Depth Distribution of Soil C in Successional Dry Tropical Forests and Agroecosystems of Guanacaste, Costa Rica

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ABSTRACT

Numerous recent studies have addressed the environmental effects of land conversion, especially forest to pasture, in tropical ecosystems. However, few studies have quantified the amount of soil C in the dry tropical forest and derived land use systems in Costa Rica. In Central America the dry tropical forest is threatened by the use of fire that favour the invasion of the introduced C_4 grass *Hyparrhenia rufa* Nees. In some areas of the Guanacaste province, in northwestern Costa Rica, there has been a reduction of the area affected by this grass, especially at the "Santa Rosa" National Park, and a transition to deciduous tropical forest with different plant associations took place instead. In this study, we evaluated C and N concentration in the different mineral soil fractions down to 50 cm depth together with other selected soil variables in four ecosystems in Santa Rosa and five ecosystems at "La Flor" sustainable center in the "Guanacaste" province. The lowest concentration of C was found in all cases in the coarse and fine sand fractions. All data were analysed with a between-within class principal component analysis (PCA) to establish a typology of ecosystems based on selected variables followed by a Monte Carlo simulation (permutation test). The dry tropical forest, the gallery forest on alluvial soils and the managed savanna with fire showed the greatest differences in soil C concentration, while the *Quercus-Acacia* dry forest association was located close to the savanna. All agroecosystems were placed around the same location in the factorial plane. The highest total soil C pool down to 50 cm was obtained in the deciduous forest (228.9 and 150.3 Mg C ha^{-1} for the >100 and 65 years-old secondary forest, respectively) and a sugarcane plantation (160 Mg C ha^{-1}). The total soil C pool in the mature dry tropical forest was very similar to that reported for the humid tropical forest in the Atlantic zone

of Costa Rica, thus being a potentially important CO_2 emitter if this ecosystem is not preserved.

Key words: Carbon, Nitrogen, dry tropical forest, Guanacaste, Costa Rica, between-within class PCA

INTRODUCTION

Costa Rica was once almost totally forested (Keogh 1984), but the country experienced severe rates of deforestation between 1950 and 1984 (Hartshorn et al. 1982; Sader and Joyce 1988). Current estimates of the forest area in Costa Rica are given at 46.8% of the total land area, and comprises $180x10^3$ ha of primary forest (no disturbance), $1,319\ x10^3$ ha of modified natural forest, and $888x10^3$ ha of semi-natural forest[1] (FAO 2005). The seasonally dry tropical forest represents 42% of all tropical forests (Brown and Lugo, 1982). This ecosystem is among the most endangered ecosystems in the world with less than 0.1% of the original dry forests of Pacific Mesoamerica under protection (Murphy and Lugo 1986, Janzen 1988b). This ecosystem has been intensively converted into cattle production by introducing grasses (Toledo 1992, Maass 1995, Quesada and Stoner 2004). In some protected areas cattle was used to control fires and to promote regeneration of the forest (Quesada and Stoner 2004) by controlling the expansion of the grass *Hyparrhenia rufa* Nees (Stepf.) and favour the natural succession of the dry tropical forest (Barboza 1995).

Global patterns in soil C and its vertical distribution across biomes were compiled and analysed by Post et al. (1982) and Jobággy and Jackson (2000). In tropical forests, 50% of the total soil C pool up to 1 m in depth is in the upper 20 cm layer (Jobággy and Jackson 2000). In Costa Rica, while many studies have been conducted on the soil C changes after conversion of the tropical humid forest into pastures, the seasonally dry forests in the Pacific area have received little attention (Johnson and Wedin, 1997). Land

[1] Modified natural forest is a forest of naturally regenerated native species where there are clearly indications of human activities. Semi-natural forest is a forest of native species established through planting, seeding, or assisted natural regeneration (FAO 2005).

conversion in the dry tropical forest may have lead to considerable losses of C in Costa Rica. When agricultural land is no longer used for cultivation and allowed to revert to natural vegetation or replanted to perennial vegetation, the SOC accumulates by processes that essentially reverse some of the effects responsible for their initial losses after land conversion. There is a large amount of variation in rates and the length of time that carbon may accumulate in soil that are related to the productivity of the recovering vegetation, physical and biological conditions in the soil, and the past history of SOC inputs and physical disturbance (Post and Kwon, 2000).

Therefore, it is of utmost importance to understand the dynamics of SOC, especially in those areas more threatened due to unrational land management options and favour the regeneration of the original vegetation. Also equally important is the role of SOC in terrestrial ecosystem C balance and the global C cycle. The loss of SOC by conversion of natural vegetation to cultivated use is well known, and numerous recent studies have assessed the environmental effects of land conversion, especially forest to pasture, in tropical ecosystems. The evidence suggests that conversion may lead to fundamental changes in C contents and cycling but the nature and extent of these changes vary with climate, soil type, vegetation, and land management (Werner 1984; Buschbacher et al., 1988; Veldkamp, 1994; de Moraes et al. 1996; Groffman et al., 2001; Powers 2004; Powers and Veldkamp, 2005). Past studies of soil C pools following conversion of tropical forest to pasture have shown a range of responses, including increases, decreases, or no net long-term changes in soil C (Cerri et al. 1991, Tiessen et al. 1992, Trumbore et al. 1995, de Moraes et al. 1996, Neill et al. 1997). However, additional empiric studies are still needed to obtain better precision of detecting changes in soil C pools, especially

in dry tropical forest with a better understanding of the biological and physical controls involved.

The present study was conducted in two different sites of the Northwestern part of "Guanacaste" separated 40 km, i.e., the "Santa Rosa" National Park and "La Flor" Sustainable Center. Our main objective was first to provide useful information on the amount of total soil C stored in the soils of the region under different land use systems, including the successional vegetation of the dry tropical forest. Secondary objectives were: (1) to assess the vertical distribution of total soil C up to 50 cm depth, (2) to quantify the amount of C in the different mineral fractions contained in the micro-aggregates (<250 μm), (3) to determine the relationship of SOC with some key soil properties, and (4) to establish a typology of the ecosystems studied in the area by using multivariable ordination techniques (between- and within-class principal component analysis). The reason why we studied both sites was to obtain a range of land uses in the area and, especially in "Santa Rosa", to follow changes in the SOC pool in secondary tropical dry forest after ca. 50 years recovery of this forest.

Material and Methods

Study site

The study was conducted in August 2005 in two sites of the northwest Pacific region of Costa Rica (10°50' N, 85°40' W) (Janzen, 2000; Allen, 2001): i) the "Santa Rosa" National Park, which is part of the "Area de Conservación Guanacaste" (ACG) and, ii) "La Flor" Sustainable Center, 15 km south Liberia (Figure 1). The mean annual temperature is 28 ºC and yearly rainfall averages 1,530 mm annually, although in some

areas of the ACG precipitation is highly variable and ranges from 915 to 2,558 mm per year. There is a marked dry season between November and May. Both sites are only a few tens of km apart and therefore can be considered identical climatically. The soils at both sites showed a darker organic layer in the first 15 cm, and texture of soils were similar in the first 50 cm (Appendix 1 and 3).

All the tropical dry forest of Costa Rica is found in the ACG and covers an area of 60,000 ha. Up to 20 distinct plant associations are identified that grow on different soil types, i.e. limestone, alluvial, recent volcanic, ancient volcanic, serpentine. Main vegetation types include: (a) mixed deciduous forest with *Calycophyllum candidissimum* (Vahl) DC. (Rubiaceae), *Bombacopsis quinatum* (Jacq.) (Bombacaceae) and *Luehea candida* (DC.) Mart (Tiliaceae) among the dominants, and with fig trees *Ficus* sp. and rosewood *Dalbergia retusa* Hemsl. (Papilonaceae) also represented; (b) evergreen gallery forests along streams and behind the occasionally flooded zone ("estero"); (c) savannahs with exotic jaragua grass *Hyparrhenia rufa* (Nees) Stapf. and scattered trees of *Byrsonima crassifolia* (L.) Kunth (Malpighiaceae) and *Curatella americana* L. (Dilleniaceae); (d) oak forests and savannahs with *Quercus oleoides* Schltdl. & Cham. (Fagaceae) ("encino") dominant and *Acacia collinsii* Saff. (Mimosaceae), and (e) mangroves. There is also beach vegetation, and areas of calabash *Crescentia* sp. forest.

The entire region encompassing "Santa Rosa" has suffered intense deforestation over the decades. Natural forests were converted into pastures with introduced grasses for cattle production (Quesada and Stoner, 2004). The other preferred land use in this area was agriculture and timber extraction. There are also areas with different land use

histories and anthropogenic events such as fire (Janzen, 2000). In Central America, the introduced African C_4 grass *H. rufa* has received the most attention from ecologists, since when it is not intensively grazed it forms tall and dense stands that burn readily and intensely. This constitutes a serious threat to preservation of both successional and pristine tropical dry forest, in contrast to fires in comparables sites dominated by native grasses which are patchy and less intense. Pasture area in the ACG has decreased since 1979. In only 6 years, 28% of the pasture land became deciduous or evergreen forest (Kramer 1997). In this area, the restoration depends on several factors, namely the seed dispersal mode of the plant species, the distance to the seed sources, the proximity to the forest patches, and the number of herbivores involved (Janzen 1988a). Cattle were formerly present in this park, although they have been eliminated from this area and are not considered to be a viable management tool for controlling fires.

Textural analysis and pH of soils indicated that these were sandy loam and sandy clay loam in the upper layers and clayey in the deeper layers (Appendix 1).

Site 1. Santa Rosa National Park

Most of the area in "Santa Rosa" has suffered intense deforestation and only one patch of mature forest (>100 years old) was present at the time of the study. The dry tropical forest is characterized by high diversity, with no dominant single species. One of the most abundant species of the deciduous forest is *Acacia collinsii* ("cornizuelo"), an example of coevolution since ants *Pseudomyrmex ferruginea* Smith live inside its spines. Other plant species include *Tabebuia ochracea* Standl. (Bignoniaceae) ("Corteza amarilla"), the fern *Selaginella* sp. ("Doradilla"), *Enterolobium cyclocarpum* (Jacq.)

Griseb. (Mimosaceae) ("Guanacaste"), *Hymenaea courbaril* L. ("Guapinol") (Fabaceae), *Cecropia peltata* L. (Moraceae) ("Guarumo"), *Bursera simaruba* (L.) Sarg. (Burseraceae) ("Indio desnudo"), *Ficus* sp. ("Matapalo"), *Bromelia pinguin* L. (Bromeliaceae) ("Pinuela"), *Q. oleoides* ("Encino"), among others. Several parts of "Santa Rosa" are covered with a mosaic of pasture and secondary growth forest in various stages of regeneration. Natural fire is totally absent from "Santa Rosa" (R. Blanco, pers. comm.), thus any fire event is human-induced. This area has been burned during the dry season over two centuries, and probably even earlier (Kalacska et al., 2004). In "Santa Rosa" *H. rufa* L. rapidly invade after burning, and woody regeneration is removed by subsequent fires that are fueled by the grass (Janzen, 1988b).

Four vegetation types were sampled in this site: mature deciduous forest (> 100 years old), "San Emilio" secondary deciduous forest (less coriaceous leaves) of 65 years old, secondary forest of *Quercus-Acacia* (more coriaceous leaves) of 65 years old, and a managed savanna plot which is purposely burnt annually to study the effect of fire on vegetation (Appendix 2).

Site 2. "La Flor" Sustainable Center.

"La Flor" is located 15 km south Liberia, and 45 min driving to "Santa Rosa" through the Panamerican highway, in Guanacaste. In some areas, the introduced African grass *H. rufa* dominates the vegetation. This pyrophyte grass was introduced to Costa Rica ca. 1900 and began aggressively invading forest preserves in Guanacaste about 30 yr ago (Parsons 1972). With annual burning, it is extremely combustible during the dry season (Daubenmire 1972). Five vegetation types were sampled in this site: a derived savanna of

H. rufa with scattered trees of *B. crassifolia* and *C. americana*; these fire-resistant species are indicative of early stages of regeneration from a recent anthropogenic fire event (Kalackska et al., 2004); a gallery forest associated to the "Santa Isabel" river; an abandoned *Mango indigofera* L. plantation; a *Citrus* sp. plantation, and a sugarcane plantation with no burning of surface residues.

