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Responses of Soil Labile Organic Carbon to a Simulated Hurricane Disturbance in a Tropical Wet Forest

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Received: 12 June 2018; Accepted: 9 July 2018; Published: 12 July 2018

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Abstract: Hurricanes are an important disturbance in the tropics that can alter forest ecosystem properties and processes. To understand the immediate influence of hurricane disturbance on carbon cycling, we examined soil labile organic carbon (LOC) in a Canopy Trimming Experiment (CTE) located in the Luquillo Experimental Forest of Puerto Rico. We trimmed tree canopy and deposited debris (CTDD) on the forest ground of the treatment plots in December 2014, and collected floor mass samples and 0–10 cm soil samples three weeks before the treatment, as well as at scheduled intervals for 120 weeks after the treatment. Within the first week following the CTDD treatment, the mean soil microbial biomass carbon (MBC) and soil LOC in the CTDD plots were significantly greater than in the control plots (soil MBC: 2.56 g/kg versus 1.98 g/kg, soil LOC: 9.16 g/kg versus 6.44 g/kg, respectively), and the mean turnover rates of soil LOC in the CTDD plots were significantly faster than in the control plots. The measured indices fluctuated temporally more in the CTDD plots than in the control plots, especially between the 12th and 84th week after the CTDD treatment. The treatment effect on soil LOC and its turnover rate gradually disappeared after the 84th week following the treatment, while higher levels of soil MBC in the CTDD plots than in the control plots remained high, even at the 120th week. Our data suggest that hurricane disturbance can accelerate the cycling of soil LOC on a short temporal scale of less than two years, but might have a longer lasting effect on soil MBC in a tropical wet forest.

Keywords: canopy trimming and debris deposition; floor mass; hurricane disturbance; Luquillo Experimental Forest; Puerto Rico; soil LOC; soil MBC; soil moisture; subtropical wet forest; turnover rate of soil LOC

1. Introduction

Natural disturbances often deposit massive amounts of litterfall in forests, such as in the case of drought [1], wind [2], rainstorms [3], and ice storms [4]. Severe hurricane-force winds instantaneously strip foliage and uproot many trees, depositing massive amounts of litterfall on the forest ground. Such canopy flux induces changes in forest structure and processes for a period ranging from short to long-term [5]. As a frequent source of disturbance in the Caribbean, hurricanes dramatically change forest dynamics and processes throughout the area covered by hurricane tracks [5–7].

Hurricanes deposit a large amount of fine litter and coarse woody debris on the forest ground. Hurricane Hugo deposited 1.08 kg/m^2 total litterfall, which is equal to 1.25 times of annual litterfall production in the Bisley Experimental Watersheds in the Luquillo Experimental Forest of Puerto Rico in 1989 [8]. In the northeastern Yucatan Peninsula, Hurricane Gilbert defoliated almost all of the trees in 1988 [9]. Hurricane Iniki generated an instantaneous fine litterfall that was equivalent to 1.4 times the annual fine litterfall input in the Na Pali-Kona Forest Reserve of Hawaii in 1992 [10]. During the period from 1992 to 2000, 16 typhoons deposited hurricane-induced debris varying from 10,800 to 3020 kg/ha in the Fushan Experimental Forest of northern Taiwan [3]. In 2017, Hurricane Irma and Hurricane Maria deposited a total amount of 32,225 kg/ha fine litter debris, which was equivalent to 1.61 times the annual litterfall production in the Luquillo Experimental Forest in Puerto Rico [11]. A massive input of hurricane debris provides a pulsed input of carbon and nutrients to forest soils.

Nutrient input to soil from hurricane-induced litterfall is well understood. A large-scale long-term manipulation experiment of canopy and deposited debris (CTDD) that spanned from 2003 to 2007 in the same research site demonstrated that the CTDD treatment had large and lasting effects on carbon and nutrient cycling [12], and soil microbial communities had strong resilience to the CTDD treatment [13]. However, the dynamics and degree of soil microbial community between the control and CTDD treatments were incomplete, because the study started too late after the CTDD treatment [13]. Although litter invertebrate [14], nutrient dynamics [12], soil microbial community [13], fungal connectivity [15], and tree recruitment [16] were studied in the canopy trimming experiment, studies on the impact of hurricane-induced litterfall on soil LOC and its turnover rate are still rare [8,9,17]. Soil microbial biomass carbon (MBC) is defined as the total carbon contained in the living component of soil organic matter [18,19], comprising only 1.4% of the world's total soil organic carbon [20], but it is the most active component of soil organic carbon, and plays an important role in regulating biogeochemical processes in terrestrial ecosystems [21–23]. Soil LOC is defined as the fraction of soil organic carbon that is degradable during soil microbial growth [24]. The definition and explanation of soil labile organic carbon (LOC) are still controversial [25–27], but it is widely acknowledged that soil LOC is an important component of soil organic carbon with rapid turnover rates, which can be drastically changed by disturbance and management [24,28,29]. Other indices of soil LOC rarely provide estimates of relative turnover rates.

