



Unravelling ecosystem functions at the Amazonia-Cerrado transition: II. Carbon stocks and CO₂ soil efflux in *cerradão* forest undergoing ecological succession[☆]



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ABSTRACT

The transition region between two major South American biomes, the Amazon forest and the Cerrado (Brazilian savanna), has been substantially converted into human-modified ecosystems. Nevertheless, the recovery dynamics of ecosystem functions in this important zone of (ecological) tension (ZOT) remain poorly understood. In this study, we compared two areas of *cerradão* (a forest-woodland of the Brazilian savanna; Portuguese augmentative of *cerrado*), one in secondary succession (SC) and one adjacent and well preserved (PC), to test whether the ecosystem functions lost after conversion to pasture were restored after 22 years of regeneration. We tested the hypothesis that the increase in annual aboveground biomass in the SC would be greater than that in the PC because of anticipated successional gains. We also investigated soil CO₂ efflux, litter layer content, and fine root biomass in both the SC and PC. In terms of biomass recovery our hypothesis was not supported: the biomass did not increase in the successional area over the study period, which suggested limited capacity for recovery in this key ecosystem compartment. By contrast, the structure and function of the litter layer and root mat were largely reconstituted in the secondary vegetation. Overall, we provide evidence that 22 years of secondary succession were not sufficient for these short and open forests (e.g., *cerradão*) in the ZOT to recover ecosystem functions to the levels observed in preserved vegetation of identical physiognomy.

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1. Introduction

The transition region between the Amazon and the Cerrado in Brazil is a zone of (ecological) tension (ZOT) that extends for more than 4500 km (Marimon et al., 2006). This region encompasses complex mosaics of savanna and forest vegetation with highly variable structure (Ratter et al., 1973) along the so-called “Arc of

Deforestation” (Nogueira et al., 2008). Land use patterns in the ZOT have changed rapidly in recent decades, with the area of transitional forests now largely reduced by deforestation (Alencar et al., 2004). In addition to increased land conversion to agriculture, forests of the ZOT are also subject to more intense seasonal variations and climate change than those in the central Amazon (Malhi et al., 2008). These conditions, allied to the contact tension between the two biomes, result in a hyperdynamic vegetation (i.e. fast mortality and recruitment), given their rapid turnover rates of individuals of trees (mortality vs recruitment) with many sites exceeding 3% annual turnover rates for stems >10 cm diameter (Marimon et al., 2014).

One of the most important forest types in the ZOT is the so-called *cerradão* (Portuguese augmentative of *cerrado*), as

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described by Ratter et al. (1973). Like other tree-dominated physiognomies of the transition zone the *cerradão* is “hyperdynamic” (Marimon et al., 2014). The *cerradões* contain a mixture of species from both the Cerrado and the Amazon (Ratter et al., 1973) and are an important vegetation type in the region that connects the two biomes (Ratter, 1992; Marimon et al., 2006). This vegetation type has been drastically reduced in the southern and southeastern Amazon since the 1970s (Marimon et al., 2014), particularly because legislation is less strict for removing *cerradão* vegetation, as this vegetation type is often considered a component of the Cerrado biome. As a result, most areas of *cerradão* are lost and only disconnected fragments remain.

Based on empirical evidence and computing modelling, approximately 2.1 million km² of vegetation is at risk of being lost in the Amazon by 2050, with only 53% of the original coverage remaining (Soares-Filho et al., 2006). Converting the native vegetation for agriculture and/or cattle causes losses of ecosystem functions on regional and local levels, resulting in changes in the CO₂ emissions (Malhi et al., 2008) and consequently in the carbon stock (Santos et al., 2004; Aragão et al., 2014). Such activities are responsible for disrupting the carbon balance, resulting in estimated emissions of 1.1 ± 0.7 Pg C to the atmosphere every year from tropical deforestation (Friedlingstein et al. (2010), often concentrated in marginal areas such as the Amazon-Cerrado where the climate is more seasonal than in core forest areas. Important ecosystem functions are endangered by this, including forest evapotranspiration, resulting in rainfall reduction (Aragão, 2012) and the consequent increase in carbon emissions (Malhi et al., 2008). As a “domino effect”, other components have also been modified through time due to land use change, such as decreasing of organic matter of the soil, which, consequently, alters the nutrient cycling (Diez et al., 1991; Varella et al., 2004) and soil respiration (Atarashi-Andoh et al., 2012).

The deleterious effects of establishing pasture include diminishing the nutrient cycling and organic matter of the soil, which, in general, makes the deforested lands subsequently unproductive and typically abandoned, leading to development of secondary vegetation (Günter et al., 2007; Houghton et al., 2012). Typically, tropical secondary landscapes may have forests at different stages of succession (Feldpausch et al., 2004), where during the first years of abandonment the successional process is slower compared to later stages (Vieira et al., 2003), and maybe affected by fragmentation (Günter et al., 2007). There is no clear evidence that such successional vegetation is fully capable of returning to its complete, original state in Amazonia, since diversity and the carbon stock, even in late stages of succession, is typically lower than in pristine vegetation (Houghton et al., 2012). Nevertheless, considering the vegetation growth of occupied areas by secondary succession, their atmospheric carbon absorption is potentially a major contributor to restoring the carbon balance in tropical regions (Aragão et al., 2014; Poorter et al., 2016). Unfortunately, due to the landscape fragmentation, the regeneration of abandoned pastures is a very slow process.