Soils at the study site are classified as Inceptisols with medium texture and low pH (Appendix 3).

Litter and soil sampling

Four soil samples distributed along a transect line and separated 100 m to avoid strong spatial autocorrelation were collected in each ecosystem. Prior to soil excavation the amount of litter in the soil surface was manually collected from 0.5 m^2 metal frames in order to estimate the amount of C (50% of dry weight of sample). Litter was then oven-dried at 60º C for 72 h. Soil samples (4 repetitions) were collected in each vegetation type up to 50 cm depth. Sampling depth was split in 0-10, 10-20, 20-30, 30-40 and 40-50 cm. Disturbance of the soil and site were reduced as much as possible. Samples were introduced in plastic bags and then air dried for several days. Samples were gently crumbled manually breaking the aggregates along planes of weakness when field moist and air-dried during several days. Samples were dropped onto a hard surface to ease aggregate separation and sieved through 8 mm to remove roots and stones. These were air-dried for subsequent aggregate analyses.

Bulk density (ρ_d) was measured in each soil layer by the core method (Blake and Hartge, 1986) using cores of 5-cm Ø and 5 cm deep for the 0- to 10, 10- to 20, 20- to 30,

30- to 40, and 40- to 50 cm depths. The core was taken in the middle of each soil layer, introduced in a labeled plastic bag and carried to the lab for weight measure. Values of ρ_d are expressed on a dry weight basis after placing a small amount of soil in the oven and dry at 105º C for 48 h to calculate moisture content in the soil.

A sub-sample of 50-60 g air-dried soil was used for isolation of aggregates by dry-sieving. Aggregates were separated mechanically by moving the column sieve of 4.75, 2.0, 1.0, 0.5 and 0.250 mm for 30 min in a shaker, obtaining 6 aggregate size-fractions, i.e. >4.75, 2.0-4.75, 1.0-2.0, 0.5-1.0, 0.250-0.5, and <0.250 mm. The distribution size classes of the different aggregates were related to their mean weight diameter (MWD) using the formula:

$MWD = \sum_{i=1}^{n} \bar{x}_i m_i$, where $\bar{x}_i$ is the mean diameter of each aggregate fraction,

and the aggregate fraction,

$(m_i) = \frac{M_{sieve\ i}}{M_{total\ \ sample}}$, where $M_{sieve\ i}$ is the dry mass of the particles

retained in the sieve i, and $M_{total\ sample}$ is the dry mass of the initial total sample.

The mean weight diameter (MWD) of each fraction was calculated simply by the average obtained between the opening of the above sieve and the one containing the fraction.

Texture was measured with the hydrometer method for all sites and depths by using one composite sample from the four soil samples. The pH was determined in 2 mm air-dried soil mixed with deionized water and let stand for 1 h, and later by adding CaCl2.

Particle size analysis (physical fractionation)

Physical fractionation methods have increased steadily to study the factors involved in the associations between soil mineralogy and soil organic matter, and hence C, differing in composition and function (Christensen, 1992; 2001). Another fifty grams of <2mm air-dry soil were dispersed in 50 ml 0.5 M Na-hexametaphosphate + 75 ml deionized water for 18 h and mechanically stirred in a multi-mixer machine for 30 minutes. Later, soil was passed through a column sieve 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. The <20 μm fraction was flocculated with $MgCl_2$ and allowed to settle before discarding the supernatant. No chemical treatment was used to remove organic debris.

Carbon and nitrogen analyses

Concentrations of total soil C and N were determined for 2 mm air-dried soil that was ground to 200 μm and for each fraction of the physical fractionation with a CN Elementar Vario Analyzer. We did not perform the HCl test to detect the presence of carbonate C, and thus, we refer to total C. The total soil C (TSC) pool, expressed as Mg ha^{-1} for a specific depth, was computed by multiplying the total C concentration (g kg^{-1}) with ρ_d (g cm^{-3}) and depth (D) of soil layer (cm). The TSC was calculated from soil C concentration and dry ρ_d with the formula provided by Batjes (1996):

$$\text{TSC pool}_{0\text{-}50}\ (\text{Mg ha}^{-1}) = \Sigma_{0\text{-}50}\ [\text{C content}_{\text{layer}}\ (\text{kg Mg}^{-1}) \times (\rho_d)_{\text{layer}}\ (\text{Mg m}^{-3}) \times \text{D (m)} \times 10^{-3}\ \text{Mg kg}^{-1} \times 10^{4}\ \text{m}^2\ \text{ha}^{-1}]$$

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 factorial analysis of variance (ANOVA-GLM procedure) with ecosystem and depth as the main fixed factors was performed to test for significant differences with ecosystem/land use and depth as the main fixed factors for total soil C and N concentrations, C:N ratio, ρ_d, MWD and distribution of size-class aggregates. When significant differences were found, multiple comparisons of means were performed with the Fisher PLSD test. The T-test was used for global significant differences in the SOC pool between ecosystems. The R-package was used to perform statistical analysis and the Sigmaplot software for graph representation.

Between-within class principal component analysis (PCA)

We aimed at extracting the main patterns and significance between sites (ecosystems) sampled by performing the namely between-within class analysis. Firstly a principal component analysis (PCA) is performed to identify those variables that better explain the separation of classes (ecosystems) followed by a within PCA to explore those factors responsible of variability of data within each ecosystem. In other words, by performing this type of analysis we examined the between- or within-classes' multivariate variability in our data, the classes being defined as groups of ecosystems or land uses. The between-class PCA thus focuses on between groups' differences (sites, e.g. forest, savanna, sugarcane crop). The between-class PCA is illustrated in (Dolédec and Chessel, 1989). A

Montecarlo randomisation test was performed to search for significant differences, if sites were different from what might be expected from a complete random data set (Manly 1991). The total between-class inertia for each random distribution of individuals within groups (sites) is computed. In contrast, the within-class PCA focuses on the remaining variability after the site 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. This operation is simply completed by centring the data by classes (Dolédec and Chessel, 1991). The within-class PCA gives very similar results (ordination) to a normal PCA (data not shown) and differences between sites would have been masked by those within each site. The data matrix contained 19 columns, i.e. number of variables, and 45 rows (9 sites x 5 depths), i.e. number of objects = samples. The discriminant analysis module included in the ADE4 software (Thiolouse et al., 1997) package was used.

RESULTS

We found highly significant differences for the main fixed factor ecosystem for all variables analysed in both sites (ANOVA, Tables 1 and 2). Regarding the main fixed factor depth only significant differences were observed for total C and N concentrations ($P<0.001$) and for large aggregates of 2-4.75 mm size ($P<0.01$) in Santa Rosa, and for C, N, and C:N ratio ($P<0.001$) and ρ_d ($P<0.05$) in "La Flor". No significant differences were found for the interaction between site and depth in Santa Rosa, and in La Flor, statistical differences were observed only for C:N ratio and 1-2 mm aggregates ($P<0.05$), and for

micro-aggregates ($P<0.001$). Differences in total soil N between all ecosystems in both sites were comparable to soil C differences.

Significant differences were observed in the C:N ratio for the fixed main factor site in "Santa Rosa" (ANOVA, $P<0.001$), but not for depth and the interaction between factors (Table 1). The effect of vegetation in the C:N ratio could be observed in the C:N ratio in the burnt savanna plot differed significantly ($P<0.001$) to the other ecosystems studied in "Santa Rosa" (Table 3). At "La Flor" the C:N ratio was slightly lower than that observed in Santa Rosa and ranged between 9 and 11 in all ecosystems, except in the sugarcane plot (11-13). In the natural savanna with scattered trees we observed a significant decrease in C:N ratio (Fisher PLSD test).

Relatively high values of total soil C were obtained in both sites. At "Santa Rosa", total soil C concentration was highest in the >100 years old deciduous forest and were significantly different to the 50 years-old deciduous forest, the *Quercus-Acacia* forest association, and the burnt savanna plot (Figure 1). The SOC concentration decreased significantly with increase in depth in all systems and ranged from 37.2 to 61.3 g kg^{-1} in the 0-10 cm layer to 8.4 to 29.5 g kg^{-1} in the 40-50 cm layer. At "La Flor" total soil C concentrations in the sugarcane were significantly higher (Figure 2) than those obtained in the other four ecosystems (Fisher PLSD test). Across the two sites studied average values of total soil C decreased significantly with depth (PLSD test) in all ecosystems (Figures 1 and 2). Total N concentrations varied significantly across the ecosystems studied in "Santa Rosa"; at "La Flor" differences were only significant between the sugarcane plot and the other land use systems (Fisher PLSD test).

Regarding soil physical variables, the ρ_d was significantly different among systems at "Santa Rosa" (Table 4), except for the >100 and 50 years-old deciduous forests (Fisher PLSD test). The MWD of aggregates in the burnt savanna plot was significantly different (Fisher PLSD test, $p<0.001$) to that observed in the three forest types at Santa Rosa (Table 5). The MWD of aggregates between the mature forest and the 50 years-old deciduous forest was also significantly different (Fisher PLSD test, $p = 0.037$). At "La Flor" the ρ_d in the sugarcane plantation was significantly different (Fisher PLSD test) to that observed in the other ecosystems (Table 4). At "La Flor", the MWD of aggregates in the natural savanna was significantly different (Fisher PLSD test) to the other systems evaluated (Table 5). There were no significant differences between the gallery forest and the *Mango* and sugarcane plantations (Table 5).

Particle-size fraction analysis of micro-aggregates

Within particle size fractions of micro-aggregates there was a decrease in SOC concentration with increase in soil depth (Figures 3 and 4). In all cases, the highest SOC concentration was observed in the silt+clay fraction (<20 μm) for all ecosystems evaluated in both sites, whereas the coarse-sand (105-200 μm) and fine-sand (53-105 μm) fractions contained less C. The SOC concentration comprises both the light fraction and the particulate organic matter (POM), since no chemical treatment or flotation technique was employed to remove the organic debris.

The variability of total C concentration in the different particle-size fractions is shown in figures 5 and 6. Since only composite samples were used by combining the four repetitions to obtain one data, we included all the data from the ecosystems for a certain

soil depth. The POM, i.e., coarse and fine sand fractions, showed less data variation than the coarse silt and the silt+clay fractions (Figures 5 and 6, box plots). The POM fractions also showed less variability in the deeper soil layers. This seem to be the general trend in all fractions, except for the silt+clay fraction, where even at 40-50 cm depth there was a higher variability than that observed for the other particle-size fractions. In Santa Rosa, the same pattern was observed. The POM fraction showed greater variability only in the 0-10 cm layer. The same variability was observed for the silt+clay and coarse silt fractions (Figure 6).

Between-class PCA

Two axes were selected in the between-class PCA which explained 90.1% of the total variability (Figure 7a, b). Axis I explained 66.5% of variability and discriminated soil samples with a high MWD, aggregates >4.75 mm and clay content, in contrast to those where micro-aggregates and sand contents were high. This axis can be interpreted as the soil type (texture) effect. Axis II (23.6% of variation) clearly separated those samples with high proportion of large aggregates and total soil C and N concentrations. The projection of objects (sites) onto the factorial plane defined by Axes I and II clearly separated the gallery forest, the burnt savanna and the deciduous forests of different age, and to a lesser extent the natural savanna with scattered trees. All the agroecosystems studied at La Flor are located at an intermediate position in the factorial plane together with the *Quercus-Acacia* forest, which is close to the natural savanna.

A Monte Carlo permutation test was performed on the partition of objects (ecosystems) to test land-use effect upon soil variables. Of the 10,000 random simulations performed, none led to an inertia higher or equal to that of the original data,

thus indicating that the effect of ecosystem was significant at the probability level $P<0.0001$. In other words, the separation of ecosystems (typology) onto the factorial plane of the between-class PCA is highly significant.

