Soil organic carbon pool under native tree plantations in the Caribbean lowlands of Costa Rica

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Abstract

We evaluated the soil organic carbon (SOC) pool and selected physico-chemical soil variables in a plantation with native tree species established in a degraded pasture of the Caribbean lowlands of Costa Rica. Studies on the rate and accumulation of aboveground biomass and C have been conducted in native tree plantations of Costa Rica. However, more studies on the SOC pool are needed since only few works provide information on the subject. The tree plantation was established in 1991 on a 2.6 ha. degraded pasture (*Ischaemum* sp.) Four species were selected: *Vochysia guatemalensis* Smith, *Calophyllum brasiliense* Cambess, *Stryphnodendron excelsum* Poeppig et Endl. and *Hieronyma alchorneoides* Allemao. Average SOC concentration ranged from 44.9-55.2 g kg^{-1} (0-10 cm), and decreased with depth up to 12.7-16.8 g kg^{-1} (40-50 cm). The highest SOC pool was measured under *H. alchorneoides* and *V. guatemalensis*, i.e. 131.9 and 119.2 Mg C ha^{-1}, respectively, whereas in the pasture it was 115.6 Mg C ha^{-1}. The SOC pool has not changed significantly under the tree species evaluated 14 years after establishment. A multivariate ordination technique named between-within class principal component analysis was used to determine the factors and trend that explain the variability in the data. The effect of vegetation in the SOC and selected soil variables measured in this study was only detected for *H. alchorneoides*. The information presented herein about the depth distribution of the SOC fraction improves our knowledge for further developing prediction models.

Keywords: soil organic carbon; native tree plantations; Costa Rica; carbon sequestration; land management; ordination analysis

1. Introduction

The soil organic carbon (SOC) pool is the third largest C reservoir in interaction with the atmosphere. The biotic (560 Pg) and the atmospheric (760 Pg) pools are considerably smaller than the pedologic pool (Lal, 2004). The SOC pool can be depleted by 15 to 40% in a 2-yr period to 1-m depth when tropical forest is converted to agricultural land use (Ingram and Fernandes, 2001) or as much as 50-75% (Lal, 2004; Post and Kwon, 2000). Such depletion of the SOC pool creates the potential to accumulate (sequester) C in soils upon adoption of a restorative land use and less harmful agricultural practices.

Native tree plantations have become an extensively used land use management option in Costa Rica during the last 20 years as a restorative tool for degraded lands and also because their potential use as providers of ecosystem services (FAO, 2006). A rapid land use change occurred in the northeastern part of Costa Rica between 1950 and 2000, with the dominant change being the conversion of forests to pastures (Read et al., 2000). The usefulness of native tree plantations' establishment in degraded pastures has been recognized (Butterfield, 1995), although some researchers argue the viability of this land use in degraded pastures to restore soil quality (Sánchez et al., 1985). Nevertheless, most studies in native tree plantations have dealt with aboveground biomass (Fisher, 1995; Montagnini and Sancho, 1990; Montagnini and Porras, 1998; Stanley and Montagnini, 1999; Tornquist et al., 1999). Several studies have provided estimates of the SOC pool sometimes assuming that the soil bulk density do not change through the soil profile, which seems not to be the valid procedure.

In Costa Rica, studies on soil C dynamics have been mainly focused on changes in total soil C following conversion of forests to pastures (Veldkamp, 1994; Veldkamp et al., 1992; Powers and Schlesinger, 2002; Powers, 2004; Powers and Veldkamp, 2005). The SOC pool may also decrease slowly upon conversion of rain forest to pasture (Veldkamp, 1994), probably because of higher root biomass production under improved pastures (Lugo and Brown, 1993); however, van Dam et al. (1997) indicated the opposite trend and found a significant C accumulation in rich volcanic soils after clearance of the natural forest for pasture establishment. Reiners et al. (1994) reported the SOC pool at 16 Mg C ha^{-1} under pasture (0-10 cm depth) compared to 15 and 21 Mg C ha^{-1}, respectively, under 5 to 10 and 10 to 15 yr-old regrowth forest. Under tree plantations the research data on the rates of SOC sequestration in Costa Rica are not abundant in the literature. Available data indicate that SOC pool does not always increase under tree plantations (Lugo et al., 1986; Bashkin and Binkely, 1998; Tornquist et al., 1999). Furthermore, the data on SOC concentrations, including in the particle-size fractions and its stabilization upon conversion to tree plantations are needed to develop rational decision support systems for adopting judicious land uses. Physical fractionation methods allow us to study the factors involved in the associations between soil mineralogy and soil C differing in composition and function (Christensen, 2001).

The general objective of our study was to quantify the SOC pool and related key physical properties under a 14 yr-old mixed tree plantation established in a degraded pasture soil in the Caribbean lowlands of Costa Rica. The area has large geographic gradients in edaphic properties such as topography, SOC concentration, soil texture, and clay mineralogy (Powers and Schlesinger, 2002). Specific objectives were to: (1) assess the depth distribution of SOC concentration up to 50 cm depth, (2) determine the trends and variations in SOC pool at the scale of the plantation, (3) establish the association of SOC with selected physical and chemical soil properties, and (4) set the determinants of the depth distribution of SOC under tree plantations.

2. Material and Methods

2.1 Study site

This study was conducted at EARTH University (10º 10’ N and 83º 37’ W; 64 m a.s.l.) at the confluence of “Parismina” and “Destierro” rivers, in the Caribbean lowlands of Limón Province, Costa Rica. The climatic zone is classified as premontane, wet forest basal belt transition (Bolaños and Watson, 1993). The terrain is flat to undulating, annual rainfall averages 3,464 mm and annual mean temperature is 25.1 ºC (iso-hyperthermy). Rainfall is evenly distributed and exceeds 100 mm in all months, with peaks during June, July, August, November, and December, and yearly mean relative humidity is 87%. Soils of the study site are predominantly Andisols, and have moderate to low fertility. Soil pH (H_2O, 1:1) ranges from 3.7-4.8 and texture from sandy clay and sandy clay loam in the surface to clay in the sub-soil layers (Table 1).

Native tree plantations were established in 1991 on a 2.6 ha degraded pasture (*Ischaemum* sp.) that had been grazed for 7 years. Tree plantations were established following a completely randomized block design, comprising 3 blocks. Eight native tree species that are normally used in agroforestry systems (Montagnini and Sancho, 1990) were planted in a 3x3 m pattern in monoculture within each block, at a density of 1,111 trees ha^{-1}. Four species were selected for this study: *Vochysia guatemalensis* Smith ("Chancho"), *Calophyllum brasiliense* Cambess ("Cedro María"), *Stryphnodendron excelsum* Poeppig et Endl. ("Vainillo") and *Hieronyma alchorneoides* Allemao ("Pilón") (Table 2). Among these species *C. brasiliense* is considered a "climax" hardwood species expected to grow relatively slow, and *V. guatemalensis* is a long-lived pioneer, an early succession species (Carpenter et al., 2004). The tree density proximity at the time of soil sampling in July 2005 was 426 trees ha^{-1}. A remaining patch of the previous pasture in close proximity to the plantation was used as control.

