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ORIGINAL PAPER

Precipitation influences on active fractions of soil organic matter in seasonally dry tropical forests of the Yucatan: regional and seasonal patterns

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Abstract In a transect study involving 15 mature seasonally dry tropical forests growing on uniform geological substrate in the Yucatan Peninsula, Mexico, we analyzed the influence of a large reduction in mean annual precipitation (1,036–537 mm year^{-1}) on carbon (C) and nitrogen (N) pools in soils. We investigated the C content in organic soil and in active fraction pools (organic matter and microbial biomass) and analyzed the dependence of these pools on precipitation. Carbon (total, inorganic and organic, and in microbial biomass) and N (total) concentrations in bulk soil decreased as rainfall increased from <600 mm year^{-1} >1,000 mm year^{-1}. Additionally, in all organic matter fractions, C and N concentrations generally decreased with greater precipitation. Soil average C mineralization decreased by 61 % from the wettest to the driest region. Reduced precipitation during the dry season increased microbial biomass C and water-extractable C concentrations and decreased the C concentration in organic matter fractions. No other significant changes were observed between seasons in C concentrations, N concentrations or C mineralization. Overall, we conclude that physical (macroclimate) and biological processes are more active in soils in the wettest region, resulting in a faster turnover of organic matter.

Keywords Carbon sequestration · Climate change · Drought · Fast carbon pools · Karstic soils

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Introduction

Climate has a dominant effect on soil organic matter (SOM) decomposition and carbon accumulation on a regional scale (Meentemeyer 1984). Although microbes have a high adaptability to both different temperatures and precipitation regimes (Tate 1995), temperature and soil moisture can be limiting factors for microbial activity. Despite the influence of site factors (such as soil properties and type of vegetation) on the partitioning of C pools, climate factors (temperature and precipitation) control C accumulation and turnover in the soils. Thus, determining the climate controls on C dynamics in tropical forest soils is essential if we want to understand their potential as source or sink of C to the atmosphere under changing climate conditions.

Seasonally dry tropical forests (SDTF) represent more than 40 % of tropical forest areas (Murphy and Lugo 1986). Previous work in these seasonally dry tropics (regions with a seasonal drought period of 4–6 months and less than 100 mm of rainfall per month during this period) indicates that precipitation is typically a key climatic state factor that directly or indirectly controls the structure and function of forest ecosystems, since seasonal variation in monthly temperature is negligible (Lugo and Murphy 1986). Macroclimatic influences on biogeochemical processes that control C accumulation in soils in these SDTF ecosystems have not been studied as extensively as in tropical moist forests (Austin and Vitousek 2000; Posada and Schuur 2011). Although the effects of

rainfall seasonality on soil C dynamics have been studied individually in SDTFs (Singh et al. 1989; Saynes et al. 2005), none of these studies have included a more general and integrated treatment of seasonal and mean annual precipitation (MAP) effects on soil C dynamics. This gap limits cross-regional, environmental assessments of tropical forest biogeochemistry, and comprehension of the C sequestration potential of such ecosystems.

Soil organic matter is usually divided into four pools on the basis of stability (Stevenson 1994): an easily decomposable organic or light fraction (partially decomposed plant residues); microbial biomass (together with the organic matter, this is what many researchers have termed *labile SOM*—the highly dynamic, rapidly recycling component of SOM responsible for supplying most of the nutrients for plant growth; Sanderman and Amundson 2005); dissolved organic matter; and substances that are more stable and recalcitrant to decomposition (humic substances). In this study, we used a transect approach with 15 SDTFs on the same bedrock to study C and N concentrations and C mineralization in soils across a precipitation gradient (550–1,050 mm year^{-1}) with similar mean annual temperatures. By comparing results from three regions in Yucatan, we assessed the effects of precipitation differences on labile C, water-extractable C, total N concentrations and C mineralization in SDTFs. The tropical soils of Yucatan, in southeast Mexico, have an exceptionally high organic matter content, between 50 and 250 g C kg^{-1} (Shang and Tiessen 2003; Gamboa et al. 2010). These soils are formed on limestone and produce a mosaic of shallow black lithosols surrounding rock outcrops and deeper red rendzinas at slightly lower relief. Our overall goal was to understand the soil organic matter dynamics, and whether these seasonal dynamics depend on annual precipitation. This is the first attempt, to our knowledge, to explore soil organic matter dynamics in seasonally dry tropical forests along both scales, seasonal and regional. In this study, we tested the hypotheses that (1) both SOC and microbial biomass decrease with an increase in precipitation from 550 to 1,050 mm year^{-1}, and (2) decreasing precipitation during the dry season results in an increase in microbial biomass. Also, we hypothesized that an increase in MAP (3) reduces the residence time of C in the soil due to faster mineralization rates and (4) results in a relative shift of organic matter fractions from light pools to heavy pools.

Materials and methods

Study sites

The study was carried out in three regions of the Yucatan Peninsula, situated along a strong north-to-south gradient in mean annual precipitation (Table 1). The study regions are between 50 and 120 km apart. Within each of the three study regions, five mature SDTFs were selected. Temperature, relief, organisms, parent material and time could be held sufficiently constant in this study to investigate the influence of precipitation on ecosystem soil C storage and dynamics.