Within-class PCA

The first and second axis of the within-class PCA accounted for 44.8% and 21.2% of the within-class inertia. The first axis discriminated those samples with high clay content in opposition to those samples with high C concentrations in the coarse (105-200 μm) and fine sand (53-105 μm) fractions (Figure 8). Axis II separated very large aggregates (>4.75 mm) from micro-aggregates (<250 μm). The projection of the objects onto the factorial plane is given in figure 8. The ecosystem effect was removed by placing all centers of classes at the origin of the factorial maps (Figure 9a), while the sampling units are scattered with the maximal variance around the origin. The samples were sorted by soil depth to examine clearly the general pattern (Figure 9b). The within-class PCA also showed that the coarse and fine sand fraction concentrations are different owing to soil depth; in other words, there is a high variability from the topsoil to deeper soil layers (as indicated in the box-plot diagrams).

Litter accumulation and SOC pool

The quantity of litter collected was significantly different in all ecosystems evaluated in both sites [check] (ANOVA, $P<0.001$). At Santa Rosa, the highest litter accumulation was observed in the >100 years-old mature forest and *Quercus-Acacia* forest (Table 6) with $1{,}326.7 \pm 240.7$ g m^{-2} and $1{,}322.0 \pm 478.1$ g m^{-2}, respectively, and the deciduous forest (50 years-old) ($1{,}104.6 \pm 726.2$ g m^{-2}). In the burnt savanna no litter accumulation

was present at the time of the study. Litter inputs in Santa Rosa equalled 6.6 Mg C ha^{-1} for the mature and *Quercus-Acacia* forests, and 5.5 Mg C ha^{-1} in the 65 years-old deciduous forest (Table 6). At la Flor the highest litter accumulation was observed in the sugarcane plot (mulching management), followed by the natural savanna with scattered trees, the gallery forest, and the *Mango* plantation. Less litter accumulation was observed in the *Citrus* plantation compared to the other ecosystems (Table 6).

Subsequently, the highest SOC pool up to 50 cm was obtained in the mature forest (228.9 Mg C ha^{-1}) at "Santa Rosa" and in the sugarcane plantation (160 Mg C ha^{-1}) at "La Flor". These pools were significantly different ($P<0.01$, t-test) to the other land uses/ecosystems studied within each site (Table 6). At "Santa Rosa" total soil C concentrations were significantly higher in the >65 years-old deciduous forest compared to the burnt savanna (Fisher PLSD test; Figure 1); however, the higher ρ_d in the latter system resulted in no significant differences in total soil C pool. All ecosystems studied at "La Flor" stored in general less below-ground C than those from "Santa Rosa". When we compared the SOC pool in the 65 years-old deciduous forest with the mature forest and the *Quercus-Acacia* forest at "Santa Rosa" the level of the significance was $P=0.01$ (t-test). At "La Flor" only significant differences ($P<0.01$; t-test) were obtained between the sugarcane plot and the rest of land uses and ecosystems. Across all ecosystems ca. 50 to 65% of the total SOC pool occurred in the first 20 cm (Table 6), a potential important emitter of CO_2 to the atmosphere.

DISCUSSION

Comparison with other studies

The comparison of our results is limited by the few number of studies conducted in dry tropical forests of Central America. For example, in the Pacific coast of Mexico García-Oliva et al. (2004) have reported total soil C concentrations in the tropical deciduous forest at 32.5 g kg^{-1}. Johnson and Wedin (1997) reported in soils developed from volcanic tuffs at the "Lomas Barbudal" biological reserve in southern "Guanacaste" that total soil C in the intact deciduous forest was 52.3 g kg^{-1} (0-15 cm) and 17% lower in the grassland (*H. rufa*) plots compared to plots in the intact forest (vegetation effect on total soil C was significant at $P < 0.01$). These values are within the range of our data, i.e. 50.9 and 61.3 g kg^{-1} in the first 10 cm for the 50 and >100 years-old deciduous forest, and 45.8 and 37.3 g kg^{-1} for the *Quercus-Acacia* forest and the burnt savanna plot, respectively, at "Santa Rosa"; at "la Flor" the total soil C (0-10 cm) in the savanna (*H. rufa*) with scattered trees was 37.6 g kg^{-1}. In another study conducted in southwestern Costa Rica ("Osa" peninsula, > 5,000 mm yr^{-1}), Cleveland et al. (2003) obtained total soil C concentrations that ranged from 50 to 65 g kg^{-1} and 56 to 68 g kg^{-1} under very humid primary forest and derived 20 years-old pasture in highly weathered Oxisols and very fertile alluvial mollisols, respectively. These values corresponded to a soil C pool in the 0-10 cm of 33.8, 37.5, 44.9 and 55.4 Mg C ha^{-1}.

In South America, Tiessen et al. (1998) provided data under different land use systems in dry tropical forests of Brazil. Trumbore et al. (1995) reported decreases of SOC when the dry tropical forest was converted to pasture, although interpretation of results is masked by the site preparation methods employed. Under savanna vegetation the total soil C pool was estimated at 54.7 Mg C ha^{-1} up to 40 cm depth in native grasslands of the Brazilian Cerrado (da Silva et al., 2004). In another study conducted in

the "Chaco" region (Argentina), Abril and Buchner (2001) reported SOC concentrations of 7.05, 3.1 and 1.5 kg m^{-2} for secondary forest, forest-grassland transition (grazing) and heavily grazed grassland, respectively, which equaled a SOC pool for the 0-20 cm of 64.2, 33.8 and 18.3 Mg C ha^{-1}. These figures are similar to those reported by Houghton (1995) for tropical open forest, i.e. 64 Mg C ha^{-1}. The restored western Chaco soils under secondary forest were comparatively rich in soil C in relation with other savanna sites, although generally lower than our data, i.e., from the *Acacia-Quercus* forest, the 65 years-old deciduous forest at "Santa Rosa", and slightly higher than those obtained in the savanna with scattered trees at "La Flor".

The losses of the soil C pool due to the conversion of the dry tropical forest into fruit tree plantations in the "Guanacaste" region ranged from 11-14% when using savanna data to 31-33% if we use the data obtained in the *Quercus-Acacia* forest, and 53-54% if we use data for the 60 years-old deciduous forest. These values, however, must be used cautiously since we ignore how much C was lost initially after replacement of the natural vegetation and what the amount of C was already incorporated into the soil after land conversion. Nonetheless, these calculations are shown to bring the attention of scientists and stakeholders in the region regarding the great variability and the discrepancies that seem to emerge between studies and the cautions when extrapolations are made to larger areas.

There seems to be a great difference regarding the total soil C pools of the gallery forests in tropical sites. For example, in the Colombian "Llanos" the mean soil carbon pool in the gallery forest of the Yucao watershed was estimated at 133 Mg ha^{-1} down to 1 m depth (Veneklass, pers. comm.), which is higher to the values obtained in the savanna.

The contribution of gallery forests to regional carbon stock seems thus to be more than proportional to their surface area. This contribution would be largely lost, however, if land use intensification were to lead to large-scale clearing of forests, as has occurred in the Brazilian "Cerrado" region (Barbosa 1993, Klink et al. 1993). In our study, on the contrary, the total soil C pool in the gallery forest was 66 Mg ha^{-1} down to 50 cm depth, 17% lower to that in the savanna with scattered trees.

Rates of soil C accumulation in the dry tropical forest

The effects of climate on soil C sequestration with forest succession are not well known. The soil C pool in tropical mature forests tend to decrease exponentially as the ratio of temperature to precipitation increases, corresponding to a gradient from wet to dry forests (Brown and Lugo, 1982). Silver et al. (2000) reported that there is a statistical significance relationship between the soil C content and forest age, at least during the first 100 years. The C accumulation rate in the soil is lower in the moist forests than in the dry forests over a 100 year period, i.e. 0.51 and 1.02 Mg C ha^{-1} yr^{-1}, respectively (Silver et al., 2000). The relationship for the dry forest follows a strongly significant linear increase in soil C with time (n = 5), which contradicts previous estimates reported by Lugo and Brown (1993), and probably indicates differences in soil organic matter content in the previous land use practice since the most fertile soils are generally used for the establishment of pastures or other agricultural land uses. The low number of samples indicates that there is an important gap in knowledge. The data analysed by Silver et al. (2000) showed that soil C concentrations in land uses derived from dry forests were high to start with. In our study, the C accumulation rate in the soil was 1.03 Mg C ha^{-1} yr^{-1},

calculated from the SOC pool variation between the 50 and the >100 years old deciduous forest at "Santa Rosa".

The review by Post and Kwon (2000) shows that globally there is considerable variation in accumulation rates of SOC across vegetation types and climate range. Many factors are involved in the different results obtained that seem not to be consistent among the studies. In the dry subtropical forest, the rates of C accumulation during forest establishment after agriculture use have been reported at -13.1 (pasture) and 38 g m^{-2} yr^{-1} (0.38 Mg C ha^{-1} yr^{-1}) after 25, and 35 years after establishment in Smith et al. (1951) and Brown and Lugo (1990), respectively. In our study, the difference in C concentration in the first 10 cm between the 50 and the >100 years-old deciduous forest indicated an accumulation rate of 0.17 Mg C ha^{-1} yr^{-1} (0.43 for 0-20 cm depth).

Factors controlling soil C accumulation

The soil ρ_d in the burnt savanna plot at "Santa Rosa" was higher than in the other ecosystems studied, which may be suggestive of significant soil compaction during past pasture use (Veldkamp 1994). Consequently, in the traditionally managed savanna (burning every year) the low concentration of SOC seems to be balanced out by the high ρ_d in this system, resulting in soil compaction and no significant changes in total SOC pool under the four systems studied.

The total soil C concentration (and pool) in the sugarcane plantation was more than doubled compared to the other ecosystems and agro-ecosystems at "La Flor". Among the factors and processes that determine the trend and rate of accumulation of total C in the soil are those that increase the rates of litter input that are later incorporated deep in the

soil through the action of soil organisms. The mixing of soil and litter is performed by the joint action of soil invertebrates like Arthropods and earthworms, producing fecal pellets and reducing the size of organic residues that can be attacked by microorganisms (bacteria and fungi) (Lavelle and Spain, 2001). This seems to happen in the sugarcane plantation where a large amount of plant residues are kept in the soil surface that favour the high activity of soil organisms (earthworms) observed and the maintenance of optimal soil moisture levels compared to the *Citrus* and *Mango* plantations at the time of the study (August 2005).

Leffler and Enquist (2001) observed a high degree of tree functional diversity by comparing the variation in $\delta^{13}C$ among co-occurring tropical dry forest species in "San Emilio" forest (60 years-old). They observed significant differences in $\delta^{13}C$ between species with tough, coriaceous leaves (*Q. oleoides*) and those with soft leaves (*T. ochracea*). Whether these differences may result in significant differences in total soil C concentrations must be further investigated. In fact this forest was clearly discriminated to the *Quercus-Acacia* association and the mature deciduous forest in the factorial plane formed by the first two axes of the between-class PCA (Figure 7a). Some of the differences observed in total soil C between the *Quercus-Acacia* association forest and the "San Emilio" deciduous forest might be a consequence of several factors, some of them linked to aboveground functional diversity and the activity of soil invertebrates. In this forest it was also observed a large number of Coleopterans (Elateridae) and biologically-formed rounded aggregates.

