

See discussions, stats, and author profiles for this publication at:
<https://www.researchgate.net/publication/292678841>

Altered soil carbon dynamics under different land-use regimes in subtropical seasonally-dry forests of central Argentina

Article in *Plant and Soil* · February 2016

DOI: 10.1007/s11104-016-2816-2

CITATION

1

READS

290

7 authors, including:



Georgina Conti

National University of Cordoba, Argent...

13 PUBLICATIONS 293 CITATIONS

SEE PROFILE



Esteban Kowaljow

National Scientific and Technical Rese...

12 PUBLICATIONS 77 CITATIONS

SEE PROFILE



Florence Baptist

BIOTOPE Bureau d'études environnem...

36 PUBLICATIONS 688 CITATIONS

SEE PROFILE



Sandra Diaz

National University of Cordoba, Argem...

209 PUBLICATIONS 14,664 CITATIONS

SEE PROFILE

Altered soil carbon dynamics under different land-use regimes in subtropical seasonally-dry forests of central Argentina

G. Conti · E. Kowaljow · F. Baptist · C. Rumpel ·
A. Cuchietti · N. Pérez Harguindeguy · S. Díaz

Received: 9 December 2015 / Accepted: 25 January 2016
© Springer International Publishing Switzerland 2016

Abstract

Background and aims Subtropical seasonally dry forests from South America are now experiencing one of the highest rates of forest-cover change globally. These changes may affect the dynamics of soil organic carbon (SOC) including long-term stabilization processes, with profound consequences for the fertility and carbon storage of these ecosystems.

Methods In order to explore the effect of different land-use regimes on SOC dynamics, we determined the amount and quality of plant litter, the amount and quality (lignin and carbohydrate content) of SOC, and the

soil basal respiration rates across seasonally dry Chaco forests of Argentina.

Results Changes in land-use regimes significantly reduced the amount of litter but not its quality. As a consequence, the SOC content was also reduced together with SOC quality. Unexpectedly, we found a higher CO₂ release per SOC unit in soils with lower amount and quality of SOC.

Conclusions The results presented here show a clear effect of different land-use regimes on SOC dynamics through a reduction in the amount and quality of SOC. Additionally, we found that potential microbial activity is somehow disconnected from substrate quantity and quality, suggesting that the molecular structure of SOC is not significantly affecting long-term soil stabilization processes across these seasonally-dry ecosystems.

Responsible Editor: Ingrid Koegel-Knabner.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-016-2816-2) contains supplementary material, which is available to authorized users.

G. Conti (✉) · E. Kowaljow · A. Cuchietti ·
N. Pérez Harguindeguy · S. Díaz
Instituto Multidisciplinario de Biología Vegetal (IMBIV-
CONICET) and Departamento de Diversidad Biológica y
Ecología, FCEFyN, Universidad Nacional de Córdoba, CC 495,
CP X5000ZAA Córdoba, Argentina
e-mail: georconti@gmail.com

F. Baptist
Biotope, 22 Boulevard Foch, BP 58, 34140 Mèze, France

C. Rumpel
CNRS, IEES (UMR 7618, UPMC-CNRS-INRA-IRD-UPEC),
Bâtiment EGER, Aile B, 78820 Thiverval-Grignon, France

C. Rumpel
CNRS, Ecosys (UMR INRA-AgroParisTech), Bâtiment EGER,
Aile B, 78820 Thiverval-Grignon, France

Keywords Land-use regime · Soil carbohydrates · Soil lignin · Soil organic matter stabilization · Semiarid ecosystems · Soil basal respiration

Introduction

Soil organic matter (SOM) formation is fundamental for the recycling of macronutrients into plant available forms. A wide range of soil properties, such as structure, water retention, and nutrient holding capacity, as well as soil biodiversity are also strongly dependent on SOM content (Dungait et al. 2012). In addition, the storage of organic carbon in soils (SOC) represents the largest and most stable stock of carbon (C) in terrestrial ecosystems

(Lal 2005). However, the magnitude, turnover and stability of SOC could be deeply affected by changes in land-use regime.

Globally, about 27 % of soils are under cultivation, and 60 % of forests are managed to some degree (Cassman and Wood 2005; Don et al. 2013). Most of the evidence on the effect of land use changes on forest soils is focused on the total replacement of forest cover by crops (Don et al. 2011; Grünzweig et al. 2004; Guo and Gifford 2002; Murty et al. 2002). However, less drastic land-use changes, such as those including forest logging and grazing, can also have profound consequences on global storage and turnover of SOC (Lal 2005; Nave et al. 2010; Tanentzap and Coomes 2012; Smith et al. 2015).

Forest logging and grazing usually result in the partial or total removal of the standing vegetation. A reduction in vegetation cover could increase soil exposure to wind and water and therefore soil erosion and compaction. The direct effect of trampling by livestock or by forest machinery could also alter the amount and dynamic of SOC (Jandl et al. 2007). Biomass extraction could also have consequences on plant species composition directly, if the forest is managed through selective species removal, or indirectly, by changes in resource availability (Garnier et al. 2004; Quedsted et al. 2007). Changes in plant species composition are expected to affect litter quantity and quality, and thus the turnover of SOM if they involved changes in dominant species functional attributes (Metcalf et al. 2011). Since plant litter is the primary source of all SOM, any changes in the quality and quantity of standing litter are expected to affect the quality and quantity of SOM (Don et al. 2011; Jandl et al. 2007; Yanai et al. 2003), but mechanisms involved in long-term stabilization processes are still under debate (Castellano et al. 2015; Cotrufo et al. 2013; Lehmann and Kleber 2015).

Carbohydrates (CH) represent about 50 % of the decomposing plant litter (Kögel-Knabner 2002), and have been traditionally considered part of the labile component of SOM because they are usually rapidly metabolized by soil microorganisms (Martens et al. 2004; Six et al. 1998). On the other hand, lignin is the most abundant aromatic plant component in terrestrial ecosystems (about 20 % of plant litter) (Kögel-Knabner 2000), generally considered more stable and resistant to biological attack (i.e., biochemically recalcitrant) compared to more labile compounds, like CH (Krull et al. 2003; Lorenz et al. 2007). Within this context, it is

expected than soils with increased amount of high-quality SOC (i.e., lower lignin to CH ratio) will show higher total potential CO₂ effluxes, as microbial communities have high availability to readily-available resources to decompose. However, recent studies have shown that regardless its chemical structure, SOM stabilization seems to be mainly driven by physical mechanisms such as aggregation and adsorption to minerals (Dungait et al. 2012; Kögel-Knabner et al. 2008; Schmidt et al. 2011; Lehmann and Kleber 2015). According to this evidence, physical properties conferring protection and physical stabilization should be of primary importance in driving potential microbial activity, rather than the amount and quality of SOC.

The Chaco forest – the geographically most extended seasonally dry forest in South America – has been experiencing profound land cover changes in the last few decades (Hansen et al. 2013; Hoyos et al. 2013). Over large areas, forests have been replaced by shrublands, as a result of historic logging and grazing in areas where agriculture is restricted by water availability (Grau et al. 2005). Consequently, the original seasonally-dry Chaco forest has given way to much more open forests and shrublands (Hoyos et al. 2013), with a marked reduction in aboveground and soil C pools (Abril and Bucher 1999; Bonino 2006; Conti et al. 2014).

In order to explore the local effects of changes in forest use on SOC quantity, quality and turnover, we determined the amount of SOC and its molecular composition (proportion of lignin to CH compounds) in soils under different ecosystem types resulting from different past and present land-use regimes. We also measured potential activity of microbial communities to investigate the effect of SOC quantity and quality change on microbial C effluxes, and so the potential stabilization of SOC (in terms of resistance to potential microbial attack) under different land-use regimes. We hypothesized that, in the seasonally-dry Chaco forest of central Argentina, changes in land-use regime lead to i) a reduction in the amount and quality of SOC by a reduction in the *quantity* and *quality* of litter decomposing into the soil. We also expected that ii) lower amounts of SOC and iii) low-quality substrate (higher lignin to CH ratio) would lead to lower C effluxes from soils (lower potential microbial activity).

