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Physical, Chemical, and Biological Properties of Soil under Decaying Wood in a Tropical Wet Forest in Puerto Rico

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Academic Editor: Björn Berg

Received: 31 May 2016; Accepted: 29 July 2016; Published: 4 August 2016

Abstract: Decaying wood is related to nutrient cycling through its role as either a sink or source of nutrients. However, at micro scales, what is the effect of decaying logs on the physical, chemical, and biotic characteristics of the soil underneath? We took samples from a 0 to 5 cm depth under and a 50 cm distance away from decaying logs (*Dacryodes excelsa* and *Swietenia macrophylla*) at 2 stages of decay, and measured soil temperature, total and available nutrients, and root length in a tropical wet forest. We found decaying wood affected physical, chemical, and biotic properties of the underlying soil. Soil temperature was less variable under the decaying logs than away from the logs. Soil under the decaying wood had fewer roots, and lower NO_3^- and Mg^{2+} availability than samples collected a distance of 50 cm away from the logs. Tree species and decay stage were important factors defining the effect of decaying wood on the distribution of available nutrients. Ca^{2+}, Mg^{2+}, and K^+ levels were higher in the soil associated with the youngest logs, and were higher near *S. macrophylla* logs. Heavy metals were also higher in the soil located near the younger logs independent of the species; other metal ions such as Al^{3+} and Fe^{3+} were higher in the soil associated with *D. excelsa* and the oldest logs. These results indicate decaying wood can contribute to and generate spatial heterogeneity of soil properties.

Keywords: coarse woody debris (CWD); wood decomposition; soil properties; available nutrients; roots; microbial biomas; tropical forest; Puerto Rico

1. Introduction

Coarse woody debris (CWD), which is defined as any decaying woody material greater than 10 cm in diameter and larger than 1 m [1], is an important component of forest structure, accounting for a considerable portion of the aboveground forest floor: 20%–30% in tropical forests [2–4] and more than the 60% in some temperate ones [5] (and references cited therein). Structurally, decaying wood can contribute to and generate a high diversity of habitats for many species of microorganisms, plants, and animals [6–8] (and references cited therein). Functionally, decaying wood is related to nutrient cycling through its role as either a sink or source of nutrients [9]. Coarse woody debris is also a site for nitrogen fixation, a cradle for seed germination, and for storage of water [6]. However, regarding the specific effect of decaying wood on the physical, chemical, and biotic properties of the underlying soil, different studies have found contrasting results.

It is well known that decaying wood can absorb many times its dry weight in water [10] because woody tissue is highly hygroscopic [11], and additionally, water is produced after fungal degradation

of wood [12,13]. In fact, Vogt et al. [14] noted that decaying logs acted as refuges for mycorrhizal fungi during dry periods or after disturbances. Therefore, it can be expected that decaying logs will contribute to keep the underlying soil moister than the soil that is covered only by the forest floor litter. However, some authors have reported no changes in soil moisture under decaying logs compared to controls (i.e., soil without a log upon it) [15,16].

Decaying wood can also change soil chemical properties. Some studies in temperate and boreal forests have found higher C and N percentages (%C and %N, respectively) in soil under decaying wood, but did not observe changes in the C:N ratios [17,18]. Conversely, in other temperate and boreal forest studies, higher C:N ratios have been observed in the soil under woody debris, due to increases in %C joined with decreases in %N [17,19]. These results suggest that decaying wood could be a source of recalcitrant organic matter that accumulates in the underlying soil, and ultimately can change the properties of soil organic matter in the vicinity of CWD. As mentioned before, CWD can be either a source or sink of nutrients and several studies attest for both roles. Studies that have focused on the changes of nutrient content along wood decomposition in temperate and boreal forests (most of them based on chronosequences after known disturbance events) indicate that CWD can temporarily act as sinks for N and sometimes also for P and Mg [5,20–23]. But, when these data were reanalyzed accounting for mass losses due to fragmentation and CO_2 respiration, it was found that even though the concentration of N can increase as decomposition progresses, there can be net losses of N and other nutrients along all the stages of decomposition [9,24].

Following a different approach, studies based on experimental addition or removal of CWD have shown that CWD in wet tropical forest can either hinder [25] or enhance [26] tree growth, by the immobilization or release of nutrients that can potentially be taken up by plants. Patterns of immobilization and release of nutrients from decaying wood are varied, depending mainly on the C:N ratio of the substrate (which in turn changes along the decomposition process) [9], and on the ability of microbes and plants to take up available nutrients. For example, Zimmerman et al. [25] performed a removal of coarse woody debris windthrow from Hurricane Hugo in a wet tropical forest in Puerto Rico and reported a short-term immobilization of nutrients by soil microbiota. The immobilization by microbes may have prevented plant uptake, since the trees recovered their canopies slower where woody debris was left on the ground of the experimental plots. Bole growth was greater over the long-term, however, in tropical wet forest plots where debris was not removed [27]. In contrast, Beard et al. [26] added CWD to non-disturbed plots in a wet tropical forest, in amounts equivalent to the inputs generated by a hurricane and observed enhanced tree growth. The results from Beard et al. [26] differ from other tropical forest studies that used modeling tools to suggest that CWD deposited on the ground during a hurricane in Puerto Rico would lower aboveground plant growth for at least a few years [25,28]. Furthermore, the results from Beard et al. [26] suggest that hurricane generated wood may increase ecosystem recovery due to its rapid rate of decomposition and associated release of nutrients. Another approach to infer effects of decaying wood on nutrient availability has been to directly measure mineralization rates in soil influenced by CWD. In this regard, Busse [15] reported higher mineralizable N under decaying pine logs in Oregon, while Kayahara et al. [17] found the opposite in British Columbia, namely higher mineralizable N away from logs. Later on, Hart [29] showed that indeed there is active N mineralization in decaying wood, presumably due to a shortage of labile carbon in the wood, but the rates do not exceed those in bare soil. Thus, decaying wood can potentially affect nutrient cycling in the underlying soil, but the factors and the mechanisms determining this effect are still not well understood. As suggested by Klinka et al. [30], the effect of decaying wood on soil can be specific for each ecosystem, as it is affected by the particularities of the physical environment as well as by biotically mediated process.