In our study we found that the total soil C pool in the mature dry tropical forest in "Santa Rosa" is very similar to values reported for the humid tropical forest in the

Atlantic zone of Costa Rica (Jiménez et al. in prep.) The dry tropical forest is not only an important reservoir of C aboveground but also belowground, and may be thus considered as the steady-state situation for C accumulation. Besides, in this forest, where the total soil C concentration was high, i.e. 61.3 and 49.3 g kg-1 for the 0-10 and 10-20 cm depth, the presence of ant hills of the genus *Atta* create local patches of soil with very low C concentrations. This results in an important spatial heterogeneity within the landscape that needs to be taken into account, especially if global estimates are intended. The amount of C in the ant hill was somewhat similar to that in the soil of the mature forest at 40-50 cm depth, indicating that part of the soil transported by ants to the soil surface must be below 50 cm. At "La Flor", the same pattern was observed for the ant hills. Regarding termites, total C concentrations were higher in the biogenic structures produced by a soil-feeding termite (94.5 g kg^{-1}) and a plant-litter feeder termite (488 g kg^{-1}) than in the (Figure 4).

In our study, all forests studied contained more C in the soil than the other ecosystems, except the gallery forest on alluvial soils at "La Flor", where the high proportion of sand in the alluvial soil has limited the concentration of C (soil type effect). The typology of ecosystems in the between-within PCA indicated a clear and significant separation of four ecosystems, i.e., the gallery forest, the >100 years (mature) deciduous forest, the natural savannah and the *Quercus-Acacia* association forest, and the traditionally managed (burnt) savanna. The agroecosystems studied occupied an intermediate position within the factorial plane formed by the first two axes.

The high total soil C concentration obtained in the sugarcane plot is not the result of differences in soil texture mainly but the contribution of surface residues that would have

been lost with burning, the usual practice in the region. These residues were observed at different stages of decomposition even at 50 cm depth. In our study we only addressed the amount of C in the mineral soil. Further studies are needed to evaluate the contribution of a C_4 plant in an area previously occupied by C_3 plants into the total soil C pool.

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References

Abril A, Bucher EH. 2001. Overgrazing and soil carbon dynamics in the western Chaco of Argentina. Appl Soil Ecol 16:243-249.

Allen W. 2001. Green Phoenix: Restoring the Tropical Forests of Guanacaste, Costa Rica, Oxford University Press, New York 310 p.

Barboza G. 1995. Pastoreo controlado para control de incendios y restauración de bosque tropical seco, en el Parque Nacional Palo Verde, Guanacaste, Costa Rica. Informe de avance de resultados de monitoreo del proyecto, 12 de junio de 1995. Organización para Estudios Tropicales, San José, Costa Rica.

Batjes NH. 1996. Total carbon and nitrogen in soils of the world. Eur J Soil Sci 47:151-163.

Blake GR, Hartge KH. 1986. Bulk density. In: Klute A, Ed. Methods of Soil Analysis. Part 1. Physical and mineralogical methods. 2nd Ed. Agron. Monogr. 9. ASA and SSSA, Madison, WI. p 363-382.

Brown S, Lugo AE. 1982. Storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14:161-187.

Brown S, Lugo AE. 1990. Tropical secondary forest. J Trop Ecol 6:1-32.

Buschbacher R, Uhl C, Serrão EAS. 1988. Abandoned pastures in eastern Amazonia. II. Nutrient stocks in the soil and vegetation. J Ecol 76: 682-699.

Cerri CC, Volkoff B, Andreaux F. 1991. Nature and behaviour of organic matter in soils under natural forest, and after deforestation, burning and cultivation, near Manaus. Forest Ecol Manage 38:247-257.

Christensen BT. 1992. Physical fractionation of soil and organic matter in primary particle size and density separates. Adv Soil Sci 20:1-90.

Christensen BT. 2001. Physical fractionation of soil and structural and functional complexity in organic matter turnover. Eur J Soil Sci 52:345-353.

Cleveland CC, Townsend AR, Schmidt SK, Constance BC. 2003. Soil microbial dynamics and biogeochemistry in tropical forests and pastures, southwestern Costa Rica. Ecol Appl 13:314-326.

da Silva JE, Resck DVS, Corazza EJ, Vivaldi L. 2004. Carbon storage in clayey Oxisol cultivated pastures in the "Cerrado" region: Brazil. Agr Ecosys Environ 103:357-363.

Daubenmire R. 1972. Ecology of *Hyparrhenia rufa* (Nees) in derived savanna in north-western Costa Rica. J Ecol 9:11-23.

de Moraes JLB, Volkoff B, Cerri CC, Bernoux, M. 1996. Soil properties under Amazon forest and changes due to pasture installation in Rondonia, Brazil. Geoderma 70:63-81.

Dolédec S, Chessel D. 1989. Rythmes saisonniers et composantes stationnelles en milieu aquatique II. Prise en compte et élimination d'effets dans un tableau faunistique. Acta Oecol 10: 207-232.

Dolédec S, Chessel D. 1991. Recent developments in linear ordination methods for environmental Sciences. Adv Ecol India 1:133-155.

Eswaran H. van den Berg E, Reich P. 1993. Organic carbon in soils of the world. Soil Sci Soc Am J. 57:192-194.

FAO 2005. Global Forest Resources Assessment 2005. Progress towards sustainable forest management. FAO Forestry Paper 147, 320 p.

García-Oliva, F., Oliva, M., Sveshtarova, B. 2004. Effect of soil macroaggregate crushing on C mineralization in a tropical deciduous forest. Plant Soil 259: 297-305.

Groffman PM, McDowell WH, Meyers JC, Merriam JL. 2001. Soil microbial biomass and activity in tropical riparian forests. Soil Biol Biochem 33:1339-1348.

Hartshorn G, Hartshorn L, Atmetlla A, Gómez LD, Mata A, Mata L, Morales R, Ocampo R, Pool D, Quesada C, Solera C, Solórzano R, Stiles G, Tosi Jr J, Umaña A, Villalobos C., Wells R. 1982. Costa Rica – Country Environmental Profile. A Field Study. Tropical Science Center, San Jose, Costa Rica, 123 p.

Houghton RA. 1995. Chages in the storage of terrestrial carbon since 1850. In: Lal R, Kimble JM, Levine E, Stewart VA, Eds. Soils and Global Change. Lewis Publisher CRC, Boca Raton, p 45-65.

Janzen DH. 1988a. Tropical dry forests: The most endangered major tropical ecosystem, In: Wilson EO, Ed. Biodiversity. National Academy Press, Washington, D.C. p 130-137.

Janzen DH. 1988b. Guanacaste National Park: tropical ecological and biocultural restoration. In: Cairns JJ, Ed. Rehabilitating Damaged Ecosystems, vol. II. CRC Press, Boca Raton, FL. p 143-192.

Janzen DH. 2000. Costa Rica's Area de Conservación Guanacaste: a long march to survival through non-damaging biodevelopment. Biodiversity 1:7-20.

Jobággy EG, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol Appl 10(2):423-436.

Johnson NC, Wedin DA. 1997. Soil carbon, nutrients, and mycorrhizae during conversion of dry tropical forest to grassland. Ecol Appl 7:171-182.

Kalacska M, Sánchez-Azofeifa GA, Calvo-Alvarado JC, Quesada M, Rivard B, Janzen DH. 2004. Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. For Ecol Manage 200:227-247.

Klink CA, Moreira AG, Solbrig OT. 1993. Ecological impacts of agricultural development in the Brazilian Cerrados. In: Young MD, Solbrig OT, Eds. The world's savannas. Man and the Biosphere (MAB) series, Vol. 12. Unesco. p. 259-282.

Lavelle P. Spain A. 2001. Soil Ecology. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Leffler, A. J., Enquist, B. J. 2002. Carbon isotope composition of tree leaves from Guanacaste, Costa Rica: comparison across tropical forests and tree life history. Journal of Tropical Ecology 18: 151-159.

Lugo AE, Brown S. 1993. Management of tropical soils as sinks or sources of atmospheric carbon. Plant Soil 149:27-41.

Manly, B.F.J. (1991) Randomization and Monte Carlo methods in Biology. Chapman and Hall, London, 281 p.

Maass JM. 1995. Conversion of tropical dry forest to pasture and agriculture. In: Bullock SH, Mooney HA, Medina E, Eds. Seasonally Dry Tropical Forests. Cambridge University, Cambridge, UK. p. 399-422.

Murphy, P.G., Lugo, A.E. 1986. Ecology of tropical dry forest. An. Rev. Ecol. Sys. 17: 67-88.

Neill C, Melillo J, Steudler PA, Cerri CC, Moraes JFL, Piccolo MC, Brito M. 1997. Soil carbon and nitrogen stocks following forest clearing for pasture in the southwestern Brazilian Amazon. Ecol Appl 7:1216-1225.

Parsons JJ. 1972. Spread of African pasture grasses to the American tropics. J Range Manage 25:12-17.

Post WM, Kwon KC. 2000. Soil carbon sequestration and land use change: processes and potential. Global Change Biol 6:317-328.

Post WM, Emmanuel WR, Zinke PJ, Stangenberger G. 1982. Soil carbon pools and world life zones. Nature 298:1586-1589.

Powers JS. 2004. Soil carbon and nitrogen storage following contrasting land-use transitions in Northeastern Costa Rica. Ecosystems 7:134-146.

Powers JS, Veldkamp E. 2005. Regional variation in soil carbon and δ13C in forests and pastures of northeastern Costa Rica. Biogeochemistry 72:315-336.

Quesada M, Stoner KE. 2004. Threats to the conservation of the tropical dry forest in Costa Rica. In: Frankie GW, Mata A, Vinson SB, Eds. Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest, University of California Press, Berkeley, CA. p. 266-280.

Sader S, Joyce AT. 1988. Deforestation rates and trends in Costa Rica 1940–1983. Biotropica 20:11-19.

Silver WL, Ostertag R, Lugo AE. 2000. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. Rest Ecol 8:394-407.

Smith RM, Samuels G, Cernuda CF. 1951. Organic matter and nitrogen build-ups in some Puerto Rican soil profiles. Soil Science 72:400-427.

Thioulouse, J., Chessel, D., Dolédec, S., Olivier, J.M., 1997. ADE-4: a multivariate analysis and graphical display software. Statistics and Computing 7, 75–83.

Tiessen H, Feller C, Sampaio EVSB. 1988. Carbon sequestration and turnover in semiarid savannas and dry forest. Clim. Change 40:105-117.

Tiessen H, Salcedo IH, Sampaio EVSB. 1992. Nutrient and soil organic matter dynamics under shifting cultivation in semi-arid northeastern Brazil. Agr Ecosys Environ 38:139-151.

Toledo VM. 1992. Bio-economic cost. In: Downing T, Hecht S, Pearson H, Eds. Development or Destruction? The Conversion of Tropical Forest to Pasture in Latin America. Westview, New York. p. 63-71.

Trumbore SE, Davidson EA, de Camargo PB, Nepstad DC, Martinelli LA. 1995. Belowground cycling of carbon in forests and pastures of Eastern Amazonia. Global Biogeochem Cycles 9:515-528.

Veldkamp E. 1994. Organic carbon turnover in three tropical soils under pasture after deforestation. Soil Sci Soc Am J 58:175-180.

Werner P. 1984. Changes in soil properties during tropical wet forest succession in Costa Rica. Biotropica 16:43-50.

Tables

Table 1. Two-way ANOVA for all variables studied in the four systems evaluated at "Santa Rosa" National Park. The F-ratios for each variable are indicated. NS, not significant; * P<0.05; ** P<0.01; *** P<0.001.

Table 2. Two-way ANOVA for all variables studied in the five systems evaluated at "La Flor" Sustainable Center National Park. The F-ratios for each variable are indicated. NS, not significant; * P<0.05; ** P<0.01; *** P<0.001.

Table 3. Average C:N ratio in all ecosystems studied in Guanacaste (Costa Rica). Mean comparisons are only valid for the same site. The Fisher PLSD minimum significant difference is 1.753 and 0.568 for ecosystems at "Santa Rosa" and "La Flor", respectively (P<0.05). Standard error within brackets.

Table 4. Soil bulk density up to 50 cm depth in all ecosystems studied in northwestern "Guanacaste" (Costa Rica). Mean comparisons are only valid for the same site. The Fisher PLSD minimum significant difference is 0.083 and 0.095 for ecosystems at "Santa Rosa" and "La Flor" respectively (P<0.05). Standard error within brackets.