Arid and semiarid ecosystems not only represent nearly one-third of continental land area –and are expanding as the result of climate change (IPCC

2013)-, but also are increasingly recognized by their important role as a driver of variations in global atmospheric CO₂ levels (Poulter et al. 2014). There is thus, an urgent need to understand the mechanisms underlying SOM formation, stabilization as well as SOC storage and potential losses in these less studied, non-acidic soils.

Materials and methods

Study area and experimental design

The study was carried out in the southern and driest extreme of the Gran Chaco (Fig. 1), in central Argentina (c. 31°15′–31°44′ S and 65°16′–65°40′ W). The climate is subtropical with a mean annual precipitation of 600 mm distributed in spring–summer

(October – March) and a mean annual temperature of 18 °C. Soils are mainly sandy-loam aridisols (typical Camborthids) of alluvial origin (Gorgas and Tassile 2003). The dominant vegetation is an open xerophytic forest with *Aspidosperma quebrachoblanco* and *Prosopis flexuosa* as canopy and subcanopy dominants, respectively. The shrub layer is often dense and dominated by *Mimozyanthus carinatus*, *Acacia gilliesii* and *Larrea divaricata* (Cabido et al. 1992).

Within the study area we selected different ecosystem types initially corresponding to the same vegetation, developed under the same climate and on very similar parental material but having experienced contrasting combinations of historic and present livestock grazing and logging. The sites corresponded to i) *primary forest*, with no significant logging or livestock grazing at least in the past 5 decades; ii) *secondary forest*, recently

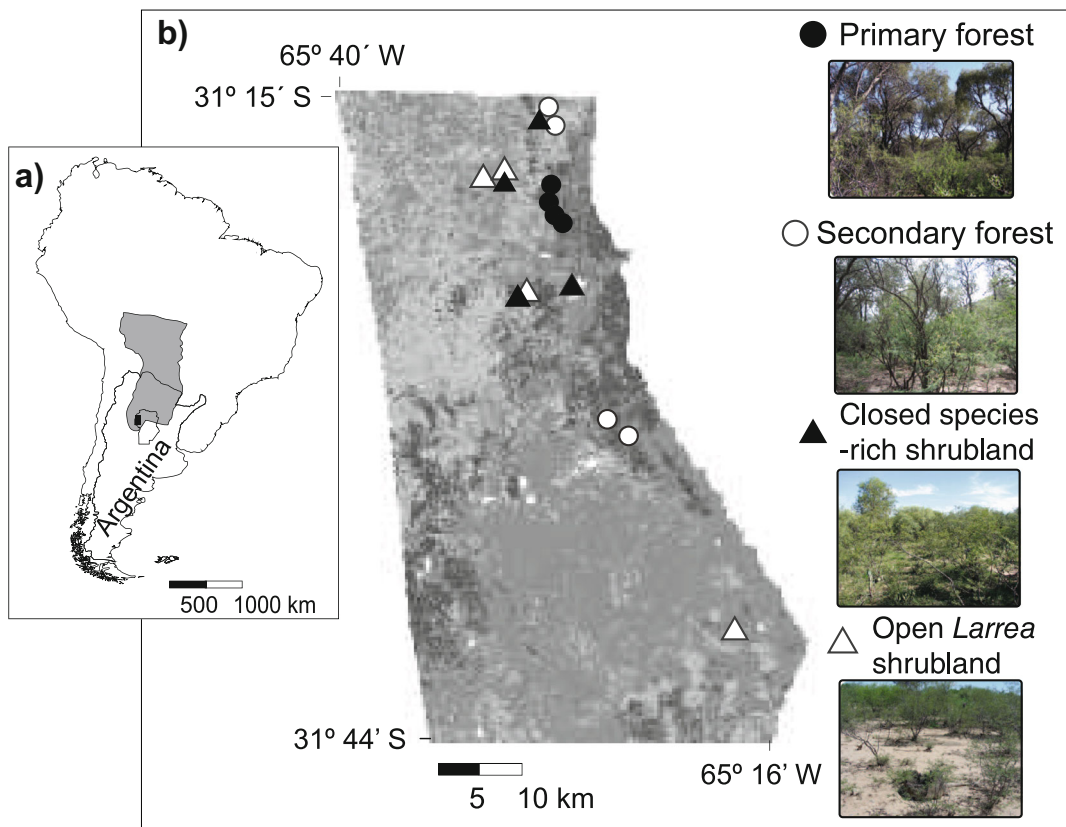


Fig. 1 Study area location in central Argentina. **a** The map shows the area represented by de Gran Chaco forest in Southern South America (in grey), the framed area corresponds to Córdoba province in central-Argentina and the black area situates the study area in the southern portion of the Gran Chaco region. **b** Detail of the

study area showing the location of the sampling plots for each ecosystem types. Ref: ● Primary forest, ○ Secondary forest, ▲ Closed species-rich shrubland, △ Open shrubland dominated by *L. divaricata*

managed forest (c. 7 years) with light selective logging and low cow and goat stocking rate; iii) *closed species-rich shrubland* showing current moderate to heavy logging and moderate cow and goat stocking rates but historically (>2 decades) intensively grazed and logged; and lastly, iv) *open shrubland* strongly dominated by *L. divaricata*, and historically characterized by past heavy logging and high cow and goat stocking rates. At present, these last sites show visible signs of soil erosion and compaction, resulting in low forage availability and agricultural productivity (Fig. 1, and additional soil and vegetation structure variables in Table S1). There is no evidence that any of these ecosystem types have been fertilized, cultivated, irrigated or burned at least in the last 50 years. In addition, there are not visible current differences of livestock stocking rate or associated manure input across sites, with the exception of the primary forests, in which there is no livestock (data not shown). We identified four 50 × 50 m sampling plots (replicates) corresponding to each ecosystem type at a distance of at least 1 km from each other. Each plot was as homogeneous as possible in terms of vegetation, soil and topography. To confirm edaphic similarities among plots, we sampled basic soil parameters at each site during winter (July 2008), including total N (%), P (ppm), pH, carbonates (%) and texture following Sparks (1996). We calculated soil bulk density by measuring the mass of dry soil contained in a metal cylinder which measured 4.5 cm in diameter and 10 cm in height. The samples were oven-dried at 105 °C for 48 h to obtain the dry mass of the soil. No adjustment for rocks or coarse fragments was necessary because their amount were negligible.

Litter quantity and quality

Total litter (composed of leaf and woody litter <5 cm diameter) was sampled by a single collection of all dead plant material accumulated on the ground surface in six subplots (0.5 m × 0.5 m) randomly distributed within a 50 m × 50 m plot. The sampling was carried out in autumn, after most of the senescent parts of deciduous and semi-deciduous species material had fallen. The material collected at each subplot was oven-dried at 80 °C for 3 days and weighed to obtain total dry mass (kg). A subsample of the collected litter was used to determine carbon (C), nitrogen (N) and lignin content. Litter C and N content was determined using an Alpkem RFA 300 auto-analyzer (Alpkem, Wilsonville, OR,

USA), whereas litter lignin content was analyzed following the procedure presented by Goering and Van Soest (1970). From these data, we calculated the C to N (C:N) and lignin to N ratio (Lignin:N) for litter.

Soil chemical analyses

During spring (October 2008), at each site we took one composite sample, consisting of three randomly selected subsamples, in the 0–10 cm layer and sieved them at 2 mm. Soil samples for subsequent chemical analysis were then air-dried and stored in closed plastic bags until processing. We determined SOC (g kg^{-1}) using an oxidation in acid medium procedure ('Walkley and Black'; Nelson and Sommers (1996)). We chose this analytical procedure that allows measuring only the organic fraction of the soil sample and thus, distinguishing it from the inorganic fraction, since these soils are known to have a significant proportion of calcium carbonate (Conti et al. 2014).