Around 800 severe disturbances of hurricane and tropical storm have crossed the Caribbean region over the last 100 years, resulting in dynamic changes in forest structure and processes [5,6]. Our objective in this study is to examine the influence of hurricane disturbance on below-ground ecosystem properties in forests. Specifically, we hypothesize that hurricane disturbance increases the pools of soil MBC and soil LOC because of the sudden massive input of hurricane-induced litterfall, thus leading to the alteration of the turnover rate of soil LOC. For testing our hypothesis, we conducted this study and measured soil MBC and soil LOC immediately after the CTDD treatment and during the initial period of forest recovery.

2. Materials and Methods

2.1. Study Sites

This study was conducted in the Canopy Trimming Experiment (CTE) plots, which are located in the Luquillo Experimental Forest, Puerto Rico [30]. This forest is a subtropical wet forest, according to the landscape life zone classification system of Holdridge, and is characterized as a tabonuco forest type [14]. The dominant tree species include *Dacryodes excelsa* Vahl, *Sloanea berteriana* Choisy ex DC., *Manilkara bidentata* (A.DC) A. Chev., and *Prestoea acuminata* (Wildenow) H.E. Moore (=*Prestoea montana*

(Graham) A. Henderson and G. Galeano) [31]. Mean air temperature was 24 °C [31], and mean annual precipitation was 3500 mm [32]. Although this is a non-seasonal forest, there is typically a weak dry season from December to March [14]. Two litterfall peaks normally occur in April and August, and the lowest litterfall rate is between December and February [23,33,34]. Soils are classified as highly weathered Oxisols derived from volcaniclastic sediments [35,36]. Three complete replicated blocks of the CTE plots were located in the northeastern and eastern areas of El Verde Field Station (18°19′16.37″ N, 65°49′11.21″ W) in El Yunque National Forest around 1 km apart, at 340–470 m a.s.l. [14].

2.2. Study Design

The three replicated blocks of the CTE are located in areas of tabonuco forest with similar biotic and abiotic factors, such as plant species, soil type, temperature, and precipitation. The original design of the CTE included four plots (i.e., four treatments) in each block: without canopy trimming or debris deposition (control), without canopy trimming and with debris deposition, with canopy trimming and without debris deposition, and a simulated hurricane treatment with canopy trimming and debris deposition (CTDD) [14,37]. Each plot of the treatment is 30 m × 30 m, with a central 20 m × 20 m measurement plot divided into 16 subplots (each subplot: 5 m × 5 m). Since the most common effect of hurricane disturbance on forest is canopy defoliation and massive amounts of debris deposition, we conducted this study using only two treatments: control and CTDD. Three subplots in each plot were randomly assigned for taking soil samples to study below-ground processing.

2.3. Soil Sampling and Processing

In the CTDD plots, forest canopy was trimmed, and debris was deposited on the forest ground in December 2014 (Figure 1). We collected floor mass and 0–10 cm deep volumetric soil cores three weeks before the treatment, and in the first, second, third, fifth, 12th, 24th, 36th, 48th, 60th, 72nd, 84th, 96th, 108th, and 120th weeks after the treatment.

Each time, we randomly threw a round plastic dish with a 0.2-m diameter onto the ground surface, cut the leaves and wood along the dish margin with a knife, and collected the forest floor mass under the dish in each of three subplots. Soil samples were collected to 10-cm depth using a PVC pipe with 0.05-m inner diameter. All of the samples of floor mass and soil were immediately processed at the field station. We weighed floor mass samples before and after they were oven-dried at 65–70 °C to constant weight for obtaining their dry weights. We weighed the soil cores, removed all of the roots, plant debris, rocks, and visible soil animals from each soil sample, weighed each component, pooled the three soil samples from the three subplots in the same plot to form one composite pool soil sample, and transported them to the lab in University of Puerto Rico-Río Piedras campus for further analysis.

(**a**) (**b**)

Figure 1. *Cont.*

(**c**)

(**d**)

Figure 1. Photos of the canopy trimming and debris deposition (CTDD) plots before and after the CTDD treatment in the Luquillo Experimental Forest, Puerto Rico. (**a**) Dense forest canopy before the CTDD treatment; (**b**) Bare trunks after the CTDD treatment; (**c**) Thick litter deposition on the forest ground after the CTDD treatment; and (**d**) Recovery of trimmed forest after 12 weeks following the CTDD treatment. These photos were taken by Sarah Stankavich.

We determined soil MBC by the modified Jenkinson and Powlson's fumigation–incubation method [38,39]. For each soil sample, we weighed two 30-g fresh soil subsamples, one for the fumigation and incubation treatment, and one for the control sample. Soil MBC was calculated by the difference of CO_2 released from the control and fumigated soil samples during a period of 10-day incubation using the following equation:

$$B = F/K \tag{1}$$

where B was soil MBC (g/kg); F was the difference of CO_2 released from two copies of soil sample; and K = 0.45, which was the rate of the biomass carbon mineralization during the fumigation—incubation process.