Furthermore, decaying wood can also influence soil biological properties. As wood decomposition proceeds, different organisms are able to catalyze different molecules at different rates while produced as byproducts of decay, and depending on the abiotic environmental regime, which may vary considerably over a small scale [31,32]. After a hurricane, production of new fine roots might be

expected as plants need to increase their acquisition of nutrients to support the growth of the new foliage [33]. In wet tropical forests in Puerto Rico, Lodge et al. [34] found higher root length away from rather than underneath the decaying logs in the dry season, but the pattern was reversed in the wet season. Conversely, a greater microbial biomass accumulation as a result of woody debris addition could result in a greater immobilization of nutrients as found by Zimmerman et al. [25] in wet tropical forests. In temperate and boreal forest ecosystems, microbial biomass immobilizes much more added nitrogen than does plant uptake [35–39], and thus retains nutrients as observed in temperate forests during spring melt [38,39]. In a pine forest in Oregon, Busse [15] found higher microbial biomass underneath rather than away from decaying logs and suggested it could be a result of higher mineralizable N. Most previous studies on the effects of decaying CWD on the underlying soil have been conducted in temperate or boreal forests while the few studies conducted in wet tropical forests have produced conflicting results [25–28]. In this study, we posited that decaying wood would affect soil biota (soil microbial biomass and roots) via changes in the physico-chemical environment of the underlying soil (temperature, moisture, increased carbon content, and altered nutrient availability) as influenced by the decay stage of the overlying wood.

Specifically, we hypothesized that the specific effect of decaying wood on soil moisture would be related to the decay stage and the seasonal variation of rainfall, being more evident for highly decayed logs and during the dry periods. Concomitant with the effect of decaying logs in soil moisture, we expected logs to have an effect on soil temperature, keeping it cooler and more constant than in the soil not affected by CWD. In addition, we hypothesized that if decomposing logs affected physical and chemical soil properties, then soil biota would respond to the associated changes. Thus, if decaying logs are sources of nutrients, we can expect an abundance of microbial biomass and/or roots under the decomposing logs compared to the soil covered only by the forest floor litter. We aimed to: (1) determine if there was an effect of decaying wood on the following physical, chemical and biological soil properties: temperature, moisture, total and extractable nutrients, nutrient supply rates, pH, microbial biomass, and root length; and (2) establish if the effect of decaying wood on soil was related to the type of wood (tree species), the stage of decomposition, or to seasonal conditions (a dry vs. a wet period).

2. Materials and Methods

2.1. Study Area

The study was performed in the Luquillo Mountains of northeastern Puerto Rico (18°18′ N; 65°50′ W; Figure 1A). Logs were selected for study in two areas: the Bisley Experimental Watersheds and the Río Chiquito plantation, 3.6 km apart [40]. The Bisley Experimental Watersheds has subtropical wet forest dominated by Tabonuco—*Dacryodes excelsa* Vahl. Some of the other more abundant species in this forest are: *Sloanea berteriana* Choisy, *Inga laurina* (Sw.) Willd. and *Manilkara bidentata* (A. DC.) Chev. There is also some planted mahogany (*Swietenia macrophylla* King). Elevation ranged between 300–330 m. The Río Chiquito area is an abandoned mahogany plantation of 32.4 ha, planted 42 years ago, and located at an elevation of 170 m [40]. Apart from *S. macrophylla*, which is the dominant species, other species present in this forest are *Ocotea leucoxylum* (Sw.) Mez. and *Syzygium jambos* (L.) Alston. [40]. Soils in both sites are ultisols and belong to the Humatas series [40]; these soils are derived from volcanic rocks, and are moderately well drained, with fine texture [41]. Texture, organic matter, nitrogen and phosphorus contents, and pH are similar between sites (Table 1), while bulk density, Ca and Mg are higher in Río Chiquito than in Bisley (Table 1, [40]).

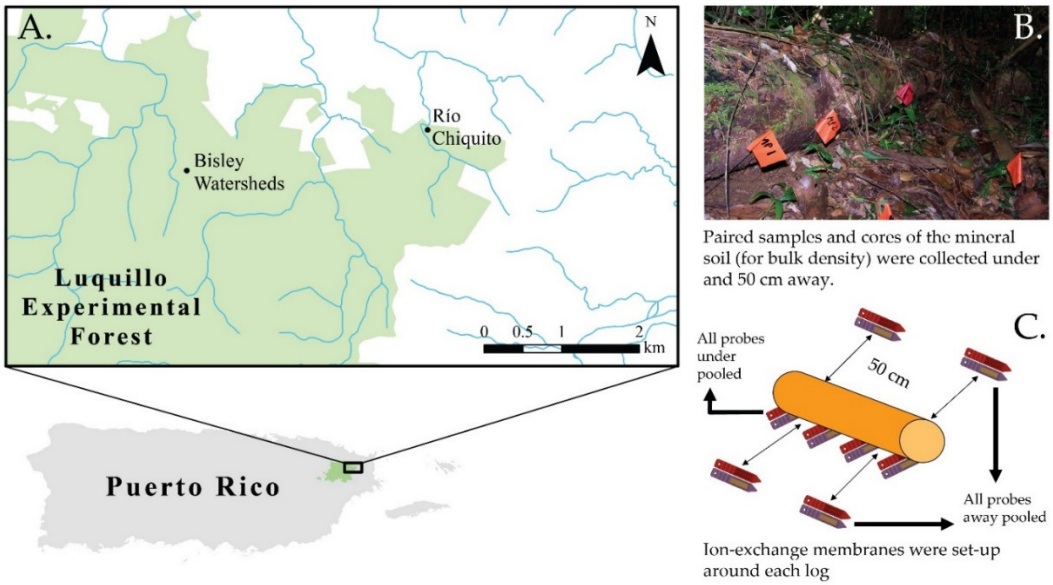

Figure 1. (**A**) The study sites were located in the Luquillo Experimental Forest in northeastern Puerto Rico; (**B**) Logs of two species and two stages of decomposition were selected (twenty logs total) and paired soil and core samples were collected and; (**C**) PRS^{TM}-probes (Plant Root Simulator) (ion exchange membranes) were collected from underneath and 50 cm away from the logs.

Table 1. Soil characteristics of the two sites where decaying logs were located. Errors are SE of the means.

Soil Property	Bisley Experimental Watershed	Río Chiquito Plantation
	Loam:	Loam/Silt Loam:
Texture [40]	45% Sand 34% Silt 21% Clay	32% Sand 48% Silt 20% Clay
Bulk density (kg/L) *	0.60	0.80
%Organic matter [40]	5.79 ± 2.5	5.11 ± 1.38
%Nitrogen [42] *	0.401 ± 0.01	0.408 ± 0.02
Phosphorus (mg·g^{-1}) *	0.3 ± 0.009	0.25 ± 0.02
pH [40]	4.6	4.9
Calcium (mg·g^{-1}) *	0.7 ± 0.2	4.2 ± 1.0
Magnesium (mg·g^{-1}) *	1.7 ± 0.4	3.0 ± 0.6

* This study, see methods for details.

