Organic carbon and nitrogen in soil particle-size aggregates under dry tropical forests from Guanacaste, Costa Rica – Implications for within-site soil organic carbon stabilization

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Abstract

In this study we report results on the soil organic carbon (SOC) pool (0-50 cm) from a chrono-sequence of dry tropical forest (dTf) of increasing age and a yearly burned ancient pasture in the “Sector Santa Rosa” at the “Área de Conservación Guanacaste” (ACG) in northwestern Costa Rica, where intense human induced land-use modifications has occurred during the past century. The effects of land conversion on soil organic carbon (SOC) have mainly been conducted in the Atlantic humid forests while overlooking dTfs. We quantified the depth distribution of SOC concentration down to 50-cm and in physically separated mineral soil fractions, as these data are scanty from the dTf. Additional objectives were to identify the relationship with selected soil physical and chemical properties, including stabilized SOC fractions by means of multivariate ordination methods. Statistically significant differences were found for the main fixed factor ecosystem for all soil variables analysed (ANOVA). SOC and N concentrations were significantly higher in the oldest dTf compared to the other dTfs. Soil physical properties like aggregate size distribution and bulk density changed with depth, and varied significantly among the three dTf stands sampled. The multivariate analysis, i.e. between-within class principal component analysis (PCA), revealed a significant ordination of dTfs ($P<0.0001$). The SOC concentration decreased in particle size fractions of <200 µm aggregates with increasing soil depth. The lowest and highest C concentrations were obtained in the fine sand (105-200 µm) and clay+silt (<20 µm) fractions, respectively. Mineral-associated and stable SOC pool increased with depth, and poorly crystalline Fe oxides and ferrihydrite were the most important minerals for SOC stabilization at 40-50 cm depth. The highest SOC pool was found in the old-growth and >80 years-old dTfs, i.e., 228.9 and 150.3 Mg C ha^{-1}, respectively, values similar to those obtained in the Atlantic humid forests of

Costa Rica. Comparatively to other studies, soils under dTf at Santa Rosa store a considerable amount of SOC with potentially large CO_2 emissions if this ecosystem is not preserved.

Key words: Soil organic carbon, Nitrogen, particle size fraction, principal component analysis, dry tropical forest.

1. Introduction

The soil organic carbon (SOC) pool is the largest pool of terrestrial organic carbon, with an estimated 2,100 Pg (1 Petagram = 10^{15} g) ca. 3 times larger than the amount of C stored in above-ground vegetation (Post et al., 1982). In tropical soils the SOC pool amounts to 30% of the global C pool, i.e., 384–506 Pg down to 1-m depth (Kimble et al., 1990; Eswaran et al., 1993; Batjes, 1996), and more specifically 119 Pg C is stored in the top 1-m in the dry tropical forest (dTf) (Jobbágy and Jackson, 2000). The SOC is thus relevant for the terrestrial ecosystem C balance and its potential to respond to the global C cycle.

Compared to other ecosystems worldwide, the dTf has experienced the greatest transformation to agriculture lands (Hoekstra et al., 2005), and the process still continues in the dTfs of South America (Grau et al., 2008). The conversion of tropical forests to agricultural land has decreased over the past ten years but continues at an alarmingly high rate in many countries (FAO, 2010), resulting in depletion of the SOC pool as much as 75% in the tropical region (Lal, 2004). Tripathi and Singh (2009) reported SOC data (0-10 cm) from dTf in the Similipal Biosphere Tiger Reserve (India) to be 19.8 g kg^{-1} while in pasture and cropland a reduction of 46 and 54% was observed, respectively. Changes on SOC pool after conversion of natural tropical ecosystems to agricultural land has been assessed by several authors (Werner, 1984; Buschbacher et al., 1988; García-Oliva et al., 1994; Veldkamp, 1994; Cerri et al., 1991; Tiessen et al., 1992; Trumbore et al., 1995; De Moraes et al., 1996; Neill et al., 1997; Groffman et al., 2001; Murty et al., 2002; García-Oliva et al., 2006; Schwendenmann and Pendall, 2006; Marin-Spiotta et al., 2009), with various responses observed, including increases, decreases, or no net long-term changes in

SOC. When agricultural land is no longer under cultivation and allowed to return to the previous vegetation cover, C accumulates in the soil by processes that essentially reverse initial losses of SOC after land conversion. SOC accumulation rates and time lag broadly vary depending on the productivity of the re-growing vegetation, physical and biological conditions in the soil, and the past history of SOC inputs and physical disturbance (Post and Kwon, 2000). Full recovery of SOC pool following deforestation depends on the length of time allowed for recovery and intensity of land use, taking several decades to achieve a new equilibrium (Ramankutty et al., 2006).

In Costa Rica, historic conversion of the dTf has potentially caused considerable loss of above- and belowground C due to extensive deforestation for land clearance following land colonization in Costa Rica during the 1950's to establish traditional livestock and agricultural land use (Calvo-Alvarado et al., 2009). Research on SOC in the dTf, as indicated by the small number of published studies (Sánchez-Azofeifa et al., 2005) in the Pacific region (Johnson and Wedin, 1997; Powers et al., 2009), has not kept pace with those conducted in humid forests at the Atlantic region (Powers, 2004; Veldkamp, 1994; Powers and Schlesinger, 2002; Powers and Veldkamp, 2005; Jiménez et al., 2007; Jiménez et al., 2008). Consequently, additional studies from the Pacific region are needed to increase our knowledge on SOC changes and the distribution and abundance of SOC in dTf, for which there are little published data, with comprehensive emphasis on the biological and physical factors involved.

Physical protection of soil C within aggregates is an important mechanism for C sequestration (Jastrow, 1996; Six et al., 2002). Assessment of SOC concentration within particle-size fractions from the dTfs and derived agro-ecosystems are not abundant in the literature either (García-Oliva et al., 1994; García-Oliva et al., 1999b).

Soil physical fractionation methods have been generally used to reveal the factors involved in C and soil mineralogy associations and in the study of the dynamics and turnover of organic matter (OM) (Christensen, 1992; 2001; Six et al., 2002). The dynamics of OM varies with soil aggregates size and physical fractionation techniques are, thus, useful to isolate C pools more sensitive to changes in land management or differences between ecosystems in order to elucidate processes and mechanisms involved in the storage of C (Six et al., 2002).

The stabilization of SOC is relevant for biogeochemical processes in ecosystems although the mechanisms are still poorly understood and new framework has been proposed (Kleber et al., 2007). It is also important for global C cycing models to assess the effect of disturbance and recovery in the dTf in addition to identifying the processes of SOC stabilization. The main goal of this study was to increase our knowledge on the vertical distribution of SOC in size-class aggregates in the dTf, in addition to a better understanding of those factors that are correlated with soil C and the environmental between- and within-site control on SOC. Additional objectives were to: (1) assess C and N distribution associated with different soil mineral fractions of <250 μm aggregates, (2) investigate SOC relationships with selected soil properties, including C stabilization data obtained from chemical extraction methods by applying multivariate ordination techniques in order to identify meaningful trends in dTf recovery. A forest chronosequence approach was used to infer SOC pool recovery after perturbation, which is a normal procedure in tropical ecology studies (Aide et al., 2000).

2. Materials and methods

2.1. Study area

The study was conducted during August 2005 in Sector Santa Rosa (85°36’54”W; 10°48’53”N) in the Área de Conservación Guanacaste (ACG, formerly Parque Nacional Santa Rosa), north-western Pacific region of Costa Rica (Janzen, 2000). The area is defined as a tropical dry zone. All the dTf of Costa Rica is located in ACG, and covers half the area of the total $120x10^3$ ha of the park, while 3,556 ha are dTf in Sector Santa Rosa (Maldonado et al., 1995; Kramer, 1997). The dTf is characterized by a well defined dry season (Mooney et al., 1995). Yearly average temperature and precipitation are 28 ºC and 1,530 mm, respectively, with a marked 6-mo dry season between November and May (Janzen, 1993). Geologic substrate at Santa Rosa is Pleistocene aeolian ash. Soils at the study area are of volcanic origin (Guanacaste volcanic Cordillera), and major soil parent material weathered in place are andesite to rhyolite ash-flow tuffs (ignimbrites) with intercalated fluvial deposits with high Fe content, and consisting mostly of plagioclase feldspar with biotite, hornblende, amphibole, and pyroxene (Weyl, 1980; PDX, 2005). Soils are classified as Inceptisols and Entisols (USDA taxonomy) defined as Typic Ustropept and Lithic Ustropept (Oficina de Planificación Sectorial Agropecuaria, 1999).

The dTf at Santa Rosa contains the highest number of plant families, genera, and species richness of all Central American dTfs (Gillespie et al., 2000). Acacia collinsii Saff. (Mimosaceae) (Spanish name “Cornizuelo”) and Quercus oleoides Schltdl. & Cham. (“Encino”) are two of the most abundant tree species (Janzen, 2000; Allen, 2001), although there is no single dominant species (Kalacska et al., 2004). Santa Rosa contains both evergreen forests dominated by live oak, Q. oleoides, but also a large number of other co-occurring species from the adjacent mixed deciduous forest where oaks are less common. These include Tabebuia ochracea Standl. (Bignoniaceae), the fern Selaginella sp., Enterolobium cyclocarpum (Jacq.) Griseb.

(Mimosaceae), Hymenaea courbaril L. (Fabaceae), Cecropia peltata L. (Moraceae), Bursera simaruba (L.) Sarg. (Burseraceae), Ficus spp., and Bromelia pinguin L. (Bromeliaceae).

Within tropical forests the dTf represents 42% of the total (Brown and Lugo, 1982), and is among the most endangered ecosystems worldwide (Mooney et al., 1995). Currently, only 0.5% of the original dTf area in Pacific Mesoamerica is under protection (Janzen, 1988; Calvo-Alvarado et al., 2009) and remains in Costa Rica (Quesada and Stoner, 2004). During the 1950's and for more than 30 years severe deforestation reduced the area covered by dTf (Sader and Joyce, 1988). Land conversion and cattle grazing and human-induced fires, hugely reduced the area covered by the dTf in Guanacaste (Houghton et al., 1991; Toledo, 1992; Maass, 1995). This favored the invasion of the exotic pyrophite grass Hyparrhenia rufa (Ness) which fueled more fires and transformed drastically the original dTf physiognomy (Daubenmire, 1972). The area affected by this grass was reduced after cattle removal in addition to a fire-suppression active program (Janzen, 1988b; Kramer, 1997). Since 1979 the area covered by pastures in the ACG has decreased and, nowadays, natural fires are totally absent from ACG (R. Blanco, pers. comm.) Fire is an important disturbance for natural succession in the dTf (Vieira & Scariot, 2006). The management strategy of fire control has promoted oak passive regeneration of secondary dTf in Costa Rica.

As analyses are expensive, only a limited number of stands were selected on the same edaphological unit, i.e., three dTf stands and a pasture plot (Figure 1): a) a remnant patch of old-growth forest >400 years old (Of), b) a secondary deciduous forest (Df), San Emilio (>80 years), c) a Q. oleoides forest of ca. 65 years old (Qu), and d) a yearly burned ancient pasture strip (Pa) (See list of plant species in appendix A). The vegetation structure of the Of is similar to the original dTf, it was never cleared except some old individual trees in the mid-forties of the last century, i.e., Swietenia macrophylla and Manilkara chicle (Janzen, pers. comm.). Some fires occurred in the late 1970s and early 1980s, when the pastures came closer to the edge of this forest, as an occasional event during late April to early May when leaf litter was extremely dry and burned very low to the ground and detached branches were converted to charcoal. Even today fire scars can be seen on the bases of the old-growth trees (Janzen, pers. comm.)