We measured soil LOC and its turnover rate using the sequential fumigation–incubation method [24]. We fumigated and incubated each soil sample repeatedly for eight cycles (10 days for each cycle), and calculated soil LOC and its turnover rate by the released CO_2 from the fumigation and incubation soil sample relative to the control soil sample over all eight fumigation and incubation cycles. We calculated soil LOC and its turnover rate using the following equation:

$$Ln\ (C_t) = Ln(kC_{labile}) - kt \qquad (t = 1,\ 2,\ 3, \ldots\ldots,\ 8) \tag{2}$$

where C_t was soil MBC at the fumigation and incubation t cycle; k was the slope, or the turnover rate of soil LOC; C_{labile} was soil LOC; $Ln(kC_{labile})$ was the intercept (a); and t was the fumigation and incubation cycle. $C_{labile} = e^a/k$.

2.4. Data Analysis

Values of soil MBC and soil LOC were expressed at a dry soil basis (oven-dried for 24 h at 110 °C to constant weight). We compared floor mass, soil moisture, soil MBC, soil LOC, and its turnover rate between the control and CTDD plots three weeks before and one week following the CTDD treatment using one-way ANOVAs (Statistical Package for the Social Sciences 20, SPSS 20, IBM Corporation, Chicago, IL, USA), and employed mixed-model ANOVA using SPSS 20 to analyze the influence of the CTDD treatment on floor mass, soil moisture, soil MBC, soil LOC, and the turnover rate of soil LOC. Dependent variables were floor mass, soil moisture, soil MBC, soil LOC, and its turnover rate. The within-subject factor was week. Independent variables were treatment (control versus CTDD treatment). All of our data for ANOVA met the homogeneity (Levene's test [40]), normality (Shapiro–Wilk test [41]), and sphericity (Mauchly's test [42]) assumptions. Significance level was set at $\alpha < 0.05$.

We constructed Figures 2 and 3 using SigmaPlot 10.0 (Systat Software, Richmond, CA, USA). Figure 2 was constructed by the multiple-scatter method, and Figure 3 was constructed using a 3D mesh plot [43]. The 3D mesh plots were interpolated based on our experimental data. A uniformly spaced grid was divided into 50 intervals from the minimum raw to maximum raw data in the x and y-dimensions. At the intersection of the x and y-grids, interpolated z-values were calculated using an inverse distance method [43–45].