Table 5. Mean weight diameter (MWD) of soil aggregates up to 50 cm depth in all ecosystems studied in northwestern "Guanacaste" (Costa Rica). Mean comparisons are only valid for the same site. The Fisher PLSD minimum significant difference is 0.667 and 0.383 for ecosystems at "Santa Rosa" and "La Flor", respectively (P<0.05). Standard error within brackets.

Table 6. Litter accumulation and SOC pool (Mg C ha^{-1}) in all ecosystems studied at Guanacaste (Costa Rica). Values followed by the same letter are statistically different at P<0.01 (t-test). Comparisons are only valid for the same site.

Figure 1. Box-plots of C fractions with depth (all ecosystems included; one data comes from a composite sample of 4 repetitions represent all ecosystems studied at “Santa Rosa”. Differences were significant according to Kolmogorov-Smirnov one sample test using logistic distribution.

Figure 2. Box-plots of C fractions with depth (the data, which were obtained from a composite sample of 4 repetitions, represent all ecosystems studied at “La Flor”. Differences were significant according to Kolmogorov-Smirnov one sample test using logistic distribution.

Figure 3. Depth C concentration in <2 mm ground soil (mean ± 1 S.E.) in the four ecosystems studied at S. Rosa. Fisher PLSD critical significance level is 4.8 at $p<0.05$.

Figure 4. Depth C concentration in <2 mm ground soil (mean ± 1 S.E.) in the five ecosystems studied at “La Flor”. Fisher PLSD critical significance level is 3.53 at $p<0.05$.

Figure 5. Soil C concentration in the different particle size fractions at “Santa Rosa”; clay+silt (<20 μm), coarse silt (20-53 μm), fine sand (53-105 μm) and coarse sand (105-200 μm)

Figure 6. Soil C concentration in the different particle size fractions at “La Flor”. Same legend as figure 5.

Figure 7. Between-class PCA of the soil variables. Projection of the sampling sites onto the factorial plane defined by axes 1 and 2. (A) Variability of scores among sites. (B) “Eigenvalues” diagram. Squares (grey) are placed at the centre of gravity of each ecosystem or land use. Lines link samples to the corresponding sites. $P<0.0001$ (Montecarlo simulation).

Figure 8. Within-class PCA of the soil variables. Projection of the sampling sites onto the factorial plane defined by axes 1 and 2. (A) Variability of scores among sites. (B) "Eigenvalues" diagram.

Figure 9. Within-class PCA of the soil variables. Projection of the sampling sites onto the factorial plane defined by axes 1 and 2. (A) Ordination of sites with all centroids (groups or ecosystems) at the origin; (B) open circles are placed at the centre of gravity of each soil depth. Lines link the different ecosystems to the corresponding soil depth.

Table 1.

Source of variation	*df*	Carbon	Nitrogen	C:N ratio	MWD	ρ_d	Aggregate size 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 **	1.29 NS
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
Error SS	60	27.50	0.24	368.51	66.77	1.02	3590.39	1282.96	4216.10	2419.76	4282.72	22374.24
Error MS	60	0.46	0.004	6.14	1.11	0.02	59.84	21.38	70.27	40.33	71.38	372.90

Table 2.

Source of variation	*df*	Carbon	Nitrogen	C:N ratio	MWD	ρ_d	Aggregate size distribution (mm)					
							<0.25	0.25-0.50	0.50-1.00	1.00-2.00	2.00-4.75	>4.75
Ecosystem (A)	4	42.44 ***	33.83 ***	19.94 ***	21.83 ***	11.75 ***	75.24 ***	7.76 ***	21.35 ***	29.19 ***	25.88 ***	10.68 ***
Depth (B)	4	36.31 ***	38.19 ***	5.47 ***	0.36 NS	3.11 *	0.27 NS	0.83 NS	0.43 NS	0.31 NS	1.61 NS	0.78 NS
AxB	16	0.61 NS	0.60 NS	1.83 *	1.31 NS	0.82 NS	2.68 **	0.78 NS	1.31 NS	2.03 *	1.08 NS	1.39 NS
Error SS	75	23.57	0.18	60.92	27.78	1.70	5392.05	2164.40	1395.21	868.96	2180.77	5114.40
Error MS	75	0.31	0.002	0.81	0.37	0.02	71.89	28.86	18.60	11.59	29.08	68.19

Table 3.

	Santa Rosa N. P.				La Flor S. C.				
Depth (cm)	Mature forest	Deciduous forest	*Quercus* forest	Burnt savanna	Natural savanna	Mango plantation	Citrus plantation	Gallery forest	Sugarcane
0-10	11.5 (0.3)	11.3 (0.3)	12.4 (0.6)	15.0 (0.8)	11.5 (0.4)	10.3 (0.4)	10.8 (0.1)	10.0 (0.2)	11.9 (0.2)
10-20	11.8 (0.7)	11.2 (0.3)	11.6 (0.7)	15.6 (1.5)	10.1 (0.2)	10.2 (0.3)	10.4 (0.3)	9.8 (0.3)	11.4 (0.2)
20-30	12.7 (0.7)	11.3 (0.1)	11.1 (0.2)	16.3 (2.6)	9.4 (0.6)	9.8 (0.2)	9.4 (0.2)	9.6 (0.2)	11.4 (0.6)
30-40	13.7 (1.1)	12.0 (0.5)	11.0 (0.6)	15.5 (2.5)	9.0 (0.6)	10.2 (0.2)	8.7 (0.2)	9.1 (0.3)	11.2 (1.0)
40-50	13.7 (1.3)	12.0 (0.4)	12.0 (1.4)	15.6 (2.6)	9.1 (0.6)	10.6 (0.5)	9.0 (0.6)	9.0 (0.3)	12.8 (0.8)

Table 4.

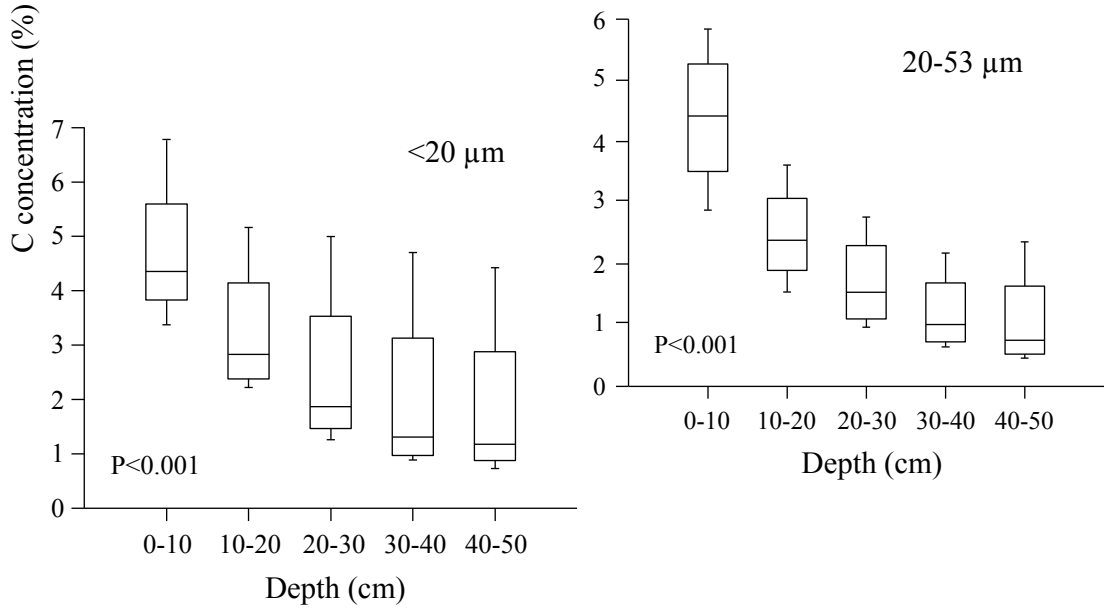
	Santa Rosa N. P.				La Flor S. C.				
Depth (cm)	Mature forest	Deciduous forest	*Quercus* forest	Burnt savanna	Natural savanna	Mango plantation	Citrus plantation	Gallery forest	Sugarcane
0-10	1.1 (0.04)	1.2 (0.07)	1.0 (0.02)	1.1 (0.06)	1.2 (0.06)	1.3 (0.10)	1.3 (0.08)	1.3 (0.05)	1.2 (0.07)
10-20	1.2 (0.05)	1.2 (0.05)	0.9 (0.03)	1.4 (0.04)	1.2 (0.05)	1.3 (0.09)	1.3 (0.05)	1.3 (0.05)	1.1 (0.03)
20-30	1.2 (0.06)	1.2 (0.05)	1.0 (0.10)	1.4 (0.04)	1.3 (0.06)	1.3 (0.11)	1.4 (0.10)	1.3 (0.04)	1.0 (0.09)
30-40	1.2 (0.04)	1.2 (0.07)	0.9 (0.14)	1.3 (0.06)	1.5 (0.14)	1.4 (0.06)	1.4 (0.05)	1.4 (0.04)	1.1 (0.11)
40-50	1.1 (0.03)	1.1 (0.08)	1.1 (0.09)	1.3 (0.04)	1.4 (0.09)	1.4 (0.04)	1.6 (0.04)	1.3 (0.07)	1.1 (0.06)

Table 5.

	Santa Rosa N. P.				La Flor S. C.				
Depth (cm)	Mature forest	Deciduous forest	*Quercus* forest	Burnt savanna	Natural savanna	Mango plantation	Citrus plantation	Gallery forest	Sugarcane
0-10	2.12 (0.17)	2.32 (0.15)	1.98 (0.38)	4.07 (0.64)	2.09 (0.07)	2.36 (0.08)	2.27 (0.08)	1.52 (0.35)	1.99 (0.14)
10-20	2.03 (0.23)	2.31 (0.15)	1.66 (0.57)	4.70 (0.84)	1.71 (0.18)	2.18 (0.11)	2.26 (0.19)	1.32 (028)	2.32 (0.08)
20-30	1.66 (0.10)	2.39 (0.39)	1.32 (0.38)	5.38 (0.72)	1.58 (0.25)	2.24 (0.09)	2.88 (0.50)	0.98 (0.24)	2.40 (0.17)
30-40	1.37 (0.11)	2.45 (0.56)	2.13 (0.77)	5.25 (0.66)	1.57 (0.16)	2.49 (0.63)	2.74 (0.45)	0.77 (0.29)	2.36 (0.12)
40-50	1.51 (0.28)	2.08 (0.09)	2.52 (0.94)	5.88 (0.44)	1.70 (0.06)	3.32 (0.56)	2.48 (0.40)	0.70 (0.22)	2.64 (0.57)

Table 6.

