

Trees modify the dynamics of soil CO₂ efflux in coffee agroforestry systems

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ARTICLE INFO

Article history:

Received 7 August 2015

Received in revised form 18 March 2016

Accepted 4 May 2016

Available online 8 May 2016

Keywords:

Climate change

Soil carbon

Soil CO₂ efflux

Tree canopy

Atlantic rainforest biome

ABSTRACT

Agroforestry systems may help significantly reduce atmospheric carbon levels in forthcoming years through photosynthesis and regulation of soil CO₂ efflux. This study aimed to characterise the soil CO₂ efflux dynamics of coffee plants cultivated under agroforestry and full-sun production systems and identify the factors that regulate this process. The study was carried out in agroforestry and full-sun coffee systems on three family farms in Minas Gerais, the Atlantic Forest Biome, Brazil during three consecutive days on each farm. Twenty 1-m² sampling areas (10 for each system), each separated by a distance of 5 × 5 m and located between coffee plant rows, were selected on each farm. Soil physical and chemical attributes, air temperature and humidity, soil temperature and moisture, the percentage of canopy cover, and soil CO₂ efflux were measured at each sampling area in the two systems. The air and soil temperature in the agroforestry systems were lower and soil moisture was higher than in the full-sun systems. Soil CO₂ efflux showed different dynamics in the two systems. Daytime soil CO₂ efflux was more stable (i.e. from morning to midday) in the agroforestry system (average 15% increase) compared to the full-sun system (average 49.1% increase). Soil CO₂ efflux was regulated by labile carbon and total nitrogen variation in the agroforestry systems, and by soil temperature variation at a depth of 10 cm in the full-sun systems. A principal components analysis with data from all grouped systems showed that soil CO₂ efflux was generally positively correlated with soil temperature at 5 and 10 cm depths, and negatively correlated with soil moisture. In conclusion, agroforestry systems promote microclimate stability and decrease soil CO₂ efflux variability compared to full-sun systems.

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1. Introduction

Greenhouse gas emissions into the atmosphere, especially carbon dioxide (CO₂), have increased considerably, due to the burning of fossil fuels and the conversion of tropical forests to agricultural land (Rogner et al., 2007) and have been identified as the cause of global climate changes (Field et al., 2014). Most CO₂ emissions due to agricultural activity originate from the soil, which is also the largest C reservoir (~2344 PgC) in the terrestrial biosphere (Stockmann et al., 2013). Although soil carbon stocks from forests

and crops management systems in tropical regions are often studied, high uncertainty remain about the size and factors controlling the carbon losses (soil CO₂ efflux) and how agricultural practices could mitigate soil CO₂ emissions in these ecosystems.

Soil CO₂ efflux results from abiotic and biotic soil processes associated to the roots and organisms respiration (Berisso et al., 2013; Hanson et al., 2000). These processes are related to various soil attributes such as temperature, moisture, texture, and aggregation (Blagodatsky and Smith, 2012; Lloyd and Taylor, 1994; Wu et al., 2010), and soil temperature and soil moisture are the main factors involved in the regulation of soil CO₂ efflux (Raich and Potter, 1995). An increase in soil temperature causes an increase in soil CO₂ efflux, because of changes in root respiration and in the decomposition rates of organic matter (Peng et al., 2009). Soil moisture is the main driver of soil microbial activity (Orchard and Cook, 1983), and interferes with gas diffusion because water replaces the air in

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Table 1

Location environmental characteristics, and history of the agroforestry (AF) and full-sun (FS) coffee systems at the three farms (RO, PA, GI).

Site code	RO	PA	GI
Location	Araponga	Araponga	Divino
Latitude	–20°41′53.9″	–20°39′28.9″	–20°38′43.3″
Longitude	–42°31′45.4″	–42°33′18.9″	–42°11′50″
Altitude (m)	1040	800	650
Average annual temperature (°C)	18	18	21
Average annual rainfall (mm)	1345	1345	1282
Soil type	Oxisol	Oxisol	Oxisol
Slope (%)	12	3	5
Estimated average trees height (m)	12	5	5
Coffee age (years)	20	9	25
Land use before coffee	Pasture and rice	Coffee yard	Pasture
Coffee spacing (m × m)	3 × 1	3 × 1	3 × 1
Year of AF implementation	1998	2006	2010
Tree density in AF (trees ha ^{−1})	240	200	170
Main plant species present in AF	<i>Inga subnuda</i>	<i>Solanum</i> sp. and <i>Musa</i> sp.	<i>I. subnuda</i> , <i>Solanum</i> sp., <i>Musa</i> sp., and <i>Toona ciliata</i>

the soil pore space (Melling et al., 2005). Soil texture and aggregation interfere with the CO₂ production process and its transport to the soil surface (Harrison-Kirk et al., 2013; Lenka and Lal, 2013), because these attributes affect soil porosity, interfere with gas diffusion, and alter the accessibility of soil organic matter to microbial decomposition (Jastrow et al., 2007). Although it is known how soil characteristics may influence soil CO₂ efflux, the role of vegetation cover on soil CO₂ efflux is not well understood.

Vegetation cover may be the main factor that controls soil CO₂ efflux, since it controls microclimate conditions, soil physical, biological and chemical quality. Agroforestry systems (AF), which use trees between crops, sequester C in plant biomass and increase the input of organic matter residue into the soil (Ehrenbergerová et al., 2015; Montagnini and Nair, 2004), and if globally implemented could remove significant quantities of C (1.1–2.2 Pg C) from the atmosphere over the next 50 years (Albrecht and Kandji, 2003). Agroforestry coffee systems are widely used in Central and South America (Bacon, 2005), but are underrepresented in Brazil (Edenhofer et al., 2014), where coffee plants are predominately cultivated under full-sun systems (FS). However, to overcome problems of land degradation, a group of farmers in the Zona da Mata of Minas Gerais, Brazil, initiated experiments with AF coffee systems in cooperation with local non-governmental organizations and researchers in 1993 (Cardoso et al., 2001) and resulted in improvement of soil quality and microclimatic conditions (Souza et al., 2010). The farmers selected the trees to use in AF systems based on many criteria, such as amount of biomass and compatibility with coffee plants (e.g., no competition for water, light and nutrients) (Souza et al., 2010). The canopy cover of trees also protects the soil against direct solar radiation (Breshears and Ludwig, 2010), reducing soil temperature and water loss by evaporation (Lin, 2010). Therefore, AF systems may positively influence soil CO₂ efflux dynamic to the atmosphere.

