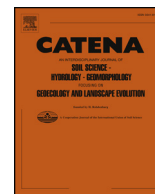




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## Organic matter composition and paleoclimatic changes in tropical mountain peatlands currently under grasslands and forest clusters

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### ABSTRACT

Tropical peatlands are important ecosystems for Planet Earth, as they store large amounts of carbon and water. A better understanding of the impact of vegetation type and altitude in content, composition, and rate of accumulation of organic matter is key for assessing the current role of such environments. This study evaluated fibric and soluble fractions as well as the lignocellulosic and the isotopic compositions of the peat organic matter from four tropical mountain peatlands located at different altitudes of the Serra do Espinhaço Meridional, state of Minas Gerais, Brazil. The peatlands are currently under grasslands and forest clusters. Samples of peat under both vegetation types were collected and analyzed for organic matter fractions, cellulose, and lignin (van Soest method), as well as carbon and nitrogen isotopes. Different depths were chosen for radiocarbon dating of selected samples. The organic matter of peatlands currently under grasslands and forest clusters presented differences in soluble fractions, lignocellulosic composition, and  $\delta^{13}\text{C}$  values. Multivariate analyses allowed grouping the peatlands by altitude and vegetation type. The chronological succession of grassland and forest clusters in tropical mountain peatlands was influenced by altitude and was related to paleoclimatic changes.

### 1. Introduction

Peatlands are transitional environments between terrestrial and aquatic ecosystems that provide essential functions for hydrology, ecology, and biogeochemistry (Rezanezhad et al., 2016). These ecosystems are formed from plant remains in places saturated with water and subjected to accumulation of organic matter of dead plant material under conditions of low pH and oxygen scarcity, resulting in slow humification and mineralization (M.L. Silva et al., 2013).

Peatlands play an important role in global water and carbon cycles, storing approximately 10% of all water and approximately 30% of the organic carbon found in soils (Rudiyanto et al., 2015; Rezanezhad et al., 2016).

Peat organic matter is derived from plant tissues composed mainly of lignin, cellulose, and hemicellulose, which together may constitute up to 85% of the dry biomass of tree species (Canellas and Santos, 2005). Lignin represents 14 to 30% of the dry biomass of herbaceous matter (Moreira et al., 2006) and 16 to 24% of the dry biomass of tree

species (Klock et al., 2005). Lignin is a significant component of peat organic matter due to slow decomposition rates under anoxic conditions (Williams and Yavitt, 2003). The vegetation type is known to influence the content and composition of lignin and polysaccharides of peat (Schellekens et al., 2012, 2015a). Chronological succession of vegetation type in peatlands may leave signs in the chemical composition of peat.

Plants discriminate carbon differently due to their photosynthetic pathways ( $\text{C}_3$ ,  $\text{C}_4$ , and CAM), with  $\text{C}_3$  species (trees and shrubs) discriminating more  $^{13}\text{C}$  ( $\sim -27\%$ ) than  $\text{C}_4$  species ( $\sim -13\%$ ) (Tippie and Pagani, 2007). The  $\delta^{13}\text{C}$  values in peat organic matter can thus be used to identify the photosynthetic pathway of the plants that colonized the site. The removal of compounds that have more or less heavy isotopes than the mean value of the plant tissue alters isotopic signatures during decomposition of peat organic matter. Additionally, the admixture of microbial organic matter in peat organic matter, which generally has a higher content of the heavy isotopes, leads to higher  $\delta^{13}\text{C}$  contents (Buurman et al., 2004).

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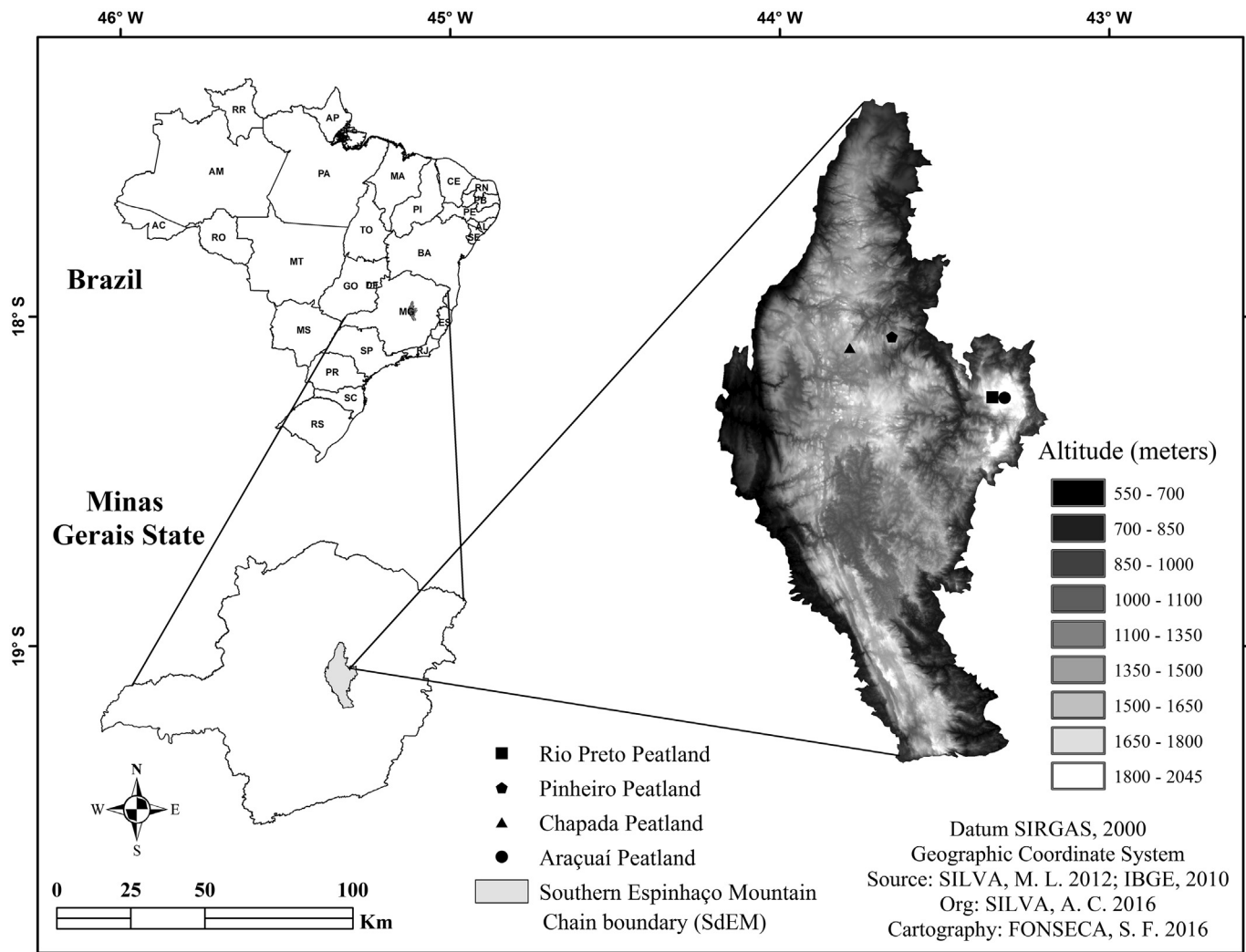


Fig. 1. Geographical location of the four peatlands, situated in the SdEM, state of Minas Gerais, Brazil.

The  $^{15}\text{N}$  content is an indicator of changes in the use of nitrate, denitrification, and  $\text{N}_2$  fixation, which in turn allows to distinguish the origin of peat organic matter (Lehmann et al., 2002). Atmospheric  $\text{N}_2$  fixing plants have slightly lower  $^{15}\text{N}$  values than non-fixing plants. Microbial processing of organic matter may lead to selective preservation of  $^{15}\text{N}$  (Evans, 2007). Enriched  $\delta^{15}\text{N}$  values in peat organic matter are indicative of algae ( $\sim +6.0\text{‰}$ ), whereas depleted values ( $\sim +0.5\text{‰}$ ) indicate terrestrial plants (Peterson and Howard, 1987).

