Journal of Tropical Forest Science 34(2): 133–141 (2022)
https://doi.org/10.26525/jtfs2022.34.2.133

DAILY AND SEASONAL VARIATION OF SOIL RESPIRATION IN A SEASONAL SEMIDECIDUAL ATLANTIC FOREST FRAGMENT AND A RESTORATION SITE IN SOUTHERN BRAZIL

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Submitted July 2020; accepted March 2021

Forest soils have a large capacity of stocking and cycling carbon, incorporated by organic matter and evaded by roots and soil microbiota as CO_2. Soil respiration can indicate ecosystem processes, but little is known about the successional, seasonal and diurnal variation in CO_2 flux. This study presents estimations of soil CO_2 efflux in a seasonal Atlantic forest fragment (FF) and an adjacent 15 years-old restoration site (RS), in two seasons (winter-dry and summer-rainy), during 24-hour periods, in southern Brazil. Measurements were performed with an infrared gas analyser at 2-hour intervals. Respiration rates were 50% higher in the rainy season, both in FF (261, against 135 mg m^{-2} s^{-1} in the dry season) and RS (237 and 127 mg m^{-2} s^{-1}), indicating that higher humidity and temperature promoted higher soil biota activity. The soil respiration was higher at FF only in the dry season, revealing that this environment may be less sensitive to water limitation. Greater overnight respiration was observed in the dry season for both sites, likely reflecting more intense microbial metabolism at night in this season. There was no rainy season diurnal variation. Seasonal and daily variation suggests that soil respiration in the RS is more sensitive to warmer and dryer conditions.

Keywords: CO_2 efflux, soil organic matter, carbon cycle, decomposition

INTRODUCTION

Soil stores a huge portion of carbon assimilated through photosynthesis by plants in the form of dead organic matter, which is continuously mineralised by soil microbiota, releasing carbon to the atmosphere as CO_2 (Grace 2004). Humidity and temperature, as well as the quality of the substratum, are the main drivers of microbiota activity (Luo 2001, Davidson et al. 2011).

Tropical forests are known for its efficient nutrient cycling and high primary productivity. However, in the semidecidual Atlantic forests two marked seasons are observed, a rainy summer and a dry winter, and this seasonality may influence carbon mineralisation (IBGE 2012).

Soil respiration, as inferred by means of CO_2 efflux, is related to the metabolic state of the soil microbiota, including decomposers and plant root-microbial associations (Janssens et al. 2010). The input of organic matter to the soil comes from litter deposition, the death of fine roots and from root exudates, all being substrata for microbial activity (Fontaine et al. 2007). Vegetation development along secondary succession leads to changes in microclimate, and the amount and quality of organic matter, therefore influencing soil respiration rates (Davidson 2000, Smith & Berry 2013).

Soil CO_2 efflux (hereafter soil respiration) can also be higher during the day, when photosynthesis occurs, gas exchange and transpiration peaks and root metabolic rate increases and is lowered at night (Kuzyakov & Cheng 2001). However, microbial activity can be limited during hot and dry days in more open environments, otherwise, in dense forests the stability of microclimate can attenuate such variations in soil respiration (Chen et al. 1999).

However, little is known about the interactions among these three sources (succession stage, season and daily time). This study presents estimations of soil CO_2 efflux in an Atlantic forest fragment and in an adjacent restoration site, in two seasons (winter-dry and summer-rainy), during 24-hour periods, aiming to track the variation in soil respiration associated with vegetation, seasonality and diurnal variation, but keeping the effects of soil type and regional climate controlled. Is it predicted that soil respiration will be higher in the forest fragment, in the rainy season and during the day, but variation will be lower in the forest fragment than in the restoration site both daily and between seasons.