In the literature, studies in situ of soil CO₂ efflux in AF coffee systems sought to quantify the C emissions and correlate this to soil attributes (Hergoualc'h et al., 2008; Nojonen et al., 2012), but the efflux dynamics and controlling factors remain unclear. To improve our understanding, it is necessary to study the relationship between soil CO₂ efflux, soil attributes and vegetation characteristics. Therefore, this study aimed to (i) determine how the tree canopy influences the microclimate and soil CO₂ efflux variability in AF versus FS coffee systems, and (ii) identify the main abiotic factors and how they control this process in each system.

2. Material and methods

2.1. Study areas

This study was carried out in Zona da Mata of Minas Gerais State, Brazil, in the Atlantic Rainforest Brazilian biome, which is one of the five *biodiversity hotspots* of the world (Myers et al., 2000). Three family farms were selected (referred to as RO, PA, and GI), which were cultivated with coffee (*Coffea arabica* L. cv. Red Catuai) under AF and FS systems. All three farms used similar agroecological management practices (e.g. skimming of weeds, no use of pesticides, cultivating maize among coffee rows leaving the straw on the field after harvest), which help keep the soil covered and add organic matter to the soil. In FS_{PA}, the farmer even chose a maize variety that produces more straw to add more organic matter to the soil. Regional soils are generally acidic and present low natural fertility, with organic matter input and nutrient cycling being required for natural quality maintenance. Table 1 provides information about the location, environmental characteristics, and history of each farm.

2.2. Study design

At each farm, we selected a coffee field of approximately 300 m². In each field, we selected 20 sampling areas of 1-m² each, which were located between the rows of coffee plants. Among the 20 sampling areas, 10 were located in the AF system and the other 10 in the FS system. The distance between sampling areas was about 5 × 5 m. AF and FS systems were considered treatments, whereas the 10 areas in each treatment were considered replicates. In total, 60 areas were sampled across the three farms. For soil CO₂ efflux analyses, we placed a polyvinyl chloride (PVC) ring (10 cm diameter and 7 cm height) on the soil at the centre of each sampling area. The rings were inserted 3 cm deep into the soil, leaving 4 cm above the soil surface to avoid changes in soil temperature, moisture, and radiation balance that affect the soil surface inside the ring. Large branches and leaves were removed from the soil surface for optimum ring installation. The rings were installed 24 h before the measurements of soil CO₂ efflux, which is the time required to recover soil CO₂ equilibrium after soil disturbance due to ring insertion (Heinemeyer et al., 2011).

2.3. Soil sampling and analysis

After 3 days of soil CO₂ efflux measurements, disturbed soil samples from inside the rings were collected from 0 to 10 cm soil depth at each sampling area. Beside each ring, three undisturbed soil sam-

ples were collected with steel rings of 5.3 cm height and 4.8 cm diameter.

Organic matter and N determination were performed on disturbed samples. Total organic carbon (TOC) was measured by the wet oxidation of organic matter, using external heat source (Yeomans and Bremner, 1988). Labile carbon (LC) was quantified by oxidation with KMnO_4 , as proposed by Blair et al. (1995) and modified by Shang and Tiessen (1997). Total nitrogen (TN) was quantified by sulphuric acid digestion (Bremner, 1996).

Soil bulk density (BD) was determined using the undisturbed soil samples (Embrapa, 2011). Soil particle density (PD) was determined by the balloon volumetric method (Embrapa, 2011). Microporosity (PMi) was calculated as the amount of water retained in undisturbed soil samples subjected to pressure -0.006 MPa ($\sim 60 \text{ cm H}_2\text{O}$). Macroporosity (PMa) was calculated as the difference between TP and PMi. All of these physical characteristics and soil texture were analysed according to Embrapa (2011). Water-filled pore space (WFPS) was calculated using soil moisture (SM, %), BD (g cm^{-3}), and TP (%).

2.4. Canopy cover

Hemispheric photographs were taken of each sampling area to estimate the canopy cover level (%), with a Canon T2i 18 megapixel camera and a fisheye lens. The camera was attached to a tripod with a spirit level. Then, the tripod with camera was set at 80 cm high above the soil surface in the centre of all sampling areas, aiming to ensure real brightness of the soil surface. The camera was pointed to the magnetic North. Light intensity is important for image quality; thus, images were taken at sunrise, thereby preventing the direct entry of sunlight into the lens and avoiding excess light in the images. We used a lens aperture of F 6.3 for all images (Pueschel et al., 2012), which were saved as 16-bit. Five images were taken at each sampling area, and the best image was analysed by the program GLA (Gap Light Analyzer) in the blue band, seeking to achieve the optimum brightness value (thresholding) of the sky (Leblanc et al., 2005).

The images were obtained with a Zenithal angle of $0-90^\circ$, generating a 180° view from the soil surface. However, pixels become mixed when the zenithal angle has high values (Jonckheere et al., 2004; Leblanc et al., 2005). Thus, to avoid this problem, a mask that limited Zenithal angle values of $0-70^\circ$ (Macfarlane et al., 2007) and nine segments azimuth were created before analysis in the GLA program. Therefore, analysed images represented a view of 140° from a height of 80 cm above the soil surface. In total, 60 images were analysed.

2.5. Microclimate evaluation

When measuring soil CO_2 efflux, we also measured air temperature, humidity, and soil temperature, in addition to collecting soil samples for moisture analysis. Air temperature and humidity were measured at a height of 80 cm by using a thermohygrometer (Incoterm, model 7666.02.0.00). Soil temperature was measured using a soil thermometer-type dipstick placed at 5 and 10 cm soil depths, 3 cm from the outside of the ring. To estimate gravimetric soil moisture, soil samples were collected at 0–5 cm depth and sent to the laboratory, where they were placed in an oven at 105°C for 48 h.

2.6. Soil CO_2 efflux and soil temperature sensitivity

To measure soil CO_2 , we used the portable LI-8100 analyzer (LiCor, USA) coupled to a dynamic chamber (model LI-8100-102). Soil CO_2 efflux was measured for 90 s in each ring. We tried to complete the measurement of all 20 rings in the 20 sampling areas at

each farm as quickly as possible to minimise variation in soil temperature and moisture between the sampling areas (Scala et al., 2005). The data were collected in the morning (8:00 to 10:00 h) and at midday (12:00 to 14:00 h) over three consecutive days at each farm during the end of October 2013 (RO farm) and the beginning of November 2013 (PA and GI farms). In total, we carried out 360 measurements of soil CO_2 efflux at the three farms.