In Brazil, peatlands occupy approximately 0.07% of the territory (Valladares et al., 2008). The Serra do Espinhaço Meridional (SdEM), located in the state of Minas Gerais, Brazil, is one of the few mountainous regions where peatlands have been formed at an altitude between 1200 m and 2000 m since the Pleistocene (Horák-Terra et al., 2014). They occupy  $> 14,000$  ha and hold approximately 142 million  $\text{m}^3$  of water and approximately 3.6 million tons of carbon (M.L. Silva et al., 2013). These tropical peats are distinguished from northern peatlands by the absence of sphagnum acid (Schellekens et al., 2015b). The SdEM separates the Atlantic Forest biome from the Cerrado biome (Ribeiro et al., 2009; Santos et al., 2011). Little is known about the influence of the Atlantic Forest and Cerrado biomes on peatland vegetation cover. Recent studies have shown that forest clusters in the east and west of the SdEM present a different floristic composition that may be related to altitude, climate, and soil (Santos et al., 2011). The microclimate is directly influenced by altitude, with a decreasing temperature of approximately  $1^\circ\text{C}/100$  m, caused by a decrease in air

density, an increasing cloudiness, and greater wind exposure (Dury, 1972; Ometto, 1981). According to the Nernst equation the increase in temperature favors oxidation and, of course, the decay of the peat organic matter.

The peatlands of SdEM are found at different altitudes colonized by herbaceous, and shrub species (grasslands - C3 and C4 photosynthetic pathways), as well as tree species (forest clusters - C3 photosynthetic pathways) (Campos et al., 2012; Horák et al., 2011). Grassland and forest clusters vary in the species composition, phytomass production, and lignocellulosic composition of the plant material (V.E. Silva et al., 2013). This work aimed at evaluating the chemical and isotopic composition of the peat organic matter of four tropical mountain peatlands of different altitudes, situated in SdEM, currently under grasslands and forest clusters.

Our hypotheses for this study are: a) altitude influences the floristic composition of grassland and forest clusters; b) vegetation type and altitude impact the content and the composition of peat organic matter; c) paleoclimatic changes promoted a chronological succession of grassland and forest clusters in peatlands.

## 2. Material and methods

### 2.1. Study area

The study area is located in the SdEM (state of Minas Gerais, Brazil),

in which quartzite rocks predominate, with altitudes varying from 1000 m and 2000 m. The relief is extremely mountainous and steep in the valleys and flat to softly undulating on the flat surfaces. The climate is C'wb (mesothermal), according to the Köppen classification; a rainy season occurs from November to March (monthly average precipitation of 223 mm) and a dry season lasts from May to September (monthly average precipitation of 8 mm). The seasons are well defined, and the average annual temperature is 18.7 °C (E.V. Silva et al., 2013). At 1600 m of altitude, the average annual temperature is 16.2 °C (Costa, 2018).

The studied peatlands are located in the depressions of plane surfaces and are currently under two vegetation types that are found at altitudes above 1000 m, on the Diamantina Plateau (Mendonça Filho, 2005): grasslands and forest clusters. The grasslands are composed predominantly by herbaceous plants, with species adapted to poor drainage conditions and dominated by families such as Cyperaceae, Eriocaulaceae, Poaceae, and Xyridaceae (Munhoz and Felfili, 2008; Ribeiro et al., 2009). The forest clusters are “islands” of semi-deciduous, high-mountain, seasonal forests (Veloso et al., 1991) surrounded by grasslands and exhibiting different but mainly circular shapes (Meguro et al., 1996a; Horák et al., 2011; Santos et al., 2011), whose local name is Capões.

The four peatlands studied are located in: A) Chapada (LCH): 18°3'46.4" and 18°3'37.3" S and 43°39'41.4" and 43°39'29.8" WGR; B) Pinheiro (LPN): 18°16'22" and 18°15'17" S and 43°41'10" and 43°39'15" WGR; C) Rio Preto (HRP): 18°14'7.02" and 18°14'3.63" S and 43°19'10.86" and 43°19'7.66" WGR; D) Araçuaí (HAR): 18°14'30.18" and 18°14'26.4" S and 43°18'37.58" and 43°18'33.94" WGR. The peatlands LCH and LPN are located, respectively, at 1320 and 1240 m of altitude (lower altitudes). The peatlands HRP and HAR are located, respectively, at 1598 and 1593 m of altitude (higher altitudes) (Fig. 1).

## 2.2. Collection of the botanical material

An inventory of plant species was performed in all four SdEM peatlands investigated. The collections were made in March 2012 (LCH and LPN) and July 2012 (LRP and LAR), periods with higher number of species with flower buds at each altitude. The collected material was georeferenced and the samples received the traditional treatment used in floristic surveys: pressing, drying in an electric dryer, and storage as exsiccata. The collected specimens were deposited in the Herbarium of Universidade Federal dos Vales do Jequitinhonha e Mucuri (Herbário DIAM), Diamantina, Minas Gerais, Brazil.

## 2.3. Peat sampling

A vibracore was used to collect two cores in each peatland (under grasslands and forest clusters). The cores were opened in the laboratory and samples were taken every 15 cm down to the depths of: 200 cm (grasslands) or 215 cm (forest clusters), for peatland HRP; 150 cm (grasslands) or 225 cm (forest clusters), for HAR; 105 cm (grasslands) or 135 cm (forest clusters) for LCH; 150 cm (grasslands) or 90 cm (forest clusters) for LPN. The collection, sampling and transport of the material followed the methodology described by Horák et al. (2011). Data from samples collected down to 90 cm, which corresponds to the depth of the shallowest peat, were used for the analysis of variance.

## 2.4. Determination of fibric and soluble fractions and lignocellulosic composition

The samples were first air-dried and passed through 2-mm sieves, and then placed in an oven with air circulating at a temperature of 50 °C, for 12 h. Fractionation of soil organic matter followed the procedure described by Canellas and Santos (2005), with fractions being classified as soluble (i.e., fulvic acids - FA, first extracted with base and then with acid; and, humic acids - HA, dissolved in base and then

precipitated with acid), and insoluble (fibric fraction - FF).

To isolate lignin and cellulose from the samples, a solution of acid detergent (van Soest, 1994) was first used to obtain cellulose, lignin, and insoluble ash residue (acid detergent fibre - ADF). To determine the contents of lignin and cellulose, two sub-samples of ADF were next separated; in the first one, lignin was oxidized with a solution of acetic acid and potassium permanganate, leaving cellulose and insoluble ash as a residue, while in the second sample, cellulose was oxidized by sulfuric acid to leave lignin and other non-oxidized materials and insoluble ash as a residue. The cellulose and lignin (cellulose and lignin van Soest method) contents were determined after heating the ADF subsamples in a muffle furnace at 500 °C for 3 h.

## 2.5. Determination of C and N isotopes

For determination of isotopic compositions, the samples were oven-dried at 40 °C, homogenized in an agate mortar, and weighed in tin capsules. Approximately 3.5 mg of each sample was used to determine the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in a mass spectrometer (Groning and Groot, 2004).

For radiocarbon dating, three samples (2-cm layers) were collected at different depths of each peatland, according to the morphological attributes and the organic carbon content of the layer. One additional sample was collected in PN under the forest cluster. After sampling, the decomposed organic matter was removed by dissolution in base and then in acid. Next, the samples were washed with distilled water and the residue (FF) was sent for dating. The radiocarbon ages of the samples were determined in the  $^{14}\text{C}$  Laboratory of CENA/USP, São Paulo, Brazil, according to a method proposed by Pessenda et al. (1983) and Stuiver et al. (2017).

## 2.6. Statistical analysis

To test the hypothesis that vegetation type and altitude influences the content and composition of peat organic matter and that paleoclimatic changes promoted a chronological succession of grassland and forest clusters, peatland (LRP, LAR, LCH, and LPN), vegetation type (grasslands and forest clusters), and depth (down to 90 cm, which corresponds to the depth of the shallowest peat) were the factors considered for analyzes. The evaluated variables were the contents of FA, HA, FF, “van Soest lignin” and “van Soest cellulose”, as well as the composition of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  and the C/N ratio. The effects of these factors on each of the variables evaluated were tested by the F test using the following model:  $y_{ijk} = m + t_i + f_j + t_{ij} + p_k + e_{ijk}$ , where  $t_i$  refers to the effect of peatland  $i$  with four levels;  $f_j$  refers to the effect of vegetation type  $j$ , with two levels;  $t_{ij}$  refers to the effect of the interaction between these two factors;  $p_k$  refers to the effect of depth  $k$ , with six levels; and  $e_{ijk}$  refers to the residue, following a cross-classification. The averages of each variable were compared using the Tukey test ( $p < 0.05$ ).

