

Priming of soil organic carbon decomposition induced by corn compared to soybean crops

Sebastián R. Mazzilli^{a,*}, Armen R. Kemanian^b, Oswaldo R. Ernst^a, Robert B. Jackson^c, Gervasio Piñeiro^d

^a Facultad de Agronomía, Estación Experimental Mario Alberto Cassinoni, Universidad de la Republica, Ruta 3, km 363, Paysandú 60000, Uruguay

^b Department of Plant Science, The Pennsylvania State University, 116 Agricultural Sciences and Industries Building, University Park, PA 16802, USA

^c Nicholas School of the Environment and Center on Global Change, Duke University, PO Box 90338, Durham, NC 27708, USA

^d IFEVA/CONICET, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, Buenos Aires C1417DSE, Buenos Aires, Argentina

ARTICLE INFO

Article history:

Received 14 October 2013

Received in revised form

31 March 2014

Accepted 3 April 2014

Available online 24 April 2014

Keywords:

Priming effect in field conditions

Soil organic carbon decomposition

Humification rate

Corn

Soybean

ABSTRACT

The rate of soil organic carbon (C_S) loss via microbial respiration (decomposition rate k , y^{-1}), and the rate of stabilization of vegetation inputs (C_V) into C_S (humification rate h , y^{-1}) are usually considered independent of C_V . However, short-term laboratory studies suggest that the quality and quantity of C_V controls k , which is often referred to as a priming effect. We investigated how the chemical composition of different residues, (corn and soybean) controls k and h under field conditions in a no-till ecosystem. Using C_V -driven shifts in $\delta^{13}C$, we estimated changes in carbon (C) stocks, k and h of both the labile particulate organic matter fraction (C_{POM}) and the stabilized mineral associated organic matter fraction (C_{MAOM}). After two years of high C inputs (corn: 4.4 $Mg\ ha^{-1}\ y^{-1}$ aboveground and C:N = 78; soybean: 3.5 $Mg\ ha^{-1}\ y^{-1}$, C:N = 17), we found no changes in C_{POM} and C_{MAOM} stocks in the top 5-cm of soil or in deeper layers. However, C_{MAOM} in corn had higher k (0.06 y^{-1}) and C output fluxes (0.67 $Mg\ ha^{-1}\ y^{-1}$) than in soybean (0.03 y^{-1} and 0.32 $Mg\ ha^{-1}\ y^{-1}$), but similar rates and fluxes in C_{POM} in the top 5-cm of soil. In addition, while C inputs to C_{POM} were also similar for both crops, C inputs from C_V to C_{MAOM} were higher in corn (0.51 $Mg\ ha^{-1}\ y^{-1}$) than in soybean (0.19 $Mg\ ha^{-1}\ y^{-1}$). Overall, corn plots had higher k and C inputs into C_{MAOM} and therefore higher C cycling in this fraction. Our data suggests that the type of crop residue strongly influences C cycling in the topsoil of no-till cropping systems by affecting both the stabilization and the decomposition of soil organic matter.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

Soil organic carbon (C_S) is a major component of the global carbon (C) cycle that influences productivity in terrestrial ecosystems; its accumulation can reduce the buildup of CO_2 in the atmosphere (Bauer and Black, 1994; Lal, 1997; Reeves, 1997; Berthrong et al., 2009). Carbon stocks and fluxes are strongly affected by land use. Agriculture is one of the main perturbations of the global C cycle with a large contribution to global atmospheric CO_2 emissions (Schimel, 1995; Foley et al., 2005). Agriculture modifies C_S stocks by changing: (1) C inputs from vegetation (C_V) or the fraction of C_V that is stabilized (or humified) in organic matter,

and (2) C outputs as CO_2 from microbial respiration of C_S . Hénin and Dupuis (1945) formalized this mass balance framework as follows:

$$\frac{dC_S}{dt} = hC_V - kC_S \quad (1)$$

where h (y^{-1}) is the humification rate and k (y^{-1}) is the decomposition rate of C_S . It is well known that microorganisms decompose fresh biomass inputs and release C as CO_2 from respiration while retaining most nitrogen (N), depending on the C:N ratio of the biomass inputs (Swift et al., 1979). The retained N and the non-respired organic C stabilizes in organo-mineral associations that decompose at a much slower rate than fresh inputs. Therefore, C_S is mostly formed by microbial byproducts such as exudates and components released through breakup of dead microorganisms that are protected from decomposition by association with clay and silt particles and occlusion in soil aggregates (Hassink and Whitmore, 1997; Balesdent et al., 2000).

* Corresponding author. Tel.: +598 99729214; fax: +598 47227950.

E-mail addresses: sebastianmazzilli@gmail.com, smazzilli@agro.edu.uy (S. R. Mazzilli).

In corn and soybean cropping systems, the residues returned to the soil by these two crops differ in amount and composition. Corn C inputs usually exceed those of soybean by 1.4- to 1.8-fold, albeit with a much higher C:N ratio (Buyanovsky and Wagner, 1986; Allmaras et al., 2000; Huggins et al., 2007). In agricultural systems, a higher return of residues is often associated with higher soil organic matter contents (e.g. Campbell et al., 1991; Rasmussen and Smiley, 1997). Nevertheless, several knowledge gaps remain regarding the specific mechanisms that determine changes in h and k as consequence of changes in quantity and composition of residue inputs.

It is often assumed that k of C_s depends mainly on temperature, humidity, and soil physical properties (Wildung et al., 1975; Bunnell et al., 1977; Kowalenko et al., 1978; Buyanovsky and Wagner, 1986; Power et al., 1986; Hendrix et al., 1988; Gregorich et al., 1998). However, experiments in laboratory conditions challenge this assumption and suggest that k is also affected by the so-called priming effect. In priming, k is a function of the amount and quality of the fresh residues being decomposed (Fontaine et al., 2003, 2007; Blagodatskaya and Kuzyakov, 2008; Crow et al., 2009; Chemidlin Prévost-Bouré et al., 2010; Guenet et al., 2010; Kuzyakov, 2010; Larionova et al., 2011; Guenet et al., 2012; Shahzad et al., 2012; Zhu and Cheng, 2012; Paterson and Sim, 2013). In forest soils, priming seems to operate because increasing net primary productivity does not translate systematically into increases in C_s , due to a simultaneous acceleration of soil organic matter decomposition (Sulzman et al., 2005; Crow et al., 2009).

The quality and quantity of C_v may affect rates of both k and h , particularly in no-till crops where mechanical breakdown and mixing with soil is absent. To evaluate the influence of C_v properties on h , it is useful to apply the decomposition cascade framework of Swift et al. (1979), in which a portion of C_v ($1 - h$) is lost through microbial respiration but most N and non-respired C remain in the soil. Based on this framework, one can propose that residues with a C:N ratio closer to that of soil organic matter may have higher h than residues with high C:N. This idea is also supported by recent results showing that decomposers decrease their C use efficiency when consuming high C:N ratio residues, therefore decreasing h (Manzoni et al., 2008). In agricultural systems, soybean and corn represent two extreme C:N ratios, and we expect that h for soybeans should be higher than that for corn. However, sparse experimental evidence suggests the opposite (Huggins et al., 1998, 2007); no clear mechanism explaining these putative differences in h rates has been proposed. Furthermore, another factor that may control h is the ratio between C_s and the corresponding C_s saturation level (Hassink and Whitmore, 1997). The C_s saturation is defined as the amount of C that can be protected in organo-mineral associations in soils and seems to depend on soil texture. A soil with C_s closer to saturation should have lower h than one with lower C_s , a concept that has been incorporated in simulation models (Kemanian and Stöckle, 2010). Therefore, the saturation effect has to be considered when interpreting experimental determinations of h .