To compare soil temperature sensitivity in the AF and FS systems of each farm, the proportional change in soil CO_2 efflux when soil temperature increased by 10°C (Q_{10}) was calculated, based on the relationship between soil temperature at a 5 cm depth and soil CO_2 efflux. An exponential regression was applied to find the relationship between soil CO_2 efflux and soil temperature (Eq. (1)):

$$\text{CO}_{2\text{ef}} = \alpha \cdot e^{(\beta_1 \cdot T)} \quad (1)$$

where $\text{CO}_{2\text{ef}}$ is the soil CO_2 efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$), T is the soil temperature, α is the intercept of soil CO_2 efflux when the temperature is zero, and β_1 is the regression coefficient obtained from the natural logarithm of the CO_2 efflux and soil temperature at 5 cm depth. Thus, the Q_{10} values were obtained according to Eq. (2) (Van't Hoff, 1898):

$$Q_{10} = e^{10 \cdot \beta_1} \quad (2)$$

To calculate the Q_{10} of AF and FS systems in each farm, the data from two daytime measurements (morning and midday) were grouped for each system. The three farms are located at different altitudes (Table 1). Moreover, soil CO_2 efflux was measured on different dates, and each site had different soil temperatures at a 5 cm depth. Therefore, to compare soil CO_2 efflux among the three farms, the efflux at each system was normalised to a temperature of 25°C , generating new soil CO_2 efflux (R_{25}) values at each sampling area. The R_{25} was calculated according to the following equation (Acosta et al., 2013):

(3) $R_{25} = \text{CO}_{2\text{ef}} \times Q_{10}^{\frac{(25-T)}{10}}$ where $\text{CO}_{2\text{ef}}$ is the soil CO_2 efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) measured at each sampling area, and T is the soil temperature at a 5 cm depth, measured at the time of soil CO_2 efflux measurements.

2.7. Statistical analysis

Soil CO_2 efflux and soil physical and chemical attributes were analysed by descriptive statistics. The spatial variability of soil CO_2 efflux was characterised for each measurement by calculating the coefficient of variation, using data from all of the sampling areas of the two systems at the three farms. The comparison of soil CO_2 efflux normalised (R_{25}) between farms was carried out by analysis of variance (ANOVA), following which a Tukey post-hoc test was applied ($p < 0.05$).

Multiple stepwise regression analyses were used to model and identify the environmental variables and physical and chemical soil attributes that most influenced soil CO_2 efflux in the two systems at each farm. In the multivariate regression analysis, soil CO_2 efflux was the dependent variable and the soil physical, chemical, and environmental characteristics were the independent variables. The relative importance of each parameter from the equations was measured and then diagnostics tests for heteroscedasticity, normality, and influential observations were applied. Principal components analysis (PCA) was also used to reduce the complex dataset to a lower dimensionality, to reveal simplified structures that explain the complex dataset. PCA analysis was performed with all variables from the three farms combined to assess how the variables were correlated. Program R (R Development Core Team, 2014) and the packages car (Fox and Weisberg, 2011), Mass (Venables and Ripley, 2002) and relaimpo (Grömping, 2006) were used to perform the statistical analysis.

Table 2

Average soil physical (n = 30 per system) and chemical (n = 10 per system) attributes from the agroforestry (AF) and full-sun (FS) coffee systems at the three farms (RO, PA, GI) at 0–10 cm soil depth.

System	AF _{RO}	FS _{RO}	AF _{PA}	FS _{PA}	AF _{GI}	FS _{GI}
Soil physical characteristics						
Textural class		Clay		Sandy Clay Loam		Clay
Particle density (g cm ⁻³)		2.37		2.52		2.42
Sand (%)		37.7		41.7		58.9
Silt (%)		11.9		13.7		10.5
Clay (%)		50.4		44.6		30.6
BD (g cm ⁻³)	0.98 (0.01)	1.06 (0.01)	1.26 (0.02)	1.21 (0.01)	1.16 (0.02)	1.10 (0.01)
TP (m ³ /m ³)	0.58 (0.00)	0.55 (0.00)	0.49 (0.00)	0.52 (0.00)	0.51 (0.00)	0.54 (0.00)
PMA (m ³ /m ³)	0.21 (0.00)	0.15 (0.00)	0.13 (0.00)	0.19 (0.00)	0.13 (0.00)	0.18 (0.00)
PMi (m ³ /m ³)	0.37 (0.00)	0.39 (0.00)	0.36 (0.00)	0.33 (0.00)	0.38 (0.00)	0.35 (0.00)
WFPS (%)	46.4 (2.5)	39.6 (1.9)	45.8 (2.8)	26.2 (1.2)	50.0 (1.8)	31.8 (1.1)
Soil chemical characteristics						
TOC (g kg ⁻¹)	35.3 (2.0)	39.7 (1.3)	28.4 (2.3)	30.7 (1.4)	28.7 (2.5)	31.5 (1.3)
TN (g kg ⁻¹)	2.7 (1.6)	3.4 (0.1)	2.2 (0.1)	2.7 (0.2)	2.0 (0.2)	2.2 (0.1)
LC (g kg ⁻¹)	4.3 (0.2)	5.2 (0.1)	4.1 (0.3)	4.9 (0.3)	3.2 (0.2)	3.7 (0.1)

The numbers between parentheses are (± standard error). BD = soil bulk density, TP = total porosity, PMA = macroporosity, PMi = microporosity, WFPS = water filled pore space, TOC = total organic carbon, TN = total nitrogen; LC = labile carbon.

Table 3

Average (n = 30) air temperature (AT), humidity (HU), soil temperature (ST) at 5 and 10 cm depths, and soil moisture content (SM) in the agroforestry (AF) and full-sun (FS) coffee systems at the three farms (RO, PA, GI).