It is important to consider that the natural regeneration of abandoned pastures depends on the management systems and the consequent impact on the soil and on the capability of receiving new species in terms of seed sources, germination, and establishment (e.g., Cheung et al., 2009). Vegetation with a history of intense and prolonged uses, usually undergo slower regeneration (Uhl et al., 1988). Indeed, the total removal of the vegetation and processes associated with introduction of grasses (e.g. soil ploughing) can damage tree seeds and hinder the capacity of restoring the vegetation (Cheung et al., 2009). In such areas, other factors may act to limit the successional process, such as the distance between the pasture to the remaining forests (Günter et al., 2007) and the

micro-climates under tropical conditions (e.g., high temperature and low soil moisture) (Nepstad et al., 1996). Cattle grazing can also affect the soils, both physically and chemically, increasing the apparent density and decreasing porosity and fertility (Reiners et al., 1994).

Throughout the different stages of succession a few key species are typically essential for providing vegetation structure and for restoring ecosystem functionality. For example, key-species of *cerradão*, such as *Tachigali vulgaris* L. G. Silva & H. C. Lima (Fabaceae), strongly influence both the vertical structure (Franczak et al., 2011) and the hyperdynamic condition of the vegetation (Marimon et al., 2014), and its nutrient cycling rates (Oliveira et al., 2017). According to Morandi et al. (2015), this species promotes a strong rate of change in the primary successional seres. The same authors identified that the fragments of *cerradões*, when protected, have the potential to expand naturally into damaged areas via ecological succession, including into land previously occupied by ‘typical cerrado’ vegetation (*cerrado típico*, i.e. *cerrado sensu stricto*), so demonstrating that these forests can occupy open environments. Similar results were observed in another Brazilian *cerradão* landscape where the reduction of human activity reduced the area occupied by ‘*cerrado típico*’, while the area occupied by *cerradão* increased (Durigan and Ratter, 2006). These observations suggest that conservation action involving *cerradões* in the ZOT may have the effect of increasing forest cover and, consequently, Net Primary Productivity (NPP), and hence resulting in a positive carbon balance. Such measures could at least partially reverse the effects of increased CO₂ emissions and recover ecosystem functions lost by clear-cutting and burning of native vegetation in the region.

Although the deforested area in the ZOT continues to increase, in this region in particular little is known about the consequences of this disturbance on primary ecosystem functions, including changes in biomass, soil CO₂ efflux and organic matter. For example, little is known about how the replacement of native vegetation by pasture in the ZOT affects soil carbon fluxes (Varella et al., 2004), which emphasizes the urgent requirement to understand the magnitude of such fluxes in natural and modified ecosystems (Santos et al., 2004). Measuring each or most components of the carbon cycle should help increase understanding of the interactions among components and of the effects that the climatic characteristics of each environment have on the components (Huasco et al., 2013). Additionally, these types of studies can reveal the effects of man-made disturbances on ecosystem functions and their consequences for NPP and carbon balance in hyperdynamic vegetation systems.

In this study, we compared the carbon stocks and soil CO₂ efflux of a preserved area (PC) and a successional area of *cerradão* (SC) that has been used as pasture for 22 years. We tested whether the ecosystem functions linked to carbon balance had recovered after two decades, and specifically, we asked whether the natural ‘hyperdynamic’ properties of the vegetation (i.e., the tendency to have much more rapid rates of stem recruitment and mortality than typical for tropical forests (Marimon et al., 2014), cf. e.g. Phillips et al. (1994) contributed to the natural recovery of vegetation and of ecosystem functions via ecological succession. Thus, we compared the carbon cycles of the PC and the SC to test the following hypotheses: 1) the SC has higher annual increments of biomass but lower aboveground biomass, soil CO₂ efflux, litter layer content, and biomass of the superficial layer of fine roots; 2) seasonal variation is observed in CO₂ efflux, litter layer content, and biomass of the superficial layer of fine roots in both areas; 3) soil moisture is the main abiotic factor of subcanopy controlling CO₂ efflux; 4) CO₂ efflux increase with the increases in litter layer, fine root biomass, and/or aboveground biomass in both areas.

2. Material and methods

2.1. Sites description

We conducted this study in two GEM-Plots (ECI-University of Oxford) in the Bacaba Municipal Park (BMP; 14°42'22" S, 52°21'07" W), Nova Xavantina, eastern Mato Grosso State, Central Brazil. The park contains approximately 500 ha located in the Cerrado-Amazon transition region (Marimon-Junior and Haridasan, 2005). The average altitude is approximately 300 m, and the climate is Köppen's Aw, with two well-defined periods: a hot and rainy period and a somewhat cooler and dry period (Silva et al., 2008). Based on climate data from 1998 to 2015 the average rainfall is 1440 mm and the average temperature is 24,8 °C (Fig. 1). The values for rainfall and average temperature for the study period (July of 2014 to May of 2015) were extremely similar to the mean climatological values observed over the preceding 16 years, being 1494 mm, and 25.1 °C, respectively (Fig. 1).