Long-term climatic data from weather stations across Yucatan show that the three regions are characterized by a distinct period of low precipitation (5–7 months with precipitation below 100 mm; García 2004). The climate is hot—semiarid to subhumid (Table 1)—and would support either tropical dry or very dry forest in the Holdridge system (Holdridge et al. 1971). Mean annual temperature in the three regions is close to 27 °C, with a difference of less than 5 °C between the coolest and the warmest months. In these regions, most of the total annual precipitation falls in the rainy season, contributing 75 % of the total MAP. Peak rainfall occurs in September, and March is the driest month.

The landscape consists of flat areas (Table 1), and the predominant lithology includes Late Pliocene material, with numerous areas of exposed limestone (Duch-Gary 1988). Soils (Lithic Ustorthents) in our study regions are mainly shallow and organic-rich and directly overlie weathered calcium carbonate. The depth of the Ah horizon varies between 50 and 100 mm, and its bulk density ranges from 0.5 to 0.6 g cm^{-3} (Table 2). Soil reaction is about pH 7.4. The range of clay contents is 22–30 %, silt is 1 %, and sand is 66–75 %.

The predominant vegetation in the three regions is the SDTF, in which mean canopy height is 3–5 m (Table 1). Floristically, *Leguminosae* are the most important family at all forest sites. The southern, driest region, Chicxulub, has the least trees (diameter at breast height, DBH $\geq$2.5 cm) per unit of area; the northern, wettest region, Hobonil, has a higher tree density; and the intermediate region, X'matkuil, has the highest tree density. At all three sites, the dominant species of trees (i.e., the most frequent) are *Bursera simaruba* (L.) Sarg. (*Burseraceae*), *Piscidia piscipula* (L.) Sarg. (*Fabaceae*) and *Lysiloma latisiliquum* (L.) Benth. (*Fabaceae*), which represent 9.4–27.6 % of the basal area of tree species at each site (González-Iturbe et al. 2002).

Soil sampling

In each region (i.e., Chixulub, X'matkuil and Hobonil), five mature forest sites were selected between one and five km apart. At each forest site, one 40 × 40 m plot was established in 2008. Soils at each forest site were sampled twice to determine C and N concentrations, C mineralization and organic mater fractions: midway through the rainy season (September) and in the dry season (March). On each

Table 1 General characteristics of the three studied regions

	Chicxulub	X'matkuil	Hobonil
Coordinates	21° 14′ N, 89° 32′ W	20° 52′ N, 89° 36′ W	20° 00′ N, 89° 02′ W
Altitude (m a.s.l.)	2	22	36
Climate	BS1	Aw0	Aw1
Mean annual temperature (°C)	25.8	26.6	26.2
Mean annual precipitation (mm $year^{-1}$)	537	993	1036
Precipitation/potential evapotranspiration (mm mm^{-1})	0.5	0.8	1.0
Tree density (stems 144 m^2)*	37.4 c ± 5.2	104.3 a ± 6.1	56.4 b ± 6.6
Tree height (m)*	3.3 b ± 0.2	3.4 b ± 0.1	4.5 a ± 0.2

Data are means ± SE of five forest sites

* DBH ≥2.5 cm. Different letters (a, b) indicate means are significantly different ($p < 0.05$), when testing for differences among regions

Table 2 Selected soil properties in the three studied regions

	Chicxulub	X'matkuil	Hobonil
Sand (%)	74.5 a ± 1.0	73.3 a ± 1.4	65.8 b ± 2.8
Silt (%)	1.0 b ± 0.0	1.0 b ± 0.0	1.3 a ± 0.5
Clay (%)	21.7 b ± 1.0	23.3 b ± 1.4	30.0 a ± 2.4
pH	7.4 a ± 0.04	7.5 a ± 0.04	7.4 a ± 0.02
Bulk density (g cm^{-3})	0.53 b ± 0.03	0.66 a ± 0.03	0.66 a ± 0.04

Data are means ± SE of five forest sites. Different letters (a, b) indicate means are significantly different ($p < 0.05$), when testing for differences among regions

sampling date, in each plot, 64 soil samples (to a depth of 0.10 m, or less, where soils were too shallow) were collected randomly on a grid (the plots of 40 × 40 m were divided into 5 × 5 m areas, giving 64 samples per plot). Samples were combined in the field and stored at 4 °C for up to 48 h before processing. In the laboratory, the composite soil samples were homogenized. A subsample (500 g of soil) was sieved (<8 mm) for organic matter fractionation and roots and stubble were removed. The remaining soil was used to measure total soil C and N, and concentrations of organic, water-extractable and microbial C in bulk soil (sieved through a 2-mm mesh). Soils collected at this time were also used in potential C mineralization assays.

Soil organic matter fractionation

The organic material was separated using the sequential Meijboom fractionation procedure (Meijboom et al. 1995). Meijboom et al. developed a particle density fractionation method to fractionate the 150 µm to 2 mm fraction by sieving into three fractions based on physical density: light (LF), intermediate (IF) and heavy (HF) fractions. Briefly, freshly collected soil samples were mixed thoroughly before removing gravel and roots using an 8-mm sieve. A subsample of soil (100 g) was then size-fractionated by wet sieving through a series of stacked sieves (2,000, 250 and 150 µm). The material retained on each sieve was then suspended in water and the floating organic material was separated by decantation. All the organic material recovered was then fractionated in Ludox colloidal silica (Du Pont Corp, Virginia) to yield three organic matter fractions: a light fraction (LF) (floating at 1.13 g cm^{-3}); an intermediate fraction (IF) (floating at 1.37 g cm^{-3} but not at 1.13 g cm^{-3}), and a heavy fraction (HF) (not floating at either density). The material coming to the surface on a given suspension was rinsed and dried to determine dry weight. These fractions were analyzed for total C and N concentrations.