	Santa Rosa N. P.				La Flor S. C.				
Depth (cm)	Mature forest	Deciduous forest	*Quercus* forest	Burnt savanna	Natural savanna	Mango plantation	Citrus plantation	Gallery forest	Sugarcane
In litter	6.6	5.5	6.6	0	4.9	4.5	1.5	3.8	7.6
0-10	65.9	63.0	48.2	42.2	37.6	28.9	27.5	26.9	44.6
10-20	49.3	30.4	21.1	27.4	17.1	17.7	16.4	14.4	38.5
20-30	39.7	25.1	12.7	16.4	10.5	9.2	10.1	9.6	28.5
30-40	40.1	18.5	10.0	12.7	8.4	7.7	7.2	7.6	26.0
40-50	33.9	13.3	10.6	11.3	6.1	6.9	6.8	7.6	22.4
Total in soil	**228.9 a**	**150.3 ab**	**102.6 b**	**110.0 b**	**79.7 b**	**70.4 b**	**68.0 b**	**66.1 b**	**160.0 a**


C concentration (%)
<20 µm
P<0.001
0-10
10-20
20-30
30-40
40-50
Depth (cm)
20-53 µm
P<0.001
0-10
10-20
20-30
30-40
40-50
Depth (cm)

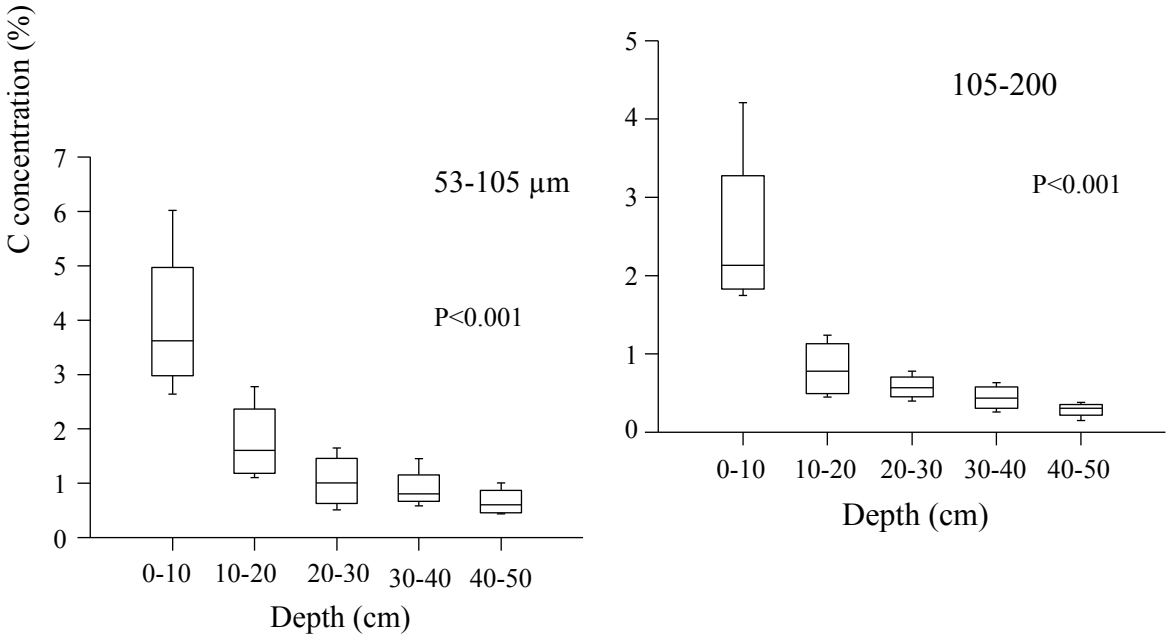

C concentration (%)
53-105 µm
P<0.001
105-200
P<0.001
0-10
10-20
20-30
30-40
40-50
Depth (cm)

Figure 1.

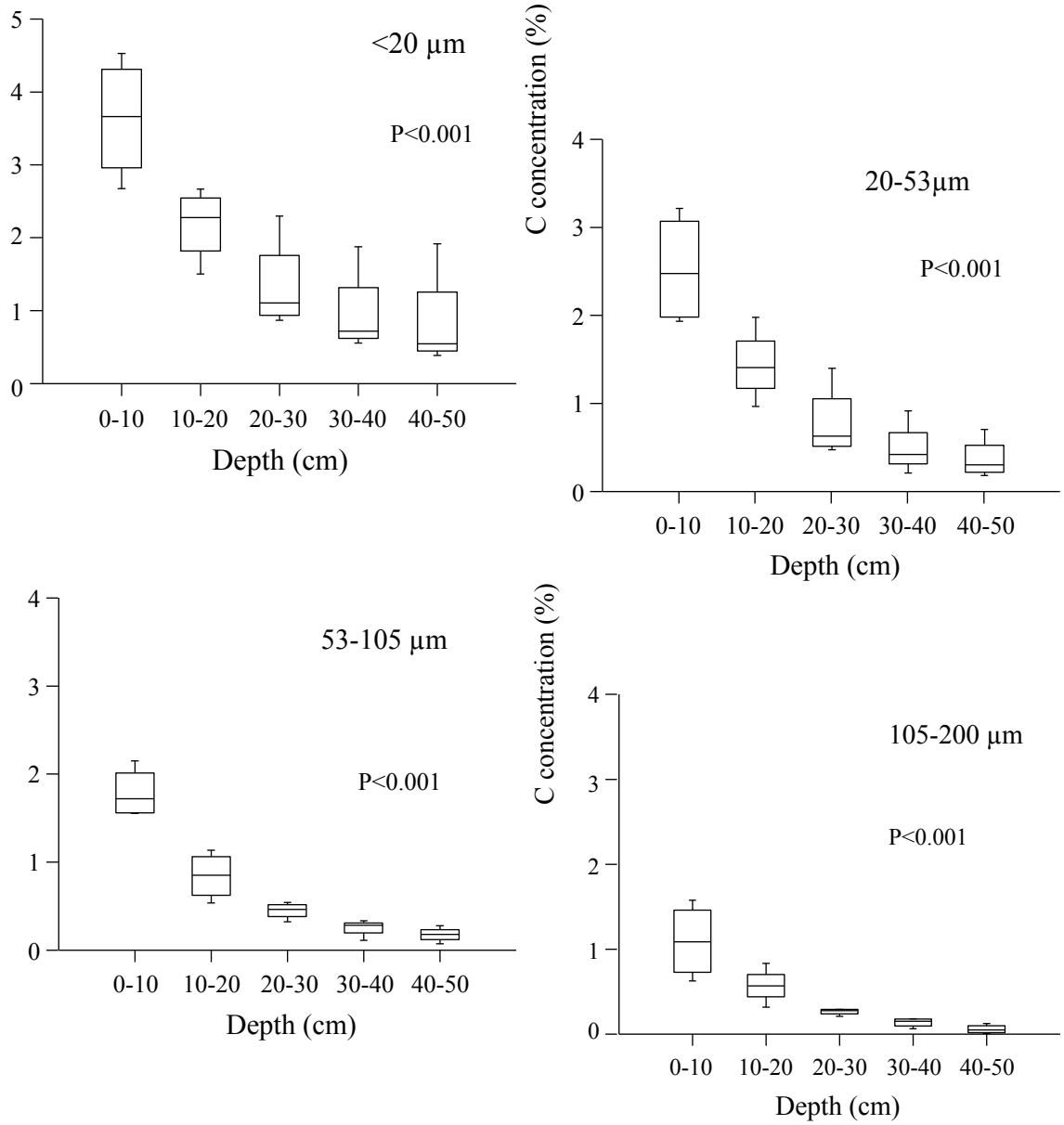

<20 µm
P<0.001
20-53µm
P<0.001
53-105 µm
P<0.001
105-200 µm
P<0.001
C concentration (%)
C concentration (%)
0-10
10-20
20-30
30-40
40-50
Depth (cm)
Depth (cm)
Depth (cm)
Depth (cm)

Figure 2.

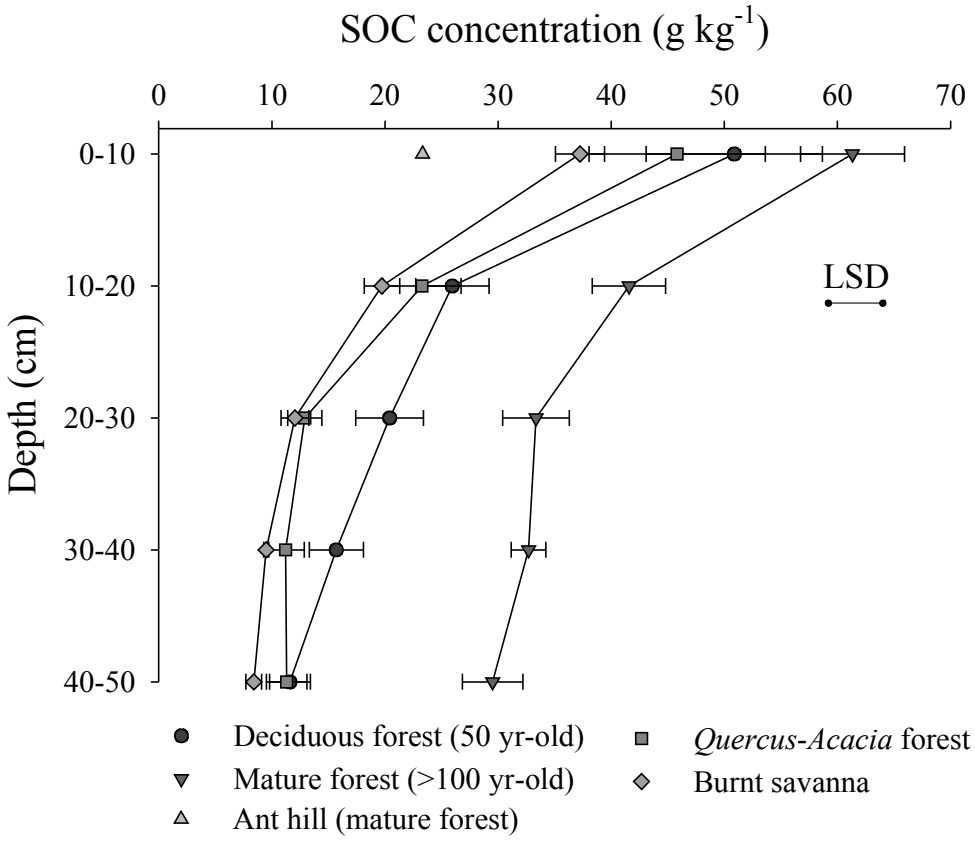

SOC concentration (g kg-1)
0
10
20
30
40
50
60
70
Depth (cm)
0-10
10-20
20-30
30-40
40-50
LSD
Deciduous forest (50 yr-old)
Quercus-Acacia forest
Mature forest (>100 yr-old)
Burnt savanna
Ant hill (mature forest)

Figure 3.

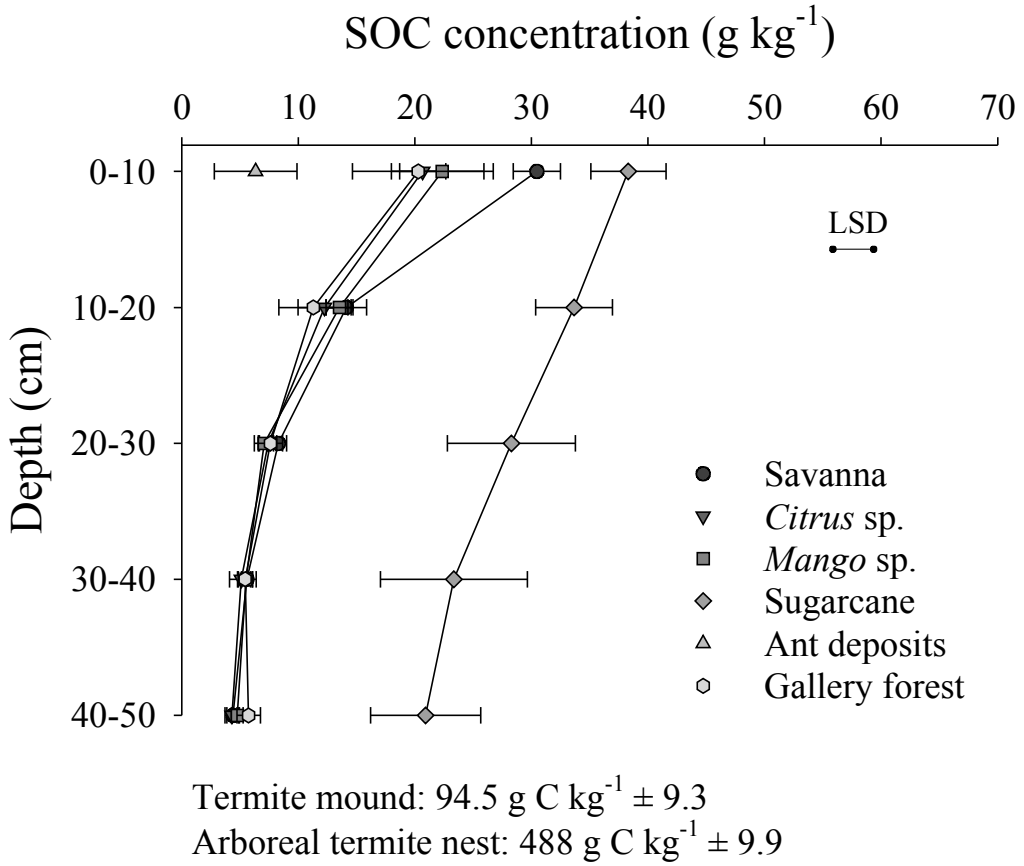

SOC concentration (g kg-1)
0
10
20
30
40
50
60
70
0-10
10-20
20-30
30-40
40-50
Depth (cm)
LSD
Savanna
Citrus sp.
Mango sp.
Sugarcane
Ant deposits
Gallery forest
Termite mound: 94.5 g C kg-1 ± 9.3
Arboreal termite nest: 488 g C kg-1 ± 9.9

Figure 4.