MATERIALS AND METHODS

Study site

Samplings were carried out in the Mata dos Godoy State Park (23° 26' S, 51° 15' W), Londrina, North of Paraná State, Southern Brazil. Annual rainfall ranges from 1400 to 1600 mm, and annual average temperature is 21.5 °C (IAPAR 2019). Soil is eutroferric red latosol, originated from basalt rock (Stipp 2002), showing consistently high fertility (averaging 1.6 ppm P, pH 5.3, base saturation 67%, N = 6 in both sites), and a high clay content (60–70% at 0–20 cm horizon, both sites). The original vegetation is a seasonal, semidecidual form of the Atlantic forest (Torezan 2002).

Two adjacent sites were sampled, a mature, well-conserved forest fragment (FF), and a restoration site (a-15-year old reforestation with native species, RS), both inside the Mata dos Godoy State Park. Estimates from the same plots used for soil respiration measurements, in the two sites, showed higher aboveground biomass, higher litter stock and litter fall in the FF (Table 1). The forest at FF has a tall (20–25m height) and moderately dense canopy (~ 70% canopy cover in the winter, ~ 90% in the summer, 30% of the trees drop their leaves in the winter), with a dense understory comprised mostly by shrubs and few native herbs. The soil is covered with a thick, continuous litter layer with no bare soil spots. The RS is still dominated by trees originated from planted seedlings, whose height range from 10–15 m, forming a sparse canopy (50–70% canopy cover, winter-summer respectively). Due to the high light penetration, the understory has few shrubs and is dominated by the non-native grass, *Megathyrsus maximus* (guinea-grass). The soil is covered by a thin litter layer with some bare soil spots. While planted seedlings that originated RS were all from regional native species, the tree species composition in the site showed a bias toward early-succession and fast-growing species.

Sampling

In each site, four sampling points were selected in existing trails, with each point spaced at least 100 m from other points and 300 m from the forest edge (50 m in the RS). At each point, a 150 mm diameter and 70 mm height polyvinyl chloride ring (PVC-ring) was inserted into the soil (leaving 50 mm aboveground in height) one month before sampling began. Soil CO_2 efflux was estimated with a closed, ventilated PVC chamber coupled to the ring, and connected to an infrared gas analysis (IRGA) system. Air was circulated between chamber and IRGA by means of an air pump. Soil CO_2 efflux was estimated from the angular coefficient of a regression line between time and CO_2 concentration (Salimon 2003).

Sampling was done on two subsequent days in each dry and rainy season. In each measuring session, CO_2 concentration in the chamber was recorded every one second and for 7 minutes. In each season, twelve, 2-hour spaced measurements per point were carried out, i.e., six during the day and six at night. Measurements at different points in the forest and the RS were spaced by 30 minutes (7-minute recording, the rest for assembling equipment and walking in trails). The 12 measuring sessions for each of the four points per site resulted in 96 measuring sessions per season.

The dry season sampling was done in September, which is considered late for regular years in the study site region, but 2017 showed a deviance from historical patterns, considering the last 45 years, of -100 mm in rainfall and

Table 1 Sampling site ecosystem indicators

Site	Aboveground biomass mg ha^{-1}	Basal area m^2 ha^{-1}	Litter stock mg ha^{-1}	Litter fall mg ha^{-1} year^{-1}
Forest fragment	273.7 ± 104.9	49 ± 18,2	1.1 ± 0.07	1.4 ± 0.2
Restoration site	46.3 ± 27.1	13.66 ± 0.03	1.0 ± 0.1	1.3 ± 0.1

Aboveground biomass and basal area for trees over 5 cm diameter at 1.3 m, litter stock and litter fall (Arcanjo 2017, Paula 2018)

3.5 °C in temperature (Figure 1) (IAPAR 2019). Rainy season sampling was carried out in February 2018.

In every CO_2 sampling session and at each point, air temperature and relative humidity were recorded with a data logger, and soil humidity and temperature were recorded with sensors coupled to a data-logging station.

Data analysis

Soil respiration and most of microclimate variables did not follow normal distribution, thus parametric analysis was avoided. Spearman rank correlation was used to investigate overall relationships among these variables, both using the full dataset and splitting data for all four site/season combinations. Microclimate, site, season and diurnal period were used to build generalised linear models with soil respiration as dependent variable, using gamma distribution and log as linkage function. In these models, hourly times were classified into 'day' (8h00–17h00) and 'night' (20h00–05h00); twilight measures (6h00, 7h00, 18h00 and 19h00) were excluded.