For a better understanding of how peatlands are grouped by vegetation type and altitude, multivariate clustering and stepwise discriminant analysis were performed. Since collinearity may negatively interfere with multivariate analyses (Hair et al., 2009), the redundant variables were eliminated, leaving only one of the highly correlated variables. Therefore, FF, “van Soest lignin”, “van Soest cellulose”,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  were included in multivariate clustering. FA and HA were eliminated, as they were highly correlated with FF. The multivariate clustering was used to elaborate a dendrogram based on dissimilarities using mean Euclidean distances and hierarchical grouping generated by the Ward method. The measurement of dissimilarities was made using the variables in their respective units of evaluation, that is, without any type of standardization. The Genes software was used for the analysis (Cruz, 2006).

The stepwise discriminant analysis was performed in all data to determine the most important variables to for differentiating the

peatlands. Thus, for each peatland, a discriminant function was generated (Johnson and Wichern, 1992):

$$f(G_i) = k_i + \sum_{j=1}^n w_{ij} p_{ij} \quad (1)$$

In this formula,  $i$  is the number of groups (grasslands),  $k_i$  is the inherent constant for each group,  $n$  is the number of parameters used to classify a sample into one of the groups,  $w_j$  is the weighted coefficient, defined by the stepwise discriminant analysis for a given parameter ( $p_j$ ). The spatial variation of the parameters analyzed in the peatlands was evaluated using the stepwise discriminant analysis method. Three discriminant functions ( $LD$ ) were generated among the four peatlands. The functions were considered statistically significant according to the Wilks lambda test.

Peatlands were considered the dependent variables, whereas the parameters measured were the independent variables. The relative contribution of each variable in the separation of groups was also evaluated. The discriminant analysis was performed with the R software.

### 3. Results

#### 3.1. Floristic composition of the grasslands and forest clusters

Forest clusters are sparsely distributed (3–17 in each peatland), with a circular shape 5 to 100 m in diameter (Fig. 2), occupying between 2.7 and 13.6% of the peatland (Table 1). M.L. Silva et al. (2013) mapped 19 isolates of forest clusters in 82 ha of peatland of the SdEM, occupying an area of 2.6 ha (3.2% of the total area). These authors identified four dominant species in forest clusters and 11 dominant species in grasslands. The number of dominant species ranged from 12 to 28 and from 6 to 10 for grasslands and forest clusters, respectively (Table 1), with nine (29%) from the grasslands and five (50%) from forest clusters common to all four peatlands.

Twenty-four families, 36 genera and 42 species were identified. Of these families, 15 families were found in grasslands, and five of these were common to all the peatlands: Cyperaceae, Eriocaulaceae, Iridaceae, Poaceae, and Xyridaceae. In forest clusters, 10 families were identified, of which five families and their respective species were common to all the peatlands studied. Nineteen of the 31 species found

**Table 1**

Number of forest clusters, area and number of dominant species in grassland (G) and forest clusters (F) in four peatlands of the SdEM.

Peatland	No of forest clusters	Area			Dominant species <sup>a</sup>	
		Total ha	F %	G %	F	G
LCH	3	9.8	6.1	93.9	6	12
LPN	6	44.9	13.6	86.4	6	12
HAR	16	80.3	2.7	97.3	10	28
HRP	17	20.8	3.8	96.2	10	28

<sup>a</sup> Identified in Table 2.

in grasslands and 5 of the 11 species found in forest clusters only occur in peatlands HAR and HRP, whereas 3 of the 31 species found in grasslands and 1 of the 11 species found in forest clusters only occur only in peatlands LCH and LPN (Table 2).

#### 3.2. Vegetation type, altitude, and content and composition of peat organic matter

##### 3.2.1. Vegetation type

The levels of FA, “van Soest lignin”, “van Soest cellulose”, and  $\delta^{13}\text{C}$  were higher in forest clusters (ANOVA,  $p = 0.046$ ,  $0.002$ ,  $0.000$  and  $0.000$ , respectively), whereas HA contents were higher in grasslands (ANOVA,  $p = 0.000$ ) and FF and  $\delta^{15}\text{N}$  contents exhibited no differences among the vegetation types (Table 3).

The levels of FF and “van Soest lignin” are higher on the surface in forest clusters and the levels of HA and  $\delta^{13}\text{C}$  are higher on the surface in grasslands. In the layer of 45 to 90 cm of depth, the levels of FF, FA, HA,  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , and C/N ratio of peat under grasslands and forest clusters tend to be similar (Figs. 3, 4, 5 and 6).

The mean, maximal and minimal values of  $\delta^{13}\text{C}$  were lower under forest clusters than under grasslands (Table 3 and Fig. 7). However, in the layer of 45 to 90 cm of depth these levels under grasslands and forest clusters were comparable (Fig. 5).

##### 3.2.2. Altitude

The LPN and LCH (lower altitudes, higher temperatures) peatlands

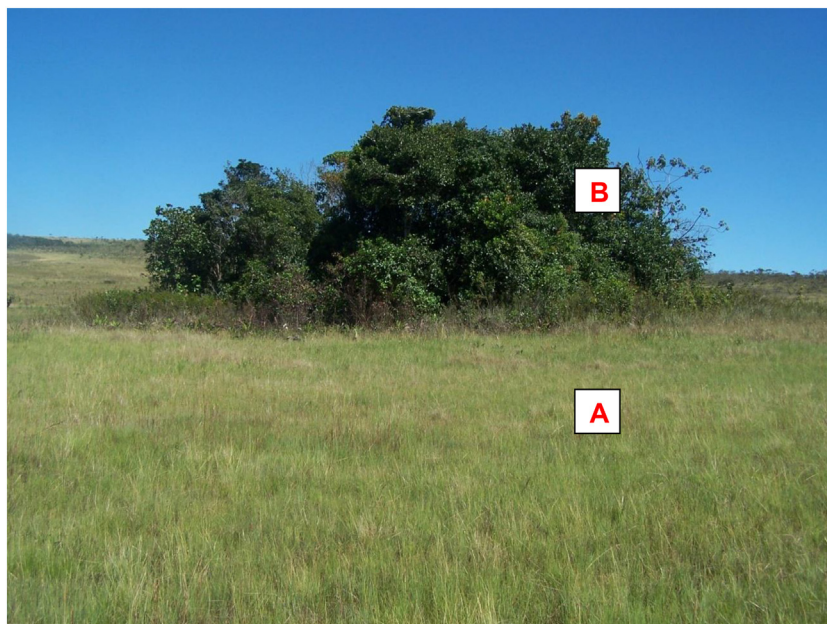


Fig. 2. Peatlands characteristic vegetation: A) grasslands (G) and B) forest clusters (F).

**Table 2**  
Predominant species in the grasslands (G) and forest clusters (F) that colonize four peatlands and their  $\delta^{13}\text{C}$ .

