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Interactions between Vegetation, Hydrology, and Litter Inputs on Decomposition and Soil CO₂ Efflux of Tropical Forests in the Brazilian Pantanal

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Abstract: Climate change has the capacity to alter water availability and the litter production of tropical forests, which will alter rates of carbon (C) cycling and storage. We conducted a short-term field experiment in two hydrologically diverse forests in the Brazilian Pantanal to assess the initial response of litter decomposition and soil respiration (Rsoil) to variations in litter pool size. Total annual Rsoil and decomposition significantly declined with litter removal and increased with litter addition, but the rate of litter decomposition was highest for plots where litter was removed. Rsoil was positively related to soil organic matter content and the rate of litter decomposition, but not soil moisture or temperature, suggesting that the litter treatment effects on decomposition and Rsoil were due to changes in C availability and not litter effects on the soil environment (i.e., temperature and moisture). Rsoil was not significantly different between the forests studied here even though they had large differences in hydrology; however, litter decomposition was significantly higher in seasonally flooded forest, especially when augmented with litter. These results suggest that alterations in litter production from land use and/or climate change will alter short-term rates of decomposition and Rsoil for these and other floodplain forests of the Pantanal and Amazon Basin.

Keywords: carbon cycle; Cerrado; climate change; hyperseasonal forests; mass-balance models; respiration; tropical savanna

1. Introduction

Climate change scenarios for the southern Amazon Basin predict an increase in the dry season length [1], and some reports suggest that dry season intensification may already be occurring [2,3]. Increases in the dry season length have the potential to affect carbon (C) storage and cycling [4–6], especially in forests and woodlands in the southern part of the Amazon Basin which already suffer from drought stress during the dry season [7–10]. In particular, understanding climate controls on litter decomposition and soil CO₂ flux dynamics are key to understanding how climate change will alter the C balance of terrestrial ecosystems [11–13]. Soil respiration (Rsoil), which includes both autotrophic and heterotrophic respiration, releases approximately 98 PgC to the atmosphere each year [12], which is >7 times the current rate of C-equivalent fossil fuel emissions [14]. Rates of Rsoil have been increasing by approximately 0.1 PgC year⁻¹ since 1989 in response to an increase in global air temperature,



and small changes in Rsoil have the potential to influence atmospheric CO₂ concentrations associated with climate change [12].

While soil CO₂ efflux has been studied extensively, there is still uncertainty about how climate change will alter spatial and temporal variations in litter decomposition and Rsoil [5,11,12]. Warming is expected to alter rates of litter decomposition and Rsoil through changes in litter and soil temperatures [14,15] and water availability [5]. However, climate change will also alter forest phenology [16], mortality [17], productivity [4,18,19], and species composition [20], which can alter litter decomposition and Rsoil through changes in soil and forest floor C quantity and quality [11,21,22]. Plant litter has been estimated to contribute between 18 and 48% to the total Rsoil in temperate [23–26], subtropical [27], and tropical forests [28,29]. Some of this contribution is due to the "priming" effect of fresh litter on rates of Rsoil [29]; however, litter pool mass and thickness also feedback on soil moisture and temperature [11,14,15,30]. Thus, climate change impacts on litter and soil C emissions are complex because changes in temperature and moisture can both directly and indirectly affect rates of litter decomposition and Rsoil.

Recent global Rsoil inventories suggest that tropical ecosystems may be responsible for approximately 67% of the total annual global CO₂ efflux [12]. This large contribution is undoubtedly driven by high net primary production and consistently warm and moist climate conditions [12,30]. However, tropical ecosystems are diverse, ranging from tall, dense forests to open grasslands, and well-drained upland to seasonally flooded landforms that have widely different rates of net primary production, litter production, soil C, species composition, and hydrology [31–33]. These differences are likely to cause variations in Rsoil, and how climate variables interact with vegetation to affect rates of Rsoil [6,11,12].

Here we describe the initial results of a field experiment designed to assess interactions between vegetation, hydrology, and litter input on tropical forest litter decomposition and Rsoil. The experiment was conducted in an upland and a seasonally flooded (hyperseasonal) forest in the Brazilian Pantanal, which is one of the largest floodplains in the world, covering 160,000 km² [34]. Because of flat topography and low elevation, the Pantanal has a variety of forests that are subject to seasonal flooding, but there are also areas with slightly higher elevation that are well-drained throughout the year [35]. These conditions are broadly similar to lowland forests of the Amazon River floodplain, and many of the tree species found in the Pantanal forests are native to the Amazon Basin, making the results described here applicable to other tropical floodplain forests [9,16,34,35]. Forests arrayed across this hydrologic gradient exhibit large differences in aboveground biomass and litter production but, interestingly, seasonally flooded and upland forests share many of the same tree species [36–38]. Furthermore, this region is sensitive to human impacts, and climate change has been intensifying and altering hydrology [39]. Thus, the aim of this work was to quantify how variation in litter input and hydrology altered the litter decomposition and Rsoil of upland and seasonally flooded forests. We hypothesized that decomposition and Rsoil would decline with litter reductions and increase with litter increases. Furthermore, we hypothesized that the direct effects of litter input would affect decomposition and Rsoil more than the indirect effects of litter manipulation on soil environmental properties (i.e., soil temperature or moisture). Finally, we hypothesized that litter decomposition and Rsoil would be higher in more well-drained soils because of the periodic anoxia that occurs in response to seasonal flooding.