2.2. Soil sampling protocol

Four sampling points were selected along a 300-m transect line in each ecosystem. Optimal sampling distance for measuring SOC varies among studies from a few meters to tens and hundreds meters (Rossi et al., 2009). Despite no real plot replicates for each ecosystem were present, no significant pseudo-replication-induced bias was introduced in our results (Oksanen, 2001), as the inter-sampling distance, i.e., 100 m was higher than the minimum 25-50 m inter-sample distance that is recommended to avoid or reduce spatial dependence of variables in soil carbon studies (Powers and Veldkamp, 2005; Powers, 2006). Moreover, this procedure has also been used in recent studies (Paul et al., 2008) to reduce the possible effect of spatial autocorrelation between soil variables.

Leaf litter was hand-sorted within 0.5 m^2 metal frames and oven-dried at 60º C for 72 h prior to excavation of ca. 1x0.5 m^2 pits. Soil samples were carefully collected down to 50 cm depth from one of the pit walls and split into 10 cm increments. Soil sampling started from the deepest layer (40-50 cm) to avoid likely contamination of deeper layers with soil from upper layers. Approximately 0.5 kg of bulk soil was taken and air-dried at ambient temperature for several days. Samples were gently crumbled manually to break the aggregates along planes of weakness at field moist conditions. Soils were dropped from 1-m height onto a hard surface to ease aggregate separation, after air-drying, and sieved <8 mm to manually remove roots and stones before packing and shipping to the lab at OSU, Columbus (Ohio).

2.3. Soil physical properties

Soil bulk density (ρ_b) was measured with the core method in each layer by using a 5x5 cm metal cylinder (Blake and Hartge, 1986). Soil ρ_b was expressed on a dry weight basis after placing a small amount of soil in the oven and drying at 105º C for 48 h to determine soil moisture content. Soil texture was determined by the hydrometer method (Bouyoucos, 1962) in a composite sample with approximately 50 g of dry soil from the four samples collected in each ecosystem. No chemical treatment was used to remove labile or light fraction organic matter. Aggregate size-class distribution and mean weight diameter (MWD) were assessed by standard dry-sieving procedure (Kemper and Rosenau, 1986). A sub-sample of air-dried soil of ca. 60 g was passed through a column of sieves of 4.75, 2.0, 1.0, 0.5 and 0.250 mm and mechanically moved in an automatic shaker for 30 min to obtain 6 aggregate size-classes. Finally, soil pH was determined in <2 mm air-dried samples in H_2O (1:1, v/v) and 0.01 M $CaCl_2$ (1:1, v/v).

Additionally, we collected soil from surface ant hills of the fungus-growing ant Atta (Formicidae) in the Of for C and N comparisons.

2.4. Simplified particle-size fractionation

Owing to the specific purpose of our study we dispersed soil aggregates followed by wet-sieving to release the primary particles, i.e., clay, silt and sand size-particles (Emerson and Greenland, 1990). Briefly, 50 g of <2mm air-dried soil were dispersed in 50 ml 0.5 M sodium-hexametaphosphate + 75 ml deionized water for 18 h, and mechanically stirred in a multi-mixer for 30 minutes. Then, the soil suspension was passed through a nest of sieves of 250, 105, 53, and 20 μm diameter to separate the fine sand (105-250 μm), very fine sand (53-105 μm), coarse silt (20-53 μm) and silt+clay (<20 μm) fractions (USDA nomenclature), respectively, in beakers that were oven-dried at 60 °C for 72 h. By following this procedure we aimed at also quantifying the C and N concentrations in micro-aggregates, i.e. <250 μm. The suspension containing the <20 µm fraction was flocculated with $MgCl_2$ and allowed to settle before discarding the supernatant. Uncomplexed OM was not determined, although likely present in some of the fractions since no chemical methods were used to remove organic debris from the mineral fractions, and thus neither free nor particulate OM was quantified.

2.5. Carbon and Nitrogen determinations

Concentrations of total C and N were determined for <2 mm air-dried soil aggregates that were ground in a mortar and passed through a 250 μm sieve, and for each particle size fraction by dry combustion using a Vario Max CN Analyzer (Elementar GmbH, Hanau, Germany). The presence of inorganic C in carbonates was tested qualitatively with HCl. This test yielded negative results, and thus C concentration data were referred as organic C. The SOC pool to 50-cm depth was computed using equation 1 (Batjes, 1996):

$$\text{Mg SOC ha}^{-1} = \Sigma_{0\text{-}50}\,[\text{SOC}_{\text{layer}}\,(\text{kg Mg}^{-1}) \times (\rho_d)_{\text{layer}}\,(\text{Mg m}^{-3}) \times \text{soil depth (m)} \times 10^{-3}\,\text{Mg kg}^{-1} \times 10^{4}\,\text{m}^{2}\,\text{ha}^{-1}] \qquad \text{[Eq. 1]}$$

2.6. Mineral-associated and stable SOC

Chemical extraction and standard selective dissolution methods of oxalate, dithionite-citrate and pyrophosphate (USDA, Table 1) were used on bulk soil from each 10-cm depth increments. Acid oxalate predominantly extracts Al, Fe, and Si (Al_o, Fe_o, Si_o) from organic complexes and poorly ordered minerals such as ferrihydrite, allophane, and imogolite (Hartwig and Loeppert, 1993). Dithionite-citrate-extractable Fe (Fe_d) represents both crystalline and poorly crystalline Fe oxides, and dithionite-citrate-extractable Al (Al_d) represents Al substituted in Fe oxides and from the partial dissolution of poorly ordered Al (oxy)hydroxides (Kleber et al., 2005). Sodium pyrophosphate extracts all organically bound Al (Al_p) and an intermediate fraction of the organically bound Fe (Hartwig and Loeppert, 1993). The Fe_o/Fe_d ratio reflects poorly crystalline fraction of total Fe oxides (Kleber et al., 2005). Thus, Fe_d-Fe_o represents crystalline Fe oxides. Fe_o-Fe_p represents the content of ferrihydrite (López-Ulloa et al., 2005), while Al_p/Al_o ratio, which is an index of allophanic soil properties (Dahlgren et al., 1993), is the relative amount of Al that is in organic complexes (Kleber et al., 2007b). The amount of sesquioxides is represented as Al_o+0.5Fe_o (Spielvogel et al., 2008). For a more complete description of the selective chemical extractions see Lorenz et al. (2009).

Sodium persulfate ($Na_2S_2O_8$) was used to determine the amount of stable SOC (Eusterhues et al., 2003; Lorenz et al., 2008). The functionally passive SOC concentration was estimated as the amount of residual SOC left after treatment with hydrogen peroxide (H_2O_2) following a method described in Eusterhues et al. (2005).

Finally, soils were de-mineralized with hydrogen fluoride (HF) to isolate SOC from organo-mineral associations (Eusterhues et al., 2003). A more complete and detailed description of the chemical oxidation and separation methods can be consulted in Lorenz et al. (2009).

2.7. Statistical analyses

Normality of data distribution was explored for all variables with the Kolmogorov-Smirnov test. When necessary data were log transformed to meet the assumption of normality. A two-way analysis of variance (ANOVA-GLM procedure) was performed to test for significant differences with ecosystem and sampling depth as the fixed main factors for SOC and N concentrations, C:N ratio, ρ_b, MWD and size-class aggregates. A Bonferroni corrected probability procedure for nested tests was used to ensure against statistical error (Cooper, 1968). The probability levels of 0.05, 0.01 and 0.001 were adjusted by dividing them by 33 (11 analyses x 3 tests). When differences were significant, multiple post-hoc comparisons of means were tested with Fisher PLSD at $P<0.05$. Correlation analysis was performed with the Pearson product moment correlation between SOC and texture, and between SOC and C concentration in particle-size fractions. Finally, the t-test was used to search for statistical differences in SOC pool among the four sampled sites. All statistical analyses were performed with the SPSS for Windows v. 17.0 (© SPSS, Chicago, Illinois), and the Sigmaplot software v. 11.0 (© Systat Inc.) was used for graphics.

The main source/s of variation and significance were investigated with the between-within principal component analysis (PCA), a specific multivariate ordination technique. Firstly, a PCA is performed that focuses on between-groups' differences, i.e., ecosystems (old-growth forest, deciduous forest, Quercus forest, and burned ancient pasture) in order to identify the variables responsible in the definition of axes. Details on the use and interpretation of this between-class PCA can be found in Dolédec and Chessel (1989). The significance of variables and ordination of objects in the plane formed by the first two axes was tested with a Monte Carlo randomisation procedure with 10,000 simulations (Manly, 1991).

The between-PCA was followed by the within-class PCA in order to focus on the remaining variability after the ecosystem effect 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 (Dolédec and Chessel, 1991). The within-class PCA gave very similar results compared to a normalized PCA (data not shown), and differences between sites would have been masked by those obtained within each site. The data matrix contained 19 columns, i.e. number of variables, and 20 rows (4 sites x 5 depths), i.e. number of objects = samples. Analyses were performed with the Discriminant module included in the ADE4 software package (Thioulouse et al., 1997).

As we were also interested in the pattern of SOC stabilization within the three different forests, i.e., Of, Df, and Qu, a second data matrix was used for a between-within PCA. This matrix included data used in the first matrix with those data on SOC stabilization provided by Lorenz et al. (2009). This new data matrix contained 36 columns (variables) and 60 rows (samples).

3. Results

Soils at the study site were slightly acidic, and texture varied from sandy loam and sandy-clay loam texture to clay loam and clay in the upper and deeper soil layers, respectively (Table 2). Summary descriptive statistics of all variables used in this study is listed in Table 3. Statistically significant differences were found for the main fixed factor ecosystem for all variables (ANOVA, Table 4), and for the main fixed factor depth but for SOC and N concentrations only (ANOVA, $P<0.01$). No significant differences were found for the site and depth interaction.

SOC concentration was significantly higher in Of compared to the other ecosystems (Figure 2). Values decreased significantly with depth ($P<0.05$, Fisher PLSD test) in all ecosystems, and ranged from 37.2 to 61.3 g kg^{-1} in 0-10 cm and from 8.4 to 29.5 g kg^{-1} in 40-50 cm depth, respectively. The SOC concentration measured in the refuse material deposited in the surface ant hill at Of was within the range similar to that at 40-50 cm soil depth. Multiple post-hoc comparisons ($P<0.05$; Fisher PLSD test) for N(%) and C/N ratio are indicated in Table 5. In each ecosystem N concentration decreased significantly with increasing depth. The C:N ratio in the Pa was significantly greater ($P<0.05$) under Pa than under the three dTfs for all depths (Table 5). The C:N ratio decreased significantly with depth only in the Of.

Regarding soil structure the MWD of aggregates at Pa did differ significantly from that at the three dTf stands (Table 6). Significant differences were found in size-class aggregate distribution with depth at Of ($P<0.05$; Fisher PLSD test) for the 0.5-1 and 2-5 mm size-class aggregates, respectively (Figure 2). Statistical differences were found between Pa (<5% of aggregates <250 µm) and the dTf stands (10-25% of aggregates <250 µm). Aggregates larger than 4.75 mm were the most abundant class in all depths, while at the forest stands the percentage of size-class aggregate was similarly distributed in all depths, except for the <0.25 mm size-class aggregates at the Df (values not significant).

The SOC concentration decreased in particle size fractions of <200 µm aggregates with increasing soil depth (Figure 3), with the highest concentration in the silt+clay fraction (<20 µm). Negative and positive significant correlation was observed between the percentage of clay (r = 0.688; $p<0.001$) and sand (r = 0.627; p=0.003) with SOC (bulk soil), respectively, while no correlation was observed between the percentage of silt and SOC (Figure 4a). Regression analysis for <200 µm aggregates indicated that SOC concentration in the bulk soil correlated significantly with all particle size fractions in the order 20-53>53-105>20>105-200 µm particles (Figure 4b).