System	AF _{RO}		FS _{RO}		AF _{PA}		FS _{PA}		AF _{GI}		FS _{GI}	
Period	8 h	12 h	8 h	12 h	8 h	12 h	8 h	12 h	8 h	12 h	8 h	12 h
AT (°C)	22.8 (0.3)	26.7 (0.4)	25.2 (0.6)	27.8 (0.6)	24.6 (0.1)	32.7 (0.2)	28.0 (0.3)	39.5 (0.4)	27.9 (0.2)	35.5 (0.3)	32.6 (0.4)	41.5 (0.7)
HU (%)	68.9 (0.3)	63.4 (0.6)	66.5 (0.7)	62.2 (1.0)	60.6 (0.7)	42.9 (0.7)	56.2 (0.7)	34.6 (0.7)	58.3 (1.0)	40.1 (0.3)	49.3 (1.0)	32.3 (1.0)
ST _{5cm} (°C)	18.7 (0.2)	20.2 (0.1)	20.4 (0.2)	22.9 (0.2)	19.6 (0.1)	23.1 (0.4)	21.1 (0.1)	30.8 (0.4)	21.9 (0.1)	27.1 (0.4)	25.3 (0.3)	35.7 (0.4)
ST _{10cm} (°C)	18.4 (0.1)	19.5 (0.1)	19.8 (0.1)	21.7 (0.1)	19.5 (0.1)	21.6 (0.2)	20.8 (0.1)	26.5 (0.3)	21.4 (0.1)	25.0 (0.3)	23.7 (0.2)	31.3 (0.3)
SM (%)	27.5 (1.6)	27.1 (1.4)	21.5 (1.3)	19.9 (1.1)	17.4 (0.7)	17.6 (0.7)	12.3 (0.6)	10.4 (0.6)	22.6 (0.9)	21.4 (0.9)	17.5 (0.9)	13.9 (0.5)

Numbers between parentheses are (±standard error).

Table 4

Average (n = 30) of soil CO₂ efflux (μmol m⁻² s⁻¹), standard error (s.e.), and the coefficient of variation (CV) measured in two periods in the agroforestry (AF) and full-sun (FS) coffee systems at the three farms (RO, PA, and GI).

System	AF _{RO}		FS _{RO}		AF _{PA}		FS _{PA}		AF _{GI}		FS _{GI}	
Period	8 h	12 h	8 h	12 h	8 h	12 h	8 h	12 h	8 h	12 h	8 h	12 h
CO ₂ efflux	2.66	2.83	2.39	2.45	4.21	4.79	3.48	6.52	6.73	8.26	5.82	8.95
s.e.	0.15	0.20	0.15	0.13	0.24	0.29	0.14	0.18	0.47	0.47	0.21	0.40
CV (%)	31.9	39.6	35.1	29.2	30.6	33.1	21.8	15.0	38.1	31.1	19.7	24.6

s.e. = standard error; CV = coefficient of variation (%).

3. Results

3.1. Soil attributes, canopy cover and climatic conditions

The soil textures were classified as clay (RO and GI systems) and sand clay loam (PA systems). Despite the differences in texture, the soils had similar values for most of physical and chemical attributes, with differences in BD and WFPS (Table 2), canopy cover (%) was higher in AF systems (RO = 47.80; PA = 72.14; GI = 84.45) compared to the FS systems (RO = 15.55; PA = 33.74; GI = 48.62).

Compared to the FS systems, the AF systems had 4.1 °C lower air temperature, 5.1% higher air humidity, 4.3 °C and 3.1 °C lower soil temperature at 5 and 10 cm depths, respectively, and 6.4% higher soil moisture content (Table 3).

3.2. Canopy cover versus climatic conditions

Air temperature was negatively correlated ($p < 0.001$) with canopy cover (%), whereas air humidity were positively correlated ($p < 0.001$) at all farms (Fig. 1). Soil temperature (at both 5 and 10 cm depths) was negatively correlated ($p < 0.001$) at all farms and soil moisture content (%) was positively correlated ($p < 0.001$) with

canopy cover (%) at PA and GI farms, but showed no correlation at RO farm (Fig. 2).

3.3. Soil CO₂ efflux analysis

Average soil CO₂ efflux was lowest in the AF_{RO} (2.66 μmol m⁻² s⁻¹) and FS_{RO} (2.39 μmol m⁻² s⁻¹) systems and highest in the AF_{GI} (8.26 μmol m⁻² s⁻¹) and FS_{GI} (8.95 μmol m⁻² s⁻¹) systems (Table 4). Spatial variation in soil CO₂ efflux (expressed as coefficient of variation [CV] in Table 4) was higher in the AF (average 34.1%) compared to the FS coffee systems (average 24.2%).

Q₁₀ was highest in AF_{RO} (2.41) and only FS_{PA} (1.84) and FS_{GI} (1.41) systems showed Q₁₀ values with significant determination coefficients (Table 5). FS_{PA} showed the highest variation in soil temperature (+9.74 °C) and in soil CO₂ efflux (+89.7%) from morning to midday. Soil CO₂ efflux normalized to 25 °C (R₂₅) increased ($p < 0.05$) from RO < PA < GI and was similar in both systems ($p > 0.05$) at farms PA and GI, but not at RO (Table 5).

