

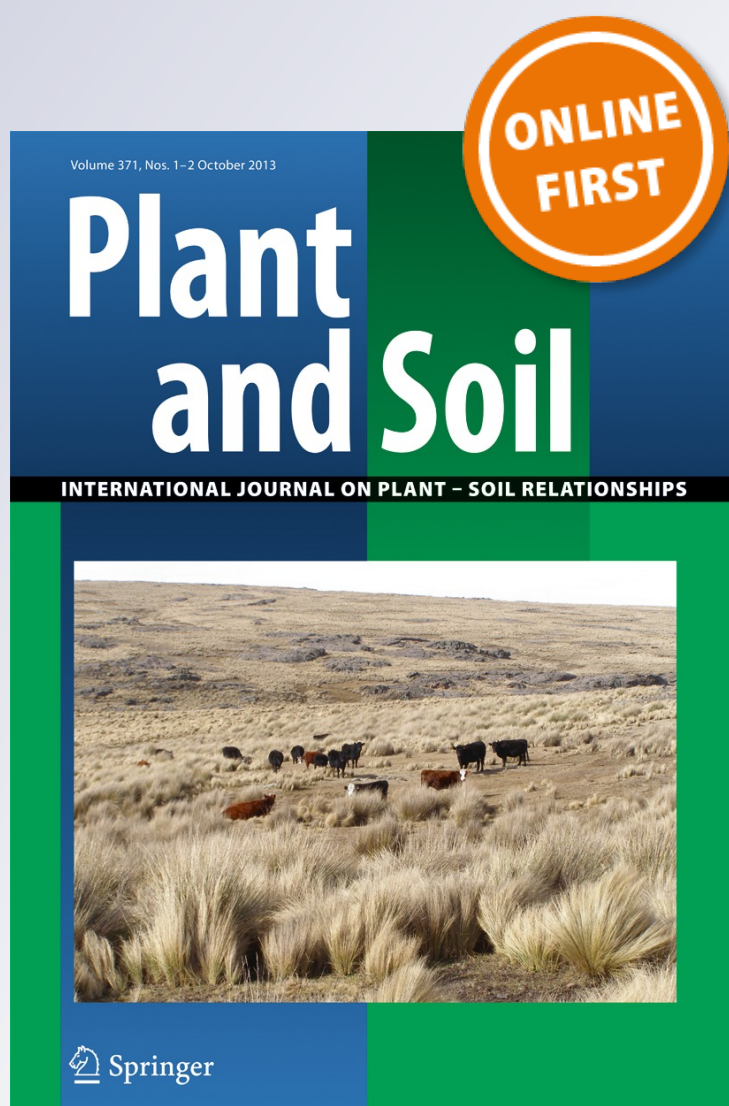
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**Pere Casals, Johanna Romero, Graciela
M. Rusch & Muhammad Ibrahim**

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Soil organic C and nutrient contents under trees with different functional characteristics in seasonally dry tropical silvopastures

Pere Casals · Johanna Romero ·
Graciela M. Rusch · Muhammad Ibrahim

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Abstract

Aims The selection of tree characteristics is critical for the outcome of the tree effects on soil fertility in silvopastoral pastures. This study aims to quantify the effects of trees on soil nutrient and C stocks, as well as assessing differences on the effects between legume (*Albizia saman*; *Enterolobium cyclocarpum*) and non-legume tree species (*Tabebuia rosea*; *Guazuma ulmifolia*). **Methods** In Central Nicaragua, soil was sampled (0–10 cm deep) in paired plots, under both a canopy and in open grassland, in 12 sites per tree species and analysed for organic C, total N stocks, available P and extractable K^+ , Ca^{2+} and Mg^{2+} . To assess the effects of herbaceous composition and cattle to soil properties, we recorded the cover of plant groups and assessed the mass of dung in each plot.

Results Soil organic C and N, available P and extractable K^+ and Ca^{2+} were higher under the tree canopy than under paired open grassland. The basal area of trees was positively related with the canopy effect on soil

variables, thus suggesting that the age or sizes of the trees are relevant factors associated with the content of soil C and nutrients. No specific effects related to the legume species group were detected.

Conclusions Our results indicate that in fertile seasonally dry subtropical pastures, scattered trees have an overall effect on soil fertility, and that the magnitude of the effect depends more on the tree characteristics (i.e. basal area, crown area) than on whether the species is a legume or not.

Keywords Legume functional group · Silvopastoral systems · Soil nutrient stocks · Tree-grass interactions · Tree leaf traits

Introduction

Pasture is a major land use in Central America, occupying more than 60 % of the agricultural land area. In many tropical pastures, isolated trees are frequently kept after forest conversion (Manning et al. 2006), and the resulting silvopastoral systems have benefitted from the total production of fodder and other products (including wood for construction and firewood, fruit for human consumption, etc.), as well as from an enhancement of animal well-being and productivity from the shelter and shade provided by trees (Souza 2002). There is also an increasing amount of evidence that silvopastoral systems have an important conservation value (Harvey and Haber 1999; Harvey et al. 2005; Sáenz et al. 2006), in addition to playing a role in mitigating global

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P. Casals (✉)
Centre Tecnològic Forestal de Catalunya (CTFC), Ctra de
St. Llorenç de Morunys, km 2, 25280 Solsona, Spain
e-mail: pere.casals@ctfc.cat

J. Romero · M. Ibrahim
Tropical Agricultural Research and Higher Education Center
(CATIE), Cartago, Costa Rica

G. M. Rusch
Norwegian Institute for Nature Research (NINA),
Norway, Norway

carbon emissions (Andrade et al. 2008). Knowledge about the effects of trees on soil nutrient contents and dynamics will help improve the theoretical basis for soil and tree management oriented towards improving or maintaining soil fertility in tropical pastures, thereby harmonizing food production systems with environmental and biodiversity preservation.

Tree diversity is one of the main evident features of tropical forests, and approximately 42 tree species were recorded growing scattered in paddocks in central Nicaragua, with most of them remaining from previous dry tropical forest (Sánchez Merlos et al. 2005). Plant species influence ecosystem nutrient dynamics through a variety of mechanisms (Craine 2009 and references therein), and trees with different characteristics are expected to have different effects on soil nutrient stocks and cycling (Kumar 2008). Grouping species according to their functional properties is an approach widely used, not only to simplify the study of functions in a broad variety of species, but also to assess emerging processes (Eviner and Chapin 2003).

Legume tree species form one of the most evident functional groups by its potential for the symbiotic fixation of atmospheric N and, even independent of this capacity, by the high levels of N in their tissues, which is in accordance with their N-demanding strategy (McKey 1994). Hence, both above- and below-ground litter inputs from legume trees are thought to enhance soil's biological activity and nutrient release from organic matter. According to this, and among other reasons, legume tree species are widespread in production systems, including agroforestry systems in the tropics.

Furthermore, several other traits of tree species may be relevant to nutrient cycling. Differences in litter nutrient concentrations and carbon quality (e.g. lignin content) are likely to affect litter decomposition rates (Cornwell et al. 2008) and, therefore, the relative abilities of different tree species to contribute to the soil fertility of tropical silvopastoral systems (Kumar 2008). Differences in root architecture (associated with the portion and depth of the soil profile explored), morphology and physiology may help explain the differences in litter composition between tree species or groups. As postulated by the nutrient uplift hypothesis, trees with deep roots can redistribute cations and P from soil deep layers to the soil surface through deep root uptake and release via litterfall or leaching from leaves by throughfall (Jobbágy and Jackson 2004; Vetaas 1992).

In addition, and independently of their physiology, the canopy characteristics of scattered trees may also, whether directly or indirectly, affect soil fertility. Since canopy surfaces intercept small particles contained in wet and dry deposition (Hanson and Lindberg 1991), species that differ in canopy characteristics (e.g. architecture, leaf area index, phenology and morphology) may markedly change atmospheric deposition. Canopy properties also indirectly alter micro-environmental conditions and change the conditions for soil biotic activity, which may further affect soil organic matter mineralization and nutrient availability. Lastly, the presence of scattered trees may attract domestic and wild animals, thereby possibly increasing the soil's nutrient content with their excreta. Consequently, if moving animals preferentially select the canopies of specific species, the spatial and temporal distribution of soil nutrients may be altered.