3.1. Between-within differences of soil physico-chemical variables (data matrix 1)

The first two axes of the between-class PCA performed on data matrix 1 were retained, explaining 92.8% of the total variability (Figure 5a). Axis I (71.9% of variability) mainly separated soil physical properties, while axis II (20.9% of variation) separated soil bulk density, pH, and SOC concentrations in the silt+clay fraction from the percentage of aggregates <250 µm. The projection of objects (sites) onto the factorial plane (Figure 5c) clearly separated the Pa from the three dTfs. The separation of ecosystems in the factorial plane of the between-class PCA was highly significant (Monte Carlo permutation test, $P<0.0001$).

With regards to the within-class PCA the first two axes captured 77.1% of variability (Figure 6a). Axis I (61.5% of the within-class inertia) discriminated soil samples with high clay content from those with high C concentrations in the coarse (105-200 µm) and fine sand (53-105 µm) fractions. Axis II (15.6% of total variability) separated soil samples with higher sand content from those with high silt content.

3.2. Between-within differences of SOC stabilization (data matrix 2)

There was a significant effect of vegetation on the C/N ratio in Pa compared to the three dTf stands at Santa Rosa (ANOVA; Table 3). Thus, we performed a second between-within analysis without data from Pa to test for significant trends between the three dTfs.

Axis I of the between-class PCA explained 58.2% of total variation and discriminated pH, silt+clay C, SOC concentration and Al_p from HF resistant C, clay%, $Na_2S_2O_8$ resistant C, coarse silt C, Si_d, soil N concentrations and percentage of 1-2 mm aggregates (Figure 7a). Thus, more alkaline soils with higher concentrations of C in finer particle-size fractions and bulk soil were discriminated from those containing relatively higher amounts of mineral associated and stable SOC, and C in coarser particle size fractions. Axis II (41.8% of total variance) separated Fe_o/Fe_d, percent <0.25 mm aggregates, Al_d, Al_o+0.5Fe_o, Al_o+Fe_o, Al_o, Si_o and Fe_o from clay%, percent 2-4.75 mm aggregates, silt%, Fe_d-Fe_o, BD and Fe_d.

Multivariate analysis also showed that concentration of crystalline Fe oxides (Fe_d-Fe_o) in 10-20, 20-30 and 30-40 cm depth were highest at Df, intermediate at Qu and lowest at Of. Crystalline Fe oxides were highly related to clay%, which also increased with depth (Figure 7a). Moreover, the ordination of variables in the PCA (Figure 7a) highlighted that the $Na_2S_2O_8$-resistant proportions at Of and Qu was negatively correlated with SOC concentration and augmented with soil depth at Df. The “eigenvalues” (Figure 7b) and projection of objects (sites) onto the factorial plane defined by both axes (Figure 7c) separated Of from Qu forest and the Df in axis I, while axis II separated the latter two (Figure 7c, top left). The mineral-associated and stable SOC pool increased with depth as revealed by axis I, while axis II resulted in soil texture differences, from a loamy to clayey soil (Figure 7c, bottom left). The ordination of the between-class PCA was highly significant ($P<0.0001$; Monte Carlo permutation test).

Regarding the within-class PCA the first two axes explained 49.8% of variation as revealed by the “eigenvalue” analysis (Figures 8a, b). Axis I (26.0% of the within-class inertia) separated soil samples containing high proportion of sesquioxides and Al-, Fe- and Si-minerals in organic complexes and poorly ordered minerals and high proportions of small aggregates, from soils with higher ratios of organically-bound to total amorphous Al, large aggregates and MWD (Figure 8a). Axis II (23.8% of total variability) separated stable SOC and clay% from C concentrations in the coarser fractions, C and N concentrations in bulk soil and sand% and silt%. The projection of objects onto the factorial plane is depicted in Figure 8c.

3.3. SOC and SON pools

The amount of litter collected was similar for Of and Qu, i.e., 1,326.7 ± 240.7 g m^{-2} and 1,322.0 ± 478.1 g m^{-2}, respectively, while it was 1,104.6 ± 726.2 g m^{-2} at Df (Table 6). No surface litter was present at Pa. The SOC pool to 50-cm depth was highest at Of, i.e., 228.9 Mg C ha^{-1}, and decreased in the order Df > Pa > Qu, with significant differences observed with the latter two (Table 7). The SOC pool under Of was 52.3% and two-fold higher than under Df and Qu and Pa, respectively (Table 7). Between 50 to 65% of the total SOC pool to 50-cm depth was found in the top 20 cm. With regards to the SON pool, soils from the Of and Df contained 18.7 and 13.1 Mg N ha^{-1}, respectively, and from 30 to 45% of total SON pool was located in the upper 0-10 cm soil layer (Table 7). Significant differences pattern was similar to that observed for the SOC pool.

4. Discussion

4.1. Comparison with other studies

Published data on SOC from several studies in dTfs from Central America are listed in Table 8. SOC concentration obtained in our study was higher to values reported by Powers et al. (2009) from the same area, while Johnson and Wedin (1997) reported a total soil C concentration in the topsoil at 52.3 and 42.6 g C kg^{-1} in dTf and H. rufa grassland, respectively, in soils developed from volcanic tuffs in southern "Guanacaste" ("Lomas Barbudal" biological reserve). More recently, at Santa Rosa total soil C concentration for 0-10 cm depth has been reported at 26.5 and 37.9 g kg^{-1} in a young Oak forest and a mixed deciduous forest, respectively, and 43.0 g C kg^{-1} in a dTf at Palo Verde National Park in the Pacific region (Powers et al., 2009). Based on another study conducted in the "Osa peninsula" of southwestern Costa Rica, total soil C concentration to 10-cm depth ranged from 65 to 68 g C kg^{-1} in a very humid lowland primary forest, and from 50 to 56 g C kg^{-1} for a 20 yr-old pasture on an Oxisol and Mollisol, respectively (Cleveland et al., 2003). These values corresponded to a total soil C pool in 0-10 cm that ranged from 33.8 to 44.9, and from 37.5 to 55.4 Mg C ha^{-1} in the primary forest and derived pasture, respectively. In the Mexican pacific coast, García-Oliva et al. (2004) reported a total soil C concentration in the dTf of 32.5 g kg^{-1} for 0-5 cm, and its conversion to pasture after slash-and-burn management reduced SOC concentration by 18%, i.e. 29 and 23 g kg^{-1}, respectively (García-Oliva et al., 2006). In the same area Paul et al. (2008) reported a SOC pool of 30.9-45.9 Mg C ha^{-1} at 0-10 cm depth in sedimentary and volcanic soils, respectively. In Puerto Rico, the SOC pool in 0-10 cm was estimated to be 61.6 and 65.8 Mg C ha^{-1} in a 50-yr and 70-yr old dTf, respectively (Erickson et al., 2002). The SOC pool at Of, i.e., 228.9 Mg C ha^{-1}, was within the range reported in humid secondary forests of northeastern Costa Rica (Powers and Veldkamp, 2005; Jiménez et al., 2008b), whereas it was lower for the 65 years-old dTf.

Our data from the dTf were lower than those globally estimated for the top 1 m of mineral soil by Jobbagy & Jackson (2000), i.e., 158 Mg C ha^{-1}. However, our data were higher and lower than those reported by Delaney et al. (1997) and Jaramillo et al. (2003) in the first 10 cm of mineral soil in mature dTf of Venezuela and Mexico, i.e., from 27.4 to 98 Mg C ha^{-1}, respectively. In a lower montane wet evergreen forest of Puerto Rico, Marin-Spiotta et al. (2009) reported SOC and SON pool of 77.2 and 88.5 Mg C ha^{-1}, and 7.0 and 6.9 Mg N ha^{-1} for 0-50 cm, during 60 and 80 years of secondary succession, respectively, values much lower than those obtained in our study (Table 7).

Comparatively to soils under moist forests from other sites in Central and South America (Schwendenmann and Pendall, 2006; Paul et al., 2008) soils in Sector Santa Rosa contained an important reservoir of SOC pool in the Of. Paul et al. (2008) reported a SOC pool from 30.9 to 45.9 Mg C ha^{-1} (0-10 cm) in sedimentary and volcanic soils under montane humid forests in Ecuador, values lower than those obtained in our study for the three dTfs stands.

N concentrations were high in the topsoil of Df and Of, i.e. 4.5 and 5.3 g kg^{-1}, respectively. These values were higher than those reported in the same area by Powers et al. (2009), i.e. 3.5 g kg^{-1} (0-10 cm), although similar to N concentrations found in a dTf at Palo Verde National Park. At Santa Rosa, soil N concentration in the Qu stand was higher than the value reported in Powers et al. (2009), i.e., 3.7 vs. 2.2 g kg^{-1} for the same area. The reason could be related to within-site soil differences in the various regenerated dTfs.

4.2. Soil organic carbon concentration in size-class aggregates

Aggregate fractionation revealed significant differences on soil structure at Sector Santa Rosa. Our data revealed a much higher proportion of >250 µm aggregates in the Pa as compared to the dTf stands. Conversion of forest into pasture leads to reduction in the distribution of >250 µm aggregates (Garcia-Oliva et al., 2006; Schwendenmann and Pendall, 2006). The proportion of >250 µm aggregates in dTf soils of the Pacific Mexican coast was 80% of the total (García-Oliva et al., 1999a), whereas these aggregates made up only 35% of the sand-free soil mass in pasture soils (García-Oliva et al., 2006). Cotler and Ortega-Larrocea (2006) found a greater content of aggregates >4.75 mm in an unburned pasture (Panicum maximum), in opposition to the burned pasture, where a higher content of <0.25 mm aggregates was observed. Between the pasture and the TDF soil, the largest differences were found among the <0.25 mm aggregates, which are dominant in the pasture soils. In our study, aggregates >4.75 mm were more than 90% of the total in the burned ancient pasture (Figure 2d), while at the dTf stands the percentage of size-class aggregate was similarly distributed in all depths. In another study, Noguez et al. (2008) found that aggregates >250 µm under forest soils were ca. 80% of the total fraction.

Data on the vertical SOC concentration within particle-size fractions in the dTf are scanty, and comparison with other studies is constrained by the few data available. A high variability exists among studies in the results obtained for C concentration in size-class aggregates. In the most recently recovered dTf, the Qu forest, SOC concentration was higher (average of the four size-class aggregates, Figure 3) than data reported in García-Oliva et al. (1994) and C concentration increased with decreasing size of aggregates in similar textured soils, i.e. sandy-clay loam as in the

Qu forest. García-Oliva et al. (1999) reported that in <53 and 53-250 µm fractions, total C ranged from 6 to 19, from 8 to 18 and from 19 to 60 g kg^{-1} in the dTf, a burned plot and a 10 yr-old pasture, respectively, while in the control dTf total C concentration was similar between >250 and <250 µm aggregates. They also reported that distribution of SOC across aggregate size fractions was strongly affected by slash-and-burn agriculture. The effect of burning on size-class aggregate C distribution was assessed by García-Oliva et al. (1994). A reduction of C concentration with decreasing size-class aggregates was observed after the dTf was converted to pasture in 0-2 cm depth. In our study the three dTfs were affected by different fire events of varying intensity and time lag that could have lead to a redistribution of size-class aggregates, in addition to other abiotic and biotic factors like tree root growth and biological activity related to the time elapsed since the last fire event. Differences are determined by fire management and duration which in the Qu forest occurred for longer periods than in the Df and Of (Lorenz et al., 2010), and continuous burning in the Pa could result in higher MWD of aggregates.

Results from different studies in Central America indicate discrepancies on the SOC concentration values reported in aggregates >250 and <250 µm differ among studies conducted in Central America dTfs. Cotler and Ortega-Larrocea (2006) found a significant positive and negative correlation between SOC concentration and >250 and <250 µm aggregates, respectively in a Mexican dTf. Ashman et al. (2003) and García-Oliva et al. (2003), on the contrary, reported that total soil C concentration in the same area was higher in <250 µm than in >250 aggregates (0-5 cm depth). These results were confirmed by Noguez et al. (2008) who reported C concentration in aggregates <250 µm at 43.6 mg C g^{-1}, higher than the values obtained in aggregates >250 µm, i.e., 28.8 mg C g^{-1}. These data are comparable to ours at Df and Qu dTfs, but lower at Of (Figure 3). Different results obtained among studies are the result of soil type, texture, clay content, and plant cover with OM of different quality.