Average total annual rainfall for both sites is around 3500 mm [41] with a weakly seasonal regime in which a typically dry season occurs between February and April and a typically wet season from August to November. Additionally, a short wet period occurs around April and May. Given the weakly seasonal rainfall regime, the dry season is better defined from the number of dry days per month than from monthly rainfall means [43]. Considering this, the driest period usually occurs in March and the wettest in May and September. Mean monthly temperatures range from a minimum of 22 °C to a maximum of 27 °C (multi-annual averages from 1993 to 2002, calculated from raw data available from the Luquillo—LTER Bisley Tower 1 data) [44].

2.2. Sampling Design

Twenty logs were selected, 10 from each of the two species, *D. excelsa* and *S. macrophylla*. Five of the logs from each tree species fell during hurricane Hugo in September 1989 and the other five during hurricane Georges in September 1998. Hugo's logs were in a more advanced stage of decomposition

(15 year) than Georges' logs (7 year). According to the four stages of decay proposed by Torres [45], the younger logs were close to the decay class II: intact bark, sapwood partially soft, and few invading roots present; while older logs belonged to class III: bark partially lost, sapwood soft, invading roots present. All logs selected were >30–80 cm in diameter, were in contact with the forest floor for most of their length [46] (Figure 1B), and had white rot based on the bleached, fibrous appearance of the wood. Information about the tree species identity and the time of fall was obtained from previous censuses carried out on each site and from personal observations of field technicians of the USDA—Forest Service in Puerto Rico. Soil sampling was done twice: in March 2005 (a typically dry month) and May 2005 (a typically wet month). A detailed description on the properties and nutrient content of the logs can be found at Zalamea et al. [42].

2.3. Soil Sampling and Analysis

Superficial soil temperature (upper 1 cm of mineral soil) was recorded with i-buttons® data loggers (Dallas Semiconductor Corporation, Whitewater, WI, USA) installed in pairs located under and 50 cm away from selected logs (2 in each position), between March and May 2005. Soil moisture was estimated gravimetrically from soil samples (Figure 1B). Additionally, air temperature was recorded with HOBO® data loggers (Onset Computer Corporation, Bourne, MA, USA) placed beside the logs during March and May 2005.

For each log and during each sampling period, one pair of samples (5cm × 10 cm, 5 cm depth) of mineral soil was extracted, one located underneath and one located away from the decaying logs. The samples, both under and away cores, were spatially paired, so that they were no more than 50 cm apart. Soil samples were then carried to the laboratory for estimation of soil properties (Tables 1 and 2). Additionally, an adjacent pair of soil cores (4.25 cm diameter × 5 cm depth) was taken for gravimetrical estimation of bulk density.

Soil texture was estimated following the Bouyucos-Hydrometer method [47]. Soil totals of C, N, and S were determined with a LECO-2000 CNS analyzer [48] following the procedure of [35]. Total nutrients (Al, Ca, Fe, K, Mg, Mn, Na, and P) were measured with a Beckman Spectra Span V (Fullerton, CA, USA) plasma emission spectrometer following [49] procedures. Extractable nutrients were obtained by titration using 1 N KCl (Ca, Mg, Na, and Al) and modified Olsen extractions (K, P, Mn, and Fe) [50]. The results from these extractions will be referred to as extractable nutrients. Nutrient supply rates were measured with Plant Root Simulator (PRS)™-probes (Western Ag Innovations Inc., Saskatoon, SK, Canada). The PRS™-probes consist of cation and anion exchange resin membranes encased in a plastic holding device, which are inserted into soil to measure nutrient supply in situ with minimal disturbance [51]. PRS™-probes were placed horizontally in the superficial mineral soil both underneath and 50 cm away from the decaying logs. Four pairs (i.e., four cation and four anion exchange) of PRS™-probes were spread throughout each position (under and 50 cm away), and incubated in the field for 17 days (Figure 1C). After removal, the PRS™-probes were washed with deionized water, combined according to position (under and away) for each one of the logs (5 per combination species-decay stage), and sent back to Western Ag Innovations laboratories for analysis. There, the probes were eluted for one hour using 0.5 N HCl/2 M KCl. The eluate was analyzed for levels of ammonium (NH_4^+) and nitrate (NO_3^-) using automated colorimetry. Total inorganic available N was calculated by adding NO_3^- and NH_4^+. Inductively-coupled plasma (ICP) spectrophotometry/Atomic absorption spectrometry (AAS)/flame emission spectrometry (FES) was used to measure levels of P, K, S, Ca, Mg, Al, Fe, Mn, Cu, Zn, B, and Pb, in the 0.5 N HCl/2 M KCl eluate. Nutrient supply rates generated with the PRS™-probes are reported as the amount of nutrient adsorbed per amount of adsorbing surface area per time of burial in soil (i.e., mg nutrient 10 cm^{-2} 17 $days^{-1}$), and are a measure of available nutrients as they could appear for plant roots in the soil [51]. Therefore, hereafter we will refer to nutrient supply rates and nutrient availability interchangeably, in contrast to total and extractable nutrients.

Microbial biomass C was estimated by the substrate induced respiration (SIR) method [52], calibrated for the study area [53] using an ER-10 Columbus Instruments respirometer. Microbial biomass C was previously measured in the same forest type as this study, and the values (0.46–1.43 $mg \cdot g^{-1}$ soil) fell within the range obtained for the same site using the chloroform fumigation-incubation method [54]. Conversion of CO_2 evolved to mg-C/g soil followed Anderson and Domsch [55]. Roots were extracted by hand using fine tongs for separating dead from live roots and sorting by size as fine (<2 mm) and coarse (>2 mm). Root length for fine roots (both dead and live) was measured with a Delta-T scanner and software, based on the line-intercept method [56]. Additional description of the methodology used for wood and soil analyses can be at found at Zalamea et al. [42].

2.4. Data Analysis

The effect of season (dry vs. wet), species (*D. excelsa* vs. *S. macrophylla*), decay stage (15 year vs. 7 year after falling), and position (underneath vs. 50 cm away from decaying logs) on the dependent variables (mean, maximum, and minimum temperature; gravimetric soil moisture; % soil C and N content; total and extractable Al, Fe, Mn, Ca, Mg, Na, K, and P; nutrient supply rates using ion exchange resins for Al, Fe, Mn, Ca, Mg, Mn, K, total N, NO_3^-, NH_4^+, S, Cu, Zn, B, and Pb; microbial biomass using substrate induced respiration with selective inhibitors; coarse, fine, and total root length) were determined by a multivariate analysis of variance (MANOVA) based on the general linear model (GLM). Analysis of soil temperature was based on mean, maximum, and minimum values to account for differences in the diurnal variation. To overcome possible bias due to differences between sites (i.e., Bisley vs. Río Chiquito) related to canopy openness, or soil chemistry, the site and total nutrients were included as covariates in the GLM-MANOVA. Correlations between biotic and abiotic soil properties were determined by the Pearson coefficient. Nutrient data were normalized for bulk density and root length data were log-transformed before performing the analysis of variance to meet assumptions of normality. The antilog of pH was used for running the statistical analysis, but the results are presented as standard pH units. All analyses were done with SPSS with a significance level of 0.05 [57].