This fractionation scheme is linked to the notion that organic matter in differently sized aggregates differs in function (Gestel and Merckx 1994) and C turnover times (Sitompul et al. 2000). The mineral-free LF consists of fresh, partly decomposed plant residues and is the major C substrate for active microbes. This LF exerts a dominant influence on soil nutrient dynamics, based on a positive correlation between C and N mineralization and the amount of C in the LF and active microbial biomass (Sitompul et al. 2000). It has a relatively rapid turnover and a specific density considerably lower than that of soil minerals (Sollins et al. 1984). The intermediate fraction consists partly of recognizable plant residues mixed with soil particles and also contains undefined particles. The heavy fraction consists of undefined organic material and includes the organo-mineral SOM complexes. It has a slower turnover rate and a higher specific density than the LF due to its intimate association with soil minerals. Thus, C turnover times increase following the order LF < IF < HF (Sitompul et al. 2000).

Chemical analyses

Carbon mineralization was determined from 50 g subsamples of soil under the following set of standard conditions. Duplicate soil subsamples were moistened to 50 % water-filled pore space following light tamping in a

graduated jar and incubated at 25 °C in a 700 mL jar containing vials with water to maintain humidity and 10 mL of 1.0 M NaOH to absord CO_2. Alkali traps were replaced at 1, 2, 3, 5, 7, 14 and 21 days and were removed at 28 days. Carbon dioxide evolved was determined by titration of alkali with 0.5 M HCl (Anderson 1982). The rate of carbon mineralization was calculated during 3–28 days to avoid the majority of the flush of activity due to drying and rewetting.

Soil total and inorganic C (carbonates) were analyzed in an automated C analyzer (SCHIMADZU 5005A), after grinding a 5-g air-dried subsample to pass through a 100-mesh screen. Soil organic C (SOC) concentration was obtained from the difference between total C and inorganic C. Total N was determined by H_2O_2–H_2SO_4 digestion followed by auto-analysis (Anderson and Ingram 1993). Microbial C concentration was determined by the fumigation–extraction method (Vance et al. 1987) using replicate samples of fresh soil. Fumigated and non-fumigated samples were incubated for 24 h at 24 °C. Microbial C was extracted from both fumigated and non-fumigated samples with 0.5 M K_2SO_4, filtered through a Wathman No. 42 paper, and the concentration of C was measured with an automated C analyzer. Concentrations of C in the non-fumigated extracts were subtracted from the fumigated extract, and a conversion factor k_C for microbial C equal to 0.45 (Vance et al. 1987) was used to estimate microbial C.

We also measured water-extractable C concentrations (inorganic, organic and total) after each soil sampling date, using deionized water extraction (soil : water = 1:5). Soil subsamples were shaken for 1 h and centrifuged at 10,000 rpm at 0 °C for 10 min. The supernatant was filtered with a 0.45-μm Millipore filter. Soil total and inorganic water-extractable C was determined by combustion at 680 °C on a SCHIMADZU C analyzer. Water-extractable organic C concentrations were calculated from the difference between total and inorganic C concentrations in water extracts.

Statistical analyses

Statistical analyses for element content in soils and potential C mineralization were performed using SYSTAT (SYSTAT, Evanson, IL, USA); all statistical tests involved nonparametric one-way analysis of variance (Kruskal and Wallis test) by season. A significance level of $p < 0.05$ was used in all of these tests. Means were compared using chi-square tests. Seasonal differences in element content and potential C mineralization in each region were compared using Kruskal and Wallis tests. All values are means plus or minus 1 SE.

Results

C and N concentrations in bulk soil

Soil total C in the three regions varied between 142 and 242 mg C g^{-1} (Table 3). The total C concentration in the soil increased significantly, from 144 mg C g^{-1} in stands with >1,000 mm $year^{-1}$ (i.e., Hobonil) to 234 mg C g^{-1} in stands with < 600 mm $year^{-1}$ (i.e., Chicxulub). A similar trend was found in organic C concentrations, where soils in the driest region had, on the average, 48 % higher C concentrations than soils receiving >1,000 mm $year^{-1}$. On the other hand, on average, Chicxulub soils contained one order of magnitude more inorganic C than Hobonil soils. No significant changes in soil total C, organic C and inorganic C concentrations between sampling dates were detected in any of the regions.

The gradient of soil C concentrations detected with MAP was not observed in the concentrations of any of the water-extractable C forms (i.e., inorganic, organic and total water-extractable C). Across all regions, organic water-extractable C concentrations changed significantly through time, with higher values in the dry season than in the rainy season. Water-extractable organic C accounted for 0.5 % of total soil organic C in the rainy season; its contribution to soil organic C was very consistent across regions. In contrast, in the dry season, it accounted for between 1.1 and 1.5 % of soil organic C and its contribution increased (by 40 %) with MAP.

