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REGULAR ARTICLE

Soil organic matter dynamics under decaying wood in a subtropical wet forest: effect of tree species and decay stage

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Abstract Decaying wood is an important structural and functional component of forests: it contributes to generate habitat diversity, acts as either sink or source of nutrients, and plays a preponderant role in soil formation. Thus, decaying wood might likely have measurable effects on chemical properties of the underlying soil. We hypothesized that decaying wood would have a stronger effect on soil as decomposition advances and that such effect would vary according to wood quality. Twenty logs from two species with contrasting wood properties (*Dacryodes excelsa* Vahl. and *Swietenia macrophylla* King) and at two different decay stages (6 and 15 years after falling) were selected, and soil under and 50 cm away from decaying logs was sampled for soil organic matter (SOM) fractions [NaOH-extractable and water-extractable organic matter -(WEOM)] and properties (WEOM aromaticity). NaOH-extractable C and WEOM were higher in the soil influenced by 15-year-old logs, while the degree of aromaticity of WEOM was higher in the soil influenced by the 6-year-old logs. Decaying logs did influence properties of the underlying soil with differing effects according to the species since there was more NaOH-extractable C in the soil associated to *D. excelsa* logs and more WEOM in the soil associated to *S. macrophylla* older logs. It is proposed that such effects occurred through changes in the relative quantity and quality of different SOM fractions, as influenced by species and advancement in decomposition. Through its effect on SOM and nutrient dynamics, decaying wood can contribute to the spatial heterogeneity of soil properties, and can affect process of soil formation and nutrient cycling.

Keywords *Dacryodes excelsa* · Dissolved organic matter · Humic substances · Puerto Rico · *Swietenia macrophylla* · Wood decomposition

Abbreviations

ASC	Acid soluble carbon
ASPS	Acid soluble poly-saccharides
FI	Fluorescence intensity
HiN	Hydrophilic neutrals
HMW-FA	High molecular weight fulvic acids
LMW-FA	Low molecular weight fulvic acids
SUV*a*	Specific UV absorption coefficient

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WSC	Water soluble carbon
WEOM	Water-extractable organic matter
WSPP	Water soluble polyphenols
WSPS	Water soluble poly-saccharides

Introduction

Decaying wood is an important structural and functional component of forests, accounting for 20–30% of aboveground litter in the tropics (Delaney et al. 1998; Clark et al. 2002) and more than 60% in temperate regions (Lambert et al. 1980). Structurally, decaying wood contribute generating high diversity of habitats for several species of plants and animals (Harmon et al. 1986; Scholz et al. 2004). Functionally, decaying wood is related to nutrient cycling through its role as either a sink or source of nutrients (Creed et al. 2004), and to soil formation because residues from lignin degradation are precursors for humus synthesis (McFee and Stone 1966; Stevenson 1982; Preston et al. 1998). Given these important roles, likely decaying wood has measurable effects on chemical properties of the underlying soil. Such effects would occur mainly through translocation of dissolved organic matter (DOM) from decaying wood to the soil underneath. Although translocation of organic matter from woody litter to soil can occur via soil fauna as well, DOM is recognized as one of the major forms for mobilization of C and N from the forest floor to the mineral soil (Qualls et al. 1991; Yano et al. 2005) and also from decaying wood to the underlying mineral soil (Yavitt and Fahey 1985; Spears and Lajtha 2005). Previous studies have found that partially decayed organic matter is leached from the wood to the soil underneath becoming part of the soil organic matter (SOM) (Yavitt and Fahey 1985; Spears et al. 2003). In this study, we compared SOM fractions (water-extractable and NaOH-extractable organic matter) from the surface mineral soil (0–5 cm depth) under decaying logs and 50 cm away. Our working hypothesis was that coarse woody debris (CWD) (defined as any woody material greater than 10 cm diameter, Harmon and Sexton 1996) affects soil properties due to the leaching of qualitatively different DOM relative to the DOM leaching from the adjacent forest floor. Consequently, SOM under decaying logs will differ from SOM away from logs. Previous studies have shown that CWD leachates can be more acid, and rich in polyphenols (Spears and Lajtha 2005), as well as lower in labile carbon fractions (Yano et al. 2005) than forest floor leachates. In the long-term, as mentioned before, residues from lignin decay are building blocks of humus. Hence, we hypothesized that greater and more complex humic substances would accumulate under decaying wood as decomposition progresses. We also hypothesized that the effect of decaying wood on soil properties would be related to wood properties; namely, different tree species with particular wood qualities would leave different chemical imprints on the underlying soil. Thus, decay of less resistant woods (e.g., with lower lignin and tannin contents) would result in less recalcitrant SOM accumulation, with a higher proportion of labile carbon fractions than SOM accumulated under more resistant woods (i.e., with high lignin and tannin contents). To infer the importance of the initial properties of the wood in determining its effects on the underlying soil, we selected logs from two species with contrasting wood quality: *Dacryodes excelsa* Vahl. and *Swietenia macrophylla* King, low and high in both lignin and tannins, respectively. To analyze how the effect of decaying wood on soil changes over the decomposition process, we selected logs at two stages of decay: 6 and 15 years after falling. In addition to measurements of soil organic carbon fractions, we estimated nutrients and carbon fractions in the wood to characterize nutrient dynamics during the decomposition processes of selected logs as well.

The study was carried out in a subtropical wet forest in Puerto Rico, where large quantities of coarse wood debris is generated periodically during tropical storms and hurricanes (Lodge et al. 1991), becoming an important episodic input of organic matter. Furthermore, considering that SOM is the largest organic carbon pool in terrestrial ecosystems (Gupta and Kaur 1998), understanding the effect of decaying wood on the amount and quality of SOM will contribute to our understanding of the formation and dynamics of SOM.

Materials and methods

Study area

The study was performed in the Luquillo Mountains in northeastern Puerto Rico (18°18′N; 65°50′W).

Logs were selected in two areas: the Bisley Experimental Watersheds and the Río Chiquito plantation, 3.6 km apart (Lugo 1992). The Bisley Experimental Watersheds bears a subtropical wet forest dominated by tabonuco –*D. 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. Some planted mahoganies (*S. macrophylla* King) were also present. Elevation ranged between 300 and 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 (Lugo 1992). In addition to *S. macrophylla*, which is the dominant species, other species present in this forest are *Ocotea leucoxylum* (Sw.) Mez. and *Syzygium jambos* (L.) Alston (Lugo 1992). Soils in both sites are mapped as Humatas series (Lugo 1992) and classified as Fine, kaolinitic, isohyperthermic Typic Hapludox according to Soil Taxonomy (Mount and Lynn 2004) and Haplic Ferralsols according to Word Reference Base (IUSS Working Group WRB 2006). Carbon, N, and P contents are similar between sites ranging between 5.1 and 5.8% C (Lugo 1992), 0.38–0.4% N (M. Zalamea et al. submitted), and 0.25–0.32 mg g^{-1} P (M. Zalamea et al. submitted). Soil texture is loam for both sites (Lugo 1992) and bulk density ranges between 0.6 and 0.8 kg l^{-1} (M. Zalamea et al. submitted). Calcium, Mg, and Na are higher in Río Chiquito than in Bisley (Lugo 1992), while Al and Fe are higher in Bisley than in Río Chiquito (M. Zalamea et al. submitted).