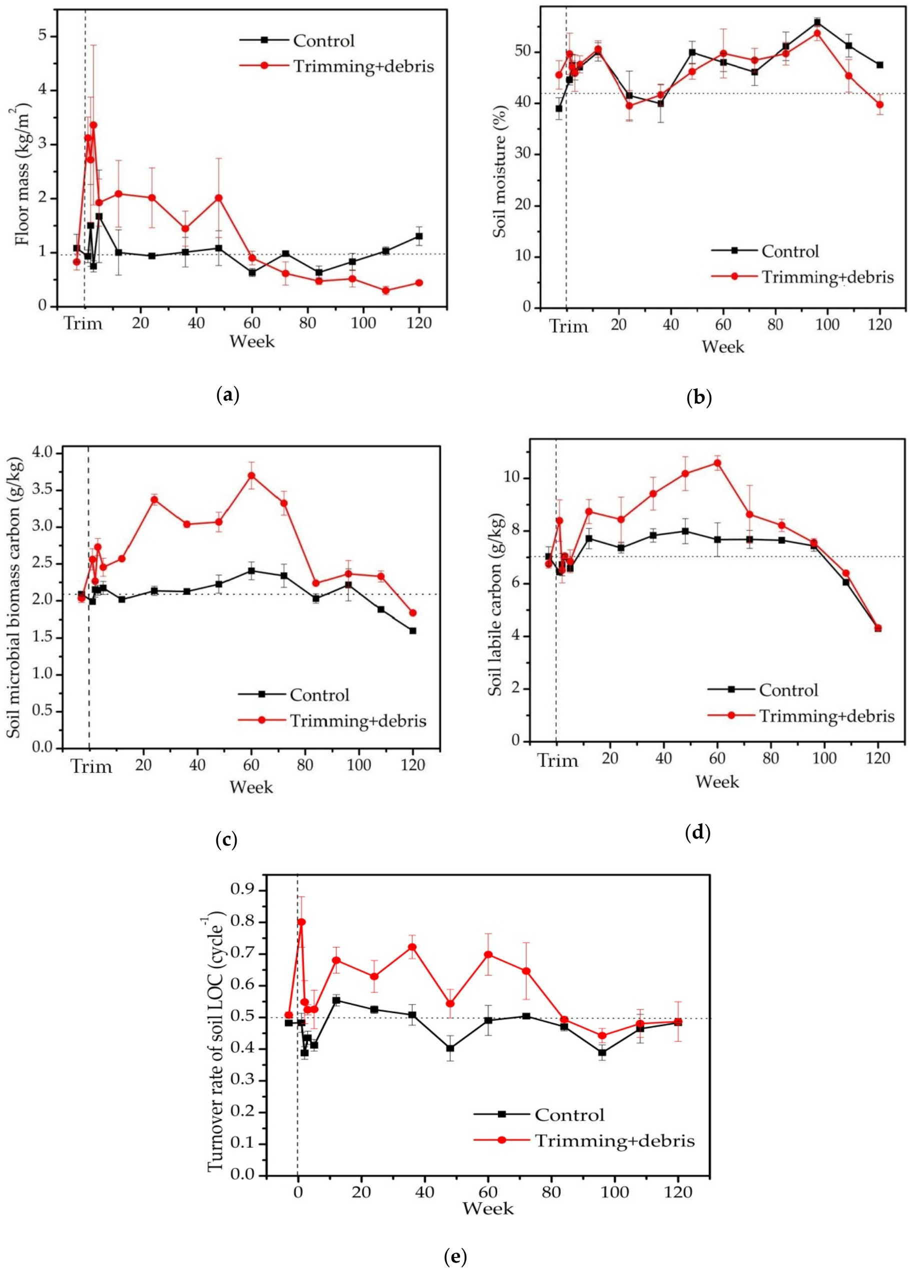

Figure 2. Dynamics of (**a**) floor mass, (**b**) soil moisture, (**c**) soil microbial biomass carbon (MBC), (**d**) soil labile organic carbon (LOC), and (**e**) turnover rate of soil LOC three weeks before and after the canopy trimming and debris deposition (CTDD) treatment for 120 weeks in the control and CTDD plots in the Luquillo Experimental Forest, Puerto Rico. Note: The week marked by the vertical dashed line was the week to trim forest canopy and deposit debris on the forest ground in the CTDD plots; the value marked by the horizontal dotted line was the corresponding value of floor mass, soil moisture, soil MBC, soil LOC, and the turnover rate of soil LOC measured in the control and CTDD plots three weeks before the CTDD treatment. Error bars represent the standard error.

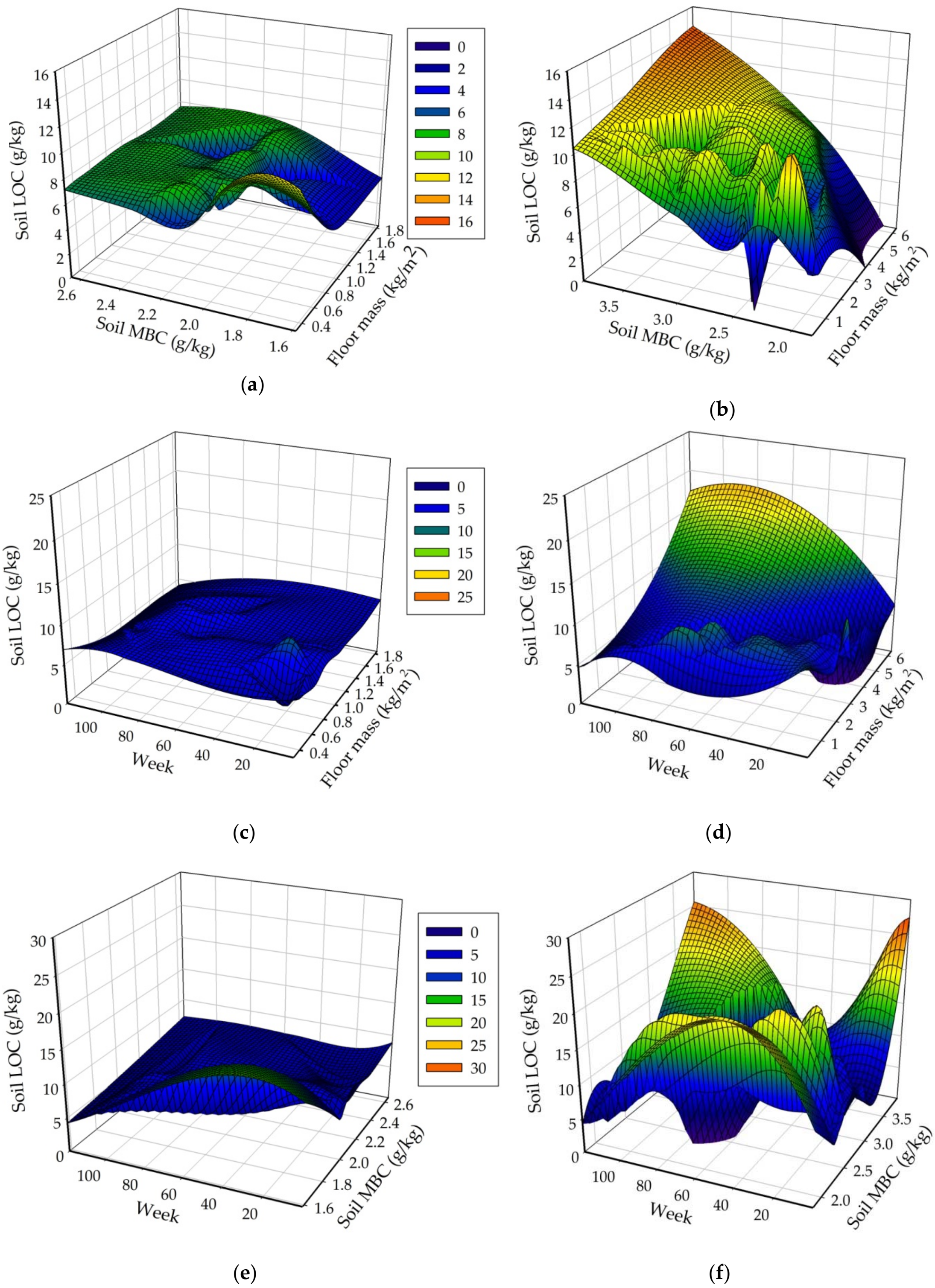

Figure 3. Soil LOC in correspondence to floor mass and soil MBC in (**a**) the control and (**b**) CTDD plots, floor mass, and weeks following CTDD treatment in (**c**) the control and (**d**) CTDD plots, and soil MBC and weeks following CTDD treatment in (**e**) the control and (**f**) CTDD plots in the Luquillo Experimental Forest, Puerto Rico.