While testing these ideas is important, estimating k and h and identifying the sources of C leaving or entering a soil C compartment remain challenging. Among the existing methods, isotopic tracing of natural ^{13}C is particularly useful, especially when a soil originally grown or managed with C_3 plants ($\delta^{13}\text{C} = -26\text{‰}$) is substituted with C_4 plants ($\delta^{13}\text{C} = -12\text{‰}$) or vice versa (Balesdent et al., 1988). A soil with an intermediate isotopic composition derived from mixed C_3 and C_4 vegetation ($\delta^{13}\text{C} = -18$ to -21‰) allows researchers to follow simultaneously the decline of $\delta^{13}\text{C}$ in the soil following the introduction of C_3 plants and its enrichment after the introduction of C_4 plants

(Andriulo et al., 1999; Bayala et al., 2006; Desjardins et al., 2006). When isotopic tracing and soil fractionation are combined (i.e. size separation of C_s into particulate organic C, C_{POM} , and mineral associated organic C, C_{MAOM} , as proposed by Cambardella and Elliot (1992)), both C inputs and outputs from each fraction can be estimated (Martin et al., 1990; Gregorich et al., 1995; Huggins et al., 1998).

Here, our objectives were to estimate decomposition rate of C_s (k) and the humification rate (h) for different soil fractions (C_{POM} and C_{MAOM}) under crop biomass inputs that differ strongly in quantity, quality, and isotopic composition. We hypothesize that, if priming influences k , soils receiving inputs from corn will have higher k than soils receiving soybean inputs in no-till systems. In addition, crop inputs from soybean with a lower C:N ratio should have higher h compared to corn residues with a high C:N. To address these hypotheses, we measured C fluxes in the plant-soil system using $\delta^{13}\text{C}$ natural abundance as a tracer, and estimated k and h in no-till corn and soybean systems. Our experiment started from an old pasture of mixed C_3 and C_4 plants that was converted to no-till agriculture, allowing us to follow both the enrichment and depletion of C_s with $\delta^{13}\text{C}$ due to inputs of corn or soybean.

2. Materials and methods

2.1. Study site and experimental design

The experiment was located in northwest Uruguay, 10 km south of Paysandú (31° 21' S and 58° 02' W; 61 m above sea level), in the Northern Campos region of the Rio de la Plata grasslands (Soriano, 1992). The climate is meso-thermal sub-humid with a mean daily temperature of 25 and 13 °C in summer and winter, respectively, and an annual rainfall of 1200 mm distributed on average uniformly throughout the year, albeit with large intra- and inter-annual variations. The soil at the site was a fertile Typic Argiudol with a 1% slope. Soil particle-size distribution is uniform throughout the first 0.20 m, with 209, 564 and 227 g kg⁻¹ of sand, silt, and clay, respectively.

Between 1940 and 1970 the study site was under continuous annual cropping of wheat (one crop per year) in conventional tillage (inversion tillage plus several secondary operations). From 1970 to 1993 annual crops were rotated with pastures in a six-year rotation consisting of three years of white clover (*Trifolium repens* L.), birdsfoot trefoil (*Lotus corniculatus* L.), and tall fescue (*Lolium arundinacea* L.) and three years of crops, with 1.7 crops per year on average (Ernst and Siri-Prieto, 2009). From 1993 until the beginning of our experiment in 2007 the site was not cultivated and was gradually colonized by bermudagrass (*Cynodon dactylon* L. – C_4 perennial), maintaining a variable abundance of annual ryegrass (*Lolium multiflorum* L.) and white clover.

Our experiment was established in April of 2007 with two treatments arranged in three randomized blocks. The treatments were continuous corn (corn) or continuous soybean (soybean). The experimental area was initially treated with glyphosate at a rate of 3.0 kg a.i. ha⁻¹ and subsequently at a rate of 1.5–2.0 kg a.i. ha⁻¹ depending on weed infestation and weather conditions. Crops were sown on December 6th in 2007 and November 28th in 2008. Pre- and post-emergent herbicides were applied in all treatments to control weeds as needed, and insects and diseases were controlled chemically as needed based on insect and diseases population monitoring. Prior to sowing, all plots were fertilized with 150 kg ha⁻¹ of ammonium phosphate (27 kg N ha⁻¹ and 30 kg P ha⁻¹). At the six-leaf stage, 69 kg N ha⁻¹ as urea were applied in corn plots. All crops were no-till planted in 30 × 5.2 m plots with 0.52-m row spacing.

2.2. Soil and crop sampling

Soils were sampled before sowing crops in November 2007 and after two years in November 2009. Samples were taken at seven depths (0–5, 5–10, 10–20, 20–30, 30–50, 50–70 and 70–100 cm). In 2007 soil samples were taken with a 7-cm diameter core per plot, while in 2009 each sample was a composite of four 2-cm diameter cores per plot to represent better soil heterogeneity and avoid soil disturbance of the plots. The location of each sample was geo-referenced. Samples were weighed, and approximately a third of each sample was dried to 105 °C to estimate soil moisture. The soil moisture was used to estimate the soil mass and bulk density. The remainder of each sample was lightly crushed and sieved through a 2 mm mesh and dried to 60 °C. Soil organic matter fractions were determined according to Cambardella and Elliot (1992) separating organic matter (and therefore C_s) into particulate (C_{POM}) and mineral-associated organic matter (C_{MAOM}). The C_{POM} fraction is relatively young, minimally transformed C compared to fresh inputs and is less associated with the soil mineral matrix. In contrast C_{MAOM} is older and more stable, likely due to its association with the mineral fraction. Briefly, 10 g of 2 mm sieved soil were shaken for 18 h in 50 ml 0.5% hexametaphosphate dispersing solution. The dispersed soil was sieved through 53-mm sieves. The sand-sized organic material (C_{POM}) retained on the sieves was thoroughly rinsed, transferred to glass beakers, and oven-dried at 60 °C to constant weight. The slurry that passed both sieves contained the mineral associated organic C (C_{MAOM}) and was subject to the same drying process. Carbon stocks for each plot were calculated on a constant soil mass basis (Davidson and Ackerman, 1993).

Inputs of C from aboveground and belowground crop biomass were measured on an annual basis. Grain yield and total aboveground biomass was determined after physiological maturity by harvesting 2 m of two adjacent center rows (2.08 m²) in each plot. Root biomass was measured at flowering using the soil core method. In each plot, soil cores of 5-cm diameter and 100-cm depth were taken on the row and in the inter-row space at the same depth intervals used for the soil samples, with two replications per plot. The soil cores were frozen immediately and kept at –20 °C. To recover roots, samples were thawed and roots were separated from the soil using water and three sieves of 2, 0.5, and 0.05 cm. Roots were collected individually with tweezers. The root biomass was calculated by averaging the row and inter-row samples.

Sub-samples of corn and soybean aboveground and belowground biomass, and samples of soil from each fraction and sampling time were milled and analyzed for C, N and ¹³C/¹²C ratio with an elemental C–N analyzer (Carlo Erba, Model NA 1500, Milan, Italy) interfaced with an isotope ratio mass spectrometer (Fisons Optima model; Fisons Middlewich-Cheshire, UK) at the Duke Environmental Isotope Laboratory (DEVIL), Duke University, USA. The C isotope ratios were expressed as δ¹³C:

$$\delta^{13}C(\text{‰}) = \left[\frac{R_{\text{sam}}}{R_{\text{std}}} - 1 \right] \times 10^3 \quad (2)$$

where R_{sam} is the ¹³C/¹²C ratio for the sample, and R_{std} is the ¹³C/¹²C ratio of the Pee Dee Belemnite standard.