2.2. Sampling methodology

Prior to digging the soil profile, litter on the soil surface was hand-sorted from 0.5 m^2 quadrats to estimate the amount of C (50% of the dry weight of the sample) input into the soil. Litter was oven-dried in the lab at 60º C for 72 h. Soil samples were obtained in all three blocks for each tree species for 0-10, 10-20, 20-30, 30-40 and 40-50 cm depth increments. Precautions were taken to minimize soil and site disturbance. Samples were gently broken manually into aggregates along planes of cleavages when at field moisture content, and air-dried for several days. Later, these aggregates were dropped onto a hard surface to ease their separation and sieved through 8 mm sieve to remove root materials and stones. Bulk soil and aggregate samples were carefully packed for shipment to The Ohio State University.

2.3 Soil physical and chemical properties

Soil bulk density (ρ_d) for each layer was measured by the core method (Blake and Hartge, 1986) using 5-cm Ø and 5 cm deep cores for all sampling depths. The soil core was obtained from the middle of each layer and weighed in the lab. Simultaneously, soil moisture content was determined gravimetrically by oven-drying a sub-sample at 105º C for 48 h to calculate the dry bulk density.

A sub-sample of 50-60 g air-dried soil was used for aggregate analyses by the dry-sieving method. Aggregates were separated into 6 size fractions, i.e. >4.75, 4.75-2.0, 2.0-1.0, 1.0-0.5, 0.5-0.250 and <0.250 mm by shaking the nest of sieves for 30 min. Size-class aggregates >250 μm were termed macro-aggregates and those <250 μm as micro-aggregates (Tisdall and Oades, 1982). The mean weight diameter (MWD) was computed with the equation provided by Kemper and Rousenau (1986):

$$MWD = \sum_{i=1}^{n} \bar{x}_i m_i ,$$

, and the aggregate fraction

$$(m_i) = \frac{M_{sieve\ \ i}}{M_{total\ \ sample}}$$

, where $\bar{x}_i$ is the mean diameter of each aggregate fraction; $M_{sieve\ i}$ is the dry mass of the particles retained in the sieve i; $M_{total\ sample}$ is the dry mass of the initial total sample.

The pH was determined in water (1:1) and $CaCl_2$ by combining the four samples of the soil collected for every tree species and the pasture.

2.4. Particle size analysis

We dispersed 50 g of <2mm air-dried soil combining the 4 samples in 50 ml of 0.5 M Na-hexametaphosphate plus 75 ml deionized water for 18 h and mechanically stirred in a multi-mixer machine for 20 minutes. Later, soil was passed through a nest of sieves of 250, 105, 53, and 20 μm to separate the coarse sand (105-200 μm), fine sand (53-105 μm), coarse silt (20-53 μm) and silt+clay (<20 μm) fractions, respectively in beakers that were oven-dried at 60 °C for 72 h. No chemical treatment was used to remove organic debris, (i.e., light organic fraction).

2.5. Aggregate-associated Carbon and Nitrogen concentrations

Concentrations of C and N in soil were determined for each aggregate size fraction by using a CN Elementar Vario Analyzer. The HCl test was performed to detect the presence of carbonate C in the samples. Because all samples tested negatively, total C was referred to as SOC. The SOC pool (Mg ha^{-1} for a specific depth) was computed by multiplying the SOC concentration (g kg^{-1}) with bulk density (g cm^{-3}) and depth (cm) (Batjes, 1996):

$$\text{C pool}_{\text{layer}}\ (\text{Mg ha}^{-1}) = \text{C content}_{\text{layer}}\ (\text{kg Mg}^{-1}) \times \text{BD}_{\text{layer}}\ (\text{Mg m}^{-3}) \times$$
$$\text{T (m)} \times 10^{-3}\ \text{Mg kg}^{-1} \times 10^{4}\ \text{m}^{2}\ \text{ha}^{-1}$$

2.6. Statistical analyses

Normality of the data was determined with the Kolmogorov-Smirnov test. All data were log transformed when necessary to meet the assumption of normality. A two-way ANOVA was performed to test for significant differences among tree species and depth as the main fixed factors. When significant differences were observed, multiple comparisons of means were performed with Tukey's significant difference (HSD) test. The Systat statistical package was used to perform ANOVA analysis and the Sigmaplot software for graph representation.

The main pattern and significance between trees sampled were searched by performing a between-within class analysis. First, a Principal Component Analysis (PCA) is performed to identify the variables that explain better the separation of classes (trees). A Montecarlo randomisation test was performed to search for significant differences (Manly 1991). Later, a test named within-class PCA was performed to explore those factors responsible of variability of data within each tree species. The between-class PCA which is illustrated in Dolédec and Chessel (1989), focuses on between groups' differences (tree species, e.g. *V. guatemalensis*, *S. excelsum* and so on). The within-class PCA, on the contrary, focuses on the remaining variability after the class effect (tree species) has been removed. Removing the class effect is achieved by placing all centers of classes at the origin of the factorial maps while the sampling units are scattered with the maximal variance around the origin. This operation is simply completed by centring the data by classes (Dolédec and Chessel, 1991). The results of the within-class PCA are very similar to a normalised PCA (data not shown). The matrix contained 19 columns (i.e. number of variables), and 25 rows, (i.e. number of objects = samples). The PCA module included in the ADE4 software package was used. The discriminant module included in the ADE4 software package (Thiolouse et al., 1997) was used.

3. Results

3.1. Soil physical properties

There were significant differences (ANOVA, $P<0.001$) in soil bulk density (ρ_d) among tree species and depths, but the interaction of both factors was not significant. In general soil ρ_d increased with increase in depth, although under some tree species differences were not significant (Tukey test, Table 3). No differences in soil ρ_d were observed among treatments for the 0- to 20 cm depth. In general, soil ρ_d was higher under pasture than under tree species, except for *S. excelsum* (30-50 cm depth).

In all cases, ca. 80-90% of aggregates were macro-aggregates, comprising 50% of very large macro-aggregates >2mm (Figure 1). These large aggregates may be the result of, among other factors, high biological activity in the topsoil. Earthworm activity was intense in all treatments, along with some conspicuous ant hills (*Atta* sp.) The visible part of this biogenic structure occupied an area of ca. 30-40 m^2 in the soil surface. Compared with the pasture, the aggregate size-class distribution was not different among tree species except in *S. excelsum*.

The mean weight diameter (MWD) decreased with increase in soil depth regardless of the treatment (Figure 1), although differences were not statistically significant (Table 4). A significant effect of tree species was also observed but the interaction was not significant. Regarding the distribution of size-class aggregates no significant differences were observed for the 1-2 mm size-class. However, values differed significantly for 0.25-0.50, 0.50-1 and 2-4.75 mm aggregate size fractions for the two sources of variation considered in this study, i.e., tree species and depth. For micro-aggregates only significant differences were observed regarding tree species (Table 4).

3.2. Carbon and Nitrogen concentrations and SOC pool

The SOC concentration decreased with increase in depth in all treatments, with the highest values measured under *H. alchorneoides* and *V. guatemalensis* (Figure 2). Average SOC concentration ranged from 44.9 to 55.2 g kg^{-1} in the 0-10 cm layer, and it decreased with increase in depth up to 12.7 to 16.8 g kg^{-1} in the 40-50 cm (Figure 2). There were significant differences in SOC concentrations for the main fixed factors and the interaction (ANOVA, P<0.001). However, the SOC concentration did not differ significantly among size-class aggregates (Figure 3).