We conducted the multiple linear regression analysis including floor mass, soil moisture, soil MBC, soil LOC, turnover rate of soil LOC, and time (in weeks) after the CTDD treatment between the control and CTDD plots, using SPSS 20. The independent variables were floor mass, soil moisture, soil MBC, week after the CTDD treatment, and the treatment of CTDD. The dependent variables were soil LOC and its turnover rate. Our data met the assumptions of linearity (scatter plots [46]), normality (Kolmogorov-Smirnov test [47]), and homoscedasticity of variance (Goldfeld-Quandt test [48]). Significance level was set at $p < 0.05$.

3. Results

3.1. Data Collected Three Weeks before the CTDD Treatment

All of the soil parameters were statistically similar between the control and CTDD plots prior to the CTDD treatment, which meant that we started our study from the similar levels of floor mass, soil moisture, soil MBC, soil LOC, and turnover rate of soil LOC in the control and CTDD plots (Table 1). However, one week after the CTDD treatment, most of the soil parameters differed significantly between the control and CTDD plots.

Table 1. One-way ANOVA statistical analyses of floor mass, soil moisture, soil MBC, soil LOC, and turnover rate of soil LOC three weeks before and one week after the CTDD treatment in the control and treatment plots in the tabonuco forest, Puerto Rico. Dependent variables are floor mass, soil moisture, soil MBC, soil LOC, and turnover rate of soil LOC. Independent variables are the control and CTDD treatment. The same superscripts indicate no significant difference between the control and CTDD plots at $\alpha = 0.05$. Same superscripts (a and b) indicate no significant difference between the control and CTDD plots.

Source	Average (±SE)		Degree of Freedom	Mean Squares	F	p
	Control	CTDD				
Floor mass (kg/m^2)						
Three weeks before	1.08 ^{a} (0.26)	0.83 ^{a} (0.15)	1	0.96	0.72	0.44
One week after	0.93 ^{b} (0.11)	3.13 ^{a} (0.38)	1	7.21	29.35	0.006
Soil moisture						
Three weeks before	0.45 ^{a} (0.03)	0.39 ^{a} (0.02)	1	0.01	3.03	0.16
One week after	0.46 ^{a} (0.01)	0.43 ^{b} (0.01)	1	0.01	71.22	0.001
Soil MBC (g/kg)						
Three weeks before	2.09 ^{a} (0.02)	2.03 ^{a} (0.06)	1	0.01	0.81	0.42
One week after	1.98 ^{b} (0.01)	2.56 ^{a} (0.14)	1	0.49	15.42	0.01
Soil LOC (g/kg)						
Three weeks before	7.04 ^{a} (0.37)	6.75 ^{a} (0.16)	1	0.12	0.52	0.51
One week after	6.44 ^{b} (0.03)	9.16 ^{a} (0.31)	1	11.03	74.72	0.001
Turnover time of soil LOC (/cycle)						
Three weeks before	0.48 ^{a} (0.01)	0.51 ^{a} (0.01)	1	0.01	3.79	0.12
One week after	0.50 ^{b} (0.01)	0.87 ^{a} (0.02)	1	0.20	161.38	<0.001

3.2. Floor Mass and Soil Moisture after the CTDD Treatment

Floor mass in the CTDD plots differed significantly from the control plots, and varied significantly with time following the CTDD treatment (Table 2). Compared with the control plots, changes of floor mass in the CTDD plots during the study period could be divided into three phases: before the treatment of CTDD, between the first and 48th week after the treatment, and after the 60th week following the treatment (Figure 2a). During the first phase, mean floor mass in the CTDD plots was 0.83 (±0.15) kg/m^2, and did not differ significantly from the control plots (1.08 ± 0.26 kg/m^2). During the second phase, mean floor mass in the CTDD plots was 2.53 (±0.26) kg/m^2, and was significantly greater than 0.92 (±0.08) kg/m^2 in the control plots. During the third phase, mean floor mass in the CTDD plots was 0.54 (±0.06) kg/m^2, and was significantly lower than 0.90 (±0.07) kg/m^2 in the control plots.

Table 2. Effects of canopy trimming and debris deposition (CTDD) treatment and time after the CTDD treatment as well as their interactions on floor mass, soil moisture, soil MBC, soil LOC, and the turnover rate of soil LOC by the mixed-model ANOVA in the Luquillo Experimental Forest, Puerto Rico. The within-subject factor is week. The dependent variables are floor mass, soil moisture, soil MBC, soil LOC, and turnover rate in the CTDD plots. Independent variables are treatment (control vs. CTDD treatment).