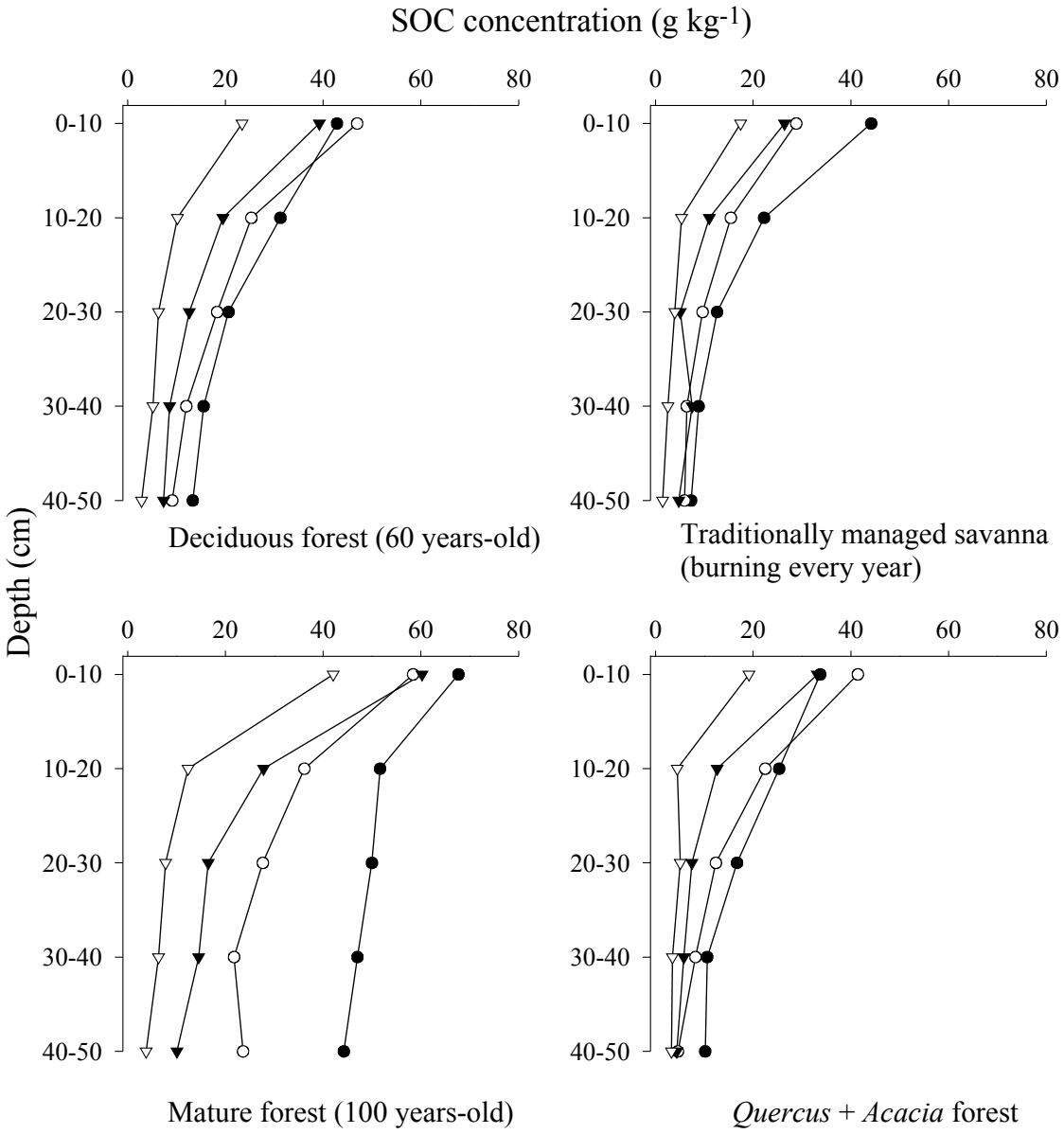

SOC concentration (g kg-1)
0
20
40
60
80
0-10
10-20
20-30
30-40
40-50
Depth (cm)
Deciduous forest (60 years-old)
Traditionally managed savanna
(burning every year)
Mature forest (100 years-old)
Quercus + Acacia forest

Figure 5.

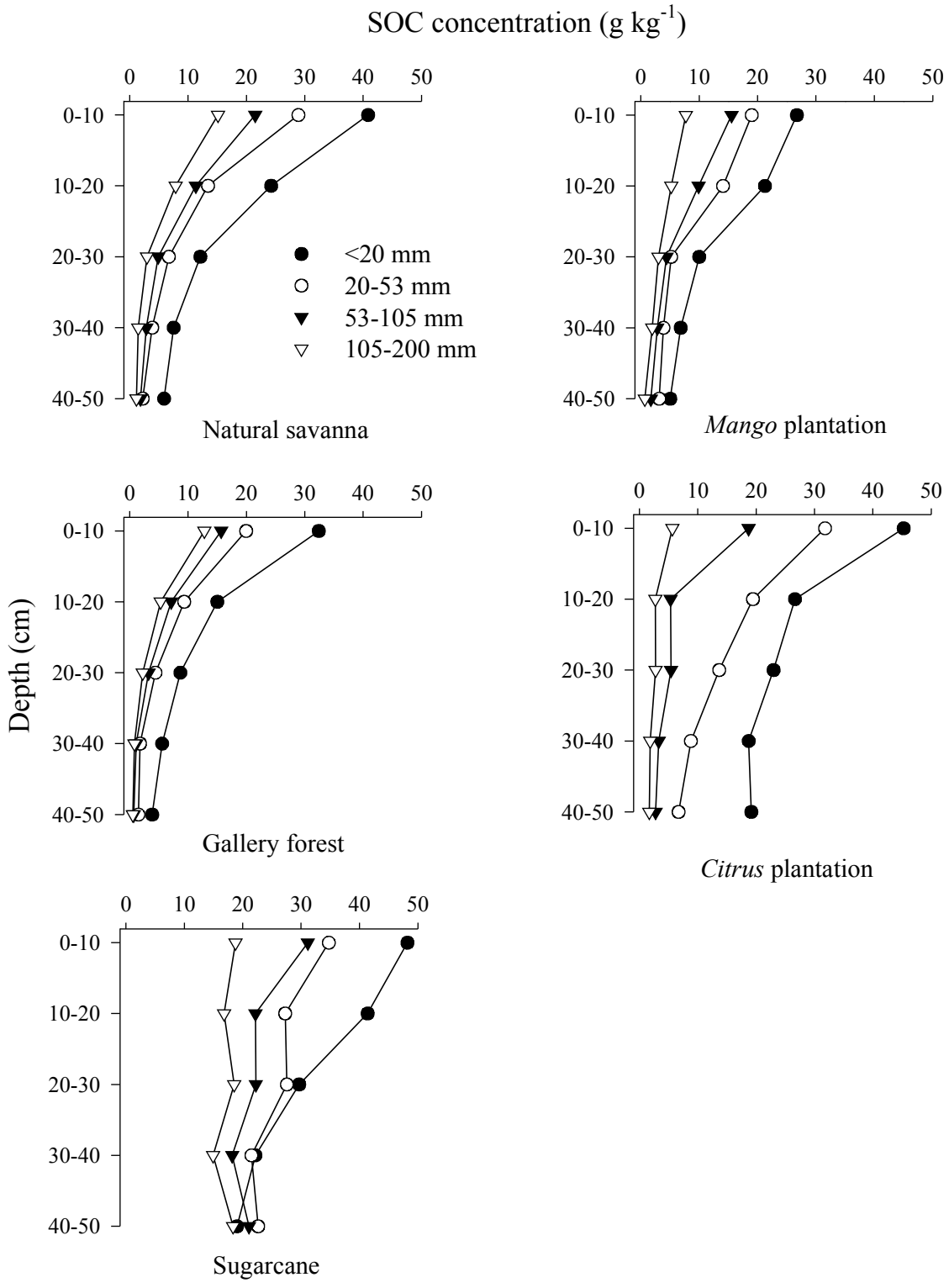

SOC concentration (g kg-1)
Depth (cm)
0-10
10-20
20-30
30-40
40-50
0
10
20
30
40
50
<20 mm
20-53 mm
53-105 mm
105-200 mm
Natural savanna
Mango plantation
Gallery forest
Citrus plantation
Sugarcane

Figure 6

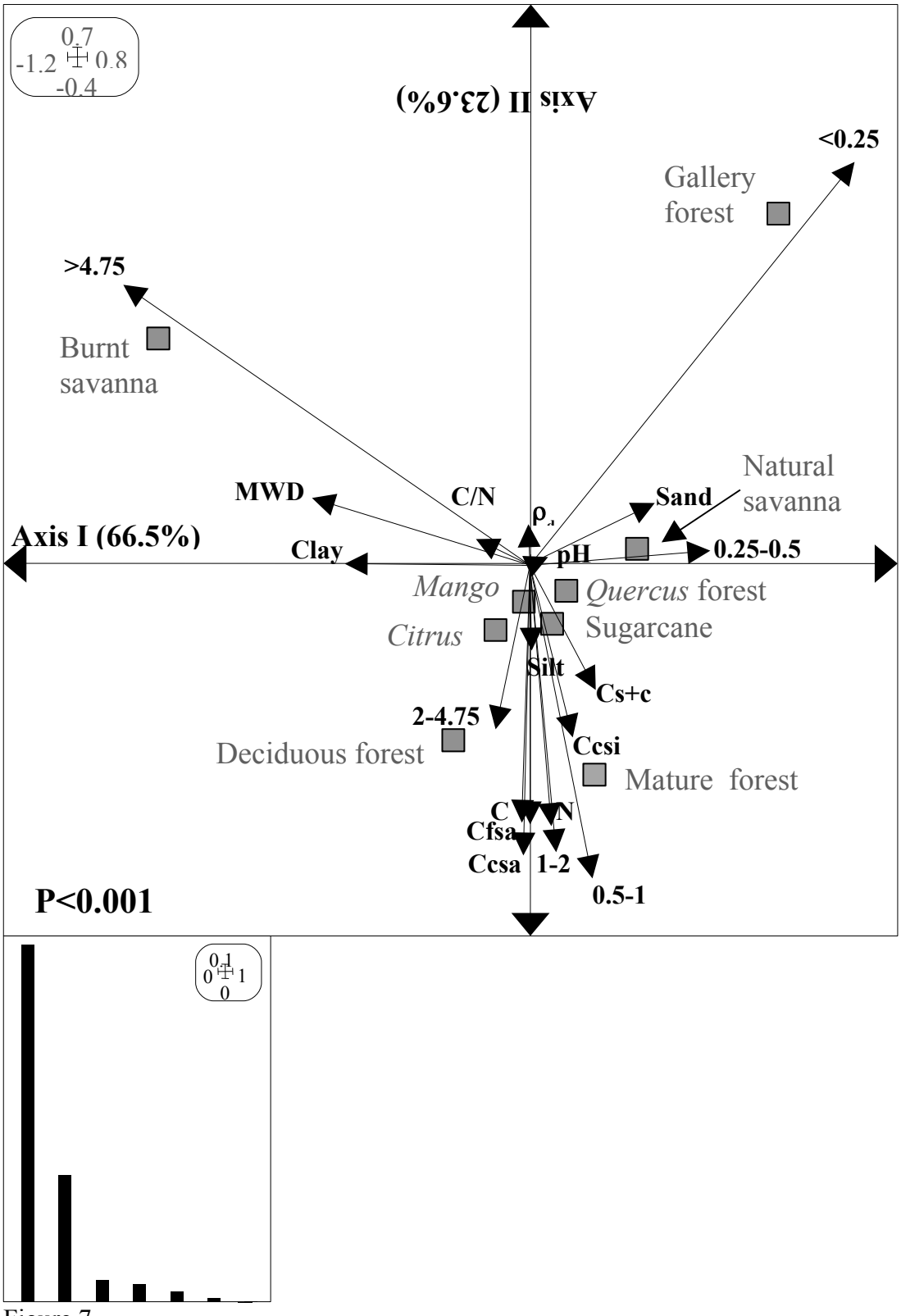

0.7
-1.2
0.8
-0.4
Axis II (23.6%)
<0.25
Gallery forest
>4.75
Burnt savanna
Natural savanna
MWD
C/N
Sand
Axis I (66.5%)
Clay
pH
0.25-0.5
Mango
Quercus forest
Citrus
Sugarcane
Silt
Cs+c
2-4.75
Ccsi
Deciduous forest
Mature forest
C
N
Cfsa
Ccsa
1-2
0.5-1
P<0.001
0.1
0
1
0

Figure 7.