Silvopastoral systems can be an alternative for the management of soil nutrients of tropical pastures, though the selection of tree species becomes critical for successful results (Galicía and García-Oliva 2004; Rhoades 1997). This study aims to quantify the effect of trees on soil nutrient and C stocks in tropical seasonally dry silvopastoral systems, in addition to evaluating possible differences in the effect between legume and non-legume tree functional groups. We hypothesized that trees would make a net contribution to soil C and nutrient contents, which would result in higher levels under trees compared with the adjacent open pasture. We also expected soil N under legume trees to be higher than under non-legume trees because of their presumably N-enriched litter. We addressed these hypotheses by comparing soil samples under two legume and two non-legume tree species and paired open grassland, while accounting for the potential effects due to differences in understory herbaceous vegetation and in the deposition of animal faeces in silvopastoral paddocks with scattered trees in central Nicaragua.

Material and methods

Study area

The research was conducted in the central region of the Matalagalpa district (Nicaragua) belonging to the Muy-Muy (85°45'N, 12°40'W) and Matiguás (85°27'N, 12°50'W) municipalities.

Silvopastoral systems in the region were located in flat landforms or moderately steep hills, and composed of Tertiary rhyolitic to dacitic tuffs. In flat areas, soils were moderately deep Vertisols or Inceptisols with vertic properties. The mean annual rainfall from the closest meteorological station, Muy Muy, is 1,547 mm (1971–2000), and the annual mean air temperature is 24.3 °C (1971–2000; Instituto Nicaragüense de Estudios Territoriales, 2011). There is a clear contrast between the rainy and dry periods, with the rainfall recorded between November–May usually being less than 10 % of the yearly total.

The native forest has been a seasonally dry tropical forest, and has been converted to semi-natural pastures consisting of various species sharing dominance, mostly prostrate grasses of the genus *Paspalum* and *Axonopus* and sown pastures dominated by *Brachiaria brizantha* Hochst (Ospina et al. 2012). In general, those grasses (natural or exotic) are perennial grasses with a high resistance to seasonal droughts, but with a low tolerance to shade. Forbs are less abundant (e.g. *Blechnum pyramidatum* Lamarck, *Baltimora recta* L), though they display a trend of being comparatively more abundant under the canopy. After deforestation, individual forest trees are kept within pastures or allowed to establish by natural recruitment, although this process is often hindered by animal trampling, browsing and management practices intended to halt the encroachment of shrubs and other woody plants in the pasture (Esquivel et al. 2008). Unfortunately, it was not possible to know exactly when the paddocks in the study had been cleared or whether the studied trees had been planted or not because these areas were occupied in the 1990s after a period of abandonment during the Nicaraguan civil war (1981–1989).

Experimental design

We studied the effects on soil C and the nutrient stocks of four of the most common tree species in silvopastures in the study area (Sánchez Merlos et al. 2005): *Guazuma ulmifolia* Lam. (guácimo), *Enterolobium cyclocarpum* (Jacq.) Griseb. (guanacaste), *Albizia saman* (Jacq.) F. Muell. (genízaro) and *Tabebuia rosea* (Bertol.) D.C. in A. D.C. (roble). To assess the effects of trees, we compared paired soil samples under the canopy and in open grassland at 12 sites per tree species (Appendix A), and we also tested the effect of legumes by comparing the two legume species (*E. cyclocarpum* and *A. saman*) and

the two non-legume ones (*G. ulmifolia* and *T. rosea*). For each species of tree, experimental sites (i.e. a pair of tree and open grassland plots) were located in different paddocks. We considered the paddock as a management unit, and we assumed that both paired plots has been submitted to the same management. Paddocks were located in seven farms in Matiguás (22 sites) and 16 farms in Muy Muy (26 sites), within an altitudinal range between 260 m a.s.l and 325 m a.s.l. (Appendix A). The site selection was done after visiting 37 farms in Matiguás and 38 in Muy Muy, where 103 possible sites were characterized by pasture and land features, soil type and the structural properties of trees. We chose sites in paddocks with low slopes (<10 %), a low density of trees and a pasture dominated by native grass species. Moreover, the selected paddocks had to have been used for grazing for at least the past 10 years, had never been fertilized or mechanized and had no pasture burning at any of them for at least the past 5 years. In the area, forest was converted to land for cattle grazing by cutting down trees and shrubs, and burning. To overcome the problem of uncertainty about the time since the forest was cleared and the age of the studied trees, and to minimize possible effects due to the time over which the tree had influenced soil properties, we chose trees with a DBH above 23 cm (Appendix A).

Due to the predominant north-eastern winds in the study area, litterfall generally spreads out in the south-west direction from the tree canopy and at a distance from the trunk of up to approximately twice the tree height (Sandoval 2006). Therefore, in each site, we located the open grassland plot in the opposite direction to the dominant wind with respect to the tree and at a location beyond the influence area of any other trees in the paddock. The canopy plot was located in the south-western tree canopy quartile, within a distance from the trunk of two-thirds the crown's radius (Fig. 1). Soil nutrient dynamics in tropical forests are strongly affected by rainfall seasonality (e.g. Toledo-Aceves and García-Oliva 2008). Hence, in each plot we took soil samples at the beginning of the rainy season (June) when the maximum nutrient contents were expected due to the absence of plant uptake and the accumulation of soluble forms during the dry season (Campo et al. 1998; García-Oliva et al. 2003). To help assess the effect of both the grassland plant composition and the contribution of animals to soil nutrients, we recorded the cover of herbaceous plant groups and the number and mass of faeces.

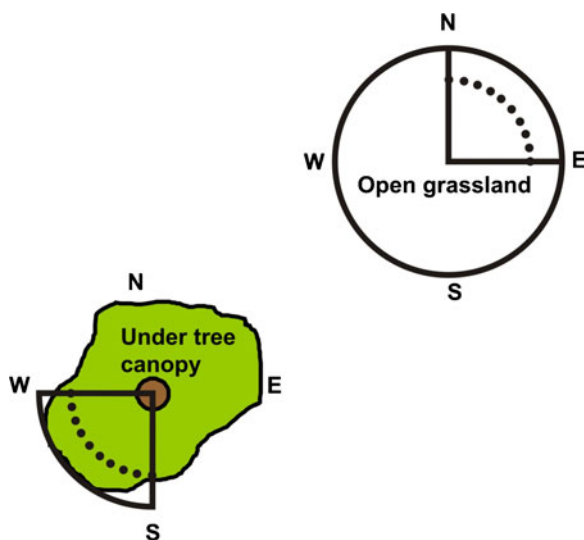


Fig. 1 Soil sampling under canopy and open grassland sketch

Tree species characteristics

The species of trees selected for this study were among the most ten abundant species growing in the areas (Sánchez Merlos et al. 2005). *A. saman* and *E. cyclocarpum* belong to the Mimosoideae sub-family of the Fabaceae, having the potential capacity to symbiotically fix atmospheric N_2 . They are up to 30–40 m tall deciduous trees with long imparipinnate leaves. *G. ulmifolia* (Sterculiaceae) is a smaller evergreen tree up to 25 m tall with simple 2–16 cm long leaves, while *T. rosea* (Bignoniaceae) is a deciduous tree with pentafoliate palmate leaves that reach up to 28–37 m in height. In the seasonally dry forest, the maximum litterfall occurs in February–March, which is before the start of the rainy season. Sandoval (2006) reported that in Muy Muy, more than 75 % of the leaf litterfall of *A. saman* and approximately 60 % of *G. ulmifolia* occurred from February to April.

Site characteristics

Experimental sites were located in paddocks with low slopes and soils with vertic characteristics (Appendix A), and the paddocks ranged in size from 1 ha to 45 ha (median of 5.6 ha), with approximately 1 to 19 trees per ha^{-1} (median of 2.9 trees per ha^{-1}). The paddocks were extensively grazed by cattle and since no pasture rotation is applied during the dry season, an exact stocking rate was difficult to determine, although we estimated

that it varied between 0.1 and 1.4 animal units per hectare ($0.50 \pm 0.04 AU ha^{-1}$; mean \pm SE, $n=48$).

Soil sampling and chemical analysis

In June 2009, we took 10 soil cores (0–10 cm deep) spaced 1 m apart under each tree and in a paired open grassland plots using an auger, mixing the 10 cores afterwards into a composite sample. In August, the soil bulk density in the first 2–7 cm was estimated in the same sampling plots in three small trenches using steel cylinders ($100 cm^3$).