Average total annual rainfall for both sites is around 3,500 mm (Scatena 1989) with a weakly seasonal regime in which a typically dry season occurs between February and April and a typically rainy season from August to November. Additionally, a short rainy 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 (Cuevas et al. 1991). 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 (multiannual averages from 1993 to 2002, calculated from raw data available in LUQ-LTER web site: http://luq.lternet.edu/data/databasesbycategory.html#Meteorology).

Sampling design

Twenty logs were selected, ten from each of two species, *D. excelsa* and *S. macrophylla*, having different wood properties (Table 1). 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 years) than Georges' logs (6 years). According to the four stages of decay proposed by Torres (1994), the younger logs were close to the decay stage II: intact bark, sapwood partially soft, and few invading roots present, while older logs belonged to stage III: bark partially lost, sapwood soft, invading roots present. All logs selected were >30 cm diameter, were in contact with the forest floor for most of their length, had white rot, and were at least 50 m apart. Sampling locations were kept as similar as possible; however, there were slight differences in slope and litter coverage. Information about the species identity and the time of fall was obtained from previous census data for each site and from personal observations of field technicians of the USDA-Forest Service in Puerto Rico. Based on that information, all *S. macrophylla* logs from hurricane Georges were found in Río Chiquito plantation, while the rest where located in Bisley area.

Wood analyses

One wood core of 2.5 cm diameter × 5.3 cm long was taken from each log using a wireless drill in February 2005. These samples were carried to the laboratory for gravimetric estimation of wood density. Subsequently, samples were oven-dried and ground in a Wiley mill (18 mesh) for chemical analysis of nutrient content and carbon fractions. Total C, N, and S were determined with a LECO-2000 CNS analyzer following Tabatabai and Bremmer (1991). For estimation of nutrient concentrations (Al, Ca, Fe, K, Mg, Mn, Na, and P), samples were digested with H_2O_2 and concentrated HNO_3 (Luh Huang and Schulte 1985) and then analyzed with a plasma emission spectrometer (Beckman Spectra Span V, Fullerton, CA, USA). Carbon fractions were analyzed following a modification of Ryan et al. (1990), McClaugherty et al. (1985), and Allen (1974) protocols, consisting of gravimetric measures of weight

Table 1 Wood properties of *D. excelsa* and *S. macrophylla*

	Dacryodes excelsa Vahl	*Swietenia macrophylla* King
Family	Burseracea	Meliaceae
Common name	Tabonuco, gommier or candlewood[c]	Bigleaf Mahogany, caoba or caoba hondureña[c]
Distribution	Native to the West Indies[c]	Yucatan peninsula (23°N) to Brasil (18°S)[c]
Durability	Very susceptible[d,e]	Moderately resistant[d,e]
Lignin (%)	32.8[f]	45.8[f]
Wood density (g/cm^3)[a]	0.52–0.61[d,e,g,h]	0.4–0.68[d,g,i,j]
Hardness (lb)[b]	690–840[c,d,f]	740–1,160[d,j,k,l]

Ranges correspond to the maximum and minimum values reported in the literature

[a] Ovendry weight/green volume

[b] For green wood

[c] Francis et al. (2000)

[d] Chudnoff (1984)

[e] Longwood (1961)

[f] Wellwood (1946)

[g] CIRAD (2003)

[h] Reyes et al. (1992)

[i] Boone and Chudnoff (1970)

[j] Wangaard and Muschler (1952)

[k] Bendtsen and Chudnoff (1981)

[l] Wangaard et al. (1955)

loss following sequential extractions. The fractions extracted were: non-polar extractives (NPE, including fats, waxes, and chlorophylls), water soluble carbon (WSC, including simple sugars, hydroxyphenol groups, and amino acids), acid soluble carbon (ASC, including polysaccharides such as cellulose, hemicellulose, and starch, as well as proteins, polypeptides, some amino acids, and nucleic acids), and lignin and lignin-based material (Lignin), water soluble polyphenols (WSPP, including small poly- and mono-aromatic compounds like tannins, water soluble poly-saccharides (WSPS, containing a variety of simple sugars), and acid soluble poly-saccharides (ASPS, consisting in glucose, xylose and other sugars resulting from the hydrolysis of cellulose, hemicellulose, and starch). All fractions, sugars, and tannins were calculated on an ash free basis and expressed as percentage of the initial wood sample (meaning the wood cored samples taken from the logs).

Soil analyses

A pair of mineral soil blocks (5 × 10 cm^2 sizes, 5 cm depth) was extracted from both under and away of each log on March 2005. The under and away samples were spatially paired, so that they were 50 cm apart. Soil was sieved through a 3.36 mm mesh and roots were removed by hand before extraction and fractionation of SOM. A second pair was taken on May 2005, and prepared in the same way for extraction of water-extractable organic matter (WEOM) and characterization of its optical properties. The two sets of samples were taken with a difference of 2 months unlikely to have significant effects over the main comparisons done in this study which involve processes occurring at longer time scales (e.g., wood decomposition and humification).

NaOH-extractable organic matter and humic substances fractionation

Extractable SOM was obtained with 0.1 N NaOH following guidelines in Ping et al. (1995). Briefly, subsamples of 20 g fresh-weight ground soil were suspended in NaOH, shaken for 10 h, and centrifuged. The suspensions obtained were pressure-filtered (0.45 μm polyethersulfone membrane filters). The material retained after filtering was scraped from