We compared a preserved area (PC) and an adjacent successional area of *cerradão* (SC). The whole sample site spans what was previously a single unit, which was partly converted to pasture in 1987, composed of palisade grass [*Urochloa brizantha* (Syn. *Brachiaria brizantha* Hochst. Ex A. Rich. Stapf)] used as livestock forage, as shown by Google Earth Engine® satellite images (<https://earthengine.google.com/>). According to the information obtained from the original managers of this pasture, the land use included cattle breeding designed for milk production and total area used as pasture (~10 ha) harbored around 10 cows on average. These managers also informed that they did not use any grazing rotation system, even during the dry season, when the pasture productivity markedly decreased. The satellite images reveal that the recovery processes in the area started in 1994. From this date the pasture was abandoned, and lacked human intervention. Nevertheless, by

2016, after 22 years, patches of *U. brizantha* still remain in the SC area.

The species with the highest Importance Value Index (IVI) in the PC were *Hirtella glandulosa* Spreng., *Tachigali vulgaris* L. G. Silva & H. C. Lima, *Xylopia aromatica* (Lam.) Mart., and *Tapirira guianensis* Aubl (Franczak et al., 2011), whereas *Qualea grandiflora* Mart., *Q. multiflora* Mart., *Aspidosperma multiflorum* A. DC., and *Hymenaea stigonocarpa* Mart. ex Hayne had the highest IVI in the SC (Melo-Santos, 2015). The soil in both areas is a dystrophic yellow oxisol (nutrient poor), characterized as acidic, Alic, with a reduced sum of the bases, low cation exchange capacity, and a deep profile that is well drained and without concretions up to 2 m deep (Table 1).

2.2. Data collection

To describe the dynamics of aboveground biomass, we used data from previous vegetation surveys conducted in 1-ha plots (subdivided into 25 20 × 20 m subplots) to the PC and 0,5 ha (subdivided into 50 10 × 10 m subplots) to the SC. The vegetation survey in the PC was conducted between 2010 (Time 1, T1) and 2013 (Time 2, T2), and all individuals with a diameter at breast height ≥ 5 cm were recorded and measured. We estimated aboveground biomass for this area using the allometric equation proposed by Scolforo et al. (2008). The survey in the SC was conducted between 2011 (Time 1, T1) and 2013 (Time 2, T2), and all individuals with a diameter at ground level ≥ 5 cm were recorded and measured. Because the vegetation structure of the successional area was more similar to that of a typical cerrado (Melo-Santos, 2015), we used the allometric equation proposed by Rezende et al. (2006). During each inventory, following standard RAINFOR criteria (Phillips et al., 2010), all trees which fulfilled the diameter criteria for inclusion were tagged permanently with a numbered aluminum tag, and the point at which diameter was measured was painted to assure that each stem would be subsequently measured at the same point of measurement (Marthews et al., 2014). Tree identity, size, location, and growth data for each plot and census are curated at the ForestPlots.net database (Lopez-Gonzalez et al., 2011).

To measure the soil respiration, the litter layer and the superficial layer of fine roots, we used, for both the PC and SC, permanent plots of 1-ha (subdivided into 25 20 × 20 m subplots). We measured total soil respiration within plots using a portable Infrared Gas Analyzer (EGM-4; PP-Systems, UK) coupled with a holding chamber (SRC-1; PP-Systems). We installed one 10 × 10 cm PVC collar at the center of each subplot in both areas. Collars remained 5 cm above the surface to minimize damage to roots and enable coupling of the gas retention chamber following the GEM (ECI/Oxford) protocol (Marthews et al., 2014). We maintained the leaf litter in place when we inserted the collar, and then, to minimize the potential effects on soil and roots, we waited for three months to initiate data collection on efflux. Measurements of efflux were conducted monthly from June 2013 to May 2014. To estimate CO₂ efflux, we used the equations proposed by Honorio-Coronado and Baker (2010). Values of CO₂ efflux were initially expressed as g m⁻² h⁻¹ and were then multiplied by the conversion factor of 6.31 and converted to μmol m⁻² s⁻¹ (Honorio-Coronado and Baker, 2010). Concurrently, we measured soil temperature with a type-K thermocouple thermometer (Hanna Instruments, RI, USA) equipped with a 15.5 cm probe. Soil moisture was measured with a TDR-Hydrosense (Campbell, UT, USA) with a 20 cm probe.

We also collected the litter layer monthly from June 2014 to May 2015 at a random point in each subplot. To the litter layer survey, we used a specific patented tool for litter collection and thickness measurement (Marimon-Hay collector-meter), following to Marimon-Junior and Hay (2008). The collector-meter consists of one piece with lances to extract the litterlayer in the forest floor and

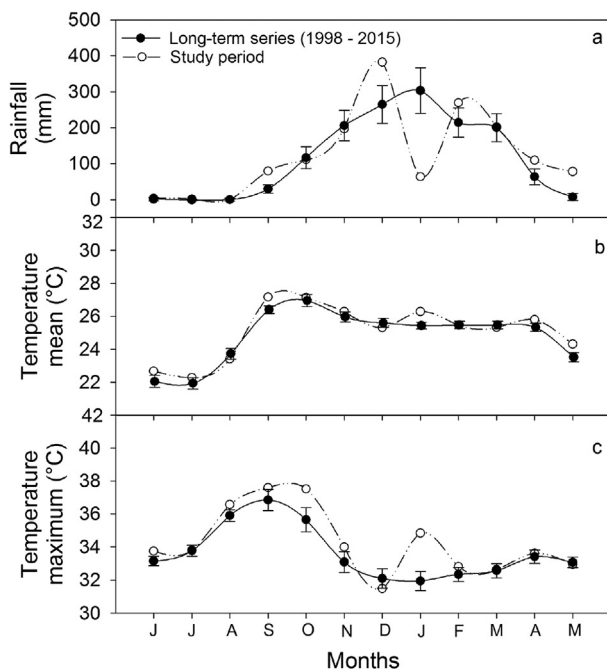


Fig. 1. Climatic variation in the study areas in Bacaba Municipal Park (BMP), Nova Xavantina, Mato Grosso State, central Brazil. Black circles indicate long-term weather series (1998–2015) and white circles weather data for the study period (June 2014; May 2015). The data for rainfall (a), temperature mean (b) and temperature maximum (c) are from meteorological station #83319 of the Brazilian National Institute of Meteorology (INMET), approximately 200 m from the study area.