Soils were air dried and sieved (2 mm) prior to chemical analyses, and a subsample of each soil core was ground using a ball mill (MM200 Retsch®) for analyses of organic C, total N and the natural abundance of $\delta^{13}C$ and $\delta^{15}N$. The total N and isotope ratios were measured using an ANCA interfaced with a 20–20 Europa isotope ratio mass spectrometer (Sercon Ltd. Cheshire, UK). Organic C was oxidized by digestion with an acidified dichromate solution in a block digester ($155^\circ C$, 30 min), and determined by colourimetry (Soon and Abboud 1991). The potentially mineralizable nitrogen (PMN), a comparative biochemical assay to estimate the capacity of soil to release inorganic N (Waring and Bremner 1964), was used to estimate N availability. PMN was estimated by a seven-day anaerobic incubation at $40^\circ C$ following Keeney's modifications (1982) of the general method by Waring and Bremner (1964). Briefly, 5.00 g of dry soil sample were added to test tubes containing 12.5 ml of distilled H_2O , sealed with rubber stoppers and incubated for 7 days in the dark at $40^\circ C$. Following incubation, 12.5 ml of KCl 4 N were added and filtered after 30 min of shaking. NH_4^+ was colourimetrically determined by use of the phenol and basic citrate method. Following Powers (1980), the initial amounts of mineral N were not subtracted because it was considered that initial N is a part of the N pool potentially available, which accounts for the storage effects of soil samples. We calculated the ratio of PMN to total soil N as a relative index to estimate the control of N mineralization by the organic matter in the tested lab conditions. This ratio places the focus on the organic matter control of N mineralization, i.e. the high PMN per unit of soil N suggests a more rapid cycling of organic matter in the tested lab conditions. The available soil phosphate (P) was extracted with 0.5 M $NaHCO_3$ (pH 8.5; soil:solution,

1:20; Olsen method following Kuo 1996) and colourimetrically determined using the ascorbic method (Murphy and Riley 1962) after the extracts had been neutralized with a dilute HCl solution, which accounts for the molybdate-reactive labile P. Cations were extracted by successive leaching with BaCl 0.2 N to a total soil:extract ratio of 1:5 following the method of Mehlich (1984), with the modification outlined by Lax et al. (1986). Concentrations of Ca^{2+} , Mg^{2+} , K^+ , Na^+ and Al^{3+} were determined by ICP-OES (inductively coupled plasma optical emission spectroscopy) in an accredited laboratory, while soil pH was determined on water extracts (soil:water, 1:5).

Dung counts and mass

At the end of the dry season (April), the number of dungs was recorded and classified by size into three categories (small, medium and large) under the tree canopy and in a paired area of equivalent size in the open grassland. Additionally, we randomly collected one excrement sample per size category in each site, and the dry mass was obtained in the laboratory and used to express the dung variable as dung dry matter per unit area (g m^{-2}). The dungs were also counted again in August during the rainy season.

Tree characteristics and grassland vegetation cover

For each tree, we recorded the total height, crown length and diameter, and trunk basal area. The tree shape was estimated as the ratio between the crown diameter and total tree height, so that a ratio larger than one corresponded to a flat ellipse tree shape. In February, leaf litterfall was collected under the canopy of three trees per each species and lumped in a composite sample for chemical analysis. A subsample was ground in a ball mill (MM2000 Retsch®), and C, N and isotope ratios were analysed as previously described for soil samples. Cations and P were determined by ICP-OES after digesting the samples with nitric acid in a microwave oven.

Grassland plant cover was visually estimated in 10 squares (1 m^2) under the canopy and open grassland plots where the soil samples were collected, both in April (dry season) and August (rainy season), and the herbaceous cover (%) of four species groups was recorded: grasses, non-grass graminoids, legumes and non-legume forbs.

Statistical analysis

We did side-by-side comparisons of soil nutrients and C and N stocks on paired plots, located under tree and in open grassland, in 48 different sites. This approach was chosen to minimize the confounding effects of climate, topography or soil type between sites on the canopy factor (under tree and open grassland). The possible correlation of functional groups with site characteristics was minimized by selecting paddocks with similar landform and soil characteristics (Appendix A). In order to account for the autocorrelation of paired plots (samples under tree and under open grassland, Canopy effect), we assessed differences due to the canopy factor on soil variables using a General Linear Model-Repeated Measures analysis. The canopy effect was considered as a within-subject factor, with two levels ($n=2$), and legume vs. non-legume (functional group effect) as a between-subject factor ($n=2$). The species factor was nested to functional group to account for species variability, and when significant ($p<0.1$) we tested the canopy effect in each tree species ($n=12$) by use of a paired two-sample student's *t*-test. Because it was not possible to estimate the time since clearing or tree establishment, we included the basal area of each tree as a covariable in the statistical model. To help avoid the bias produced by inter-specific differences in trunk growth rates, which would maximize the canopy effect on species with a low basal area (i.e. *T. rosea*), as well as minimize it in the large basal area species (i.e. *E. cyclocarpum*), we standardized the basal area for each species. The standardized basal area ranged between 0 and 1, and was calculated by dividing each basal area by the maximum basal area for each species. We considered that a significant interaction between the canopy factor and the standardized basal area of each tree indicated that differences between the tree and open grassland were related to the size of the tree or the time over which the trees had influenced soil properties.

Dung and plant differences between under canopy and open grassland paired plots were analysed similarly to soil variables by a GLM-repeated measures analysis. The relations between soil variables, tree characteristics, plant cover and dung mass were analysed by Pearson correlation, including all the samples together in the analysis ($n=48$). All the analysis were performed with the software SPSS (v.12.0).

Results

Leaf and canopy tree species characteristics

Leaf litter ^{13}C natural abundance ($\delta^{13}\text{C}$) of the four tree species was representative of the C_3 photosynthesis pathway, ranging from -26.26‰ to -28.51‰ (Table 1). The leaf litter of *A. saman* (Mimosaceae) exhibited a higher N concentration (2.07 %) and lower ^{15}N natural abundance ($\delta^{15}\text{N}$, 2.56‰) than the rest of the species

(Table 1). The other legume species, *E. cyclocarpum*, and the Sterculiaceae, *G. ulmifolia*, had an intermediate leaf N content (1.54 % and 1.52 %, respectively), while the leaves of *T. rosea* (Bignoniaceae) had the lowest N concentration (0.85 %). Therefore, both the C:N and lignin:N ratios were lowest in *A. saman* and highest in *T. rosea*, with intermediate values for the other two species (Table 1). The ^{15}N natural abundance ($\delta^{15}\text{N}$) of the legumes species was lower than that of the non-legumes ones (Table 1). The P and K concentrations in

Table 1 Species, leaf litter and tree characteristics of species studied

		<i>Tabebuia rosea</i>	<i>Guazuma ulmifolia</i>	<i>Albizia saman</i>	<i>Enterolobium cyclocarpum</i>
<i>Species characteristics^a</i>					
Family		Bignoniaceae	Sterculiaceae	Mimosaceae	Mimosaceae
Potentially N-fixer		No	No	yes	Yes
Leaf phenology ^b		deciduous (XII-IV)	evergreen (II-IV)	semi-deciduous (I-III)	semi-deciduous (II-III)
Leaf shape		penta-palmatisect	simple, ovate-lanceolate	bipinnatisect	bipinnatisect
Leaf size	cm	31–72×42–84	8–16×3–7	6–30×5–12	19–35×8–24
Foliolate size	mm	51–183×113–555	–	15–35×9–20	6–14×1–4
<i>Leaf litter^c</i>					
N	%	0.85	1.52/1.13	2.07/2.21	1.54
$\delta^{13}\text{C}$	‰	-27.09	-28.51	-28.25	-26.26
$\delta^{15}\text{N}$	‰	7.29	13.59	2.56	5.94
P	%	0.06	0.10/0.15	0.06/0.07	0.05
K	%	0.41	1.15/0.71	0.22	0.16
Ca	%	2.17	2.74/3.91	1.50/1.70	1.19
Mg	%	0.42	0.42/0.46	0.10/0.16	1.51
Lignin	%	10.66	8.21	7.08	7.25
C:N ratio		50.6	30.0/39.2	25.0/23.4	31.5
lignin:N ratio		12.5	5.4	3.4	4.7
C:P ratio		716.4	455.8/294.9	861.5/738.3	966.9
<i>Tree characteristics^d</i>					
Basal area	dm ²	12.9 (2.7) a	21.5 (4.8) a	36.1 (6.3) b	50.7 (9.1) b
DBH	cm	38.5 (3.9) a	43.6 (5.5) a	62.8 (5.9) b	77.7 (7.8) b
Tree height	m	11.2 (0.9) a	11.6 (1.9) a	12.8 (0.9) a	16.5 (1.5) b
Crown length	m	7.4 (0.8) a	7.9 (1.3) a	6.7 (0.8) a	9.3 (1.1) a
Crown diameter	m	12.2 (0.8) a	14.8 (0.9) a	21.0 (1.4) b	22.7 (1.8) b
Crown area	m ²	12.2 (1.6) a	18.0 (2.2) a	36.1 (4.8) b	43.2 (6.5) b
Crown diameter : tree height		1.1 (0.1) a	1.7 (0.1) c	1.7 (0.1) c	1.4 (0.1) b