4.3. Abiotic and biotic soil C stabilization processes

Results of the between-within PCA were interpreted to characterize the relationship between soil minerals and stabilized SOC fractions in 30-40 and 40-50 cm depth. The between PCA confirmed the analysis performed by Lorenz et al. (2009), i.e., mineral-associated and stable SOC pool increased with depth and C was preferentially bound to soil minerals (HF extraction) at both Of and Df compared to Qu, while the pool of functionally passive SOC was larger at Of than at Df and Qu forests. In other words, H_2O_2-resistant SOC pool in each depth and the total C pool down to 50-cm depth was higher in the order Of > Df > Qu.

Stabilization of SOC by Al-complexes has been revealed by Powers and Schlesinger (2002). In our study, this was the case in the Qu forest, as indicated by the positive relationship with Al_p/Al_o ratio, which was also related to Al- and Si-minerals (Figure 8a). The mineral-associated and stable SOC pool increased with depth as indicated by the multivariate analysis. Particularly, poorly crystalline Fe oxides and ferrihydrite were the most important minerals for SOC stabilization at 40-50 cm depth. High Fe_o/Fe_d ratios indicated that poorly crystalline Fe oxides were important for SOC stabilization at Of. Ferrihydrite was more relevant for SOC stabilization at Df and Qu forests as indicated by Fe_d-Fe_o with increasing depth and clay% in the PCA. No statistical differences were reported between stable SOC among the three dTfs (Lorenz et al., 2009). The regressions among selective dissolution data, mineral phase indicators and stabilized SOC indicate that poorly crystalline Fe oxides are most important for SOC stabilization in secondary dTf sub-soils (Lorenz et al., 2009).

Non-crystalline clays and metal-humus complexes also increase soil C residence times and pool sizes by decreasing the accessibility of soil C to microbes (Sollins et al, 1996). Regarding soil texture, Powers and Schlesinger (2002) reported that Al_p/Al_o was positively correlated with %clay and negatively correlated with Fe_o in volcanic soils from very humid forest soils at La Selva Biological Station (northeastern Costa Rica). They found that ferrihydrite was negatively related to clay% and positively related to silt%. In our study Fe_o was indeed negatively correlated with clay% but also with silt% in the between-PCA (Figure 7a). Regarding Al_p/Al_o the relationship with clay% was very weak, and the within-PCA indicated a negative correlation with Fe_o (Figure 8a).

Soil C concentration was positively correlated with Al-humus complexes (Powers and Schlesinger, 2002), and the stabilization of soil C is determined by Al-humus complexes and non-crystalline hydroxides (Masiello et al., 2004), which are important for C stabilization at time scales longer than several decades (Paul et al., 2008). We also found a correlation of SOC with Al_p in the within-PCA (Axis II, negative axis, Figure 8a), especially in the topsoil of the Qu forest, but not in the between-PCA, where both variables were in opposite sides of Axis I (Figure 7a). The within-PCA revealed intra-site differences, mainly related to soil texture variations with increasing depth. This relationship can thus be useful to determine within-site differences. Other studies have reported this relationship in different soil types, including volcanic ash soils (de Koning et al., 2003). The different results obtained reflect variation in climate, parent material, weathering processes and land management like fire use, between more humid and drier forests in Costa Rica.

Clay mineralogical composition varies with soil development. Clays are transformed through weathering processes from non crystalline, allophanic minerals to Al/Fe–humus complexes and crystalline minerals such as kaolinite and gibbsite. Soils in the dTf of Sector Santa Rosa contain a high proportion of Al_p/Al_o which indicates that Si-minerals have been removed and gibbsite and goethite are the most likely dominant residual minerals. The relative amounts of Al in organic complexes (Al_p/Al_o) are not statistically different among depths and sites (Lorenz et al., 2009). The dTf at Santa Rosa is characterized by less-weathered, allophanic soils, as revealed by the Al_p/Al_o ratios below 0.5 throughout the profile at Of whereas this ratio is >0.5 at Df indicating that Al complexed by organic acids may have been present (Lorenz et al., 2009). Compared to soils in humid forests from northeastern Costa Rica, soils at dTfs in the Pacific region seem to have higher potential to stabilize SOC.

Knowledge of soil C stabilization mechanisms is necessary as these are varied. Among the factors that determine accumulation and stabilization of SOC are those related to soil biological activity, i.e. the rates of litter and OM inputs that are incorporated into the soil by invertebrates, such as diplopods, ants, beetles and earthworms, and belowground inputs from roots, root exudates, microorganisms, and stabilization by association with soil minerals. We do know little about the factors controlling the stability of carbon in deep soil layers. Some studies have highlighted that the stability of OC in deep soil layers is maintained in the absence of fresh organic C, an essential source of energy for soil micro-organisms, i.e. bacteria and fungi (Fontaine et al., 2007). A strong role for organo-mineral interactions in C stabilization within aggregates <250 µm has been demonstrated by Lehmann et al. (2007). The higher content of aliphatic and carboxylic C of microbial origin than the OM of the aggregates <250 µm indicated that interactions between microbial metabolites and surface of minerals are important in initiating SOC stabilization (Lehmann et al., 2007). However, the stability of SOC in deep soil layers cannot entirely be ascribed to SOC fixation on minerals (Fontaine et al., 2007). These authors demonstrated that stabilization of SOC in deep soil layers was controlled by the incorporation of fresh C supply. SOC in deeper layers can persist because it is bound to soil minerals and exists in forms that decomposers cannot access (Baldock and Skjemstad, 2000).

Soil invertebrates excrete faecal pellets and reduce the size of organic residues that are then decomposed by micro-organisms, and also protect OM from further decomposition by occlusion within aggregates (Lavelle and Spain, 2001). Important soil biological activity was observed in the Df and Of where abundant beetles (Elateridae, Coleoptera) and earthworms (Oligochaeta) were present. In the Of, ant nests of the genus Atta (Formicidae, Hymenoptera) were also present and SOC concentration in the ant hill equaled that observed at 40-50 cm depth. Low C concentration in the ant hills have been reported in other studies from tropical sites (Decaëns et al., 2001; Jiménez et al., 2008a). This soil translocation contributes to patchy distribution of low SOC concentration areas (Figure 2). More studies are needed on the ecology of soil invertebrates from the dTfs and their influence on SOC accumulation and stabilization in aggregates.

4.4. Preliminary SOC accumulation rates in the dTf at Santa Rosa

The SOC accumulation rates across global vegetation types and climates vary considerably (Post and Kwon, 2000). Furthermore, SOC varies regionally with stand age and vegetation composition (Powers, 2004). For instance, the SOC pool in tropical old-growth forests tends to decrease exponentially as the temperature/precipitation ratio increases, corresponding to a gradient from wet to dry forests (Brown and Lugo, 1982). The soil C accumulation rate in wet forests is half the value observed in the dTf over a 100-year time period, i.e. 0.51 and 1.02 Mg C ha^{-1} yr^{-1}, respectively (Silver et al., 2000). A strong significantly linear relationship between soil C and forest age exists, at least during the first 100 years after recovery (Silver et al., 2000), although previous estimates are inconclusive (Lugo and Brown, 1993). This may indicate differences in organic matter contents due to previous land use since most fertile soils are generally used for pasture establishment or other agricultural land uses, even during the pre-hispanic period (Janzen, pers. comm.) The data analysed by Silver et al. (2000) showed that soil C concentrations in land uses derived from dTfs were initially high to start with, but the low number of replicates indicates the need for additional studies.

Our results agree with Vargas et al. (2008), who have reported increases in the SOC pool after recovery of the dTf. In the dry subtropical forest, the rates of C accumulation during forest establishment after agriculture use have ranged from loss, i.e. -13.1 g C m^{-2} yr^{-1} in the pasture to gain of 0.38 Mg C ha^{-1} yr^{-1} after 25 and 35 years after establishment (Smith et al., 1951, op. cit. in Post and Kwon, 2000, and Brown and Lugo, 1990), respectively. In our study, the SOC pool increased with age of the restored dTf (Table 7), from 0.009 and 0.25 Mg C ha^{-1} yr^{-1} in the 0-10 and 0-20 cm between the Df and Of, respectively. No conclusion is to be drawn from these figures as no information was available about how much C was initially lost after replacement of the dTf and what the amount already incorporated into the soil after land conversion. From 18 to 25% reduction in SOC concentration in fire-affected dTf soils has been reported (García-Oliva et al., 2006; Erickson et al., 2002), and more recently SOC changes related to history of fire events have been revealed (Lorenz et al., 2009).

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Appendix A. List of vascular plant species in the burned ancient pasture of Sector Santa Rosa[1]

Family	Genus/Species	Descriptor
Poaceae (= Gramineae)	*Axonopus aureus*	Beauv.
	Hyparrenia rufa	(Nees) Stapf.
	Ischaemum rugosum	Salisb.
	Lasiacis ruscifolia	(Kunth) Hitchc.
	Lasiacis sorghoidea	(Desv. ex Hamilton) A.S. Hitchc. & Chase
	Melinis minutiflora	Beauv.
	Oplismenus burmannii	(Retz.) Beauv.
	Oryza latifolia	Desv.
	Panicum maximum	Jacq.
	Panicum sp.	
	Panicum trichoides	Sw.
	Paspalum sp.	L.
	Paspalum virgatum	L.
	Rottboellia cochinchinensis	(Lour.) W.D. Clayton
Cyperaceae	*Scleria* sp.	Wall.
	Fimbristylis spadicea	(L.) Vahl
	Eleocharis sp.	
	Cyperus sp.	L.
	Cyperus surinamensis	Rottb.
	Rhynchospora sp.	
	Rhynchospora barbata	(Vahl.) Kunth
Asclepiadaceae	*Asclepia woodsianiana*	
	Asclepia oenotheroides	
Asteraceae	*Baltimora recta*	L.
Boraginaceae	*Heliotropium filiforme*	Lehm.
Fabaceae/papillonaceae	*Crotalaria incana*	L.
	Eriosema diffusum	(Kunth)G.Don
	Indigofera costaricensis	Benth.
	Indigofera suffruticosa	P. Mill.
	Tephrosia vicioides	Schldl.
Fabaceae/mimosaceae	*Acacia farnesiana*	L.
	Dalea cliffortiana	Willd.
	Mimosa pigra	L.
Iridaceae	*Cipura campanulata*	Ravenna
Malvaceae	*Sida barclayi*	Baker f.
Ponteridaceae	*Heteranthera limosa*	Sw. Willd
	Heteranthera spicata	J. Presl.
Rubiaceae	*Spermacoce exilis*	(L.O. Williams) C. Adams
Scrophulariaceae	*Bacopa* sp	

Bacopa salzmannii	(Benth.) Wettst.
Buchnera pusilla	Kunth
Polypremum procumbens	L.
Scoparia dulcis	L.
Stellaria ovata	Willd. ex Schlecht.
Stemodia durantifolia	(L.) Sw.

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[1] Prepared by A. Guadamuz, “Area de Conservación Guanacaste”.

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Figure captions

Fig 1. Vertical SOC concentration (mean ± 1 S.E.) in the four ecosystems studied at Santa Rosa. Fisher PLSD test critical significance level is 4.3 and 4.8 ($P<0.05$) for ecosystem and depth, respectively.

Fig 2. Size-class aggregate distribution with depth in the four ecosystems analysed. Only significant differences for each size-class aggregate are indicated ($P<0.05$, Fisher PLSD). NS = Not significant.

Fig 3. Vertical SOC concentration in the different particle size fractions at Santa Rosa; clay+silt (<20 µm), coarse silt (20-53 µm), very fine sand (53-105 µm) and fine sand (105-200 µm).