Table 1
Soil attributes in preserved (PC) and secondary succession (SC) *cerradões* in Nova Xavantina, Mato Grosso, central Brazil. ECC = effective cation exchange capacity; V(%) = base saturation level; SOM = soil organic matter; \pm Standard Deviation.

Site	Depths	V	pH	Clay	Silt	Sand	SOM	P	Fe	K	Ca	Mg	Al	ECC
	(cm)	(%)	(H ₂ O)	(g/kg)			(g/dm ³)	(mg/dm ³)		(cmol _c /dm ³)				
PC	0–10	13.3 \pm 14.2	5.2 \pm 0.19	172.4 \pm 14.2	80.0 \pm 11.2	747.6 \pm 13.1	19.7 \pm 2.9	4.6 \pm 0.4	189.0 \pm 25.8	0.13 \pm 0.02	0.09 \pm 0.03	1.10 \pm 1.7	1.30 \pm 0.2	8.70 \pm 1.5
	10–20	12.5 \pm 15.0	5.4 \pm 0.17	207.2 \pm 27.6	65.2 \pm 29.0	727.6 \pm 28.3	11.8 \pm 1.1	2.2 \pm 0.5	199.3 \pm 30.8	0.09 \pm 0.03	0.02 \pm 0.01	0.85 \pm 1.4	1.31 \pm 0.1	6.43 \pm 1.4
SC	0–10	6.9 \pm 1.9	5.4 \pm 0.15	212.4 \pm 17.6	60.0 \pm 21.8	727.6 \pm 28.3	13.0 \pm 1.2	2.2 \pm 0.5	165.8 \pm 6.2	0.13 \pm 0.03	0.08 \pm 0.04	0.23 \pm 0.07	1.39 \pm 0.23	6.31 \pm 0.4
	10–20	4.6 \pm 2.2	5.2 \pm 0.08	237.2 \pm 43.3	55.2 \pm 11.6	707.6 \pm 48.3	11.4 \pm 1.1	1.7 \pm 0.6	152.2 \pm 12.4	0.08 \pm 0.03	0.03 \pm 0.02	0.14 \pm 0.08	1.64 \pm 0.25	5.43 \pm 0.23

another piece to insert into the material after the collection to measure the thickness of the litter layer. The procedures of litter layer collection was also according to the protocol suggested by Marimon-Junior and Hay (2008). We dried the litter in a forced-air oven at 65 °C until constant weight and then used precision scales to record the weights. To estimate the biomass of the litter layer, we used with inputs of sample dry weight and area of the collector.

To estimate the surface fine root mat we collected one soil sample in each subplot from a depth of 0–14 cm, for a total of 25 samples per plot. Soils were sampled twice a year: at the end of the dry period (September 2014) and at the end of rainy period (March 2015). Deformed samples of soil were collected as a soil sampler of 8 cm of diameter \times 14 cm of length (50.27 cm²) constituted by convex cutting blades. After collection of soils, we separated roots with diameters up to 5 mm, which were washed and then dried in a forced-air oven at 65 °C to constant weight. To estimate the biomass of the fine root, we used with inputs of sample dry weight and area of the collector.

In order to determine and account for the variation in the soil within each area, five sub-plots were randomly selected. At each, we collected composite samples of soil (from three different localities within the sub-plot) at depths of 0–10 cm and 10–20 cm each. After collection, the samples were air dried and sent to the laboratory for analysis and classification. Soil variables assessed were texture, pH, exchangeable Al, cation exchange capacity, sum of bases and macronutrients concentration, following to Embrapa (1997).

2.3. Numerical analysis

To compare total aboveground biomass, soil CO₂ efflux, litter layer content, and biomass of fine roots between the two areas, we used independent samples *t*-tests or unequal variances *t*-tests when the requirement for homogeneity of variances was not met. We used paired *t*-tests to test for an increase in aboveground biomass between surveys and for differences in fine root biomass between the dry and rainy periods in each area. We tested for seasonal variation in CO₂ efflux and litter layer content using a Friedman test followed by a Wilcoxon post-hoc test.

We used simple linear regressions to test the influence of aboveground biomass and fine root biomass on soil CO₂ efflux.

Then, we used multiple linear regression to test the influence of litter layer biomass, soil moisture and temperature, and rainfall (independent variables) on soil CO₂ efflux (dependent variable). Before these analyses, we log-transformed the data and tested for normality, linearity, and residual homoscedasticity assumptions. We removed variables with a Pearson product-moment correlation >0.75 to avoid collinearity. In all analyses, we assumed an alpha level of 5%.