The SOC concentration was significantly higher under *H. alchorneoides* and *V. guatemalensis* than in the pasture for all depths. The lowest SOC concentration was measured in the soil aggregates collected in the leaf-cutting ant deposit, i.e. 10 g kg^{-1}

(Figure 2), indicating that this soil is transported from even lower depths. Finally, the C:N ratio (Table 3) was similar among treatments and ranged from 10.5 in the pasture (0-10 cm) to 13.9 under *H. alchorneoides* plot (10-20 cm).

There was a decrease in SOC concentration within particle size fractions with increase in soil depth (Figure 4). With increasing depth the SOC concentration was higher in the silt+clay fraction under all treatments, except in *H. alchorneoides*. In the pasture, the highest SOC concentration was observed in the silt+clay fraction (<20 μm). The SOC concentration in the coarse-sand fraction was higher in *V. guatemalensis* and *S. excelsum*, whereas in *H. alchorneoides* and *C. brasiliense* the highest SOC concentration was observed in the fine-sand fraction.

Finally, the highest SOC pool was measured under *H. alchorneoides* (131.9 Mg C ha^{-1}) and *V. guatemalensis* (119.2 Mg C ha^{-1}). The SOC pools under *S. excelsum* and *C. brasiliense* were similar, i.e., 112.6 and 113.5 Mg C ha^{-1}, respectively (Figure 5), whereas in the pasture it was 115.6 Mg C ha^{-1}. However, differences were not statistically significant. The SOC pool down to 50 cm depth was two or three-fold higher than the amount of C aboveground. Compared to the pasture, the SOC pool did not change significantly in the tree plantations 14 years after establishment.

3.3. Ordination analysis. Between-within classes PCA

The first and second axis of the between-class PCA explained 90.8% and 7.4% of the total data inertia, respectively (Figure 6a, b). The first axis represented the soil type effect and the physico-chemical properties of soil under different tree species as many of the variables measured in this study were displayed along the first axis. Those samples with high values of C in the different particle size fractions were clearly distinguished. The second axis showed an opposition between those sites with high MWD and percentage of very large aggregates, versus those samples with high amounts of aggregates 0.5-1 and 1-2 mm size and C:N ratio. This axis represents the effect of vegetation type or land management. The ordination of samples within the plane formed by the first two axes of the PCA is represented in Figure 6c. It showed an opposition between those samples collected in the first soil layer (0-10 cm) in all treatments, and therefore where SOC concentrations were high, and the soil collected at 40-50 cm. Axis II separated *H. alchorneoides* from the rest of tree species and the pasture, i.e. the vegetation effect. The Monte Carlo permutation test performed on the partition of objects to test the tree effect upon soil variables was highly significant; none of the 1,000 random simulation matrices led to an inertia higher or equal to that of the original data ($P<0.001$).

The first two axes of the within-class PCA explained 42.5 and 29.9% of the within-variability, respectively (Figure 7a, b). Again, it was observed the effect of aggregation and soil texture in Axis I and II, respectively. The effect of C is removed with this analysis, since most variables related to C concentrations are displayed around the origin of coordinates. The ordination of objects in the factorial plane showed that the most different land use systems were the pasture and the *H. alchorneoides* plantation (Figure 7c).

4. Discussion

The SOC pool has been reported to decline after woody plant invasion of pastures (Jackson et al., 2002) and conversion from pasture to pine plantation (Guo and Gifford, 2002). Tornquist et al. (1999) did not observe any significant difference in SOC pool under agroforestry and pastures (i.e., 50 and 62.6 Mg C ha^{-1} for 0-15 cm depth). In our study, the SOC pool was higher in the tree plantation compared with the pasture. In general, SOC concentrations measured in were slightly higher than those reported in other studies (Table 5). Fisher (1995) reported increases in the SOC pool under two exotic tree species, i.e., *Pinus tecunumanii* and *Gmelina arborea* out of 11 species just after 3 years of establishment in a degraded pasture, and decreased under the pasture control. In contrast, Montagnini (2000) reported increase in SOC concentration within 2.5 years, from 4.8% under fallow (pasture) to 5.3-6.6% under tree plantations. Our data showed that both the SOC concentrations and the SOC pool increased under tree plantations although not significantly. The reasons are probably in several factors like for example, other C sources in the pasture, i.e. higher root biomass contribution, or reduced ρ_b in the tree plantations compared with the pasture, or the time lag elapsed since the establishment of the plantation.

Regarding the amount of litter our results must be cautiously interpreted since no temporal variation in litter production was addressed. Thus, it is difficult to draw general conclusions on the effect of litter input on SOC concentration after 14 years of establishment. Nonetheless, it is worth noticing that the understory vegetation under *H. alchorneoides* was the highest observed. In fact, ferns and *Heliconia* sp. were abundant under this system, even if high litter production was observed under *V. guatemalensis*. No understory vegetation was observed under *C. brasiliense*. Understory vegetation may contribute to SOC increases. In fact, Cusack and Montagnini (2004) observed levels of understory vegetation significantly higher under *H. alchorneoides*, *V. guatemalensis* and *C. brasiliense* in the same region.

The formation of aggregates occurs through flocculation of clay colloids and their cementation by organic and inorganic materials (Jiménez and Lal, 2006). Several factors affect this process, like land use and management, soil mineralogy, texture, quantity and quality of the organic matter incorporated, diversity and abundance of soil organisms (bacteria, fungi, earthworms and others). Soils thus can be fractionated according to the aggregates that configure their structure. In our study, the highest SOC concentrations were obtained in the silt+clay, which are important in the longer term due to the complex associations of C with the structure of clays (Jiménez and Lal, 2006). This is the general rule observed in other tropical sites (Desjardins et al, 1994; Feller and Beare, 1997). The sand-size (20-2000 μm) macro-aggregates are important in the short-term dynamics of C. Our data showed that under *S. excelsum* and *V. guatemalensis*, the highest SOC concentrations were obtained in the coarse-sand sized fraction (105-200 um). This is likely the result of contribution of litter and other plant fragments to this fraction.

Estimates of C sequestration are mainly based on the aboveground biomass, which represent about 90% of the total tree biomass, and growth belowground represents between 2-4% (Montagnini and Sancho, 1994), sometimes higher around 10% of total biomass (Enquist and Niklas, 2002; Jenkins et al., 2003).

Finally, the between-within analysis PCA was very useful to explore the links between the variables analysed and the trend in SOC concentrations 14 years after establishment of the tree plantations. At the local scale of our study this trend may indicate a long-lasting residual effect of the pasture and the effect of *H. alchorneoides* (Figures 6 and 7), although further studies are needed to obtain complete and accurate estimations of C sequestration belowground.

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Tables

Table 1. Soil textural analysis (hydrometer method) and pH under the different tree species and pasture.

Table 2. List of tree species used in the on-farm agroforestry systems and associated characteristics

Table 3. Soil ρ_b and C:N ratio (mean ± stand. error) up to 50 cm depth under the tree plantations and the pasture (control). Values followed by the same letter within a column are not statistically different (Tukey HSD test, $P<0.05$).