3. Results

3.1. Soil Physical Properties

3.1.1. Soil Temperature

Mean soil temperature was 21.8 °C (SE = 0.1), while the mean air temperature was 23.2 °C (SE = 0.09). Overall, the soil temperature was 6.2% lower than the air temperature. Air and soil temperatures increased from March to May, as expected given the normal annual variation in temperature. The mean soil temperature did not differ between away and under positions ($p = 0.6$), nor between species ($p = 0.4$), but maximum and minimum temperatures did change between under and away positions ($p \leqslant 0.02$), and were affected by the stage of decay ($p = 0.001$). Patterns of diurnal variation of soil temperature under decaying logs had lower maximum and higher minimum values than the patterns observed away from the logs, and such a buffering effect was stronger underneath the older logs rather than underneath the younger logs (Figure 2).

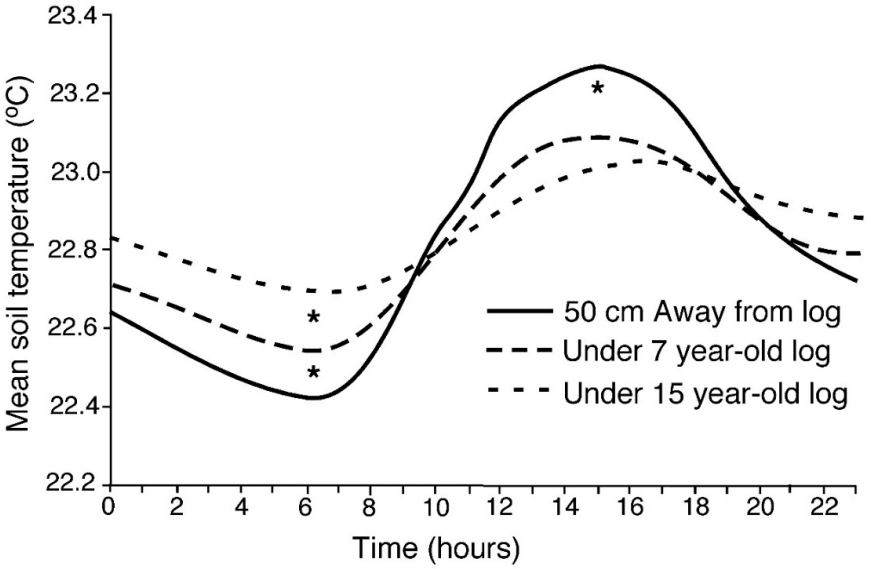

Figure 2. Mean soil temperature 50 cm away and underneath decaying logs that fell 7 years and 15 years previously. Differences were significant for maximum and minimum values as indicated by the asterisks. $n = 10$. * represents significant differences ($p < 0.05$).

3.1.2. Soil Moisture

Soil moisture did not differ between under and away positions ($p > 0.05$). During the dry period (March), water content for soil under and away from all logs ranged between 0.5–0.6 g water/g dry soil, equivalent to 70.8%–84% of the water holding capacity (WHC). For the wet season the water content was between 0.89–0.91 g water/g dry soil equivalent to 126%–128.5% of the WHC. Soil texture was similar for both sites (Table 1). In Bisley, surface soil texture was silty clay loam: 20% Sand, 47% Silt, and 33% Clay, whereas in Río Chiquito it was boarderline clay-clay loam: 30% Sand, 30% Silt, and 40% Clay. Soil bulk density was 0.6 g/cm^3 (SE = 0.02) and 0.8 g/cm^3 (SE = 0.04) for Bisley and Río Chiquito, respectively.

3.2. Soil Chemical Properties

There were no significant effects of season, tree species, decay stage, or position on the percentages of carbon and nitrogen. Mean carbon content was 6.4% (SE = 0.2) for all soil samples, while mean nitrogen content was 0.47% (SE = 0.02). Consequently, no differences were found in C:N ratios.

Differences in the content of total elements such as Ca, Mg, Al, Fe, and Mn reflected more the effect of the site (Bisley vs. Río Chiquito) than trends due the presence of decaying logs. Calcium, Mg, Na, and Mn were higher in the Río Chiquito plantation than in Bisley ($p < 0.001$), while metals Al, and Fe were higher in Bisley than in Río Chiquito ($p < 0.05$). When the site was included as a covariate in the MANOVA, there were no effects of season, species, decay stage, or position on most of the nutrients. The only exceptions were Al, Fe, and Mg. Total Al and Fe were higher in the soil near *D. excelsa* 7 year-old and *S. macrophylla* 15 year-old logs than in the soil collected near the other two pairs of logs ($p < 0.001$, Table 2). Total magnesium was higher in the soil near the younger logs, for both species ($p = 0.05$), although the absolute amounts were higher for the *S. macrophylla* logs, again showing the effect of the site (Table 2).

Table 2. Total, extractable, and % extractable nutrients in the soil near decomposing logs (under and away positions averaged) belonging to the two species and decay stages. Units are $mg \cdot g^{-1}$; exchangeable acidity was converted from m-eq. 100 g^{-1} based on the atomic weight. Errors (in parentheses) are SE of the mean (n = 10).

