associated with a lower range in soil temperature, an increase in soil respiration for certain soil temperature ranges (i.e., up to 25°C) would have been observed, as suggested by Flanagan and Veum (1974). A positive relationship exists for much lower temperature ranges, such as those not found

in a tropical climate. In the hilly region of Mount Taihang, R_s was positively correlated with soil temperature, which ranged from -4.98 to $26.23°C$ (Zeng et al., 2014).

The PDDF site had a greater soil moisture content and lower soil temperature than in the SDDF site, and was undisturbed by human activity, with a more stable forest structure and mineral and nutrient contents. The basal area and density of trees were lower in the PDDF site than in the SDDF site since the trees in the SDDF site were in the recovery phase and still growing. R_s rates are strongly correlated with elevation, temperature, precipitation, and litterfall production (Huang et al., 2017). Therefore, higher R_s rates occur at lower elevations because of increased temperature, litterfall production, and active plant growth rates and decreased precipitation ($<1,700\,mm$), which contribute to lower soil moisture (Kane et al., 2003; Litton et al., 2011; Berryman et al., 2014). Soil pH and soil bulk density were significantly lower in the PDDF site than in the SDDF site ($p < 0.05$) and soil carbon and nitrogen contents and SOC were significantly greater in the PDDF site than in the SDDF site ($p < 0.05$). Liu et al. (2018) reported that R_s was positively correlated with soil pH. The CO_2 flux from R_s was 2–12 times less in soil with a pH of 3 than in soil with a pH of 4. Soil with a pH above 7 also release less CO_2 flux from R_s (Kowalenko et al., 1978). Soil pH affects the activities of soil microbes, the main drivers of R_s. Zeng et al. (2014) reported that R_s was negatively correlated with SOC and soil nitrogen content, indicating decreased soil respiration due to increased SOC and nitrogen content. In addition, litterfall production was significantly lower in the PDDF site than in the SDDF site. Greater litterfall production tended to enhance R_s (Huang et al., 2017). According to Raich (1998), R_s increased with an increasing rate of litterfall production. Aboveground litterfall production regulates energy flow and nutrient cycling in forest ecosystems (Attiwill and Adam, 1993). Changes in aboveground litterfall production inputs can potentially affect soil respiration through the direct decomposition of litterfall and indirect effects on biological processes in the underlying soil (Bowden et al., 1993; Crow et al., 2009; Huang and Spohn, 2015).

Conclusion

R_s experienced diurnal variations corresponding to air and soil temperatures while soil moisture and litterfall production determined the seasonal variations. The seasonal variations of R_s in the primary dry dipterocarp forest (PDDF) site and secondary dry dipterocarp forest (SDDF) site were significantly positively correlated with soil moisture, and significantly negatively correlated with litterfall production. R_s produced higher CO_2 emissions during the wet season at both sites. The cumulative CO_2 flux from R_s was $2.99\,kg\,CO_2\,m^{-2}\,yr^{-1}$ (8.16 tons C ha$^{-1}\,yr^{-1}$) in the PDDF site and $3.24\,kg\,CO_2\,m^{-2}\,yr^{-1}$ (8.83 tons C ha$^{-1}\,yr^{-1}$) in the SDDF site. R_s was significantly lower in the PDDF site than in the SDDF site because R_s respond differently to environmental factors, such as climate, soil properties, litterfall production, and forest structure.

The research results estimating and comparing CO_2 emissions from soil respiration (Rs) in primary dry dipterocarp forests (PDDF) and secondary dry dipterocarp forests (SDDF) can serve as valuable knowledge and baseline information on CO_2 release from soil respiration in tropical forests. This information can help link forest carbon release data with other data from Asia. For future research, it is suggested that data collection be extended over the long term to provide clearer information on changes in carbon emissions in forest ecosystems under climate change conditions. This approach will allow for a more comprehensive understanding of the dynamics of carbon emissions and their implications for forest management and conservation.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

WT: Data curation, Formal analysis, Investigation, Methodology, Project administration, Writing – original draft. BS: Data curation, Methodology, Formal analysis, Writing – original draft. PC: Conceptualization, Formal analysis, Funding acquisition, Resources, Supervision, Writing – review & editing. AC: Conceptualization, Formal analysis, Funding acquisition, Resources, Supervision, Writing – review & editing. PH: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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