A further check of diurnal variation in soil respiration (using the full set of measures) was carried out using circular analysis (Rayleigh test of uniformity, general unimodal alternative). All analyses were completed in the R environment, by means of the Vegan and Circular packages (Agostinelli & Lund 2017, Oksanen et al. 2019).

RESULTS

Microclimatic variables showed larger diurnal amplitude in the RS than in the FF, in both dry and rainy season (Table 2). Maximum recordings for air and soil temperature were higher and air humidity showed lower values in RS. The difference between the two sites was higher in the rainy season. Soil humidity showed relative

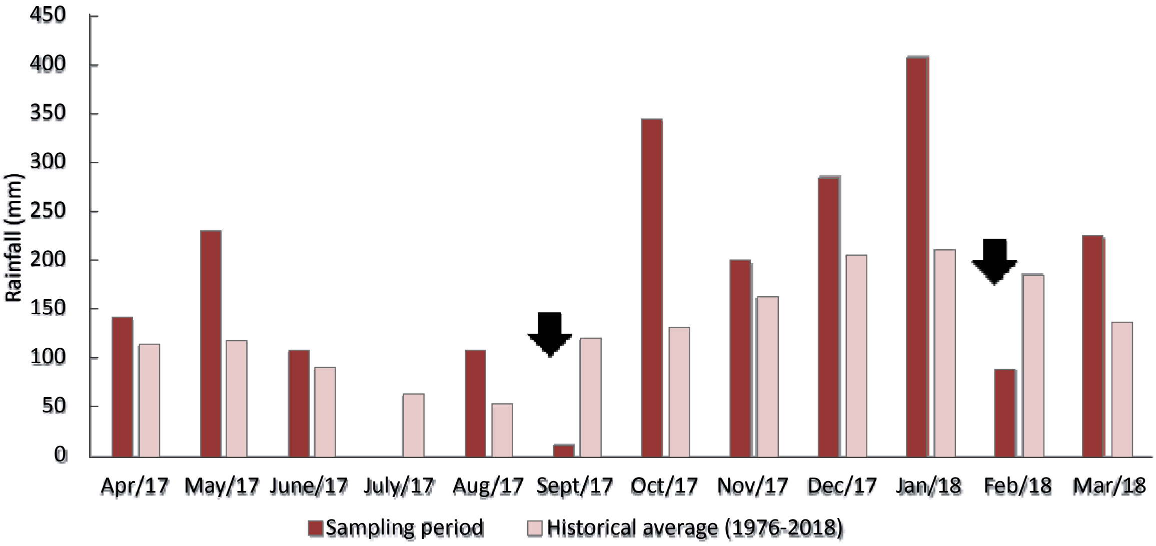

Figure 1 Monthly rainfall at the Londrina meteorological station IAPAR (2019); light bars indicate 1976–2018 average and dark bars the 2017 records, arrows point to the two samplings

Table 2 Air and soil temperature and humidity averages (and range) recorded in an Atlantic forest fragment (FF) and a restoration site (RS) in the Mata dos Godoy State Park (Southern Brazil), during dry season (September 2017) and rainy season (February 2018)

	Dry season		Rainy season	
	FF	RS	FF	RS
Air temperature (°C)	23.8 (18.5–30.5)	25.1 (18.0–35.0)	20.8 (17.0–25.0)	22.2 (16.9–28.0)
Soil temperature (°C)	20.3 (19.5–21.3)	21.4 (19.7–23.7)	21.1 (20.1–21.8)	21.6 (20.0–23.1)
Air relative humidity (%)	59.5 (41.5–75.0)	54.3 (32.5–70.0)	84.4 (75.1–92.1)	78.3 (63.8–91.6)
Volumetric soil humidity (%)	17.3 (17.0–17.5)	21.4 (21.1–22.1)	19.2 (18.4– 9.8)	30.9 (30.7–31.4)

diurnal stability and was higher in the RS, with a higher difference in the dry season (Figure 2). Soil respiration was broadly related to air temperature and humidity and, in a lesser extent, to soil humidity and soil temperature. Considering all sites and seasons together, soil respiration was higher with lower air temperature and higher air humidity (Table 3). The responses of soil respiration to soil temperature and humidity, however, were quite different across sites and seasons.