membranes and combined with the residual soil after centrifugation. This entire fraction was analyzed for total C content, using a LECO-1000 CHN analyzer according to Tabatabai and Bremmer (1991) procedure. These values were subtracted from the unextracted C content to obtain the percentage of total extractable carbon. Dissolved organic carbon (DOC) was analyzed in the filtrates, by the persulfate oxidation method (EPA 1979) using an Oceanographic International-Model 700 TOC Analyzer. Filtrates were then adjusted to pH 2 by adding HCl (1:1 volume aqueous solution) to promote the precipitation of the hydrophobic acid fraction, operationally defined as humic acids. Afterward, filtrates were centrifuged and pressure-filtered (0.45 μm membrane filters) to separate humic from fulvic acids. The DOC was determined again on the new filtrates (containing acid hydrophilic fraction operationally defined as the fulvic acid fraction). Fulvic acids were then separated into large, small and neutral fulvic fractions by passing them through XAD-8 and XAD-4 resin columns placed in tandem (Aiken et al. 1992). The DOC of effluents flowing from each column was determined as above and used to calculate amounts of DOC retained by each column. Based on the DOC of column effluents after pH adjustment and filtration (total fulvic acid fraction) and the proportions of fulvic acids retained by each of the resins, the fulvic acids fraction was further divided into high molecular weight fulvic acids—HMW-FA (relatively large molecules still with abundance of functional groups retained on the XAD-8. Includes phenolic acids and protein-tannin complexes); low molecular weight fulvic acids—LMW-FA (smaller molecules with an abundance of functional groups retained on the XAD-4. Also called transphilic acids); and hydrophilic neutrals (HiN) as sugar and smaller yet molecules passing both resin columns (Malcolm and MacCarthy 1992). Total extractable organic carbon was calculated as the sum of humic and fulvic fractions as mg NaOH-extractable C g SOC (soil organic carbon).

Water-extractable organic matter and optical characterization

Water-extractable organic matter was obtained from fresh soil samples using a 1:20 soil to water ratio. The soil-water suspensions were shaken, centrifuged, and vacuum-filtered (0.7 μm glass fiber filter). Carbon content in the extracts was determined as described above. Optical characterization of the WEOM was done by analysis of the absorbance and fluorescence spectra. Absorbance (A) of WEOM was measured with a UV-visible spectrophotometer (Agilent 8453), using a quartz cuvette, over 190–900 nm wavelength range, and 2 nm of resolution. A blank was established with deionized water (TOC = 8–10 ppm). From absorbance values the absorption coefficient (a m^{-1}) was calculated as: $a(\lambda) = 2.303 \times A/L$, where A is absorbance and L is the optical path length (0.01 m = cuvette dimensions). Specific UV absorption coefficient for 254 nm (SUVa L/mg C m^{-1}) was calculated as $a(254)$/DOC, as a measure of the abundance of aromatic structures in dissolved humic substances (Hood et al. 2005).

Fluorescence emission spectra of WEOM were measured with a spectrofluorometer (Fluoromax-3 Jobin Yvon) using a quartz cuvette of 0.01 m width, at an excitation wavelength of 370 nm, recommended for detecting humic substances of terrestrial origin (Guéguen et al. 2005). Emission spectra were recorded between 400 and 700 nm, since humic substances of terrestrial origin show emission peaks between 400 and 490 nm (Senesi et al. 1991). Fluorescence intensity-FI at 450 nm was chosen for comparisons because that was the wavelength at which all samples showed the highest fluorescence intensity. Results are presented in arbitrary units as counts per second (cps).

Data analysis

The effects of tree species (*D. excelsa* versus *S. macrophylla*), decay stage (6 years vs. 15 years after fell), and position (under vs. 50 cm away from decaying logs) as independent variables, on dependent variables measured in wood (nutrients and C fractions) and soil (humic substances, WEOM, and optical properties) were analyzed by a MANOVA based on the general linear model (GLM). According to our sampling design, decaying logs constitute the replicates ($n = 5$ for each combination of tree species, decay stage, and position). Given that logs were scattered around two areas (Bisley and Río Chiquito), site was included as a covariate in the analyses of variance. When the effect of position was not significant, values were averaged and referred as soil

near or associated to decaying logs for further analysis of the effects of tree species and decay stage. Independent samples *t*-tests were performed to determine differences between specific combinations of tree species and decay stage. Differences in wood density between fresh and decaying wood were also tested with independent samples *t*-tests. Fresh wood data corresponded to oven-dry weight/green volume and were taken from Longwood (1961), Chudnoff (1984), and Reyes et al. (1992) for *D. excelsa*, and Wadgaard and Muschler (1952), Wangaard et al. (1955), Bultman and Southwell (1976), Chudnoff (1984), and Francis (2003) for *S. macrophylla*. All data sources used for fresh wood physical and chemical properties refer to Caribbean woods. All tests were performed with SPSS (2002) and significance was established for $P < 0.05$.

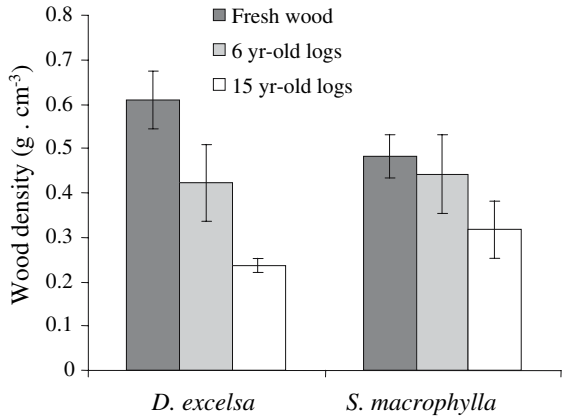

Fig. 1 Wood density for the two stages of decay and two species studied contrasted to fresh wood density reported in literature. *Error bars* are standard errors ($n = 5$). For literature-derived data, *n* represent the number of sources used

Results

Wood properties

Wood density decreased as decomposition progressed, but this trend was only statistically significant for *D. excelsa* (*t*-test $P < 0.05$, Fig. 1). Calcium was higher in *S. macrophylla* than in *D. excelsa* logs, especially for the younger logs (GLM-MANOVA $P_{\text{Tree species}} = 0.002$, $P_{\text{Tree species} \times \text{Decay stage}} = 0.08$); Mn was higher in *D. excelsa* logs than in *S. macrophylla* independent of the stage of decay (GLM-MANOVA $P_{\text{Tree species}} = 0.02$, $P_{\text{Decay stage}} = 0.72$); and *D. excelsa* older logs had more ash than the younger logs, while the opposite was true for *S. macrophylla* logs (GLM-MANOVA $P_{\text{Tree species} \times \text{Decay stage}} = 0.004$). Aluminium was higher in *D. excelsa* older logs than in any other log (*t*-test $P = 0.03$); and N was lower in younger *D. excelsa* logs than in any other log (*t*-test $P = 0.004$). When compared with fresh wood, nutrients in decaying wood were in general less concentrated, except for Al and Fe in *D. excelsa* wood and N in *S. macrophylla* (Table 2). Nutrient concentration's decrease after 15 years of decomposition ranged between 5 and 95% depending on the element (Table 2). Carbon fractions did not differ for *S. macrophylla*; in contrast, for *D. excelsa* we found a consistent pattern of wood decomposition characterized by an increase of simple sugars (i.e., higher WSC and WSPS), and a decrease in the percentages of polysaccharides (i.e., lower ASC and ASPS), from 6- to 15-year-old logs (*t*-test $P \leq 0.03$, Table 3). As expected, wood from *S. macrophylla* had more lignin and tannin than wood from *D. excelsa* (Table 3). Based on lignin contents of fresh wood obtained from literature (Table 1), 14.3 and 24.2% of the lignin had been lost in the first 15 years of decomposition for *D. excelsa* and *S. macrophylla*, respectively.