Family	Species	Vegetation types	Peatland				$\delta^{13}\text{C}^*$ ‰
			LCH	LPN	HAR	HRP	
Cyperaceae	<i>Lagenocarpus rigidus</i> Nees	G	x	x	x	x	27.60
Cyperaceae	<i>Lagenocarpus tenuifolius</i> Kuntze	G	x	x	x	x	26.85
Cyperaceae	<i>Rhynchospora speciosa</i> (Kunth) Boeckeler	G	x	x	x	x	26.01
Eriocaulaceae	<i>Leiothrix flavescens</i> (Bong) Ruhland	G	x	x	x	x	–
Eriocaulaceae	<i>Paepalanthus macrocephalus</i> (Bong) Körn	G	x	x	x	x	26.08
Xyridaceae	<i>Xyris</i> sp. 1	G	x	x	x	x	25.60
Iridaceae	<i>Trimezia juncifolia</i> (Klatt) Benth. & Hook	G	x	x	x	x	–
Poaceae	NI	G	x	x	x	x	–
Poaceae**	<i>Loudetiopsis chrysothrix</i> (Nees) Conert	G	x	x	x	x	13.37
Xyridaceae	<i>Abolboda pulchella</i> Humb.	G	x	x	–	–	–
Eriocaulaceae	<i>Paepalanthus</i> sp. 2	G	x	x	–	–	27.66
Xyridaceae	<i>Xyris</i> sp. 2	G	x	x	–	–	27.88
Araceae	<i>Philodendron uliginosum</i> Mayo	G	–	–	x	x	25.62
Asteraceae	<i>Achyrocline satureioides</i> (Lam.) DC.	G	–	–	x	x	–
Asteraceae	<i>Baccharis trimera</i> (Less.) DC.	G	–	–	x	x	28.75
Asteraceae	<i>Trixis nobilis</i> (Vell.) Katinas	G	–	–	x	x	–
Ericaceae	<i>Gaylussacia brasiliensis</i> (Spreng) Mart.	G	–	–	x	x	26.01
Eriocaulaceae	<i>Comanthera xeranthemoides</i> (Bong) L.R.Parra & Giul.	G	–	–	x	x	–
Eriocaulaceae	<i>Syngonanthus</i> sp.	G	–	–	x	x	–
Eriocaulaceae	<i>Syngonanthus elegans</i> (Bong.) Ruhland	G	–	–	x	x	–
Eriocaulaceae	<i>Syngonanthus nitens</i> Ruhland	G	–	–	x	x	–
Euphorbiaceae	<i>Croton campestris</i> A.St.-Hil	G	–	–	x	x	–
Fabaceae	<i>Chamaecrista distichoclada</i> (Benth.) H.S.Irwin & Barneby	G	–	–	x	x	–
Fabaceae	<i>Crotalaria flavicoma</i> Benth.	G	–	–	x	x	–
Lythraceae	<i>Cuphea micrantha</i> Kunth	G	–	–	x	x	–
Melastomataceae	<i>Microlizia glandulifera</i> Cogn.	G	–	–	x	x	–
Melastomataceae	<i>Lavoisiera imbricata</i> (Thunb.) DC.	G	–	–	x	x	–
Poaceae	<i>Chusquea pinifolia</i> (Nees) Nees	G	–	–	x	x	–
Polygalaceae	<i>Polygala celosioides</i> Mart. Ex A.W.Benn.	G	–	–	x	x	–
Rubiaceae	<i>Galianthe</i> sp.	G	–	–	x	x	–
Verbenaceae	<i>Stachytarpheta reticulata</i> Mart. ex Schauer	G	–	–	x	x	–
Anacardiaceae	<i>Tapirira guianensis</i> Aubl.	F	x	x	x	x	–
Araliaceae	<i>Schefflera calva</i> (Cham.) Frodin & Fiaschi	F	x	x	x	x	–
Burseraceae	<i>Protium heptaphyllum</i> Marchand	F	x	x	x	x	29.39
Calophyllaceae	<i>Calophyllum brasiliense</i> Cambess	F	x	x	x	x	30.85
Melastomataceae	<i>Tibouchina</i> sp.	F	x	x	x	x	29.30
Chloranthaceae	<i>Hedyosmum brasiliense</i> Mart.	F	x	x	–	–	–
Lauraceae	<i>Nectandra</i> sp.	F	–	–	x	x	–
Lauraceae	<i>Ocotea</i> sp.	F	–	–	x	x	–
Myrtaceae	<i>Myrcia splendens</i> (Sw.) DC.	F	–	–	x	x	–
Rubiaceae	<i>Rudgea sessilis</i> (Vell.) Müll. Arg.	F	–	–	x	x	–
Sapindaceae	<i>Matayba</i> sp.	F	–	–	x	x	–

NI: unidentified; \*: M.L. Silva et al. (2013); x: present; \*\*: photosynthetic cycle C4.

**Table 3**

Average values and standard deviation (SD) of FA, HA, FF, “van Soest lignin”, “van Soest cellulose”,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in four peatlands of the SdEM currently under grasslands (G) and forest clusters (F).

Vegetation types	FA	HA	FF	Lig	Cel	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
	% of POM					‰	
G	11.6b (3.1)*	14.0a (3.1)	74.4a (5.3)	16.2b (5.4)	17.4b (5.9)	–20.9b (1.4)	4.0a (1.7)
F	13.1a (5.9)	10.8b (1.9)	76.2a (6.7)	22.2a (6.4)	22.3a (6.1)	–23.4a (1.8)	4.6a (1.5)

POM: peat organic matter; \*: SD. Means followed by the same letter in the columns did not differ by Tukey's test ( $p < 0.05$ ). Number of observations (n) = 24.

had higher mean levels of FA (ANOVA,  $p = 0.000$ ), lower FF and “van Soest cellulose” (ANOVA,  $p = 0.000$  and  $0.000$ , respectively) and higher values of  $\delta^{13}\text{C}$  (ANOVA,  $p = 0.000$ ). The contents of HA and “van Soest lignin” as well as the  $\delta^{15}\text{N}$  values did not differ among peatlands (Table 4).

In peat under grasslands of higher altitudes, the levels of FA and HA (peatland LRP), and “van Soest lignin” (peatland LAR) tend to increase

with depth. Opposite trends are found in peat under grasslands of lower altitudes (LPN and LCH). In peat under forest clusters of higher altitudes (LRP and LAR), the levels of FA and “van Soest cellulose” tend to increase with depth and the levels of “van Soest lignin” tend to decrease with depth. Opposing trends are found in peat under forest clusters of lower altitudes (LPN and LCH).

The mean levels of FA (soluble) are higher and the mean levels of FF are lower in peats of lower altitudes (LPN and LCH - older) (Table 4).

The C/N ratio increases with depth (ANOVA,  $p = 0.000$ ). In the layer of 45 to 90 cm of depth, the levels of  $\delta^{13}\text{C}$  and C/N ratio under grasslands and forest clusters in all peatlands tend to be comparable (Figs. 3 and 5).

### 3.3. Grouping of peatlands by vegetation type and altitude

The dendrogram (Fig. 8) illustrates the formation of the two main blocks separating the peatlands LRP and LAR (higher altitudes) and LPN and LCH (lower altitudes). Differences were also observed between the variables in grasslands and forest clusters, but this difference is smaller than that verified between the higher (LRP and LAR) and lower peatlands (LPN and LCH).

The data analysis of the variables at all depths under the two vegetation types, considering the first two discriminant functions (LD1

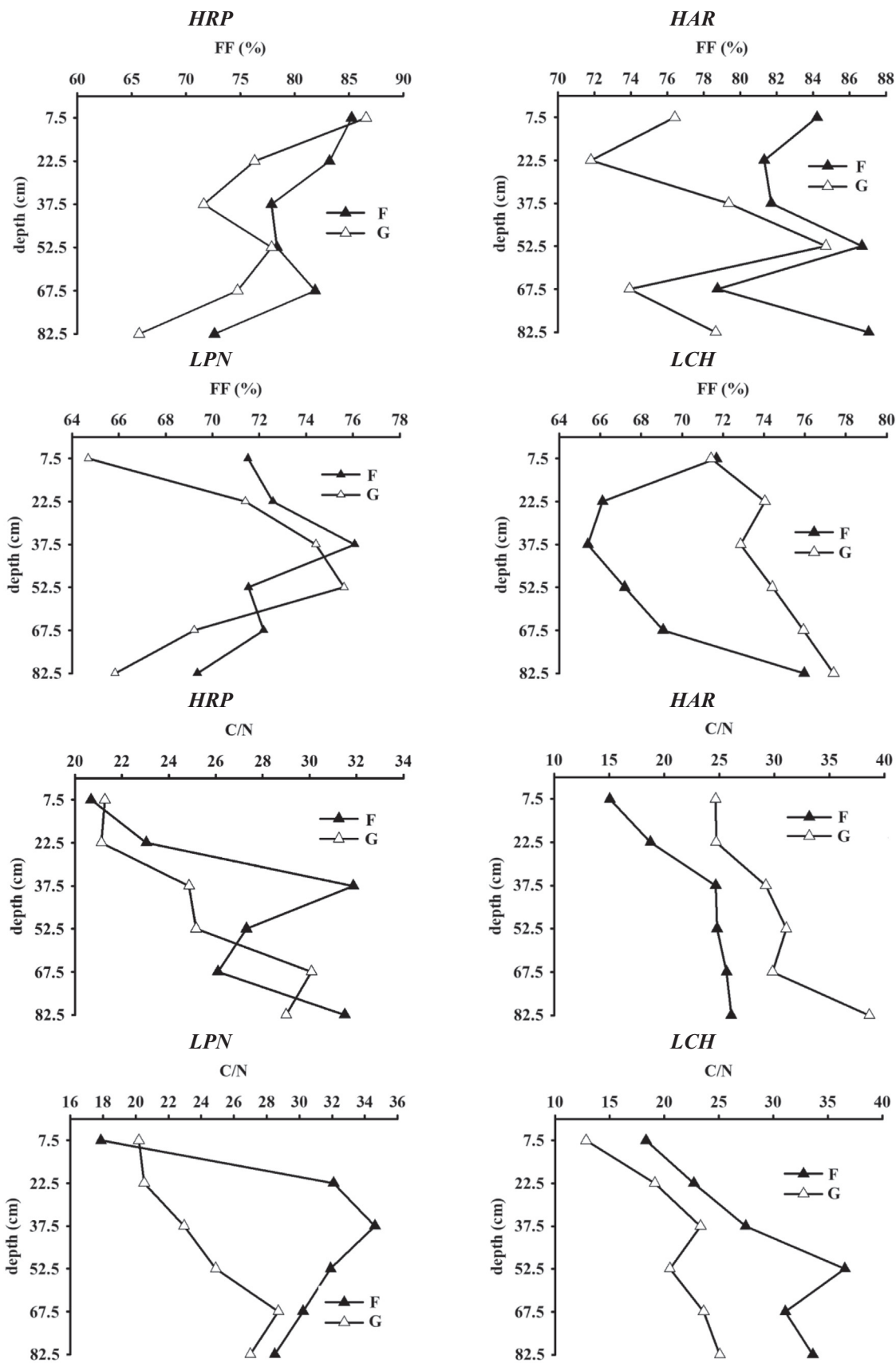


Fig. 3. Values of FF and C/N ratio with respect to depth in LPN, LCH, HRP, and HAR peatlands, under grassland (G) and forest clusters (F).