Table 4. Tukey HSD two-way ANOVA for aggregate size distribution and MWD in the tree plantation and pasture (control), with tree species and sampling depth as main fixed factors. The F-ratios for each variable are indicated. NS, not significant; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Table 5. The SOC pool concentration under tree plantations of different ages in Costa Rica.

Table 1.

System	Depth (cm)	Texture (%)			pH	
		Sand	Silt	Clay	H_2O 1:1	$CaCl_2$
Pasture (“degraded”)	0-10	54.1	11.0	34.9	4.5	4.1
	10-20	49.9	11.2	39.9	4.7	4.0
	20-30	55.5	6.0	38.5	4.7	4.0
	30-40	47.2	6.7	46.2	4.7	4.0
	40-50	48.7	9.4	41.9	4.8	4.0
Hieronyma alchorneoides	0-10	62.8	13.6	23.6	4.1	3.8
(Pilón)	10-20	56.8	10.7	32.5	4.2	3.8
	20-30	61.7	8.7	29.6	4.6	4.0
	30-40	45.4	12.7	41.9	4.6	4.0
	40-50	45.5	12.6	41.9	4.7	4.0
Stryphnodendron excelsum	0-10	49.3	13.8	36.9	3.7	3.6
(Vainillo)	10-20	21.4	9.7	68.9	4.3	3.9
	20-30	11.4	15.7	72.9	4.4	3.9
	30-40	27.4	13.8	58.8	4.6	4.0
	40-50	37.4	13.7	48.8	4.7	4.0
Vochysia guatemalensis	0-10	65.0	9.40	25.6	4.2	4.0
(Chancho)	10-20	43.7	14.8	41.5	4.1	3.9
	20-30	45.8	11.8	42.4	4.5	4.0
	30-40	31.9	13.7	54.4	4.6	4.0
	40-50	27.5	15.1	57.4	4.5	3.9
Calophylum brasiliense	0-10	50.0	11.1	38.9	3.8	3.7
(Cedro María)	10-20	22.3	16.9	60.8	4.1	3.9
	20-30	18.2	17.0	64.8	4.6	4.0
	30-40	20.6	15.8	63.6	4.7	4.1
	40-50	22.2	14.3	63.6	4.5	4.0

Table 2.

Scientific name (family)	Spanish common name	Distribution	Growth[1] (9 years)	Characteristics[2]
Hieronyma alchorneoides (Euphorbiace)	“Pilón”	Belize to Amazon region	21.7; 17.5	Good litter-producer, moderately fast growth
Stryphnodendron excelsum (Mimosaceae)	“Vainillo”	Nicaragua, Costa Rica, Panamá	26.6; 15.8	N-fixing, low litter-producer, fast growth
Vochysia guatemalensis (Vochysiaceae)	“Chancho blanco”	All Central America	28.7; 20.8	Good litter-producer, Al accumulator, fast growth
Calophylum brasiliense (Clusiaceae)	“Cedro María”	Mexico to North South America	18.3; 16.2	Mature forest, slower growth

[1] Numbers refer to diameter at breast height (DBH) and tree height, respectively.

[2] Montagnini (2000)

Table 3.

Depth (cm)	Tree Species									
	H. alchorneoides		*S. excelsum*		*V. guatemalensis*		*C. brasiliense*		Pasture (control)	
	ρ_d	C:N	ρ_d	C:N	ρ_d	C:N	ρ_d	C:N	ρ_d	C:N
0-10	0.76 a	11.8 ± 0.22 a	0.76 a	10.7 ± 0.21 b	0.67 a	11.4 ± 0.25 a	0.78 a	11.3 ± 0.28 ac	0.94 a	10.5 ± 0.3 bc
10-20	0.94 b	12.2 ± 0.20 a	0.90 a	10.7 ± 0.16 b	0.90 a	11.1 ± 0.05 a	0.91 a	10.8 ± 0.14 bc	0.99 a	11.0 ± 1.0 ac
20-30	0.90 b	13.8 ± 0.22 a	0.98 a	12.2 ± 0.09 b	0.91 a	11.5 ± 0.12 c	0.91 a	11.0 ± 0.11 b	1.07 b	11.4 ± 0.8 b
30-40	0.97 b	13.9 ± 0.17 a	1.06 b	13.0 ± 0.08 b	0.96 a	11.5 ± 0.08 b	0.93 a	11.3 ± 0.06 c	1.06 b	11.7 ± 0.5 c
40-50	0.91 b	12.7 ± 0.11 a	1.02 b	13.7 ± 0.09 bd	0.89 a	11.0 ± 0.07 b	0.98 a	11.1 ± 0.02 c	1.02 b	11.6 ± 0.4 d

Table 4.

Source of variation	*df*	MWD[1]	Aggregate size (mm)					
		(cm)	<0.25	0.25-0.50	0.50-1.00	1.00-2.00	2.00-5.00	>4.75
Tree species (A)	4	4.145 **	2.783 *	3.470 *	3.441 *	1.305 NS	3.087 *	5.106 **
Depth (B)	4	2.348 NS	1.590 NS	3.803 **	2.552 *	0.584 NS	6.353 ***	2.184 NS
AxB	16	0.819NS	0.413 NS	0.651 NS	0.923 NS	0.606 NS	0.687 NS	1.058 NS

[1] Mean weight diameter

Table 5

Tree species	Soil type (FAO)	Age (years)	Depth (cm)	SOC (g kg^{-1})	Reference
Erythrina peoppigiana	Cambisol	10	0-20	19.0	Oelbermann et al., 2004 (1)
E. peoppigiana	Cambisol	19	0-20	29.0	(1)
Gliricidia sepium	Cambisol	10	0-20	29.9	(1)
Vochysia ferruginea	Acrisol	10	0-15	36.5	Tornsquist et al., 1999
E. peoppigiana	Cambisol	9	0-15	27.3	Fassbender, 1998
E. peoppigiana	Cambisol	10	0-10	27.8	Mazzarino et al., 1993 (2)
G. sepium	Cambisol	10	0-10	27.5	(2)
E. peoppigiana	Cambisol	6	0-20	18.5	Haggar et al., 1993 (3)
G. sepium	Cambisol	6	0-20	14.8	(3)
Calophylum brasiliense	Inceptisol (Fluvent. Dystr.)	4	0-15	34.0-36.7	Montagnini and Porras, 1998 (4); Montagnini, 2000 (5)
C. brasiliense	Inceptisol (Fluvent. Dystr.)	4	0-30	90.0	(4)
Stryphnodendron microstachyum	Inceptisol (Fluvent. Dystr.)	4-5	0-30	98.1-120.9	(5)
V. guatemalensis	Inceptisol (Fluvent. Dystr.)	4-5	0-30	104.4-102.3	(4), (5)
Jacaranda copaia	Inceptisol (Fluvent. Dystr.)	4-5	0-30	97.5-137.4	(4), (5)
Dipteryx panamensis	Inceptisol (Fluvent. Dystr.)	4-5	0-30	86.1-105.0	(4), (5)
Albizia guachapele	Inceptisol (Fluvent. Dystr.)	4-5	0-30	88.2-102.0	(4), (5)
Terminalia amazonia	Inceptisol (Fluvent. Dystr.)	4-5	0-30	90.0-124.5	(4), (5)
Virola koschnyi	Inceptisol (Fluvent. Dystr.)	4-5	0-30	85.5-123.9	(4), (5)
Genipa Americana	Inceptisol (Fluvent. Dystr.)	4	0-30	82.8	(4)
Hieronyma alchorneoides	Inceptisol (Fluvent. Dystr.)	4	0-30	81.6	(4)

Pithecellobium elegans	Inceptisol (Fluvent. Dystr.)	4	0-30	98.1	(4)
V. ferruginea	Inceptisol (Fluvent. Dystr.)	4	0-30	87.9	(4)
H. alchorneoides	Andosol	14	0-30	112.6	This study
S. excelsum	Andosol	14	0-30	82.2	This study
V. guatemalensis	Andosol	14	0-30	108.1	This study
C. brasiliense	Andosol	14	0-30	100.3	This study
Pasture (control)	Andosol	21?	0-30	97.4	This study

[1] Calculated by multiplying the SOC concentration (g kg^{-1}) and bulk density (Mg m^{-3})

Figure captions

Figure 1. Aggregate size distribution and mean weight diameter (MWD, number above the bars) under the different tree species and the pasture.