Fig 4. a) Regression analysis between the percentage of clay (black dots), silt (blue triangles) and sand (red squares) and SOC concentration in the bulk soil; b) correlation between SOC concentration in the bulk soil and SOC in the different particle size fractions in <250 µm aggreagates.

Fig 5. Between-class PCA of the soil variables (data matrix 1). a) ordination of variables; b) “Eigenvalues” diagram; c) projection of sampling sites owing to categories soil depth and texture onto the factorial plane defined by the first two axes. $P<0.0001$ (Montecarlo simulation).

Fig 6. Within-class PCA of the soil variables (data matrix 1). a) Projection of the sampling sites onto the factorial plane defined by axes 1 and 2; b) “eigenvalues” diagram; c) the ecosystem effect is removed by placing the center of classes (representing the 4 stands) at the origin of the factorial maps (top left); open circles are placed at the centre of gravity of each soil depth and texture (the lines connect the different ecosystems to their corresponding category).

Fig 7. Between-class PCA of the soil variables (data matrix 2). a) ordination of variables; b) projection of sampling sites onto the factorial plane defined by the first two axes extracted in the analysis. $P<0.0001$ (Montecarlo simulation).

Fig 8. Within-class PCA of the soil variables (data matrix 2). a) Projection of the sampling sites onto the factorial plane defined by axes 1 and 2; b) “eigenvalues” diagram; c) ordination of sites with all centroids (representing the three dTfs) at the origin; open circles are placed at the centre of gravity of each soil depth and texture (the lines connect the different ecosystems to the corresponding category).

Tables

Table 1. Overview of chemical extraction and separation treatments for targeted SOC-related and mineralogical variables (from Lorenz et al. 2009).

Table 2. Soil texture and pH in the four ecosystems, Sector Santa Rosa, Costa Rica.

Table 3. Summary statistics for all soil variables analysed in this study.

Table 4. Two-way ANOVA for all soil variables studied in the four ecosystems, Sector Santa Rosa, Costa Rica. The F-ratios for each variable are indicated. Bonferroni corrected P for 0.05, 0.01 and 0.001 are 0.0015(*), and 0.0003 (**), and 0.00003(***), respectively; NS, not significant.

Table 5. Mean N concentrations and C:N ratios in all ecosystems studied, Sector Santa Rosa, Costa Rica. Within rows, different capital letters indicate significant differences between mean values for ecosystems (P<0.05, Fisher PLSD test). Within columns, different lowercase letters indicate significant differences between mean values for depth (P<0.05, Fisher PLSD test). Standard error within parentheses.

Table 6. Mean values of soil bulk density (ρ_b) and mean weight diameter (MWD) of soil aggregates down to 50 cm depth in the four systems studied in “Sector Santa Rosa”, Guanacaste. Within columns, different lowercase letters indicate significant differences between mean values for depth (P<0.05, Fisher PLSD test). Standard error within parentheses.

Table 7. Litter C pools and vertical distribution of SOC pools (Mg C ha^{-1}) by 10-cm depth increments in the ecosystems studied. Values followed by the same letter are statistically different at P<0.01 (t-test).

Table 8. SOC concentrations in selected studies conducted in different successional dry tropical forests (dTfs) and pastures in Central America.

Table 1

Treatment/Ratio	Extraction and separation output
Hydrogen fluoride	Mineral-associated SOC pool
Hydrogen peroxide	Functionally passive SOC pool
Sodium persulfate	Stable SOC pool
$Al_o + 0.5\ Fe_o$	Sesquioxides
Al_p/Al_o	Ratio organically-bound to total amorphous Al, relative amount of Al in organic complexes
$Fe_o - Fe_p$	Ferrihydrite
$Fe_d - Fe_o$	Crystalline Fe oxides
Fe_o/Fe_d	Poorly crystalline fraction of Fe oxides
Pyrophosphate	Organically-bound Al and intermediate fraction of organically-bound Fe
Dithionate-citrate	Fe in crystalline and poorly crystalline Fe oxides, Al substituted in Fe oxides and Al in partial dissolved poorly ordered Al (oxy) hydroxides
Acid ammonium-oxalate	Al, Fe, Si in organic complexes and poorly ordered minerals

Table 2

Ecosystem	Soil depth (cm)	Soil separates (%)			Textural class	pH	
		Sand	Silt	Clay		H_2O 1:1	$CaCl_2$
> 400 years-old growth deciduous forest (Of)	0-10	60.8	21.9	17.3	Sandy loam	6.7	6.6
	10-20	55.0	25.8	19.2	Sandy loam	6.9	6.6
	20-30	50.6	26.2	23.2	Sandy clay loam	6.8	6.3
	30-40	44.4	26.2	29.4	Clay loam	6.8	6.2
	40-50	55.1	20.8	24.1	Sandy clay loam	6.7	6.1
>80 years-old deciduous forest (Df)	0-10	52.3	22.7	25.0	Sandy clay loam	6.5	6.2
	10-20	38.6	26.6	34.9	Clay loam	6.5	6.1
	20-30	38.9	24.3	36.8	Clay loam	6.5	6.1
	30-40	23.3	24.9	51.8	Clay	6.3	6.1
	40-50	15.8	27.4	56.7	Clay	6.2	5.9
65 years old Quercus forest (Qu)	0-10	61.4	14.2	24.5	Sandy loam	6.1	5.6
	10-20	45.4	20.2	34.4	Sandy clay loam	6.0	5.2
	20-30	45.4	20.2	34.4	Sandy clay loam	5.9	5.3
	30-40	46.8	21.1	32.1	Sandy clay loam	5.7	5.2
	40-50	38.9	27.0	34.1	Clay loam	5.6	5.1
Burned ancient pasture (Pa)	0-10	21.6	28.0	50.4	Clay	5.8	5.2
	10-20	17.9	25.8	56.3	Clay	5.8	5.3
	20-30	37.8	13.9	48.3	Clay	5.8	5.5
	30-40	34.8	14.8	50.4	Clay	6.1	5.7
	40-50	11.6	23.2	65.2	Clay	6.2	5.8

Table 3

Variables	Mean	Std Dev	Std. Error	C.V.^{1}	Skewness	Kurtosis	K-S^2
SOC_HF	43.13	15.295	1.975	35.47	0.768	0.253	**0.038**
SOC_H_2O_2	4.61	2.164	0.279	46.93	1.499	2.252	**<0.001**
SOC_$Na_2S_2O_8$	10.65	6.786	0.876	63.72	1.608	3.207	**0.002**
C(%)	2.84	1.685	0.218	59.31	0.856	0.108	**0.088**
N(%)	0.24	0.145	0.019	60.67	0.922	0.107	**0.019**
C/N	11.97	1.521	0.196	12.71	1.620	3.043	**<0.001**
MWD (mm)	2.04	0.926	0.120	45.46	1.341	2.506	**0.045**
Bulk density (g cm^{-3})	1.11	0.164	0.021	14.74	-0.802	1.453	0.287
<0.25 mm	13.10	10.052	1.298	76.76	1.279	1.199	**<0.001**
0.25-0.5 mm	12.64	5.098	0.658	40.34	-0.170	0.401	0.510
0.5-1 mm	20.81	8.983	1.160	43.18	2.510	13.393	**<0.001**
1-2 mm	19.86	5.542	0.715	27.91	0.732	4.190	**0.026**
2-4.75 mm	20.76	9.093	1.174	43.79	-0.252	-0.482	0.105
>4.75 mm	12.84	13.585	1.754	105.80	2.445	6.717	**<0.001**
Fe_o/Fe_d	0.07	0.031	0.004	44.40	0.168	-0.404	0.285
Fe_d-Fe_o	14.53	4.454	0.575	30.65	0.394	-0.847	**0.008**
Al_o+0.5Fe_o	1.43	1.225	0.158	85.48	2.742	8.957	**<0.001**
Al_o+Fe_o	1.93	1.437	0.186	74.38	2.746	9.455	**<0.001**
Al_p/Al_o	0.66	0.681	0.088	102.87	3.162	11.578	**<0.001**
Al-Dit	2.26	1.326	0.171	58.70	1.467	2.148	**<0.001**
Fe-Dit	15.53	4.473	0.577	28.80	0.337	-0.900	**0.016**
Si-Dit	0.90	0.243	0.031	27.00	-0.141	-0.744	0.339
Al-Oxa	0.93	1.022	0.132	109.42	2.676	7.997	**<0.001**
Fe-Oxa	1.00	0.468	0.061	46.89	2.136	8.563	**<0.001**
Si-Oxa	0.41	0.559	0.072	135.68	2.965	9.293	**<0.001**
Al-Pyr	0.36	0.214	0.028	59.78	1.468	1.541	**<0.001**
Fe-Pyr	0.31	0.172	0.022	55.13	1.227	2.267	0.121
Si-Pyr	0.41	0.356	0.046	85.99	4.397	22.810	**<0.001**

C.V. = Coefficient of variation (%)
K-S = Kolmogorov-Smirnov probability test

Table 4

Source of variation	*df*	C	N	C/N ratio	MWD	ρ_d	Aggregate size-class distribution (mm)					
							<0.25	0.25-0.50	0.50-1.00	1.00-2.00	2.00-4.75	>4.75
Ecosystem (A)	3	42.38 **	39.09 **	11.61 **	42.68 **	21.92 **	18.64 **	28.08 **	20.04 **	22.83 **	7.71 **	41.55 **
Depth (B)	4	66.60 **	53.84 **	0.28 NS	0.71 NS	0.57 NS	1.26 NS	1.04 NS	0.73 NS	0.32 NS	4.64 NS	1.29 NS
Interaction AxB	12	0.34 NS	0.75 NS	0.31 NS	0.76 NS	1.56 NS	1.19 NS	0.74 NS	0.95 NS	0.79 NS	1.14 NS	0.71 NS
Sum of squares	60	27.50	0.24	368.51	66.77	1.02	3590.39	1282.96	4216.10	2419.76	4282.72	22374.24
Mean of squares	60	0.46	0.004	6.14	1.11	0.02	59.84	21.38	70.27	40.33	71.38	372.90

Table 5

Depth (cm)	Variable	Forest stands			Grassland
		Of	Df	Qu	Pa
0-10	N (%)	0.53 (0.06) A,a	0.45 (0.13) B,a	0.37 (0.12) C,a	0.25 (0.04) D,a
	C/N	*11.5 (0.3) B,a*	*11.3 (0.3) B,a*	*12.4 (0.6) B,a*	*15.0 (0.8) A,a*
10-20	N (%)	0.36 (0.09) A,b	0.23 (0.05) B,b	0.21 (0.07) B,b	0.13 (0.05) C,b
	C/N	*11.8 (0.7) B,a*	*11.2 (0.3) B,a*	*11.6 (0.7) B,a*	*15.6 (1.5) A,a*
20-30	N (%)	0.27 (0.07) A,c	0.18 (0.05) B,c	0.12 (0.03) C,c	0.08 (0.04) D,c
	C/N	*12.7 (0.7) B,ab*	*11.3 (0.1) BC,a*	*11.1 (0.2) C,a*	*16.3 (2.6) A,a*
30-40	N (%)	0.24 (0.06) A,cd	0.13 (0.04) B,d	0.10 (0.03) BC,c	0.07 (0.02) C,c
	C/N	*13.7 (1.1) B,b*	*12.0 (0.5) C,a*	*11.0 (0.6) C,a*	*15.5 (2.5) A,a*
40-50	N (%)	0.22 (0.08) A,d	0.10 (0.03) B,d	0.08 (0.02) B,c	0.06 (0.02) B,c
	C/N	*13.7 (1.3) B,b*	*12.0 (0.4) C,a*	*12.0 (1.4) C,a*	*15.6 (2.6) A,a*