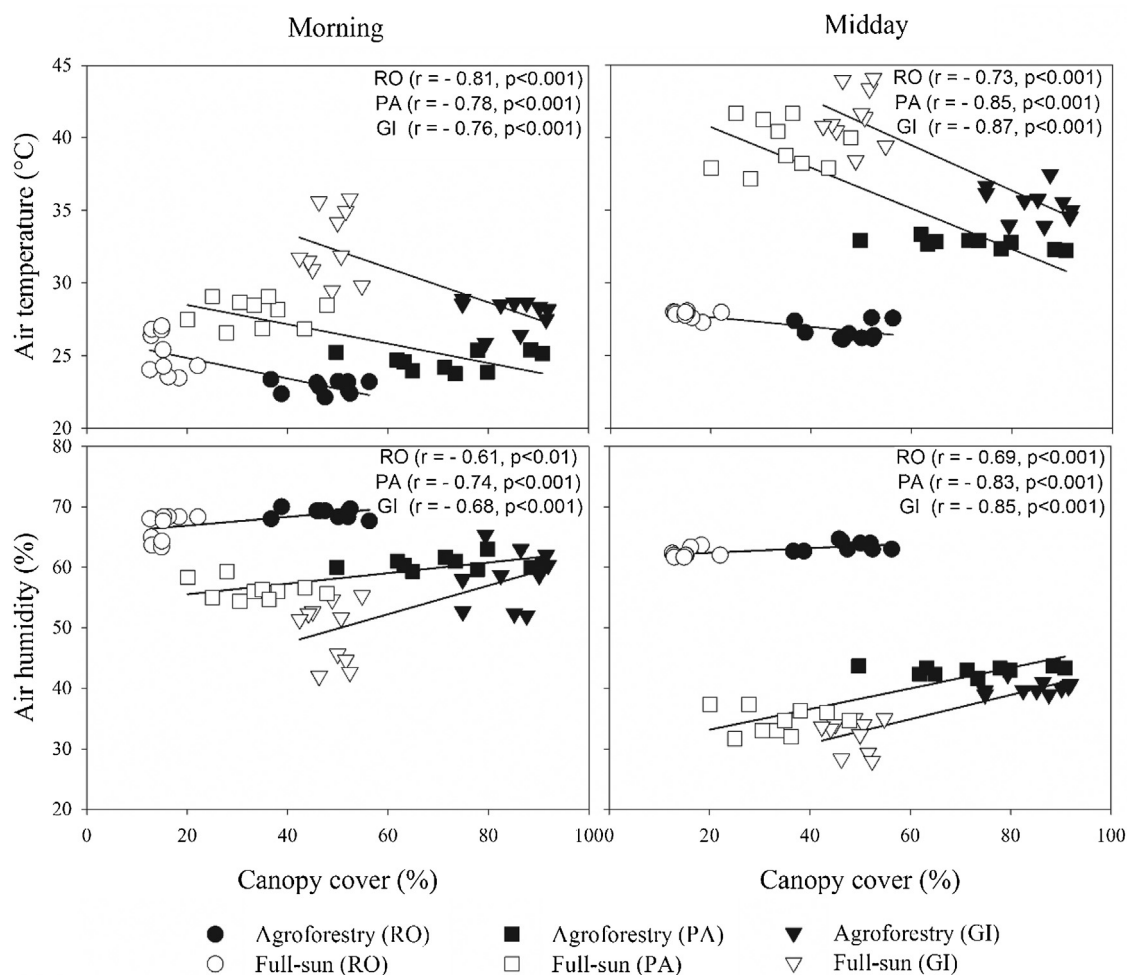


Fig. 1. Scatterplots with Pearson correlations between canopy cover (%) and air temperature and humidity in the morning (08:00–10:00 h) and midday (12:00–14:00 h) in the agroforestry and full-sun coffee systems at the three farms (RO, PA, and GI).

Table 5
Q₁₀ values and coefficients of determination (R²) for the mean (n=60 evaluations of soil CO₂ efflux), variation in soil temperature (Δ T5 cm) and soil CO₂ efflux (Δ CO₂) at each sampling point from the morning to midday periods and soil CO₂ efflux normalised to 25 °C soil temperature (R₂₅) in the agroforestry (AF) and full-sun (FS) coffee systems at the three farms (RO, PA and GI).

System	AF _{RO}	FS _{RO}	AF _{PA}	FS _{PA}	AF _{GI}	FS _{GI}
Q ₁₀	2.41	1.9	1.26	1.84	1.49	1.41
R ²	0.09	0.11	0.02	0.73	0.14	0.45
Δ T5 cm (°C)	+1.48	+2.45	+3.46	+9.74	+5.18	+10.45
Δ CO ₂ (μmol m ² s ⁻¹)	+0.16	+0.05	+0.58	+3.03	+1.51	+3.13
Δ CO ₂ (%)	+5.17	+4.21	+14.46	+89.73	+26.61	+53.36
R ₂₅	3.32 d	2.62 c	4.65 b	4.75 b	7.51 a	6.77 a

Numbers with different letters are significantly different (p < 0.05) among all systems.

3.4. Canopy cover versus soil CO₂ efflux

Increasing canopy cover was related to decreasing soil CO₂ efflux variability (difference between the efflux from morning to midday)(Fig. 3). Daytime soil CO₂ efflux variability (%) was negatively correlated with canopy cover (%) in PA ($r = -0.78, p < 0.001$) and GI ($r = -0.71, p < 0.001$) and not correlated in RO ($r = -0.02, p > 0.1$).

3.5. Multivariate analysis of soil CO₂ efflux

The multivariate equations (Table 6) showed that different factors control soil CO₂ efflux in the AF and FS coffee systems. Soil CO₂ efflux variability correlated most with variations of LC and TN in the AF systems, and soil temperature at 10 cm depth explains up to 97% of the soil CO₂ efflux variation in FS_{PA} and 55% in FS_{GI}.

The PCA analysis of total data indicated the correlation among the variables and which variables were responsible for soil CO₂ efflux variation among all systems (Fig. 4). Overall, soil CO₂ efflux was positively correlated with soil temperature at 5 and 10 cm depths and negatively correlated with soil moisture, WFPS, and PMi.

4. Discussion

4.1. Influence of tree canopy cover on soil and air variables

Plants that grow spontaneously between coffee plant rows in AF and FS coffee systems are controlled and not completely removed. In addition, corn straw is left on the soil after harvesting, which also increases the carbon input into FS systems. Therefore, these practices may explain why a similar amount of total organic carbon was found in the two systems investigated in the current study (Table 2).