Figure 2. Distribution of SOC through the soil profile under the different treatments. Different letters indicate significant differences among soil layers for the same treatment.

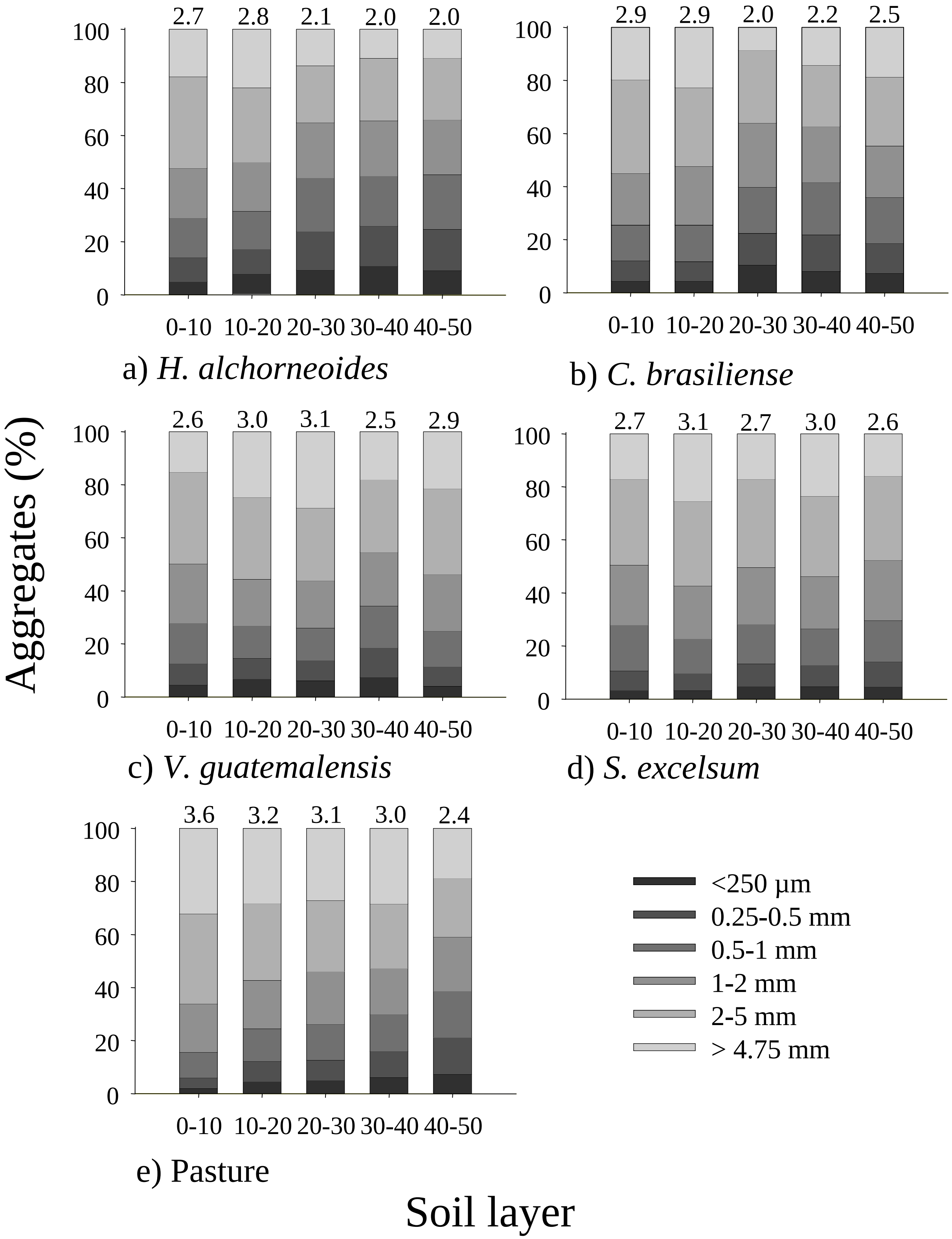
Figure 3. SOC concentration in the different size-class aggregates. Capital letters refer to differences between treatments for the same soil layer, and lowercase letters indicate differences between soil layers within treatments (HSD Tukey ANOVA test, $P<0.05$). NS = Not significant for comparisons between different size-class aggregates within the same treatment in the same soil layer.

Figure 4. SOC concentration in micro-aggregates (<250 µm) after particle-size fractionation analysis.

Figure 5. Above- and belowground C pools in a native tree plantation compared with the pasture (control). Data for aboveground C accumulation are from Leblanc et al. (unpubl.), except litter (this study). Different letters indicate significant differences between land use systems at $P<0.05$ level (ANOVA), NS = Not significant.

Figure 6. Between-class PCA of the data from the tree plantations and the pasture: (a) variability of data retained in the first two axes retained in the PCA (98.2% of total variance); (b) “Eigenvalue” diagram; (c) ordination of samples on F1-F2 plan according to tree plantation and depth. Codes are: Ha = *H. alchorneoides*, Vg = *V. guatemalensis*, Se = *S. excelsum*, Cb = *C. brasiliense*, Pa= Pasture. Numbers 1 to 5 indicate soil depth (1 = 0-10 cm and so on). Cs+c = C concentration in the silt+clay fraction (<20 µm); Ccsi = id. for the coarse silt fraction (20-53 µm); Cfsa = id. for the fine sand fraction (53-105 µm); Ccsa = id. for the coarse sand fraction (105-200 µm).

Figure 7. Within-class PCA: (a) Variability of data retained in the first two axes retained in the PCA (98.2% of total variance); (b) “Eigenvalue” diagram; (c) ordination of samples on F1-F2 plan according to tree plantation. Same legend as figure 6.



a) *H. alchorneoides*

b) *C. brasiliense*

c) *V. guatemalensis*

d) *S. excelsum*

e) Pasture

Figure 1 – Jimenez et al.