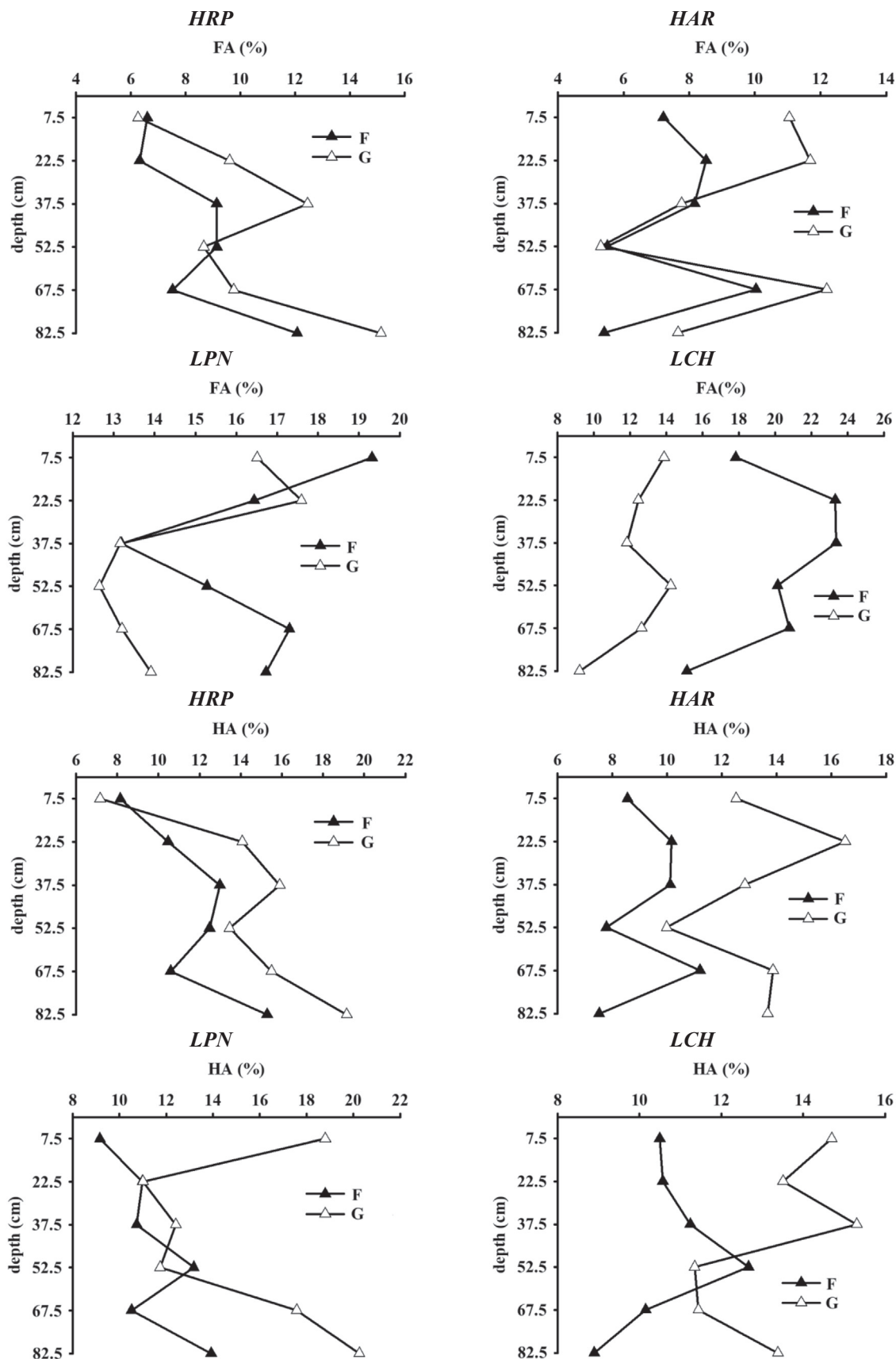


Fig. 4. Values of FA and HA with respect to depth in LPN, LCH, HRP, and HAR peatlands, under grassland (G) and forest clusters (F).

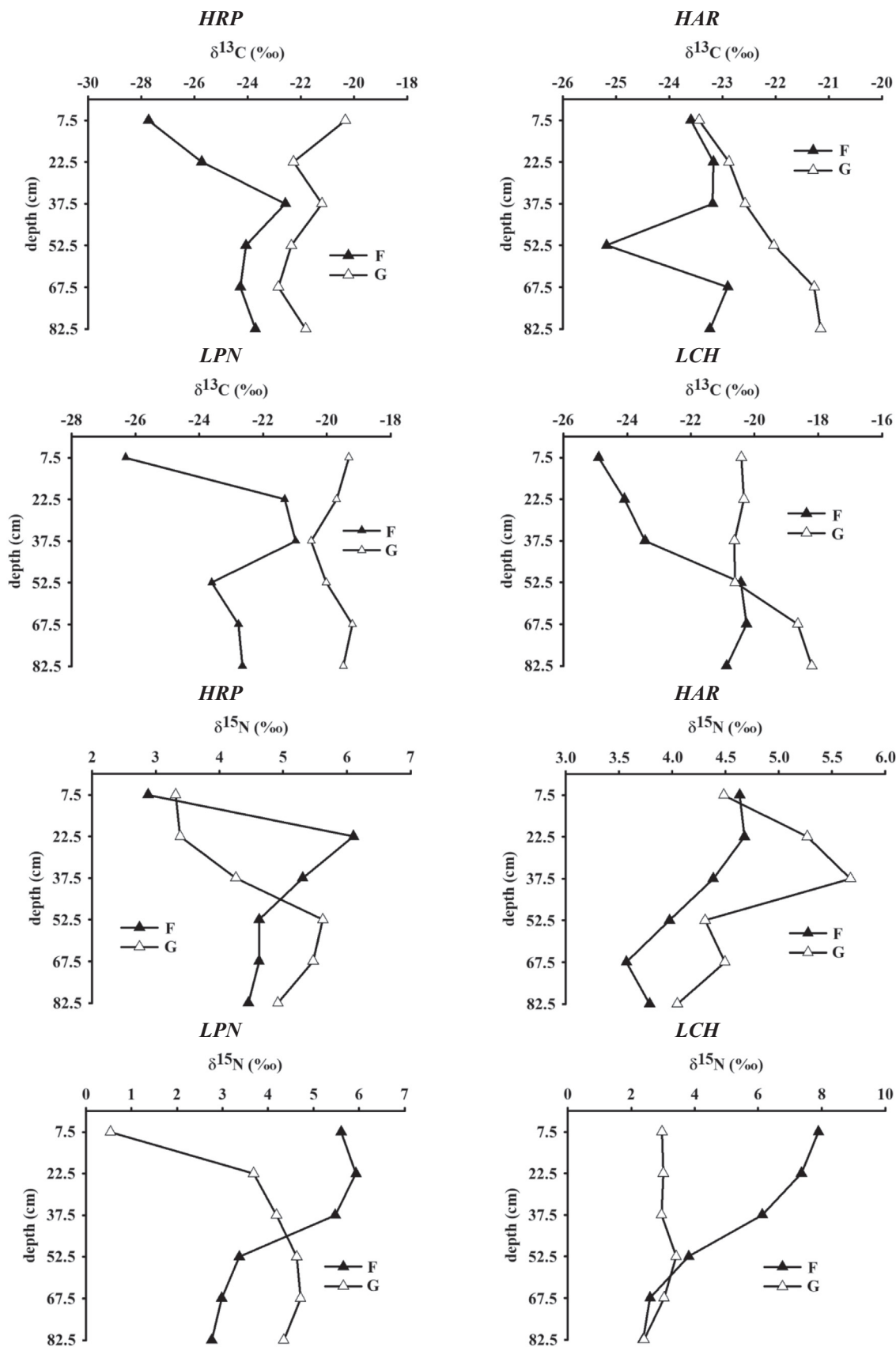


Fig. 5. Values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  with respect to depth in LPN, LCH, HRP, and HAR peatlands, under grassland (G) and forest clusters (F).