In the FF at dry season, neither temperature nor humidity influenced soil respiration, but in the rainy season soil respiration decreased with soil humidity (suggesting air displacement by water) and increased with soil temperature. In the RS, soil temperature showed a significant negative correlation with soil respiration at dry, but not at rainy season. Soil humidity showed the opposite trend, i.e. weak relationship with soil respiration at dry season, and strong negative correlation in the rainy season.

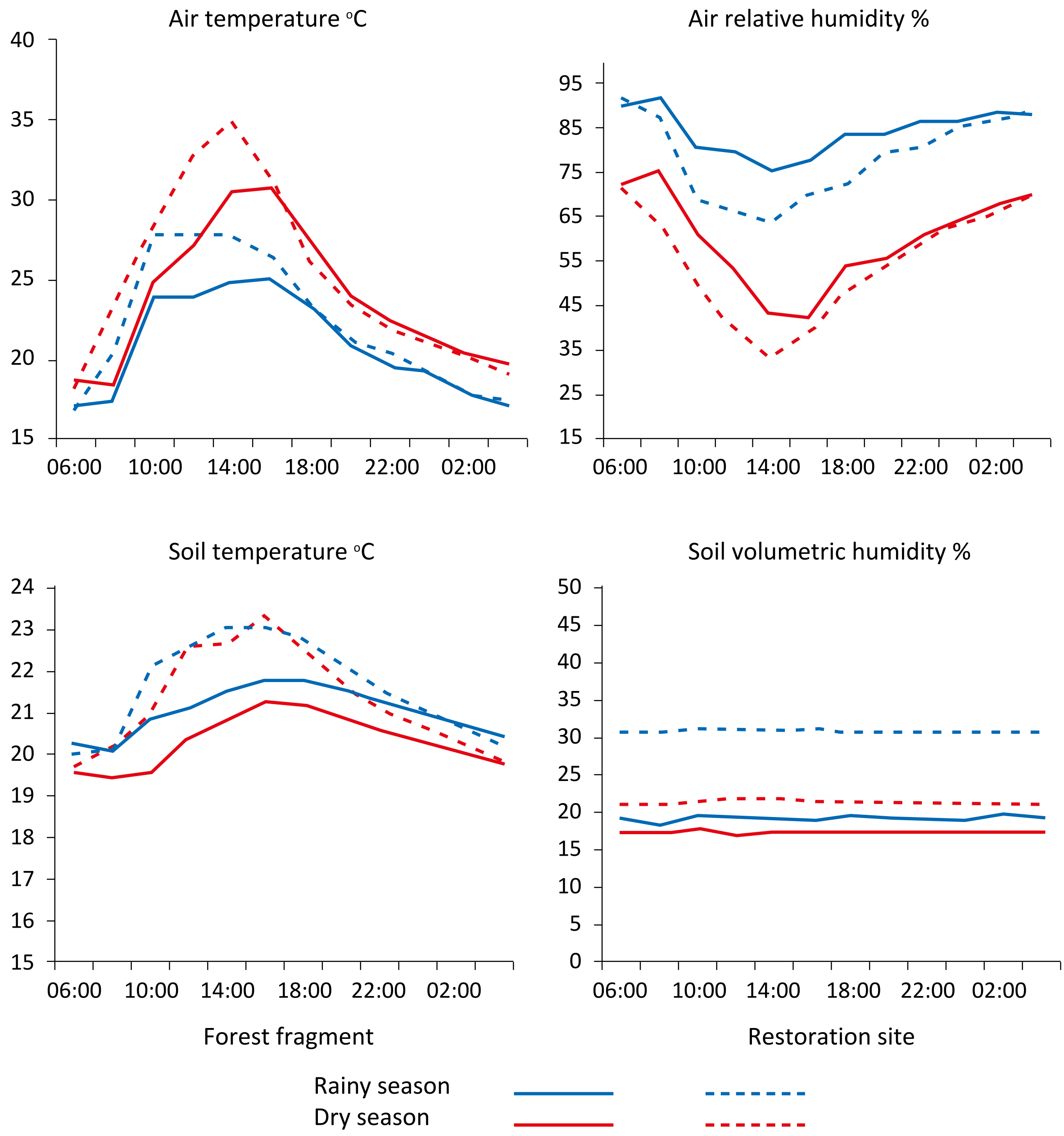

Figure 2 Average values (N = 4) for microclimatic variables in an Atlantic forest fragment (FF) and a restoration site (RS) (a native species reforestation with 15 years) in rainy season (February 2018) and dry season (September 2017)

Table 3 Spearman rank correlation coefficients for variables recorded from two adjacent sites (Atlantic forest fragment, FF, and a restoration site, RS), and in two seasons (dry season-September 2017, rainy season-February 2018)

		All sites and seasons					
		AT	AH	ST	SH		
	AH	-0.76					
	ST	0.58	-0.24				
	SH	0.07	0.13	0.35			
	SR	-0.37	0.53	0.12	0.07		
		Restoration site					
		AT	AH	ST	SH	SR	
	AT	-	-0.88	0.78	0.05	-0.01	
	AH	-0.92	-	-0.81	0.22	-0.30	
Dry	ST	0.81	-0.77	-	0.04	0.12	Rainy
	SH	0.36	-0.49	0.20	-	-0.69	
	SR	-0.47	0.29	-0.47	-0.20	-	
		Forest fragment					
		AT	AH	ST	SH	SR	
	AT	-	-0.55	0.80	0.27	0.07	
	AH	-0.92	-	-0.51	0.18	-0.71	
Dry	ST	0.63	-0.52	-	0.18	0.29	Rainy
	SH	0.16	-0.17	0.09	-	-0.37	
	SR	-0.28	0.16	0.09	0.07	-	

AT = air temperature, AH = air relative humidity, ST = soil temperature, SH = soil volumetric humidity, SR = soil respiration; highlighted coefficients are significant at $p < 0.05$