Soil organic matter

Most of the SOM fractions did not differ between soil under and 50 cm away from the decaying logs, but there were significant differences according to decay stage and tree species. Therefore, hereafter we will refer to the soil near or associated to specific combinations of tree species and decay stage. Total NaOH-extractable C, both absolute and relative (% Total C) was higher near older logs for both species (Fig. 2, Table 4). There were less HA near older *S. macrophylla* logs than either younger logs for this species or any of the *D. excelsa* logs (Fig. 3a, Table 4), while the opposite was true for FA, namely there were more FA near older *S. macrophylla* logs than either younger logs for this species or *D. excelsa* logs (Fig. 3b, Table 4). For FA fractions we found more HMW-FA in soil associated with older *S. macrophylla* logs, while

Table 2 Mean and standard error (in parentheses) of nutrient contents in fresh and decaying wood

Element	*Dacryodes excelsa*				*Swietenia macrophylla*			
	Fresh wood[a]	Decaying wood		Concentration decrease after 15 years (%)[c]	Fresh wood[a]	Decaying wood		Concentration decrease after 15 years (%)[c]
		6 years	15 years			6 years	15 years	
Carbon		52.0 (0.29)	51.6 (0.43)			52.4 (0.45)	53.1 (0.7)	
Nitrogen	0.83	0.26 (0.02)	0.44 (0.06)	60.6	0.58	0.39 (0.02)	0.43 (0.13)	29.3
C : N		312	158			134	123	
Sulfur		0.05 (0.01)	0.07 (0.01)			0.05 (0.005)	0.06 (0.02)	
Ash	4.66	1.21 (0.23)	3.15 (0.62)	32.4	3.80	3.46 (0.77)	1.87 (0.63)	50.8
P	0.25	0.03 (0.06)	0.06 (0.01)	82.5	0.94	0.07 (0.01)	0.08 (0.03)	91.7
K	3.64	0.17 (0.02)	0.21 (0.02)	94.8	6.34	0.40 (0.16)	0.19 (0.04)	95.3
Ca	4.93	1.00 (0.18)	2.10 (0.73)	57.5	12.99[b]	9.32 (2.13)	4.76 (1.73)	63.4
Mg	0.76	0.27 (0.05)	0.39 (0.07)	56.4	0.53[b]	0.42 (0.04)	0.50 (0.14)	13.1
Na		0.10 (0.01)	0.20 (0.04)			0.16 (0.02)	0.16 (0.02)	
Mn	0.23	0.06 (0.02)	0.05 (0.03)	76.4		0.005 (0.001)	0.03 (0.01)	
Fe	0.17	0.15 (0.12)	0.31 (0.15)	−33.3		0.24 (0.13)	0.16 (0.07)	
Al	0.19	0.06 (0.04)	0.27 (0.12)	−44.5		0.24 (0.13)	0.13 (0.06)	

Units are mg g^{-1}, except for C, N, S, and Ash that are %

[a] From Beard et al. (2005), Sánchez et al. (1997), and M. J. Sánchez (2005) Personal communication

[b] Data not available for *S. macrophylla*. The values correspond to *S. macrophylla* × *S. mahagony* (Sánchez et al. 1997)

[c] When there were not differences between decay stages the average was used for calculate the percentage

Table 3 Wood carbon fraction means and standard errors (in parentheses) for the two species and stages of decay

Carbon Fractions[a]	*Dacryodes excelsa*		*Swietenia macrophylla*	
	Decay stage		Decay stage	
	6 years	15 years	6 years	15 years
Non-polar extractives	3.93 (0.53)	5.30 (0.96)	2.90 (0.65)	4.45 (0.86)
Water soluble carbon	4.10 (0.17)[b]	6.12 (0.62)	6.69 (0.71)	5.99 (0.52)
Water soluble polysaccharides	0.89 (0.07)[b]	1.90 (0.45)	1.17 (0.11)	1.01 (0.10)
Acid soluble carbon	65.1 (1.57)[b]	59.2 (1.70)	56.0 (2.35)	54.7 (4.55)
Acid soluble polysaccharides	55.4 (1.12)[b]	48.2 (2.08)	41.4 (2.04)	37.8 (4.79)
Lignin	26.8 (1.80)	29.4 (1.51)[c]	34.4 (2.41)	34.9 (3.91)
Tannins	0.57 (0.04)	0.71 (0.04)[c]	1.04 (0.12)	1.17 (0.35)

[a] Units are percentages, except for water and acid soluble polysaccharides which are Glucose-equivalents

[b] Indicates significant differences ($P < 0.05$) between decay stages

[c] Indicates significant differences ($P < 0.05$) between tree species

there was no difference for *D. excelsa* logs regardless of position or decay stage (Fig. 4). For LMW-FA the two tree species presented opposite patterns (Table 4: Interaction Tree species × Decaying stage): soil near younger *D. excelsa* logs had more LMW-FA than soil near older logs, while soil near older *S. macrophylla* had more LMW-FA than soil near younger logs. HiN were the only fraction affected by position (Table 4). HiN fraction was higher away than under logs, especially for *S. macrophylla* older logs (Table 4). Overall, FA fraction was higher than HA (Fig. 4). WEOM was

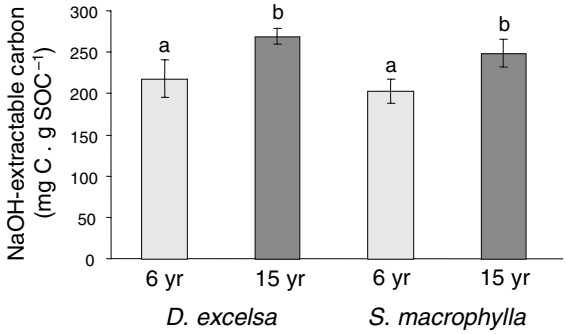

Fig. 2 NaOH extractable carbon from soil near (under and away averaged) decaying logs according to species and decay stage. *SOC* soil organic carbon. *Error bars* represent standard errors (n = 10). Letters denote significantly different groups