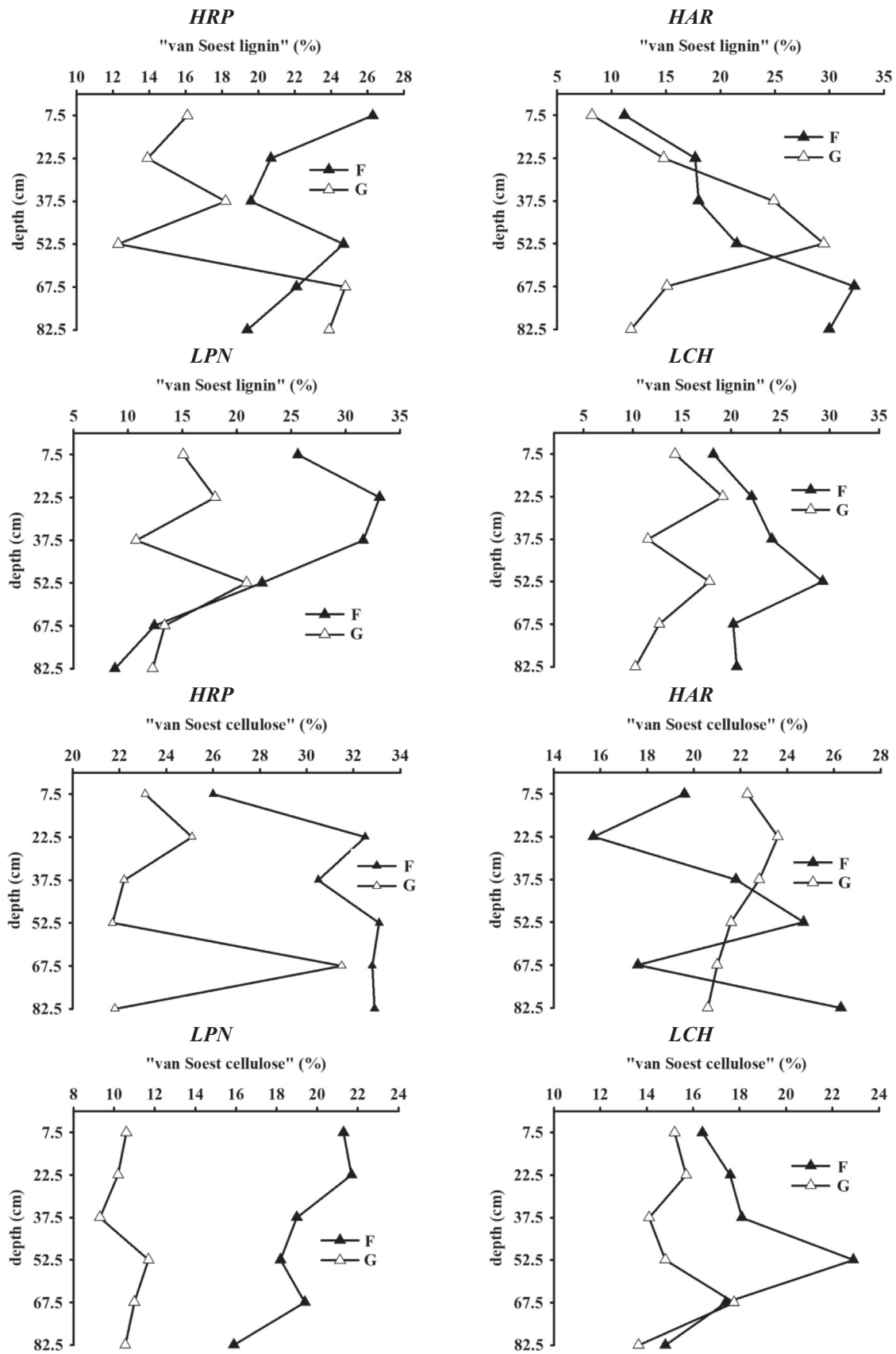


Fig. 6. Values of “van Soest lignin” and “van Soest cellulose” with respect to depth in LPN, LCH, HRP, and HAR peatlands, under grassland (G) and forest clusters (F).

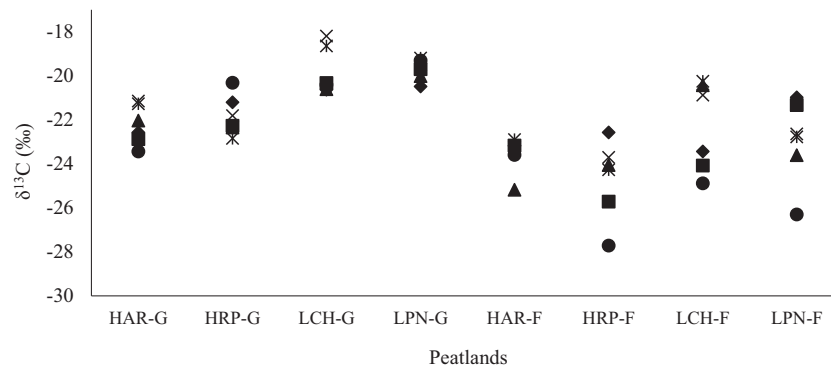


Fig. 7. Values of  $\delta^{13}\text{C}$  in peat organic matter in LPN, LCH, HRP, and HAR peatlands, under grassland (G) and forest clusters (F).

Table 4

Average contents and standard deviation (SD) of FA, HA, FF, “van Soest lignin”, “van Soest cellulose” and mean values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of four peatlands of the SdEM.

Peatland	FA	HA	FF	Lig	Cel	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
	% of POM					‰	
HAR	8.4b (2.4)*	11.2a (2.7)	80.4a (4.8)	19.6a (8.0)	21.5b (2.9)	-22.9a (1.1)	4.4a (0.6)
HRP	9.4b (2.7)	12.9a (3.4)	77.7a (6.0)	20.2a (4.4)	27.7a (4.9)	-23.2a (2.0)	4.6a (1.0)
LPN	15.4a (2.2)	13.4a (3.7)	71.2b (3.6)	18.7a (8.1)	14.9c (4.8)	-21.3b (2.1)	4.0a (1.5)
LCH	16.2a (4.7)	12.0a (1.9)	71.8b (4.0)	18.4a (5.6)	16.6c (2.6)	-21.1b (2.0)	4.0a (2.0)

POM: peat organic matter; \*: SD. Means followed by the same letter in the columns did not differ by Tukey's test ( $p < 0.05$ ).  $n = 12$ .

and LD2) shows a clear differentiation of peatlands by altitude. There is a greater proximity between samples of RP and AR peatlands, located at 1600 m in altitude, and between samples of PN and CH, located at an altitude of 1300 m (Fig. 9).

The larger number of exclusive dominant species in the higher peatlands (LAR and LRP - Tables 1 and 2) in grasslands and forest clusters areas and the composition of organic matter (variables AF, FF, “van Soest cellulose” and  $\delta^{13}\text{C}$  - ANOVA,  $p = 0,000$ ) show differences in the composition and stage of peat decomposition.