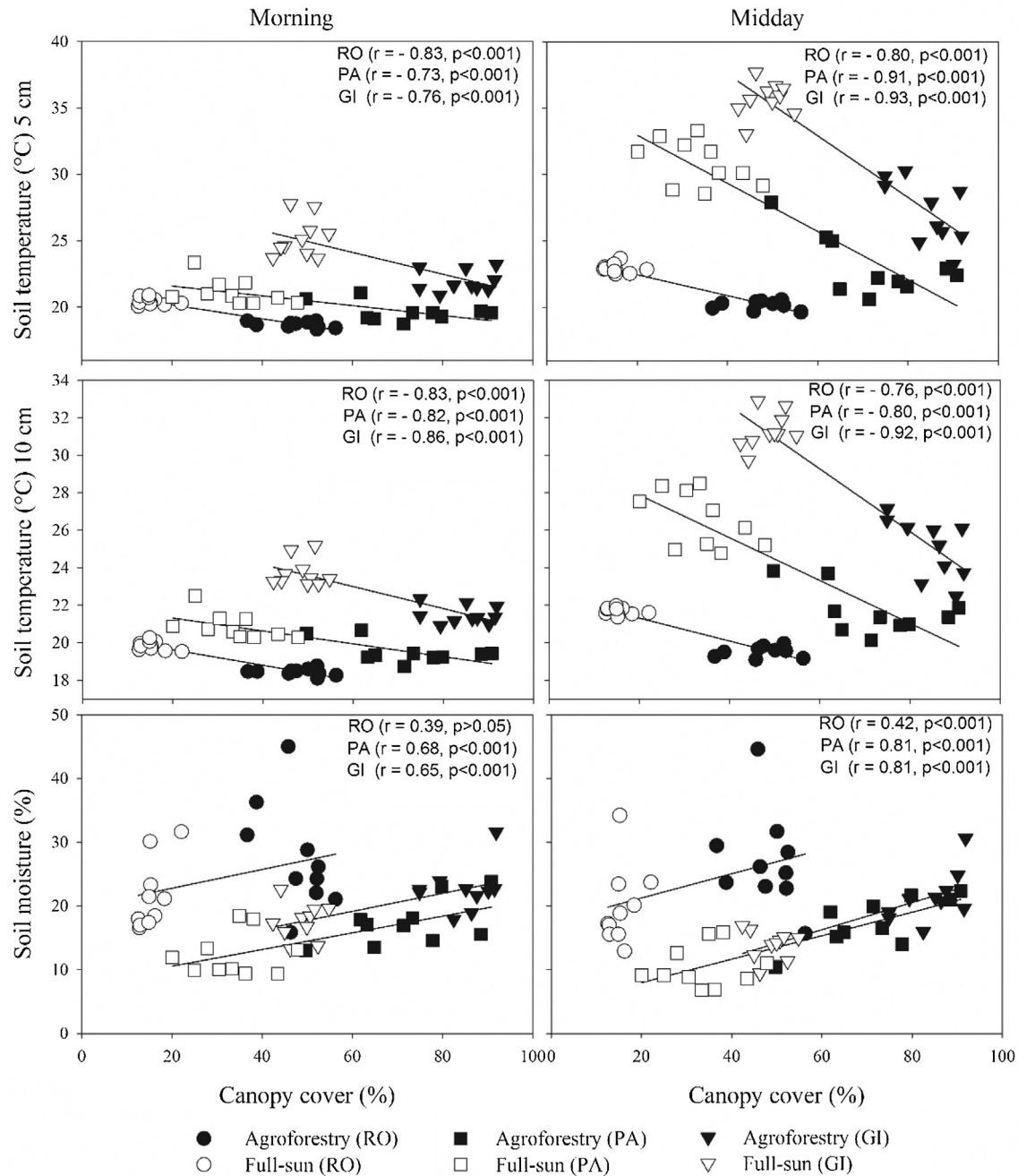


Fig. 2. Scatterplots with Pearson correlations between canopy cover (%) and soil temperature at 5 and 10 cm depths and soil moisture in the morning (08:00–10:00 h) and midday (12:00–14:00 h) in the agroforestry and full-sun coffee systems at the three farms (RO, PA and GI).

Table 6

Regression equations of soil CO₂ efflux in relation to soil microclimatic, chemical, and physical attributes of the agroforestry (AF) and full-sun (FS) coffee systems at the three farms (RO, PA and GI).

System	Parameters	Regression Equation	R ²	p
AF _{RO}	TN (47%), LC (29%), PMi (24%)	$Y = -3.49 + 2.25TN^{**} - 0.96LC^{*} + 11.35PMi$	0.52	0.007
FS _{RO}	TN (30%), LC (60%), ST _{10cm} (9%), SM (1%)	$Y = -1.41 + 0.018 ST_{10cm}^{*} + 0.85LC^{**} - 0.02SM$	0.77	<0.001
AF _{PA}	TN (18%), LC (21%), ST _{10cm} (7%), SM (9%), BD (36%), PMi (9%)	$Y = 2.57 + 0.20 ST_{10cm} + 2.50TN - 1.15LC - 9.32BD + 20.83PMi + 0.09SM$	0.30	0.495
FS _{PA}	ST _{10cm} (97%), LC (1%), TOC (1%), BD (1%)	$Y = -9.78 + 0.51 ST_{10cm}^{***} + 0.22TOC + 0.28BD + 0.36LC$	0.82	<0.001
AF _{GI}	TN (27%), ST _{10cm} (28%), SM (23%), BD (10%), PMi (12%)	$Y = 35.1 + 0.689 ST_{10cm}^{**} - 5.58 TN^{**} - 6.01 BD - 92.50PMi^{*} + 0.38 SM^{*}$	0.66	0.005
FS _{GI}	ST _{10cm} (55%), TN (23%), SM (22%)	$Y = 11.17 + 0.36 ST_{10cm}^{**} + 4.31TN^{*} - 0.06SM$	0.68	<0.001

TN = total nitrogen; LC = labile carbon; PMi = microporosity; ST_{10cm} = soil temperature at 10-cm depth; BD = soil bulk density; TOC = total organic carbon; and SM = soil moisture. The percentages between parentheses shows the relative importance of each parameter for the soil CO₂ efflux. (**) $p < 0.001$ and (*) $p < 0.05$.