2. Materials and Methods

2.1. Study Area

The study was conducted at Baía das Pedras (16°29′52″ S; 56°24′46″ W) in the northern Brazilian Pantanal, which is approximately 130 km SSW from Cuiabá, Mato Grosso, Brazil. This location has an average annual rainfall and temperature of 1420 mm and 26.5 °C, respectively [33,35]. The climate is defined by a prominent dry season from May–September and a wet season from October–April,

and during the wet season, low-lying areas within the northern Pantanal can experience 0.5–2.0 m of flooding [40].

The field experiment was conducted at two stands within Baía das Pedras, a seasonally flooded gallery forest and an upland forest that were located on flat, level terrain at an elevation of about 125 m above sea level and separated by approximately 200 m [37]. Both forests were composed of 7–15 m tall trees and had a closed canopy with minimal understory vegetation [41]. Both forests had similar tree density (1479 and 1441 trees/ha), and approximately 34% of the tree species encountered were found at both sites [37]. The seasonally flooded gallery forest was situated on a broad flat floodplain and was dominated by the tree species Mouriri elliptica Mart., Vochysia divergens Pohl, and Eugenia florida DC [37]. During the wet season, this forest experienced a 0.3–0.5 m seasonal flood pulse that began in late February and lasted approximately 4–6 weeks. This type of forest is considered to be "hyperseasonal" because it is subjected to both wet season flooding and dry season drought [34,38]. The upland forest was situated on a slightly higher (ca. 5 m) flat plain than the gallery forest, and was never flooded during the study period [42]. This forest was dominated by a palm Scheelea phalerata (Mart.) and by the broad-leaved trees M. elliptica and Aspidosperma cylindrocarpon M. Arg. [37]. Both sites had clay-rich soil with a sand:silt:clay ratio of 16:33:51% for the upland forest and 12:37:51% for the hyperseasonal forest [41], with similar bulk density, total N, and cation exchange capacity [37]. In addition, both forests have an O-horizon that is on average 5 cm deep and an A-horizon that extends to at least 30 cm. Both study sites were located in a protected area and have not experienced fire for >35 years [41].

2.2. Experimental Design

The experiment [37] was conducted from February 2014 to February 2015. Six blocks were randomly located at each site. Blocks were separated by 2–15 m, and each block consisted of three 2×2 m treatment plots; an unmanipulated control plot, a plot with the surface litter removed (removal plot), and a plot with additional surface litter (addition plot). During the initial treatment and each month following, litter was removed from the removal plot, weighed, recorded, and evenly dispersed on the addition plot.

Litter pool stocks were measured monthly in each block, but outside of the treatment plots to preserve the surface litter pool, by randomly collecting surface litter from a 25 cm diameter (490 cm²) circular quadrat. Litter was weighed fresh in the field, returned to the lab, dried at 72 °C, and re-weighed to determine the moisture content of the surface litter each month. The litter moisture content was used to calculate the dry litter mass of fresh litter taken from the removal plots and added to the litter addition plots. The average monthly dry mass of the surface litter pool in the control plot was assumed to equal the dry mass of the surface litter pool randomly sampled within each block. The average monthly dry mass of the surface litter for the addition plot was assumed to be equal to the dry mass of the control plot + the dry mass of the litter produced during the previous month + the dry mass of the litter added to the plot from the removal plot.

Monthly litter production was also measured by harvesting the litter trapped in a 1 m² circular collector consisting of a 1 mm nylon mesh affixed to an aluminum frame that was approximately 1 m tall (n = 1 collector/block, 6 collectors/site). Litter (leaves, stems, fruits, and flowers) retained by the collectors was removed, dried at 72 °C, and weighed to determine the dry mass of each litter fraction produced per month. Nearly all of the litter retained (ca. 88–96%) was in the form of leaves (76% and 52% for the seasonally flooded and upland forests, respectively) and small stems (20% and 36% for the seasonally flooded and upland forests, respectively).