Soil respiration was roughly 50% higher in the rainy season; thus, season was the most significant factor to explain soil respiration variation in both sites (generalised linear model, $p < 0.001$, Figure 3). Soil respiration also differed between FF and RS, being higher in FF and with a higher difference in the rainy season ($p < 0.001$, Figure 3). Soil respiration varied throughout the day in both seasons (Rayleigh test, rainy season $p = 0.006$ and dry season $p = 0.045$, Figure 4), showing values slightly higher at night. Variation among data points was higher in both sites during the rainy season, following differences in soil humidity among points.

DISCUSSION

The microclimate differences between FF and RS were expected due to the higher foliage density, leading to higher interception of solar radiation and total transpiration in the FF environment (Chen 1999, Smith & Berry 2013). However, soil humidity was lower in FF in both seasons, likely because of the higher water uptake in the forest where tree biomass is higher, compared to the RS (Bruno et al. 2006). The higher difference between the two sites in the rainy season corroborates the influence on vegetation structure, as more water remain in the soil of RS during the rainy season.

Both air temperature and humidity (negatively correlated) influenced soil respiration. This is likely due to the effect on the litter layer decomposing microbiota (Pandey et al. 2007, Wang & Gu 2017). Within the range of air temperatures in September and February at the study site, higher temperatures (corresponding to lower humidity) showed lower microbial activity in the exposed litter layer.