Source	Week	Trimming + Debris	Week × Trimming + Debris
Floor mass	<0.001	0.03	0.001
Soil moisture	<0.001	0.01	0.10
Soil MBC	<0.001	<0.001	<0.001
Soil LOC	<0.001	0.007	0.26
Turnover rate of soil LOC	<0.001	0.01	0.001

Mean floor mass did not differ among these three phases in the control plots. Mean floor mass in the CTDD plots was significantly lower during the first phase than the second phase, but was not significantly different from the third phase, showing an apparent interaction between treatment and time.

Soil moisture in the CTDD plots differed from the control plots, and varied with weeks following the CTDD treatment (Table 2). Considering fluctuations in both the control and CTDD plots, we divided soil moisture status into four phases: before the treatment, between the first and 12th week after the treatment, between the 24th and 96th week after the treatment, and after the 108th week following the treatment (Figure 2b). During the first and second phases, mean soil moisture in the control plots was not different from the CTDD plots. During the third phase, mean soil moisture in the control plots was 45% (±1), which was significantly lower than the 49% (±1) recorded in the CTDD plots. In contrast, mean soil moisture in the control plots was 49% (±1) during the last phase, which was significantly higher than the 42% (±1) recorded in the CTDD plots.

There was a strong seasonal drop in soil moisture in the both control and CTDD plots between the 20th and 50th week caused by a drought with no interactions between treatment and time, regardless of the shift in relative value of soil moisture during the third and fourth phases. Between the 24th and 36th week, the mean soil moisture in both the control and CTDD plots was lower than in the other weeks. The variation of soil moisture in the CTDD plots was slightly more pronounced than in the control plots.

3.3. *Soil MBC after the CTDD Treatment*

Soil MBC in the CTDD plots differed significantly from the control plots, and varied significantly with time after the CTDD treatment (Table 2). Mean soil MBC in the CTDD plots was significantly higher than in the control plots on every sampling date during the study period, except for the 96th week and three weeks before the CTDD treatment (Figure 2c). According to the ratio between soil MBCs in the CTDD plots and the control plots, changes of soil MBC could be divided into four following phases: the first phase occurred during the period three weeks before the treatment, with insignificant difference in the soil MBC between the control and CTDD plots; the second phase occurred between the first and 12th week after the treatment, during which period the mean soil MBC in the CTDD plots was 1.20 times that of the control plots; the third phase occurred between the 24th and 72nd week after the treatment, during which period the mean soil MBC in the CTDD plots was 1.47 times that of the control plots; and the fourth phase occurred after the 84th week following the treatment, during which period the mean soil MBC in the CTDD plots was 1.14 times that of the control plots. The third phase corresponded largely to the drought.

In the control plots, the only significant difference in mean soil MBC was between the third (drought) phase and the fourth phase. In the CTDD plots, the mean soil MBC in the first phase was significantly lower than the second and third phases, but was insignificantly different from the fourth phase. There is a strong interaction between treatment and time for soil MBC.

3.4. Soil LOC and Its Turnover Rate after the CTDD Treatment

Soil LOC in the CTDD plots differed significantly from the control plots, and varied greatly with time of the CTDD treatment (Table 2), showing both treatment and time effects. We divided the entire study period into four phases: the first phase, three weeks before the treatment; the second phase, from the first to fifth week after the treatment; the third phase, from the 12th to 72nd week after the treatment; and the fourth phase after the 84th week following the treatment (Figure 2d). Among these four phases, the mean soil LOC of the CTDD plots during the third phase was significantly higher than the control plots, and did not differ from the control plots during the other three phases. The mean soil LOC in both the control and CTDD plots was significantly lower in the fourth phase than in the other three phases, and did not differ among the other three phases. There is a significant interaction between treatment and time on soil LOC.

The turnover rate of soil LOC in CTDD plots also differed significantly from the control plots, and varied significantly with time after the CTDD treatment (Table 2). According to the differences between the control and CTDD plots, the mean turnover rate of soil LOC showed dynamic changes in four phases: the first phase during the three weeks before the treatment, the second phase from the first to fifth week after the treatment, the third phase between the 12th and 72nd week after the treatment, and the fourth phase after the 84th week since the treatment started (Figure 2e). Among these four phases, the mean turnover rate of soil LOC during the second and third phases in the CTDD plots was significantly higher than the control plots, and was significantly faster than during the first and fourth phases. The turnover rate of soil LOC did not differ among the four phases in the control plots, showing apparent treatment and time interactions.

3.5. Correlation Analysis

Using data pooled from both the control and CTDD plots, we found that soil LOC correlated significantly with floor mass, soil MBC, and time after the CTDD treatment, but was not correlated with soil moisture (Table 3). In contrast, soil MBC was only correlated with the turnover rate of soil LOC.

Table 3. Linear correlations of soil LOC and its turnover rate with floor mass, soil moisture, soil moisture, soil MBC, for the week after the CTDD treatment in the control and CTDD plots in the Luquillo Experimental Forest, Puerto Rico.