2.3. Estimating h , k , and C fluxes for C_{POM} and C_{MAOM}

We assumed that the system has three C pools (dead biomass from crops (C_V), C_{POM} and C_{MAOM}) and that the C transfers mediated by decomposers are as follows: C from C_V can stabilize in C_{POM} or C_{MAOM} , and C from C_{POM} can stabilize in C_{MAOM} (Fig. 1, see also Table 1 for abbreviations used throughout the manuscript). Based

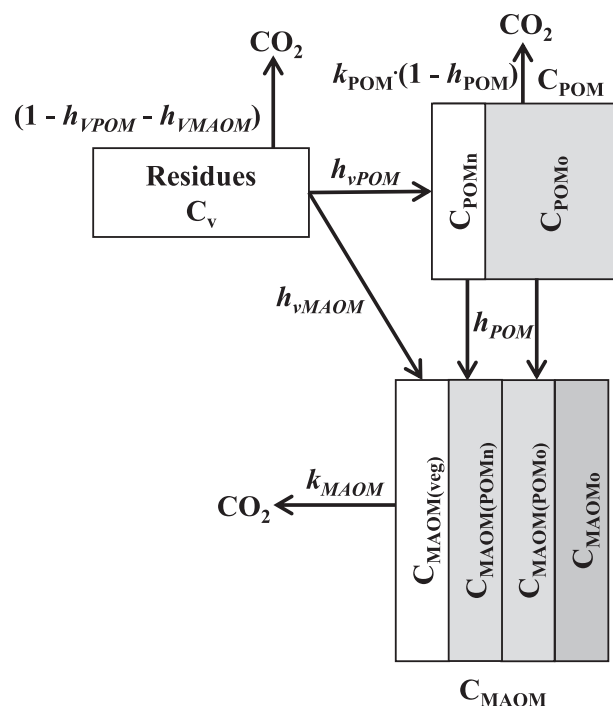


Fig. 1. Diagram of estimated carbon fluxes. C_V : Carbon inputs from vegetation; C_{POMn} = C_{POM} new from from C_V ; C_{POMo} = C_{POM} old or native that was present at the beginning of the experiment; $C_{MAOM(veg)}$ = C_{MAOM} new that came from C_V ; $C_{MAOM(POMn)}$ = C_{MAOM} new that came from C_{POMn} ; $C_{MAOM(POMo)}$ = C_{MAOM} new that came from C_{POMo} ; C_{MAOMo} = C_{MAOM} old or native that was present at the beginning of the experiment; h_{POM} = humification rate of C_{POM} into C_{MAOM} ; h_{VPOM} = humification rate of C_V into C_{POM} ; h_{VMAOM} = humification rate of C_V into C_{MAOM} ; k_{POM} = decomposition rate of C_{POM} ; k_{MAOM} = decomposition rate of C_{MAOM} .

on this framework we calculated h in each transfer and k of each pool by assuming that each pool has uniform properties and is well mixed. Carbon in C_{POM} and C_{MAOM} was partitioned into old C (or original C that was present at the beginning of the experiment) (C_{POMo} and C_{MAOMo}) and C new derived from plant residues incorporated during the experiment. For C_{POM} , new C (C_{POMn}) comes from C_V (crop litter and dead roots). For C_{MAOM} , the new C may come from C_V forming $C_{MAOM(veg)}$ or from C_{POMn} forming

Table 1
List of abbreviations.

Abbreviations	Units	Description
C_n	Mg ha ^{−1}	Soil organic carbon formed during the experiment
C_{fn}	—	Fraction of C_n from the crops (either soybean or corn)
C_e	Mg ha ^{−1}	Total soil organic carbon at the end of the experiment
C_o	Mg ha ^{−1}	Old soil organic carbon.
C_V	Mg ha ^{−1} y ^{−1}	Carbon inputs to the soil from vegetation (litter or crop residues)
C_{POM}	Mg ha ^{−1}	Carbon in particulate soil organic matter
C_{POMn}	Mg ha ^{−1}	C_{POM} formed during the experiment (from C_V)
C_{POMe}	Mg ha ^{−1}	C_{POM} at the end of the experiment
C_{POMi}	Mg ha ^{−1}	C_{POM} at the beginning of the experiment
C_{POMO}	Mg ha ^{−1}	C_{POM} old, i.e. formed before the beginning of the experiment
C_{MAOM}	Mg ha ^{−1}	Carbon in mineral associated soil organic matter
C_{MAOMO}	Mg ha ^{−1}	C_{MAOM} old, i.e. formed before the beginning of the experiment

(continued on next page)

Table 1 (continued)

Abbreviations	Units	Description
C_{MAOMn}	$Mg\ ha^{-1}$	C_{MAOM} new (from C_{POMo} , C_{POMn} and C_V)
$C_{MAOM(POMo)}$	$Mg\ ha^{-1}$	C_{MAOM} originated from C_{POMo}
$C_{MAOM(veg)}$	$Mg\ ha^{-1}$	C_{MAOM} originated from C_V without passing through C_{POM}
C_x	$Mg\ ha^{-1}$	Final amount of soil organic carbon in a pool (C_{POM} or C_{MAOM})
C_{xo}	$Mg\ ha^{-1}$	Initial amount of soil organic carbon in a pool (C_{POM} or C_{MAOM})
$C_x(t)$	$Mg\ ha^{-1}$	Amount of C in the compartment of interest in the sampling date
C:N	–	Relation between amount of carbon and nitrogen
h_{VPOM}	y^{-1}	Humification coefficient from C_V into C_{POM}
h_{POM}	y^{-1}	Humification coefficient of C_{POMo} into C_{MAOM}
h_{VMAOM}	y^{-1}	Humification coefficient of C_V into C_{MAOM}
k_{POM}	y^{-1}	C_{POM} decomposition rate
k_{MAOM}	y^{-1}	C_{MAOM} decomposition rate
δ_e	‰	$\delta^{13}C$ of the soil organic carbon at the end of the experiment
δ_i	‰	$\delta^{13}C$ of soil organic carbon at the beginning of the experiment
δ_v	‰	$\delta^{13}C$ of vegetation (crop) inputs to soil
Δt	Years	Time elapsed since the beginning of the experiment

$C_{MAOM(POMn)}$, both with the same $\delta^{13}C$ signal, or from C_{POMo} forming $C_{MAOM(POMo)}$, which has a different $\delta^{13}C$ than C_V (Fig. 1).

We began our calculations by partitioning total C_S ($C_{POM} + C_{MAOM}$), and C_{POM} into old C (C_o) and new C (C_n) present in each pool using the equations proposed by Balesdent (1987) (Table 2, Eqs. (3)–(5)). Since C_n is the sum of C_{POMn} and C_{MAOMn} , we estimated C_{MAOMn} as the difference between C_n and C_{POMn} (Table 2, Eq. (6)). The $\delta^{13}C$ signal measured in C_{MAOM} at the end of the experiment (C_{MAOMe}) is necessarily a weighted average of $\delta^{13}C_{MAOMo}$, $\delta^{13}C_{MAOM(POMo)}$, and the $\delta^{13}C_{MAOMn}$ which is the same than δ_v (Table 2, Eq. (7)). The only unknown variable in this equation is $C_{MAOM(POMo)}$, which can be readily solved (see Equation (12), Appendix I).