Nutrient		*D. excelsa*				*S. macrophylla*			
		7 Year-Old		15 Year-Old		7 Year-Old		15 Year-Old	
Al	Total	42.3	(3.2)	25.5	(2.5)	21.4	(2.1)	49.5	(2.5)
	Extractable	0.4	(0.1)	0.7	(0.1)	0.02	(0.003)	0.2	(0.02)
	%	1.0	(0.2)	3.3	(0.6)	0.1	(0.03)	0.3	(0.1)
Fe	Total	53.3	(1.4)	46.5	(2.2)	37.8	(3.8)	70.2	(3.2)
	Extractable	1.4	(0.3)	2.6	(0.3)	0.2	(0.05)	1.2	(0.1)
	%	2.8	(0.6)	5.8	(0.7)	0.7	(0.1)	1.6	(0.2)
Mn	Total	0.6	(0.2)	0.1	(0.02)	1.5	(0.2)	0.5	(0.1)
	Extractable	0.1	(0.03)	0.0	(0.01)	0.3	(0.05)	0.2	(0.04)
	%	28.3	(3.5)	36.8	(5.3)	24.9	(4.6)	25.6	(3.2)
Ca	Total	0.7	(0.2)	0.44	(0.1)	4.2	(1.0)	0.9	(0.2)
	Extractable	0.7	(0.2)	0.39	(0.1)	2.4	(0.5)	0.8	(0.1)
	%	100.0	(3.9)	88.4	(9.0)	58.8	(33.4)	91.5	(3.0)
Mg	Total	1.7	(0.4)	0.6	(0.1)	3.0	(0.6)	0.8	(0.03)
	Extractable	0.3	(0.1)	0.2	(0.02)	0.7	(0.1)	0.3	(0.02)
	%	21.4	(3.3)	27.4	(3.1)	37.0	(10.8)	32.9	(1.9)
Na	Total	0.1	(0.01)	0.1	(0.01)	0.2	(0.03)	0.1	(0.01)
	Extractable	0.1	(0.01)	0.1	(0.01)	0.2	(0.1)	0.1	(0.01)
	%	55.4	(6.4)	60.4	(6.6)	93.6	(20.3)	82.8	(11.1)
K	Total	0.5	(0.1)	0.3	(0.03)	0.4	(0.1)	0.2	(0.03)
	Extractable	0.2	(0.02)	0.1	(0.02)	0.1	(0.02)	0.1	(0.02)
	%	51.8	(10.4)	56.1	(15.4)	80.4	(19.7)	76.0	(11.4)
P	Total	0.3	(0.02)	0.3	(0.02)	0.3	(0.02)	0.4	(0.01)
	Extractable	0.04	(0.02)	0.1	(0.02)	0.02	(0.02)	0.03	(0.01)
	%	11.8	(1.9)	19.0	(5.2)	7.9	(1.1)	6.8	(1.1)

Extractable nutrients did not change between seasons ($p > 0.06$), but there were significant effects of tree species, decay stage, and position. Extractable Ca^{2+} and K^{+} were higher near the younger logs ($p < 0.02$). Extractable Mg^{2+} was higher away from rather than underneath the logs, independent of species or decay stage ($p = 0.002$). Extractable P, Al, and Fe were higher in the soil near *D. excelsa* logs compared to the soil located near *S. macrophylla* logs ($p < 0.03$). For P, this pattern was independent of the stage of decay, but Al and Fe were higher in the soil located near the 15 year-old logs ($p = 0.001$), for both species and positions. Extractable Mn was higher in the soil located near the youngest *D. excelsa* logs ($p = 0.02$).

Nutrient supply rates were significantly affected by season, tree species, decay stage, position, and several interactions (Table 3). With the exception of NO_3^-, P, and B, all other nutrients showed higher supply rates during the wet season than during the dry season. Tree species, decay stage, and some interactions significantly affected the availability of N and some cations such as Ca, Mg, Al, Fe, and Mn (Table 3), while position was significant only for NO_3^-, Ca^{2+}, and Mg^{2+} (Table 3). These nutrients were higher away from as opposed to underneath the decaying logs. Soil located under the younger logs had more NO_3^- than soil located under the older logs; and soil samples collected near *S. macrophylla* logs had more NO_3^- than soil samples located near *D. excelsa*. In contrast, NH_4^+ was higher during the wet season as opposed to the dry season, especially for *D. excelsa* logs (Table 3: interaction season * tree species), but did not differ between positions. Nitrate (NO_3^-) accounted for 80% of the total inorganic available N (NO_3^- + NH_4^+).

Table 3. Results from multivariate analysis of variance assessing the effect of season (S), tree species (SP), decay stage (DS), position (P), and significant interactions on nutrient supply rates as estimated with the PRS™-probes. Significant effects are in bold.

Soil Nutrient	*p*-Values								
	S	**SP**	**DS**	**P**	**S * SP**	**S * DS**	**SP * DS**	**SP * P**	**DS * P**
Al	**<0.001**	**<0.001**	**0.03**	0.78	**<0.001**	0.12	**0.01**	0.25	0.26
Fe	**<0.001**	**<0.001**	0.13	0.08	**0.001**	0.13	0.18	0.09	0.16
Mn	**<0.001**	**0.001**	0.43	0.55	**0.01**	0.39	**0.02**	0.98	0.27
Ca	**<0.001**	**<0.001**	**<0.001**	0.85	**0.03**	0.44	0.06	0.69	**0.02**
Mg	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.76	0.85	0.19	0.19	0.28
K	**0.02**	0.98	0.84	0.78	0.93	0.97	0.57	0.99	0.13
Total N	0.18	**0.05**	**<0.001**	**0.002**	0.08	**0.04**	0.85	0.20	0.10
NO_3^-	0.43	**0.002**	**<0.001**	**0.002**	0.29	**0.01**	0.76	0.09	0.07
NH_4^+	**0.04**	**0.006**	0.37	0.24	**0.007**	0.54	0.78	0.38	0.80
S	**<0.001**	0.09	0.99	0.34	0.13	0.51	**0.02**	**0.02**	**0.04**
Cu	**<0.001**	0.68	**0.002**	0.50	0.43	0.07	0.46	0.39	0.46
Zn	**<0.001**	**0.05**	**<0.001**	0.30	**0.01**	0.75	**<0.001**	0.58	0.34
B	0.39	**<0.001**	**0.001**	0.49	**0.02**	0.44	0.30	0.42	0.78
Pb	**0.001**	0.67	0.96	0.23	0.51	0.77	**0.05**	0.42	0.21

* represents "by" in interactions.

Nutrient supply rates for Ca and Mg were higher in the soil associated with *S. macrophylla* logs. Calcium and Mg were also higher in the soil associated with younger logs, for both tree species. As mentioned before, Mg was higher away from as opposed to underneath the decaying logs, while Ca was higher away from younger logs only (Table 3: interaction Decay stage * Position). Phosphorus was not affected by any of the factors considered. Sulfur was higher underneath the younger logs of *D. excelsa* (Table 3: significant interactions). Metal ions such as Al^{3+} and Fe^{3+} were higher in the soil associated with *D. excelsa* logs compared to the soil near *S. macrophylla* logs. These elements were also higher in the soil located near older rather than younger logs (Table 3: significant interactions). Manganese was higher in the samples near *D. excelsa* younger logs only. Other ions such as B^{2+}, Cu^{2+}, Pb^{2+}, and Zn^{2+} were higher in soil associated with younger logs. For Cu and Pb this was independent of the species or the position, but B and Zn were higher in the soil near *S. macrophylla*.

Soil pH was higher in Río Chiquito than in Bisley (pH = 5.7 and 4.5 respectively, $p < 0.001$). However, when site was included as a covariate in the MANOVA, soil influenced by older logs had lower pH values (pH = 4.2 and 4.6 for 15 year-old and 7 year-old logs, respectively, $p = 0.003$).