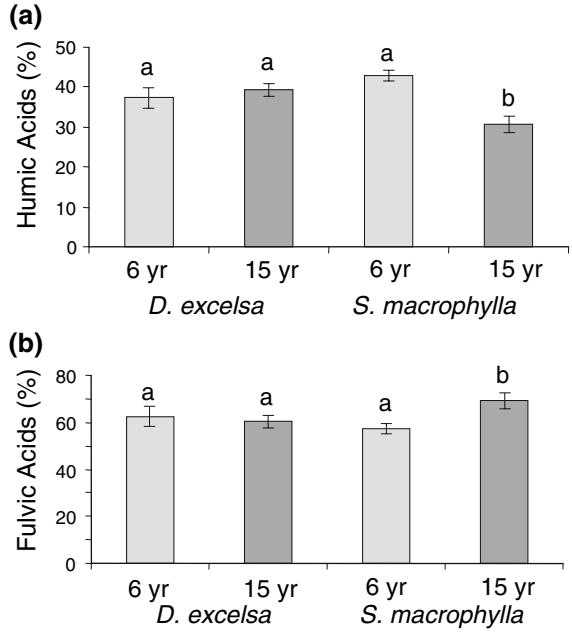

Fig. 3 Percentage of humic (**a**) and fulvic (**b**) acids in the soil near (under and away positions averaged) decaying logs, according to species and decay stage. *Error bars* represent standard errors (n = 10). Letters denote significantly different groups

higher under than 50 cm away from logs (GLM ANOVA P = 0.04) and when averaged for position, it was higher for the soil associated with *S. macrophylla* logs (GLM ANOVA $P < 0.001$) as well as for soil collected near the 15-year-old logs (t-test $P < 0.01$) as compared with the less decayed logs (Fig. 5). Specific UV absorption coefficient at 254 nm was higher for the 6 years-old for both tree species (t-test $P < 0.03$, Fig. 6). Fluorescence intensity at 450 nm was lower for soils under *S. macrophylla* older logs compared with all the others. Emission spectra were similar for all samples, showing main peaks at the same wavelength (around 450–460 nm). This means that the constitution of humic substances in terms of abundance of poly-aromatic groups and degree of humification is similar for the compared soils (Senesi et al. 1991; Zsolnay 2003).

Discussion

Changes in wood properties through decomposition

It is well known that wood density decreases through the decay process as a result of loss of matter through respiration, fragmentation and leaching (Harmon

Table 4 Results from multivariate analysis of variance for assessing the effect of tree species, decay stage, position, and the interaction tree species (*SP*) × decay stage (*DS*), upon NaOH-extractable matter and soil organic matter fractions

SOM Fractions (%)	*P*-values			
	Tree species	Decay stage	Position	SP × DS
NaOH-extractable matter[a]	0.02	0.002	0.94	0.56
% Total C[b]	0.04	0.001	0.37	0.69
Humic acids	0.39	0.01	0.76	<0.001
Total Fulvic acids (FA)	0.39	0.01	0.76	<0.001
High-molecular-wt. FA	0.90	0.02	0.40	0.21
Low-molecular-wt. FA	0.37	0.47	0.45	0.05
Hydrophilic neutrals	0.06	0.05	0.06	0.13

[a] mg-C g dry soil^{-1}; all the other fractions are percentages

[b] Total C—NaOH-extractable C × 100

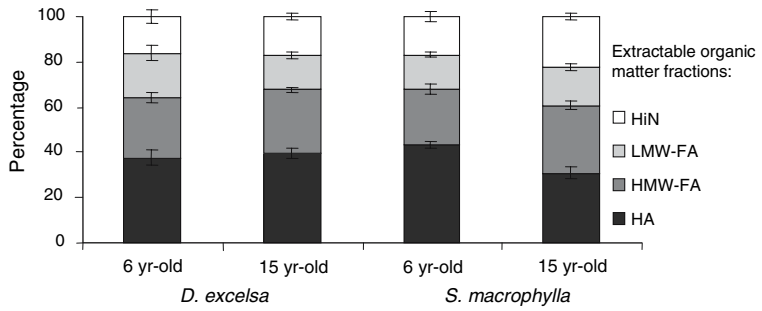

Fig. 4 Percentage of extractable organic matter fractions in the soil near (under and away positions averaged) decaying logs. *HiN* hydrophilic neutrals, *LMW-FA* low molecular weight fulvic acids, *HMW-FA* high molecular weight fulvic acids, *HA* humic acids

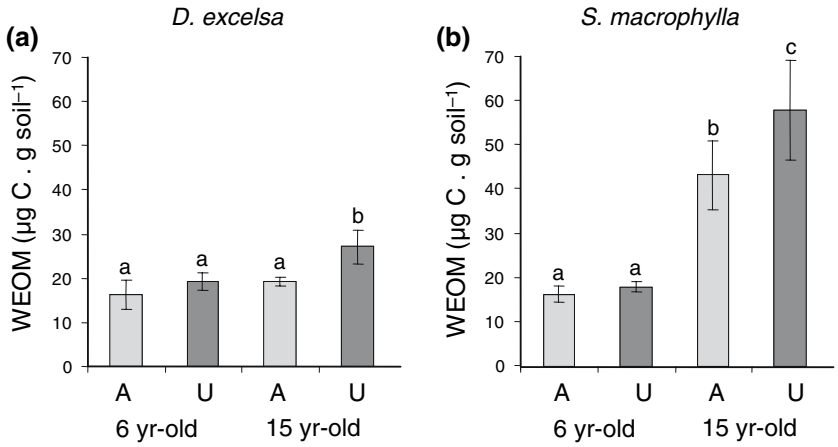

Fig. 5 Water-extractable organic matter (*WEOM*) in soil under (*U*) and 50 cm away (*A*) from decaying logs. **a** *D. excelsa*, **b** *S. macrophylla*. *Error bars* represent standard errors (n = 5). Letters denote significantly different groups

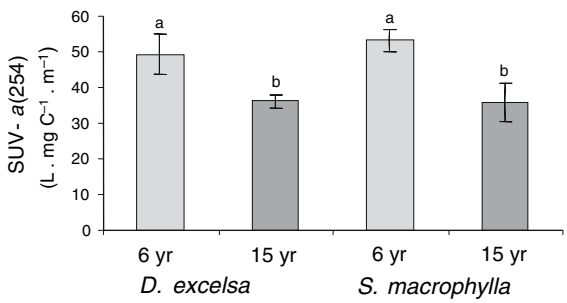

Fig. 6 Specific UV absorption coefficient at 254 nm [SUV—*a* (254)] as a measure of aromaticity in WEOM, according to species and decay stages. *Error bars* represent standard errors (n = 10). Letters denote significantly different groups

et al. 1986). In this study, we observed a decrease in wood density in the *D. excelsa* logs but not in *S. macrophylla*. Torres (1994) found that significant changes in wood density of *Cyrilla racemiflora* only occurred in advanced stages of decay. Therefore, it is possible that the two stages analyzed here were not sufficiently decayed to show changes in wood density for *S. macrophylla*, like *C. racemiflora* has high lignin content in wood (cf. Table 1). This could delay the structural and chemical deterioration of wood by decomposers and implies that these two species have distinctly different decomposition rates over the 15-year period. However, it is also possible that we were unable to detect statistically significant changes in wood density in the case of *S. macrophylla* due to the small sample size used in this study.