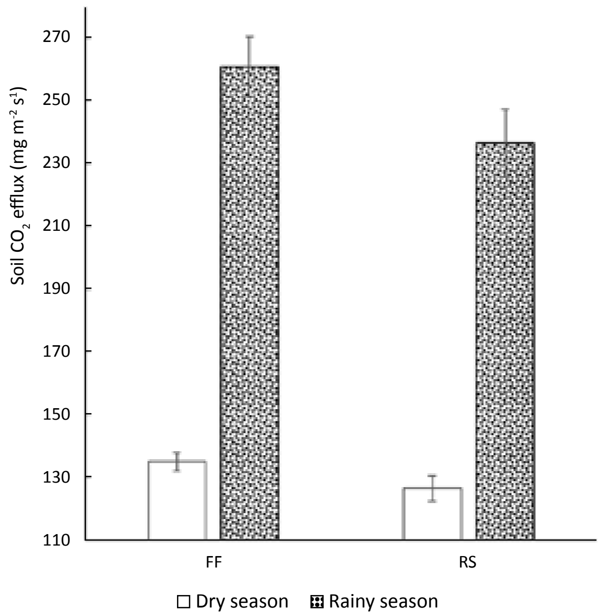

Figure 3 Soil CO_2 efflux in a seasonal Atlantic forest fragment (FF) and a restoration site (RS) in the Mata dos Godoy State Park (Southern Brazil); white columns indicate dry season (September 2017) and dotted columns the rainy season (February 2018), bars indicate standard error

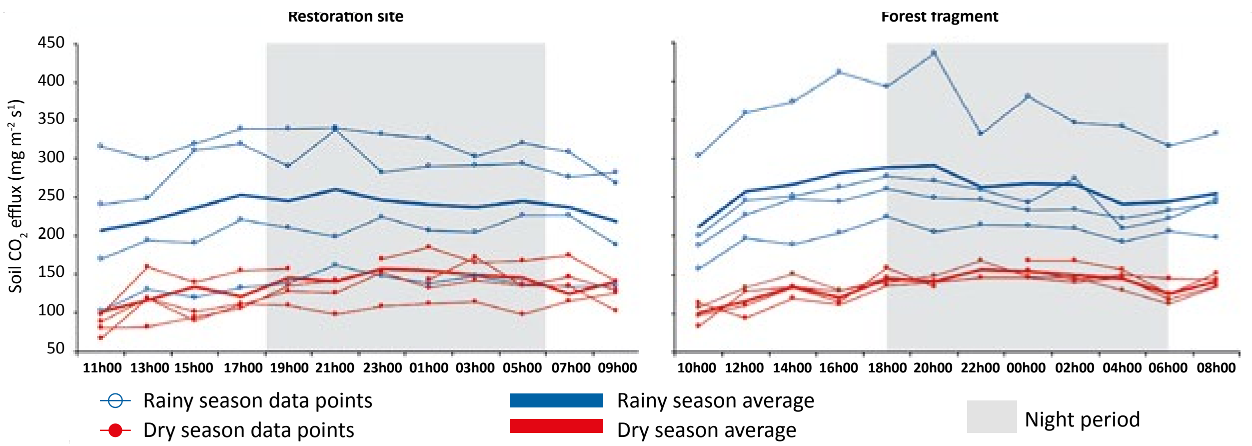

Figure 4 Soil CO_2 efflux in a seasonal Atlantic forest fragment (FF) and a restoration site (RS) in the Mata dos Godoy State Park; tiny lines with circles are individual data points, bold lines are the 4-point average; blue color indicates rainy and red color dry season

The recorded range in soil humidity at the study site may not include real drought situations, but varied water availability. During the rainy season, high water volume in the high-clayey content soil of both study sites can lead to air displacement, leading to oxygen limitation for soil microbiota, thus reducing soil respiration (Linn & Doran 1984). This occur at the FF but is more intense in the RS, where water uptake by vegetation is lower, given its lower tree biomass. Indeed, there was no significant correlation between soil respiration and soil humidity during dry season, but negative correlations at rainy season.