Using Eq. (1), which is based on a mass balance approach, and bulking aboveground and belowground C inputs (ignoring C inputs from rhizodeposition), we set Eqs. (8) and (9) (Table 2) for each soil C fraction (C_{POM} and C_{MAOM}) to solve for the humification coefficients (h_{VPOM} , h_{VMAOM} , h_{POM}), decomposition rates (k_{POM} and k_{MAOM}), and the C transfers among pools (see equations and details in Appendix I). The decomposition rates k_{POM} and k_{MAOM} were computed using first order kinetics based on the loss of C_3 (corn plots) or C_4 (soybean plots) from both C_{POM} and C_{MAOM} given that C inputs = 0 (Table 2, Eq. (10)). At this stage, the only variable that needs to be calculated is the amount of C_{MAOM} that came directly from C_V ($C_{MAOM(veg)}$), which is resolved in Eq. (11) (Table 2).

2.4. Statistical analysis

Treatment effects on the response variables were analyzed using a split-plot design with treatment (corn and soybean) as main plots and time of sampling as subplots. We focused our analysis on the effect of time of sampling and the interaction between time and treatment. Both k and h were obtained for each plot. Treatment effects were tested using analysis of variance and analysis of variance of regression with the software Infostat 2011/p.

2.5. Sensitivity analysis of $\delta^{13}C$ changes

We did a sensitivity analysis to evaluate the effect of the mass spectrometer detection limit on the differences found among

Table 2

Equations used to estimate model parameters and the size of the carbon pools shown in Fig. 1. Equations (1) and (2) are presented in the text.

Equation	
$C_{fn} = \frac{(\delta_e - \delta_i)}{(\delta_v - \delta_i)}$	(3)
$C_n = C_{fn} \times C_e$	(4)
$C_o = (1 - C_{fn}) \times C_e$	(5)
$C_{MAOMn} = C_n - C_{POMn}$	(6)
$\delta_{MAOMe} \times C_{MAOMe} = \delta_{POMi} \times C_{MAOM(POMo)} + \delta_v \times C_{MAOMn} + \delta_{MAOMi} \times (C_{MAOMe} - C_{MAOM(POMo)} - C_{MAOMn})$	(7)
$\frac{C_{POMe} - C_{POMi}}{\Delta t} = h_{VPOM} \times C_V - k_{POM} \times \frac{(C_{POMi} + C_{POMe})}{2}$	(8)
$\frac{C_{MAOMe} - C_{MAOMi}}{\Delta t} = h_{VMAOM} \times C_V + h_{POM} \times k_{POM} \times \frac{(C_{POMi} + C_{POMe})}{2} - k_{MAOM} \times \frac{(C_{MAOMi} + C_{MAOMe})}{2}$	(9)
$k = -\frac{1}{\Delta t} \times \ln\left(\frac{C_x(t)}{C_{xo}}\right)$	(10)
$C_{MAOM(veg)} = C_{MAOMn} - C_{MAOM(POMn)}$	(11)

^a C_V is in annual basis. The time step or time elapsed since the beginning of the experiment is $\Delta t = 2$ years.

treatments in $\delta^{13}C$. Based on 24 replicates of standard samples of Costech acetanilide analyzed in-between our soil and plant samples, the detection limit of our mass spectrometer was estimated to be 0.06‰. With these samples we also estimated the variance attributable to the instrument (0.005‰). To remove any potential bias in our isotopic analyses from the precision of the mass spectrometer, we created 100 new datasets by adding a normally distributed random error attributable to the mass spectrometer to each $\delta^{13}C$ determination, based on the calculated variance. With these datasets we recalculated k_{MAOM} values (since the smallest differences in $\delta^{13}C$ were found in the C_{MAOM} fraction) for each plot and performed the corresponding ANOVAs for both corn and soybean treatments.

3. Results

3.1. Residue inputs

Corn left significantly greater amounts of residues into the soil and with a greater C:N ratio than soybean (Table 1). Aboveground C inputs were 8.8 and 6.9 $Mg\ ha^{-1}$ for the two-year period for corn and soybean, respectively. Aboveground C:N ratio was 4.5 times larger in corn (77.8 ± 5.0) than in soybean (17.4 ± 0.3), but the difference was only twice as large in belowground biomass (60.8 ± 1.5 and 33.4 ± 1.5 for corn and soybean, respectively) (Table 3, Fig. 2). In the top 0.2 m of soil, belowground corn biomass inputs were three times larger than those of soybean. Approximately 82% of the corn and 56% of the soybean

Table 3

Cumulative crop biomass after two years, carbon and nitrogen concentration, and $\delta^{13}\text{C}$ (mean and s.e.) in aboveground and belowground (0–5 cm soil depth) for corn and soybean crops.

Variable	Corn		Soybean	
	Aboveground ^a	Belowground ^b	Aboveground ^a	Belowground ^b
Crop production (Mg of C ha ⁻¹)	8.8 ± 0.1 (a)	1.53 ± 0.03 (c)	6.9 ± 0.6 (b)	0.53 ± 0.03 (d)
Crop biomass Carbon concentration (g Kg ⁻¹)	440 ± 12 (ab)	372 ± 43 (b)	500 ± 12 (a)	385 ± 43 (b)
Crop biomass Nitrogen (Mg of N ha ⁻¹)	0.12 ± 0.001 (b)	0.02 ± 0.01 (c)	0.38 ± 0.023 (a)	0.02 ± 0.01 (c)
Crop biomass Nitrogen concentration (g Kg ⁻¹)	5.2 ± 0.7 (c)	6.5 ± 0.8 (c)	28.7 ± 0.3 (a)	11.5 ± 0.5 (b)
Crop biomass C:N ratio	77.5 ± 5.0 (a)	57.3 ± 3.7 (b)	17.4 ± 0.3 (d)	33.3 ± 1.4 (c)
Crop biomass $\delta^{13}\text{C}$ (‰)	-13.0 ± 0.2 (a)	-13.7 ± 0.3 (b)	-27.1 ± 0.2 (d)	-25.1 ± 0.3 (c)

^a Grain is not included.

^b In the first 5 cm of soil; Means with a common letter within variable are not significantly different ($P \leq 0.05$).