Patterns of nutrient change through decomposition in general suggest a loss of P, K, Mn, N, Ca, and ash, through leaching and fragmentation. It has been observed that elements such as Ca, K, Na, and in some cases Mg are easily leached from decaying wood during the early stages of decomposition (Holub et al. 2001). Although there is no data available for Ca content in the wood of *S. macrophylla*, data for the hybrid *S. macrophylla* × *S. mahagoni* suggests that these species tend to accumulate Ca in their biomass, compared to other tree species. Indeed, Lugo et al. (1990) found enhanced Ca levels in the litterfall of a *S. macrophylla* plantation in Puerto Rico when compared to other tree species.

Many of the early studies investigating changes in nutrient content during wood decomposition found increases in the concentration of N as decay progresses, suggesting that decaying wood could act as a sink for this element (Grier 1978; Lambert et al. 1980; Sollins et al. 1987; Keenan et al. 1993; Preston et al. 1998; Krankina et al. 1999; Cotrufo and Ineson 2000). However, there is now enough evidence showing that N immobilization and mineralization can co-occur during wood decomposition (e.g., Hart 1999; Holub et al. 2001; Creed et al. 2004). Our results, although not conclusive, are consistent with the last statement because on one hand N concentrations found in the decaying logs are lower than the values reported in the literature, and on another hand, the 15-year-old logs of *D. excelsa* had more N than the 6 year-old logs, suggesting that there may have been N immobilization in the decaying process.

The pattern observed for carbon fractions in the wood of *D. excelsa* suggests a loss of polysaccharides such as cellulose and hemicellullose (measured as %ASC) from 6 years after fallen toward the more advanced stage of decay after 15 years. The degradation of cell wall constituents produces simple sugars that become available for decomposers and this is indicated by the increase of water-soluble fractions (%WSC and %WSPS). We did not find such trend in *S. macrophylla*'s wood probably because the decrease in ASC coupled with an increase in WSC may be slower for this species than for *D. excelsa* due to the higher lignin and tannin content in *S. macrophylla*'s wood. High contents of lignin and tannins can slow down the degradation of cell wall polysaccharides and affect decomposers activity (Rayner and Boddy 1988; Hammel 1997). Moreover, these findings are consistent with the aforementioned pattern for wood density.

Effect of decaying wood on soil organic matter fractions

We found more NaOH-extractable C and WEOM under more decayed logs for both species (cf. Figs. 2, 5), showing that the stage of decay is an important determinant of the effect of decaying wood on the properties of the underlying soil. Our findings support the idea that as decomposition proceeds and as polymers in wood are degraded, soluble residues are released and transferred to the soil as DOC, and later on condensed to form heavier organic matter fractions. Moreover, considering that more than 70% of the DOC can be easily decomposed (i.e., labile carbon) (Cleveland et al. 2004), our results support the notion of decaying wood as a source of labile C, that leaches into the soil and influence processes in the soil underneath.

Wood quality was also an important factor determining the effect of decaying wood on soil. For example, NaOH-extractable organic carbon was higher near *D. excelsa* logs (cf. Table 4). Berg et al. (2001) found evidence suggesting that forests with litter richer in N tend to accumulate more humus because, in spite of the fact that richer litter has a higher initial decomposition rate, the asymptotic point after which only recalcitrant material remains is reached earlier in richer than in poorer substrates. This trend could explain why we found more NaOH-extractable organic carbon under *D. excelsa* logs, given that wood of this species has higher N content than *S. macrophylla* wood.

Results from the optical characterization of DOM may seem at first glance counterintuitive, because an increasing degree of humification should be associated with an advanced stage of wood decay. However, specific absorbance at 254 nm as a measure of aromaticity was higher in the soil under the less decayed logs (i.e., 6-year-old logs), and the intensity of fluorescence emission at 450 nm was lower under *S. macrophylla* older logs than under any other. It should be considered that the water soluble humic portion that was present in the analyzed WEOM is lighter (probably close to the LMW-FA) than the fractions extracted with NaOH. Therefore, what our results indicate is that a higher degree of condensation of water soluble fulvic acids and other related poly-aromatic residues occurred in the soil associated with the youngest logs. This could be part of the early stages of condensation that will ultimately lead to the formation of more complex humic acids (Stevenson 1982; Baoshan and Zhengqi 1999; Chefetz et al. 2002). Additionally, large humic molecules tend to fold and plicate acquiring complex tertiary structures (Hayes and Swift 1978). As a result of this folding the absorbance of large humic compounds can decrease (Hayes and Swift 1978), which explains why we found lower a (254) in the soil influenced by the more decayed logs.

Effect of decaying wood on soil nutrients

Following our working hypothesis, the effect of decaying wood on soil properties is mediated by the leaching of DOM and the subsequent transformations of and interactions between these substances in the underlying soil matrix. In another study using the same sampling design presented here, it was shown that the relative abundance of two groups of polyvalent cations: Ca^{2+}, Cu^{2+}, Zn^{2+}, and Pb^{2+} on one side, and Al^{3+} and Fe^{3+} on the other, were affected differently by advancement of log decay (M. Zalamea et al., submitted). More divalent cations were available in the soil influenced by younger logs, and decreased as decomposition increased. While trivalent cations were more available near the older logs as decomposition advanced. The authors suggested that this pattern is the result of biotical and chemically mediated processes. Results obtained from organic matter fractions are consistent with the distribution of nutrients found the aforementioned study: divalent cations as well as highly aromatic dissolved organic compounds (measured as the specific UV absorbance of WEOM at 254 nm) were more abundant in the soil influenced by 6-year-old logs (cf., Fig. 6). In contrast, Al^{3+} and Fe^{3+} were more available where the amount of humic substances, both HA and FA (measured as total NaOH-extractable organic carbon) were the highest (cf., Fig. 2). This suggests that the availability of the two groups of polyvalent ions is mediated by different fractions of SOM. In addition, these results may indicate important differences in the mobility of divalent cations such as Ca versus trivalent ions such as Al and Fe. It has been found that SOM promotes release and retention of trivalent ions as well as solubility and loss of divalent ones (Birkeland 1984). Our data shows this in a consistent way: even with higher Ca input from *S. macrophylla* wood, there was a reduction of soil Ca for both tree species as decomposition advanced, suggesting that Ca coming from decaying wood to soil has been lost probably through the formation of soluble organic matter complexes. In contrast, Al and Fe concentrations in the soil influenced by decaying logs increased with decomposition for both species also, suggesting that these ions are being retained by interactions with the SOM. It is known that Al and Fe are strongly linked with larger fractions of SOM like HA and FA (Cancès et al. 2003). These results show the importance of both species and decomposition on the specific effects of decaying wood on soil properties and nutrient availability.