Values are means of 4 replicates

Table 6

Depth (cm)	Variable	Of	Df	Qu	Pa
0-10	ρ_b	1.07 (0.04) B,a	1.24 (0.07) C,a	1.05 (0.02) A,b	1.13 (0.06) B,a
	MWD	*2.12 (0.17) A,a*	*2.32 (0.15) A,a*	*1.98 (0.38) A,abc*	*4.07 (0.64) B,a*
10-20	ρ_b	1.19 (0.05) B,b	1.17 (0.05) B,a	0.91 (0.03) A,a	1.39 (0.04) C,c
	MWD	*2.03 (0.23) A,a*	*2.31 (0.15) A,a*	*1.66 (0.57) A,ab*	*4.70 (0.84) B,ac*
20-30	ρ_b	1.19 (0.06) B,b	1.23 (0.05) B,a	0.98 (0.10) A,b	1.36 (0.04) C,c
	MWD	*1.66 (0.10) A,a*	*2.39 (0.39) B,a*	*1.32 (0.38) A,a*	*5.38 (0.72) C,bc*
30-40	ρ_b	1.23 (0.04) B,b	1.18 (0.07) B,a	0.89 (0.14) A,a	1.34 (0.06) C,b
	MWD	*1.37 (0.11) A,a*	*2.45 (0.56) C,a*	*2.13 (0.77) B,bc*	*5.25 (0.66) D,bc*
40-50	ρ_b	1.15 (0.03) A,a	1.14 (0.08) A,a	1.08 (0.09) A,c	1.34 (0.04) B,b
	MWD	*1.51 (0.28) A,a*	*2.08 (0.09) AB,a*	*2.52 (0.94) B,c*	*5.88 (0.44) C,b*

Values are means of 4 replicates

Table 7

Depth (cm)		Of	Df	Qu	Pa
Litter C		6.6	5.5	6.6	0
0-10	C	65.9	63.0	48.2	42.2
	N	*5.71*	*5.54*	*3.89*	*2.82*
10-20	C	49.3	30.4	21.1	27.4
	N	*4.26*	*2.70*	*1.88*	*1.85*
20-30	C	39.7	25.1	12.7	16.4
	N	*3.19*	*2.22*	*1.15*	*1.14*
30-40	C	40.1	18.5	10.0	12.7
	N	*3.00*	*1.54*	*0.92*	*0.89*
40-50	C	33.9	13.3	10.6	11.3
	N	*2.57*	*1.09*	*0.89*	*0.77*
Total[1]	SOC	228.9 a	150.3 ab	102.6 b	110.0 b
	SON	*18.72 a*	*13.09 ab*	*8.72 b*	*7.47 b*

[1] Litter not included

Table 8

Region, Country	Site	Plant community composition[1]	Soil type	Soil depth (cm)	SOC ($\text{g kg dry soil}^{-1}$)	Reference
Mexico	Chamela-Cuixmala reserve	Deciduous forest	Entisol	0-2	37.4	García Oliva et al., 1994
Mexico	Chamela	Deciduous forest	Entisol	2-5	21.1	García Oliva et al., 1994
Mexico	Chamela	Recently burned forest	Entisol	0-2	27.2	García Oliva et al., 1994
Mexico	Chamela	Recently burned forest	Entisol	2-5	21.1	García Oliva et al., 1994
Mexico	Chamela	10 yr-old pasture	Entisol	0-2	25.6	García Oliva et al., 1994
Mexico	Chamela	10 yr-old pasture	Entisol	2-5	15.3	García Oliva et al., 1994
Mexico	Chamela	Deciduous forest	Eutric Regosol	0-5	86.1	Cotler and Ortega-Larrocea, 2006
Mexico	Chamela	Unburned pasture	Eutric Regosol	0-5	27.0	Cotler and Ortega-Larrocea, 2006
Mexico	Chamela	burned pasture	Eutric Regosol	0-5	36.6	Cotler and Ortega-Larrocea, 2006
Mexico	Chamela	Deciduous forest	Eutric Regosol	0-5	28.3-44.1	Noguez et al., 2008
Puerto Rico	Guánica forest reserve	Deciduous, semi-deciduous forest	Calciustolls (Mollisol)	0-10	50.7[2]-72.5[3]	Erickson et al., 2002
Puerto Rico		70 yr-old semi-deciduous forest	Calciustolls (Mollisol)	0-10	77.9-78.8	Erickson et al., 2002
Costa Rica	Guanacaste, Lomas Barbudal	Dry tropical forest	Inceptisol	0-15	52.3	Johnson & Wedin, 1997
		Pasture	Inceptisol	0-15	42.6	Johnson & Wedin, 1997
Costa Rica	Guanacaste, ACG; Sector Santa Rosa	Dry tropical forest, Quercus	Inceptisol	0-10	26.5	Powers et al. 2009
		Dry tropical forest	Inceptisol	0-10	37.9	Powers et al., 2009
Costa Rica	Guanacaste, Palo Verde	Deciduous forest	Inceptisol	0-10	43.0	Powers et al., 2009
Costa Rica	Guanacaste, Osa peninsula	Wet deciduous forest	Oxisol	0-10	50-65[4]	Cleveland et al., 2003
		20 years old pasture	Mollisol	0-10	56-68[4]	Cleveland et al., 2003
Costa Rica	Guanacaste, ACG; Sector Santa Rosa	Old-growth forest (Of)	Inceptisol	0-10 to 40-50	61.3; 41.6; 33.4; 32.7; 29.5	This study
		Deciduous forest (Df)	Inceptisol	0-10 to 40-50	50.9; 26.0; 20.4; 15.7; 11.6	This study
Costa Rica	Guanacaste, ACG; Sector Santa Rosa	Quercus forest (Qu)	Inceptisol	0-10 to 40-50	45.8; 23.3; 12.9; 11.2; 9.9	This study

	Burned ancient pasture (Pa)	Inceptisol	0-10 to 40-50	37.3; 19.7; 12.1; 9.5; 8.4		This study

[1] Forest types are named as they were originally in the published paper.

[2] Pasture until 1950s

[3] Pasture until 1950s, then burned in 1970s

[4] Figures refer to SOC concentration in a pasture and forest, respectively [4] Pasture until 1950s, then burned in 1970s

Figure 1

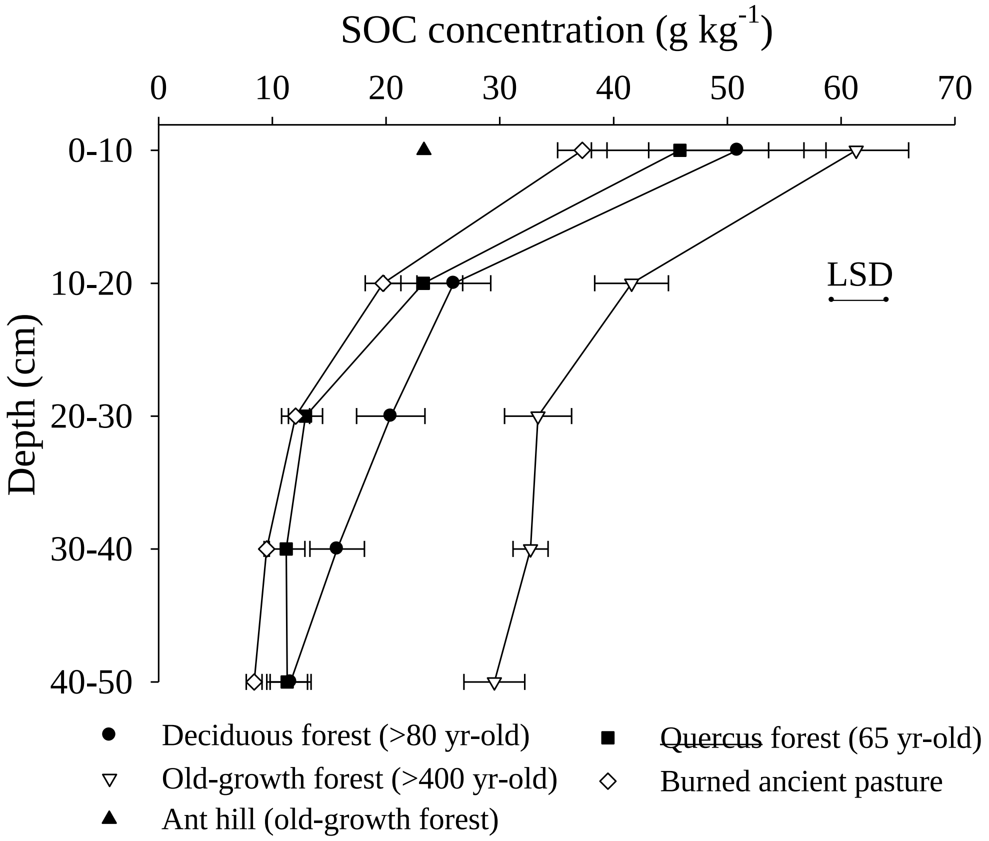


Fig 1.

Figure 2

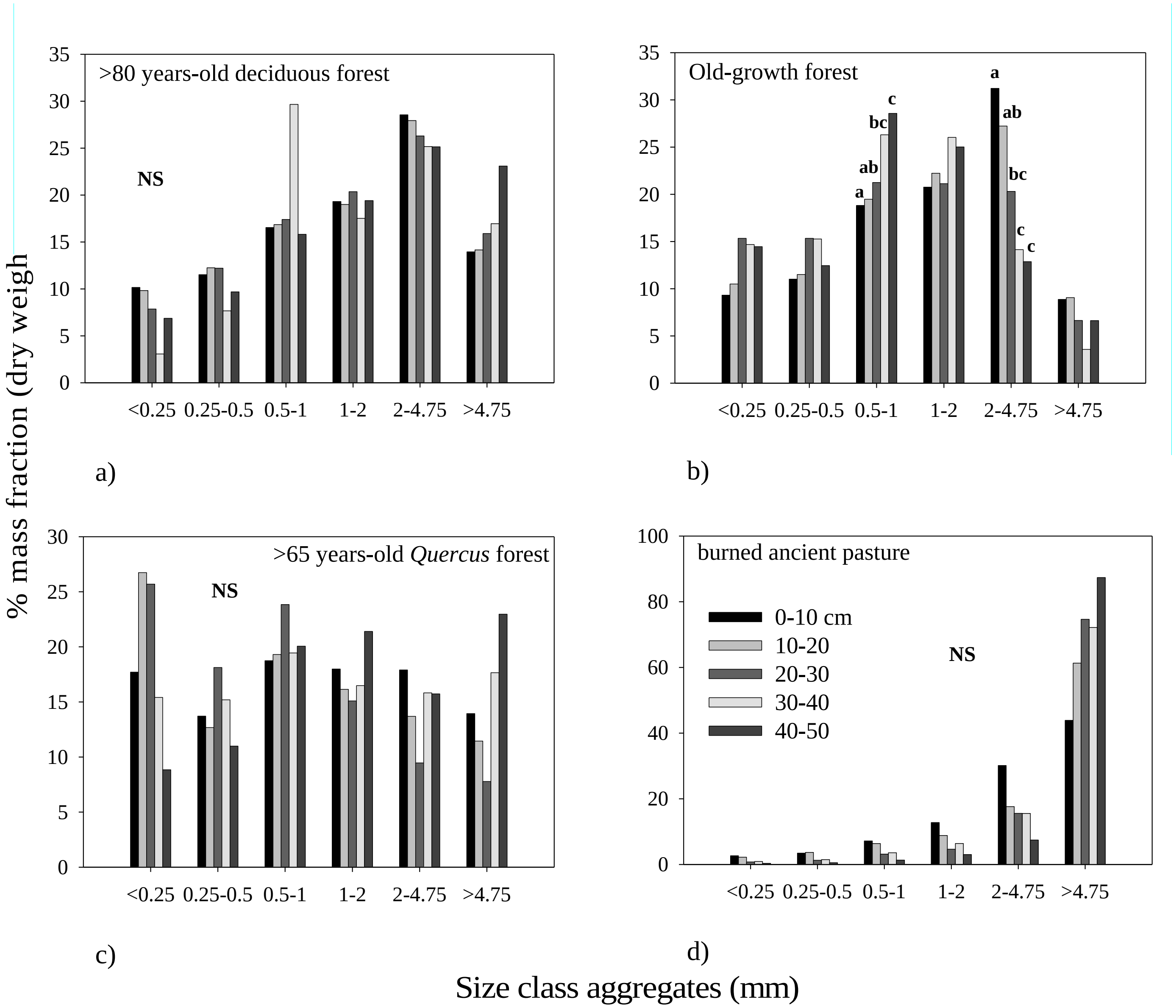


Fig 2.