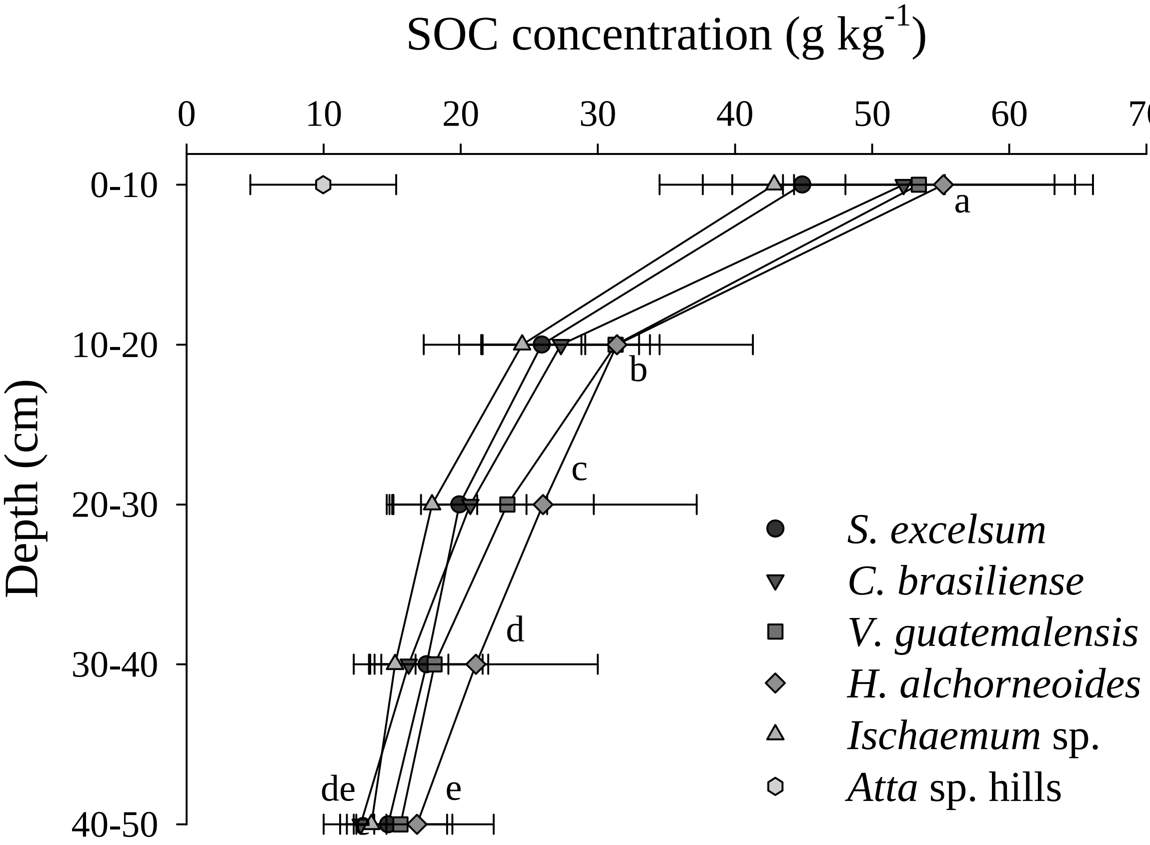


Figure 2 – Jimenez et al.

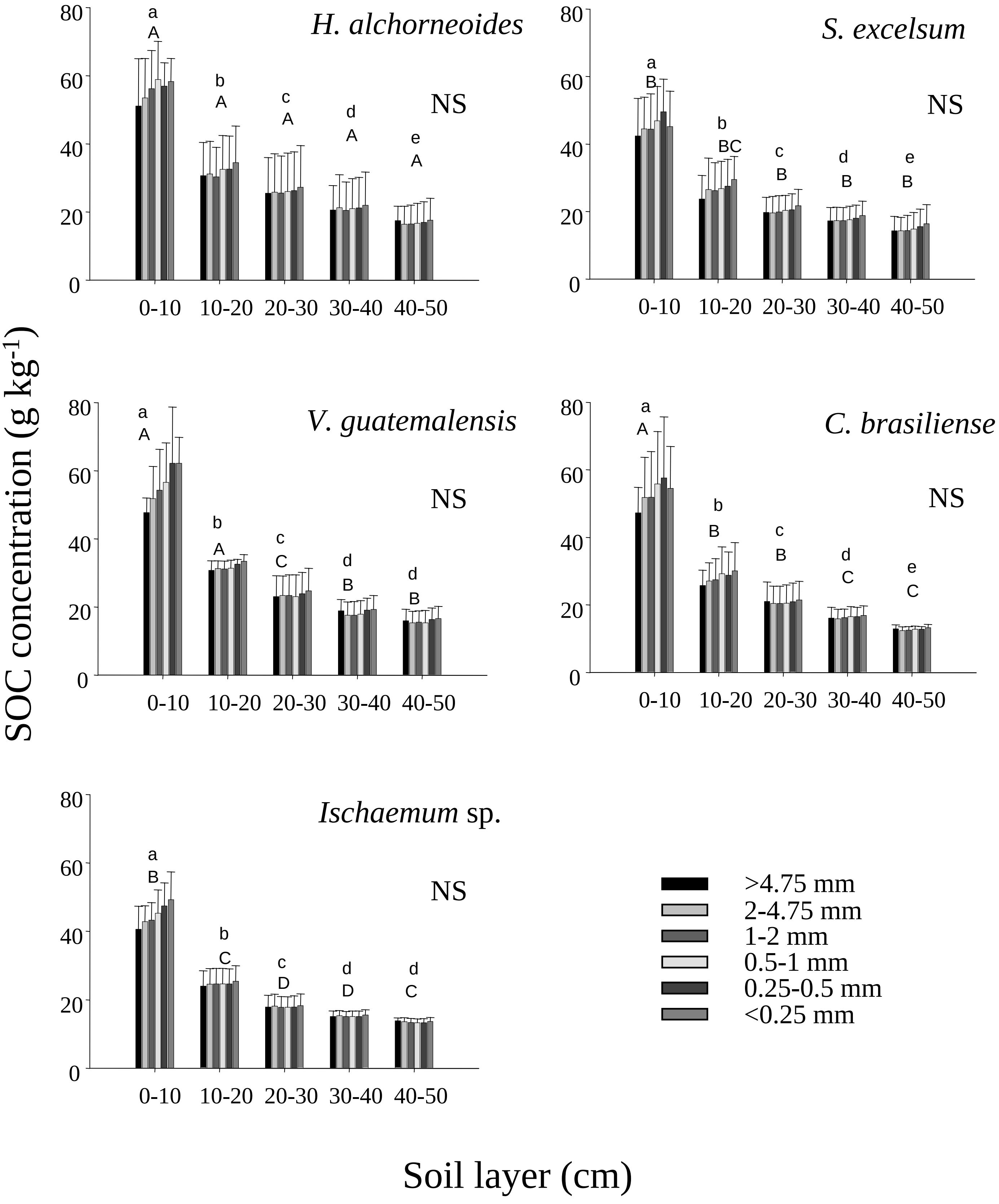


Figure 3 – Jimenez et al.