Soil microbial biomass C concentrations varied significantly among regions, but changes were not consistent across sampling seasons (Table 3). Soils from the driest region had the highest concentration of microbial biomass C, whereas soils from the wettest region had the lowest concentration in the dry season. However, in the rainy season, precipitation did not have a significant effect on soil microbial biomass C. The relative contribution of mean microbial C to organic C (measured as the ratio between the C concentrations in microbial biomass and organic C concentrations) (mean proportion ranged from 0.4 to 1.3 %) tended to increase (by a factor of 1.8) with precipitation in the rainy season, while it decreased (by 66 %) from dry sites to moist sites in the dry season.

The microbial biomass C concentration in soils differed considerably between the two sampling dates according to MAP of the region (Table 3). Soils from the driest region had 2.7 times more microbial biomass C in the dry season than in the rainy season. In contrast, soils from the southern, wettest region had a significantly higher (2.1 times greater) microbial C concentration in the rainy season than in the dry season. However, sampling date did not affect the concentration of microbial biomass C (i.e., seasonal

Table 3 Soil carbon and nitrogen concentrations in the three studied regions

	Chicxulub		X'matkuil		Hobonil	
	Rainy season	Dry season	Rainy season	Dry season	Rainy season	Dry season
Total C (mg C g^{-1})	226 aA ± 17	242 aA ± 18	190 abA ± 22	185 abA ± 13	145 bA ± 14	142 bA ± 9
Organic C (mg C g^{-1})	200 aA ± 19	215 aA ± 15	177 abA ± 23	173 abA ± 10	142 bA ± 11	139 bA ± 9
Inorganic C (mg C g^{-1})	25.6 aA ± 1.1	27.2 aA ± 0.8	13.2 bA ± 1.8	11.7 bA ± 1.3	2.6 cA ± 0.8	2.7 cA ± 0.3
Microbial biomass C (μg C g^{-1})	1,008 aB ± 204	2,721 aA ± 79	1,477 aA ± 228	1,033 bA ± 109	1,278 aA ± 175	602 cB ± 90
Total N (mg N g^{-1})	18.9 aA ± 0.8	17.7 aA ± 0.5	13.7 bA ± 1.3	13.8 bA ± 0.5	12.3 bA ± 0.9	12.3 bA ± 0.5
C: N ratio	10.6 aA ± 0.9	12.1 aA ± 0.6	12.9 aA ± 0.3	12.5 aA ± 0.7	11.5 aA ± 0.6	11.3 aA ± 0.6
Water-extractable Ci (μg C g^{-1})	417 aB ± 35	598 aA ± 41	411 aA ± 38	416 aA ± 18	378 aA ± 23	428 aA ± 31
Water-extractable Co (μg C g^{-1})	978 aB ± 34	2434 aA ± 112	929 aB ± 47	2,323 aA ± 84	728 aB ± 27	2,115 aA ± 35
Water-extractable C total (μg C g^{-1})	1,395 aB ± 74	3,032 aA ± 166	1,341 aB ± 94	2,738 aA ± 91	1,106 aB ± 71	2,543 aA ± 91

Data are means ± SE of five forest sites. Different lowercase letters (a, b, c) indicate means are significantly different ($p < 0.05$), when testing for differences among regions within each season. Different capital letters (A, B) indicate means are significantly different ($p < 0.05$), when testing season within region

differences were not significant) of soils collected in the intermediate region.

Soil total N concentration in the northern, driest region, Chicxulub, was significantly larger than that of X'matkuil and Hobonil in both sampling seasons (Table 3). Across all regions, variation between seasons was generally very low and the differences were not significant.

The average soil organic C-to-N ratio was ~11–13. Mean soil C-to-N ratios were not significantly different among regions, and this stoichiometry ratio did not change over the course of the study in any of the regions.

C and N in organic matter fractions

The C concentration was lowest (mean values ranged from 223 to 345 mg C g^{-1} fraction) in the organic matter heavy fraction (HF), higher in the organic matter intermediate fraction (IF) (359–409 mg C g^{-1} fraction) and highest in the organic matter light fraction (LF) (382–439 mg C g^{-1} fraction) (Table 5). In contrast, differences in N concentration among fractions at each region were low and non-significant. In the driest region, the mean values of the C-to-N ratio in the fractions decreased following the order LF $\underline{\approx}$ IF > HF. Generally, in wetter regions, the C-to-N ratio did not vary among fractions (except in dry season samples from Hobonil).

In all three organic matter fractions, C and N concentrations generally decreased with MAP, while the C-to-N ratio increased with MAP (Table 4). Across all regions, C concentrations in organic matter fractions generally were significantly higher in the rainy season than in the dry season (the exception being Hobonil's LF). However, seasonal patterns in N concentrations were only significant for the IF and the HF in Chicxulub. Rainfall seasonality did not have a significant effect on the C-to-N ratio in any of the fractions within each region.

The amount of organic matter varied with MAP and rainfall seasonality (Table 5). Their masses decreased from the driest region to the wettest region and generally from the dry season to the rainy season (except for the LF). It accounted for 6–13 % of total soil C and 4–12 % of total soil N. Differences in C and N amounts between rainy and dry periods largely reflected organic matter mass variation. Thus, larger amounts of these elements were accumulated in the dry season. Carbon and N amounts in organic matter were higher in the driest region than in other regions.