^aSpecies characteristics from literature: Stevens et al. (2001); Cordero and Boshier (2003)

^bPeriod of maximum leaf litterfall between parenthesis

^cLeaf litter from a composite litterfall sample collected in the field from three trees per species during the maximum litterfall In *G. ulmifolia* and *A. saman* data from Sandoval (2006) of nutrient contents of leaf litter from six trees per each species collected during maximum litterfall in the nearby paddocks were added after “/” symbol

^dCharacteristics of the studied trees; Mean (\pm SE); $n=12$. For each tree characteristic, different lowercase letters indicated significant post-hoc differences (LSD test, $p<0.05$)

the *G. ulmifolia* leaf litter were more than twice the concentrations in the rest of the species (Table 1).

The tree basal area was higher in the legume species than in the non-legume ones (Table 1), and was correlated with the crown area and tree height (adj R²=0.83 and 0.46, respectively, *p*<0.001, *n*=48). The crown area was lower in *T. rosea* than in the rest of the species, while the tree height was similar in all species; hence, most of the studied *T. rosea* trees had a spherical shape compared with *G. ulmifolia* and *A. saman*, which had a predominantly flat ellipse shape (Table 1). The tree shape in *E. cyclocarpum* ranged from spherical to flat ellipse.

Dung under canopy and open grassland

The number of dung was higher at the end of the dry season than in the mid-rainy season (Table 2), and in each season the number of dung under the tree canopy was correlated with that in the paired open grassland (adj R²=0.46 and 0.51, for dry and rainy seasons, respectively, *p*<0.001; *n*=48).

No clear overall effects of the tree canopy or legume functional group were found. However, both the mass and number of dung at the end of the dry season tended to be higher under the canopies of *E. cyclocarpum* and *T. rosea* than in paired open grasslands (Canopy × Sp. (F.G.) nested factor; Table 2).

Plant functional groups under canopy and open grassland

Graminoids represented more than 90 % of the total herbaceous cover, and most of them corresponded to grasses (97 % of the total graminoid cover). Additionally, there were seasonal differences in the herbaceous cover composition, with non-leguminous forbs increasing in the rainy season, although these differences were minor (Table 3).

The graminoid cover was higher in open grassland than under the paired tree canopy, independent of the sampling season or tree species. In contrast, the relative cover of legume forbs in the rainy season tended to be higher under the canopy of *T. rosea* compared to their respective paired open grassland, although no differences were detected in the other species (Canopy × Sp. (F.G.) nested factor; Table 3).

Furthermore, neither bare soil nor the covers of plant functional groups were correlated with dung mass under trees or in the open grassland.

Table 2 Dung mass (dry mass) and counts at the end of the dry season and counts in the mid-rainy season in open grassland and under tree canopy in the four tree species; mean and SE in brackets (*n*=12). The significance from the Repeated Measures GLM was indicated (*p*-values <0.1 in bold) for the within-subject factor (Canopy) and the interactions with the legume-non legume functional groups and the species (Sp) nested within legume-non legume functional groups (FG) as between-subject factors. The significance level of the paired *t*-student test for the canopy factor (*p*-value) in each species is also indicated

<i>Tabebuia rosea</i>		<i>Guazuma ulmifolia</i>		<i>Albizia saman</i>		<i>Enterolobium cyclocarpum</i>		Canopy × FG	Canopy × Sp (FG)								
Grassland	Tree	<i>p</i> -value	Grassland	Tree	<i>p</i> -value	Grassland	Tree	<i>p</i> -value	Canopy								
<i>Dung dry mass (g m⁻²), dry season</i>																	
154.2 (21.9)	195.5 (34.8)	0.153	193.9 (33.9)	162.4 (22.2)	0.300	118.9 (23.4)	122.2 (20.0)	0.778	95.5 (9.8)	0.141	81.8 (8.7)	0.29	0.33 (0.03)	0.165 (0.03)	0.532	0.867	0.059
<i>Dung counts (number m⁻²), dry season</i>																	
0.54 (0.07)	0.67 (0.12)	0.148	0.63 (0.11)	0.52 (0.07)	0.225	0.39 (0.08)	0.42 (0.07)	0.611	0.07 (0.02)	0.288	0.07 (0.02)	0.07 (0.02)	0.07 (0.02)	0.165 (0.03)	0.497	0.753	0.041
<i>Dung counts (number m⁻²), rainy season</i>																	
0.13 (0.02)	0.16 (0.04)	0.473	0.17 (0.06)	0.12 (0.03)	0.321	0.12 (0.04)	0.09 (0.02)	0.288	0.07 (0.02)	0.713 (0.02)	0.601	0.907	0.231				

Table 3 Plant and soil cover in open grassland and under tree in the four tree species at the end of the dry season and in the mid-rainy season and wet season; mean and SE in brackets ($n=12$). The significance probability in the Repeated Measures GLM is indicated (p -values <0.1 in bold) for the within-subject factor (Canopy) and their interactions with the legume-non legume functional groups and the species (Sp) nested within legume-no legume functional groups (FG) as between-subject factors. The significance of the paired t -student test (p -value) for the canopy factor in each species is also indicated

	<i>Tabebuia rosea</i>			<i>Guazuma ulmifolia</i>			<i>Albizia saman</i>			<i>Enterolobium cyclocarpum</i>			Canopy \times FG		Can \times Sp (FG)
	Grassland	Tree	p -value	Grassland	Tree	p -value	Grassland	Tree	p -value	Grassland	Tree	p -value	Canopy	Canopy	
Dry season															
Bare soil	3.0 (0.8)	3.7 (0.9)	0.317	5.2 (0.7)	6.2 (0.9)	0.315	4.3 (0.6)	5.0 (0.9)	0.417	3.5 (0.6)	4.5 (0.7)	0.023	0.027	0.978	0.947
Graminoids	95.1 (0.8)	93.2 (1.2)	0.146	90.7 (1.5)	90.2 (1.1)	0.761	92.2 (1.0)	89.1 (2.2)	0.178	94.5 (0.8)	92.2 (1.0)	0.031	0.017	0.350	0.864
Legume forbs	1.2 (0.3)	1.1 (0.3)	0.852	1.0 (0.3)	1.1 (0.3)	0.843	1.3 (0.3)	0.8 (0.3)	0.259	0.8 (0.3)	0.6 (0.2)	0.528	0.343	0.367	0.820
Non-legume forbs	1.3 (0.5)	2.4 (0.5)	0.082	3.3 (1.2)	2.7 (0.5)	0.543	2.7 (0.5)	5.1 (1.8)	0.257	1.5 (0.4)	2.9 (0.6)	0.033	0.077	0.182	0.753
Rainy season															
Bare soil	0.4 (0.3)	0.3 (0.3)	0.851	12.5 (9.0)	17.9 (9.0)	0.695	1.3 (1.0)	1.5 (1.3)	0.900	0.0 (0.0)	1.0 (0.7)	0.166	0.624	0.764	0.720
Graminoids	94.5 (1.9)	72.3 (7.9)	0.020	72.1 (10.0)	70.1 (8.5)	0.886	76.6 (6.2)	75.8 (8.5)	0.873	92.3 (4.0)	84.0 (7.6)	0.380	0.089	0.413	0.144
Legume forbs	1.9 (0.6)	8.7 (4.3)	0.150	2.2 (0.9)	1.9 (0.4)	0.736	3.8 (2.2)	2.9 (1.7)	0.760	1.8 (0.7)	9.6 (7.7)	0.528	0.170	0.995	0.099
Non-legume forbs	3.5 (1.9)	18.9 (7.1)	0.049	14.2 (6.5)	17.2 (7.1)	0.756	19.2 (6.0)	20.9 (8.3)	0.736	5.9 (4.0)	6.2 (1.5)	0.944	0.136	0.216	0.397

Soil C, N and isotope natural abundances in soils under tree and in open grassland