#### 4. Discussion

##### 4.1. Influence of altitude in the floristic composition of the peatlands

Almost all analyzed species present a  $\text{C}_3$  photosynthetic path, except for the two species of the Poaceae family, whose photosynthetic pathway is  $\text{C}_4$ . Occurrence of  $\text{C}_3$ - and  $\text{C}_4$ -cycle plants have been identified in tropical peatlands (Hillaire-Marcel et al., 1989; Aucour et al., 1994; Parolin et al., 2006) including those of SdEM (Campos et al., 2012; Horák et al., 2011; E.V. Silva et al., 2013; Horák-Terra et al., 2015). The  $\text{C}_4$  species occur in the grasslands alone and are commonly found, especially in peatlands at higher altitudes. V.E. Silva et al. (2013) evaluated the values of  $\delta^{13}\text{C}$  in plant species that colonized a

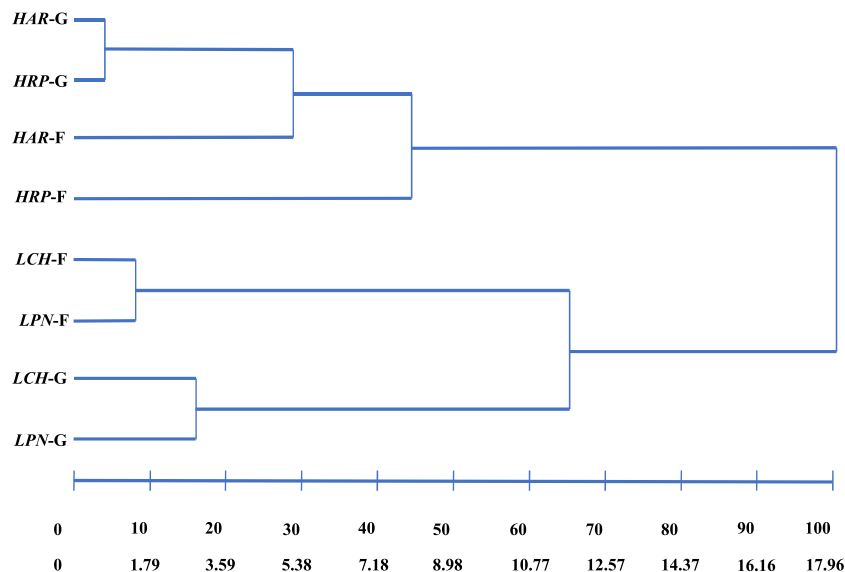


Fig. 8. Dendrogram of hierarchical cluster analysis concerning the locations and vegetation type of peatlands, in relation to FF, “van Soest lignin”, “van Soest cellulose”,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$ .

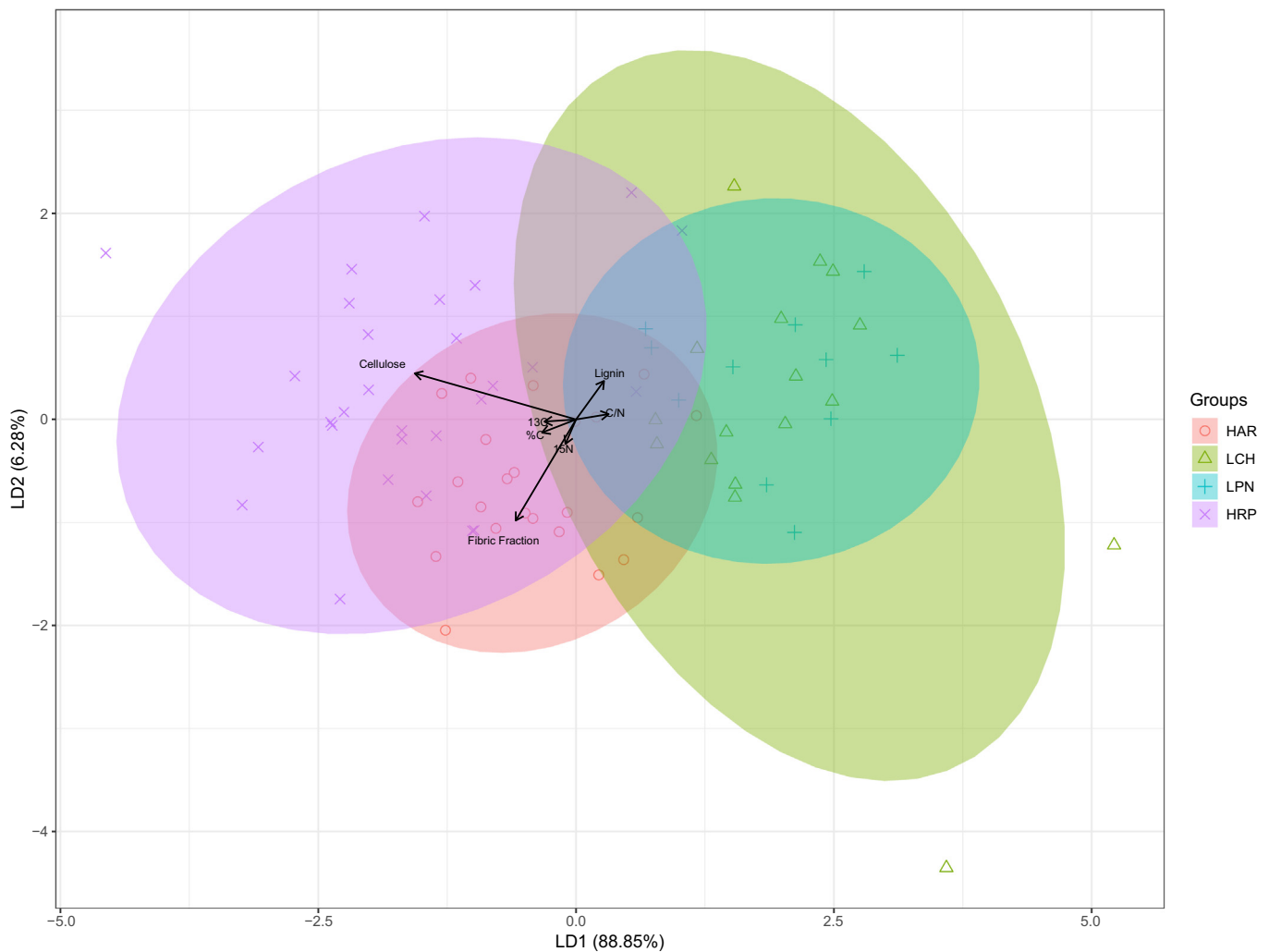


Fig. 9. Dispersion of the samples obtained in the four peatlands (LPN, LCH, HRP, HAR), considering the first two discriminant functions generated, with 95% confidence ellipses.

peatland of SdEM situated at 1370 m altitude and obtained an average value of  $-25.89\%$  for grasslands species and  $-29.91\%$  for forest clusters species.

The families Cyperaceae, Eriocaulaceae, Iridaceae, Poaceae, and Xyridaceae, common to all the peatlands (Table 2) are among the most important in wetlands of SdEM and Central Brazil (Munhoz and Felfili, 2008). The Eriocaulaceae and Xyridaceae are small and thin herbs that, according to Munhoz and Felfili (2008), cover small areas in the grassland compared to species that form dense clumps, such as the Poaceae. Among the Cyperaceae, *Lagenocarpus rigidus* was one of the most frequently occurring species. According to Munhoz and Felfili (2008), this species is restricted to areas with a shallow water table. Meguro et al. (1996a) observed that *Lagenocarpus* species, together with other herbaceous species of different families are common in more humid grasslands.

The species *Tapirira guianensis* and *Calophyllum brasiliense* also occur in forest clusters situated in the Serra do Cipó, and in the Gallery Forest and Seasonal Semi-deciduous Forest (Meguro et al., 1996a,b; Santos et al., 2011). *T. guianensis* is very important in the initial colonization of grassland areas along watercourses, because it competes with herbaceous species, and it is also found in the dense forest clusters. The species *Protium heptaphyllum* and *C. brasiliense* were also found in the SdEM (Meguro et al., 1996a), including forest clusters of peatlands (E.V. Silva et al., 2013). All of these species are adapted to stress conditions resulting from area flooding (Meguro et al., 1996a), thus are of extreme

importance for forest clusters formation in the peatlands.

Differences in floristic composition in the SdEM peatlands evaluated in this study were associated with altitude. LCH and LPN presented floristic composition different from LRP and LAR (Table 2).

#### 4.2. Influence of vegetation type and altitude on the content and composition of soil organic matter

##### 4.2.1. Vegetation type

The FA mean contents were higher in peat under forest clusters, whereas the HA mean contents were higher in peat under grasslands (Table 3). The FA contents of soils of Brazilian Forest Biomes (Amazonian Forest, Atlantic Forest, Caatinga and Cerrado) are higher than the HA contents and the inverse is observed in the Brazilian Grassland Biome (Pampa) and in pastures (Santos et al., 2013).

The higher “van Soest lignin” content in forest clusters (Table 3) can be explained by the dominance of woody species. The organic matter produced by tree species is predominantly lignified (Christensen et al., 2000; Moreira et al., 2006).