Source	Regression Coefficient	*p*-Value	Correlation Coefficient	*p*-Value
Soil LOC				
Floor mass	−0.39	0.002	−0.13	0.03
Soil moisture	3.68	0.10	0.26	0.008
Soil MBC	1.92	<0.01	0.68	<0.001
Week	−0.01	0.006	−0.22	0.01
Constant	2.05	0.05		
Turnover rate of soil LOC				
Floor mass	0.01	0.15	0.27	0.006
Soil moisture	0.02	0.89	0.14	0.09
Soil MBC	0.12	<0.001	0.56	<0.001
Week	0.01	0.59	−0.22	0.02
Constant	0.21	0.03		

Soil LOC was apparently affected by both floor mass and soil microbial activity in both the control and CTDD plots (Figure 3a,b). This influence was more pronounced in the CTDD plots than in the control plots, which was largely due to the extrapolated scales in both floor mass and soil MBC. Soil LOC also fluctuated with time, and this fluctuation was more pronounced in the CTDD plots than the control plots, too (Figure 3c–f). High levels of soil LOC occurred about 10 months after the deposition of canopy debris (Figure 3d). High soil MBC was associated with high soil LOC immediately or 60 weeks after the CTDD treatment (Figure 3f).

4. Discussion

The pulsed input of vast litter debris generated by hurricanes provides sources of soil LOC and food for soil communities. It is consequently expected that soil LOC and soil MBC will increase following hurricanes. Indeed, our manipulated hurricane disturbance showed an immediate increase in both soil LOC and soil MBC. As hurricane-induced debris decomposition proceeds, the increased soil LOC and soil MBC are expected to decrease, and eventually return to background levels or fall below pre-hurricane levels. Our data showed that soil LOC returned to control plot levels after 82 weeks, and remained at the control plot levels thereafter. Soil MBC behaved differently from soil LOC; although it decreased at week 82, it remained higher than in the control plots even at 120 weeks, showing a much longer residual effect from the pulse of hurricane-induced debris. This lasting residual effect on soil MBC following hurricane disturbance suggested an alteration of other soil physical and biological factors during forest recovery following hurricane disturbance.

The rates of forest canopy recovery after hurricanes vary among forests and storm events. After Hurricane Hugo crossed Puerto Rico in September 1989, it took 60 months for the total litterfall (fallen leaves and fine wood) to return to the pre-hurricane level in a tabonuco forest of the Bisley Experimental Watersheds [49]. After Hurricane George defoliated the tabonuco forest in Puerto Rico in September 1998, total forest floor mass and fallen leaves continually decreased to below pre-hurricane levels during the first year [50]. In our study, total floor mass in the CTDD plots continually decreased after the CTDD treatment in December 2014, with elevated floor mass lasting for only 65 weeks, after which it fell below litter standing stocks in the control plots. Total floor mass had not returned to the control plot level, even after 120 weeks. The slow recovery of forest litterfall and floor mass might result the decline of soil LOC in the CTDD plot during the later phase of forest recovery.

In previous studies, litterfall accumulation was shown to decrease solar radiation on mineral soil surface, together with reduced forest transpiration in the trimmed plots, causing soil to retain more moisture [14,50,51]. However, during our study, soil moisture did not differ significantly between the control and CTDD plots until the 12th week after treatment. An extreme drought that started in March 2015 (12 weeks after the CTDD treatment) and lasted until November 2015 (around the 50th week after the CTDD treatment) might have caused soil moisture to converge between treatments during this period. Convergence in soil moisture is also seen after torrential rain. In addition, the complicated differences in terrain among the three replicate blocks may have contributed to higher variation and a lack of soil moisture differences between treatments. Between the 24th and 96th week after the treatment, mean soil moisture in the CTDD plots was significantly higher than in the control plots, perhaps because dense canopy in the control plots intercepted rainfall water [48], soil in the CTDD plots received more rainfall, and the trimmed trees in the CTDD plots transpired less water than the untrimmed trees in the control plots. However, the situation after the 108th week following the CTDD treatment was reversed, with significantly higher mean soil moisture in the control plots compared with the CTDD plots. It might be because of a stronger transpiration rate at a lower canopy height of the recovering trees and dense understory tree seedlings, shrubs, and herbs in the CTDD plots than at a higher canopy height in the control plots [52–54], or because the reduced floor mass in the CTDD plots allowed for greater evaporation than the control plots with thicker floor mass cover.

Multiple factors can influence soil MBC. A previous study conducted in the same area showed that soil MBC was not directly regulated by soil temperature, moisture, or litterfall input [23]. Soil fungal biovolume was previously found to vary directly with soil moisture [55], and soil bacteria in this forest was also found to be sensitive to drought stress [56]. This study showed that soil MBC peaked when both soil LOC and soil moisture were high. Mean soil MBC in the CTDD plots was significantly higher than in the control plots in every sampling week, except for the three weeks before the treatment and the 96th week after the treatment. A sudden deposition of massive hurricane-induced litterfall in various forests was shown to increase soil carbon input and the heterogeneity of the microenvironment for soil microbes [5], change soil C/N ratios [3,8], increase and then decrease competition for soil nutrients between soil microorganisms and plant species [23,57], and alter the biomass and biodiversity of litter invertebrates [14], all of which could be potential factors that might have jointly elevated soil MBC. These potential factors in the CTDD plots may lead to a persistent higher soil MBC in the CTDD plots.