3.3. Soil Biota

3.3.1. Soil Microbial Biomass

We did not detect differences in the microbial biomass according to season, species, decay stage, or position. The mean microbial biomass during the dry season was 0.72 mg-C·g-soil^{-1} (SE = 0.046) and 0.60 mg-C·g-soil^{-1} (SE = 0.06) for *D. excelsa* and *S. macrophylla* logs, respectively; during the wet season, microbial biomass was 0.64 mg-C·g-soil^{-1} (SE = 0.1) and 0.64 mg-C·g-soil^{-1} (SE = 0.08).

3.3.2. Roots

Total root length was higher during the dry season compared to during the wet season ($p < 0.001$). There were more roots away from rather than underneath the logs ($p < 0.001$) and more in the soil located near older rather than younger logs ($p < 0.001$), independent of the species (Table 4). The same pattern was observed for total (coarse plus fine) live root length, while for total dead root length, the increase during the dry season was due only to dead roots near *D. excelsa* logs (Table 4: significant interaction Season * Tree species). For the other categories of roots, there were also more roots during the dry season, located near the older logs and away from the logs (Table 4).

Table 4. Results from multivariate analysis of variance assessing the effect of season (S), tree species (SP), decay stage (DS), position (P), and significant interactions upon the different root size and status classes. Coarse: >2 mm, Fine: <2 mm. Significant effects are in bold.

Root Length Category	*p*-Values						
	S	**SP**	**DS**	**P**	**S * SP**	**S * DS**	**SP * DS**
Live							
Coarse	**<0.001**	0.73	**<0.001**	**0.02**	0.49	**0.04**	0.09
Fine	**<0.001**	0.32	**<0.001**	**<0.001**	**0.03**	0.37	0.92
Total	**<0.001**	0.56	**<0.001**	**<0.001**	**0.05**	0.25	0.58
Dead							
Coarse	0.20	**0.05**	**<0.001**	**0.01**	0.82	0.21	**<0.001**
Fine	**0.02**	**0.04**	**<0.001**	**0.01**	**0.009**	0.78	**0.02**
Total	**0.03**	0.06	**<0.001**	**0.01**	**0.01**	0.68	**0.007**
Total coarse	0.06	0.47	**<0.001**	**<0.001**	0.44	0.42	**<0.001**
Total fine	**0.009**	**0.05**	**<0.001**	**<0.001**	**0.006**	0.83	0.07
Total	**<0.001**	0.11	**<0.001**	**<0.001**	**0.01**	0.71	**0.02**

* represents "by" in interactions.

Interestingly, fine roots were more abundant underneath *D. excelsa* logs rather than underneath *S. macrophylla* logs. The difference was mainly due to the presence of more dead roots under the *D. excelsa* logs. A greater abundance of total roots was related to a greater abundance of fine and live roots (Figure 3). We did not find any correlation between roots, microbial biomass, and nutrient availability (either as extractable or as nutrient supply rates).

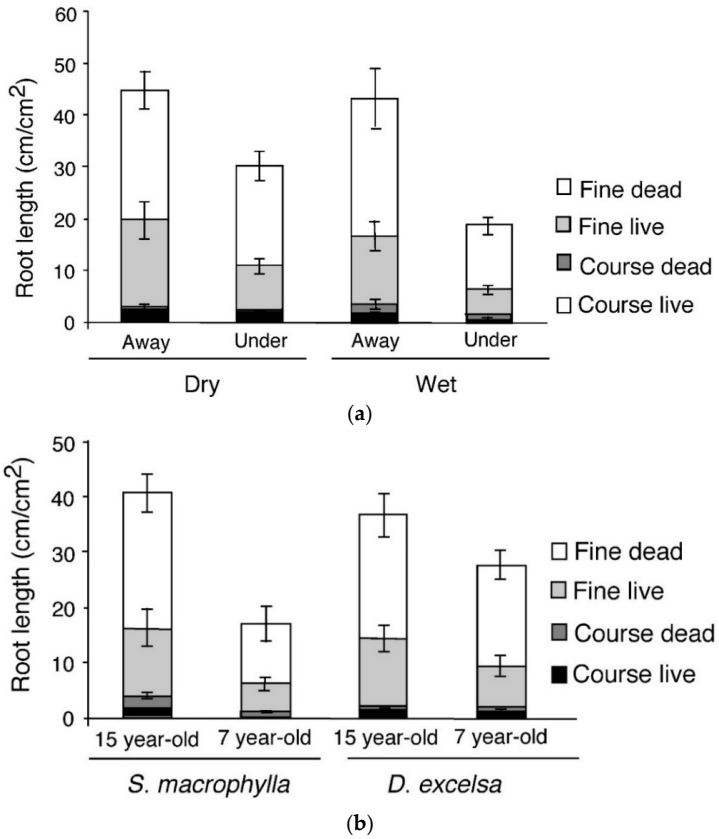

Figure 3. (**a**) Root length for coarse, fine, live, and dead roots according to season and position; (**b**) decay stage and species. Bars represent standard errors (n = 10).

4. Discussion

4.1. Effects on Soil Physical Properties

We found that decaying logs effectively created a different environment underneath them, where the range between maximum and minimum daily soil temperatures was narrower. This finding is consistent with other studies e.g., [16]. Contrary to our initial belief, logs were not effective in preserving moisture in the soil underneath them. Soil moisture increased from the dry to the wet season as expected, but within each season, the variability in the data was not related to the presence of the decaying logs. There are two explanations for this lack of effect of logs on soil moisture. First, topography in the forests studied is a complex of slopes, ridges, and valleys. Lateral movements of water are common [58], blurring the effects of logs on soil moisture. Second, it is possible that the effect of wood on soil moisture will be evident at more advanced stages of decay as opposed to the oldest stages considered here (15 years after falling). In fact, Harmon and Sexton [10] argued that the amount of water captured by decaying wood increased with the degree of decay, because of progressive degradation of sapwood and heartwood which allowed a higher infiltration of water.

4.2. Effects On Soil Chemical Properties

We hypothesized that decaying logs would increase %C, while decreasing %N in the underlying soil, due to the leaching of recalcitrant organic matter. Although we did not find an effect on total C or N, a carbon fractionation analysis by Zalamea et al. [42] of the same soil samples from this study revealed higher water-extractable organic matter under logs and in soil associated with older logs. The percentages of C and N found here are within the range reported in previous studies [52–62], but did not show any particular trend regarding the presence of decaying logs. A prior study [63] performed in the same forest type as our study, and using 7–24 month and 9.5–11 year old decaying logs of *D. excelsa* and *Guarea guidonia* (L.) Sleumer (Family Meliacea, as well as *S. macrophylla*) that had fallen during hurricanes Hugo (1989) and Georges (1998), showed higher %C and C:N ratios in soil samples collected under decaying logs as compared to samples taken 50 cm away from decaying logs at both the 0–10 and 10–20 cm depths. Percentages of C were 8.6% (SE = 0.9) and 6.4% (SE = 1.2) for the under and away positions, respectively, in the upper 10 cm of soil and included humus that often is present under decaying wood [64]. Although inclusion of the thin humus layer in the prior study may have contributed to higher %C and %N under logs than observed here, differences between the two studies are more likely caused by differences in sampling depth. The previous study detected higher %C and %N in soils at both 0–10 and 10–20 cm depths versus the 0–5 cm depth sampled in this study. The shallower soils we sampled are more strongly influenced by leaf litter inputs. Higher C and N inputs from leaf litter away from the logs may have balanced greater inputs from wood underneath the logs, thus dampening differences in surface soil C and N. It is also possible that C and N accumulated differently in the different soils and conditions at the two study sites.