Even though we find significant effects for tree species and decay stage, we did not find a significant effect of position on the soil organic fractions measured. This suggests that a distance of 50 cm could have been either too short or too wide. In the first case, the soil 50 cm away could have been still influenced by the adjacent log, whereas in the second, the influence of other nearby trees or fine and CWD could have masked the effect of the targeted logs.

In conclusion, decaying logs indeed influenced the properties of the underlying soil. We found that SOM (measured as humic substances and WEOM) accumulated under and near decaying logs as decomposition advanced (cf., Figs. 2, 5). We also found that the effect of decaying wood on soil was dependent of the decay stage and that decaying logs can have a long-lasting imprint on soil. Such effect is also attributed to wood quality, as different amounts of HS accumulated in the soil influenced by decaying logs from the two tree species studied. Moreover, the effect of decaying wood on SOM fractions seems to be influencing the distribution of nutrients around decaying logs (e.g., divalent versus trivalent cations, and NO_3^-), and this in turn could affect the spatial and temporal patterns of root distribution (M. Zalamea et al., submitted). We have shown that decaying wood, through its effect on SOM and nutrient dynamics, contributes to the spatial heterogeneity of soil properties in a subtropical forest, and can affect process of soil formation and nutrient cycling. Furthermore, our results are novel considering that few reports have been made up to date pointing to a greater accumulation of SOM under decaying wood and its potential effect over soil chemical properties in tropical forests.

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References

Aiken GR, McKnight DM, Thorn KA, Thurman EM (1992) Isolation of hydrophilic organic acids from water using non-ionic macroporous resins. Org Geochem 18:567–573

Allen SE (1974) Chemical analysis of ecological materials. Wiley, New York, pp 285–287

Baoshan X, Zhengqi C (1999) Spectroscopic evidence for condensed domains in soil organic matter. Soil Sci 164:40–47

Beard KH, Vogt KA, Vogt DJ, Scatena FN, Covich AP, Sigurdardottir R, Siccama TG, Crowl TA (2005) Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. Ecol Monogr 75:345–361

Bendtsen BA, Chudnoff M (1981) Properties of seven colombian woods. United States Department of Agriculture, Forest Service, Forest Products Laboratory Note, FPL-0242. http://www.fpl.fs.fed.us/documnts/fplrn/fplrn242.pdf. Citied Oct 2005

Berg B, McClaugherty C, Virzo De Santo A, Johnson D (2001) Humus build-up in boreal forests: effects of litter fall and its N concentration. Can J For Res 31:988–998

Birkeland PW (1984) Soils and geomorphology. Oxford University Press, USA

Boone RS, Chudnoff M (1970) Variations in wood density of the mahoganies of Mexico and Central America. Turrialba 20:369–371

Bultman JD, Southwell CR (1976) Natural resistance of tropical American woods to terrestrial wood-destroying organisms. Biotropica 8:71–95

Cancès B, Ponthieu M, Castrec-Roulee M, Aubry E, Benedetti MF (2003) Metal ions speciation in a soil and its solution: experimental data and model results. Geoderma 113:341–355

Chefetz B, Tarchitzky J, Deshmukh AP, Hatcher PG, Chen Y (2002) Structural characterization of soil organic matter and humic acids in particle-size fractions of an agricultural soil. Soil Sci Soc Am J 66:129–141

Chudnoff M (1984) Tropical timbers of the world. Agriculture Handbook #607. Madison, WI. U.S. Dept. of Agriculture, Forest Service, Forest Products Laboratory. 464p. Center for wood anatomy and research. USDA-FPL. Tropical hardwoods. http://www2.fpl.fs.fed.us/TechSheets/tropicaaD-G.html. Citied Sept 2005

CIRAD (2003) TROPIX 5.0. Technological characteristics of 215 tropical species. Technical datasheets, South American woods. Centre de coopération internationale en recherche agronomique pour le développement (CIRAD), Forest Department, Forest Products Programme. http://wwww.cirad.fr/activites/bois/en/syst/america.html. Citied Nov 2005

Clark DB, Clark DA, Brown S, Oberbauer SF, Veldkamp E (2002) Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. For Ecol Manag 164:237–248

Cleveland CC, Neff JC, Townsend AR, Hood E (2004) Composition, dynamics, and fate of leached dissolved organic matter in terrestrial ecosystems: results from a decomposition experiment. Ecosystems 7:275–285

Cotrufo MF, Ineson P (2000) Does elevated atmospheric CO_2 concentrations affect wood decomposition? Plant Soil 224:51–57

Creed IF, Morrison DL, Nicholas NS (2004) Is coarse woody debris a net sink or source of nitrogen in the red spruce—Fraser fir forest of the southern Appalachians, USA? Can J For Res 34:716–727

Cuevas E, Brown S, Lugo AE (1991) Above- and belowground organic matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest. Plant Soil 135:257–268

Delaney M, Brown S, Lugo AE, Torres-Lezama A, Bello-Quintero N (1998) The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. Biotropica 30:2–11

EPA (1979) Methods for chemical analysis of water and wastes. Environmental Protection Agency (EPA)-600/4-79-020, Environmental Monitoring and Support Laboratory, Method 415.1

Francis JK (2003) Wood densities of mahoganies in Puerto Rican plantations. In: Lugo AE, Figueroa-Colón JC, Alayón M (eds) Big-leaf mahogany: genetics, ecology and management, vol 159. Springer, Ecological Studies, pp 358–361

Francis JK, Lowe CA, Trabanino S (2000) Silvics of native and exotic trees of puerto rico and the Caribbean Islands. Gen Tech Rep IITF-15. Río Piedras, PR: U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry. 582 p. http://www.fs.fed.us/global/iitf/native.htm. Citied June 2005

Grier CC (1978) A *Tsuga heterophylla-Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. Can J For Res 8:198–206

Guéguen C, Guo L, Tanaka N (2005) Distribution and characteristics of colored dissolved organic matter in the Western Arctic Ocean. Cont Shelf Res 25:1195–1207

Gupta SR, Kaur B (1998) The soil-decomposer system: processes, controls and management. In: Gopal B et al (eds) Ecology today: an anthology of contemporary ecological research. International Scientific Publications, New Delhi, pp 217–161

Hammel KE (1997) Fungal degradation of lignin. In: Cadisch G, Giller KE (eds) Driven by nature: plant litter quality and decomposition. CAB International, Wallingford, pp 33–45

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack JR, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15:133–302

Harmon ME,Sexton J (1996) Guidelines for measurements of woody detritus in forest ecosystems. USA LTER Network. http://www.lternet.edu/documents/Publications/woodydetritus/. Citied Sept 2003

Hart SC (1999) Nitrogen transformations in fallen tree boles and mineral soil of an old-growth forest. Ecology 80:1385–1394

Hayes MHB, Swift RS (1978) The chemistry of organic colloids. In: Greenland DJ, Hayes MHB (eds) The chemistry of soil constituents. Wiley, New York, pp 179–320

Holub SM, Spears JDH, Lajtha K (2001) A reanalysis of nutrient dynamics in coniferous coarse woody debris. Can J For Res 31:1894–1902

Hood E, Williams MW, McKnight DM (2005) Sources of dissolved organic matter (DOM) in a Rocky Mountain stream using chemical fractionation and stable isotopes. Biogeochemistry 74:231–255

IUSS Working Group WRB (2006) World reference base for soil resources. World Soil Resources Reports 103, FAO, Rome

Keenan RJ, Prescott CE, Kimmins JP (1993) Mass and nutrient content of woody debris and forest floor in western red cedar and western hemlock forests on northern Vancouver Island. Can J For Res 23:1025–1059

Krankina ON, Harmon ME, Griazkin AV (1999) Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. Can J For Res 29:20–32

Lambert R, Lang GE, Reiners WA (1980) Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61:1460–1473

Lodge DJ, Scatena FN, Asbury CE, Sánchez MJ (1991) Fine litterfall and related nutrient inputs resulting from hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico. Biotropica 23:336–342

Longwood FR (1961) Puerto Rican woods: their machining, seasoning and related characteristics. Agric Handbook 205, USDA Forest Service, Puerto Rico

Lugo AE, Cuevas E, Sánchez MJ (1990) Nutrients and mass in litter and top soil of ten tropical tree plantations. Plant Soil 125:263–280

Lugo AE (1992) Comparison of tropical tree plantations with secondary forests of similar age. Ecol Monogr 62:1–41

Luh Huang CY, Schulte EE (1985) Digestion of plant tissue for analysis by ICO emission spectroscopy. Commun Soil Sci Plan 16:943–958

Malcolm RL, MacCarthy P (1992) Quantitative evaluation of XAD-8 and XAD-4 resins used in tandem for removing organic solutes from water. Environ Int 18:597–607

McFee WW, Stone EL (1966) The persistence of decaying wood in humus layer of northern forests. Soil Sci Soc Am Proc 30:513–516

McClaugherty CA, Pastor J, Aber JD, Melillo JM (1985) Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66:266–275

Mount HR, Lynn WC (2004) Soil survey laboratory data and soil descriptions for Puerto Rico and the U.S. Virgin Islands. Soil Survey Investigation Report No. 40. U.S. Department of Agriculture, Natural Resources Conservation Service, National Soil Survey Center, Lincoln, NB

Ping CL, Michaelson GL, Malcolm RL (1995) Fractionation and carbon balance of soil organic matter in selected cryic soils in Alaska. In: Lal R, Kimble J, Levine E, Stewart BA (eds) Soils and global change: advances in soil science. CRC Lewis Publishers, USA, pp 307–314

Preston CM, Trofymow JA, Niu J, Fyfe CA (1998) CPMAS-NMR spectroscopy, chemical analysis of coarse woody debris in coastal forests of Vancouver Islands. Forest Ecol Manag 111:51–68

Qualls RG, Haines BL, Swank WT (1991) Fluxes of dissolved organic nutrients and humic substances in a deciduous forest. Ecology 72:254–266

Rayner ADM, Boddy L (1988) Fungal decomposition of wood—its biology and ecology. Wiley, UK

Reyes G, Brown S, Chapman J, Lugo AE (1992) Wood densities of tropical tree species. USDA-FS-Southern Forest Experimental Station, New Orleans, Louisiana, General Technical Report SO-88

Ryan MG, Melillo JM, Ricca A (1990) A comparison of methods for determining proximate carbon fractions of forest litter. Can J For Res 20:166–171

Scatena F (1989) An introduction to the physiography and history of the Bisley experimental watersheds in the Luquillo Mountains of Puerto Rico. USDA-FS-Technical Report No. SO-72

Scholz O, Erickson K, Azevedo J (2004) Restoring the Forest in a young coastal douglas-fir plantation. 16th International Conference, Society for Ecological Restoration, August 24-26, 2004, VIC., Canada, http://www.galiano-conservancy.ca/downloads/restoration_paper.pdf. Citied Oct 2005

Senesi N, Miano TM, Provenzano MR, Brunetti G (1991) Characterization, differentiation and classification of humic substances by fluorescence spectroscopy. Soil Sci 152:259–271

Sollins P, Cline SP, Verhoeven T, Sachs D, Spycher G (1987) Patterns of log decay in old-growth Douglas-fir forests. Can J For Res 17:1585–1595

Spears JDH, Holub SM, Harmon ME, Lajtha K (2003) The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, USA, Can J For Res 33:2193–2201

Spears JDH, Lajtha K (2005) The imprint of coarse woody debris on soil chemistry in the western Oregon Cascades. Biogeochemistry 71:163–175

SPSS (2002) SPSS 11.5 for Windows. SPSS Chicago, IL, USA

Stevenson FJ (1982) Humus chemistry: genesis, composition and reactions. Wiley, USA

Tabatabai MA, Bremmer JM (1991) Automated instruments for determination of total carbon, nitrogen, and sulfur in soils by combustion techniques. In: Dekker M (ed) Soil analysis, modern instruments, and techniques. New York, USA, pp 261–286

Torres JA (1994) Wood decomposition of *Cyrilla racemiflora* in a tropical montane forest. Biotropica 26:124–140

Wadgaard FF, Muschler AF (1952) Proprieties and uses of tropical woods III. Trop Woods 98:190

Wangaard FF, Stern WL, Goodrich SL (1955) Proprieties and uses of tropical woods V. Trop Woods 103:139

Wellwood RW (1946) The physical-mechanical properties of certain West Indian timbers. Caribb Forester 7:151–173

Yano Y, Lajtha K, Sollins P, Caldwell BA (2005) Chemistry and dynamics of dissolved organic matter in a temperate coniferous forest on andic soils: effects of litter quality. Ecosystems 8:286–300

Yavitt JB, Fahey TJ (1985) Chemical composition of interstitial water in decaying lodgepole pine bole wood. Can J For Res 15:1149–1153

Zsolnay A (2003) Dissolved organic matter: artifacts, definitions, and functions. Geoderma 113:187–220