Potential C mineralization

Precipitation regime influenced potential C mineralization (Table 6). We found an increasing gradient of potential C mineralization in the direction of Chicxulub < X'matkuil < Hobonil. The corresponding Kruskal and Wallis test indicated that this gradient is significant, and paired comparisons using the chi-square test showed that soils from the driest region consistently sustained lower levels of C mineralization ($p < 0.05$ in both cases), while soils from the wettest region showed the highest levels ($p < 0.05$ in both cases). Soils from X'matkuil constituted an intermediate group in both sampling seasons. The relative rankings of regions with regard to potential C mineralization did not change between seasons. Across all regions, potential C mineralization did not vary significantly between seasons, though it tended to increase in the rainy period.

Table 4 Carbon and nitrogen concentrations, and carbon-to-nitrogen ratio in soil organic matter fractions (light, LF; intermediate, IF; heavy, HF) in the three studied regions

Fraction	Chicxulub		X'matkuil		Hobonil	
	Rainy season	Dry season	Rainy season	Dry season	Rainy season	Dry season
C concentration (mg C g^{-1} fraction)						
Macro-organic matter LF	439 aA ± 3	401 aB ± 4	415 bA ± 5	382 bB ± 5	433 aA ± 2	386 bA ± 6
Macro-organic matter IF	409 aA ± 5	366 aB ± 10	392 aA ± 6	367 aB ± 3	393 aA ± 8	359 aB ± 3
Macro-organic matter HF	346 aA ± 18	280 aB ± 14	326 aA ± 12	259 abB ± 16	325 aA ± 27	223 bB ± 13
N concentration (mg N g^{-1} fraction)						
Macro-organic matter LF	29.1 aA ± 0.9	26.1 aA ± 1.5	25.7 abA ± 0.9	26.7 aA ± 1.4	25.1 bA ± 1.1	25.4 aA ± 2.5
Macro-organic matter IF	30.2 aA ± 1.1	25.7 aB ± 2.0	25.7 abA ± 1.7	24.2 aA ± 0.5	24.3 bA ± 0.5	23.0 aA ± 1.7
Macro-organic matter HF	30.2 aA ± 1.6	23.3 aB ± 1.6	25.3 abA ± 2.2	22.5 aA ± 2.9	21.0 bA ± 1.7	17.9 bA ± 1.6
C: N ratio						
Macro-organic matter LF	15.2 bA ± 0.5	15.6 aA ± 0.8	16.3 abA ± 0.6	14.6 aA ± 0.8	17.4 aA ± 0.7	16.2 aA ± 1.8
Macro-organic matter IF	13.6 bA ± 0.5	14.8 aA ± 1.2	15.7 abA ± 1.2	15.2 aA ± 0.2	16.2 aA ± 0.5	16.1 aA ± 1.1
Macro-organic matter HF	11.5 aA ± 0.5	12.1 aA ± 0.4	13.6 aA ± 1.4	12.4 aA ± 1.2	16.4 aA ± 3.0	12.9 aA ± 1.1

Data are means ± SE of five forest sites. Different lowercase letters (a, b, c) indicate means are significantly different ($p < 0.05$), when testing for differences among regions within each season. Different capital letters (A, B) indicate means are significantly different ($p < 0.05$), when testing season within region

Table 5 Mass and carbon and nitrogen contents in soil organic matter fractions (light, LF; intermediate, IF; heavy, HF) in the three studied regions

	Chicxulub		X'matkuil		Hobonil	
	Rainy season	Dry season	Rainy season	Dry season	Rainy season	Dry season
Soil mass (g kg^{-1} soil)						
Macro-organic matter LF	25.9 aA ± 8.4	42.4 aA ± 4.7	23.1 aB ± 4.3	43.6 aA ± 8.0	14.7 aA ± 2.9	22.8 bA ± 3.1
Macro-organic matter IF	3.4 aB ± 0.8	17.2 aA ± 2.2	3.5 aB ± 0.7	12.5 bA ± 2.0	3.9 aB ± 0.8	9.8 bA ± 1.6
Macro-organic matter HF	4.2 aB ± 0.6	12.0 aA ± 0.9	4.1 aB ± 0.8	8.3 bA ± 0.7	4.3 aB ± 0.6	9.3 bA ± 0.8
Recovery (% of bulk soil mass)	3.3	7.1	3.0	6.4	2.3	4.2
C content (g C kg^{-1} soil)						
Macro-organic matter LF	11.3 aA ± 3.6	17.1 aA ± 2.1	9.7 aB ± 1.9	16.7 abA ± 3.4	6.4 aA ± 1.2	8.9 bA ± 1.3
Macro-organic matter IF	1.4 aB ± 0.3	6.4 aA ± 0.9	1.4 aB ± 0.3	4.6 abA ± 0.8	1.6 aB ± 0.3	3.5 bA ± 0.6
Macro-organic matter HF	1.4 aB ± 0.2	3.4 aA ± 0.3	1.4 aB ± 0.3	2.2 bA ± 0.3	1.4 aB ± 0.3	2.1 bA ± 0.3
Recovery (% of C in bulk soil)	6.3	11.1	6.5	12.8	6.5	10.3
N content (g N kg^{-1} soil)						
Macro-organic matter LF	0.78 aA ± 0.26	1.10 aA ± 0.13	0.59 aA ± 0.11	1.19 aA ± 0.30	0.37 aA ± 0.08	0.55 aA ± 0.09
Macro-organic matter IF	0.10 aB ± 0.03	0.46 aA ± 0.09	0.09 aB ± 0.02	0.31 aA ± 0.06	0.09 aB ± 0.02	0.23 bA ± 0.05
Macro-organic matter HF	0.13 aB ± 0.02	0.28 aA ± 0.03	0.11 abB ± 0.03	0.19 bA ± 0.02	0.08 bB ± 0.01	0.17 bA ± 0.02
Recovery (% of N in bulk soil)	5.5	10.4	5.8	12.2	4.4	7.7