Permanganate oxidizable carbon was revealed as a more sensitive fraction of the soil organic carbon [58], and soil LOC was believed to be an active component to trigger increases in soil MBC [59,60]. In our study, soil LOC was significantly related to soil MBC (Table 3). However, other factors can also influence soil MBC. It was found that soil MBC fluctuated one month ahead of plant litterfall in the same forest [23], but soil MBC in this study increased immediately after the treatment of CTDD, and this increase persisted to the end of this study. Unlike soil MBC, soil LOC increased beginning 12 weeks after treatment, and returned to the control level 84 weeks following the CTDD treatment. This might be because the more recalcitrant carbon in the CTDD plots continually stimulated soil MBC accumulation after the initial pulse of debris deposition even after the 84th week, or because the reduced floor mass in CTDD plots might have fewer predators for microbes [61]. A long-term study is needed to follow changes in soil MBC and floor mass in order to detect the lasting effect of CTDD treatment to forest ecosystems.

Since soil LOC in this study was defined as the fraction of soil organic carbon that was degradable during soil microbial growth [24], the factors controlling the growth and reproduction of soil microbes would also affect the dynamics of soil LOC. In addition, the altered accompanying environmental factors with the CTDD treatment played an important role in regulating soil LOC. Unlike the significant soil MBC difference persisting to the 120th week after the treatment, soil LOC in CTDD plots converged on that of the control plot 96 weeks after the treatment. This suggests that other factors may have played a more important role than soil LOC in regulating soil MBC during the later stages after the CTDD treatment. Except for the uneven distribution of litter deposition in forest, hurricanes changed the microenvironmental conditions in forest ecosystem over the long term [5], which might be explain the complex relationship between soil LOC, its turnover rate, and the other factors such as floor mass, soil moisture, and soil MBC.

The turnover rate of soil LOC is predominately determined by the quality of soil LOC (e.g., C/N) [62,63]. It was demonstrated that fresh debris decayed faster than senesced litter, and fresh debris released more N, P, K, Mg, Mn, Na, and S than senesced litter [8,61]. These additional materials with high decomposition rates elevate the decomposition rate of the total soil carbon and non-hydrolyzable carbon at the surface soil layer [64]. Compared with the control plots, the CTDD plots deposited thick green debris, which might decay faster and release more nutrients into soil than senesced litter in the control plots. This quickly decaying debris released mineral nutrients as well as labile carbon, which stimulated soil MBC more than soil LOC in our study, thus elevating the turnover rate of soil LOC at the initial stage. As the green CTDD debris gradually disappeared, sources of soil LOC gradually reverted back to plant litterfall with no difference in litter quality between the CTDD plant control plots, leading to the convergence in the turnover rates of soil LOC between these treatment plots.

5. Conclusions

It has been previously demonstrated that hurricanes can induce short and long-term changes in forest structure and composition, nutrient cycling, physical environmental conditions, animal biomass and diversity, and forest developmental process and successional trajectories. Our study suggested that extensive canopy removal, together with sudden massive amounts of debris deposition after a simulated hurricane treatment, significantly increased soil MBC, soil LOC, and the turnover rate of soil LOC. Soil MBC in the CTDD plots was still significantly higher than in the control plots after 120 weeks following the CTDD treatment, whereas soil LOC returned to background levels after 96 weeks. Massive accumulation of both soil LOC and recalcitrant pools offered abundant available carbon resource for soil microbes during an extended period. The elevated turnover rate of soil LOC shortened the recycling time of organic carbon, caused the pulse of soil microbial growth and reproduction, and might have mobilized more stable soil carbon pools. Our data suggest that the pulsed input of green debris and nutrients from the simulated hurricane input can alter carbon cycling by increasing the production of soil LOC and elevating its turnover rate in tropical forests.

Author Contributions: X.L., S.S., D.J.L. and S.A.C. collected floor mass and soil samples from field forest plots, and sorted soil samples; X.L. and X.Z. (Xiucheng Zeng) determined soil microbial biomass carbon and soil labile organic carbon at Zou's lab in University of Puerto Rico-Río Piedras campus; X.Z. (Xiaoming Zou), D.J.L., S.A.C. and G.G. designed the study; S.S. took the photos in the CTDD plots; X.L. wrote the manuscript; X.Z. (Xiaoming Zou), G.G., D.J.L. and S.S. revised the manuscript.

Funding: Support for this study was provided by a joint venture agreement (14-JV-11120101-018) from IITF to UPR. GG was supported by the Luquillo Critical Zone Observatory (National Science Foundation grant EAR-1331841) and the Luquillo Long-Term Ecological Research Site (National Science Foundation grant DEB-1239764).

Acknowledgments: All research at the USDA Forest Service International Institute of Tropical Forestry is done in collaboration with the University of Puerto Rico. We thank all volunteers at El Verde Field Station for helping to collect soil samples in forest field plots and sorting out soil samples at the field station. We thank the managers at El Verde Field Station for offering necessary space and experimental instrument to pretreat our samples. International Institute of Tropical Forestry (USDA forest service) provided all chemicals for determining soil microbial biomass carbon and soil labile organic carbon. Chao Wang, a graduate student of Environmental Sciences, University of Puerto Rico, helped us to analyze partial data.

Conflicts of Interest: The authors declare no conflict of interest.

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