Content of non-cellulosic neutral carbohydrates (CH)

Non-cellulosic CH were analyzed by gas chromatography as acid alditols after hydrolysis using boiling trifluoroacetic acid (TFA) (Rumpel and Dignac 2006). TFA is known to hydrolyze only non-cellulosic plant or microbial derived CH. Briefly, 250 mg of surface soil were hydrolyzed at 110 °C for 4 h in 5 ml 4 M TFA. After samples cooled down, the internal quantification standard myoinositol was added, soil was removed and TFA evaporated. Thereafter, reduction of the aldoses to alditols and acetylation was performed. The derivatized monosaccharide units were extracted by liquid–liquid extraction using a vortex mixer after addition of 1 ml dichloromethane. The gas chromatographic measurements of the monosaccharides were performed with a HP GC 6890 gas chromatograph equipped with a flame ionization detector. Split injection (1:10) was used. Separation of the monosaccharide units was achieved with a 60 m fused silica capillary column (BPX70, 0.32 mm of internal diameter, 0.25 μm film thickness) and the following temperature program: from 200 to 250 °C at 3 °C/min., 15 min isothermal at 250 °C. Carrier gas was Helium with a flow rate of 1.0 ml min^{-1} . The injector was kept at 250 °C and the detector at 260 °C. The concentrations of specific monosaccharides were calculated based on the total ion current of the internal standard myoinositol. From the suite of non-

cellulosic neutral monosaccharides yielded with this method, the ratios of arabinose + xylose to galactose + mannose (C5/C6) and rhamnose + fucose to arabinose + xylose (desoxy/C5) were calculated to know their origin (Oades 1984). CH in vascular plant organs are mainly composed of pentoses (arabinose and xylose), while microbial populations synthesize larger amounts of the hexoses like galactose and mannose (Moers et al. 1990). Desoxysugars such as rhamnose and fucose are also indicative of microorganism synthesis (Cheshire 1979). As a consequence, a higher amount of pentoses (C5/C6 ratio > 1) indicates a higher amount of CH from plant origin, while a ratio below 1 will be related to a higher microbial activity. A high ratio of rhamnose + fucose to arabinose + xylose (higher desoxy/C5 ratio) also indicates a high microbial CH synthesis. We also test the ratio proposed by Jolivet et al. (2006) to take account of all microbial derived sugars together (galactose + mannose + rhamnose + fucose to arabinose + xylose). Analytical precision was 5 %.

Lignin content assessed by CuO oxidation

The soil lignin content of the samples was determined after release of the phenol monomers by alkaline CuO oxidation (Hedges and Ertel 1982). Briefly, 500 mg of surface soil were oxidized with 250 mg CuO and 2 M NaOH at 172 °C under N₂ for 2 h. After oxidation, a standard containing ethylvanillin was added for elucidating the recovery of lignin products after the whole procedure, which is usually about 60–75 %. The solution was quantitatively transferred to glass beakers, adjusted to pH 1.8–2.2. Thereafter, the solution was made up to a constant volume and left over night to wait for humic acid precipitation. The generated lignin-derived phenols were cleaned through passage on a C18 column (International Sorbent Technology) as suggested by Kögel and Bochter (1985). They were subsequently quantified as trimethylsilyl derivatives by gas chromatography with a HP GC 6890 gas chromatograph equipped with a flame ionization detector using phenylacetic acid as internal standard. Separation of the individual monomers was achieved with a SGE BPX-5 column (50 m length, 0.25 mm inner diameter, 0.32 µm coating). The temperature was programmed from 100 °C (1 min isotherm) to 150 °C at 3 °C min⁻¹ and from 150 to 300 °C at 1 °C min⁻¹. The detector temperature was kept at 350 °C. Helium was used as carrier gas (1 ml min⁻¹). This method yields phenols,

such as vanillyl (V), syringyl (S), and cinnamyl (C) compounds with aldehydic, ketonic, and acidic side chains. The sum of these CuO oxidation products (V + S + C, hereafter VSC) is considered as an indicator of the total amount of lignin (Hedges et al. 1988). Analytical precision is 10 % for VSC. It is important to note that the CuO oxidation method, as all the molecular approaches based on the chemical release of lignin monomers, may underestimate lignin concentrations (Bahri et al. 2006). The syringyl and cinnamyl to vanillyl ratios (S/V and C/V, respectively) and the ratios of acid-to-aldehyde forms of the V- and S-type CuO oxidation products (vanillic acid to vanillin, (Ac/Al)_V and syringic acid-to-syringaldehyde, (Ac/Al)_S) are classically used to follow lignin degradation (Kögel 1986). The S-to-V ratio can only be used as an indicator of lignin degradation when comparing similar vegetation systems as in the present work, since gymnospermous and angiospermous plants differ in their monomeric composition (Duboc et al. 2014). In a system where the total VSC content is constant, the degree of lignin degradation in soil is indicated by the (Ac/Al)_V and (Ac/Al)_S ratios and by S/V ratio of the CuO oxidation products (decrease in C/V and S/V and increase in (Ac/Al)_V and (Ac/Al)_S, indicate progressing lignin decomposition) (Ertel and Hedges 1984; Kögel 1986). VSC and the sum of neutral CH were expressed as C derived from the analyzed substances and referred to total SOC. From these values we calculated the ratio of lignin to CH compounds as an indicator of SOC quality, where higher values of this ratio indicate low quality SOC and vice versa.

Basal respiration

Composite samples were collected from the first 10 cm of soil at each plot and carried out to the laboratory to start the incubation experiment. A sample of 48 g of fresh soil was placed in a 50-mL sterile polypropylene tube. Distilled water was added to each tube until 40 % of water holding capacity was reached, and the tubes were placed in controlled conditions at 23 °C. CO₂ fluxes were measured using an infra-red gas analyzer (IRGA, EGM-4, pp-system Company) coupled to a chamber adapted to the tubes (e.g., Meier and Bowman (2008)). This closed dynamic chamber system measured the increase of CO₂ in the chamber at 8 s intervals during 8 to 10 min depending on signal fluctuations. The rate of increase was used to calculate CO₂ flux (mg

CO₂ g dry soil⁻¹ h⁻¹). Measurements were taken after 8 h (day 1), and after 4, 6, 8, 13 and 35 days, respectively and used to calculate the cumulative CO₂ efflux across the incubation time. Air temperature (23 °C) and soil water content (c.a. 40 % of WHC) were maintained constant throughout the experiment. The obtained measure of soil basal respiration has been used as a good estimator of total potential microbial activity of soils, since roots are excluded and environmental conditions are maintained constant along the time elapsed during the experimental incubation (Vanhala et al. 2005).

Statistics

Differences in SOC related variables across ecosystem types were tested by one-way ANOVA following linear models when residuals had normal distribution and homogeneous variance. Normal distribution was tested using Shapiro-Wilks analysis and homogeneous variance was analyzed according to Levene's test. When residuals did not present normal distribution, a log transformation to data was applied, and when presented heterogeneous variance we used linear mixed models, and evaluated their fit using the Akaike information criterion (Burnham and Anderson 2002). Multiple comparisons were performed using Fisher's LSD post hoc test with $\alpha=0.05$. We also perform linear regression analysis to test potential associations between SOC quantity and quality, and microbial potential activity across sites. Normal distribution of residuals and homogeneity of variance was also checked as described

before. Statistical analyses were performed using Infostat v. 2011 Statistical Package (Di Rienzo et al. 2011)

Results

Land-use regimes significantly affected SOM dynamics and stabilization processes across the study area, whereas basic soil parameters (i.e., C to N ratio, pH, phosphorus, carbonate content, silt and sand content) remained fairly constant across sites (Table 1 and Table S1). Only bulk density and clay content showed some statistical differences among ecosystem types. Bulk density was lowest in the most conserved soils (primary forest) while clay content was lowest in the sites with the lowest aboveground biomass (open *Larrea* shrublands).

Litter quantity and quality

The total amount of litter input was strongly affected by land-use regime, being highest in primary forests (1.55 kg m⁻²) and lowest in shrublands (0.48 kg m⁻² in closed shrublands and 0.23 kg m⁻² in open *Larrea* shrublands) (Fig. 2a); while litter quality remained unchanged across sites (Fig. 2b).