2.3. Field Data Collection

Soil (autotrophic + heterotrophic) respiration (Rsoil) was measured at two randomly chosen points in each plot approximately every month between February 2014 to February 2015 using a

closed chamber system by circulating air between an infrared gas analyzer (EGM-4, PP systems, Amesbury, MA, USA) and an 1170 cm³ opaque chamber (SRC-1, PP systems, Amesbury, MA, USA). During each measurement, the chamber was affixed to the soil surface on a randomly located point in each plot. The bottom surface of the chamber was slightly beveled to ensure a tight seal to the soil surface to minimize the potential for leaks. Litter was not cleared from the measurement point prior to measurement, ensuring that Rsoil measurements in control and added litter treatments were influenced by respiration from both litter and mineral soil. After affixing the chamber to the soil surface, the infrared gas analyzer (IRGA) was automatically re-zeroed and a chamber fan was activated to mix the chamber. Chamber air was passed through the IRGA at a flow rate of 1 L/min, and the change in the CO₂ concentration within the chamber during the measurement period (dC/dt) was calculated using a quadratic function. The Rsoil rate was calculated using system software as dC/dt × V/A, where V is the volume of the chamber (1170 cm³) and A is the area of soil enclosed by the chamber (78.5 cm²). Each measurement took approximately 1–2 min per plot, and measurements were made at each site during the mid-day period (i.e., 1000–1400 h local time). Both sites were measured on the same day, except in the gallery forest in March 2014 when the site was flooded.

Soil temperature was measured at a soil depth of 5 cm during each respiration measurement with a soil temperature probe (STP-1, PP systems, Amesbury, MA, USA). Immediately after the measurement of Rsoil, a 10 cm deep \times 10 cm diameter (860 cm³) soil core was extracted from the Rsoil measurement point (2 per plot) for determination of soil water content, organic matter content, and root (>2 mm in size) density. Soil water content was measured gravimetrically as [(Mf – Md)/Md] \times 100, where Mf was the fresh mass of the sample and Md was the dry mass of the sample after drying the soil at 105 °C. Root fragments were removed from the soil samples by sieving, cleaned of debris, and dried at 72 °C. Root density was calculated as the dry root mass per unit core area (g dry weight/m²). Soil organic matter (SOM) was analyzed using the Walkley–Black method [43] and converted to a pool size (g/m²) by multiplying the SOM concentration by the soil bulk density.

2.4. Data Analysis

Rates of annual total (leaf + stem + flower + fruit) litter decomposition were calculated for each treatment plot using a simple mass-balance model [44,45], which assumes that the rate of change in the forest floor litter mass (dF/dt) is calculated as the difference between litter production (P) and decomposition (D),

$$dF/dt = P - D \tag{1}$$

Assuming that litter accumulation reaches a steady state over an annual basis [44], dF/dt = 0 and Equation (1) can be modified such that D can be calculated as a function of the average forest floor mass (F) multiplied by a rate constant (k; year⁻¹),

$$dF/dt = 0 = P - Fk$$
⁽²⁾

In this respect, k can be approximated as P/F; however, P is not strictly continuous because it varied due to both treatment and phenology. Thus, k was estimated over an annual time scale for each treatment (kT) as the total annual litter production for each treatment (PT) divided by the average annual forest floor mass of each treatment (FT),

$$kT = PT/(FT + PT)$$
(3)

where PT for the control and removal treatments was assumed to equal the total annual litterfall collected from the litter fall traps while P for the litter addition treatment was assumed to equal the total annual litterfall + the litter added from the removal plots. The denominator of Equation (3) is adjusted for the total P for each treatment because PT varies due to both ecosystem phenology and/or litter manipulation [44]. Thus, annual rates of decomposition for each treatment (DT) = $kT \times FT$.

Time series of Rsoil, soil moisture, organic matter content, temperature, root density, and litter pool size were analyzed using a 3-way repeated-measures analysis of variance (ANOVA) (RM-ANOVA), with site (S), treatment (T), and time (M) as fixed-effects, while a 2-way RM-ANOVA was used to assess the effects of site and time on litter production. Box's M and Mauchly's tests were used to test the assumptions of equality and compound-symmetry (sphericity), respectively (p < 0.10) of the between-group covariance matrices, and probability values were calculated using the Geisser-Greenhouse corrections for data that violated these assumptions [46].

Annual totals (Rsoil and litter decomposition) and averages (kT, litter pool size, root density, and soil temperature, moisture, and organic matter content) were analyzed using a randomized-complete block ANOVA with each treatment repeated within each block and site treated as a fixed effect. However, blocking did not increase the mean square of the site and treatment effects sufficiently to justify the loss of error degrees of freedom associated with blocking, and, more importantly, to affect the interpretation of the main effects or their interactions, so we re-ran the ANOVAs as 2-way ANOVAs with site and treatment as the main effects to increase the error degrees of freedom. In the event of a significant 2-way ANOVA, a Tukey–Kramer post-hoc test was used to determine which means were significantly different (p < 0.05). Differences in total litter production between the upland and flooded forests were analyzed using a 2-sample *t*-test.