3. Results

Aboveground biomass was 50% lower in the SC than in the PC (Table 2). Whereas the biomass of the PC increased by 9.39 Mg ha⁻¹ between 2010 and 2013, the biomass in the SC remained almost entirely stable between surveys. The soil CO₂ efflux, litter layer biomass, and fine root biomass (annual and dry periods) of the PC were higher than those of the SC (Table 2). The only exception was the stock of fine roots during the rainy period, which was similar between areas.

The smallest efflux values occurred in the dry period (June–August), particularly when rainfall and soil moisture were very low (Fig. 2). However, the efflux rates increased sharply with the first rains in September, which then remained high throughout the rainy period. These results clearly demonstrated the seasonal variation in soil CO₂ efflux.

The seasonal variation in litter layer biomass was minor, and a clear peak was not observed in either area because the months with more litter (October in the PC and March in the SC) did not differ from the most of other months (Fig. 3). The stock of fine roots was the only component without seasonal variation, with the dry and rainy periods similar in the PC (paired *t*-test = 1.84; DF = 24; *P* = 0.07) and in the SC (paired *t*-test = 0.01; DF = 24; *P* = 0.99).

Relationships between aboveground biomass and soil CO₂ efflux (preserved: *P* = 0.19; successional: *P* = 0.95) and between efflux and stock of fine roots (preserved: *P* = 0.20; successional: *P* = 0.27) were not significant in either area. However, rainfall and litter layer biomass were positively correlated with soil CO₂ efflux (Table 3), with rainfall more highly correlated than the litter layer, which showed significant influence of climate on this ecosystem function.

Table 2
Aboveground biomass, soil CO₂ efflux, litter layer biomass, and fine root stock and its respective levels of liberty (DF) estimated for preserved (PC) and secondary succession (SC) *cerradões* in Nova Xavantina, Mato Grosso, central Brazil.

Variables	PC	SC	Statistical results
Aboveground biomass (Mg ha ⁻¹) - T1	45.09	24.55	T1 \times T2 in PC (n = 25): <i>t</i> _{paired} = 8.02; DF = 24; <i>P</i> < 0.001 T1 \times T2 in SC (n = 50): <i>t</i> _{paired} = 0.19; DF = 49; <i>P</i> = 0.84
Aboveground biomass (Mg ha ⁻¹) - T2	54.48	24.71	n = 25; <i>t</i> = 9.57; DF = 48; <i>P</i> < 0.001
Soil CO ₂ efflux (μmol m ⁻² s ⁻¹)	4.54 \pm 0.37	3.60 \pm 0.36	n = 25; <i>t</i> = 3.60; DF = 48; <i>P</i> < 0.001
Litter layer (Mg ha ⁻¹)	5.98 \pm 0.31	3.94 \pm 0.28	n = 25; <i>t</i> = 9.69; DF = 48; <i>P</i> < 0.001
Fine roots (Mg ha ⁻¹) - Annual	3.83 \pm 0.46	3.16 \pm 0.26	n = 25; <i>t</i> _{var. sep.} = 2.49; DF = 37.69; <i>P</i> = 0.02
Fine roots (Mg ha ⁻¹) - Dry	4.13 \pm 0.68	3.16 \pm 0.54	n = 25; <i>t</i> = 2.18; DF = 48; <i>P</i> = 0.03
Fine roots (Mg ha ⁻¹) - Rain	3.53 \pm 0.41	3.16 \pm 0.32	n = 25; <i>t</i> = 1.43; DF = 48; <i>P</i> = 0.15

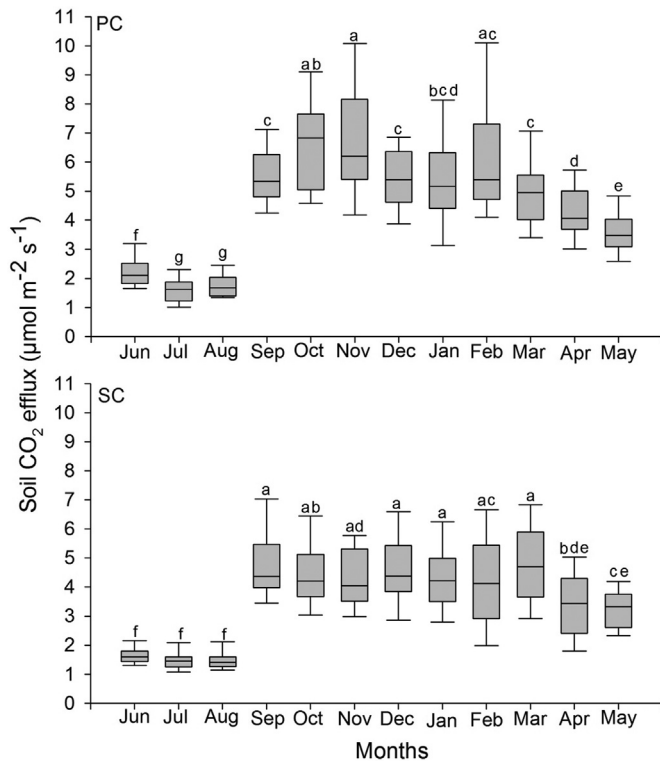


Fig. 2. Seasonal variation in soil CO₂ efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) in preserved (PC) and secondary succession (SC) *cerradões* in Nova Xavantina, Mato Grosso, central Brazil. PC: Friedman = 224.09, DF = 11, $P < 0.001$; SC: Friedman = 192.37, DF = 11, $P < 0.001$. Letters indicate comparisons between months. The central line represents the average and the extremes of the graphics and minimum and maximum values of the samples.