SOC content and composition, non-cellulosic CH and lignin

The amount of SOC in the 0–10 cm soil layer was also significantly affected by land-use regime, being highest

Table 1 Basic soil properties under different ecosystem types (mean values with standard error) in the seasonally dry Chaco forest of central Argentina

Soil properties	Ecosystem types				Statistical descriptors	
	Primary forest	Secondary forest	Closed species-rich shrubland	Open <i>Larrea</i> shrubland	<i>P</i>	<i>F</i>
C:N	9.68 ± 0.27a	12.41 ± 2.90a	7.76 ± 0.48a	8.46 ± 1.19a	0.1854	1.89
P (ppm)	30.60 ± 7.64a	37.13 ± 21.87a	14.79 ± 2.22a	17.97 ± 2.61a	0.5138	0.81
Bulk density (g cm ⁻³)	1.22 ± 0.03a	1.43 ± 0.02b	1.46 ± 0.04b	1.50 ± 0.06b	0.0008	11.29
pH	6.9 ± 0.1a	6.7 ± 0.4a	7.1 ± 0.2a	7.0 ± 0.2a	0.5603	0.72
CaCO ₃ (%)	1.63 ± 0.31a	1.88 ± 0.30a	1.31 ± 0.12a	1.38 ± 0.16a	0.3653	1.16
Clay (%)	12.35 ± 0.41a	12.20 ± 0.36a	12.65 ± 0.59a	9.78 ± 0.66b	0.0074	6.48
Silt (%)	28.55 ± 1.26a	28.73 ± 1.15a	33.40 ± 2.57a	32.45 ± 2.77a	0.2740	1.46
Sand (%)	53.95 ± 2.90	57.78 ± 3.20	59.10 ± 1.43	59.08 ± 1.27	0.4026	1.06

Different letters indicate significant differences between the same compartment across different ecosystem types (Test Fisher's LSD, $P \leq 0.05$, $n = 4$)

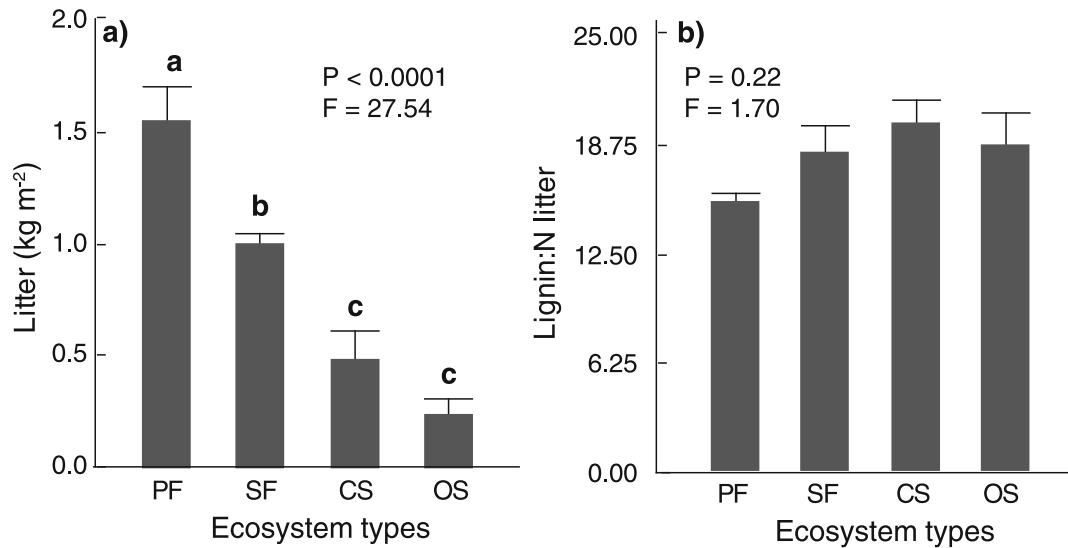


Fig. 2 Effect of different past and present land-use regimes on **a** litter quantity (kg m⁻²) and **b** litter quality (Lignin:N) a) in the seasonally dry Chaco forest of central Argentina. Different letters indicate significant differences across ecosystem types (Test

Fisher's LSD, $P < 0.05$). Error bars indicate standard errors. Ref: *PF* Primary forest, *SF* Secondary forest, *CS* Closed species-rich shrubland, *OS* Open shrubland dominated by *L. divaricata*

in primary forests (17.3 g kg⁻¹) and lowest in *Larrea* shrublands (8.26 g kg⁻¹) (Fig. 3a). Non-cellulosic CH content ranged between 185.03 mg g SOC⁻¹ and 136.36 mg g SOC⁻¹ decreasing from forests to shrublands, although this pattern was statistically not significant (Table 2). Neither the C5/C6 ratio, the

desoxy/C5 ratio, nor the index used by Jolivet et al. (2006) differed significantly across ecosystem types (Table 2).

Soil lignin content normalized to SOC was significantly lower in forests as compared to shrublands (Table 2). None of the indices calculated to reflect the

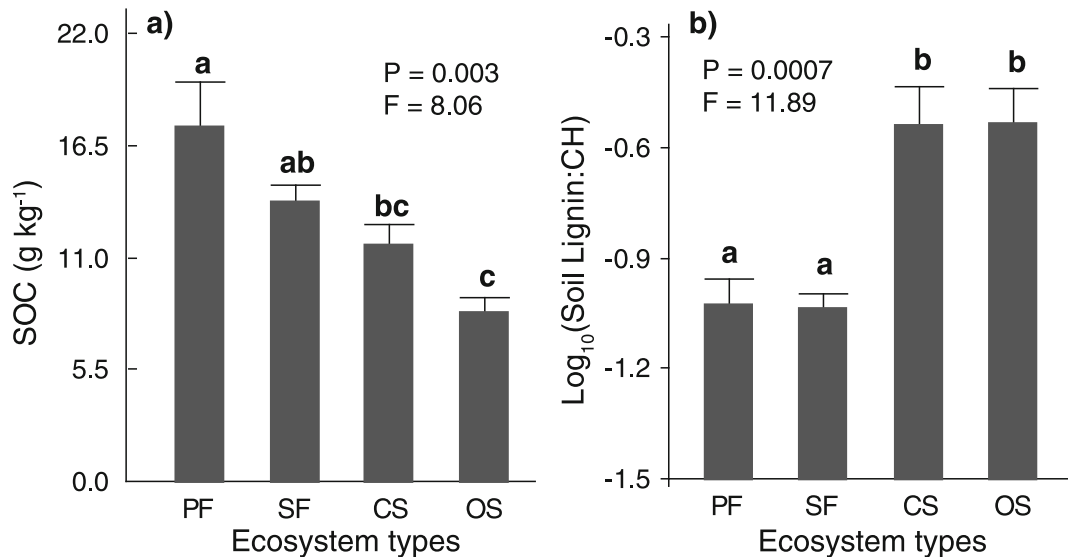


Fig. 3 Effect of different past and present land-use regimes on **a** the amount of soil organic C (SOC, g kg⁻¹) and **b** Logarithm of soil lignin to carbohydrate (CH) ratio in 0–10 cm depth soil layer in the seasonally dry Chaco forest of central Argentina. Different letters indicate significant differences across ecosystem types (Test

Fisher's LSD, $P < 0.05$). Error bars indicate standard errors. Original variables where logarithmically transformed to meet the assumption of residual's normal distribution. Ref: *PF* Primary forest, *SF* Secondary forest, *CS* Closed species-rich shrubland, *OS* Open shrubland dominated by *L. divaricata*

Table 2 Soil lignin and carbohydrates-derived compounds under different ecosystem types (mean values with standard error) the seasonally dry Chaco forest of central Argentina