Data are means ± SE of five forest sites. Different lowercase letters (a, b, c) indicate means are significantly different ($p < 0.05$), when testing for differences among regions within each season. Different capital letters (A, B) indicate means are significantly different ($p < 0.05$), when testing season within region

Discussion

The concentrations of organic C in the SDTFs studied (139–215 mg C g^{-1} soil) are similar to the regional means reported by Balbontín et al. (2009), but our means are higher than the soil organic C concentrations reported for other SDTF soils in Latin America (9.8–47 mg C g^{-1}; García-Oliva and Jaramillo 2011). Shang and Tiessen (2003) suggest that carbonate impregnation plays a major role in the stability and accumulation of SOM in Yucatan soils. Our data show that inorganic C concentration is high, mainly at the driest location, where organic C measurements were

Table 6 Potential carbon mineralization in soils from the three studied regions

	Chicxulub		X'matkuil		Hobonil	
	Rainy season	Dry season	Rainy season	Dry season	Rainy season	Dry season
C mineralization (μg CO_2 g^{-1} C d^{-1})	150 cA ± 11	136 cA ± 9	199 bA ± 16	162 bA ± 11	240 aA ± 15	221 aA ± 10

Data are means ± SE of five forest sites. Different lowercase letters (a, b, c) indicate means are significantly different ($p < 0.05$), when testing for differences among region s within each season. Different capital letters (A, B) indicate means are significantly different ($p < 0.05$), when testing season within region

greatest; this may constitute indirect evidence for the proposed role of carbonates in stabilizing organic matter in these soils.

In this study, the C content in organic matter fractions represented about 6–12 % of the total organic C in soils. Across all regions and seasons, the main C pool obtained by density fractionation was in the LF, which represents—together with microbial biomass—the active organic matter in the soil (Janzen et al. 1992). Although Meijboom's fractionation cannot be used to separate organo-mineral complexes (Cambardella and Elliott 1994), nor even to determine specific stabilization mechanisms (von Lützow et al. 2007), the lower C-to-N ratio in the HF indicates a higher degree of decomposition in this fraction and suggests that the stability of organic matter increases from the LF to the HF.

Seasonal patterns

The microbial biomass C concentration in the forest soils analyzed was affected by rainfall seasonality. Interestingly, this study shows a striking contrast between the effects of rainfall seasonality on forests in the driest region and its effects on forests in the wettest region. The rainy season leads to a substantial increase in the microbial biomass C concentration in the soils of forests in the wettest region, where C mineralization is highest and organic C content in the soil is lowest, whereas in forests in the driest region, the rainy season leads to a decrease in soil microbial biomass concentration. Studies of soils of other SDTFs (Singh et al. 1989; Saynes et al. 2005) also have reported a large decrease in microbial biomass C during the rainy season. Moreover, our data show that microbial C concentrations in soils during the dry season are nearly triple than those recorded during the rainy season. Elevated immobilization during the dry period in SDTFs may occur because microbes are active when plants and microbial grazers are not (Singh 1969; Campo et al. 1998). Differences in the response of soil microbial biomass to rainfall seasonality in the forests under study have important consequences for soil C dynamics (see C concentration and content in soil organic matter fractions) and sequestration (C concentration in bulk soil) in these seasonal ecosystems.

Based upon previous studies in SDTFs (Campo et al. 1998), we hypothesized that the rainless period enhances the accumulation of soluble C in the soil resulting from microbial biomass that dies or exudates accumulates during dry periods (Kieft et al. 1987). In Yucatan soils, this hypothesis is supported, as the concentration of water-extractable organic C in soils was enhanced across all regions during the dry season (by a factor of 2.5 in drier regions, i.e., Chicxulub and X'matkuil, and by a factor of 2.9 in the wettest region) compared to rainy season levels. In the dry season, most of the trees are leafless and fine roots are mostly dead. Thus, the accumulation of fresh litter, combined with the expected decrease in microbial activity and leaching during the rainless period, favors the accumulation of soluble C in these forest soils. Moreover, the rainless period may also promote the accretion of organic matter in the soils. Our measurements of organic matter masses in soils during the dry season were nearly twice those obtained during the rainy season. We cannot determine whether such increases in organic matter masses in the soil resulted from the observed increased in litter standing crop itself during the dry season in these ecosystems (Campo and Vázquez-Yanes 2004), or whether it reflects decreased decomposition (an indirect consequence of the decrease in soil moisture) (cf. Cárdenas and Campo 2007), or both.