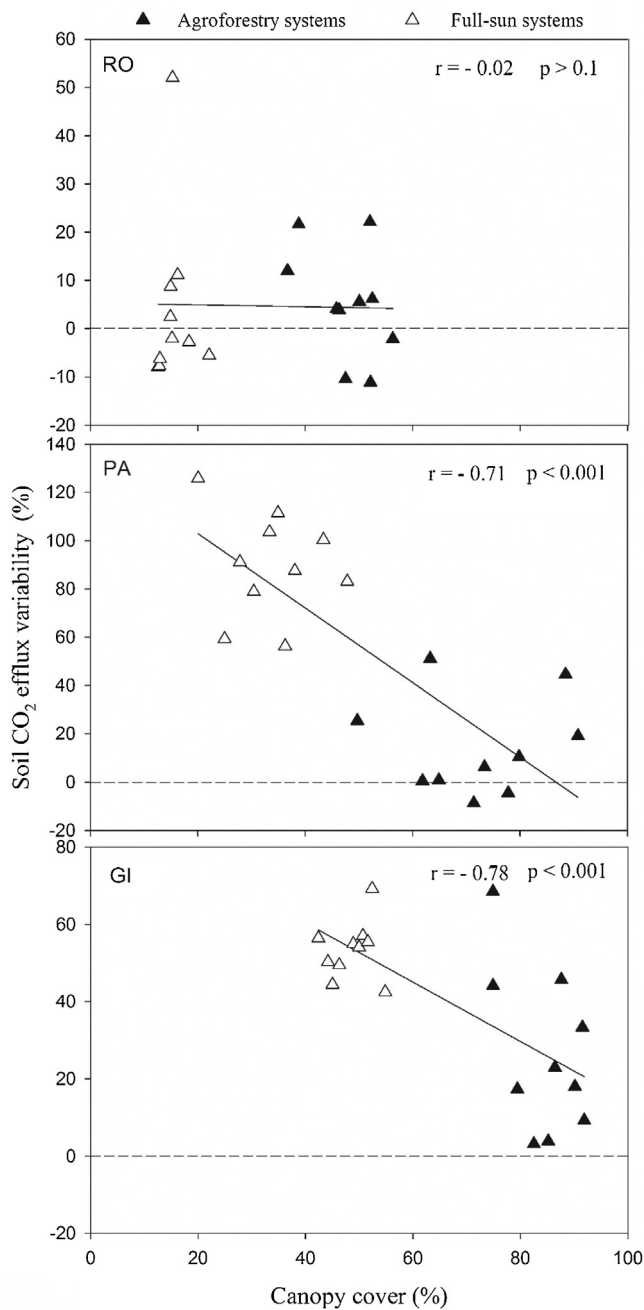


Fig. 3. Scatterplots with Pearson correlations between canopy cover (%) and soil CO₂ efflux variability (%), from the morning (08:00–10:00 h) to midday (12:00–14:00 h), at each sampling area in the agroforestry and full-sun coffee systems at the three farms (RO, PA, and GI).

Coffee plants can be intercropped with a diversity of different tree species in an agroforestry system (Souza et al., 2010), resulting in different canopy dimensions, tree phenology, and leaf density. These characteristics led to different percentages of soil surface cover by the canopy, affecting the amount of solar radiation that reached the soil (Bremen and Kessler, 1995). The main tree species in AF_{RO} (*Inga subnuda*) were pruned during the summer of 2012 (i.e. the year before the study was conducted), it may explain why the AF_{RO} and FS_{RO} had lower canopy cover than the other two sites. Trees in the AF systems provide stability to the microclimate (Beer et al., 1997; Kiepe and Rao, 1994; Lin, 2007; Nair, 1997), for instance, by reducing air temperature (Akpo et al., 2005; Lin et al., 2008; Souza et al., 2012), as shown in our study (Fig. 1) despite

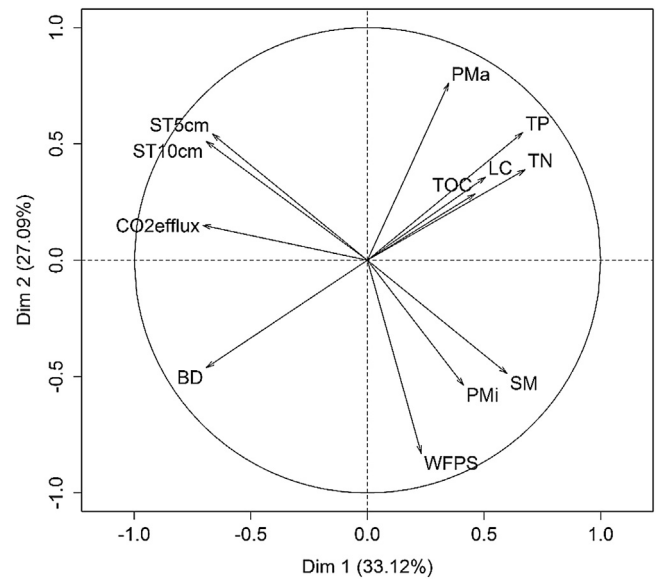


Fig. 4. Principal component analysis of data from the agroforestry and full-sun coffee systems at the three farms (RO, PA, GI). The plot shows the soil characteristics and environmental factors that influence soil CO₂ efflux (CO₂efflux). ST5 cm = soil temperature at 5 cm depth; ST10 cm = soil temperature at 10 cm depth; PMA = macroporosity; LC = labile carbon; TP = total porosity; TOC = total organic carbon; TN = total nitrogen; SM = soil moisture; PMi = microporosity; WFPS = water filled pore space; and BD = soil bulk density.

differences in altitude, different vegetation types, and different ages of the systems (Table 1). Therefore, under the climate-change scenarios (Stocker et al., 2013) the microclimate provided by the tree canopy may become crucial for *C. arabica* cultivation, which requires temperatures between 18 to 21 °C for optimal growth (Alegre, 1959).

Moreover, the humidity of the agroecosystem is also an important issue due to predicted global climatic change. Increased canopy cover maintains soil moisture (Lin et al., 2006; Liu et al., 2013), as observed in our study (Fig. 2), due to a decrease in soil evaporation (Lin, 2010). Coffee production is extremely vulnerable to water availability, which is necessary for the development of coffee beans and, consequently, determines fruit size (Cannell, 1983). In the region, water availability is also important in January and February (rainy season), when short dry periods may occur leading to the bad formation of the coffee beans. Thus, agroforestry coffee systems may provide better conditions to retain the water in the system (Liu et al., 2013) and enhance coffee bean size (Vaast et al., 2006); therefore, decreasing the risk of economic losses from coffee production.

4.2. Soil CO₂ efflux dynamics

Existing publications state that soil CO₂ efflux is one of the largest uncertainties when analysing the global carbon cycle, because it involves several processes, including different sources and multiple and varied controllers (Moyes et al., 2010; Ryan and Law, 2005). Therefore, soil CO₂ efflux is characterised by high spatial and temporal variability (Hanson et al., 1993; Xu and Qi, 2001a). To our knowledge, the study of soil CO₂ dynamics has not been previously conducted in agroforestry systems. Our study showed the highest spatial variation in CO₂ efflux in AF compared to FS coffee systems (Table 4), which may be explained by the presence of different tree species that promote different environmental conditions due to their specific biological characteristics. Tree characteristics such as root biomass, organic matter contribution, and distance between trees influence the pattern of spatial variability

in soil respiration (Katayama et al., 2009; Sørensen and Buchmann, 2005) and, therefore, CO₂ efflux.

Soil CO₂ efflux dynamics between morning and midday differed between AF and FS coffee systems, despite the mean soil CO₂ efflux was similar in both systems at all three farms (Table 4). We found that soil CO₂ efflux variability during the day decreases with increasing canopy cover (Fig. 3) and that the efflux is more stable in AF systems, showing less diurnal variation from morning to midday than in FS systems (Table 5), except for the RO farm. During the three days of the soil CO₂ efflux measurements at the RO farm, air humidity was very high and the air temperature was low compared to other farms, and did not change much from the morning to midday period, with these factors probably being due to its altitude (1000 m). Consequently, the effect of tree canopy cover on the microclimate (Fig. 1) and on the soil CO₂ efflux variability (Fig. 3) at this farm was not pronounced.