We found lower pH near the more decayed logs, which could be a result of the leaching of acidic dissolved organic matter from decaying wood [17,30]. Zalamea et al. [53] previously found more humic and fulvic acids in soil underneath some of the same logs used in this study, which is consistent with higher Al^{3+} and Fe^{3+} availability and the results of studies by Kayahara et al. [17] and Klinka et al. [30]. Lower soil pH values can alter some soil properties such as cation availability [65], as well as some processes such as nitrification [66]. In fact, we found less nitrate near the oldest logs.

The higher nutrient supply rates for Ca^{2+}, Mg^{2+}, K^{+}, Al^{3+}, Fe^{3+}, Mn^{2+}, and Cu^{2+} during the wet season as opposed to the dry season can be explained because nutrient supply rates measured by the PRS™-probes tend to increase with soil moisture, as the mobility of ions in the soil solution increases [67]. In contrast, mobility of N and P is more related to processes mediated by soil biota. Therefore, it is not surprising that nutrient supply rates for these nutrients were not particularly affected by seasonal changes in physical soil conditions. However, NH_4^{+} was more abundant during the wet season rather than during the dry season, while the more soluble form of inorganic nitrogen

(NO_3^-) did not change among seasons. There could be two reasons for this. First, NH_4^+ is easily immobilized in the interlayer of clays, even more so during dry periods, when clay structure tends to collapse [65]. Second, it is possible that during the wet season more dissolved organic nitrogen (DON) leaches from decaying wood to the soil and, once there, is actively mineralized to NH_4^+. The process would be favored by the lack of labile C, which would force the decomposition of organic N (e.g., amino acids, amino sugars, and peptides) into the carbon skeleton and ammonia [65]. This is supported by the fact that indeed, DOC leaching from decaying wood is poor in labile carbon and high in hydrophobic acid fraction [42,68]. The higher levels of NH_4^+ during the wet season would then indicate higher N mineralization, which apparently was not coupled with more nitrification, since NO_3^- did not change between seasons.

Most of the available nitrogen was in the form of nitrate, suggesting that most of the ammonia produced by decay is being converted to nitrate, in contrast to ammonium dominance in the same forest type on the opposite side of the mountain except for after hurricane disturbance [25]. Another possibility is that NH_4^+ is being taken up very quickly either by plants or soil microbiota and then is not found in large quantities free in the soil solution. However, this would lead to low levels of NO_3^-, since substrate availability is one of the factors controlling nitrification [66], and this was not the case. The dominance of NO_3^- as the form of available N, independent of the season indicates that nitrification is not being affected by low oxygen availability. It is known that oxygen levels can decrease considerably after rainfall events in these forests [69]. Nitrate availability was lower underneath rather than away from the logs, suggesting either lower rates of nitrification or higher N uptake.

In spite of the fact that NH_4^+ was higher in the soil associated with *D. excelsa*, lower amounts of NO_3^- were observed there, probably due to active immobilization either by plants or micro-organisms, though we did not find more roots or microbial biomass in these samples. Nevertheless, these results suggest that whatever the mechanisms, the decomposition of *D. excelsa* logs can influence ammonification and nitrification processes. Thus, wood quality would be playing an important role of defining the effect of decaying wood on N cycling in the underlying soil. Such an effect would be mediated by the leaching of dissolved forms of organic nitrogen. For example, Hafner et al. [19] found the same amount of NO_3^-, but much more DON in leachates from CWD, compared to litter leachates or throughfall. Hafner et al. [19] also found no difference on SO_4^{2-} concentrations but more dissolved organic S (DOS) in CWD leachates. Following the same trend, Yavitt and Fahey [70] found that most of the dissolved N and P coming from decaying wood to the soil were organic rather than NH_4^+, NO_3^- or PO_4^-. Therefore, decaying logs can be influencing N and S pools in the underlying soil via flows of DON and DOS rather than inorganic forms.

Wood quality also can have an effect on the relative abundance of other nutrients such as Ca^{2+} and Mg^{2+}. We found higher availability of Ca^{2+} and Mg^{2+} near *S. macrophylla* logs, both as extractable amounts and as nutrient supply rates. Mahogany wood has high concentrations of Ca^{2+} and Mg^{2+} [53,61]. These elements are leached easily from the early stages of decomposition [70], which can result in an enrichment of the soil beneath decaying wood.

Our results show that the stage of decay can also play an important role in defining the effect of decomposing wood on nutrient availability, as can be inferred from the fact that more NO_3^-, Ca^{2+}, Mg^{2+}, and heavy metal ions (e.g., Cu^{2+} and Zn^{2+}) have higher supply rates near the younger logs rather than near the older logs. Conversely, we found more Al^{3+} and Fe^{3+} near the oldest logs. Regarding nitrogen, it could have been immobilized in the more decayed 15 year-old logs. This is supported by the fact that we also found less NO_3^- underneath rather than away from the decaying logs. Depletion of resources as wood decomposition progresses could have promoted nutrient immobilization in the biomass of wood decomposers [19]. The lower N abundance under decaying logs can also result from adsorption of ammonia onto soil organic matter [65]. This is plausible since higher concentrations of DOC have been reported in leachates from CWD [19]. The availability of cations can in turn be related to the formation of complexes with the soil organic matter [53,71]. Therefore, it is

possible that divalent cations are being retained more strongly in the soil influenced by the older logs, where the accumulation of humic substances is higher [53]. A similar pattern has been observed in other forests. For example, Kayahara et al. [17] found more exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}) in alignin pedons (i.e., without decaying wood on it) compared to lignin pedons (i.e., under decaying wood). The availability of trivalent cations such as Al and Fe is also related to soil organic matter, but our results suggest that the complexation and sorption/desorption processes differ from the ones operating on divalent cations.