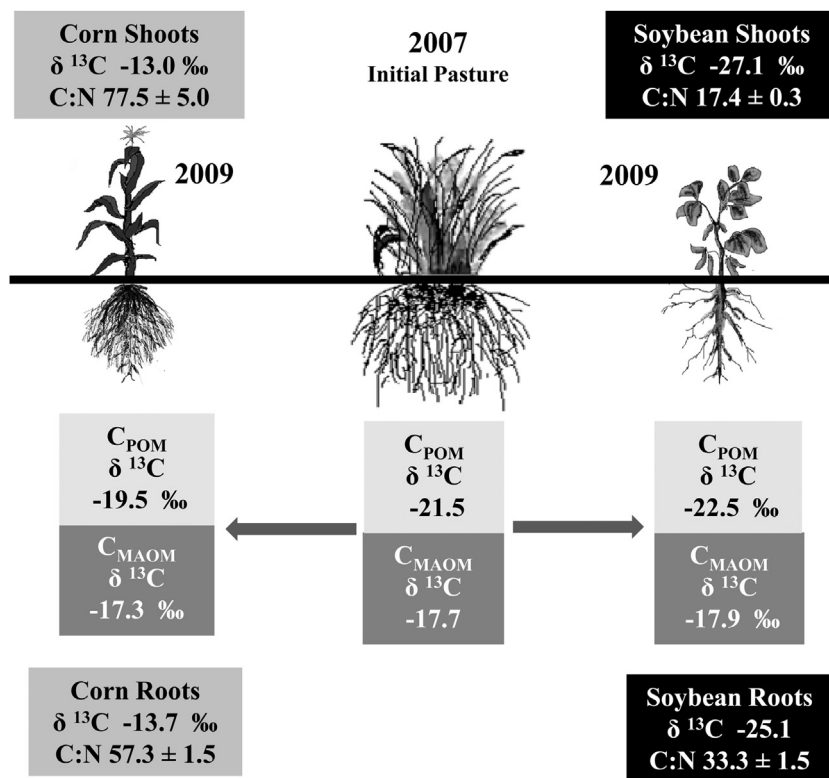


Fig. 2. Schematic representation of initial and final $\delta^{13}\text{C}$ values in different soil fractions (average 0–5 cm) and treatments. Initial conditions are represented in the center of the figure. C_{POM} = particulate organic matter; C_{MAOM} = mineral associated organic matter.

belowground biomass in the 0–20 cm soil layer was in the top 5-cm (Table 4).

3.2. Soil organic C dynamics

We detected significant changes in the $\delta^{13}\text{C}$ signal of both C_{POM} ($P < 0.05$, $n = 3$) and C_{MAOM} ($P < 0.04$, $n = 3$) in the top 5-cm of soil, and no changes in C stocks in any soil fraction or depth analyzed (Table 5 and Fig. 2). Therefore, C fluxes are only reported for the top

Table 4

Total belowground carbon inputs for corn and soybean in two years.

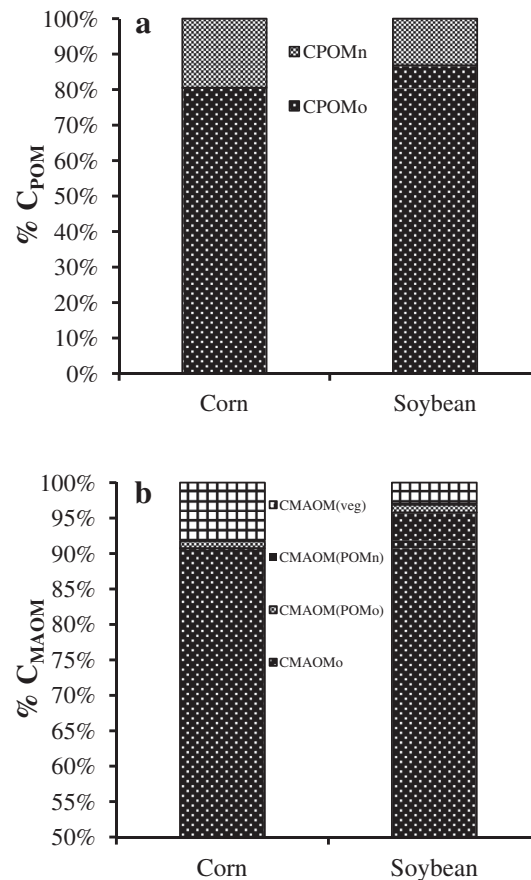
Depth (cm)	Belowground input (Mg C ha ⁻¹)	
	Corn	Soybean
0–5	1.53 ± 0.03	0.53 ± 0.03
5–10	0.23 ± 0.07	0.23 ± 0.03
10–20	0.10 ± 0.01	0.17 ± 0.03

5 cm of the soil, although changes in $\delta^{13}\text{C}$ followed similar trends in the top 20 cm of the soil (Table 5). No changes were observed below 20 cm (data not reported), probably due to the combination of low C inputs per year below 20 cm in no-till systems (Table 4) and the relatively short duration of the experiment. Nevertheless, the smallest significant difference in $\delta^{13}\text{C}$ in the topsoil was 0.4‰ (in C_{MAOM}), near an order of magnitude higher than the sensitivity of our mass spectrometer (0.06‰).

Changes in soil $\delta^{13}\text{C}$ showed that the proportion of new C present in the C_{POM} (C_{POMn}) was similar for both crops ($P < 0.99$) (Fig. 3a), but the proportion of new C from crop inputs (C_v) in the C_{MAOM} fraction ($C_{\text{MAOM(veg)}}$) was higher under corn (8%) than under soybean (3%) ($P < 0.017$) (Fig. 3b). The opposite was true for old C in C_{MAOM} (lower contents of C_{MAOMo} under corn), since total C stocks remained constant in the two-year period (Fig. 3b). Therefore, decomposition rates of C_{POM} (k_{POM}) were similar under both crops, but k_{MAOM} was three times higher under corn than under soybean ($P < 0.035$, Table 6; Fig. 4), suggesting that the more stable organic

Table 5Carbon stock and $\delta^{13}\text{C}$ signal per depth and time.

Depth (cm)	Crop	C_{POM}				C_{MAOM}			
		Mg C ha^{-1}		$\delta^{13}\text{C} (\text{‰})$		Mg C ha^{-1}		$\delta^{13}\text{C} (\text{‰})$	
		2007	2009	2007	2009	2007	2009	2007	2009
0–5	Corn	1.2	1.3	–22.5b	–20.5a	11.7	12.0	–17.7ab	–17.3a
	Soybean	1.6	1.7	–20.5a	–21.5ab	12.8	12.3	–17.6ab	–17.9b
5–10	Corn	0.3	0.3	–20.7	–20.6	13.3	11.8	–16.7	–16.7
	Soybean	0.3	0.4	–21.7	–22.6	12.4	12.0	–16.7	–16.7
10–20	Corn	0.4	0.4	–22.1	–21.9	23.0	22.6	–16.0	–16.0
	Soybean	0.4	0.5	–22.3	–22.3	24.1	23.5	–16.4	–16.6

†Means with a common letter within depth are not significantly different ($P \leq 0.05$).**Fig. 3.** The proportion of original and new carbon in the soil top 5 cm for C_{POM} (a) and C_{MAOM} (b) after two years of corn or soybean. For C_{MAOM} the new carbon is apportioned as in Fig. 2.

matter associated with the mineral fraction decomposed faster in corn plots. Our sensitivity analyses showed that k_{MAOM} of corn and soybean was different in 90% of the datasets generated adding a random error at $P < 0.05$ (and in all the datasets at $P < 0.1$). The

Table 6

Decomposition (k_{POM} and k_{MAOM}) and residue humification rates in C_{POM} (h_{VPOM}) and in C_{MAOM} (h_{VMAOM}) for corn and soybean crops in the 0–5 cm soil depth. Each value is the average of three plots.

Fraction	Variable	Corn	Soybean	<i>P</i> -value <i>n</i> = 3
		y^{-1}		
C_{POM}	k_{POM}	0.12	0.08	0.438
	h_{VPOM}	0.03	0.04	0.580
C_{MAOM}	k_{MAOM}	0.06	0.03	0.035
	h_{VMAOM}	0.10	0.05	0.349

higher k_{MAOM} of corn plots resulted in significantly greater C output fluxes from C_{MAOM} ($0.67 \text{ Mg ha}^{-1} \text{ y}^{-1}$) compared to soybean plots ($0.32 \text{ Mg ha}^{-1} \text{ y}^{-1}$) (Fig. 4). As expected for a labile fraction, k_{POM} was two to four times larger than k_{MAOM} for corn and soybean, respectively (Table 6; Fig. 4).