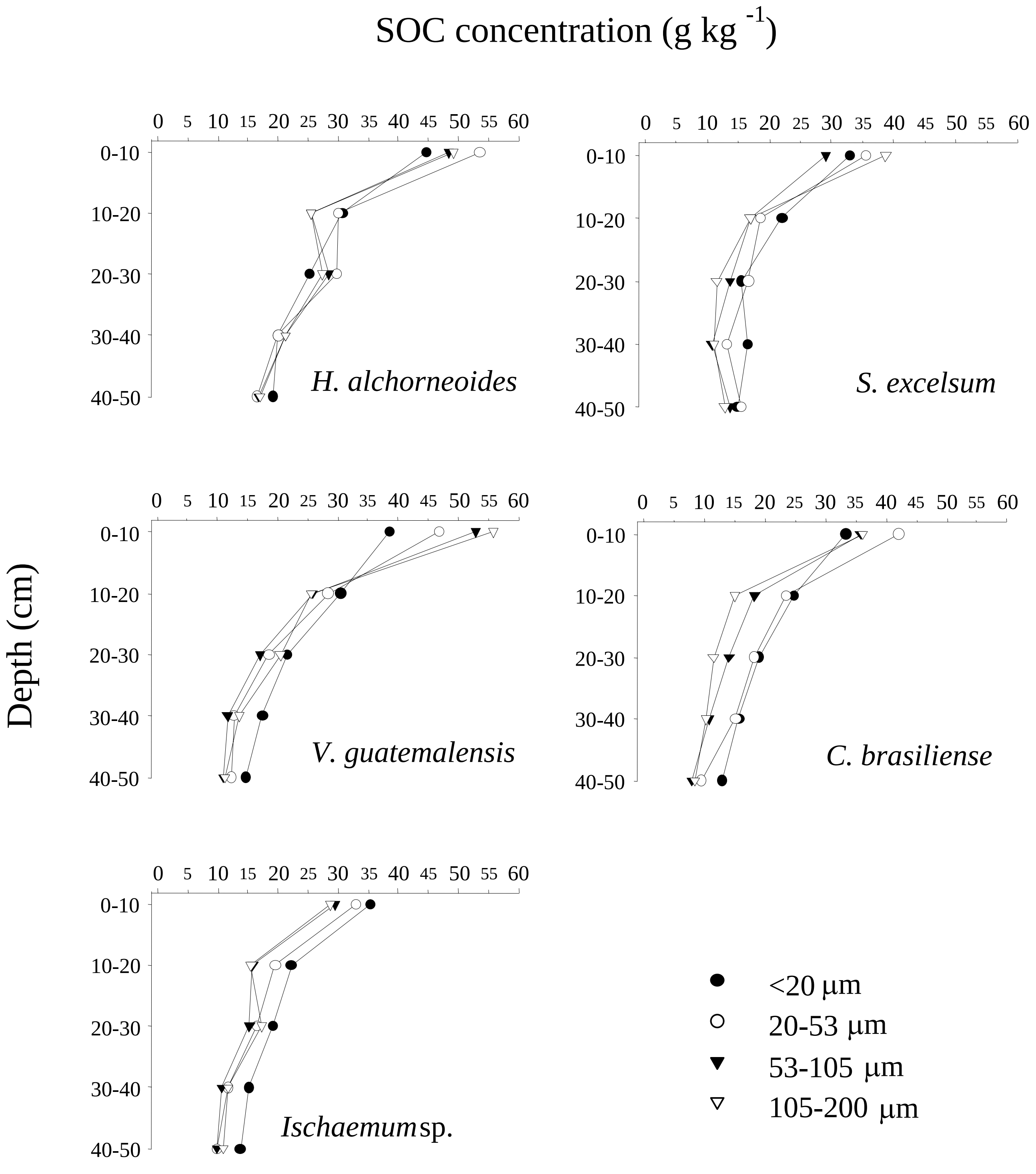


Figure 4 – Jimenez et al.

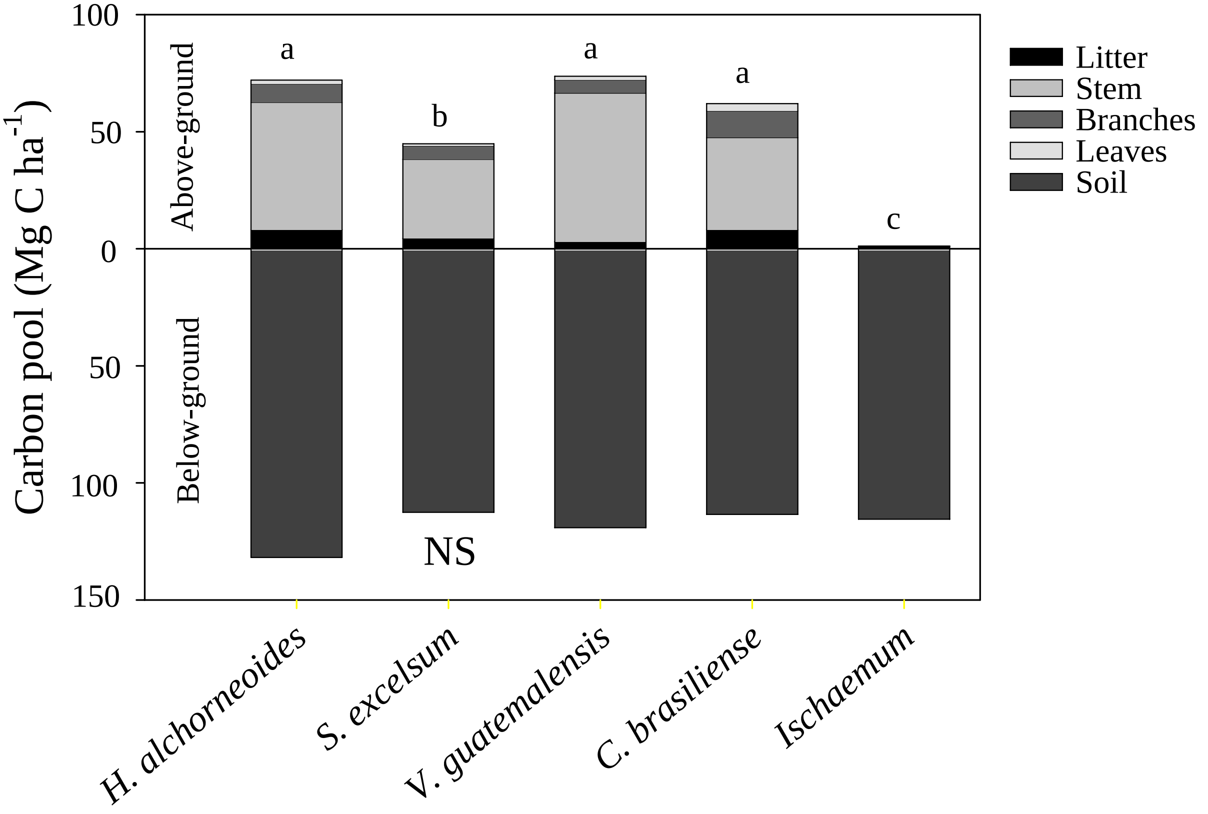


Figure 5 – Jimenez et al.