4.3. Effects on Soil Biota

We hypothesized that soil biota would respond to the changes induced in soil physical and chemical properties due to the presence of the decaying wood. This was the case for roots, but we did not detect differences in microbial biomass. Microbial biomass basically refers to the amount of matter contained in microbial structures, but it does not inform about the differences in structure and composition of functional groups in the microbial community. Therefore, it is possible that decaying wood is affecting soil microbiota qualitatively more than quantitatively. However, Spears et al. [16] analyzed the composition of functional groups in the microbial community under decaying wood and compared it with soil without decaying wood upon it, and did not find any difference. Therefore, a more plausible explanation would be related to the metabolic versatility of microbiota, a fact demonstrated by several authors in many different forest types [66,72].

Our estimation of microbial biomass using SIR was comparable to the values obtained for other wet forests in northeastern Puerto Rico [53], but was lower than the amount reported in other studies where other techniques had been used. For example, Ruan et al. [54] reported an average of 1.3 mg-C·g-soil^{-1}, obtained by the chloroform-fumigation-incubation procedure. This difference is due to the fact that SIR gives an estimation of glucose-responsive microorganisms, while chloroform-fumigation techniques include microbes susceptible to chloroform fumigation including dormant ones [73]. Lodge et al. [34] using fumigation-incubation found 0.2–0.8 mg-C·g-soil^{-1} in the dry season, comparable to our dry season mean of 0.72 mg-C·g-soil^{-1}, but their wet season estimations of microbial biomass were higher (0.4–10.2 vs. our mean of 0.65 mg-C·g-soil^{-1}). The disparity in wet season estimates is likely due to the positive response of humicolous fungi to moisture in these forests together with their relative lack of responsiveness to glucose additions [72,74,75]. Using direct observation and the agar film method, fungal biomass was found to be significantly higher in wet soils rather than in dry soils in two previous studies [75,76]. Lodge [75] found a mean fungal biomass of 2.7 mg-C·g-soil^{-1} in the upper 9 cm of soil, while Lodge and Ingham [76] estimated 6.1 mg-C·g-soil^{-1} in the upper 5 cm of soil at a nearby secondary forest.

In contrast to microbial biomass, roots responded negatively to the presence of decaying wood, being more abundant away from rather than underneath logs. A previous study also found higher root length away from rather than underneath decaying logs, but only for a dry period [34]. The temporal distribution of roots observed in this study followed the same pattern as some of the nutrients such as NO_3^-, Ca, Mg, and Al. Nutrient availability as measured with the PRS™-probes is positively correlated with nutrient uptake by plants [77]. Our results then suggest more active uptake of N by plant roots is taking place away from rather than underneath the decaying logs. Root distribution according to decay stage showed an inverse pattern compared to NO_3^- availability, as we found more roots in soils associated with older logs, while there was less NO_3^-. The low levels of NO_3^- where roots were abundant could be a result of faster absorption of this nutrient by the roots than adsorption to the ionic membranes [67]. Finally, the higher abundance of roots during the dry season could have resulted from a better aeration of soil during that time of year.

5. Conclusions

To summarize, our results suggest that the effect of decaying wood on the underlying soil changes through the decomposition process and that wood properties play an important role on defining

this effect. This suggests that decaying wood can contribute to the spatial heterogeneity of soil characteristics. Soil underneath and located near decaying logs presented distinctive patterns of root and nutrients distributions, demonstrating that processes such as nitrogen cycling and availability of cations in the soil solution can be influenced by decomposing wood.

Decaying wood can influence patterns and processes in the soil both in the short- and the long-term, and a major implication of these findings is that decomposing wood can be responsible for part of the spatial heterogeneity in soil properties. Though we did not find differences in microbial biomass C, we likely underestimated the microbial biomass present in the soil located near decaying wood in the wet season, because an important percentage of the associated microbes (i.e., humus degrading fungi) were not responsive to glucose addition. The range between maximum and minimum daily soil temperatures was narrower underneath the decaying logs but soil moisture was unaffected. Extractable soil Ca and K levels were lower underneath the younger logs of both species, while the extractable soil Mn level was only lower underneath the youngest *D. excelsa* logs. Total Al and Fe levels were higher in the soil located near *D. excelsa* 7 year-old and *S. macrophylla* 15 year-old logs, rather than in the soil collected near the other two pairs of logs. Total magnesium was higher in the soil located near the younger logs, for both species. Supply rates of NO_3^-, Ca^{2+}, and Mg^{2+} were significantly lower underneath rather than located away from the logs. Roots lengths were higher away from rather than underneath the logs, which is concordant with higher supply rates for nitrate, calcium, and magnesium located away from the decaying logs. Given the high diversity of tree species in tropical forests and considering that wood quality is strongly related to tree species, decaying wood can create differences at the scale of microsites on the soil properties. The differences we found between fallen logs of different ages dating to different storm events further contributes to the spatial heterogeneity of soil nutrients.

Acknowledgments: This research was performed under grants DEB-0218039 and 1239764 from the National Science Foundation to the Institute of Tropical Ecosystem Studies, University of Puerto Rico, and the United States Department of Agriculture, Forest Service, International Institute of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support was provided by the Luquillo Critical Zone Observatory (EAR-1331841), the Forest Service (U.S. Department of Agriculture), CREST—Center for Applied Tropical Ecology and Conservation, the Biology Graduate Program at the University of Puerto Rico, and the Organization for Tropical Studies and Conservation (OTS). We are thankful to Samuel Moya and Carlos Estrada who helped locate and identify logs; Maria M. Rivera, Mary Jeane Sánchez, Maysaá Ittayem, Edwin Lopéz, Carmen Marrero, Maribelís Santiago, and other staff at the International Institute of Tropical Forestry—Soil Laboratory who helped process soil samples; Verónica Cruz and Jesús Santiago who helped with microbial biomass estimation and root separation; Andrés Fernández who helped grind soil samples; Ligia Lebrón for methodological guidance; Maya Quiñones and Olga Ramos helped with Figure 1. Elvira Cuevas from the University of Puerto Rico kindly provided the Delta-T scanner and software, and her advice was very helpful to Marcela Zalamea. Ryan Hangs from Western Ag Innovations and Jeff Schoenau from University of Saskatchewan—Saskatoon, Canada, provided helpful comments on the discussion section, while Juan C. Bello Edmund Tanner, and Ariel E. Lugo commented on an earlier version of the manuscript.

Author Contributions: Marcela Zalamea, Deborah Jean Lodge and Grizelle González conceived and designed the study; Marcela Zalamea performed the field measurements with technical help from Grizelle González; Marcela Zalamea and Grizelle González analyzed the data; Marcela Zalamea initially wrote the paper based on revisions by Deborah Jean Lodge and Grizelle González. Deborah Jean Lodge -reproduced Figures 2 and 3 to higher resolution. Grizelle González and Deborah Jean Lodge revised the manuscript based on the reviewers and editors comments.

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

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