Figure 3

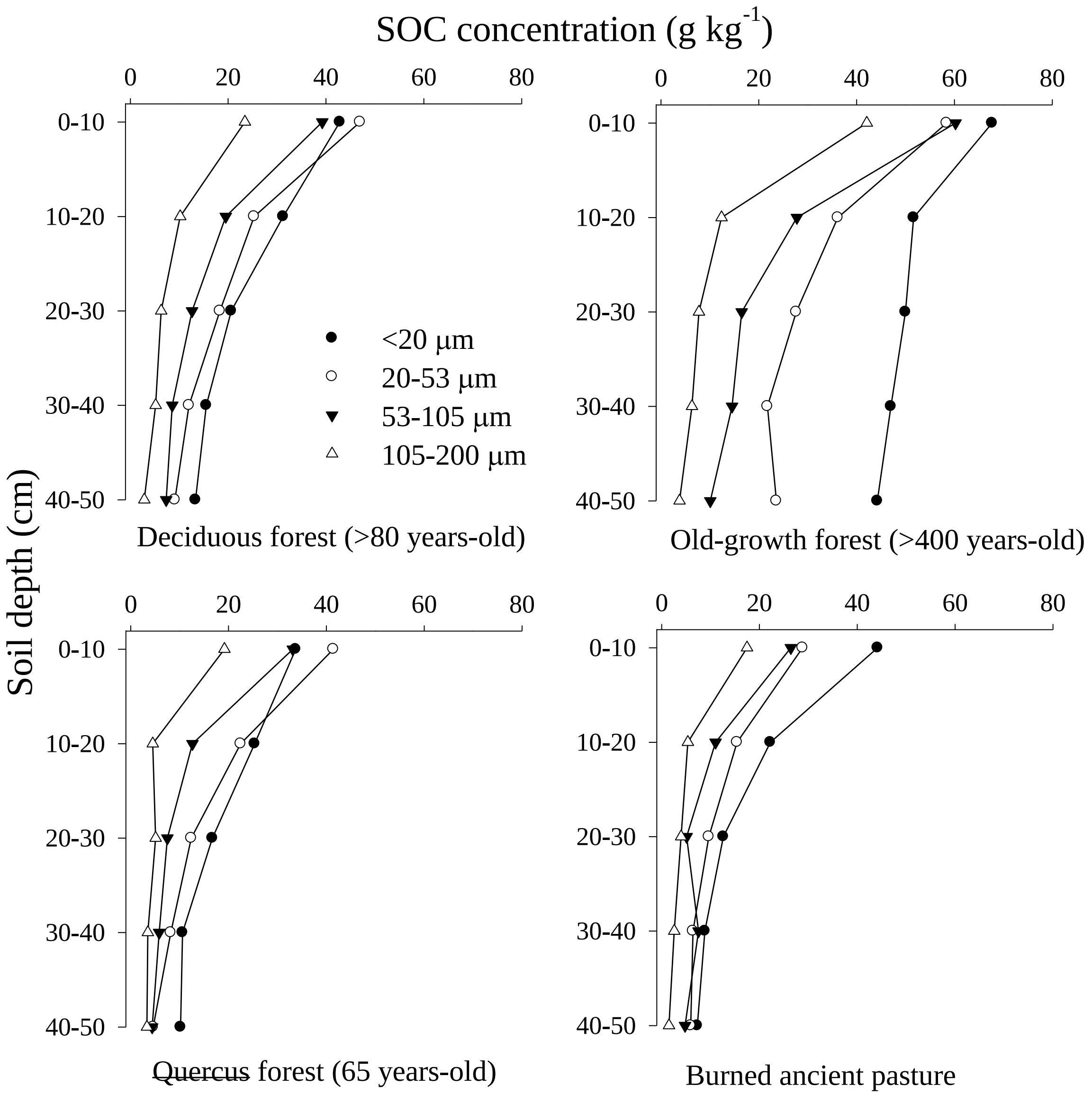
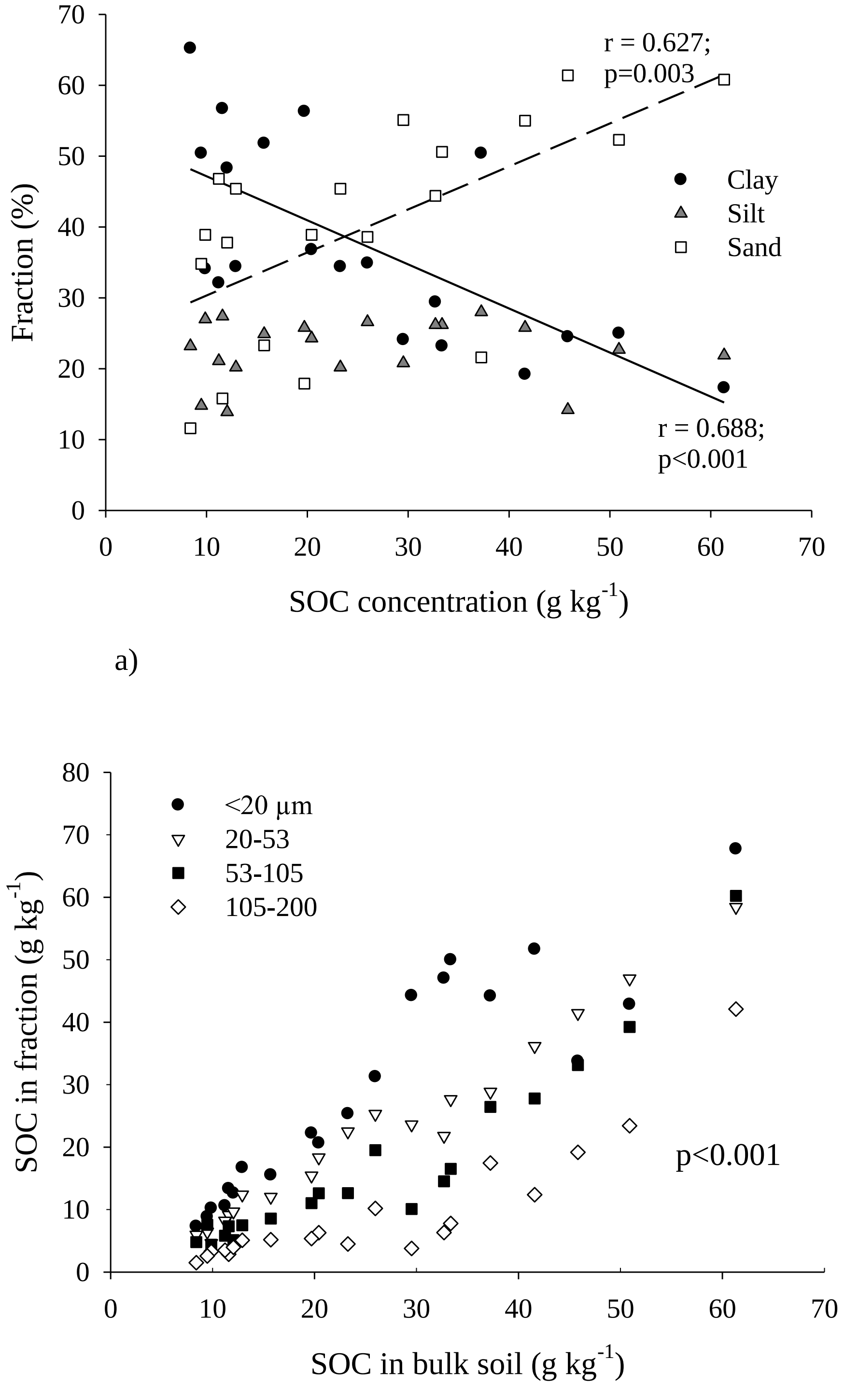


Fig 3.

Figure 4



a)

b)

Fig 4.

Figure 5

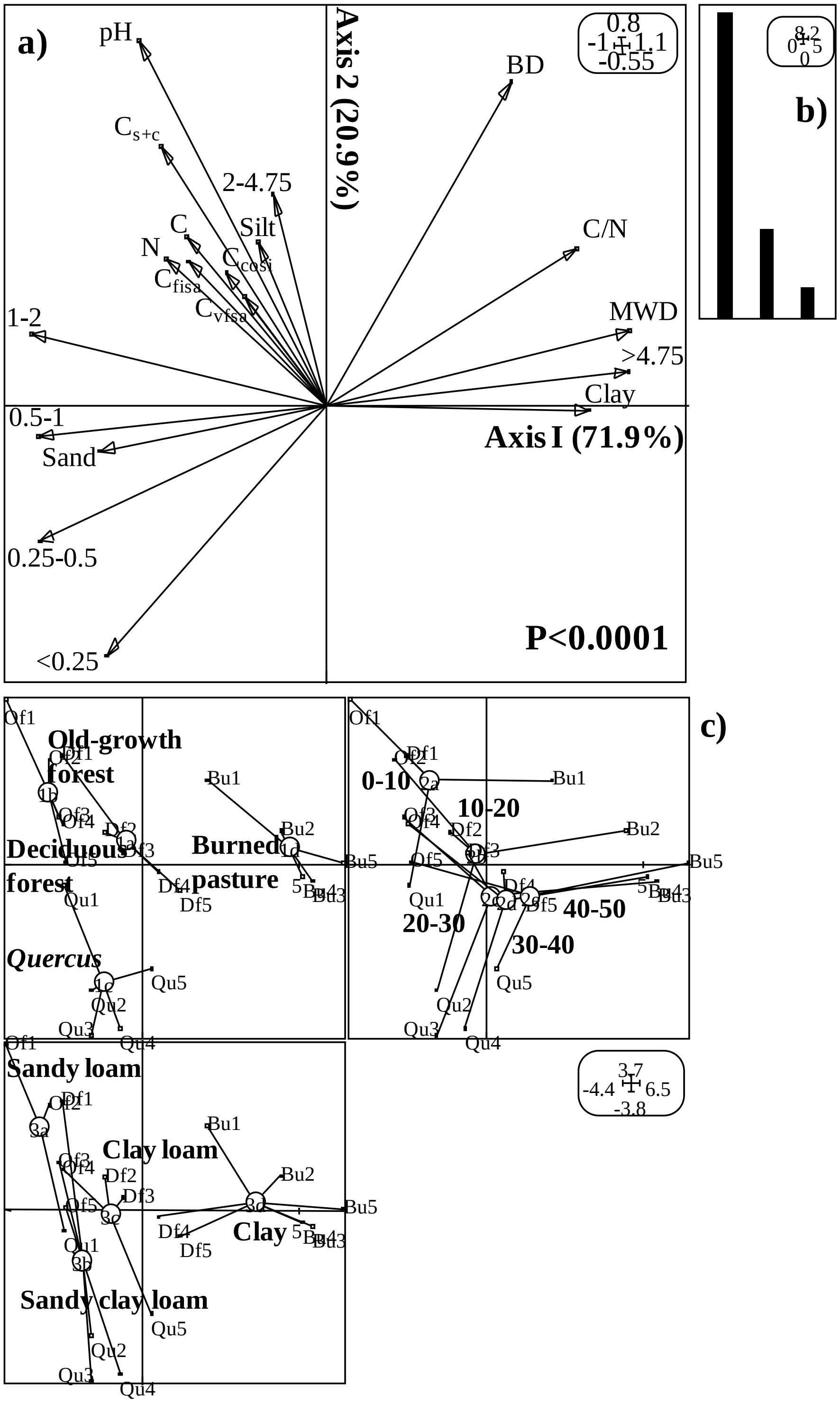


Fig 5.