4. Discussion

The most surprising results was the marked gain in biomass in the PC, and the failure of the SC to recover any biomass. We discuss this in turn, focusing first on the PC. This gain may be partly explained by the thicker litter layer and its abundant superficial root mat, components that provide for and indicate more robust nutrient cycling, therefore sustaining higher primary productivity (Oliveira et al., 2017). The litter layer also represents the main source of CO₂ flux from the soil (Martins and Rodrigues, 1999; Davidson et al., 2002), and so is expected to correlate with the magnitude of decomposition and nutrient release of the whole ecosystem (Xuluc-Tolosa et al., 2003). Indeed, the association between the litter layer and fine roots is a key factor promoting nutrient availability for the vegetation (Bréchet et al., 2009) and plant nutrition in general in the dystrophic soils of the region. This increase in nutrient availability, as previously determined by Oliveira et al. (2017) in the same area, might be a factor affecting the net accumulation of biomass noted in tropical forests (Phillips et al., 1998), and potentially also allows vegetation to respond preferentially to the long-term increase in atmospheric carbon dioxide which may be stimulating tree growth in Amazonia (Brienen et al., 2015). In this case, we believe that the fast ('hyperdynamic') turnover of vegetation registered in the same area by Marimon et al. (2014), is a key factor in promoting the hypercycling of nutrients at Amazonia/Cerrado transition (Oliveira et al., 2017), and so favoring high biomass growth (Valadão et al., 2016).

The growth rate of biomass is normally accelerated on secondary forest, with large capability of capturing carbon in short periods (Feldpausch et al., 2004). Therefore, we expected the increase in

aboveground biomass between surveys to be greater in the SC than in the PC because the competition for space (Vieira and Pessoa, 2001) and other limiting factors, such as water, nutrients, and light (Zanine and Santos, 2004), was lower in the regenerating area. However, the results were contrary to this expectation, and therefore, our first hypothesis was rejected in part. We believe that several factors might hinder the biomass increment on the SC. The deforestation, followed by the implementation of the pasture and the overgrazing, result in severe nutrient loss (Uhl and Jordan, 1984), a temporal decrease in the seed bank (Gronbone-Guaratini and Rodrigues, 2002), and soil compaction (Mendonça et al., 2009) which all may hamper both the development of mature trees and the establishment of new individuals, and might have influenced negatively the biomass growth. Alternatively, some authors demonstrate that the rate of aboveground carbon accumulation might decrease as the abandonment period increases (Feldpausch et al., 2004), as fast-growing pioneer species are replaced by species of slower growth (Aryal et al., 2014). The observation that the palisade grass (*U. brizantha*) remained in the SC, which shades and competes with tree seedlings, limiting their development (Holl, 2002), suggests that the legacy of the previous land use itself has provided a long-term brake on the biomass growth and carbon sequestration capacity of the secondary Cerradao vegetation at our study site.

When pastures are abandoned secondary succession is initiated, with woody species being slowly added to the community (Guariguata and Ostertag, 2001). However, although the first years of succession in land originating from agricultural abandonment is marked by the fast accumulation of aboveground biomass, the process slows down in the following phases (Vieira et al., 2003; Feldpausch et al., 2004). Because of that, preserved ecosystems usually sustain a much larger biomass than recovering ecosystems (Guariguata and Ostertag, 2001). It is also important also to consider that during the initial stages of succession, the microclimate of disturbed environments, which are generally open areas, does not favour colonization by most tree species (Nepstad et al., 1996), which limits the regeneration to pioneer species (Esquivel et al., 2008). On the other hand, through following stages, once secondary species are well established, other issues might hinder the biomass accumulation, such as the formation of edges (Aragão et al., 2014) and the distance between the vegetation and recovering and the remaining vegetation affecting the availability of propagules of late successional taxa (Günter et al., 2007; Holl et al., 2000). However, our study areas were adjacent to one another. This should facilitate and accelerate species dispersal (Augspurger and Franson, 1988) and suggests that dispersal limitation is not a barrier to biomass gains in our secondary Cerradao site. Regardless, clearly substantially more time is apparently required to attain complete recovery.

On the other hand, our hypothesis that lower aboveground biomass in the SC would yield lower soil CO₂ efflux rates was supported. The structural differences between the two areas might explain the higher emissions in the PC because the biomass of an ecosystem is one of the primary factors that determines carbon emissions (Houghton et al., 2009). Thus, vegetation types with high aboveground biomass usually have high soil CO₂ efflux (Pinto-Junior et al., 2009) due to increased autotrophic and heterotrophic respiration. Additionally, the previous land use of the SC might have contributed to soil compaction, which reduces the size of micro- and macropores, restricting gas diffusion (Ferreira et al., 2004) and altering decomposer activity. Furthermore, the PC had a more closed canopy and a thicker litter layer than those in the SC. With this greater availability of organic matter, nutrients are released via decomposition, which favors the development of a fine root layer (Sayer et al., 2006; Valadão et al., 2016; Oliveira et al.,