	Ecosystem types				Statistical descriptors	
	Primary forest	Secondary forest	Closed species-rich shrubland	Open Larrea shrubland	<i>P</i>	<i>F</i>
Carbohydrates-derived compounds						
Total carbohydrates (mg g SOC ⁻¹)	185.03 ± 16.64 _a	191.45 ± 15.09 _a	141.31 ± 20.84 _a	136.36 ± 16.23 _a	0.0893	2.74
C5/C6	1.24 ± 0.08 _a	1.30 ± 0.14 _a	1.07 ± 0.06 _a	1.16 ± 0.10 _a	0.4449	0.96
desoxy/C5	0.32 ± 0.03 _a	0.29 ± 0.02 _a	0.35 ± 0.03 _a	0.31 ± 0.02 _a	0.4909	0.85
Jolivet et al. (2006) index	1.13 ± 0.08 _a	1.09 ± 0.09 _a	1.30 ± 0.09 _a	1.17 ± 0.08 _a	0.4021	1.06
Lignin-derived compounds						
V + S + C (mg g SOC ⁻¹)	17.86 ± 2.39 _a	18.07 ± 2.85 _a	45.52 ± 13.29 _b	41.46 ± 9.57 _b	0.0249	4.48
(Ac/Al) _V	0.42 ± 0.04 _{ab}	0.55 ± 0.02 _a	0.37 ± 0.07 _b	0.39 ± 0.02 _b	0.0435	3.68
(Ac/Al) _S	0.43 ± 0.08 _a	0.45 ± 0.03 _a	0.33 ± 0.10 _a	0.28 ± 0.02 _a	0.2544	1.54
C/V	0.34 ± 0.13 _a	0.26 ± 0.01 _a	0.38 ± 0.07 _a	0.36 ± 0.05 _a	0.7365	0.43
S/V	1.41 ± 0.06 _a	1.20 ± 0.04 _a	1.44 ± 0.14 _a	1.11 ± 0.08 _a	0.0608	3.23

Different letters indicate significant differences between the same compartment across different ecosystem types (Test Fisher's LSD, $P \leq 0.05$, $n = 4$)

state of degradation of lignin (C/V, S/V and (Ac/Al)_S) was significantly affected by ecosystem type (Table 2). Only (Ac/Al)_V marginally differed across sites with the highest value in secondary forests (Table 2). SOC quality, expressed as the ratio between soil lignin to carbohydrate content (Lignin:CH) differed across ecosystem types, being significantly lowest (high soil Lignin:CH) under shrublands (Fig. 3b).

Basal respiration

Soil basal respiration -measured as cumulative soil CO₂ efflux during 35 days of incubation under controlled conditions- showed significant differences in soils under different ecosystem types, being significantly higher under open *Larrea* shrublands (200.5 mg CO₂ g SOC⁻¹) compared to all other sites (106 mg CO₂ g SOC⁻¹ in primary forests, 134 mg CO₂ g SOC⁻¹ in secondary forests and 134.6 mg CO₂ g SOC⁻¹ in closed shrublands) (Fig. 4a).

Links between basal respiration and SOC quality and quantity

In order to investigate the effect of change in SOC quantity and quality on microbial C effluxes we

performed linear regression analysis between SOC concentration (SOC quantity) and lignin to CH ratio (SOC quality) with potential microbial activity. The resulted patterns showed that, unexpectedly, SOC quantity and quality were significantly but negatively related to changes in soil basal respiration (low SOC quantity and quality related to higher potential microbial activity) (Fig. 4b and c).

Discussion

In the subtropical seasonally-dry Chaco forest of central Argentina, land-use regime, associated mainly to past and present forest logging and grazing, has profound consequences for the storage and dynamics of SOC.

The amount of fallen litter decreased across ecosystem types from forests to open shrublands, although litter quality remained unchanged. There are several other studies showing lower quantity of litter decomposing into the soil as a result of a reduction in the aboveground standing biomass (Don et al. 2011; Jandl et al. 2007; Yanai et al. 2003). The fact that the dominant vascular plant species remain similar across these ecosystem types (although in different abundances) (Conti and Díaz 2013), explains the lack of significant change in litter quality.

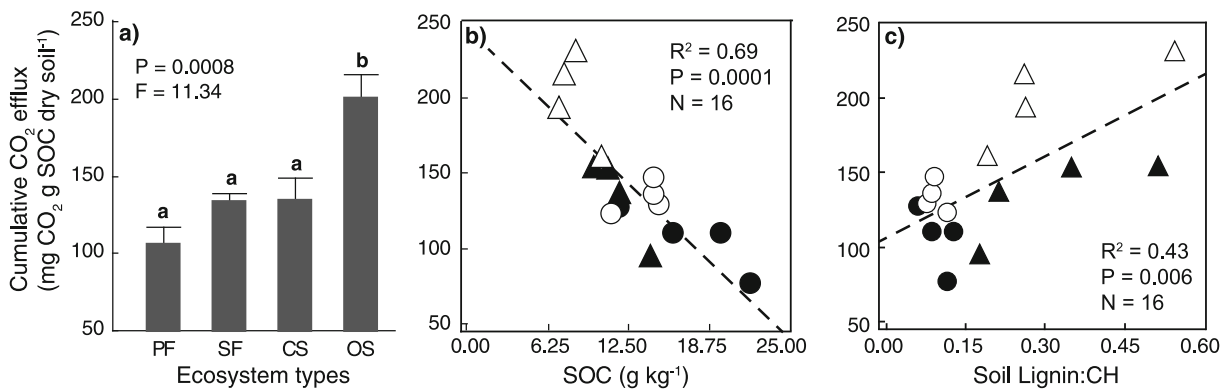


Fig. 4 Effect of different past and present land-use regimes on **a** cumulative CO₂ efflux per gram of SOC (mg g⁻¹) during 35 days, in 0–10 cm depth soil layer in the seasonally dry Chaco forest of central Argentina. Different letters indicate significant differences across ecosystem types (Test Fisher's LSD, $P < 0.05$). Error bars indicate standard errors. Simple linear regression analysis between **b** cumulative soil CO₂ efflux per gram of SOC (mg g⁻¹) during

35 days and soil organic matter content (g kg⁻¹); and **c** simple linear regression analysis between normalized cumulative soil CO₂ efflux per gram of SOC (mg g⁻¹) during 35 days and soil lignin to carbohydrate (CH) ratio (as indicative of SOC quality). Ref: ● Primary forest (PF), ○ Secondary forest (SF), ▲ Closed species-rich shrubland (CS), △ Open shrubland dominated by *L. divaricata* (OS)

The reduction in the amount of accumulated litter was reflected in a decrease in the total amount of SOC across ecosystem types. This pattern has been widely tested in the conversion of forest to crops in previous works, reporting losses of at least 30 % of SOC (Don et al. 2011; Guo and Gifford 2002; Murty et al. 2002). However, the effect on SOC of other land-use regimes related to forest use have shown no clear pattern, and seems to depend on several variables including forest type, soil type, sampling depth, past uses, among others (Nave et al. 2010; Yanai et al. 2003). We found that >50 % of SOC was lost between the most conserved primary forests and the lowest-biomass open *Larrea* shrublands, which is very substantial. Previous studies carried out in the study area have shown similar values of SOC content for sites with natural vegetation, and a profound reduction under forest management (Abril et al. (2005): -38.1 % on 0–20 cm depth; Bonino (2006): -46.37 % on 0–20 cm depth; Conti et al. (2014): -59.2 % on 0–10 cm depth; Mazzarino et al. (1991): -21 % on 0–10 cm depth). It is important to note that basic soil properties across sites were fairly homogeneous. The fact that clay content showed lower values in open *Larrea* shrublands seems to be mainly related to a visible process of soil erosion at these sites, as was previously reported in Conti et al. (2014). In any case, we have tested if these changes in clay content could have any influence on SOC content or any other response variables considered, with no statistical significance in any case.

Although we have not analyzed the effect of the removal of aboveground biomass on the amount of belowground biomass or litter input, it is expected that any change in belowground biomass and turnover should have direct consequences on the accumulation and stabilization of SOC (Rasse et al. 2005). The effect of root dynamics on the quantity and quality of SOC of these sites needs further research.

Regarding the quality of SOC, we found that, in the least productive sites, it showed the lowest values (highest Lignin to CH content of SOC), mainly due to significant changes in the amount of soil lignin content. The amounts of CH found across ecosystem types were within the range of values reported by Bongiovanni and Lobartini (2006) for Haplustols from Central Córdoba, Argentina under different managements. The indicators of carbohydrate origin (C5/C6 and desoxy/C5) remained relatively constant and close to one across all ecosystem types, whereby decomposition products seems to be not significantly affected by ecosystem types.