Structural equation modeling (SEM) [47] was used to evaluate the direct and indirect effects of average litter pool size (F), soil moisture (Sw), temperature (Ts), SOM, and root density (Root) on annual rates of litter decomposition (D) and Rsoil calculated over the study period. Structural models were developed from six linear multiple regression models, including (1) Rsoil = f(F, D, Sw, Ts, SOM, Root); (2) D = f(F, T, Sw); (3) SOM = f(F, Root, Sw); (4) Root = f(F); (5) Sw = f(Ts, F, Root); and (6) Ts = f(F). Partial least-squares analysis was used to quantify the standardized partial-regression coefficient for each independent and response variable [47]. Direct effects of the hypothesized variables on Rsoil and D were taken to be the standardized partial-regression coefficients quantified from models (1) and (2), respectively, while indirect effects of hypothesized variables on Rsoil and D were quantified as the product of the standardized partial regression coefficients summed across each possible path [47]. All statistical analyses were conducted using NCSS statistical software (version 7, NCSS, LLC, Kaysville, UT, USA).

3. Results

3.1. Site Characteristics and Climate

Total annual precipitation was 1549 mm during the study period, which was approximately 120 mm above the long-term average of 1420 mm for the region. Rainfall was distinctly seasonal, with a 5-month dry season (defined as the consecutive months when rainfall < 10 cm) between June–October (Figure 1a), which is typical for the northern Pantanal [33,35]. February 2014 was the wettest month, with rainfall exceeding 32 cm, and August was the driest month with no measureable rainfall.

Surface (0–10 cm) soil moisture content was significantly higher in seasonally flooded forest than in upland forest, and there was no effect of litter manipulation on soil moisture (Table 1). Soil water content was consistently 10–20% higher in the flooded than in the upland forest, even during the dry season (Figure 1a). There was also a statistically significant site \times time (S \times M) interaction (Table 1), which was due to site differences in soil moisture between March and June 2014. During this time, the flooded forest soil was saturated because of the arrival of 0.3–0.5 m of surface flooding, while the upland forest exhibited a decline in soil moisture (Figure 1a). Temporal trends in soil water content were qualitatively similar to trends in precipitation, with the highest values observed in the wet season months (March and January for the upland forest and May for the flooded forest), and the lowest values observed during the dry season months (Figure 1a). On average, soil water content in the flooded forest was over 2-times higher in the flooded forest than in the upland forest over the study period. Average monthly temperature varied by 6.5 °C over the study period, with the warmest temperatures observed during the wet season and the coolest temperatures observed during the dry season (Figure 1b). Soil (0–5 cm) temperature was significantly higher in flooded forest than in upland forest, but there was no effect of litter manipulation on soil temperature (Table 1). There was a significant S × M interaction, which was due to differences in soil temperature observed between December 2014 and January 2015 (Figure 1b).



Figure 1. (a) Total monthly precipitation (white bars) and mean (\pm se; *n* = 6) soil moisture for control plots located in the seasonally flooded (closed symbols) and upland (open symbols) forests and (b) mean monthly air temperature (dashed line) and mean (\pm se; *n* = 6) soil temperature for control plots located in the seasonally flooded (closed symbols) and upland (open symbols) forests in the Pantanal. Precipitation and air temperature data are from a 25 m tall tower located approximately 1 km away from the study sites. The grey shaded region in the figure depicts the dry season.

Table 1. Repeated measured analysis of variance (ANOVA) results for litterfall and litter pool, soil CO₂ efflux, soil temperature, moisture, and organic matter content, and root density as a function of litter treatment (T), site (S), time (M), and their interactions.

Source _{df}	Litterfall ⁺	Litterpool	Respiration	Soil Moisture	Soil Temperature	Organic Matter	Root Density
T _{2.30}	NA	18.7 ***	2.0	0.1	0.6	0.1	1.0
S _{1.30 (1.94)}	1.5	0.1	0.4	25.5 ***	793.2 ***	2.9	0.8
$S \times T_{2,30}$	NA	0.1	0.8	0.2	0.6	0.1	0.1
M _{10,282} (10,94)	33.5 ***	44.5 ***	27.4 ***	93.0 ***	497.3 ***	47.1 ***	9.5 ***
$T \times M_{20,282}$	NA	12.7 ***	2.8 ***	1.1	2.0	1.5	1.1
$S \times M_{10,282 (10.94)}$	7.0 ***	2.4 *	6.6 ***	33.6 ***	319.0 ***	8.8 ***	4.4 **
$S \times T \times M_{20,282}$	NA	1.0	0.8	1.2	1.3	1.7	0.9

Shown are the F-statistics for each response variable as a function of the main effects and their interactions, the effect, error degrees of freedom (df), and the probability of type-I error * (p < 0.05); ** (p < 0.01); *** (p < 0.00). ⁺ For litterfall, degrees of freedom are displayed in the parentheses under the source column. NA = not applicable.