The overall levels of the soil's total C associated with operationally defined soil organic matter fractions were lower in the rainy season (by 6 % of total soil C), but were almost twice as high as those reported for tropical climates (Barrios et al. 1996; Phiri et al. 2001; Payán et al. 2007). Moreover, the high inputs of litterfall to the forest floor during the first half of the dry season (November to February; mean monthly dry mass of 106, 109 and 108 g per meter square for Chicxulub, X'matkuil, and Hobonil, respectively; J. Campo unpublished data) combined with the low rainfall (mean monthly precipitation of 23 mm for Chicxulub, 30 mm for X'matkuil and 45 mm for Hobonil; Lilia Roa-Fuentes et al. in preparation) and microbial activity during this season may promote the accumulation of plant residues in the soil (as indicated by the seasonal changes in the size of the light and intermediate fractions separated by Ludox colloidal silica). These seasonal

changes confirm the need to quantify not only the weight but also the dynamics of the C content in the soil organic matter pool. On the other hand, our data show that the organic matter pool in these Yucatan soils is much larger than the pools reported for any other tropical soil.

The size density fractionation method has been proposed as an alternative to the litter-bag approach for determining litter decomposition, since a closer contact between organic matter and the soil can be maintained (Magid et al. 1997). The decreasing trends of organic matter C content observed in Yucatan soils both with MAP and between seasons are evidence that significant regional and temporal variations in the size of density fractions can be determined. However, the critical question is the extent to which the size of these organic matter fractions accurately reflects recent inputs of soil organic matter or alternatively the amount of C in the "active" pool. Our study followed the dynamics of organic matter by comparing amounts in the middle of the rainy season (September, the wettest month) and in the middle of the dry season. The higher levels of C concentrations in rainy season fractions than in dry season fractions suggest that more fresh, new matter is incorporated in soil during the wet season. On the other hand, a decline in C content in these fractions during the rainy season across regions also implies fast disintegration and thus a low stability of the relatively less-decomposed organic matter in this seasonally dry ecosystem, irrespective of the differences in MAP.

Comparison of C content in organic fractions during the dry season with those in the rainy season suggests that the IF offers some resolution with respect to the impact of seasonal rainfall that affects labile SOM decomposition; for example, C content in organic matter increased in the dry season with respect to rainy season levels by 51 % in the LF, by a factor of 4 in the IF and by a factor of 2 in the HF; in the driest region, by 72 %, by a factor of 3 and by 57 % in the LF, IF and HF, respectively; in X'matkuil, by 39 % in the LF, by a factor of 2 in the IF, and by 50 % in the HF, in the wettest region. This result was expected because the I fraction is an intermediate stage between the LF and HF. Furthermore, variations in C contents in the IF—as well as in the HF—between seasons and across regions followed a decreasing gradient with MAP, but this trend was not observed in the LF. This suggests that the C contained in the IF may reflect the decomposition rate of labile SOM in SDTFs over short periods. On the other hand, the content of C in organic matter decreases by approximately 50 % with MAP in the dry season, when the pool is largest. We cannot determine whether such a decrease in the content of C in organic matter with MAP reflects differences among regions in microbial activity during the dry season, as a consequence of differences in rainfall across regions during that period (Lilia Roa-Fuentes et al. in preparation). This decline in C in organic matter fractions with MAP, particularly in the dry season, shows the importance of rainfall during the dry period.

Regional trends

In the moist climate region (Hobonil), the wet environment provides conditions that enhance litterfall (by a factor of 1.3 relative to Chicxulub; J. Campo, unpublished data) and decomposition, as indicated by lower organic matter mass and C and N contents, whereas in driest climate, greater drought in this region limits decomposition and favors C and N accumulation in soils—in both bulk soil and organic matter. Inter-site experiments conducted across Yucatan show that rainfall is positively related to decay rates in these seasonally dry tropical forests (the decomposition rate of leaves from the dominant tree species *Piscidia piscipula* increases by a factor of 1.6 in Hobonil relative to Chicxulub; Marilyn Bejarano personal communication). In contrast to the results of Franzluebbers et al. (2001) for temperate forests (they found that the ratios of C mineralization-to-SOC tended to decrease with higher MAP in a precipitation range from 449 to 1,250 mm yr^{-1}), Yucatan soils from wettest region showed consistently higher C mineralization (per gram of soil C), suggesting a more active microbial biomass with an increase in MAP. Differences between Franzluebbers's trends and those observed in our study suggest differences in the amount of labile organic matter that accumulates in temperate North American forest soils and in tropical Yucatan forest soils.

The standing stock of soil C in tropical moist forests is generally greater in wetter climates than in drier ones (Posada and Schuur 2011). In contrast to this trend, our study reveals a substantial reduction in the soil C concentration in mature SDTFs with an increase in annual rainfall; forest stands with more than 1,000 mm $year^{-1}$ had only 61 % of the soil organic C of forest stands receiving less than 550 mm $year^{-1}$. These trends also held true in our analysis of soil inorganic C concentrations, as well as in soil total N concentrations. This decrease in soil C and N could be caused by higher decomposition rates of soil organic matter, considering that wetter forests tend to have higher litterfall input to soil than driest forests. Despite that there was no significant trend in soil microbial biomass with MAP in the rainy season (in contrast to the dry season), C mineralization in the laboratory was greatest in soils from wetter regions. This positive trend in potential C mineralization matched the trend in decreased soil C concentration with increased MAP observed in these SDTFs. Thus, our study also suggests that although increased precipitation leads to higher organic C input to soil, it also leads to greater decomposition in these forest ecosystems.