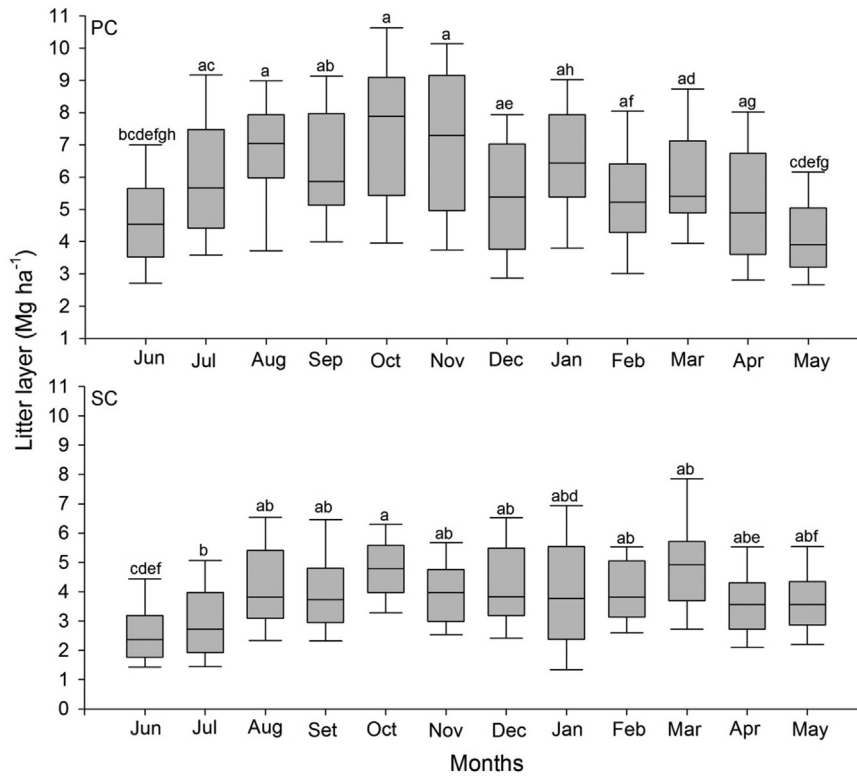


Fig. 3. Seasonal variation in litter layer biomass (Mg ha^{-1}) in preserved (PC) and secondary succession (SC) *cerradões* in Nova Xavantina, Mato Grosso, central Brazil. PC: Friedman = 53.50, DF = 11, $P < 0.001$; SC: Friedman = 53.62, DF = 11, $P < 0.001$. Letters indicate comparisons between months. The central line represents the average and the extremes of the graphics and minimum and maximum values of the samples.

Table 3

Results based on a multiple regression model for soil CO_2 efflux as predicted by microclimate ($n = 12$ months) in preserved and secondary succession *cerradões* in Nova Xavantina, Mato Grosso, central Brazil. SE = standard error.

Variables	Preserved <i>cerradão</i>				Successional <i>cerradão</i>			
	$R^2_{\text{model}} = 0.96; F_{(4, 7)} = 45.70; P < 0.001$				$R^2_{\text{model}} = 0.96; F_{(4, 7)} = 44.04; P < 0.001$			
	R^2_{partial}	F	Beta \pm SE	P	R^2_{partial}	F	Beta \pm SE	P
Precipitation	0.70	133.18	0.95 ± 0.08	<0.001	0.36	66.08	0.99 ± 0.12	<0.001
Litter layer	0.06	10.66	0.39 ± 0.11	0.01	0.03	5.60	0.23 ± 0.09	0.04
Soil moisture	0.01	1.32	0.09 ± 0.07	0.24	0.03	5.42	-0.25 ± 0.10	0.06
Temperature soil		1.61	-0.14 ± 0.12	0.28		0.00	0.004 ± 0.08	0.96
Interaction	0.19	—	—	—	0.54	—	—	—

2017). Moreover, the synergy between decomposition of the litter layer and activity of fine roots is key in determining soil CO_2 efflux (Davidson et al., 2002).

The *cerradão* is often classified as a forest and not a savannah, but compared with other typical Amazonian vegetation, *cerradão* has substantially fewer trees and a less dense canopy (Marimon-Junior and Haridasan, 2005; Hoffmann et al., 2009). These differences could explain the low efflux in the PC compared with that in other forests of the ZOT. For example, Rocha et al. (2014) recorded an average efflux of $11.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ and Valentini et al. (2008) with a flux of $\sim 7.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is 60% and 40% greater than in the PC, respectively. However, in the same PC this current study, Butler et al. (2012) used similar equipment (CIRAS; PP systems) and found a soil CO_2 efflux of $5.2 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is only slightly higher than the value that we recorded in 2013–2014. These among-site differences, including the low values recorded by us and Butler et al., might therefore be due to slight climatic variations between locations or between study periods, which can affect soil CO_2 emissions (Bae et al., 2013), as much as to the density

of tree populations per se.

Notably, soil respiration decreased dramatically in the very dry months in both study plots. Such a decrease is likely related to the influence of moisture on decomposition rates (e.g., Meir et al., 2008), with soil moisture much lower in dry periods (e.g., Luizão and Schubart, 1987). Other authors also report a decrease in soil respiration rates during periods of low moisture (Butler et al., 2012; Schwendenmann et al., 2003). In our sites, after the first rains in September, efflux increased sharply and rapidly in both areas, similar to the observations of Davidson et al. (2002) further north in Mato Grosso. This type of strong relationship with climatic seasonality was also recorded in a different forest in the ZOT, 180 km from our study area, with the highest values of efflux coincident with the highest levels of soil moisture (Rocha et al., 2014). A similar relation is also observed in secondary forests grown on abandoned pastures in southwestern Amazonia (Salimon et al., 2004). Evidently, in Amazonia and perhaps especially in its more seasonal border zones, soil respiration can be quite tightly controlled by moisture supply.