3.2. Temporal Trends in Soil Respiration, Litter Pool, Organic Matter Content, and Root Density

The litter manipulation treatments were effective in modifying the surface litter mass over the study period (Table 1; Figure 2a,b). Temporal trends in litter pool size varied significantly as a function of treatment and time, and there was a significant treatment × time (T × M) and S × M interaction (Table 1). Litter pool size was smallest during the wet season and increased to a peak in November for the upland forest and September for the flooded forest (Figure 2a,b). Thereafter, litter pool size declined in the upland forest but remained high in the flooded forest until mid-January (Figure 2a,b), which caused the significant S × M interaction (Table 1). In terms of the treatment effect, the biggest differences were observed between the removal plots and the control and addition plots; however, differences between the treatments were generally larger during the dry–wet season transition when litter pool size was at a seasonal maximum (Figure 2a,b), accounting for the significant T × M interaction (Table 1). When averaged over the study period, litter pool size was 10 times smaller in removal plots than in control plots, while addition plots had nearly 2 times more litter than the control plots during the study period (data not shown).



Figure 2. Mean (\pm se; *n* = 6) (**a**,**b**) litterpool mass and (**c**,**d**) soil respiration for control (closed circles; solid line), and added-litter (open circles; dotted line), and litter removal (inverted triangles; dashed lines) plots for the upland-forest (panels **a**,**c**) and seasonally flooded-forest (panels **b**,**d**) sites in the Pantanal. The grey-shaded region in the figure depicts the dry season.

Temporal trends in soil respiration (Rsoil) varied significantly over time but there were significant $T \times M$ and $S \times M$ interactions (Table 1). The $T \times M$ interaction was caused by an increase in the litter treatment effect over time, while the $S \times M$ interaction was due to differences in the temporal pattern of Rsoil during the March–June wet-dry season transition (Figure 2c,d). For the upland forest, Rsoil consistently declined between March and July, increased during the peak of the dry season in July–September, exhibited a transient decline in October, but increased thereafter (Figure 2c). For the flooded forest, Rsoil increased between March and June, declined to a seasonal minimum in July, and increased thereafter (Figure 2d).

Soil organic matter content varied significantly over time and there was a significant $S \times M$ interaction (Table 1) due to differences during the wet–dry season transition in March–July (Figure 3a,b). Both sites exhibited an increase in soil organic matter during the dry season, a transient decline during the dry–wet season transition in November–December, and an increase in January (Figure 3a,b).

As with soil organic matter, temporal variations in root density also varied over time and there was a significant $S \times M$ interaction due to differences during the March–July wet–dry season transition (Figure 3c,d). Root density was highest during the dry season for both forests; however, the upland forest had a distinct peak in August while the flooded forests had a broad peak that extended between May and August.



Figure 3. Mean (\pm se; *n* = 6) (**a**,**b**) soil organic matter content and (**c**,**d**) root density for control (closed circles; solid line), and added-litter (open circles; dotted line), and litter removal (inverted triangles; dashed lines) plots for the upland-forest (panels **a**,**c**) and seasonally flooded-forest (panels **b**,**d**) sites in the Pantanal. The grey shaded region in the figure depicts the dry season.

3.3. Annual Patterns of Soil Respiration, Decomposition, Root Density, and Soil Organic Matter

Total annual Rsoil was significantly altered by the litter treatments, and litter addition significantly increased Rsoil compared to control and removal plots (Figure 4a). Similar patterns were observed for litter decomposition; however, there was a significant treatment \times site (T \times S) interaction that was due to a significantly higher litter decomposition for the litter addition plots in the flooded forest (Figure 4b). In general, litter decomposition was lowest in the litter removal treatments and highest in the litter addition treatments; however, differences in decomposition between control plots in the flooded forest and the added litter plots in the upland forest were not statistically significant.

The differences in annual litter decomposition were not due to differences in the rate constant (k) but to differences in the amount of forest floor litter mass (F) between the treatments. This is because the k values for the removal plots were significantly higher than the litter addition or control plots (Figure 4c). Removal plots had k values that were 2 and 3 times higher than added litter and control plots, respectively, and the significant $T \times S$ interaction was caused by differences in k for flooded and upland forests in the litter addition treatment.

The fraction of Rsoil that was explained by litter decomposition (fD) was on average 8% for the control treatment, 9-15% for the litter addition treatment, and <3% for the litter removal treatment (Figure 4d). As with annual litter decomposition, fD was significantly higher in flooded (15%) than upland forests (9%) exposed to added litter, accounting for the significant T × S interaction. Litter manipulation did not significantly affect mean annual root density (Figure 4e) or SOM content (Figure 4f); however, there were significant differences between the forests. On average, the seasonally flooded forests had a higher root density than the upland forest (Figure 4e) while the upland forest had significantly higher SOM content than the flooded forest (Figure 4f).



Figure 4. Mean (±se; n = 6) soil respiration (**a**), litter decomposition (**b**), litter decomposition rate constant (**c**), the fraction of soil respiration that was composed of litter decomposition (**d**), soil organic matter (SOM) content (**e**) and root density (**f**) for control, added-litter, and litter removal treatment for the seasonally flooded (white bars) and upland (grey-bars) forests in the Pantanal during the study period. Also shown are the results of a 2-way ANOVA (degrees of freedom and F-statistics) for the effects of litter treatment (T), site (S), and the treatment and site interaction (S × T). ** (p < 0.01); *** (p < 0.001). Bars with a different litter are significantly different (p < 0.05) according to a Tukey–Kramer test.