Both soil organic carbon (OC) and total N were higher under tree than in the open grassland ($7.33 \pm 1.19 \text{ mg g}^{-1}$ and $0.33 \pm 0.10 \text{ mg g}^{-1}$ higher, respectively; Fig. 2 and Appendix B), whereas no clear differences existed in C:N ratios or potentially mineralizable N (PMN). As a result, the PMN per unit of soil total N was higher in the open grassland than under trees ($30.48 \pm 14.10 \text{ } \mu\text{g gN}^{-1}$ higher, $p=0.033$; Fig. 2). Soil $\delta^{13}\text{C}$ was clearly more depleted and $\delta^{15}\text{N}$ slightly higher under trees than in open grassland (Fig. 2). Differences in soil OC and in total N under tree and in open grassland positively correlated with the standardized basal area of the tree, but the correlations were weak with the standardized canopy area projection and non-significant with the difference on the dung mass (Table 4). The canopy

factor in OC, total N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ interacted with the basal area of the tree (Canopy \times BA interaction; Fig. 2, Appendix B), indicating that the magnitude of the canopy effect was affected by the size of the tree. In contrast, the effect of the tree on the soil variables was not related to whether the tree species was a legume or not (Canopy \times F.G. interaction; Fig. 2, Appendix B), but was species-specific for the soil OC (Canopy \times Sp. (F.G.) nested factor); Fig. 2, Appendix B). Thus, the difference in soil OC between under the tree and the open grassland was twice as high in *G. ulmifolia* and in *A. saman* than in *T. rosea* and *E. cyclocarpum*.

Extractable soil P and cations under tree and open grassland

Available P and extractable Ca^{2+} and K^{+} were higher under the tree than in the paired open grassland (Fig. 3;

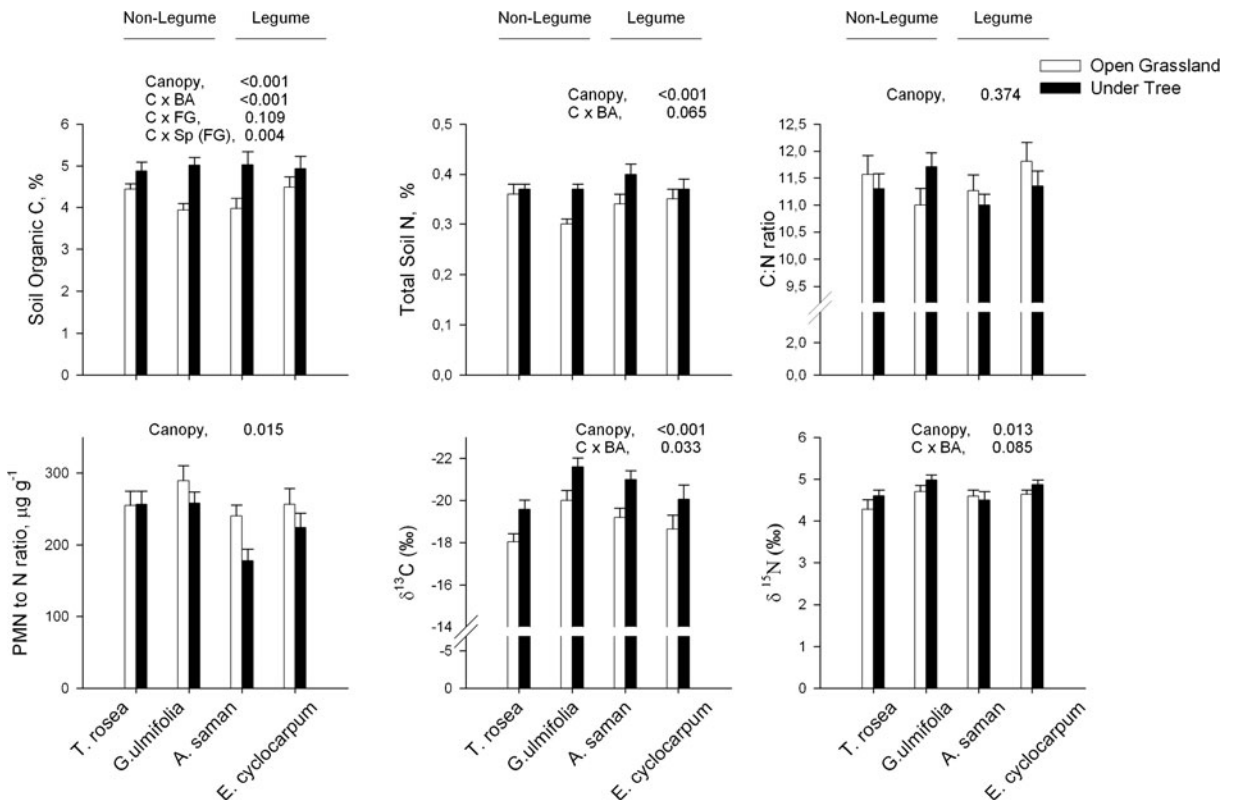


Fig. 2 Organic C, total N, C:N ratio, potentially mineralizable N to total N ratio and isotopes natural abundance in the first 10 cm of soil under paired tree and open grassland. The significance of the within-subject factor (Canopy) and the interactions with the standardized basal area (BA) of the trees; legume-non legume functional groups (FG) or the species (Sp) nested within the

functional groups as between-subject factors in the Repeated Measures GLM are indicated for each parameter when significant. The canopy factor tested the paired differences between soil parameters under trees and under open grassland. The canopy and legume-non legume functional groups interaction was never significant

Table 4 Pearson correlation coefficients (r) between the log-transformed standardized basal area, standardized canopy area or the difference on dung mass under the canopy and open

grassland and the difference between under canopy and open grassland in soil variables. The significance of the obtained r values is given (p -values <0.1 in bold; $n=48$)

	Standard basal area ^a		Standard canopy area ^a		Dung mass difference ^a	
	r	p	r	p	r	p
Standard canopy area ^a	0.78	<i>0.001</i>				
Dung mass ^a	0.25	<i>0.078</i>	0.10	<i>0.509</i>		
Organic C	0.46	<i>0.001</i>	0.35	<i>0.015</i>	-0.16	<i>0.285</i>
Total N	0.30	<i>0.038</i>	0.16	<i>0.258</i>	-0.03	<i>0.864</i>
Available P	0.30	<i>0.034</i>	0.32	<i>0.027</i>	-0.11	<i>0.451</i>
Extractable Ca ²⁺	0.31	<i>0.030</i>	0.18	<i>0.204</i>	0.04	<i>0.776</i>
Extractable Mg ²⁺	0.22	<i>0.136</i>	0.19	<i>0.198</i>	-0.03	<i>0.847</i>
Extractable K ⁺	0.30	<i>0.036</i>	0.27	<i>0.064</i>	-0.09	<i>0.547</i>
PMN	0.30	<i>0.038</i>	0.16	<i>0.258</i>	-0.03	<i>0.864</i>
PMN vs. N ratio	-0.27	<i>0.056</i>	-0.25	<i>0.081</i>	-0.16	<i>0.271</i>

^a Standardized basal area, standardized canopy area and the difference on dung mass variables were log transformed

Appendix B). Since the standardized basal area of trees correlated with the differences in these nutrients under the canopy and open grassland (Table 4), there was also a significant interaction effect of the tree canopy and basal area. There were also interspecific differences in the content of extractable Ca²⁺, which was slightly higher under *G. ulmifolia* and *A. saman* trees than in their paired grassland soils (Canopy \times Sp. (F.G.) nested factor; Fig. 3, Appendix B). By contrast, no effects of the canopy on soil variables were related to whether the tree species was a legume or not (Canopy \times F.G. interaction; Fig. 3, Appendix B).

The soil pH was higher under trees than in open grassland (*ca.* 0.30 pH units higher), although in the case of *T. rosea* there was an opposite effect (Fig. 3; Canopy \times Sp. (F.G.) nested factor). Moreover, no tree effect was detected on soil bulk density (Appendix B).

Both extractable Ca²⁺ and Mg²⁺ were correlated with soil OC ($r=0.58$ and 0.46 , respectively; $p<0.001$, $n=48$), but neither mineral P nor K⁺ demonstrated any relationship with soil OC ($r=0.15$ and 0.07 , respectively; $n=48$).

Discussion

Effects of tree presence on pasture soil fertility

Our results show that scattered trees in silvopastoral systems in seasonally dry neotropics increase soil

organic matter and stocks of available P and extractable Ca²⁺ and K⁺ in the area under the influence of their canopy. These results are in agreement with studies on a wide range of systems (Belsky et al. 1993; Mordelet et al. 1993; Rhoades 1997; Vetaas 1992 and references therein). Organic matter in the first 10 cm of soil was approximately 20 % higher under the tree than in the paired open grassland. This increase is lower than that reported in the first 5 cm of top soil in Mediterranean silvopastures (50 % in Gallardo 2003; 150 % in Casals et al. 2009), which is probably because the tree net contribution to soil organic matter is larger in unproductive systems than in more productive ones. Our results referred only to the first 10 cm of soil depth, where most of the herbaceous and fine tree roots occur in this system (Ospina 2011). We sampled this layer because our study focused on soil nutrients that are derived from litter or root decomposition. The likelihood of detecting differences that can be attributed to the vegetation cover is largest within the zone with highest biological activity and will probably be reduced if integrating a thicker soil layer. Since no clear evidence of higher dung deposition under the tree canopy compared with open grassland was found, a higher soil organic matter under scattered trees seems to be primarily related to either higher above- and below ground litter inputs or lower decomposition rates than in open grassland. The effect of the tree also seems to be positively related with tree size or age, as indicated by the

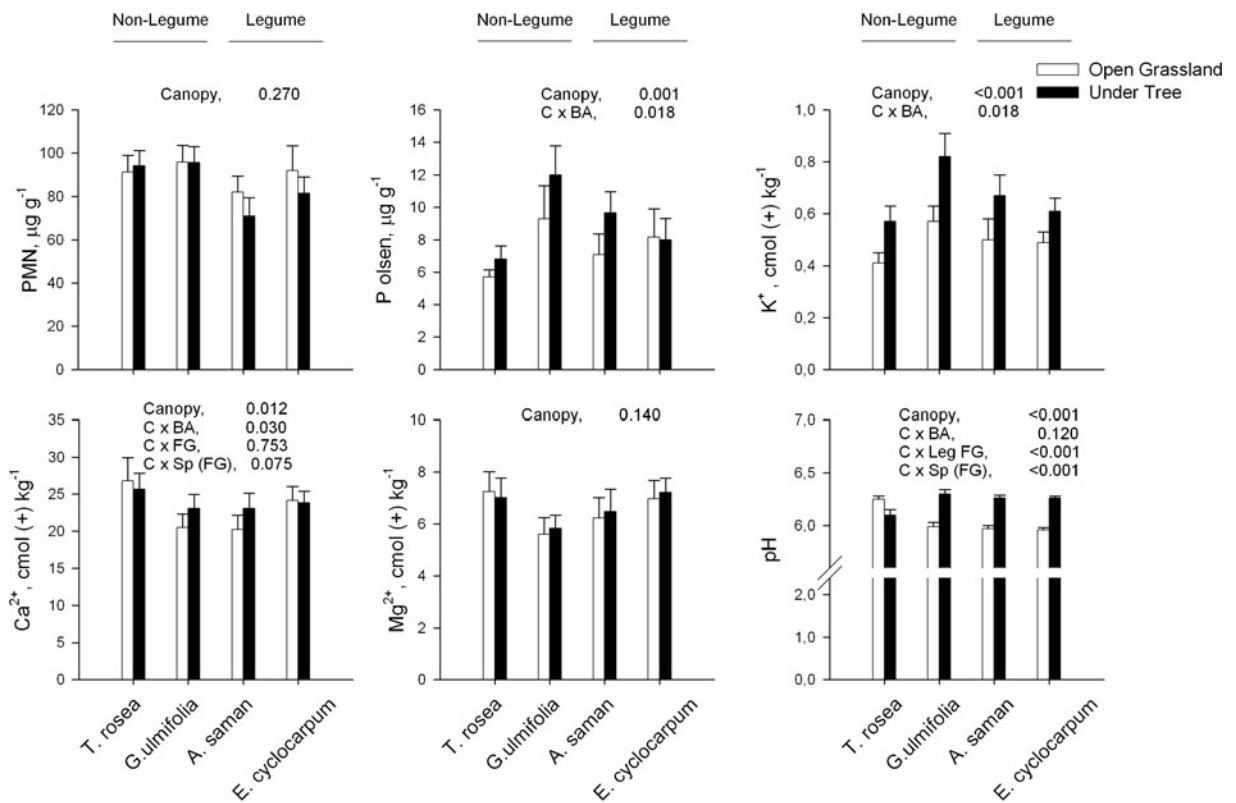


Fig. 3 Potentially mineralizable N, available P and extractable cations and pH in the first 10 cm of soil under paired tree and open grassland. The significance of the within-subject factor (Canopy) and the interactions with the standardized basal area (BA) of the trees; legume-non legume functional groups (FG) or the species (Sp) nested within the functional groups as between-

subject factors in the Repeated Measures GLM were indicated for each parameter when significant. The canopy factor tested the paired differences between soil parameters under trees and under open grassland. The canopy and legume-non legume functional groups interaction was never significant

positive correlation between the standardized basal area and the canopy effect on soil properties. In general, a higher standardized tree basal area corresponds to a taller tree with a more developed crown. However, the weak interaction with the standardized canopy projection may suggest that the size of the trees per se did not affect the soil properties per unit of soil surface. In addition to the age of the tree, the time since clearing may also contribute to the differences found between sites, though any further discussion is limited because we could not obtain specific information about when the forest was cleared in each farm.

Plants with C_3 metabolism produce lower values of the $\delta^{13}\text{C}$ signal than C_4 ones. Since the grassland has a predominance of grasses with a C_4 photosynthetic pathway, while trees and forbs have a C_3 metabolism, the lower soil $\delta^{13}\text{C}$ observed under tree canopies indicates that the organic matter in the soil under trees should have

originated, at least in part, from the trees. Furthermore, the cover of herbaceous C_3 species (forbs) was low, thereby strengthening the evidence that tree litterfall or root turnover are important sources of the soil OC under the tree canopy. A higher soil organic matter may be also explained by lower decomposition rates under the canopy through a microclimatic effect (Luizão et al. 1998) or differences in the quality of the litter (Cornwell et al. 2008). Compared with those from open grassland, a lower potential mineralization of N (PMN) per unit of soil N in samples from under canopy gives further indications that differences in the quality of the litter may have contributed to the higher organic matter stocks under the trees compared to the open grassland.

The presence of trees increased the available P and extractable K^+ in the first 10 cm of the soil compared with paired open grassland soil, which is of importance because soils with a low P content are common in the

region (Nieuwenhuys et al. unpublished data). By contrast, no clear differences were found in N availability measured as PMN or in extractable Mg^{2+} . Higher K^+ and Ca^{2+} contents in soils under the tree compared to the open grassland may contribute to explaining the lower soil acidity found under trees in this and other similar studies (e.g. Alfaia et al. 2004; Reich et al. 2005, 2010).

Effects of tree functional groups on soil organic matter and nutrients

We hypothesized that the differences in soil N would be greater between tree and paired grassland plots for legume tree species compared to non-legume ones. Even so, we did not detect any differential effect related to the legume functional group despite the fact that the leaf litterfall of both legume species had a higher N content and a lower lignin-to-N ratio than non-legume species. Compared with non-legume species, the lower $\delta^{15}N$ of legume tree species leaf litter may be related with their capacity to fix atmospheric N.

In contrast, differences in soil C stocks and extractable Ca^{2+} under canopy and paired open grassland emerged at the tree species level, regardless of whether they were leguminous or not, as indicated by the interaction between the canopy and the species nested within the functional group. Compared with the grassland, soil C stocks were higher under *G. ulmifolia* and *A. saman* than under *T. rosea* and *E. cyclocarpum*. This stands in contrast to the leaf litter characteristics, which suggest a higher decomposability of the litter of the former species. Compared to *T. rosea*, the leaf litter of *G. ulmifolia* had lower C:N, C:P and lignin:N ratios. In the case of *A. saman*, some studies indicate that the leaf litter is easily decomposable in accordance with their high N and low phenolic contents (Palm and Sánchez 1991).

In addition to organic matter decay rates, the amount of litterfall is one of the main determinants of the effects of trees on soil carbon and nutrient pools. Litterfall has been reported as the major flux of Ca^{2+} to the soil in dry tropical forests (Campo et al. 2000, 2001). Thus, higher extractable Ca^{2+} in soils under *G. ulmifolia* and *A. saman* compared with soils under *T. rosea* and *E. cyclocarpum* may indicate higher amounts of litterfall in the former species. Hence, despite the litter quality, a higher litterfall may counteract litter decomposition and explain both higher soil organic C and extractable Ca^{2+} under *G. ulmifolia* and *A. saman*. In addition, tree height and crown architecture also affect the spatial distribution

and concentration of litterfall. Both *G. ulmifolia* and *A. saman* had a flat ellipse shape that may favour litter deposition within the area of the canopy projection, which could be one of the contributing factors to higher C stocks under these species. On the other hand, both *T. rosea* and *E. cyclocarpum* had architectures that could have favoured a more spread out litter deposition pattern. *T. rosea* had a more cylindrical shape, while *E. cyclocarpum* are higher trees.

The effect of trees on a grazing animal's behaviour can further influence the amount and distribution of nutrients in the soil, as animals resting under trees can contribute to the accumulation of nutrients through a disproportionately higher deposition of faeces and urine (Skarpe 1991). In our study, we could detect differences in dung deposition between under the canopy and in the open grassland in two cases, namely *E. cyclocarpum* and in *T. rosea*. However, these differences were not reflected in higher nutrient contents in the soil under trees compared to paired open grassland, thus requiring deeper studies.

Conclusions

The presence of scattered trees in seasonally dry tropical pastures increases soil organic matter, available P and extractable Ca^{2+} and K^+ . While there is clear evidence that trees have a set of traits and attributes different from those of herbs, with important effects on soil fertility, a differential effect between legume and non-legume tree species was not detected. Instead, the study points to some characteristics at the tree level, such as the basal area, which is probably related to the time since the tree has influenced soil properties, the amount of litterfall produced and the tree architecture, which may help explain both higher soil organic C and extractable Ca^{2+} under the canopy of the *G. ulmifolia* and *A. saman* than under *T. rosea* and *E. cyclocarpum* compared to grassland.

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Appendix A

Table 5 Tree and site characteristics per each individual sampled species

Lat	Long	Altitude m asl	Soil colour	Texture	Cracks	Macrorelief	Slope %	Tree species	DBH cm	Tree height m	Branching height m	Crown diameter m	Principal herbs species
665781	1419234	304	Gley 2.5	clay	yes	Plain	<2	<i>T rosea</i>	27.7	10	27	9.7	<i>Cynodon dactylon</i> , <i>Paspalum notatum</i> , <i>Blechnum pyramidalatum</i>
665748	1419240	304	Gley 2.5	clay	yes	Plain	<2	<i>Gulmifolia</i>	30.5	8	3	12.8	<i>C. dactylon</i> , <i>P. notatum</i> , <i>B. pyramidalatum</i>
652005	1417663	289	2.5 year 2.5/1	clay loam	yes	rolling hills	<2	<i>Gulmifolia</i>	20.5+22.5+18	7	3	11.9	<i>P. virgatum</i>
652071	1417756	289	Gley 2.5	clay loam	yes	undulating plain	<2	<i>A saman</i>	39	105	45	16.9	<i>P. virgatum</i> , <i>B. pyramidalatum</i>
651771	1418610	304	Gley 2.5	clay loam	yes	undulating plain	<2	<i>T rosea</i>	23	9	4	8.9	<i>C. dactylon</i> , <i>P. conjugatum</i>
664865	1419008	301	Gley 2.5	clay	yes	undulating plain	2-6	<i>E cyclocarpum</i>	65.5+57.3	16	5	27.8	<i>P. virgatum</i> , <i>P. notatum</i>
664799	1419067	300	Gley 2.5	clay	yes	undulating plain	2-6	<i>T rosea</i>	41	10	4	14.4	<i>P. conjugatum</i> , <i>P. notatum</i>
664805	1419187	311	7.5 year 2.5/1	clay	yes	undulating plain	2-6	<i>A saman</i>	47	9	45	14.9	<i>P. notatum</i>
652972	1417072	275	10 year 3.1	clay	yes	undulating plain	<2	<i>E cyclocarpum</i>	48	105	55	16.8	<i>P. virgatum</i>
665770	1418462	320	7.5 year 3/2	clay	no	undulating plain	<2	<i>A saman</i>	59.5	12	5	21.7	<i>P. conjugatum</i> , <i>B. pyramidalatum</i>
652867	1417097	285	10 year 3/3	clay	yes	undulating plain	<2	<i>A saman</i>	39.5	95	5	15.0	<i>P. virgatum</i>
665738	1418542	312	7.5 year 2.5/1	clay	no	undulating plain	2-6	<i>T rosea</i>	27	8	3	11.2	<i>P. notatum</i> , <i>P. conjugatum</i>
653771	1415754	269	10 year 3/1	clay loam	yes	undulating plain	<2	<i>A saman</i>	69	15	6	22.0	<i>Oplismedium burmanni</i> , <i>P. conjugatum</i>
653882	1414429	300	2.5 Y 2.5/1	clay loam	yes	undulating plain	<2	<i>A saman</i>	85	15	7	28.0	<i>P. notatum</i> , <i>P. conjugatum</i> , <i>C. dactylon</i>
664993	1418577	326	7.5 year 2.5/1	clay	no	rolling hills	<2	<i>T rosea</i>	29	6	25	9.3	<i>P. virgatum</i> , <i>P. notatum</i>
653856	1414584	288	Gley 2.5	clay loam	yes	undulating plain	<2	<i>Gulmifolia</i>	78.5+48.2	9	4	19.0	<i>P. notatum</i> , <i>P. conjugatum</i>
665155	1418457	323	Gley 2.5	clay	no	rolling hills	<2	<i>Gulmifolia</i>	32.5+28	7	3	13.3	<i>P. virgatum</i> , <i>P. notatum</i>
653296	1414787	301	Gley 2.5	clay loam	yes	undulating plain	<2	<i>Gulmifolia</i>	58.4	9	2	12.4	<i>P. virgatum</i>
652349	1414380	307	Gley 2.5	clay loam	yes	rolling hills	<2	<i>T rosea</i>	67.2	17	6	17.5	<i>P. virgatum</i> , <i>P. plicatulum</i>
652309	1414340	313	Gley 2.5	clay loam	yes	rolling hills	<2	<i>Gulmifolia</i>	39	7	2	11.9	<i>P. virgatum</i> , <i>P. plicatulum</i>
650124	1412761	294	Gley 2.5	clay	yes	rolling hills	<2	<i>T rosea</i>	49.8	14	4	15.4	<i>C. dactylon</i> , <i>P. notatum</i>
663824	1418875	318	Gley 2.5	clay	yes	rolling hills	2-6	<i>E cyclocarpum</i>	54	15	6	18.3	<i>P. notatum</i> , <i>P. virgatum</i>
648022	1412535	331	2.5 Y 4.2	silty clay	no	rolling hills	<2	<i>T rosea</i>	50	135	35	10.6	<i>P. notatum</i> , <i>P. plicatulum</i>
663766	1418755	316	7.5 year 2.5/1	clay	yes	rolling hills	2-6	<i>T rosea</i>	59	9	3	10.8	<i>P. notatum</i> , <i>P. virgatum</i>
663836	1418782	315	10 year 3/1	clay	yes	undulating plain	6-13	<i>E cyclocarpum</i>	94	15	5	26.8	<i>P. notatum</i>

Table 5 (continued)

Lat	Long	Altitude m asl	Soil colour	Texture	Cracks	Macrorelief	Slope %	Tree species	DBH cm	Tree height m	Branching height m	Crown diameter m	Principal herbs species
660183	1480099	283	Gley 2.5	clay	yes	valley	<2	<i>T rosea</i>	52	15	4	15.1	<i>P. virgatum, P. notatum</i>
658401	1420526	313	2.5 Y 2.5/1	clay	yes	valley	<2	<i>Gulmifolia</i>	57.5	11	4	19.3	<i>P. conjugatum, H. rufa</i>
658804	1420399	300	Gley 2.5	clay	yes	valley	<2	<i>Gulmifolia</i>	68	13	35	18.9	<i>H. rufa</i>
652362	1407110	329	5Y 3/1	clay loam	no	rolling hills	<2	<i>T rosea</i>	38	14	3	14.5	<i>P. conjugatum</i>
652045	1417634	288	2.5 Y 2.5/1	clay loam	no	undulating plain	<2	<i>Gulmifolia</i>	32.5+35	10	2	17.6	<i>P. virgatum</i>
652663	1414717	301	2.5 Y 2.5/1	clay loam	no	undulating plain	<2	<i>Gulmifolia</i>	45	85	22	13.7	<i>P. virgatum, P. plicatulum</i>
653394	1417561	270	10 year 3/1	clay	no	undulating plain	<2	<i>A saman</i>	44.6+60.6	15	7	22.7	<i>P. notatum, C. dactylon, B. pyramidatum</i>
657507	1414451	273	Gley 2.5	clay loam	no	undulating plain	<2	<i>E cyclocarpum</i>	48.8	14	7	16.4	<i>P. virgatum, Panicum maximum, H. rufa</i>
657977	1415627	264	Gley 2.5	clay loam	no	undulating plain	<2	<i>A saman</i>	46	11	8	18.6	<i>P. virgatum, C. dactylon, B. pyramidatum</i>
655905	1406683	304	Gley 2.5	clay loam	no	undulating plain	<2	<i>E cyclocarpum</i>	77	17	8	18.2	<i>P. notatum, P. conjugatum</i>
665192	1416822	283	7.5 year 2.5/1	clay loam	no	undulating plain	<2	<i>T rosea</i>	29.6	10	4	10.1	<i>P. virgatum, B. pyramidatum</i>
665249	1417068	288	Gley 2.5	clay loam	no	undulating plain	<2	<i>T rosea</i>	27.5	10	6	11.1	<i>P. conjugatum, P. notatum</i>
651933	1413614	280	2.5 year 2.5/1	clay loam	no	undulating plain	<2	<i>E cyclocarpum</i>	111	21	11	29.6	<i>P. notatum, B. pyramidatum</i>
665869	1418450	311	2.5 year 2.5/1	clay loam	no	rolling hills	6–13	<i>E cyclocarpum</i>	95	16	7	30.4	<i>P. conjugatum, B. pyramidatum</i>
653043	1417248	285	2.5 year 2.5/1	clay loam	no	undulating plain	<2	<i>E cyclocarpum</i>	68+42.6	16+11	9+6	22.8	<i>Panicum maximum, P. virgatum, B. pyramidatum</i>
651989	1417455	295	7.5 year 2.5/1	clay loam	no	undulating plain	<2	<i>Gulmifolia</i>	19.9+26+21	15.5	3–3	15.8	<i>B. pyramidatum</i>
651955	1413610	282	Gley 2.5	clay loam	no	undulating plain	<2	<i>Gulmifolia</i>	26.2+26	25	8	11.5	<i>P. virgatum, B. pyramidatum, P. conjugatum</i>
664840	1419163	311	10 year 3/2	clay loam	no	undulating plain	2–6	<i>E cyclocarpum</i>	61.5	18	6	18.7	<i>P. notatum, P. virgatum</i>
658447	1414828	270	7.5 year 2.5/1	clay loam	no	undulating plain	<2	<i>A saman</i>	95.5	18	7	29.7	<i>P. virgatum, C. dactylon,</i>
658467	1414310	270	10 year 3/2	clay loam	no	undulating plain	<2	<i>A saman</i>	54.4	11	7	16.7	<i>P. virgatum, B. pyramidatum</i>
657271	1413883	316	Gley 2.5	clay loam	no	undulating plain	<2	<i>A saman</i>	96	18	7	22.2	<i>P. virgatum</i>
664938	1419041	317	Gley 2.5	clay loam	no	undulating plain	2–6	<i>E cyclocarpum</i>	44.5	10	6	15.8	<i>P. virgatum, P. notatum, H. rufa</i>
653902	1407871	272	10 year 3/1	clay loam	no	undulating plain	<2	<i>A saman</i>	72	10	6	23.2	<i>C. dactylon, P. conjugatum</i>
664633	1418018	325	10 year 3/1	clay loam	no	undulating plain	<2	<i>E cyclocarpum</i>	118	30	12	31.5	<i>P. virgatum, C. dactylon, P. notatum</i>

Appendix B

Table 6 Soil parameters differences between open grassland and under tree in the four tree species; mean (SE ($n=12$)). The significance from the Repeated Measures GLM was indicated (p -values <0.1 in bold) for the within-subject factor (Canopy) and their interactions with the covariable Basal area of the trees (Canopy \times BA) and the functional group (Canopy \times FG) and the species nested within functional group (Canopy \times Sp(FG)) as between-subject factors. For each species, the significance of the differences of soil variables between under tree and under grassland plots from the paired t -student test was indicated (p -value)

	<i>Tabebuia rosea</i>			<i>Guazuma ulmifolia</i>			<i>Albizia saman</i>			<i>Enterolobium cyclocarpum</i>						
	Grassl.	Tree	p -value	Grassl.	Tree	p -value	Grassl.	Tree	p -value	Grassl.	Tree	p -value				
Bulk Density	0.98 (0.03)	0.99 (0.02)	0.691	1.04 (0.03)	1.01 (0.03)	0.399	1.03 (0.03)	1.02 (0.03)	0.887	1.01 (0.04)	1.00 (0.04)	0.771	0.435	0.537	0.798	0.651
OC	4.44 (0.13)	4.88 (0.21)	0.069	3.93 (0.16)	5.02 (0.18)	0.001	3.97 (0.25)	5.03 (0.31)	0.002	4.49 (0.25)	4.93 (0.30)	0.061	<0.001	<0.001	0.109	0.004
Nt	0.36 (0.02)	0.37 (0.01)	0.639	0.30 (0.01)	0.37 (0.01)	0.037	0.34 (0.02)	0.40 (0.02)	0.026	0.35 (0.02)	0.37 (0.02)	0.154	0.001	0.065	0.702	0.172
C/N	11.57 (0.35)	11.30 (0.28)	0.343	11.00 (0.31)	11.71 (0.26)	0.225	11.27 (0.29)	11.00 (0.20)	0.502	11.81 (0.35)	11.35 (0.28)	0.045	0.374	0.750	0.245	0.161
PMN	91.14 (7.77)	94.17 (6.98)	0.755	95.79 (7.89)	95.66 (7.37)	0.990	82.01 (7.37)	70.96 (8.40)	0.379	91.97 (11.53)	81.37 (7.60)	0.299	0.270	0.445	0.367	0.973
PMN/N	25.48 (2.03)	25.66 (1.81)	0.951	28.91 (2.14)	25.79 (1.65)	0.318	24.05 (1.45)	17.77 (1.62)	0.038	25.65 (2.20)	22.41 (2.03)	0.268	0.015	0.110	0.516	0.540
$\delta^{13}C$	-18.03 (0.40)	-19.58 (0.44)	0.001	-20.00 (0.47)	-21.59 (0.42)	0.001	-19.19 (0.45)	-21.00 (0.42)	<0.001	-18.64 (0.67)	-20.05 (0.68)	0.007	<0.001	0.033	0.365	0.610
$\delta^{15}N$	4.28 (0.23)	4.60 (0.14)	0.139	4.70 (0.15)	4.98 (0.12)	0.168	4.59 (0.15)	4.50 (0.20)	0.697	4.64 (0.10)	4.87 (0.11)	0.101	0.013	0.085	0.086	0.452
P	5.70 (0.46)	6.82 (0.81)	0.132	9.28 (2.05)	12.00 (1.79)	0.035	7.08 (1.29)	9.65 (1.30)	0.177	8.18 (1.71)	8.01 (1.28)	0.863	0.001	0.018	0.193	0.178
Mg ²⁺	7.24 (0.77)	7.02 (0.74)	0.689	5.59 (0.65)	5.82 (0.52)	0.557	6.23 (0.78)	6.86 (0.86)	0.550	6.96 (0.72)	7.21 (0.56)	0.473	0.140	0.175	0.880	0.734
Ca ²⁺	26.82 (3.09)	25.69 (2.14)	0.525	20.49 (1.82)	23.10 (1.86)	0.187	20.25 (1.93)	23.10 (2.03)	0.064	24.16 (1.90)	23.83 (1.58)	0.728	0.012	0.030	0.753	0.075
K ²⁺	0.41 (0.04)	0.57 (0.06)	0.024	0.57 (0.06)	0.82 (0.09)	0.056	0.50 (0.08)	0.67 (0.08)	0.066	0.49 (0.04)	0.61 (0.05)	0.051	<0.001	0.018	0.167	0.708
pH	6.25 (0.03)	6.10 (0.05)	0.009	5.99 (0.04)	6.30 (0.04)	0.001	5.97 (0.03)	6.26 (0.03)	0.001	5.96 (0.02)	6.26 (0.02)	0.001	<0.001	0.120	<0.001	<0.001

OC organic Carbon; Nt Total N; PMN potentially mineralizable N; P, available P (Molybdate-reactive P)

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