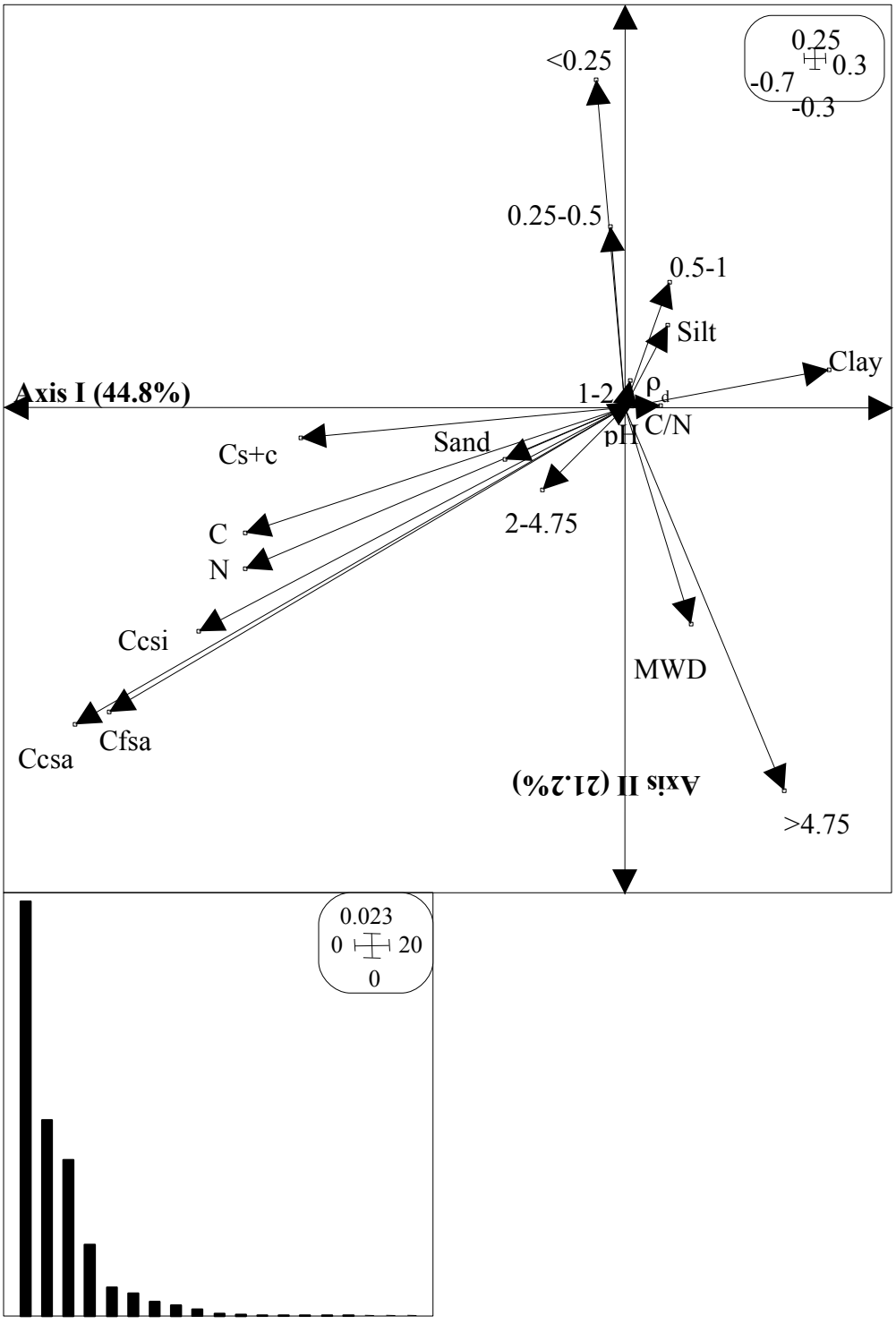

0.25
0.3
-0.7
-0.3
<0.25
0.25-0.5
0.5-1
Silt
Clay
Axis I (44.8%)
1-2
ρd
pH
C/N
Sand
Cs+c
2-4.75
C
N
Ccsi
Ccsa
Cfsa
MWD
Axis II (21.2%)
>4.75
0.023
0
20
0

Figure 8.

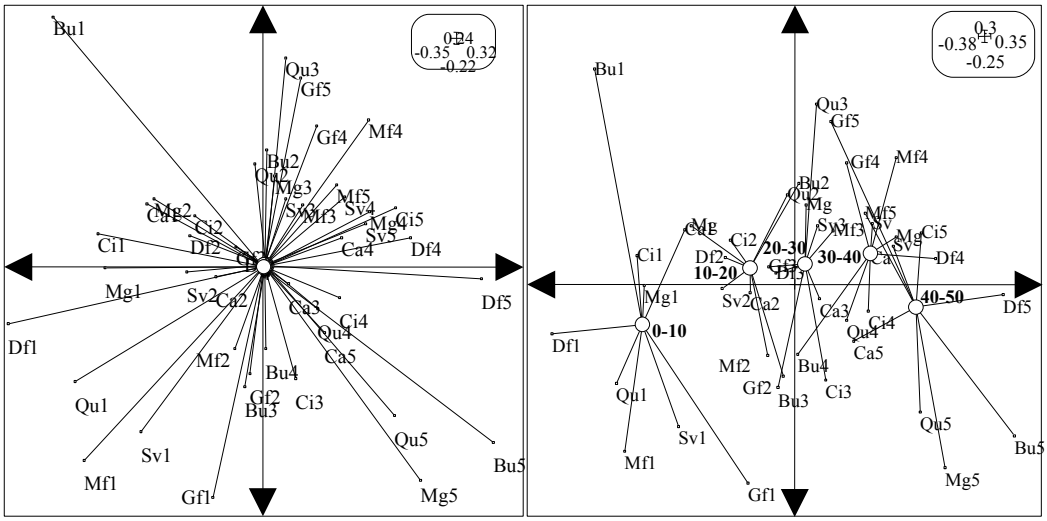

Bu1
Qu3
Gf5
Gf4
Mf4
Bu2
Qu2
Mg3
Mf5
Sv4
Mf3
Mg4
Ci5
Sv5
Ca4
Df4
Df5
Ci1
Df2
Mg1
Sv2
Ca2
Ca3
Ci4
Qu4
Ca5
Df1
Mf2
Bu4
Gf2
Bu3
Ci3
Qu1
Qu5
Sv1
Bu5
Mf1
Gf1
Mg5
Mg2
Ci2
Ca1
Mg
Sv3
Sv
0-10
10-20
20-30
30-40
40-50

Figure 9.

Appendix 1. Soil textural analysis (hydrometer method) and pH under the different ecosystems evaluated at "Santa Rosa" National Park.

System	Soil layer (cm)	Texture (%)			pH	
		Sand	Silt	Clay	H_2O 1:1	$CaCl_2$
> 100 years-old deciduous forest	0-10	60.8	21.9	17.3	6.7	6.6
Enterolobium cyclocarpum	10-20	55.0	25.8	19.2	6.9	6.6
	20-30	50.6	26.2	23.2	6.8	6.3
	30-40	44.4	26.2	29.4	6.8	6.2
	40-50	55.1	20.8	24.1	6.7	6.1
65 years-old deciduous forest	0-10	52.3	22.7	25.0	6.5	6.2
Calycophyllum candidissimum	10-20	38.6	26.6	34.9	6.5	6.1
	20-30	38.9	24.3	36.8	6.5	6.1
	30-40	23.3	24.9	51.8	6.3	6.1
	40-50	15.8	27.4	56.7	6.2	5.9
Dry tropical forest (65 years-old)	0-10	61.4	14.2	24.5	6.1	5.6
Quercus olenoides – Acacia forest	10-20	45.4	20.2	34.4	6.0	5.2
	20-30	45.4	20.2	34.4	5.9	5.3
	30-40	46.8	21.1	32.1	5.7	5.2
	40-50	38.9	27.0	34.1	5.6	5.1
Burnt savanna	0-10	21.6	28.0	50.4	5.8	5.2
	10-20	17.9	25.8	56.3	5.8	5.3
	20-30	37.8	13.9	48.3	5.8	5.5
	30-40	34.8	14.8	50.4	6.1	5.7
	40-50	11.6	23.2	65.2	6.2	5.8

Appendix 2. List of vascular plant species in the fire-prone savanna area of the Santa Rosa National Park (prepared by A. Guadamuz)

Family	Genus/Species	Descriptor
Poaceae (= Gramineae)	*Axonopus aureus*	Beauv.
	Hyparremia 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.

Appendix 3. Soil textural analysis (hydrometer method) and pH under the different ecosystems evaluated at "La Flor" Sustainable Center.

System	Soil layer (cm)	Texture (%)			pH	
		Sand	Silt	Clay	H_2O 1:1	$CaCl_2$
Savanna with scattered trees	0-10	62.7	26.6	10.7	6.0	5.3
	10-20	62.7	26.8	10.5	6.3	5.4
	20-30	52.6	30.0	17.4	6.1	5.3
	30-40	46.6	30.0	23.4	6.3	5.3
	40-50	43.0	32.6	24.4	5.7	5.2
Gallery forest	0-10	68.6	18.0	13.4	6.9	6.6
	10-20	69.0	18.8	12.3	6.8	6.4
	20-30	72.8	14.9	12.3	6.8	6.3
	30-40	62.5	19.2	18.3	6.8	6.2
	40-50	62.7	20.1	17.2	6.9	6.4
Mango plantation	0-10	59.4	25.1	15.5	6.7	6.1
	10-20	56.8	26.6	16.6	6.7	6.0
	20-30	46.0	29.6	24.4	6.6	6.0
	30-40	37.1	29.4	33.5	6.3	5.9
	40-50	40.2	23.5	36.3	6.3	5.9
Citrus plantation	0-10	48.4	32.1	19.5	6.1	5.8
	10-20	45.4	28.7	25.9	6.3	5.8
	20-30	42.5	26.9	30.6	6.2	5.6
	30-40	34.6	28.8	36.6	5.6	5.1
	40-50	28.3	28.7	43.0	5.2	4.7
Sugarcane	0-10	49.1	32.6	18.3	5.8	5.5
	10-20	45.0	34.1	20.9	6.2	5.8
	20-30	37.4	35.8	26.8	6.3	6.1
	30-40	31.9	39.4	28.7	6.6	6.0
	40-50	37.7	35.9	26.4	6.5	6.0