SEM revealed that annual totals of Rsoil were significantly positively correlated with litter decomposition and SOM, and while Rsoil was significantly affected by litter manipulation, variations in average annual forest floor mass (F) were not significantly correlated with Rsoil (Figure 5; Table 2). Rather, the effect of F was on litter decomposition, which was positively correlated with F (Figure 5; Table 2). The direct effects of root mass on Rsoil were not statistically significant; however, the indirect effects of root density were positive and almost as large as the direct effect of SOM (Table 2). This is because root density was significantly positively correlated with SOM, which in turn was significantly

positively correlated with Rsoil (Figure 5). Soil moisture and temperature were not important predictors of Rsoil even though litter decomposition was positively correlated with soil moisture (Figure 5). Variations in forest floor mass significantly affected soil temperature, but soil temperature had little direct or indirect effect on Rsoil or litter decomposition (Figure 5; Table 2).



Figure 5. Structural equation diagram showing the direct and indirect links between soil respiration (Rsoil) and the hypothesized variables that control Rsoil, including litter decomposition (D), pool size (F), root density (Root), soil temperature (T_s), moisture (S_w), and SOM for the upland and flooded forests. Arrows show links between variables, and numbers on arrows display the standardized partial coefficients for the relationship between each variable. Bold coefficients are statistically significant (p < 0.05). Models were run on averages (Ts, Sw, SOM, F, and root) and totals (D and Rsoil) calculated for the study period with study sites (upland vs. flooded) and litter treatments (control, reduced, and added) combined (n = 36 plots per site).

Table 2. Standardized partial regression coefficients calculated from the structural equation model (see Figure 5) showing the direct and indirect effects of average annual litter decomposition, litter pool size, root density, and soil moisture, temperature, and organic matter content on the total annual soil respiration and litter decomposition measured from the upland and flooded forests over the study period. Partial coefficients for direct-effects marked with an asterisk (*) are statistically significant (n = 36; p < 0.05), while partial coefficients for indirect-effects in italic font are larger in magnitude that direct effects. NA = not applicable.

	Soil Re	spiration	Decomposition		
Variable	Direct Effect	Indirect Effect	Direct Effect	Indirect Effect	
Decomposition	0.290 *	NA	NA	NA	
Litter pool	0.037	0.158	0.858 *	0.089	
Soil moisture	-0.002	NA	0.318 *	NA	
Soil temperature	-0.163	-0.053	-0.189	0.051	
Soil organic matter	0.870 *	NA	NA	NA	
Root density	0.011	0.863	NA	-0.039	

4. Discussion

4.1. Effects of Litter Pool Size on CO₂ Emission and Decomposition

Our results support our hypothesis that decomposition and Rsoil would decline with litter reductions and increase with litter increases. These changes in decomposition and Rsoil were due to the direct effects of litter input on decomposition and Rsoil, such as changes in the amount of labile C for decomposition and Rsoil, and not because litter manipulation altered soil environmental properties (i.e., soil temperature or moisture). Thus, climate change effects on litter production, due to changes in plant species composition, mortality, and disturbance [17,18,23,45,48], can significantly

affect decomposition and heterotrophic respiration by directly altering the amount of C available in the forest floor.

The direct effects of litter production on Rsoil described here are consistent with results reported from other ecosystems, indicating that the effect of litter production on ecosystem C emission may be general across diverse forest types. For example, we compiled results from litter manipulation experiments reported in the literature [23,25,27–29,49–54] and used linear regression to determine if there were consistent trends in the log response ratio of Rsoil [LN(Rsoil treatment/Rsoil control)] as a function of relative litter pool size (Figure 6). Litter addition and/or removal resulted in surprisingly similar relative responses in Rsoil in spite of widely varying experimental methods (plot sizes, measurement intervals) and forest types (Figure 6). Rsoil declined by on average 27% when litter was removed, which is slightly higher than the 10–20% reduction that we observed for the forests here, while doubling the litter pool led to a mean increase in Rsoil of about 40%, which is almost identical to that calculated for the forests observed here.