The amount of soil lignin found was within the range of values reported by Grünwald et al. (2006) and De Baets et al. (2012) for non-acidic soils (i.e., between 16 and 49.4 mg g⁻¹ SOC). The amount of lignin per C unit is expected to increase toward the ecosystem types that experienced the highest historical biomass removal, since SOC labile compounds are usually more rapidly metabolized by soil microorganisms after disturbances than SOC recalcitrant compounds (Thevenot et al. 2010), so the ratio of recalcitrant vs. labile compounds

in SOC is expected to increase, and thus reducing the quality of SOC. Accordingly, closed and open shrublands showed the highest amount of lignin content, reflecting a reduction on the SOC quality as compared to forests. Previous work suggests that roots of certain species could also be an important source of soil-lignin derived phenols (Crow et al. 2009), so the presence of particular species could be a variable affecting the amount of soil lignin in some on these sites.

Across ecosystem types, we found lower values and variation of indicators of lignin degradation (C/V , S/V , $(Ac/Al)_V$ and $(Ac/Al)_S$). Only $(Ac/Al)_V$ was slightly but significantly higher in secondary forests compared to other ecosystem types. It has been suggested that soils under forests may have lignin in a higher state of degradation since they are characterized by favorable environmental conditions for hosting adapted and abundant lignin-degrading microbial communities (Thevenot et al. 2010). As a general pattern, however, there was no consistent variation in the indicators of lignin degradation across the sampled ecosystem types, suggesting that long-term lignin chemical stabilization is not profoundly affected by changes in land-use regime on these semiarid ecosystems.

As hypothesized, we found a reduction in the amount of aboveground litter, but its quality did not change as expected. The change in the total amount of litter was reflected in a reduction in the amount of SOC across ecosystem types. The fact that aboveground litter quality (lignin to N ratio) did not significantly change across sites, but the amount of soil lignin to CH ratio did, supports the idea that litter quality (at least aboveground litter quality) is not the main control of long-term SOM formation as was previously proposed (Gentile et al. 2011; Schmidt et al. 2011).

We expected changes in SOC to be accompanied by changes in soil heterotrophic respiration (lower SOC quality and quantity leading to lower potential microbial activity). However, basal soil respiration did not change as expected across ecosystem types, where respiration per C unit in the least productive open shrublands doubled the levels found in the most conserved forests. The fact that these shrublands had also lower SOM quantity and quality (higher Lignin:CH) is in conflict with previous works, which have suggested that either substrate concentration (SOC) (Don et al. 2013), or its chemical nature (proportion of labile or recalcitrant compounds) are the main controls of SOC cycling (Lorenz et al. 2007). Our results clearly demonstrate that under these

ecosystems, higher SOC quality and quantity are not positively related to potential microbial activity, as proposed. The fact that soils under forests presented higher amount of SOC, lower soil compaction and higher vegetation cover, which are all indicators of increased soil aggregation (Bronick and Lal 2005), could suggest that changes in land-use regime potentially reduce the physical protection of soil aggregates allowing oxygen diffusion into the soil and making physically-protected SOC available as a respiratory substrate (Gupta and Germida 2015; Kimetu et al. 2009; Six et al. 2002; Zakharova et al. 2015). Moreover, reduced vegetation cover could increase the drying/rewetting cycles of soils under these semiarid conditions, stimulating a physical disruption of macro- and micro-aggregates by shrinking, and so leading to the exposure of previously protected SOM (Borken and Matzner 2009; Navarro-García et al. 2012). The decrease in aboveground biomass could also had an effect on the composition and activity of decomposer communities, as found by Abril and Bucher (1999) for these semiarid forests. Potential explanations include the idea that under stress conditions a selective degradation of SOC components occurs, mainly driven by changes in belowground microbial community composition (i.e., varying fungal to bacterial ratios across sites) (Collins et al. 2008; Smith et al. 2014). Further research is needed to understand the dynamic of microbial communities and changes in SOM physical properties associated to changes in land-use regime in arid and semiarid ecosystems.

Release of CO_2 from soils is usually considered as a by-product of microbial and root respiration. However, the fact that these semiarid soils have a significant amount of carbonates, open the discussion on the relative importance of soil carbonates as a potential source of CO_2 fluxes, as a result of calcareous soil weathering. It is generally presumed that this abiotic component of the soil CO_2 efflux is generally marginal since weathering of carbonate bedrock proceeds at comparably low rates and because most of the released C is considered to be leached out of the soil (Kuzyakov 2006). This subject has been increasingly addressed in the literature with still inconsistent patterns (e.g., Ramnarine et al. 2012; Schindlbacher et al. 2015). In any case, the role of carbonates in the dynamics of non-acidic soils deserves further investigation.

In summary, changes in land-use regime are expected to affect both, the quantity and quality of litter decomposing into new SOM. This study investigates

the impact of these changes on (1) the amount and quality of SOM remaining in the soil, and (2) the potential microbial activity expressed as C mineralization rates, both which determine the fertility and potential C storage of these ecosystems. In the subtropical seasonally dry Chaco forest of central Argentina, different ecosystem types that are the result of different past and present land-use regimes the amount and quality of SOC has been profoundly affected, by a reduction in the input of new decomposing material. However, these changes are not reflected by potential microbial activity as expected, making long term SOM stabilization processes somehow disconnected with SOC quantity and quality on these forests. Our results support the idea that, in contrast with mesic environments, where SOM processes seems to be mainly driven by biotic factors, in arid and semiarid ecosystems physicochemical drivers seems to play a fundamental role in SOM formation and stabilization (Collins et al. 2008).

Subtropical seasonally dry forests of southern South America have been converted into systems under different degree of degradation, in an accelerating process (Hoyos et al. 2013). If so, a severe reduction in the amount and quality of SOC in the Chaco forest is likely. This would add to the broader set of losses of ecosystem services associated with these land-use trajectories at local, regional and global scales.

Acknowledgments We are grateful to land dwellers, owners and managers for allowing us to work in their properties and to the Secretaría de Ambiente de Córdoba. This study is a contribution of the MIRA program from the Rhone-Alpes region, France; and of Núcleo DiverSus, endorsed by DIVERSITAS and the IGBP Global Land Project, and supported by FONCyT (PICT-0365 and PICT-0554), CONICET, SECyT - Universidad Nacional de Córdoba and the Inter-American Institute for Global Change Research (IAI) CRN 2015 and SGP-CRA2015 (which were supported by the US National Science Foundation grants GEO-0452325 and GEO-1138881). GC postdoc grant was supported by Fundación Bunge y Born Argentina and CONICET. We acknowledge Charlene Thedevuide for carrying out the lignin and CH analyses and to two anonymous reviewers for their insightful comments on this manuscript.