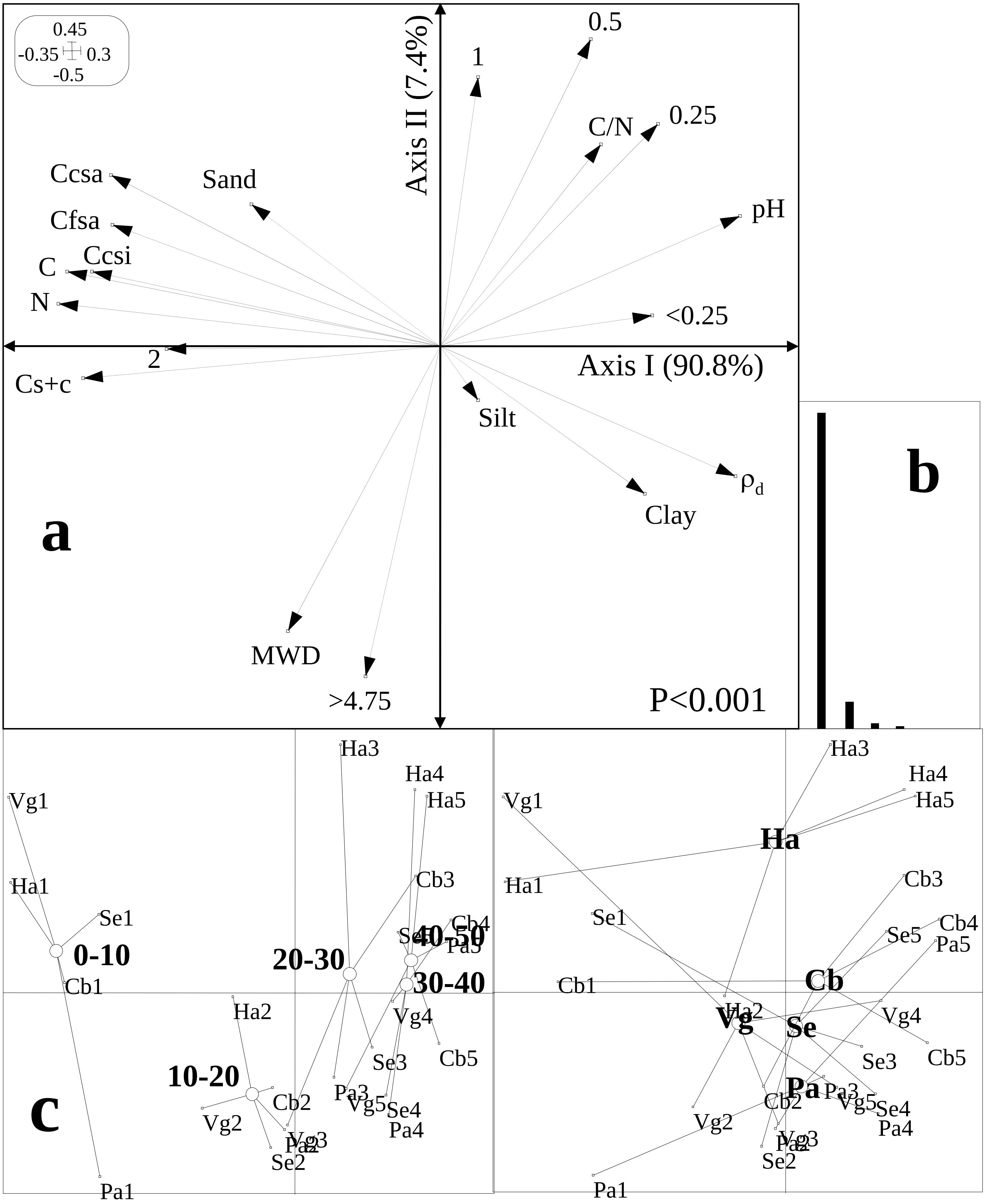


Figure 6 – Jimenez et al.

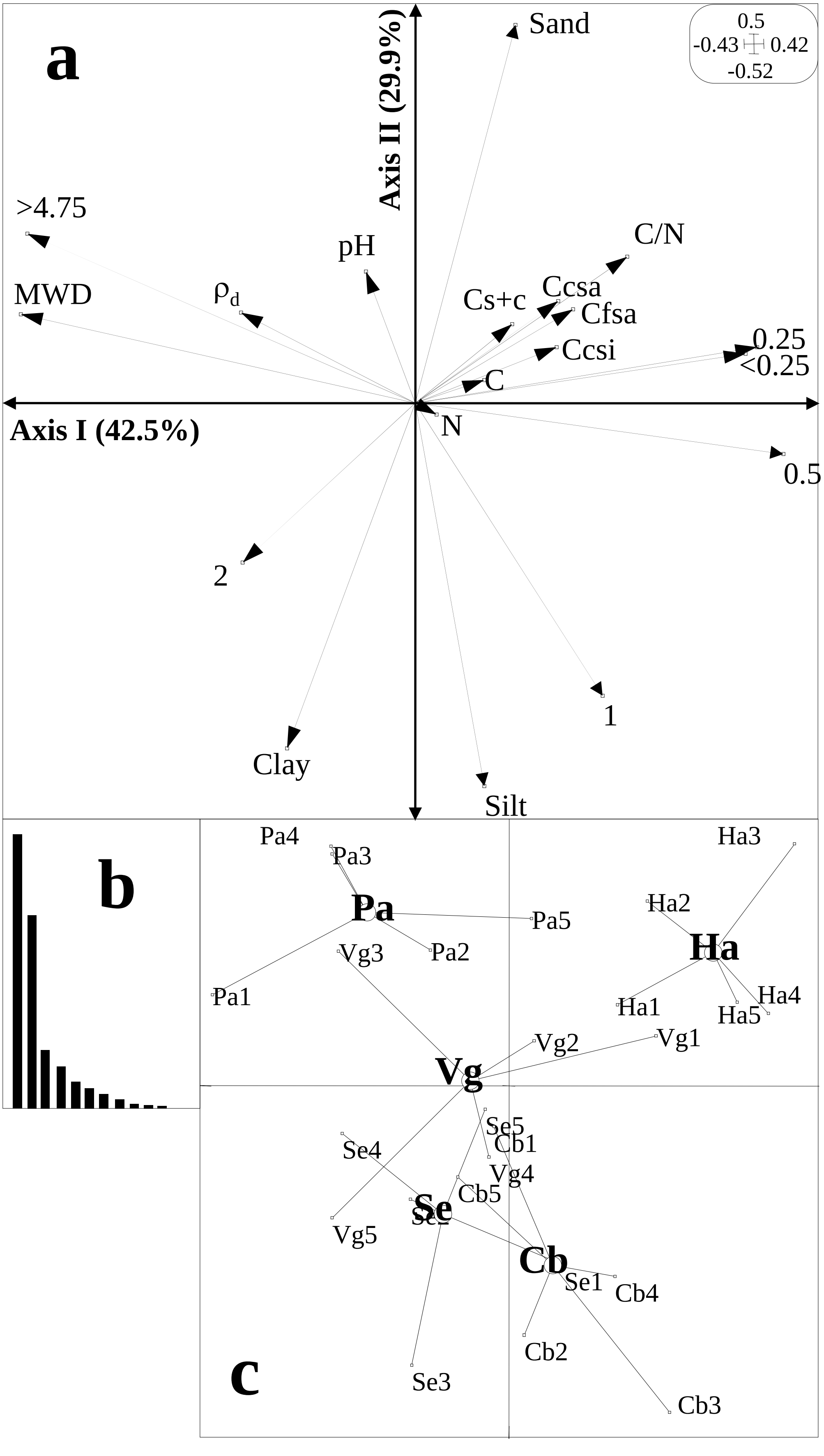


Figure 7 – Jimenez et al.