Figure 6. Summary of effects of litter pool size on soil respiration (Rsoil) from selected experiments where litter was removed and/or augmented. The relative litter pool size (x-axis) was calculated as litter treatment/control litter pool size (0 = litter removal and >1 = litter addition) and the response of Rsoil to litter manipulation calculated as the log response ratio [LN(Rsoil treatment/Rsoil control]). Data are from this study and the following sources: Biudes (12) [49], total R_{soil} during a 65 day laboratory incubation experiment of chaparral soil with and without litter; Bréchet (10) [53], Rsoil from temperate and tropical forests calculated at a soil water content of 40% using regression equations provided by the authors; Fekete (13) [23], Rsoil from double litter (DL), control (C), and no litter (NL) treatments in a deciduous forest in NE Hungary; Fuentes (13) [50], average basal Rsoil from the 0-9 cm surface soil in control and litter removal (LE) plots in Chilean shrublands; Han (15) [27], average seasonal Rsoil from a litter removal experiment in three Chinese subtropical successional forests; Prévost (10) [25], average maximum and minimum monthly Rsoil from temperate forests in France; Li (04) [51], average Rsoil from a plantation and secondary tropical forest in Puerto Rico over a 7-year litter removal experiment; Sayer (07) [29], average Rsoil from a tropical forest in Panama over a 5-year litter removal/addition experiment; Sulzman (05) [54], annual Rsoil for 2001, 2002, and 2003 for a temperate coniferous forest in Oregon over a 3-year litter manipulation experiment; Vasconcelos (04) [52], total annual Rsoil from a litter removal experiment in Amazonia; Zimmerman (09) [28], average daily Rsoil from a litter removal experiment in a Peruvian tropical cloud forest. The best-fit line (\pm 95% confidence interval) and equation were fit using linear regression. Also shown is the coefficient of determination (r^2) of the regression and the probability (*p*) that the linear trend is not significantly different from zero.

The increase in Rsoil with litter addition is likely due to the "priming effect," where an increase in labile C available to microorganisms enhances rates of microbial activity and degradation of SOM [21,22,25,29,53]. This could explain in part why Rsoil was positively related to SOM content (Figure 5; Table 2). For the forests studied here, temporal increases and reductions in Rsoil in response to litter addition and removal became larger over time (Figure 2c,d), indicating a possible substitution in the respiratory C pool [55] or an increase in priming over time [53]. Litter decomposition accounted for, on average, <3% of the Rsoil in the removal plots and between 9–15% of the Rsoil in addition plots, indicating that labile C associated with litter inputs was a more important respiratory pool in the addition plots [27], and while rates of litter turnover for our forest (ca. 1–3 years; Figure 4c) are slower than other tropical forests [44,45,48], high rates of turnover result in a lower amount of C to be incorporated into SOM, and thus a lag in the priming effect of litter [53].

Total litter decomposition over the 1-year study period was significantly affected by litter manipulation (Figure 4b), but total litter decomposition was not correlated with the rate of decomposition (Figure 4c). Rates of litter decomposition (k) were highest in the litter removal plots, intermediate in the litter addition plots, and lowest in the control plots. Litter bag experiments conducted in northern temperate [56] and tropical [57] forests indicate that decomposition was faster when litter was incubated within a deep litter layer or below ground, especially in forests exposed to seasonal drought, because litter burial can reduce water limitation of macro- and micro-organisms that are fragmenting and decomposing surface litter. Given the significantly positive relationship between decomposition for the addition plots, especially during the dry season. However, k was even higher in the litter removal plots, which may have been caused by higher rates of fragmentation and leaching during the wet season or when surface litter was temporarily flooded (described in more detail below) [56,57].

We also hypothesized that litter-induced changes in decomposition and Rsoil would be due more to changes in C availability rather than changes in soil environmental properties (i.e., soil temperature or moisture). While litter manipulation did significantly affect soil temperature (Figure 5), direct and indirect effects of soil temperature and moisture on Rsoil were small (Table 2). These results are similar to those reported for other tropical forests [53], and are not surprising given the structural and hydrological properties of the Pantanal forests. Both the upland and hyperseasonal forest have essentially closed canopies, with a leaf area index of $5.8-7.4 \text{ m}^2/\text{m}^2$ [36]. Thus, the closed canopy, coupled with small temperature variation [33], failed to influence decomposition or Rsoil as much as in more sparsely covered canopies and/or seasonal environments where spatial and temporal fluctuations in temperature have a larger influence on Rsoil [23,26,50,53]. However, increases in soil moisture did increase litter decomposition, which is qualitatively similar to results reported for more arid environments [26,50]. As mentioned above, the positive relationship between soil moisture and litter decomposition may have been due to a reduction in dry season drought and an increase in the leaching and fragmentation during the wet season [45,48,57].