The mean values of  $\delta^{13}\text{C}$  were lower under forest clusters than under grasslands (Table 3), and they were similar to those found by E.V. Silva et al. (2013) in the SdEM peatland under forest cluster and under grasslands. The grasslands currently present species of the  $\text{C}_4$  photosynthetic pathway (Poaceae - Table 2), which discriminate less against  $\delta^{13}\text{C}$  than the  $\text{C}_3$  photosynthetic pathway species that currently

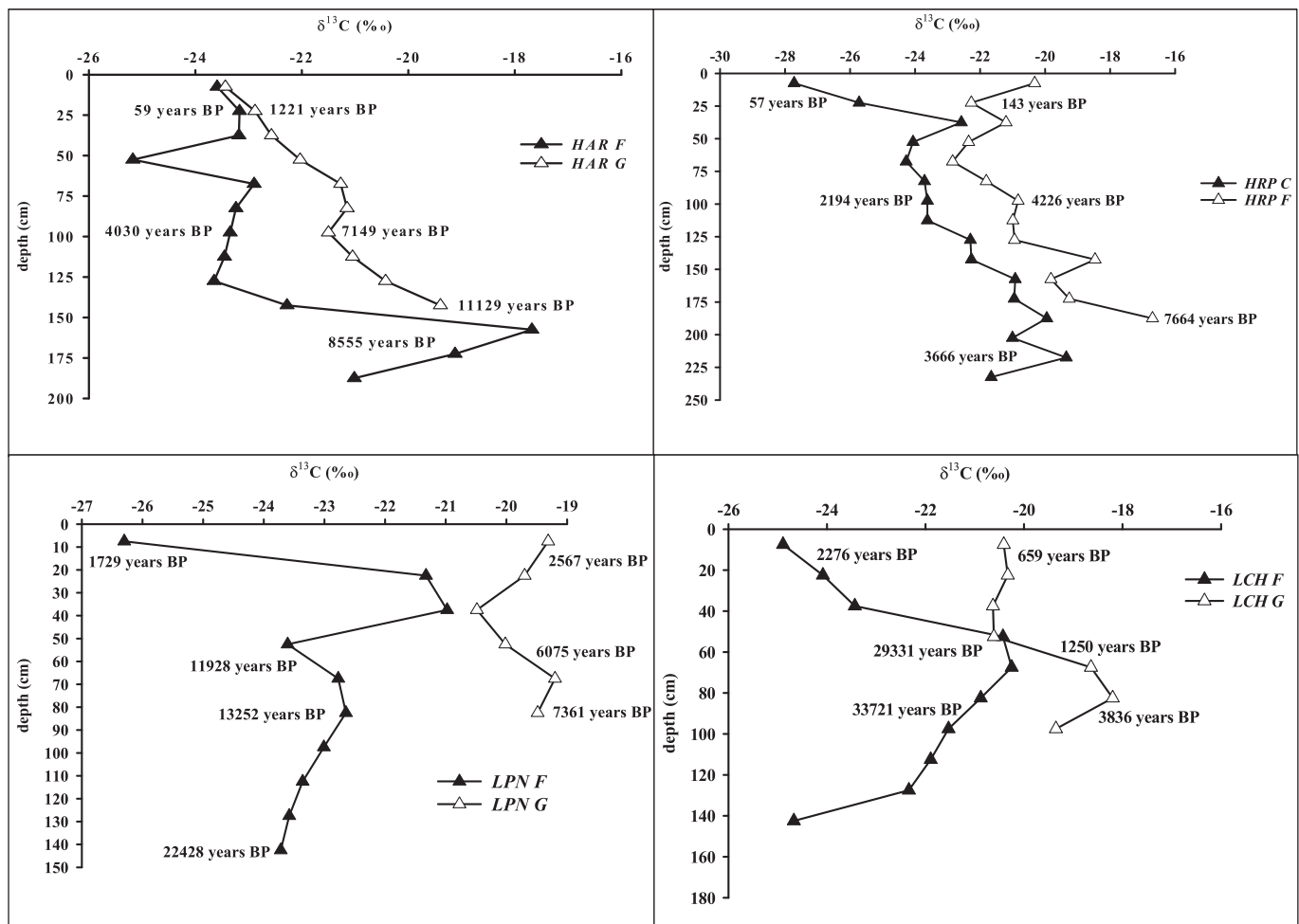


Fig. 10.  $\delta^{13}\text{C}$  values and radiocarbon dating with respect to depth in LPN, LCH, HRP, and HAR peatlands, under grassland (G) and forest clusters (F).

colonized by forest clusters. These C4 plant species are very abundant in the grassland. The lower mean values of  $\delta^{13}\text{C}$  in the superficial layer under forest clusters than under grasslands exhibit isotopic composition of peat organic matter similar to those of the vegetation type that currently colonizes it.

When the values of  $\delta^{13}\text{C}$  under the two vegetation types are considered, grasslands and forest clusters were clearly separated (Fig. 7), demonstrating the different isotopic composition of the peat organic matter between vegetation types that currently colonizes it. Similar results were found by E.V. Silva et al. (2013) in another peatland of SdEM.

**4.2.1.1. Altitude.** The LCH and LPN peatlands present differences in the levels of FF, FA, van Soest cellulose and  $\delta^{13}\text{C}$  compared to HRP and HAR peatlands (Table 4). The peatlands of higher altitudes, where annual average temperatures are 2 to 3 °C lower, present a different species than peatlands of lower altitudes (Table 2). According to the Nernst equation the increase in temperature favors oxidation and, of course, the decay of the peat organic matter. Jassey et al. (2013) detected that the increase in temperature of the peats stimulated microbial activity, leading to slight increases in levels of nutrients and labile C in peat water.

The mean levels of FA (soluble) are higher and the mean levels of FF are lower in peats of lower altitudes (LPN and LCH - older) (Table 4), since decomposition is more pronounced at higher temperatures, and is accentuated over time. Schnitzer (1967) detected in peatlands of Canadá that the increased in humification of peat organic matter was associated with increases in FA concentrations. The positive correlation

between the peat ages and FA ( $r = 0.37$ ,  $n = 24$ ;  $t$ -test,  $p = 0.038$ ) also corroborates the continuous decomposition in the lower peatlands.

The higher mean value of  $\delta^{13}\text{C}$  found in the LCH and LPN peatlands (Table 4) may be related to a more advanced decomposition stage and indicates the admixture of microbial organic matter in peat organic matter, which generally has a higher content of the heavy isotopes (Buurman et al., 2004). The values of  $\delta^{13}\text{C}$  tend to increase in the deeper layers in all peatlands, under both vegetation types (Fig. 5), as observed by other authors (Horák-Terra et al., 2015; Bispo et al., 2016; Campos et al., 2016) in peatlands of the SdEM.

The C/N ratio increases with depth (ANOVA,  $p = 0.000$ ). In graminoid-dominated peat from northern Spain, the C/N ration showed a gradual increase with depth (Martínez-Cortizas et al., 2007). In contrast to what was observed for peats with presence of sphagnum acid in temperate and boreal regions (Clymo, 1984; Kuhry and Vitt, 1996), the higher values of the C/N ratio at depth can indicate greater decomposition of soil organic matter in these peatlands (Horák-Terra et al., 2014; Schellekens et al., 2015a). In several peatlands of SdEM, the superficial layers are fibric, the intermediates are hemic and the lower are sapric (van Post scale) indicating more advanced decomposition of the peat organic matter in depth (Bispo et al., 2015; Horák et al., 2011; Campos et al., 2011).

#### 4.3. Chronological succession of grassland and forest clusters in peatlands

Forests clusters of lower altitudes peatlands began to settle in the Late Pleistocene and forests clusters of higher altitudes peatlands settled in the Holocene (Fig. 10). According to Parenin et al. (2013), ice cores

showed average temperatures in the Antarctic from  $-9$  to  $-5$  °C and  $-5$  to  $-2$  °C below the current mean, respectively between 55,000 and 16,400 years BP and between 16,400 and 12,800 years BP. Between 12,800- and 8800-years BP, the average temperatures varied from  $+2$  to  $-1$  °C in relation to the current average temperatures. These data are in line with most of the paleoclimatic changes identified in the SdEM peatlands by multi-proxy studies (Horák-Terra, 2014; Horák-Terra et al., 2015; Costa, 2018) and are related with the colonization of peatlands of higher altitudes by forest clusters only in the Holocene.

## 5. Conclusions

1. The organic matter of peatlands currently under grasslands and forest clusters presented differences in the soluble fractions, the lignocellulosic composition, and  $\delta^{13}\text{C}$  values.
2. Multivariate analysis (FF, “van Soest lignin”, “van Soest cellulose”, C/N,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$ ) allowed the peatlands to be grouped by altitude and vegetation type.
3. The chronological succession of grassland and forest clusters in tropical mountain peatlands was influenced by altitude and was related to paleoclimatic changes.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2019.04.017>.

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