Figure 6

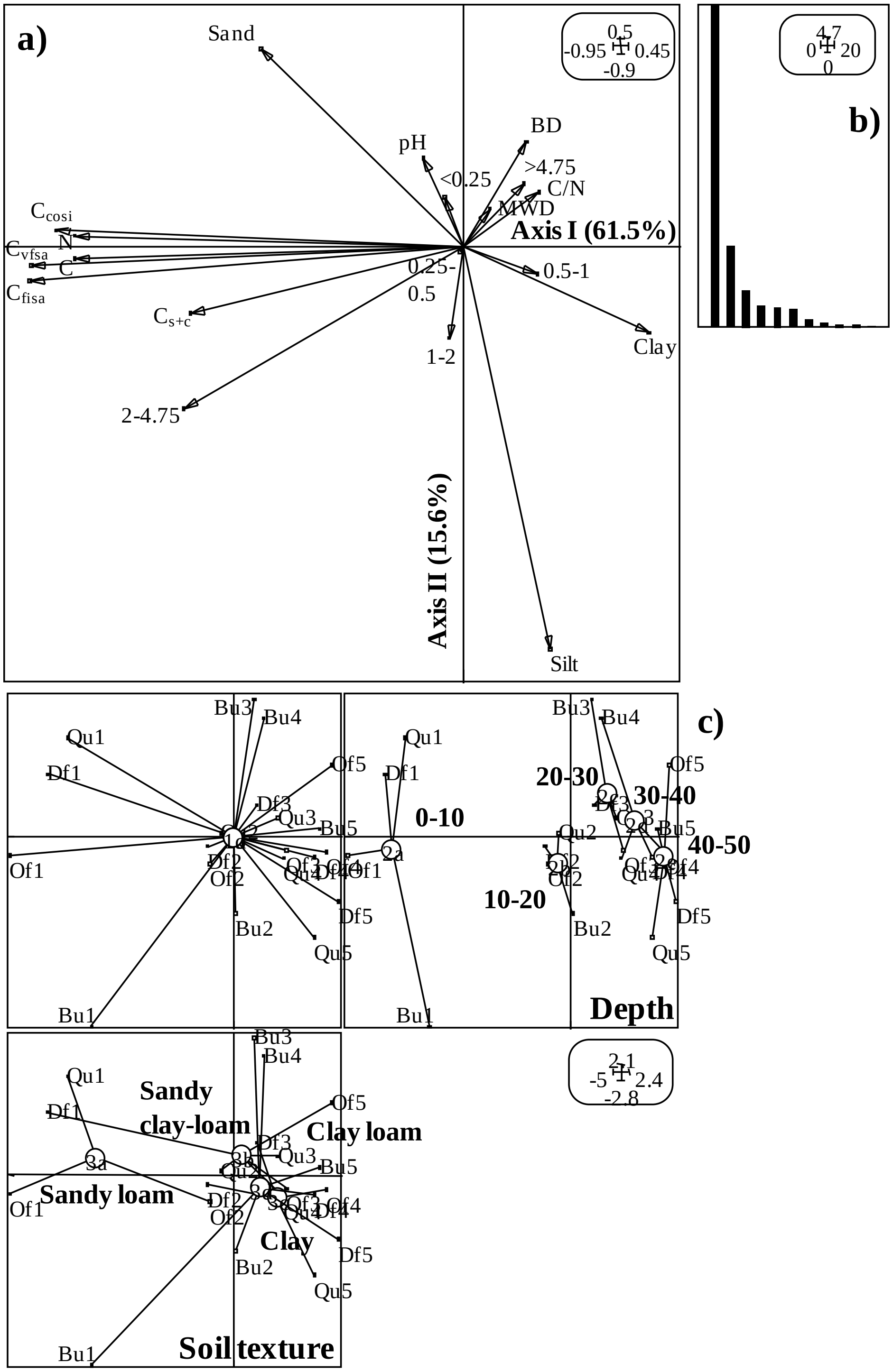


Fig 6.

Figure 7

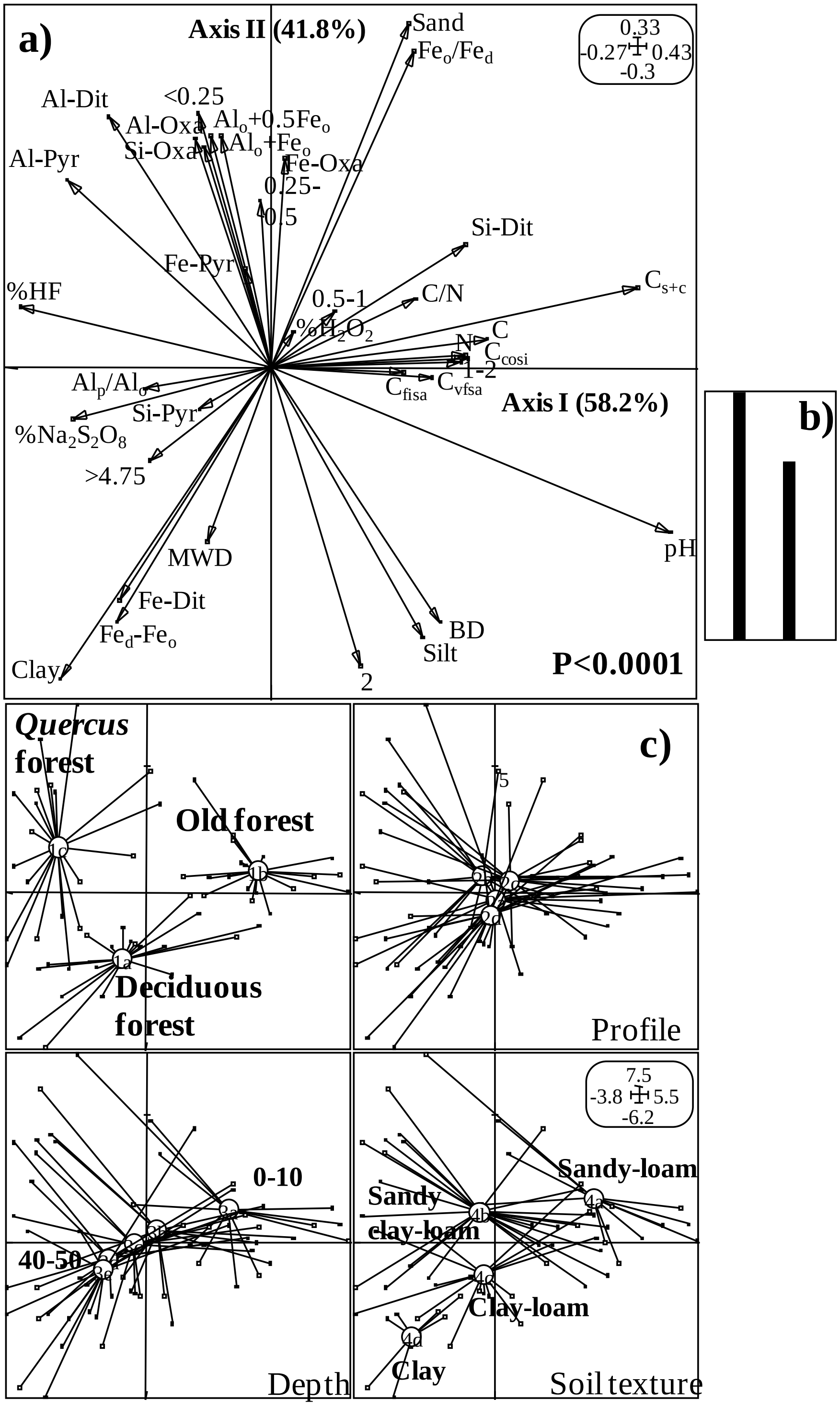


Fig 7.

Figure 8

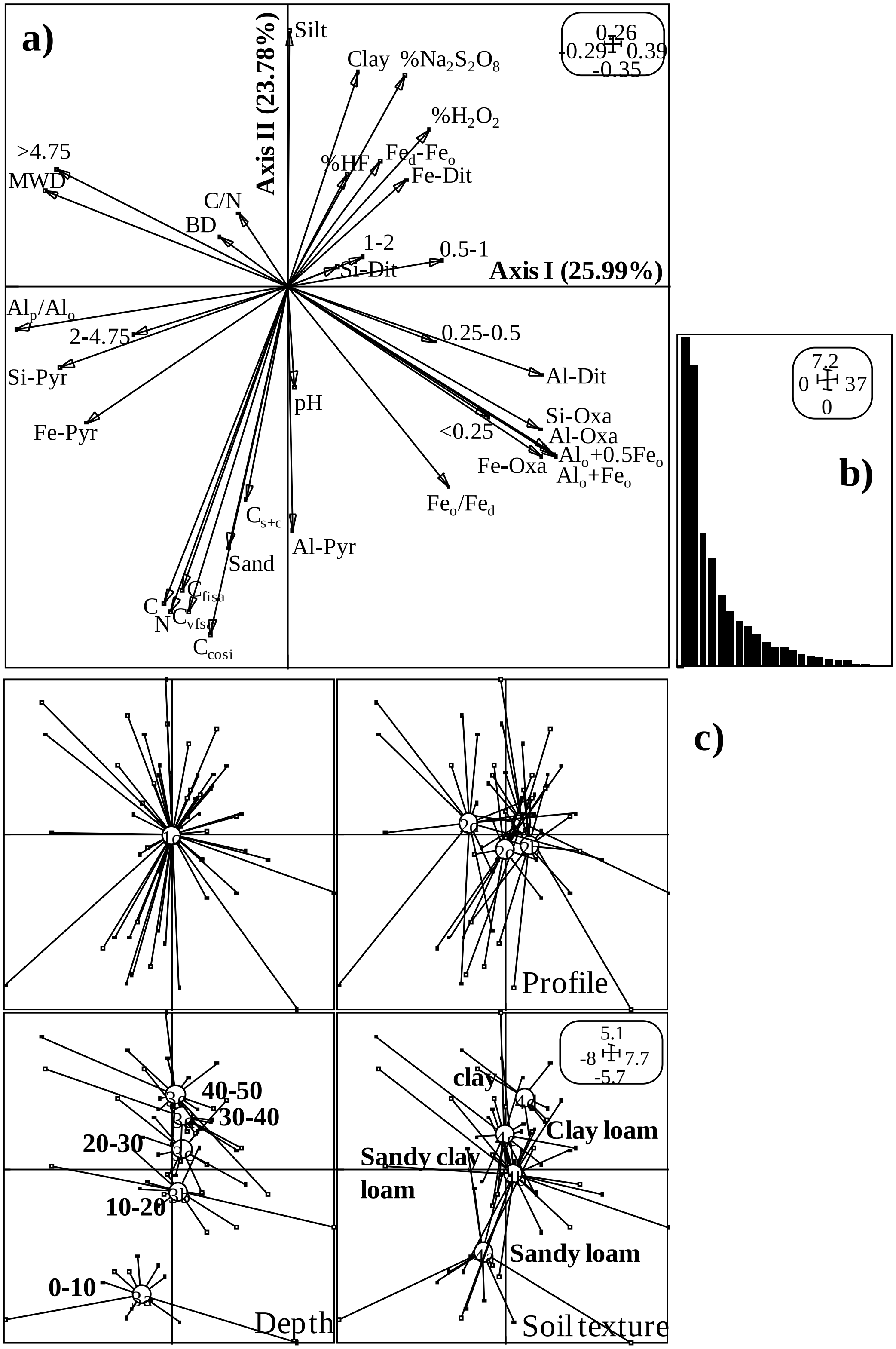


Fig 8.