The CO₂ efflux remained high in both areas in months with rainfall, regardless of the frequency, intensity, or duration of the rains. Consequently, CO₂ efflux apparently was not limited by the amount of rainfall but by the occurrence. Thus, in months of low rainfall within the rainy season (e.g., January), CO₂ efflux in the PC and SC was not affected because even a little rainfall was apparently sufficient to maintain the moisture of the litter layer, stimulate the activity of decomposers, and maintain a high efflux of CO₂ (Amundson and Davidson, 1990).

We expected the litter layer in the PC to be thicker than that in the SC because the amount of soil organic matter is typically regulated by the incorporation of aboveground biomass, which was higher in the PC, into the litter and soil (Batjes, 1996). Sanches et al. (2008), working in a transition forest at Northern Mato Grosso State, Brazil, found values for the litter layer (~6 Mg ha⁻¹) similar to those observed in the PC area. Our results supported the hypothesis of seasonal variation in the litter layer biomass, which was notably similar in both areas. This result indicated that this ecosystem function might be approaching equilibrium, despite the lower biomass of the litter layer in the SC. However, the temporal variation in the litter layer in both areas was small, and values were constantly high even during the rainy period, which was in contrast to our hypothesis that predicted a smaller litter layer on the soil during the rainy period. In these ecosystems, litter accumulation usually occurs when plants experience water stress during drought and leaves are eliminated to avoid water loss (see Pinto-Junior et al., 2009). Thus, our results suggested that plant physiological responses to water stress possibly started during the dry period but extended to rainy months. However, a severe decrease in rainfall in January might also have contributed to reduced decomposition rates, and therefore, a thick litter layer remained in the following months.

The PC had the highest annual productivity of fine roots, which was likely due to the combined influence of aboveground biomass and the thickness of the litter layer because an increase in the availability of soil organic matter facilitates root development, as discussed earlier (Sayer et al., 2006; Valadão et al., 2016; Oliveira et al., 2017). Generally, the development of roots increases in dry periods to meet plant water demands (Meinzer et al., 1999). However, no evidence of seasonal changes in fine root biomass in the PC and SC was observed. By contrast, plants of the PC were apparently more efficient in responding to water stress because they produced more fine roots during the dry period than were produced in the SC. Nevertheless, when moisture conditions were equally favorable for root growth in both areas, fine root production was similar, which showed that root growth and associated biogeochemical cycles might be recovering in the SC.

Litter layer biomass and rainfall influenced soil CO₂ efflux in both areas, and our results indicated that efflux was equally influenced by both variables. Therefore, a thick litter layer does not compensate for a lack of rainfall because moisture activates decomposition processes (Luizão and Schubart, 1987). The opposite is also true because leaf litter is essential to maintain microbial activity. For example, we recorded low efflux in August even with a thick litter layer because rainfall was close to zero in this period. Conversely, with the accumulation of litter at the end of the dry months and the increase in moisture at the start of the rainy period, a favorable environment was created for decomposition to resume, increasing soil CO₂ efflux (Malhi et al., 1998; Williams et al., 1998). This increase was particularly evident in September in both areas.

The SC had lower values of all variables analyzed (i.e., biomass, soil CO₂ efflux, litter layer biomass, and surface fine root biomass), which indicated that the functions of the ecosystem had not yet completely recovered. However, the similarity in aboveground biomass between the two surveys in time indicated that the

recovery of the successional area might be limited. Generally, in the SC, the low aboveground biomass most likely caused lower soil CO₂ efflux and lower carbon stock in both the litter layer and in fine roots. Thus, although regrowth and secondary forest establishment can be key to restoring the carbon balance (Aragão et al., 2014), our results indicated that ecosystem functions were not yet fully recovered even after more than two decades and where the intact vegetation has a very modest and relatively low biomass compared to most tropical forest ecosystems. Carbon stocks and flows within the SC continued to differ substantially from those of the PC, despite 22 years since the pasture was abandoned. Although some studies report that pasture regeneration is slow (Günter et al., 2007), it is not currently possible to determine when ecosystem functions of the SC will be similar to those of the adjacent PC or other undisturbed forests. The fact that our SC effectively failed to gain any biomass over the period observed suggests that overall recovery will likely take decades more, but the total time required cannot be directly predicted from our current results. Clearly, very extended monitoring of forest dynamics, biomass gain, and ecosystem carbon cycling processes are needed to assess the long-term trajectories of recovery in this important vegetation type.

5. Conclusions

Our results indicated that the restoration of ecosystem functions of more open and less degraded forests (e.g., *cerradão*) converted to other uses (e.g., pasture) will likely take at least several decades. Here, we provide evidence that 22 years were not sufficient for complete recovery of these forests, even though the vegetation in the ZOT is hyperdynamic in terms of stem, biomass and nutrient cycling. However, also based on the results, some ecosystem functions, such as growth of the surface fine root mat and litter layer carbon stocks, were clearly recovering. Overall, the results suggest that *cerradões* and other transition zone forests, which are all highly threatened by deforestation in the ZOT, may lack full resilience in terms of capability of restoring ecosystem carbon storage and carbon uptake functions after the intense disturbances associated with the combination deforestation and subsequent cattle pasture.

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