References

- Abril A, Bucher EH (1999) The effects of overgrazing on soil microbial community and fertility in the Chaco dry savannas of Argentina. *Appl Soil Ecol* 12:159–167. doi:10.1016/S0929-1393(98)00162-0
- Abril A, Bartfeld P, Bucher EH (2005) The effect of fire and overgrazing disturbs on soil carbon balance in the Dry Chaco forest. *For Ecol Manag* 206:399–405. doi:10.1016/j.foreco.2004.11.014
- Bahri H, Dignac M-F, Rumpel C, Rasse DP, Chenu C, Mariotti A (2006) Lignin turnover kinetics in an agricultural soil is monomer specific. *Soil Biol Biochem* 38:1977–1988. doi:10.1016/j.soilbio.2006.01.003
- Bongiovanni MD, Lobartini JC (2006) Particulate organic matter, carbohydrate, humic acid contents in soil macro- and microaggregates as affected by cultivation. *Geoderma* 136:660–665. doi:10.1016/j.geoderma.2006.05.002
- Bonino EE (2006) Changes in carbon pools associated with a land-use gradient in the Dry Chaco, Argentina. *For Ecol Manag* 223:183–189. doi:10.1016/j.foreco.2005.10.069
- Borken W, Matzner E (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Glob Chang Biol* 15:808–824. doi:10.1111/j.1365-2486.2008.01681.x
- Bronick CJ, Lal R (2005) Soil structure and management: a review. *Geoderma* 124:3–22. doi:10.1016/j.geoderma.2004.03.005
- Burnham KP, Anderson DR (2002) Model selection and inference. A practical information-theoretic approach. 2nd ed. Springer Berlin Heidelberg, New York
- Cabido M, Acosta A, Carranza ML, Diaz S (1992) La vegetación del Chaco Árido en el W de la provincia de Córdoba, Argentina. *Doc Phytosociologues* 14:447–456
- Cassman KG, Wood S (2005) Current state and trends: cultivated systems. In: Hassan R, Scholes R, Ash N (eds) The millennium ecosystem assessment: ecosystems and human well-being. Island Press, Washington, pp 747–794
- Castellano MJ, Mueller KE, Olk DC, Sawyer JE, Six J (2015) Integrating plant litter quality, soil organic matter stabilization, and the carbon saturation concept. *Glob Chang Biol* 21(9):3200–3209. doi:10.1111/gcb.12982
- Cheshire MV (1979) Nature and origin of carbohydrates in soils. Academic, London
- Collins SL, Sinsabaugh RL, Crenshaw C, Green L, Porras-Alfaro A, Stursova M, Zeglin LH (2008) Pulse dynamics and microbial processes in aridland ecosystems. *J Ecol* 96:413–420. doi:10.1111/j.1365-2745.2008.01362.x
- Conti G, Diaz S (2013) Plant functional diversity and carbon storage – an empirical test in semi-arid forest ecosystems. *J Ecol* 101:18–28. doi:10.1111/1365-2745.12012
- Conti G, Pérez-Harguindeguy N, Quétier F, Gorné LD, Jaureguiberry P, Bertone GA, Enrico L, Cuchietti A, Diaz S (2014) Large changes in carbon storage under different land-use regimes in subtropical seasonally dry forests of southern South America. *Agric Ecosyst Environ* 197:68–76. doi:10.1016/j.agee.2014.07.025
- Cotrufo MF, Wallenstein MD, Boot CM, Deneff K, Paul E (2013) The microbial efficiency-matrix stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Glob Chang Biol* 19:988–995. doi:10.1111/gcb.12113
- Crow SE, Lajtha K, Filley TR, Swanston CW, Bowden RD, Caldwell BA (2009) Sources of plant-derived carbon and stability of organic matter in soil: implications for global change. *Glob Chang Biol* 15:2003–2019. doi:10.1111/j.1365-2486.2009.01850.x

- De Baets S, Van Oost K, Baumann K, Meersmans J, Vanacker V, Rumpel C (2012) Lignin signature as a function of land abandonment and erosion in dry luvisols of SE Spain. *Catena* 93:78–86. doi:10.1016/j.catena.2012.01.014
- Di Rienzo JA, Casanoves F, Balzarini MG, Gonzalez L, Tablada M, Robledo CW (2011) InfoStat v.2014 <http://www.infostat.com.ar/>
- Don A, Schumacher J, Freibauer A (2011) Impact of tropical land-use change on soil organic carbon stocks – a meta-analysis. *Glob Chang Biol* 17:1658–1670. doi:10.1111/j.1365-2486.2010.02336.x
- Don A, Rödenbeck C, Gleixner G (2013) Unexpected control of soil carbon turnover by soil carbon concentration. *Environ Chem Lett* 11:407–413. doi:10.1007/s10311-013-0433-3
- Duboc O, Dignac M-F, Djukic I, Zehetner F, Gerzabek MH, Rumpel C (2014) Lignin decomposition along an Alpine elevation gradient in relation to physicochemical and soil microbial parameters. *Glob Chang Biol* 20:2272–2285. doi:10.1111/gcb.12497
- Dungait JAJ, Hopkins DW, Gregory AS, Whitmore AP (2012) Soil organic matter turnover is governed by accessibility not recalcitrance. *Glob Chang Biol* 18:1781–1796. doi:10.1111/j.1365-2486.2012.02665.x
- Ertel JR, Hedges JI (1984) The lignin component of humic substances: distribution among soil and sedimentary humic, fulvic, and base-insoluble fractions. *Geochim Cosmochim Acta* 48(10):2065–2074. doi:10.1016/0016-7037(84)90387-9
- Garnier E, Cortez J, Billès G, Navas M-LL, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C, Toussaint J-PP (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85:2630–2637. doi:10.1890/03-0799
- Gentile R, Vanlauwe B, Six J (2011) Litter quality impacts short-but not long-term soil carbon dynamics in soil aggregate fractions. *Ecol Appl* 21:695–703. doi:10.1890/09-2325.1
- Goering HK, Van Soest PJ (1970) Forage fiber analysis: apparatus, reagents, procedures, and some applications. *Agric handbook* 379. USDA, Washington
- Gorgas J, Tassile J (2003) Recursos naturales de la provincia de Córdoba. Los suelos. Agencia Córdoba Ambiente SE - INTA EEA, Manfredi, Córdoba
- Grau HR, Gasparri NI, Aide TM (2005) Agriculture expansion and deforestation in seasonally dry forests of north-west Argentina. *Environ Conserv* 32:140–148. doi:10.1017/S0376892905002092
- Grünwald G, Kaiser K, Jahn R, Guggenberger G (2006) Organic matter stabilization in young calcareous soils as revealed by density fractionation and analysis of lignin-derived constituents. *Org Geochem* 37:1573–1589. doi:10.1016/j.orggeochem.2006.05.002
- Grünzweig JM, Sparrow SD, Yakir D, Stuart Chapin F (2004) Impact of agricultural land-use change on carbon storage in boreal Alaska. *Glob Chang Biol* 10:452–472. doi:10.1111/j.1365-2486.2004.00738.x
- Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: a meta-analysis. *Glob Chang Biol* 8:345–360. doi:10.1046/j.1354-1013.2002.00486.x
- Gupta VVSR, Germida JJ (2015) Soil aggregation: influence on microbial biomass and implications for biological processes. *Soil Biol Biochem* 80:A3–A9. doi:10.1016/j.soilbio.2014.09.002
- Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. *Science* 342:850–853. doi:10.1126/science.1244693
- Hedges JI, Ertel JR (1982) Characterization of lignin by gas capillary chromatography of cupric oxide oxidation products. *Anal Chem* 54:174–178. doi:10.1021/ac00239a007
- Hedges JI, Blanchette RA, Weliky K, Devol AH (1988) Effects of fungal degradation on the CuO oxidation products of lignin: a controlled laboratory study. *Geochim Cosmochim Acta*. doi:10.1016/0016-7037(88)90040-3
- Hoyos LE, Cingolani AM, Zak MR, Vaieretti MV, Gorla DE, Cabido MR (2013) Deforestation and precipitation patterns in the arid Chaco forests of central Argentina. *Appl Veg Sci* 16:260–271. doi:10.1111/j.1654-109X.2012.01218.x
- IPCC (2013) Summary for policymakers. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Contribution of working groups I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, New York, p 27
- Jandl R, Lindner M, Vesterdal L, Bauwens B, Baritz R, Hagedorn F, Johnson DW, Minkinen K, Byrne KA (2007) How strongly can forest management influence soil carbon sequestration? *Geoderma* 137(3):253–268. doi:10.1016/j.geoderma.2006.09.003
- Jolivet C, Angers D, Chantigny M, Andreaux F, Arrouays D (2006) Carbohydrate dynamics in particle-size fractions of sandy spodosols following forest conversion to maize cropping. *Soil Biol Biochem* 38:2834–2842. doi:10.1016/j.soilbio.2006.04.039
- Kimetu JM, Lehmann J, Kinyangi JM, Cheng CH, Thies J, Mugendi DN, Pell A (2009) Soil organic C stabilization and thresholds in C saturation. *Soil Biol Biochem* 41:2100–2104. doi:10.1016/j.soilbio.2009.07.022
- Kögel I (1986) Estimation and decomposition pattern of the lignin component in forest humus layers. *Soil Biol Biochem* 18(6):589–594. doi:10.1016/0038-0717(86)90080-5
- Kögel I, Bochter R (1985) Characterization of lignin in forest humus layers by high-performance liquid chromatography of cupric oxide oxidation products. *Soil Biol Biochem* 17:637–640. doi:10.1016/0038-0717(85)90040-9
- Kögel-Knabner I (2000) Analytical approaches for characterizing soil organic matter. *Org Geochem* 31:609–625. doi:10.1016/S0146-6380(00)00042-5
- Kögel-Knabner I (2002) The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biol Biochem* 34:139–162. doi:10.1016/S0038-0717(01)00158-4
- Kögel-Knabner I, Guggenberger G, Kleber M, Kandeler E, Kalbitz K, Scheu S, Eusterhues K, Leinweber P (2008) Organo-mineral associations in temperate soils: integrating biology, mineralogy, and organic matter chemistry. *J Plant Nutr Soil Sci* 171:61–82. doi:10.1002/jpln.200700048
- Krull ES, Baldock JA, Skjemstad JO (2003) Importance of mechanisms and processes of the stabilisation of soil organic