4.2. Differences in Rsoil and Litter Decomposition between the Seasonally Flooded and Upland Forests

We hypothesized that decomposition and Rsoil would be higher in more well-drained soils because of the anoxia that develops in response to seasonal flooding; however, total annual Rsoil was not statistically different between upland and flooded forests (Figure 4a), and litter decomposition (Figure 4b) was significantly higher in the flooded forest. Rsoil for control plots was on average 2 kg C m⁻² y⁻¹, which is comparable to that reported for tropical forests and woodlands of the southern Amazon Basin [15,58] and Brazilian savanna [59]. While we cannot rule out the possibility that the similarity in Rsoil between these forests might be an artifact of a small sample size and/or the short duration of our field study, the similarity in Rsoil between sites is striking given the large variations in hydrology. However, even though the upland forest was never flooded, occasional high water tables can cause intermittent soil anoxia [42,60]. Furthermore, C mineralization in soils that experience

temporary anoxia can be higher than in soils that experience continuous aerobic conditions because iron reduction can release C that is protected in Fe-oxides, especially when aerobic conditions are established after soil becomes unsaturated [61]. Vourlitis et al. [37] found that mineralization of soil organic C increased significantly in the flooded forest as soon as flooding subsided, and respiration rates for the flooded forest were higher than the upland forest during the wet–dry season transition (May–June) (Figure 2c,d). Potential reductions in microbial respiration caused by anoxia in the hyperseasonal forest could have also been compensated by a combination of higher litter decomposition and higher root respiration due to significantly higher surface root mass (Table 2).

The higher litter decomposition observed in the seasonally flooded forest was presumably caused by an increase in leaching losses that occurred when the litter was inundated, as increases in rainfall and inundation increase leaching of labile C and an increase in litter mass loss during the initial stages of decomposition [45,48,53,57,62]. Differences in species composition and/or litter quality between the two stands may have also contributed to the higher rate of litter decomposition in the seasonally flooded forest [57]. While species-specific differences in litter quality are not known, foliar N and P concentrations were higher in the flooded forests than in the upland forest [41], which may have stimulated litter decomposition [21,22,52,53].

4.3. Limitations

Our data suggest that climate change-induced alterations to litter production will have important implications for Rsoil and decomposition in tropical floodplain forests. However, the small scale of the litter manipulation treatments (4 m^2), duration of the field study (1 year), and coarse sampling frequency of Rsoil limit our understanding of how climate change will alter long-term microbial respiration and decomposition kinetics. The plot sizes used here are equivalent to some experiments [23–27,51] but smaller than others [26,28,29,50,52]; however, climate change will alter whole-forest productivity and/or species composition that will affect litter dynamics on a much larger scale [17–20]. These dynamics are difficult to experimentally simulate over a short temporal scale and small spatial scale. There is also the possibility that environmental conditions during the 1-year sampling campaign were anomalous, thus confounding our interpretation of how litter manipulation and forest type affected Rsoil and decomposition. However, temperature trends were almost identical to long-term averages, precipitation was only slightly higher (ca. 112 mm) than the long-term average, and the seasonal flood regime was typical for the flooded forest [33–42,60], so even though the experimental campaign was short, the environmental conditions were typical for these forests. A potentially larger question surrounds whether the initial responses in Rsoil and decomposition will hold over a longer period of time, and while we cannot answer this question with the data at hand, data collected from litter manipulation experiments in temperate and tropical forests suggest that the initial priming effect of litter holds over at least 3 years [53]. Finally, our measurements of Rsoil were done on approximately monthly time scales, which is similar to [23,25,53], or more frequent than [29,51], other field litter manipulation experiments reported above. However, it is possible that monthly measurements of Rsoil missed potentially important transient dynamics [60] that could affect our interpretation of spatial (upland vs. flooded forest) and treatment effects. Continuous measurements of soil CO_2 concentration in our upland forest indicate that seasonal variations in CO_2 production were relatively stable but within-season variations were more transient [42], and thus it is possible that Rsoil varied more within a given season than reported here.

4.4. Conclusions

Short-term (1 year) manipulations in the surface litter pool significantly altered the Rsoil and litter decomposition of seasonally flooded and upland tropical forests in the Brazilian Pantanal. For the forests studied here, alterations in Rsoil appeared to be due to direct C inputs from litter as opposed to the indirect effects of litter on the soil environment. However, for litter decomposition, rates of mass loss (k) were higher for removal plots and the rate of litter decomposition (but not Rsoil) was higher in

the forest exposed to seasonal flooding. These results suggest that C limitations are important controls on both Rsoil and litter decomposition but that environmental limitations may become important for litter decomposition. These results are novel because little is known about the Rsoil and litter decomposition of tropical floodplain forests, and litter removal and augmentation resulted in relatively similar changes in Rsoil regardless of the forest type, plot size, and/or experiment duration (Figure 6).

While the duration of the study and spatial extent were limited, these results suggest that alterations to litter pool mass due to land use and/or climate change are likely to alter soil CO₂ emissions for these, and similar, forests significantly [29,53]. Increases in temperature and dry season duration are anticipated for the southern Amazon Basin and the Pantanal [4,39], which is likely to alter litter production [19,21,48], and perhaps litter quality due to drought-induced mortality and changes in species composition [17]. An intensification of the dry season, coupled with warming, may increase the surface litter pool and, ultimately, Rsoil in these forests. Given the fact that tropical ecosystems may be responsible for approximately 67% of the total annual global CO₂ efflux [12], changes in litter production due to climate and land-use change have important implications for global CO₂ cycling.

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