When we consider the results for soil organic C and total N concentrations and soil bulk density in SDTFs in

Yucatan, it may appear that precipitation has substantially less impact on the content of these elements in surface soils, despite the increase in litterfall with increased MAP. For example, the estimated contents of C in soils, calculated from Tables 2 and 3, were 11.0 Mg C ha^{-1} for Chicxulub, the driest region, 11.5 Mg C ha^{-1} for X'matkuil, the intermediate region, and 9.3 Mg C ha^{-1} for Hobonil, the wettest region. Also, the variation in total N content in soils calculated from Tables 2 and 3 is low, with average values of 0.97, 0.90 and 0.81 Mg N ha^{-1} for Chicxulub, X'matkuil and Hobonil, respectively. So, C and N contents in soils also suggest that higher precipitation regimes are related to faster C turnover in SDTF surface soils.

The overall levels of C concentration in the light fractions (LF and IF) were similar across regions, except for some minor variations in the LF, which contained fresh, partly decomposed plant residues as indicated by high C-to-N ratios, with low values in X'matkuil and Hobonil soils possibly due to differences in precipitation. Therefore, our study also indicates that the differences in C storage among soils are in finer particles not included in the soil organic matter fractionation scheme used, rather than in newly sequestered C.

This study shows that there are differences in newly sequestered C between ecosystems with a low supply of water, such as Chicxulub and X'matkuil forests, and those with a higher water supply, such as the Hobonil forest. Although in these forests, the LF is the predominant pool of newly sequestered C (Table 5)—in low-water-supply systems this fraction represents 75–77 % and 59–68 % of C in organic matter fractions during rainy and dry seasons, respectively—participation is higher than in the region where water is less limiting (as might be expected by the simple precipitation–evapotranspiration ratio) (64 % in the rainy season and 54 % in the dry season). Nonetheless, this suggests a faster disintegration of incoming organic matter (LF) into the IF and HF in the wettest region.

Despite the striking difference in organic C concentrations in the whole soil across regions, when results of C concentration in organic matter fractions are considered, we observe similar C levels in the light fractions (LF and IF) across regions, except for some variations in the LF, which contained fresh, partly decomposed plant residues as indicated by high C-to-N ratios. Therefore, our study also suggests that the strong differences in organic C storage among Yucatan soils analyzed along this natural precipitation gradient are in finer particle sizes (i.e., those not included in the soil organic matter fractionation scheme used) rather than in newly sequestered C.

In Yucatan, there are strong differences in inorganic C concentrations across regions (on average, soils from the driest region contained twice as much inorganic C as X'matkuil soils, and one order of magnitude more than those from the wettest region) suggesting that carbonates have been lost faster with increased MAP. However, no data are available to assess the protective effect of carbonates on soil organic C mineralization, required for the exploration of its influence on soil C storage. Consequently, we cannot determine whether the decrease in soil C storage with increased MAP results from the observed increase in site moisture itself (thus relaxing a possible direct water limitation on microbial activity), or whether it reflects a decreased protective effect of carbonate (an indirect consequence of an increase in carbonate lost during soil weathering), or both.

The trends in soil carbon content showed by our results are in contrast to the findings obtained at sites distributed across mesic-to-wet precipitation gradients (Schuur et al. 2001), where net primary productivity and decomposition rates increase with rainfall, peaking at approximately 2,200 mm of mean annual precipitation, and then decrease with additional precipitation (Schuur 2001, 2003). The new climate relationships observed at Yucatan sites, where water acts predominantly as a resource in these dry-to-mesic ecosystems, add to our conceptual understanding of the effects of precipitation amount in tropical forests. On the other hand, the trends observed at our study sites have implications for the response of carbon sequestration in seasonally dry tropical forest to global change and reflect the mechanistic control of moisture on decomposition under soil moisture extremes, proposed recently by Davidson et al. (2012).

Aside from these differences in C concentration- and C content-patterns, our study of the consequences of spatio-temporal variation in rainfall amount in the Yucatan Peninsula allows us to conclude that physical (macroclimate) and biological processes in the wettest region soils are more active, resulting in a faster turnover of organic matter. Given the potential for tropical forest C sequestration and release subsequent to the massive impact of land use on tropical ecosystems, the topic of the present study warrants subsequent investigation.

Conclusions

We investigated macro-organic matter and microbial dynamics in Yucatan because they involve some of the most active components of soil organic matter and thus play a critical role in the response of soil C to climate change. This study used the natural precipitation gradient in Yucatan, which offers the advantage that most site conditions can be assumed to be relatively similar across the gradient (e.g., temperature and seasonal precipitation patterns, elevation and topography, rock material and soil

type, vegetation and ecosystem age). In so doing, we have provided an understanding of soil-level responses to this natural environmental gradient in the seasonally dry tropics. Our study suggests that water limitation may act as an important control on soil C accumulation. When these ecosystems in Yucatan are released from water stress (e.g., during the rainy season or in regions with a greater precipitation amount), macro-organic matter pools and soil organic C concentrations are sustained at levels lower than those detected during the dry season or in regions with lower annual precipitation, respectively. This study highlights the importance of natural precipitation gradients that may exert control over the capacity of seasonally dry ecosystems for C storage in tropical regions. Given the massive influence of tropical forests on the global C cycle, and in view of projected global environmental changes, it is critical that we understand the sensitivity of the soil C storage to climate changes in tropical landscapes.

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