The difference in the variation from morning to midday between AF and FS coffee systems may be an indication of different sources of soil CO₂. The low variation in soil CO₂ efflux between the morning and midday at AF systems (Table 5) combined with higher spatial variation (Table 4) indicates that probably soil CO₂ efflux is mainly due to heterotrophic soil respiration (soil microorganisms), rather than autotrophic respiration (roots). Thus, AFs resemble natural forests, with trees creating a soil microclimate that is suitable for the growth of soil microorganisms (Bach et al., 2010). Higher variation in soil CO₂ efflux between morning and midday (Table 4) in the FS systems indicates that soil CO₂ efflux is mainly the result of autotrophic respiration. FS systems are subject to more stress on autotrophic and heterotrophic soil respiration because of the higher soil temperature at midday. Root respiration is driven by recent photosynthesis (Hogberg et al., 2008) and increases with air temperature (Atkin et al., 2000; Burton et al., 2002). Therefore, an increase in air and soil temperature due to lower canopy cover (Table 3) is probably responsible for the increase in soil CO₂ efflux (Table 5). Therefore, CO₂ is returned faster to the atmosphere in FS systems compared to AF systems, and is probably achieved by root respiration, which releases 8–52% of the total CO₂ fixed by photosynthesis per day (Lambers et al., 1996).

Several studies have used Q₁₀ to analyse soil CO₂ efflux and determine soil temperature sensitivity (Acosta et al., 2013; Davidson and Janssens, 2006; Kirschbaum, 2006; Reichstein et al., 2003), because Q₁₀ is sensitive to ecosystem and climatic variation (Raich and Schlesinger, 1992). However, in our study, Q₁₀ only showed significant coefficients of determination in FS_{PA} and FS_{GI}, due to low average variation in soil temperature and soil CO₂ efflux in the other systems during the study period (Table 5). Increasing altitude is correlated with a decrease in soil CO₂ efflux (Wang et al., 2011), with this trend being observed in the current study at RO (located at 1000 m altitude), which had the lowest R₂₅ values (soil CO₂ efflux normalised to a temperature of 25 °C) (Table 5). Air and soil temperature, which are important factors that regulate soil CO₂ efflux, decrease with increasing altitude, and may explain the lower values of soil CO₂ efflux that were obtained at high altitudes.

4.3. Drivers of soil CO₂ efflux

Soil CO₂ efflux is a complex phenomenon because it is the result of the combination of the respiration by plant roots and microorganisms (Kuzyakov, 2002), which are influenced by biotic and abiotic factors (Buchmann, 2000). Multivariate analysis demonstrated to be a useful tool to identify the main drivers of soil CO₂ efflux in each system (Table 6) and also among all systems (Fig. 4). Certain soil physical attributes (such as bulk density and porosity) are important in soil CO₂ efflux because they interfere with gas diffusion processes (Blagodatsky and Smith, 2012). However, as the soil physical attributes of the farms evaluated in this study were

similar (Table 2), the effects of these attributes on soil CO₂ efflux variation were not detectable.

In the current study, variation in CO₂ efflux in the AF systems was mainly explained by TN and LC (Table 6), which was probably due to the favourable soil microclimate for high microbial activity under the tree canopy. Soil temperature at 10 cm depth primarily explained variation in CO₂ efflux in the FS systems (Table 6), probably due to the absence of the tree canopy, leading to higher soil temperature and lower soil moisture (Fig. 2). The optimal soil depth temperature measurement that best explains the relationship between soil CO₂ efflux and soil temperature is still uncertain. Tang et al. (2003) and Xu and Qi (2001b) found the highest correlation of soil CO₂ efflux with soil temperature at depths of 8 and 10 cm. In our case, soil temperature at 10 cm depth best explained the detected variation in soil CO₂ efflux (Table 6), probably due to there being more microbial and root activity at 10 cm than at 5 cm soil depth. Closer to the surface, the soil is subject to more variation, due to environmental conditions, which may interfere with the activity of organisms (Cardoso et al., 2003).

Generally, CO₂ efflux correlates positively with soil temperature and negatively with soil moisture (Davidson et al., 1998; Kosugi et al., 2007; Liu et al., 2013), as verified by our study (Fig. 4). Soil temperature affects microbiota activity and root respiration (Atkin et al., 2000; Schindlbacher et al., 2011) and long-term studies (1 year or more) have reported higher soil CO₂ efflux in summer, when temperatures are higher (Bilgili et al., 2013; Liu et al., 2011; Olajuyigbe et al., 2012; Thomazini et al., 2015). Together with soil temperature, soil moisture has the greatest influence on soil CO₂ efflux (Fang and Moncrieff, 2001; Fenn et al., 2010). Soil moisture affects gas exchange in soil because it fills the soil pore space, which lowers the amount of oxygen available for aerobic microorganisms (Melling et al., 2013) and prevents CO₂ diffusion to the soil surface (Melling et al., 2005). Therefore, when the vegetation cover regulates soil temperature and moisture, it becomes a major driver of soil CO₂ efflux dynamics.

5. Conclusions

The trees in AF coffee systems promote stability of microclimate conditions, maintaining the soil moisture and preventing the increase of air and soil temperatures. Consequently, the microclimatic stability determines the soil CO₂ efflux dynamics, of which the variation tends to decrease with increases in canopy cover.

In the AF coffee system, soil attributes (TN and LC) are the main factors that explain soil CO₂ efflux variation, whereas the climatic factor soil temperature explains the variation in the FS coffee system.

This study shows the importance of evaluating soil CO₂ efflux at different periods of the day in tropical agroecosystems, to avoid overestimating or underestimating total soil respiration values. However, our study was performed in a short period and future studies are needed to evaluate this variable throughout the year and to identify the source of CO₂ efflux (i.e. autotrophic versus heterotrophic respiration) to improve our understanding of soil CO₂ efflux under AF and FS coffee systems.

Our study also shows that combining measurements of soil CO₂ efflux, soil temperature and moisture conditions, soil characteristics, and vegetation cover are promising and will help us to understand the mechanisms underlying soil CO₂ efflux to improve agricultural practices to capture and retain more carbon in the soil.

Acknowledgements

We thank the farmers for providing access to their farms for the study and the knowledge shared and to CAPES (Coordenação de

Pessoal de Ensino Superior) for providing a scholarship to the first author.

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