In agreement with the higher proportion of $\text{C}_{\text{MAOM(veg)}}$ under corn, h in the C_{MAOM} fraction (h_{VMAOM}) tended to be higher in corn compared soybean plots, although differences were not statistically significant, while h_{VPOM} was similar for both crops (Table 6). We detected a significantly higher amount of residues stabilizing into C_{MAOM} in corn ($0.51 \text{ Mg ha}^{-1} \text{ y}^{-1}$) than in soybean plots ($0.19 \text{ Mg ha}^{-1} \text{ y}^{-1}$), probably because corn residues were larger in quantity (Table 3). However, C input fluxes or C stabilization into C_{POM} was similar between crops (0.14 and 0.12 for corn and soybean, respectively) despite the larger amount of residues provided

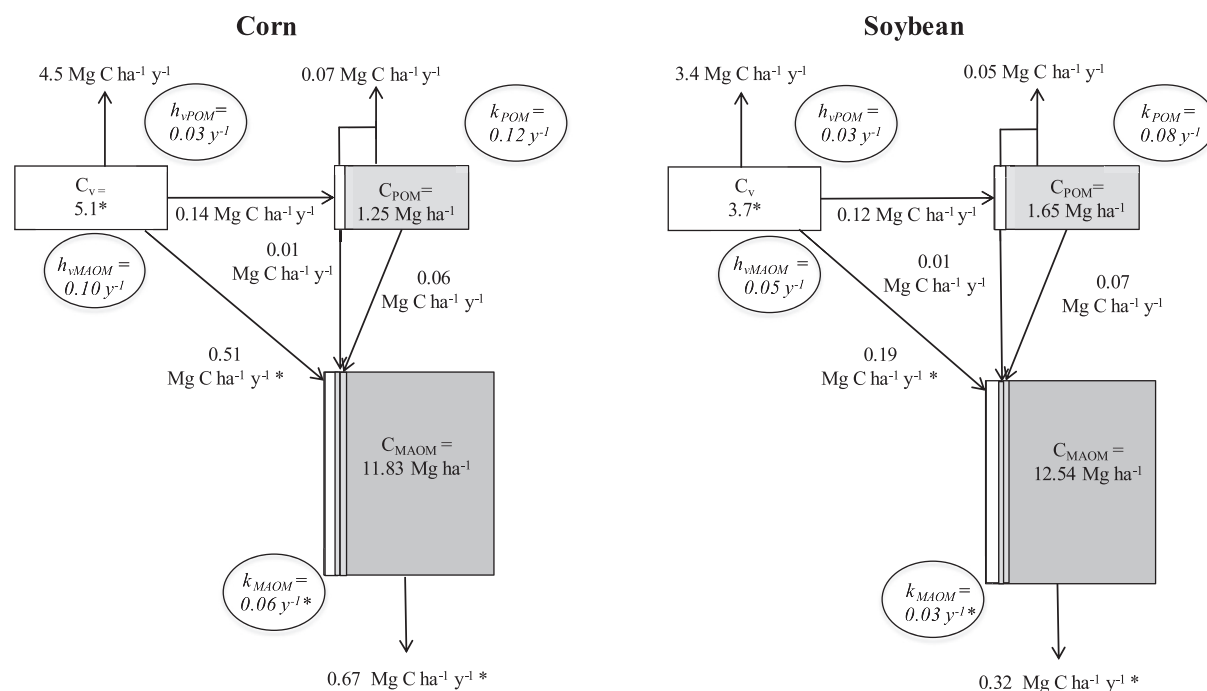


Fig. 4. Carbon flows ($\text{Mg C ha}^{-1} \text{ y}^{-1}$), decomposition rates (k , y^{-1}), and humification rates (h , y^{-1}) in the soil during two years under no-till corn and soybean. An asterisk indicates statistically significant differences between crops ($P < 0.05$).

by corn (Fig. 4). Overall, corn plots had higher k_{MAOM} but also higher stabilization of C_V inputs compared to soybean, and therefore higher C turnover in the C_{MAOM} , but not in the C_{POM} during the period studied (Table 6; Fig. 4). Our data also show that C_V moved to C_{MAOM} predominately by direct transfer (mediated by microorganisms) rather than by cascading from C_V to C_{POM} and from C_{POM} to C_{MAOM} , because fluxes from C_{POM} to C_{MAOM} were similar for both crops (on average $0.07 \text{ Mg ha}^{-1} \text{ y}^{-1}$) and an order of magnitude smaller than C fluxes from C_V directly into C_{MAOM} ($0.51 \text{ Mg ha}^{-1} \text{ y}^{-1}$ and $0.19 \text{ Mg ha}^{-1} \text{ y}^{-1}$ for corn and soybean, respectively) (Fig. 4).

4. Discussion

Our results suggest that corn inputs enhanced the decomposition of C_{MAOM} and the stabilization of C_V inputs into this soil fraction compared to soybean inputs. This interpretation is strongly supported by the changes in the $\delta^{13}\text{C}$ signal. The C derived from corn seems to have been stabilized in C_{MAOM} in a larger proportion than

the C derived from soybean (Fig. 4). The higher turnover of C_{MAOM} under corn can be caused by priming. Thus, this effect, which was previously detected in laboratory experiments (Kuzyakov, 2010), forest soils (Sayer et al., 2011) and pastures (Shahzad et al., 2012), also occurs in no-till ecosystems.

No-till systems can be especially suitable for the expression of priming. Contrary to tilled soils in which residues are mixed in the top 10–30 cm of topsoil, aboveground and belowground residues are concentrated in the topsoil, particularly in the residue–soil interface. In our experiment, the mass of fresh C inputs in the top 5 cm of soil is equivalent to $\sim 30\%$ of C_V ($C_{\text{POM}} + C_{\text{MAOM}}$). Decomposing such large amounts of fresh residues of corn requires N inputs due to its high C:N ratio and the low C:N ratio of microbial biomass. Thus, the topsoil of no-till corn systems is, in theory, conducive to priming because its microbial community has access to C from the fresh residues and N from an N-rich source such as C_{MAOM} (Kuzyakov et al., 2000; Fontaine et al., 2007; Zhu and Cheng, 2011; Guenet et al., 2012; Paterson and Sim, 2013). It is possible that priming was more related to the magnitude of the fresh inputs rather than their composition. If so, doubling the input of soybean should show priming, and halving the inputs of corn should more than proportionally reduce k_{MAOM} . Such treatments are not part of the experimental design, but plotting k_{MAOM} vs. C_V obtained in each plot and for each crop shows no relationship between these variables and indicates that priming was more related to the type of residues than to the magnitude of the C inputs (Fig. 5).

The general mechanism proposed for priming is that a C-rich substrate promotes the growth of microorganisms that produce exo-enzymes that de-polymerize N-rich compounds associated with C_{MAOM} (Talbot et al., 2008; Guenet et al., 2012). Microorganisms stimulated by fresh inputs with high C:N ratio are K-strategists (Fontaine et al., 2003; Blagodatskaya et al., 2007; Fierer et al., 2007), mostly fungi (Godbold et al., 2006) that predominantly degrade cellulose, hemicellulose, and lignin, while bacteria degrade the soluble fraction of residues and other organic inputs (sugars, amino acids) (Swift et al., 1979; Henriksen and Breland, 1999; Boer et al., 2005). In contrast, the addition of low C:N soybean residues

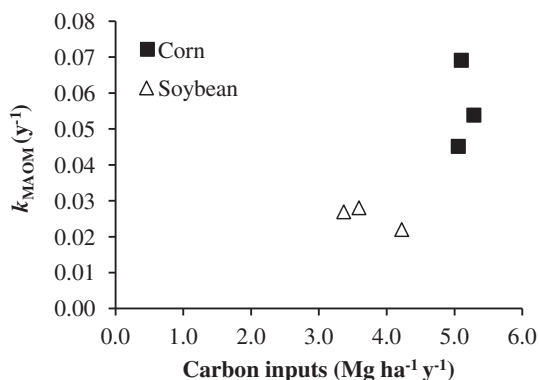


Fig. 5. Ordination of the amount of carbon input versus decomposition rate of C_{MAOM} . There was no relationship between variables ($P = 0.66$ and $P = 0.15$ for corn and soybean respectively).

would promote the growth of *r*-strategist microorganisms, mostly bacteria, that grow quickly and outcompete the *K*-strategists microorganisms (Fontaine et al., 2003; Blagodatskaya et al., 2007). The *r*-strategist would rely primarily on the soybean input biomass as a source of C and N (Fontaine et al., 2003; Blagodatskaya et al., 2007; Nottingham et al., 2009).

The priming effect has not been incorporated in models that simulate the coupled C and N cycling (e.g. Parton et al., 1988; Coleman and Jenkinson, 1996; Kemanian and Stöckle, 2010), yet, as our results show, the differences in composition between corn and soybean caused k_{MAOM} to vary by a factor of two (Table 4), and can therefore be as influential in C_5 dynamics as environmental factors such as soil temperature and moisture. The short duration of the experiment raises interesting questions regarding the long-term (years) consequence of the operation of priming in the soil C balance. (1) Will the higher k , C input (and perhaps h) in soils under corn result in similar steady state C_5 levels than under soybean? Evidence from experiments with tillage suggests that soybean-based rotations have lower steady state C_5 than corn-based rotations, but the few results reported for no-till are less certain (Andriulo et al., 1999; Huggins et al., 2007). (2) Is it possible that increasing C_V can produce the counterintuitive effect of reducing C_V due to increased turnover, as shown for cases in which rhizodeposition increases in ecosystems exposed to elevated CO_2 (Körner and Arnone, 1992)? Current literature supports the suggestion that higher C_V (not rhizodeposition) is associated with higher C_5 (Rasmussen and Parton, 1994; Huggins et al., 1998). Therefore, for this to apply in our experiment, we should detect in the future (the experiment continues) a decrease in k or an increase in h in corn plots, or conversely, an increase in k in soybean plots without an increase in h , so that the higher C_V in corn reflects in higher C_5 .

Interestingly, the higher k_{MAOM} observed in corn plots were coupled with a higher C stabilization into C_{MAOM} and a weak tendency of higher h , compared to soybean plots. The higher C input flux to C_{MAOM} in corn plots can be simply explained by the higher amount of residues leftover by the crop, however we did not detect differences in C inputs into C_{POM} between crops (Fig. 4). Higher h of corn was previously reported by (Huggins et al., 1998) and supports the concept that low C:N ratios will not cause *per se* a higher h . Therefore our results suggest that humification or C stabilization into different soil fractions is controlled by both the quality of crop inputs and other soil or ecosystem properties (Schmidt et al., 2011).

The greater C stabilization of corn residues into C_{MAOM} can be related to the degree of C saturation in soils. Based on Hassink and Whitmore (1997) and the clay concentration of 23 g kg^{-1} in our experimental site in the top 5-cm of the soil, we estimated a C_5 saturation of $\sim 15 \text{ Mg C ha}^{-1}$. Measured C_5 was $13.5 \text{ Mg C ha}^{-1}$ (1.5 and 12 Mg C ha^{-1} in C_{POM} and C_{MAOM} , respectively), suggesting that the soil is relatively close to saturation. This can explain why higher C input fluxes to C_{MAOM} occurred in corn plots: the higher output fluxes (potentially because of priming) may have released soil C slots which were refilled with byproducts of corn residue decomposition. Since soil C saturation has been related to C storage in organo-mineral fractions (i.e. C_{MAOM}) and not in labile organic matter fractions (i.e. C_{POM}) (Stewart et al., 2008), this accelerated turnover should be detected in C_{MAOM} , which is in agreement with our results.

5. Conclusions

Adding large amounts of corn residues with a high C:N ratio enhanced the turnover of C_{MAOM} when compared to adding soybean residues with a lower C:N ratio. The turnover of C_{POM} , however, was similar under both crops. The balance between increased

decomposition and higher C inputs into C_{MAOM} in corn plots resulted in constant C_{MAOM} stocks in the two years of the experiment. The same result was achieved in soybean plots but with lower decomposition rates and C inputs, suggesting that microbes fed mainly on soybean residues and not on soil C_{MAOM} . The enhanced turnover of C_{MAOM} strongly suggests that priming operated in the soil surface layer of corn plots. By extension, priming may be important in no-till cropping systems where large amounts of crop residues with high C:N ratios are left in the soil surface, and should therefore be explicitly considered in biogeochemical models.

Acknowledgments

This research is part of the doctoral dissertation of Sebastián Mazzilli at the University of Buenos Aires. Research funded by the Instituto Nacional de Investigación Agropecuaria – Fondos de Promoción de Tecnología Agropecuaria #283 (Uruguay), Proyecto de Investigaciones Plurianuales #132 (Argentina), Proyectos de Investigación Científica y Tecnológica #2008–2199 (Argentina), Universidad de Buenos Aires programa Ciencia y Tecnología #20020110100156 (Argentina), Keystone Innovation Starter Kit grant to the Penn State Institutes of Energy and the Environment, and USDA-NIFA #2012-68002-19795 grant to the Center on Global Change at Duke University. Lorena Grion, Priscila Pinto and Lucia Ciuffoli (Universidad de Buenos Aires) and Edith Elliot, Dario Frost and Gonzalo Ferreira (Universidad de la República, Uruguay) provided expert help in laboratory analysis. We thank an anonymous reviewer who made valuable comments. To all of them we are grateful.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.soilbio.2014.04.005>.

References

- Allmaras, R., Schomberg, H., Douglas Jr., C., Dao, T.H., 2000. Soil organic carbon sequestration potential of adopting conservation tillage in U.S. croplands. *Journal of Soil and Water Conservation* 55, 365–373.
- Andriulo, A., Guerif, J., Mar, B., 1999. Evolution of soil carbon with various cropping sequences on the rolling pampas. Determination of carbon origin using variations in natural ^{13}C abundances. *Agronomie* 19, 349–364.
- Balesdent, J., 1987. The turnover of soil organic fractions estimated by radiocarbon dating. *Science of the Total Environment* 62, 405–408.
- Balesdent, J., Wagner, G.H., Mariotti, A., 1988. Soil organic matter turnover in long-term field experiments as revealed by Carbon-13 Natural Abundance. *Soil Science Society of America Journal* 52, 118–124.
- Balesdent, J., Chenu, C., Balabane, M., 2000. Relationship of soil organic matter dynamics to physical protection and tillage. *Soil & Tillage Research* 53, 215–230.
- Bauer, A., Black, A.L., 1994. Quantification of the effect of soil organic matter content on soil productivity. *Soil Science Society of America Journal* 58, 185–193.
- Bayala, J., Balesdent, J., Marol, C., Zapata, F., Teklehaimanot, Z., Ouedraogo, S., 2006. Relative contribution of trees and crops to soil carbon content in a parkland system in Burkina Faso using variations in natural ^{13}C abundance. *Nutrient Cycling in Agroecosystems* 76, 193–201.
- Berthrong, S.T., Schadt, C.W., Piñeiro, G., Jackson, R.B., 2009. Afforestation alters the composition of functional genes in soil and biogeochemical processes in South American grasslands. *Applied and Environmental Microbiology* 75, 6240–6248.
- Blagodatskaya, E.V., Blagodatsky, S.A., Anderson, T.H., Kuzyakov, Y., 2007. Priming effects in Chernozem induced by glucose and N in relation to microbial growth strategies. *Applied Soil Ecology* 37, 95–105.
- Blagodatskaya, E.V., Kuzyakov, Y., 2008. Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. *Biology and Fertility of Soils* 45, 115–131.
- Boer, W.D., Folman, L.B., Summerbell, R.C., Boddy, L., 2005. Living in a fungal world: impact of fungi on soil bacterial niche development. *FEMS Microbiology Reviews* 29, 795–811.
- Bunnell, F.L., Tait, D.E., Flanagan, P.W., Van Clever, K., 1977. Microbial respiration and substrate weight loss-I: a general model of the influences of abiotic variables. *Soil Biology and Biochemistry* 9, 33–40.

- Buyanovsky, G., Wagner, G., 1986. Post-harvest residue input to cropland. *Plant and Soil* 93, 57–65.
- Cambardella, C.A., Elliot, E.T., 1992. Particle soil organic-matter changes across a grassland cultivation sequence. *Soil Society of America Journal* 56, 777–783.
- Campbell, C.A., Zentner, R.P., Bowren, K.E., Townley-Smith, L., Schnitzer, M., 1991. Effect of crop rotations and fertilization on soil organic matter and some biochemical properties of a thick Black Chernozem. *Canadian Journal of Soil Science* 71, 377–387.
- Coleman, K., Jenkinson, D., 1996. RothC-26.3 – a model for the turnover of carbon in soil. In: Powlson, D.S., Smith, P., Smith, J.U. (Eds.), *Evaluation of Soil Organic Matter Models*. Springer-Verlag, Berlin, pp. 237–246.
- Crow, S.E., Lajtha, K., Bowden, R.D., Yano, Y., Brant, J.B., Caldwell, B.A., Sulzman, E.W., 2009. Increased coniferous needle inputs accelerate decomposition of soil carbon in an old-growth forest. *Forest Ecology and Management* 258, 2224–2232.
- Chemidlin Prévost-Bouré, N., Soudani, K., Damesin, C., Berveiller, D., Lata, J.C., Dufrêne, E., 2010. Increase in aboveground fresh litter quantity over-stimulates soil respiration in a temperate deciduous forest. *Applied Soil Ecology* 46, 26–34.
- Davidson, E.A., Ackerman, I.L., 1993. Changes in soil carbon inventories following cultivation of previously untilled soils. *Biogeochemistry* 20, 161–193.
- Desjardins, T., Folgarait, P.J., Pando-Bahuon, A., Girardin, C., Lavelle, P., 2006. Soil organic matter dynamics along a rice chronosequence in north-eastern Argentina: evidence from natural ^{13}C abundance and particle size fractionation. *Soil Biology and Biochemistry* 38, 2753–2761.
- Ernst, O., Siri-Prieto, G., 2009. Impact of perennial pasture and tillage systems on carbon input and soil quality indicators. *Soil and Tillage Research* 105, 260–268.
- Fierer, N., Bradford, M.A., Jackson, R.B., 2007. Toward an ecological classification of soil bacteria. *Ecology* 88, 1354–1364.
- Foley, J.A., De Fries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. *Science* 309, 570–574.
- Fontaine, S., Barot, S., Barre, P., Bdioui, N., Mary, B., Rumpel, C., 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature* 450, 277–280.
- Fontaine, S., Mariotti, A., Abbadie, L., 2003. The priming effect of organic matter: a question of microbial competition? *Soil Biology and Biochemistry* 35, 837–843.
- Godbold, D., Hoosbeek, M., Lukac, M., Cotrufo, M.F., Janssens, I., Ceulemans, R., Polle, A., Velthorst, E., Scarascia-Mugnozza, G., Angelis, P., Miglietta, F., Peressotti, A., 2006. Mycorrhizal hyphal turnover as a dominant process for carbon input into soil organic matter. *Plant and Soil* 281, 15–24.
- Gregorich, E.G., Monreal, C.M., Ellert, B.H., 1995. Turnover of soil organic matter and storage of corn residue carbon estimated from natural ^{13}C abundance. *Canadian Journal of Soil Science* 75, 161–167.
- Gregorich, E.G., Rochette, P., McGuire, S., Liang, B.C., Lessard, R., 1998. Soluble organic carbon and carbon dioxide fluxes in maize fields receiving spring-applied manure. *Journal of Environmental Quality* 27, 209–214.
- Guenet, B., Juarez, S., Bardoux, G., Abbadie, L., Chenu, C., 2012. Evidence that stable C is as vulnerable to priming effect as is more labile C in soil. *Soil Biology and Biochemistry* 52, 43–48.
- Guenet, B., Neill, C., Bardoux, G., Abbadie, L., 2010. Is there a linear relationship between priming effect intensity and the amount of organic matter input? *Applied Soil Ecology* 46, 436–442.
- Hassink, J., Whitmore, A.P., 1997. A model of the physical protection of organic matter in soils. *Soil Science Society of America Journal* 61, 131–139.
- Hendrix, P.F., Han, C.R., Groffman, P.M., 1988. Soil respiration in conventional and no-tillage agroecosystems under different winter cover crop rotations. *Soil and Tillage Research* 12, 135–148.
- Hénin, S., Dupuis, M., 1945. Essai de bilan de la matière organique du sol. *Annales Agronomiques* 15, 17–29.
- Henriksen, T.M., Breland, T.A., 1999. Nitrogen availability effects on carbon mineralization, fungal and bacterial growth, and enzyme activities during decomposition of wheat straw in soil. *Soil Biology and Biochemistry* 31, 1121–1134.
- Huggins, D.R., Allmaras, R.R., Clapp, C.E., Lamb, J.A., Randall, G.W., 2007. Corn-soybean sequence and tillage effects on soil carbon dynamics and storage. *Soil Science Society of America Journal* 71, 145–154.
- Huggins, D.R., Clapp, C.E., Allmaras, R.R., Lamb, J.A., Layese, M.F., 1998. Carbon dynamics in corn-soybean sequences as estimated from natural carbon-13 abundance. *Soil Science Society of America Journal* 62, 195–203.
- Kemanian, A.R., Stöckle, C.O., 2010. C-Farm: a simple model to evaluate the carbon balance of soil profiles. *European Journal of Agronomy* 32, 22–29.
- Körner, C., Arnone, J.A., 1992. Responses to elevated carbon dioxide in artificial tropical ecosystems. *Science* 257, 1672–1675.
- Kowalenko, C.G., Ivarson, K.C., Cameron, D.R., 1978. Effect of moisture content, temperature and nitrogen fertilization on carbon dioxide evolution from field soils. *Soil Biology and Biochemistry* 10, 417–423.
- Kuzyakov, Y., 2010. Priming effects: interactions between living and dead organic matter. *Soil Biology and Biochemistry* 42, 1363–1371.
- Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. *Soil Biology and Biochemistry* 32, 1485–1498.
- Lal, R., 1997. