

## Lignin signatures of vegetation and soils in tropical environments

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(Received June 02, 2015, Revised December 08, 2015, Accepted December 09, 2015)

**Abstract.** The few lignin biomarker studies conducted in tropical environments are hampered by having to use references signatures established for plants and soils characteristic of the temperate zone. This study presents a lignin biomarker analysis (vanillyls (V), p-hydroxylys (P), syringyls (S), cinnamyls (C)) of the dominant plant species and soil horizons as well as an analysis of the interrelated terrigenous organic matter (TOM) dynamics between vegetation and soil of the Tapajós river region, an active colonization front in the Brazilian Amazon. We collected and analyzed samples from 17 fresh dominant plant species and 48 soil cores at three depths (0-5 cm, 20-25 cm, 50-55 cm) from primary rainforest, fallow forest, subsistence agriculture fields and pastures. Lignin signatures in tropical plants clearly distinguish from temperate ones with high ratios of Acid/aldehyde of vanillyls ((Ad/Al)v) and P/V+S. Contrary to temperate environments, similarly high ratios in tropical soils are not related to TOM degradation along with pedogenesis but to direct influence of plants growing on them. Lignin signatures of both plants and soils of primary rainforest and fallow forest clearly distinguish from those of non-forested areas, i.e., agriculture fields and pastures. *Attalea speciosa* Palm trees, an invasive species in all perturbed landscapes of the Amazon, exhibit lignin signatures clearly distinct from other dominant plant species. The study of lignin signatures in tropical areas thus represents a powerful tool to evaluate the impact of primary rainforest clearing on TOM dynamics in tropical areas.

**Keywords:** Lignin turnover; tropical soils; Amazon basin; land use change; plant material

### 1. Introduction

By demonstrating the relevance of using lignin oxidation products to identify the tissues of different groups of plants, Hedges and Mann (1979) laid the foundations of a method in which lignin phenols can be used as biomarkers for terrigenous organic matter (TOM). As lignin is a macromolecule appearing in vascular plants, and is fairly resistant to degradation (Louchouart *et*

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*al.* 1999), it allows studying the composition, the origin and the fate of TOM in the environment (Hedges *et al.* 1986, Onstad *et al.* 2000, Farella *et al.* 2001, Caron *et al.* 2008, Teisserenc *et al.* 2010). Recently, lignin biomarkers have been used to evaluate the environmental impacts of human activities such as reservoir impoundment, mining and forestry on TOM dynamics (Houel *et al.* 2006, Teisserenc *et al.* 2010, Petit *et al.* 2011). Lignin studies have also been conducted to determine soil organic matter (SOM) pool size as well as its turnover, or to establish plant-soil carbon models (Thevenot *et al.* 2010).

The vast majority of lignin studies that have flourished over the last 30 years have been conducted in temperate zones and have thus contributed to our understanding of TOM dynamics in those environments (Thevenot *et al.* 2010). In comparison, research using lignin biomarkers and lignin proxies obtained from specific biomarkers ratios has remained scarce in tropical environments. As such, there are no readily available data banks of lignin biomarkers and proxies in common tropical plants or typical tropical soils. Applying reference lignin biomarkers and proxies established for temperate environments (Hedges and Mann 1979) to TOM studies in the tropics represents a strong limitation since lignin fate in soils is related to the type of vegetation, land-uses, climate and soil characteristics (Thevenot *et al.* 2010). Singularities of lignin biomarkers and proxies, also called lignin signatures, in tropical environments have been highlighted in few studies (Hedges *et al.* 1986, Dittmar and Lara 2001, Zocatelli *et al.* 2011). Certain macrophytes (Hedges *et al.* 1986, Zocatelli *et al.* 2011) and mangrove tree species (Dittmar and Lara 2001) have similar lignin signatures to non-woody material or SOM. Thus, the accepted lignin signatures for non-woody material could be in fact showing the presence of macrophytes, as well as SOM lignin signatures could in reality be pointing out the dominance of mangrove trees. To our knowledge, only one study (Farella *et al.* 2001) has evaluated the characteristics of lignin signatures in Amazonian soils. We are not aware of any other study in a tropical environment that has evaluated the differences between the lignin signatures observed in fresh vegetation with respect to those in soils. It thus appears a prerequisite to characterize lignin signatures of local vegetation classes in order to interpret lignin trends in tropical environments.

In this study, we realize for the first time an inventory of the lignin signatures characterizing the dominant vegetation of the Tapajos region, an active colonization front in the Brazilian Amazon. We take into consideration dominant native tree species of the primary tropical rainforest as well as ubiquitous fallow forest trees, most common subsistence crops and local grass growing in cattle pastures. We then characterize the lignin signatures of SOM in a series of sampling sites covering the various land uses of the region. The distinct soil lignin signatures are then interpreted to represent the plant species assemblages growing on them after pedogenesis. We then propose to relate the differences in lignin signatures along various soil horizons to distinguish SOM dynamics in environments impacted by massive deforestation from those in pristine forest areas.

## **2. Materials and methods**

### *2.1 Study region*

This study was conducted in the Lower Tapajós River region (state of Pará, Brazil), between the cities of Itaituba and Aveiro (Fig. 1). The study region was chosen because it is affected by rampant deforestation typical of many Amazonian regions nowadays. The most common soil types in the region are oxisols and ultisols, as well as some alfisols (from American Soil Taxonomy

classification) (Baillie 2001). The oxisols and ultisols are formed on sediments of the Alter do Chão formation and are considered to be very impoverished by millions of years of weathering (Jordan 1985). They are generally acidic and have a low cation exchange capacity (Roulet *et al.* 1998). The clayey oxisols dominate the high plateaus, whereas podzolization increases down slopes that lead to waterways (Roulet *et al.* 1998). The region experiences alternating wet and dry seasons. High levels of precipitation in the rainy season, between 1800 and 2200 mm of rain between December and April (Grupo de Trabalho Interministerial 2006) result in water level changes of up to six meters and flooding of adjacent flatlands (Salati 1986). The native vegetation on the plateaus is dense tropical rainforest (Embrapa 2007).

## 2.2 Sampling

The study area was prospected prior to data collection to construct a non-random sampling design that would be representative of the distribution patterns of palms species prone to Triatominae infestation (Romaña *et al.* 1999, Abad-Franch *et al.* 2005). Sampling site selection based on observed floristic variations insures that the majority of the variability is sampled but may exaggerate group distinction during subsequent classification (Richards 1996). This limitation (non-independent samples) will be taken into account during data analysis. In 2010, 14 sampling sites were selected based on observed land-uses variations and corresponding vegetation cover and georeferenced with a Garmin eTrex Venture HC handheld GPS device. On these sites, 14 transects were sampled following the surface drainage flow axes (Fig. 1). The length of each transect (median 270.8 m, min.: 90.2 m, max.: 629.3 m) varied according to the length of the slope and accessibility. Each transect consisted of three quadrats (75 m by 25 m,  $n = 43$ ) (except for #4 with 4 quadrats) with the longer side oriented perpendicular to the site's surface drainage flow. The central quadrat of each transect was placed approximately halfway between the other two. Care was taken to insure that slope, vegetation cover, soil color and texture were constant within each quadrat. Four land use/land cover classes were defined: subsistence agriculture, cattle pasture, fallow forest and fragmented primary rainforest. For each site, three soil cores were retrieved using a stainless steel auger equipped with a 100 cm<sup>3</sup> cartridge and subsampled at different depths incorporating both organic and inorganic horizons: 0–5 cm, 20–25 cm and 50–55 cm. The dominant plant species were chosen in collaboration with another researcher who undertook an exhaustive inventory of plant species from the initial and successive rainforest ecosystems of the Tapajós region, as part of a structural analysis (Gonçalves 2010). Fresh plant samples were collected in February 2010 from the same sample plots as the soil samples. In total, 17 plant species were collected: five in primary rainforest, six in fallow forest, five in subsistence agriculture fields and one in pasture lands, actually the only herbaceous species grown for cattle grazing in the study region. For each species, fresh leaves and dead leaves from the soil litter were collected, as well as the rigid part of the plant, i.e., wood for tree species and stems for crop and grass species (Table 1).

Wood, dead leaves, fresh leaves and stems are referred to as “plant parts”. All samples were kept frozen until laboratory analysis. The dominant plant specimens are used to define pure lignin compound sources. On the other hand, lignin signatures of soil samples represent an integrated picture of an assemblage of these plant species after pedological processes. All variables used in this study are summarized in Table 1.

TOM was characterized based on soil samples ( $n = 141$ ) and dominant plant species ( $n = 38$ ), followed by an analysis of their lignin composition.

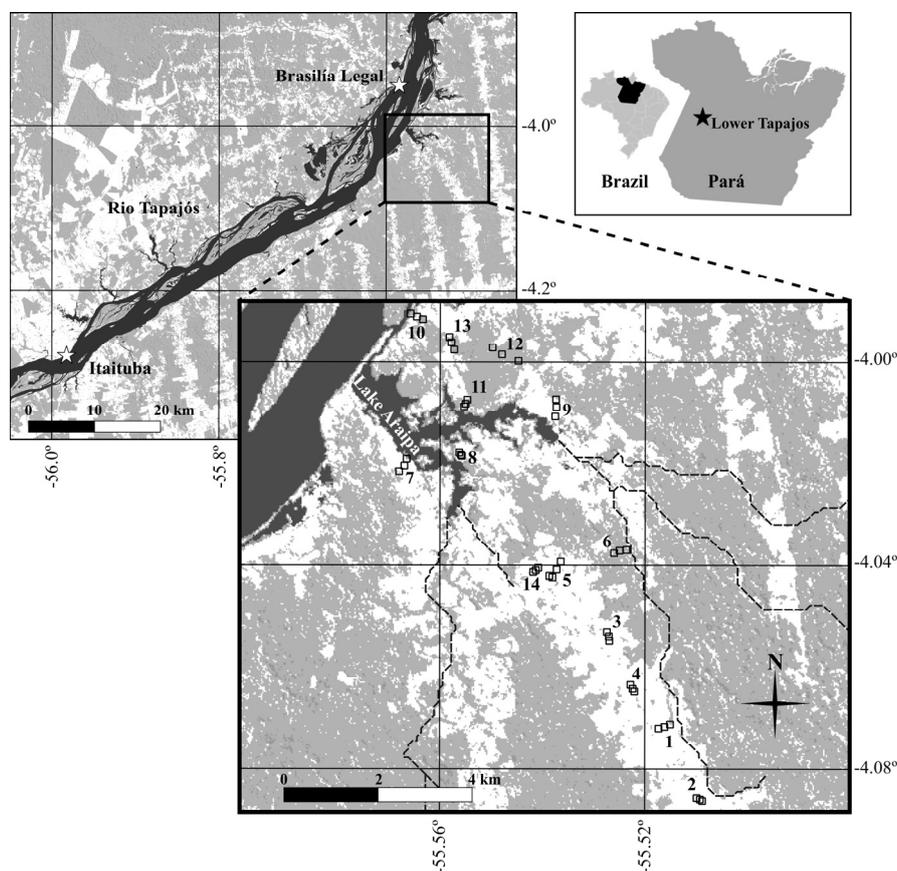


Fig. 1 Map of Lower Tapajós River Region. The study area is presented in the black square. Water appears in black, forest areas in grey and deforested areas in white. Numbers illustrate soil transects and squares represent the cores sample location

### 2.3 Chemical analyses

All soil and plant parts samples were freeze-dried, ground to a fine powder and homogenized. Total carbon (C) and nitrogen (N) concentrations were determined using a Carlo Erba (NA-1500) elemental analyzer with a relative precision of  $\pm 5\%$  and atomic C/N ratios were calculated. Two soil horizons were distinguished according to carbon content: the organic A horizon (0-5 cm) and the mineral B<sub>1</sub> and B<sub>2</sub> horizons (20-25 cm and 50-55 cm respectively) (Table 1). Samples were subjected to alkaline cupric oxide (CuO) oxidation according to a modified protocol from Goñi and Montgomery (2000) and described in Moingt *et al.* (2014). Briefly, for each sample,  $3.0 \pm 0.1$  mg of organic carbon (OC) and CuO ( $330 \pm 4$  mg) were mixed in about 3.2 mL of 2N NaOH in a reaction bomb purged with N<sub>2</sub>. Oxidations were conducted with a Hewlett Packard 5890A™ gas chromatograph oven modified by Prime Focus Inc. (Seattle, WA). Reaction bombs were heated from room temperature to 150°C for 150 min with an initial temperature gradient of 4.2°C/min for 30 min. After cooling, 50  $\mu$ L of internal standards (cinnamic acid and ethyl-vanillin) were added to the bomb and the supernatant was decanted and acidified to pH 1 with HCl (2N). Then, the

Table 1 Summary of the variables used in the study for vegetation samples and soil samples, as well as studied vegetation species

VEGETATION SAMPLES		SOIL SAMPLES			
Land-Use/Land-Cover		Land-Use/Land-cover			
Fragmented primary rainforest		Fragmented primary rainforest			
Fallow forest		Fallow forest			
Cattle pasture		Cattle pasture			
Subsistence agriculture					
Plant part		Soil Horizon			
Wood		A Horizon (0-5 cm)			
Dead leaf		B <sub>1</sub> Horizon (20-25 cm)			
Fresh leaf		B <sub>2</sub> Horizon (50-55 cm)			
Stem					
VEGETATION SPECIES		Common Name		Latin name	
Fragmented primary rainforest species		Tucuma palm		<i>Astrocaryum aculeatum</i> G. Mey	
		Envira Surucucu		<i>Duguetia echinophora</i> R.E. Fries	
		Embaubarana		<i>Pouroma guianensis</i> Aubl	
		Fava tucupi		<i>Parkia multijuga</i> Benth	
		Matamata		<i>Eschweilera amazonica</i> Knuth	
Fallow forest species		Embauba		<i>Cecropia distachya</i> Huber	
		Inga vermelho		<i>Inga alba</i> (SW) Willd	
		Lacre		<i>Vismia latifolia</i> Choisy	
		Burra leiteira		<i>Sapium marmieri</i> Huber	
		Babassu palm		<i>Attalea speciosa</i>	
Cattle pasture species		Tachi preto		<i>Tachigali myrmecophila</i> (Ducke )	
		Signal grass		<i>Brachiaria decumbens</i>	
Subsistence agriculture species		Banana		<i>Musa acuminata</i>	
		Cassava		<i>Manihot esculenta</i>	
		Cowpea		<i>Vigna unguiculata</i>	
		Maize		<i>Zea mays</i>	
		Rice		<i>Oryza sativa</i>	

organic phase was liquid-liquid extracted and dried by rotary evaporation. Finally, the extract was resuspended in pyridine and derivatized with N,O-bis(trimethylsilyl)trifluoroacetamide (BSTFA) and trimethylchlorosilane (TCMS; 99:1). A 2- $\mu$ L extraction fraction was injected in splitless mode on a GC/MS (Varian 3800/Saturn 2000<sup>TM</sup>) fitted with a fused capillary column (DB-1 from J&W, 60 m, 320  $\mu$ m). Injector and detector were both held at 300°C whereas He was used as carrier gas. The initial column oven temperature was set at 100°C with a temperature gradient of 4°C/min to 320°C followed by a holding time of 10 min. A replicate was analyzed after every 12 samples in order to ensure that the results remained reliable. The standard deviation of lignin biomarkers used

in this study is below 15%. Moreover, replicate analyses of a reference sediment sample (SAG-05) were included in each sample injection series allowing intercalibration between series through time (Moingt *et al.* 2014).

#### 2.4 Lignin biomarkers and proxies

The lignin-derived phenols are classified according to family: vanillyls (V), p-hydroxyls (P), syringyls (S) and cinnamyls (C) (Hedges and Ertel 1982). Vanillyls are ubiquitous in vascular plants, while cinnamyls are generally limited in woody plant parts (trees, bark) and abundant in those that are non-woody (herbaceous plants, leaves and needles) (Hedges and Mann 1979). Therefore, the C/V ratio is used as a proxy to differentiate woody from non-woody plant parts. As Syringyls are abundant in angiosperms and absent in gymnosperms, the S/V ratio is generally used as a proxy to estimate the relative contribution of angiosperm species to TOM content (Hedges and Mann 1979, Tesi *et al.* 2008). Other lignin proxies can also be indicative of the state of degradation of the TOM, as certain ratios tend to increase during diagenesis and/or pedogenesis processes. The Acid/aldehyde ratio of vanillyls ((Ad/Al)<sub>v</sub>) increases during degradation processes (aldehydes being oxidized into acids) (Hedges *et al.* 1986, Opsahl and Benner 1995) and in leaching and sorption processes (Hernes *et al.* 2007). The P/(V+S) ratio also increases during diagenesis and humification since demethoxylation leads to the loss of a methoxy group in V and S families whereas the P family is not affected (Prahl *et al.* 1994, Goñi and Hedges 1995, Dittmar and Lara 2001). The 3,5-Bd (3,5-dihydroxybenzoic acid) is a degradation byproduct of terrigenous plants and is commonly found in soils (Ugolini *et al.* 1981, Houel *et al.* 2006). It tends to accumulate with the degradation of plant cells (De Leeuw and Largeau 1993). Although the 3,5-Bd precursors are not lignin compounds but tannins and flavonoids, this molecule has been incorporated into the lignin indicators with the 3,5-Bd/V ratio, and used as a proxy of soil humification (Houel *et al.* 2006). Finally, two important indicators are commonly used to quantitatively evaluate TOM: lambda ( $\lambda$ ) and Sigma8 ( $\Sigma 8$ ).  $\lambda$  represents the sum of V, S and C families per 100 mg of OC whereas  $\Sigma 8$  corresponds to the same sum of lignin byproducts but per 10 g of sample (Houel *et al.* 2006).

#### 2.5 Statistical analyses

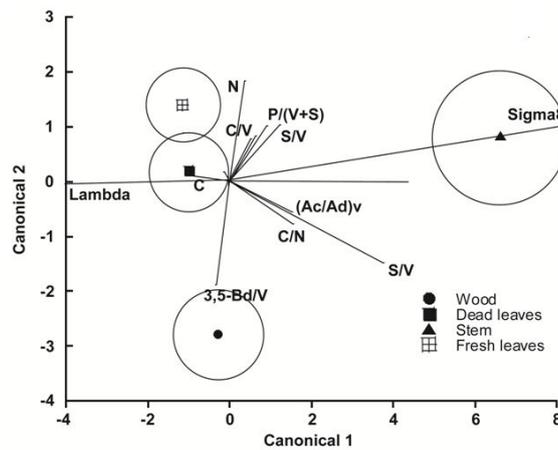
A Discriminant Analysis (DA) was performed to test the discrepancy between lignin signatures of the different plant parts (i.e., leaves, stems and wood) and condition of plant tissues (i.e., fresh or dead material) obtained for all plant samples. A second DA was also carried out to test the influence of land use/land cover classes on lignin signatures of the various plant species. Multiple comparisons Tukey's test was performed on projection of the canonical scores on each axis to identify which groups (plant parts and conditions on the first DA and land use/land cover on the second DA) would display significant differences ( $p$  value < 0.05). In soil profiles, a MANOVA analysis with one criteria of classification was performed for each lignin indicator according to soil horizons as a dependant factor and land use/land cover as classification variables. Contrast tests were carried out for lignin indicators measured in given soil horizons (A to B<sub>1</sub> and B<sub>1</sub> to B<sub>2</sub>). This last procedure allowed us to identify significant differences among the various land-cover/land-use types ( $p$  value < 0.05). In addition, a one-way ANOVA analysis was run for the surface soil horizon only (A), with a Tukey's test to identify which land use/land cover groups would display significant differences ( $p$  value < 0.05).

### 3. Results

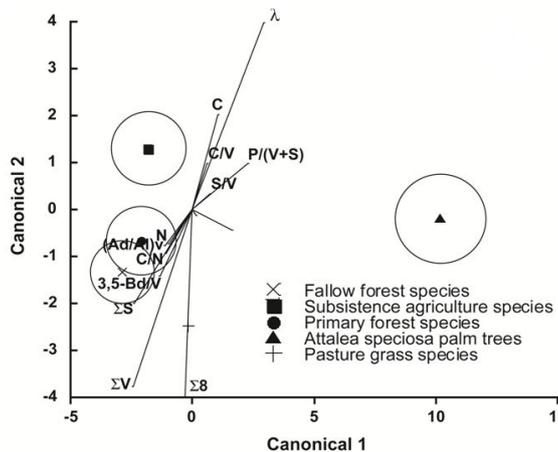
#### 3.1 Lignin signatures of dominant plant species

Lignin results for vegetation and soil samples are presented in Tables 2 and 3, respectively. Lignin indicators for vegetation samples generally fall within the range of values reported by Hedges *et al.* (1986) for pure vegetation sources of temperate regions.

The DA run for plant parts of all vegetation species revealed that the lignin signatures of fresh leaves and dead leaves were undistinguishable as the software tended to classify them interchangeably (Fig. 2(a)). Consequently, fresh and dead leaves were further regrouped together in our study. Stems, representing the rigid part of cultivated plants and the trunk of *Attalea*



(a)



(b)

Fig. 2 First two canonical dimensions of the discriminant analyses on vegetation samples according to plant parts (a) and land-use/land-cover (b). Each marker represents the center of the centroid for the corresponding group

Table 2 C/N ratios and lignin parameters for vegetation samples (standard deviations are presented into brackets)

	n	C/N	Lambda	Sigma $\delta$	Sum S	Sum V	Sum C	Sum P	S/V	C/V	P/(V+S)	3,5-Bd/V	(Ad/Al)v	
Fragmented primary rainforest	Wood	3	58.7 (6.0)	5.28 (4.58)	252.54 (213.25)	1.50 (1.69)	3.02 (2.46)	0.75 (0.65)	0.48 (0.38)	0.73 (0.38)	0.38 (0.28)	0.22 (0.24)	0.06 (0.08)	0.34 (0.18)
	Fresh leaf	4	26.1 (5.6)	6.29 (1.50)	310.75 (80.30)	2.62 (1.14)	3.22 (0.73)	0.46 (0.36)	0.56 (0.23)	0.83 (0.38)	0.14 (0.11)	0.11 (0.06)	0.02 (0.01)	0.28 (0.07)
	Dead leaf	3	27.7 (5.5)	11.39 (9.40)	532.08 (410.95)	5.13 (4.14)	5.81 (5.05)	0.45 (0.28)	0.71 (0.76)	0.93 (0.22)	0.09 (0.06)	0.06 (0.02)	0.01 (0.00)	0.37 (0.02)
Fallow forest	Wood	5	79.7 (45.9)	7.72 (3.41)	365.29 (153.19)	3.19 (1.64)	4.15 (2.41)	0.38 (0.58)	0.29 (0.14)	0.98 (0.60)	0.09 (0.10)	0.05 (0.03)	0.04 (0.06)	0.54 (0.36)
	Fresh leaf	6	23.3 (7.2)	6.39 (3.22)	312.31 (150.82)	3.14 (2.18)	2.61 (1.26)	0.64 (0.54)	1.37 (1.93)	1.19 (0.56)	0.29 (0.25)	0.26 (0.31)	0.06 (0.06)	0.32 (0.07)
	Dead leaf	6	37.0 (10.7)	6.46 (3.47)	304.13 (165.34)	2.36 (1.25)	3.27 (2.03)	0.83 (0.44)	2.88 (3.23)	0.77 (0.28)	0.28 (0.13)	0.51 (0.48)	0.05 (0.02)	0.32 (0.06)
Cattle pasture	Stem	2	91.3 (8.1)	7.40 (2.57)	378.42 (121.54)	3.80 (1.86)	2.95 (1.03)	0.65 (0.32)	10.09 (1.22)	1.25 (0.19)	0.26 (0.20)	1.60 (0.51)	0.02 (0.01)	1.67 (1.24)
	Grass	1	39.5	5.20	229.05	1.78	1.65	1.77	0.49	1.08	0.14	0	0	0.23
Subsistence agriculture	Fresh leaf	5	20.5 (5.8)	4.06 (3.74)	207.81 (179.95)	1.29 (1.37)	1.49 (1.41)	1.27 (1.13)	0.63 (0.29)	0.78 (0.32)	1.36 (1.84)	0.56 (0.59)	0.22 (0.33)	0.24 (0.08)
	Dead leaf	3	47.2 (23.4)	6.51 (4.26)	317.91 (208.47)	3.72 (3.40)	1.72 (0.54)	1.06 (0.62)	0.47 (0.15)	1.88 (1.44)	0.58 (0.26)	0.16 (0.18)	0.07 (0.08)	0.21 (0.03)
	Stem	2	104.3 (92.2)	15.77 (5.84)	780.69 (349.39)	12.35 (3.05)	2.98 (3.35)	0.45 (0.56)	0.27 (0.26)	9.77 (9.98)	0.70 (0.98)	0.02 (0.03)	0.04 (0.05)	0.20 (0.10)
Palm	Fresh leaf	1	32.2	7.88	391.02	4.01	2.21	1.67	5.26	1.81	0.76	0.85	0.03	0.45
	Dead leaf	2	42.9 (2.2)	7.63 (1.41)	346.58 (93.55)	2.99 (0.83)	3.47 (0.17)	1.18 (0.41)	7.04 (0.20)	0.86 (0.20)	0.34 (0.10)	1.10 (0.14)	0.03 (0.01)	0.33 (0.11)
	Stem	2	91.3 (8.1)	7.40 (2.57)	378.42 (121.54)	3.79 (1.86)	2.95 (1.03)	0.65 (0.32)	10.10 (1.22)	1.25 (0.19)	0.26 (0.20)	1.60 (0.51)	0.02 (0.01)	1.67 (1.24)

Table 3 C/N ratios and lignin parameters for soil samples (standard deviations are presented into brackets)

	n	C/N	Lambda	Sigma $\delta$	Sum S	Sum V	Sum C	Sum P	S/V	C/V	P/(V+S)	3,5-Bd/V	(Ad/Al)v	
Fragmented primary rainforest	A	9	13.9 (1.3)	3.6 (2.47)	7.81 (3.29)	1.27 (0.80)	1.89 (1.28)	0.41 (0.43)	0.87 (0.64)	0.69 (0.14)	0.20 (0.07)	0.27 (0.09)	0.10 (0.03)	0.73 (0.18)
	B1	9	12.0 (1.9)	0.87 (0.42)	0.92 (0.43)	0.32 (0.19)	0.45 (0.21)	0.10 (0.06)	0.25 (0.12)	0.69 (0.23)	0.23 (0.08)	0.35 (0.10)	0.17 (0.07)	0.72 (0.13)
	B2	9	9.3 (2.4)	1.36 (2.65)	0.56 (0.93)	0.74 (1.74)	0.61 (0.93)	0.01 (0.01)	0.41 (0.47)	0.79 (0.47)	0.04 (0.06)	0.63 (0.38)	0.14 (0.20)	0.78 (0.35)
Fallow forest	A	9	13.7 (1.7)	2.59 (0.81)	8.26 (4.92)	1.14 (0.64)	1.30 (0.60)	0.15 (0.05)	0.58 (0.39)	0.88 (0.19)	0.12 (0.05)	0.24 (0.14)	0.09 (0.03)	0.66 (0.17)
	B1	9	10.8 (3.2)	1.33 (0.73)	1.09 (1.07)	0.59 (0.47)	0.68 (0.38)	0.06 (0.05)	0.90 (0.89)	0.80 (0.31)	0.13 (0.11)	0.85 (0.71)	0.10 (0.09)	0.53 (0.14)
	B2	8	7.7 (3.5)	0.90 (2.65)	0.44 (0.46)	0.35 (0.33)	0.51 (0.44)	0.03 (0.06)	0.65 (0.42)	0.79 (0.48)	0.04 (0.07)	1.21 (1.23)	0.09 (0.07)	0.46 (0.09)
Cattle pasture	A	29	14.8 (1.9)	2.99 (0.95)	8.56 (5.80)	1.43 (0.60)	1.16 (0.30)	0.40 (0.22)	0.56 (0.23)	1.24 (0.41)	0.36 (0.18)	0.23 (0.09)	0.07 (0.04)	0.60 (0.18)
	B1	30	11.7 (2.6)	1.22 (0.65)	1.35 (1.66)	0.60 (0.37)	0.47 (0.23)	0.15 (0.11)	0.50 (0.25)	1.26 (0.53)	0.30 (0.17)	0.57 (0.40)	0.09 (0.04)	0.51 (0.21)
	B2	29	9.8 (2.9)	0.75 (0.70)	0.59 (1.15)	0.31 (0.36)	0.36 (0.31)	0.08 (0.09)	0.52 (0.58)	0.81 (0.59)	0.27 (0.23)	0.98 (1.09)	0.12 (0.15)	0.52 (0.30)

*speciosa* palm trees, which is in fact a stipe i.e., a thick shoot composed of leafstalk rather than wood, presented lignin signatures distinct from those of wood and leaves (Fig. 2(a)).

The ANOVA confirmed significant differences ( $p < 0.0001$ ) between the three plant parts: leaves (fresh and dead), stems and wood. Atomic C/N ratios of fresh and dead leaves (24 and 33.9 respectively) were much lower than those of wood (70.4) and stems (97.8). S/V ratios and (Ad/Al)<sub>v</sub> ratios in stems were also greater than in any other plant parts.

The DA conducted on plant parts as a function of land-use/land-cover types revealed commonalities between primary rainforest trees and fallow forest trees, as well as between agriculture field plants and pasture grass (Fig. 2(b)). This suggests that forests and non-forested environments represented two significantly distinct groups. The ANOVA conducted on lignin indicators and C/N ratios determined that there were three indicators showing marked differences between the plant species growing in forests or non-forested areas.

Higher S/V and C/V ratios were found in non-forested areas (agriculture fields and pastures) ( $p = 0.0332$  and  $p = 0.0002$ ), while (Ad/Al)<sub>v</sub> ratios were higher in forests ( $p = 0.0285$ ). The difference between woody and non-woody plant groups illustrated by distinct C/V ratios is comparable to the findings of several other researchers (Hedges *et al.* 1986, Farella *et al.* 2001, Bernardes *et al.* 2004, Rezende *et al.* 2010).

The DA of plant parts according to land-use/land-cover also revealed that the lignin signatures of *Attalea speciosa* palm trees were significantly different from all other dominant plant species growing in the various land-use/land-cover types (Fig. 2(b)). The statistical model did not reclassify palm trees as it did for other plants, thus classifying them as a distinct group. An ANOVA performed on the overall results of the first factor of the DA indicated significant differences between *Attalea speciosa* palm trees and other plant species in the four land-use/land-cover types ( $p < 0.0001$ ). It appears that both (Ad/Al)<sub>v</sub> and P/(V+S) ratios differentiated palm trees from other plant species, while the P/(V+S) one allowed us to distinguish them categorically. This indicator appeared significantly higher in *Attalea speciosa* palm trees than in any other plant species growing in any of the four land-use/land-cover types of the study region. No other tree species collected in the primary rainforest or in the fallow forest exhibited lignin signatures that were significantly distinct from those of the average signatures of primary rainforest or fallow forest vegetation.

### 3.2 Lignin signatures of soils

The type of land-use/land-cover (primary rainforest, fallow forest, subsistence agriculture, pasture) had no significant influence on soil lignin contents as expressed by  $\lambda$  and  $\Sigma 8$  indicators (Fig. 3). However,  $\lambda$  and  $\Sigma 8$  indicators varied significantly with soil depth ( $p < 0.0001$ ). On the surface,  $\Sigma 8$  values were 8.35 mg/10 g of sample  $\pm$  0.40, falling rapidly to 1.06 mg/10 g of sample  $\pm$  0.40 in the 20-25 cm layer, and to 0.55 mg/10 g of sample  $\pm$  0.54 at a depth of 50 to 55 cm. We observed the same trend with  $\lambda$  values, decreasing from 3.03 mg/100mg of OC at the surface to 0.90 mg/100mg of OC at depth (Fig. 3). Farella *et al.* (2001) also recorded a major difference in lignin signatures between the organic A and the mineral B<sub>1</sub> and B<sub>2</sub> soil horizons. However, these authors recorded  $\Sigma 8$  values between 300 and 350 mg/10g of sample in A horizon, while we recorded values between 3 and 28 mg/10 g of sample for the same horizon. On the other hand, we observed  $\Sigma 8$  values for B<sub>1</sub> and B<sub>2</sub> horizons in the same range as those found by Farella *et al.* (2001).

The P/(V+S) ratio, a proxy for organic matter degradation in soils, also showed a marked

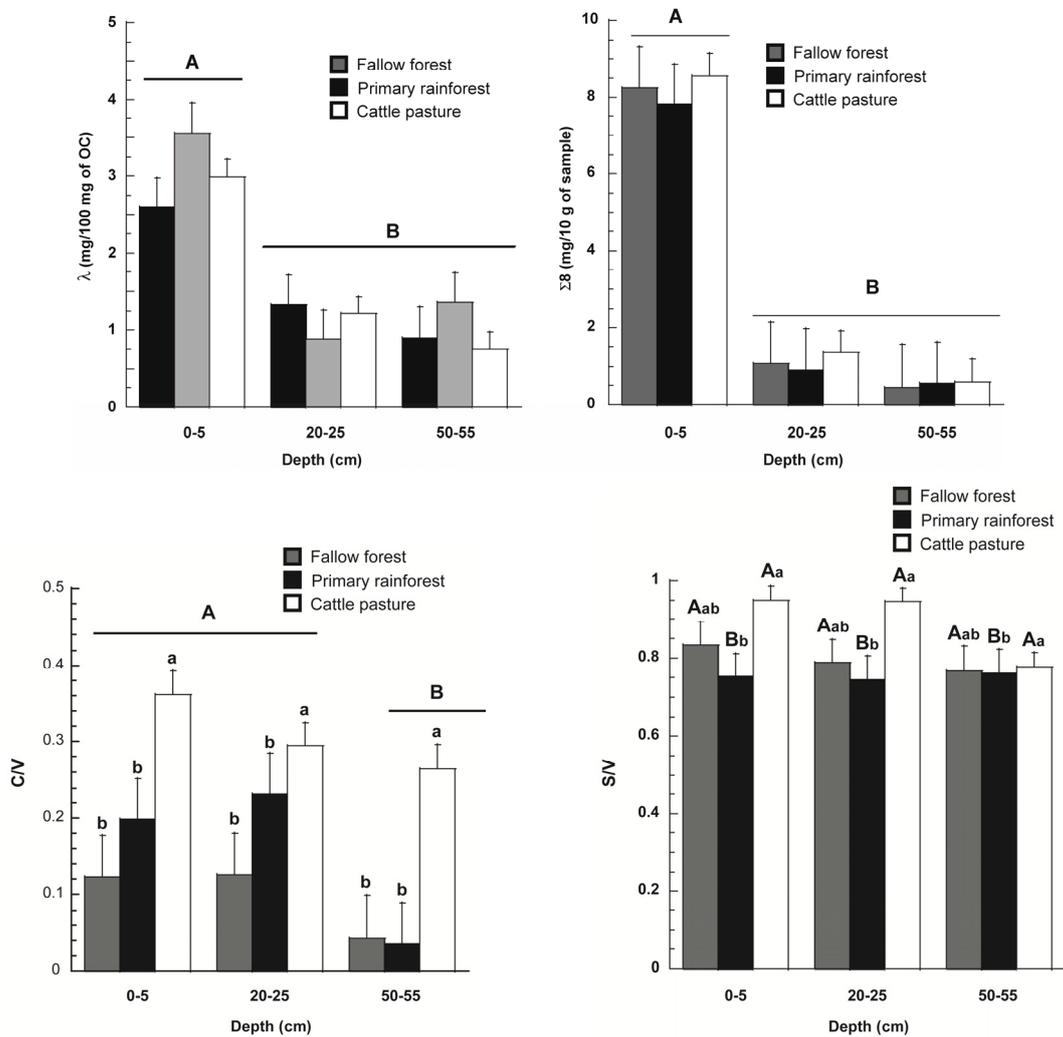


Fig. 3 Lignin indicators in soil profiles as a function of depth and land-use/land-cover for organic matter quantity ( $\lambda$  and  $\Sigma 8$ ) and quality (C/V and S/V).  $\lambda$  values have been transformed ( $\log_{10} \lambda + 1$ )

difference between the surface horizon and the deeper horizons ( $p = 0.0030$ ). This ratio increased from  $0.24 \pm 0.04$  in the 0-5 cm horizon to  $0.95 \pm 0.15$  in the deeper horizon (Fig. 4). Surprisingly, P/(V+S) ratio is the only proxy of organic matter degradation that exhibited significant differences from surface to deep soil horizons (Fig. 4). While Farella *et al.* (2001) found increasing values of 3,5-Bd/V and (Ad/Al)<sub>v</sub> ratios with deeper soil horizons, no such observation was made in our study. The (Ad/Al)<sub>v</sub> ratio exhibited significant differences between land-use/land-cover types, with greater levels in forests (Fig. 4). At all depths, the (Ad/Al)<sub>v</sub> ratio in rainforest soils was greater than in pasture or fallow forest soils. Finally, the S/V and C/V ratios were both significantly higher in pasture soils than in other land-use/land cover soils (Fig. 3). For the C/V ratio, this marked difference was observed at all soil depths and decreased with soil depth.

## 4. Discussion

### 4.1 Tropical soil lignin signatures in relation to vegetation cover

For both soils and dominant plant species of the Tapajós River region in the Amazon, C/V ratios appear to powerfully distinguish forests and non-forested areas. C/V ratios are significantly higher in tissues of grass growing in pastures or in plants cultivated in agriculture fields (average values of 1.08 and 1.36 respectively; Table 2) than in wood and leaves samples from forested areas (average values ranging from 0.09 to 0.38; Table 2). This marked difference in C/V ratios seems to be due to the fact that vegetation in non-forested areas displays both higher content in cinnamyls and lower content in vanillyls compared to vegetation in forested areas, resulting in significantly

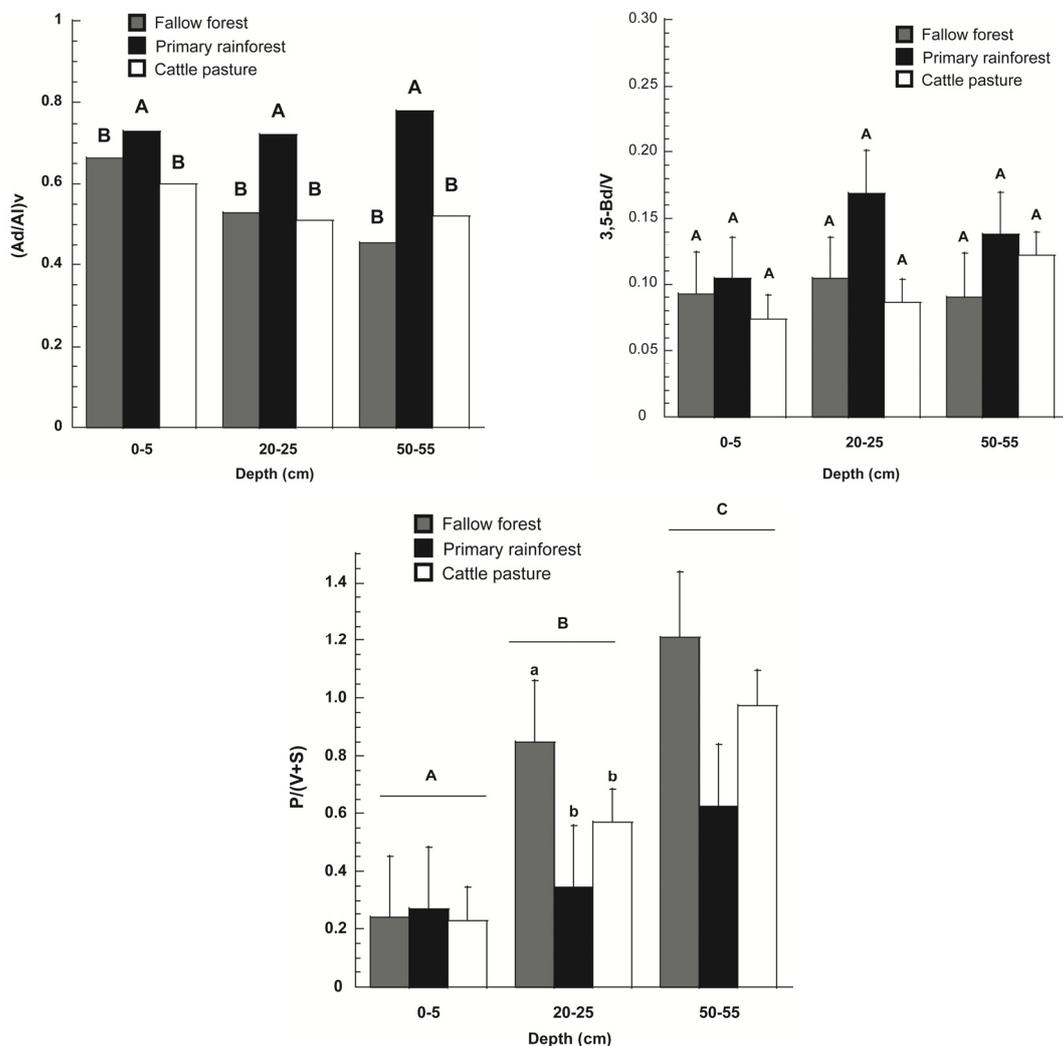


Fig. 4 Lignin indicators of organic matter degradation ( $(Ad/Al)_v$ ,  $P/(V+S)$ ,  $3,5-Bd/V$ ) in soil profiles as a function of depth and land-use/land-cover

higher C/V ratios (Table 2).

A higher content in cinnamyl phenols is expected in vegetation from non-forested areas since it is primarily composed of herbaceous species. Hedges AND Mann (1979) reported that cinnamyls were only abundant in non-woody tissues of angiosperms. Similar observations were also made in subsequent studies (Hedges *et al.* 1986, Farella *et al.* 2001, Bernardes *et al.* 2004, Rezende *et al.* 2010). In the other hand, higher vanillyls contents in forested areas vegetation is unforeseen although important variations of vanillyl phenols concentrations according to the plant species has been observed in the Amazon region (Dittmar and Lara 2001). C/V ratios are also significantly lower in all soil horizons where woody vegetation is growing compared to soils from non-forested areas (Fig. 3).

Farella *et al.* (2001) reported almost identical C/V ratios in wood samples from trees or from surface litter (0.08 and 0.09), as well as in green leaves or dead leaves of the same tree species found in the soil litter (0.19 and 0.12). In the present study, C/V ratios decrease from plants to soils on which they grow from 1.08 to 0.36 in non-forested areas and from 0.28 to 0.16 in forests (Table 3). In forests, both cinnamyls and vanillyls decrease from vegetation to soils in relatively equivalent proportions but this decrease is more important in fallow forest than in fragmented primary forested environments (Tables 2 and 3). By contrast, C/V ratios significantly decrease from plants to soils in non-forested environments. For those environments, cinnamyls levels drop far more than vanillyls, yielding low C/V ratios (0.3). Cinnamyl phenols were recognized by Opsahl and Benner (1995) to be more prompt to degradation. It should be noted that despite their decrease with depth, C/V ratios always remain significantly higher in non-forested soils than in forest soils.

SOM found in deeper horizons is normally more degraded than that found in surface litter. However, in agreement with Farella *et al.* (2001)'s study, we did not observe any statistical correlation between higher values of specific lignin degradation indicators (i.e., P/(V+S), (Ad/Al)<sub>v</sub> and 3,5-Bd/V, Fig. 4) and lower C/V ratios in forest soils (Fig. 3). This suggests that the low C/V ratios found in primary forest soils and fallow forest soils are not directly caused by SOM degradation. Low C/V ratios observed in forest soil therefore seem to be related to low C/V ratios in the forest vegetation growing on them.

Lignin indicators in stems are distinctly different from those in other parts of non-woody vegetation. Stems contain more syringaldehydes than vanillyls, resulting in fairly high S/V ratios (Table 2). According to Hedges and Mann (1979), high S/V ratios normally indicate a dominance of angiosperms in comparison to gymnosperms. Because gymnosperms are uncommon in the Amazon (Hedges *et al.* 1986), it seems relevant to explain the significance of higher or lower values of S/V ratios within the angiosperm family. The stems that we analyzed came from banana and cassava, plants most frequently cultivated in the study area as well as from the stipe of *Attalea speciosa* palm trees. Although many palm trees species grow in the primary rainforest, *Attalea speciosa* palm trees constitute a dominant species in fallow forests and represent an invasive species in the pastures of the study region (Anderson *et al.* 1991, Gonçalves 2010). High S/V ratios in the vegetation of non-forested areas then result in high S/V ratios in non-forested soils ( $p < 0.0001$ ), with the highest values found in pasture soils. Hernes *et al.* (2007) reported that S/V ratios could increase as much as two fold through sorption and leaching of SOM. But our results show no significant increase of S/V ratios with soil depth (Fig. 3), nor between plants and soils on which they grow. It thus appears that along with C/V ratios, S/V ratios can be used to discriminate forests and non-forested areas, for both plant and soil samples and despite the pedogenetic processes transforming the original plant organic matter to SOM.

As noted by Guggenberger *et al.* (1994) in temperate soils, SOM in Amazonian forest soils is characterized by (Ad/Al)<sub>v</sub> ratios higher than those measured in non-forested areas (Table 2). Hedges *et al.* (1988) presented an inversely proportional relationship between TOM degradation proxies ((Ad/Al)<sub>v</sub>, P/(V+S)) and S/V ratios. As far as SOM degradation goes, S/V ratios were expected to decrease while (Ad/Al)<sub>v</sub> ratios would increase due to the effects of fungal degradation (Hedges *et al.* 1988). However, we did not observe this correlation in our study ( $r^2 = 0.012$ ) and (Ad/Al)<sub>v</sub> ratios were higher in wood and stems than in non-woody vegetation (Table 2). While stems may be found in vegetation growing in forest and in non-forested areas, wood is restricted to trees in older fallow forests and primary rainforests. Moreover, vanillyls levels are much higher in fresh and dead plant parts of forest environments than those of non-forested areas (Table 2). Then, in forest soils of the Amazon, high (Ad/Al)<sub>v</sub> ratios seem to be related to wood and stems inputs rather than to advanced SOM degradation. This is consistent with the fact that other degradation biomarkers (P/(V+S) and 3,5-Bd/v) do not show significant differences between land-use/land-covers types. Our findings corroborate Hernes *et al.* (2007) questioning the use of the (Ad/Al)<sub>v</sub> ratio as a proxy of SOM degradation without any further considerations. Then, the increase of (Ad/Al)<sub>v</sub> ratios for forest and deforested environments from plants to soil samples (Tables 2 and 3) could rather be due to leaching and sorption processes. However, as the same phenomenon is observed for forest and deforested environments, forest plant and soils still present significantly higher (Ad/Al)<sub>v</sub> ratios.

Benner *et al.* (1990) have shown a rapid increase of P/(V+S) and (Ad/Al)<sub>v</sub> ratios, known as TOM degradation proxies, for fresh plant material collected in red mangroves (*Rhizophora mangle*) in the Bahamas when incorporated in sediments. Their laboratory degradation tests resulted in atypical lignin values with abnormally high (Ad/Al)<sub>v</sub> ratios for fresh material (0.4 average). The researchers then cautioned against using the (Ad/Al)<sub>v</sub> ratio as an “infallible” degradation indicator in plant covers dominated by mangroves. As a matter of fact, similarly high (Ad/Al)<sub>v</sub> ratios were found in fresh wood (0.54), stems (1.67) and forest soils (0.73) in the present study (Tables 2 and 3).

#### 4.2 Unique lignin signatures of *Attalea speciosa* palm trees

Two lignin indicators ((Ad/Al)<sub>v</sub> and P/(V+S)) allow to distinguish *Attalea speciosa* palm trees from all other plant samples, both in terms of plant parts and land-use/land-cover. Both indicators are commonly used to determine degradation levels but are found at high levels in fresh palm tree samples. For the first indicator, (Ad/Al)<sub>v</sub> ratios are significantly higher ( $p = 0.025$ ) in palm trees (0.83) than in fallow forest vegetation (0.39), primary rainforest vegetation (0.33), pasture grass (0.23) and agriculture plants (0.22) (Table 2 and Fig. 2(b)). But (Ad/Al)<sub>v</sub> ratios by themselves do not constitute a unique distinctive signature for *Attalea speciosa* palm trees, probably because there are differences between the different plant parts (Table 2). Indeed, palm stems have (Ad/Al)<sub>v</sub> levels that are significantly higher than those of all other samples, but fresh and dead palm leaves are comparable to those of other plants found in pastures and fallow forests (Table 2). For the second indicator, P/(V+S) ratios are markedly higher in fresh *Attalea speciosa* palm trees samples than in any other plant samples from the various land-use/land-cover categories (Table 2). These high P/(V+S) ratios (average of 0.85 to 1.60; Table 2) derive from tremendous levels of *p*-hydroxyphenols in fresh palm tree samples (average of 5.26 to 10.10 mg/100 g of OC; Table 2). Hedges *et al.* (1986) already reported extremely high P/(V+S) ratios in several plant species (1.5 to 6.9) however contrary to palm trees, corresponding (Ad/Al)<sub>v</sub> values were low (0.15 to 0.24). Since

vascular plant represent a significant input of plant OM to soils (Otto and Simpson 2006, Thevenot *et al.* 2010), the intense regrowth of *Attalea speciosa* palm trees in fallow forests and pastures in the Amazon following rainforest clearing (Anderson *et al.* 1991, Gonçalves 2010) could translate into higher P/(V+S) ratios in soils. Then, high (Ad/Al)<sub>v</sub> and P/(V+S) ratios in soil could be induced by important contributions of palm trees to the SOM pool rather than to high degradation state of lignin in soils.

## 5. Conclusions

This study has shown that lignin biomarkers and lignin proxies in tropical environments cannot readily be interpreted using reference values commonly used for temperate environments for decades. The new tropical lignin data set established for dominant plant species and typical soils of the Tapajos region proved to be a powerful tool to distinguish the TOM nature of forest environments ranging from primary rainforest to fallow forest from that of subsistence agriculture fields and pastures. The nature of SOM in tropical areas also appears to be strongly correlated to the vegetation growing on them rather than to plant organic matter degradation during pedological processes. In addition, *Attalea speciosa* palm trees, becoming an invasive species in fallow forests, pastures and subsistence agriculture fields, exhibited distinctive lignin signatures that can serve as tracers of these perturbed environments at the watershed level. Lignin biomarkers studies may thus be used to study the disruption of the terrestrial carbon cycle after massive deforestation of the tropical rainforest. They may also serve to evaluate the qualitative and quantitative shifts of TOM transfers from terrestrial environment towards aquatic systems in tropical environments.

## Acknowledgments

Special thanks to Sophie Chen for her invaluable analytical support. We also want to thank Pierre Taillardat, Armand Resneau and Bastien Jarzaguet for their help in the laboratory. For all the months working together in Brazil, thanks to Leandra Fatorelli, Deusilene Amaral, Stéphane Tremblay, Annie Béliveau, the community of Lago Araipa and Lago Bom Intento. Thanks to Jordan S. Oestreicher for manuscript revision. This work was carried out with support from the Global Health Research Initiative (GHRI), a collaborative research funding partnership of the Canadian Institutes of Health Research, the Canadian International Development Agency, Health Canada, the International Development Research Centre, and the Public Health Agency of Canada. The sponsor was not involved in any aspect of the research nor in the interpretation of the scientific data.

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