Soil temperature became an important factor to explaining the soil respiration in the RS during the dry season. In this situation, soil respiration decreases with soil temperature, suggesting that the warmer/drier conditions of the season combined with the open canopy of

RS, lead soil temperature to stressful levels for soil microbiota (Yuste et al. 2007). In the FF, during rainy season, the opposite was observed, i.e. no soil water limitation and the dense canopy allowing milder air conditions, leading to higher soil temperatures that boost microbial activity and higher soil respiration (Yuste et al. 2007, Han et al. 2016).

Higher soil respiration in the rainy season is related to higher water availability, which allows a higher decomposition rate (Davidson et al. 2011). Meir et al. (2008) in an Amazonian forest reported similar patterns, and Butler et al. (2012) reported 75% higher soil respiration during the rainy season in a Brazilian savanna site. Davidson et al. (2000) suggests that water availability is the main driver of soil respiration. However, the optimal point for soil water content should be near field capacity, because above this threshold the water in the soil will displace air and thus limit the oxygen availability, thus decreasing microbial respiration (Linn & Doran 1984). Nonetheless, soil temperature is the control for microbiota activity when there is no water shortage (Han et al. 2016).

Soil respiration is also responsive to changes in stand photosynthetic rate (Kuzyakov & Cheng 2001). Higher soil water availability, allowing higher photosynthetic rate, can increase the production and release of root exudates, stimulating rhizosphere microbial activity in the rainy season. Yan et al. (2011) pointed to soil water availability as a key factor in determining both photosynthesis and rhizospheric respiration. Indeed, most of the active, fine root biomass thrive at 0–10 cm depth in many forest types (Fiala et al. 2017), thus influencing surface CO_2 efflux. However, autotrophic respiration, and thus total soil respiration, can be underestimated due to upward CO_2 transport in transpiration stream during daytime (Grossiord et al. 2012). Thus, soil respiration differences between dry and rainy season may be even greater.

The difference in soil respiration between sites was lower during the dry season, suggesting that dry season conditions may limit CO_2 sources in both environments. In the rainy season, when there are no water or temperature limitations, the difference in soil respiration between sites is greater, responding to differences in ecosystem structure (FF presents higher biomass and higher litterfall) and soil aeration.

Soil respiration was slightly higher at night. Han et al. (2016) reported higher soil respiration during daytime, due to higher soil temperature in a temperate forest under high soil humidity. Cavelier & Peñuela (1990) reported higher soil respiration at night, both in a cloud forest and a decidual forest, with lesser diurnal differences in the latter. The authors explained such patterns, firstly by CO_2 displacement by water from nocturnal fog interception in the cloud forest (which also increased soil resistance to gas diffusion during the day), and increased microbial activity following elevated temperature in the first hours at the night. In the present study, given the relative diurnal stability of soil humidity, increased soil respiration was possibly due to a higher microbial metabolism in the surface litter layer when air humidity was higher. Further, as suggested by Grossiord et al. (2012), heterotrophic respiration can be negatively correlated with transpiration rate, being lower at daytime, when transpiration is higher.

The seasonal climate of the semideciduous interior Atlantic forests influences soil respiration, which was ~ 50% higher during the rainy season. However, it is not possible to attribute such variability to any of the components of respiration, i.e., hetero or autotrophic, with the present sampling design. Soil respiration was higher in FF than RS, as expected, with higher difference during rainy season. Soil respiration was higher at night, but only during the dry season, suggesting a limitation for microbial and/or plant metabolism during hot and dry days.

CONCLUSION

Soil respiration, as predicted, was higher in the forest fragment and in the rainy season, but contrary to prediction, lower during the day. The differences in soil respiration between FF and RS were higher during the rainy season, but seasonal differences among seasons were similar in both sites. Soil respiration is sensible to the microclimate in a complex way, suggesting that more research is necessary on soil respiration responses in mature forests and sites undergoing restoration to climate change.

ACKNOWLEDGEMENTS

The authors would like to thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) for finance assistance (finance code 001). The authors are greatful for the research grants from CNPq (447561/2014-6, 309244/2015-3 and 441540/2016-3) and Fundação Araucária (Paraná state research support agency). The authors would also like to thank Cavalheiro AL and Santos EM for invaluable help in the field work.

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