- matter for modelling carbon turnover. *Funct Plant Biol* 30: 207–222. doi:10.1071/FP02085
- Kuzyakov Y (2006) Sources of CO₂ efflux from soil and review of partitioning methods. *Soil Biol Biochem* 38:425–448. doi: 10.1016/j.soilbio.2005.08.020
- Lal R (2005) Forest soils and carbon sequestration. *For Ecol Manag* 220:242–258. doi:10.1016/j.foreco.2005.08.015
- Lehmann J, Kleber M (2015) The contentious nature of soil organic matter. *Nature* 528(7580):60–68. doi:10.1038/nature16069
- Lorenz K, Lal R, Preston CM, Nierop KGJ (2007) Strengthening the soil organic carbon pool by increasing contributions from recalcitrant aliphatic bio(macro)molecules. *Geoderma* 142: 1–10. doi:10.1016/j.geoderma.2007.07.013
- Martens DA, Reedy TE, Lewis DT (2004) Soil organic carbon content and composition of 130-year crop, pasture and forest land-use managements. *Glob Chang Biol* 10:65–78. doi:10.1046/j.1529-8817.2003.00722.x
- Mazzarino MJ, Oliva L, Abril A, Acosta M (1991) Factors affecting nitrogen dynamics in a semiarid woodland (Dry Chaco, Argentina). *Plant Soil* 138:85–98. doi:10.1007/bf00011811
- Meier CL, Bowman WD (2008) Links between plant litter chemistry, species diversity, and below-ground ecosystem function. *Proc Natl Acad Sci U S A* 105:19780–19785. doi:10.1073/pnas.0805600105
- Metcalfe DB, Fisher RA, Wardle DA (2011) Plant communities as drivers of soil respiration: pathways, mechanisms, and significance for global change. *Biogeosciences* 8:2047–2061. doi:10.5194/bg-8-2047-2011
- Moers MEC, Baas M, De Leeuw JW, Boon JJ, Schenck PA (1990) Occurrence and origin of carbohydrates in peat samples from a red mangrove environment as reflected by abundances of neutral monosaccharides. *Geochim Cosmochim Acta* 54: 2463–2472. doi:10.1016/0016-7037(90)90233-B
- Murty D, Kirschbaum MUF, McMurtrie RE, McGilvray H (2002) Does conversion of forest to agricultural land change soil carbon and nitrogen? A review of the literature. *Glob Chang Biol* 8:105–123. doi:10.1046/j.1354-1013.2001.00459.x
- Navarro-García F, Casermeiro MA, Schimel JP (2012) When structure means conservation: effect of aggregate structure in controlling microbial responses to rewetting events. *Soil Biol Biochem* 44:1–8. doi:10.1016/j.soilbio.2011.09.019
- Nave LE, Vance ED, Swanston CW, Curtis PS (2010) Harvest impacts on soil carbon storage in temperate forests. *For Ecol Manag* 259:857–866. doi:10.1016/j.foreco.2009.12.009
- Nelson DW, Sommers LE (1996) Total carbon, organic carbon, and organic matter. In: Sparks DL (ed) *Methods of soil analysis. Part 3. Chemical Methods*. ASA, SSSA, CSSA, Madison, pp 961–1010
- Oades JM (1984) Soil organic matter and structural stability: mechanisms and implications for management. *Plant Soil* 76:319–337. doi:10.1007/BF02205590
- Poulsen B, Frank D, Ciais P, Myrneni RB, Andela N, Bi J, Broquet G, Canadell JG, Chevallier F, Liu YY, Running SW, Sitch S, van der Werf GR (2014) Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature* 509:600–603
- Quested H, Eriksson O, Fortunel C, Garnier E (2007) Plant traits relate to whole-community litter quality and decomposition following land use change. *Funct Ecol* 21:1016–1026. doi: 10.1111/j.1365-2435.2007.01324.x
- Ramnarine R, Wagner-Riddle C, Dunfield KE, Voroney RP (2012) Contributions of carbonates to soil CO₂ emissions. *Can J Soil Sci* 92:599–607
- Rasse DP, Rumpel C, Dignac M-F (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant Soil* 269:341–356. doi:10.1007/s11104-004-0907-y
- Rumpel C, Dignac M-F (2006) Gas chromatographic analysis of monosaccharides in a forest soil profile: analysis by gas chromatography after trifluoroacetic acid hydrolysis and reduction–acetylation. *Soil Biol Biochem* 38:1478–1481. doi: 10.1016/j.soilbio.2005.09.017
- Schindlbacher A, Borken W, Djukic I, Brandstätter C, Spötl C, Wanek W (2015) Contribution of carbonate weathering to the CO₂ efflux from temperate forest soils. *Biogeochemistry* 124:273–290. doi:10.1007/s10533-015-0097-0
- Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kogel-Knabner I, Lehmann J, Manning DAC, Nannipieri P, Rasse DP, Weiner S, Trumbore SE (2011) Persistence of soil organic matter as an ecosystem property. *Nature* 478:49–56. doi:10.1038/nature10386
- Six J, Elliott ET, Paustian K, Doran JW (1998) Aggregation and soil organic matter accumulation in cultivated and native grassland soils. *Soil Sci Soc Am J* 62(5):1367–1377. doi: 10.2136/sssaj1998.03615995006200050032x
- Six J, Conant RT, Paul EA, Paustian K (2002) Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant Soil* 241:155–176. doi:10.1023/A:1016125726789
- Smith AP, Marin-Spiotta E, de Graaff MA, Balsler TC (2014) Microbial community structure varies across soil organic matter aggregate pools during tropical land cover change. *Soil Biol Biochem* 77:292–303. doi:10.1016/j.soilbio.2014.05.030
- Smith P, House JI, Bustamante M, Sobocká J, Harper R, Pan G, West P, Clark J, Adhya T, Rumpel C (2015) Global change pressures on soils from land use and management. *Glob Chang Biol*. doi:10.1111/gcb.13068
- Tanentzap AJ, Coomes DA (2012) Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? *Biol Rev* 87(1):72–94. doi:10.1111/j.1469-185X.2011.00185.x
- Thevenot M, Dignac M-F, Rumpel C (2010) Fate of lignins in soils: a review. *Soil Biol Biochem* 42:1200–1211. doi:10.1016/j.soilbio.2010.03.017
- Vanhala P, Tamminen P, Fritze H (2005) Relationship between basal soil respiration rate, tree stand and soil characteristics in boreal forests. *Environ Monit Assess* 101:85–92. doi:10.1007/s10661-005-9134-0
- Yanai RD, Currie WS, Goodale CL (2003) Soil carbon dynamics after forest harvest: an ecosystem paradigm reconsidered. *Ecosystems* 6:197–212. doi:10.1007/s10021-002-0206-5
- Zakharova A, Beare MH, Cieraad E, Curtin D, Turnbull MH, Millard P (2015) Factors controlling labile soil organic matter vulnerability to loss following disturbance as assessed by measurement of soil-respired $\delta^{13}\text{C}$. *Eur J Soil Sci* 66: 135–144. doi:10.1111/ejss.12209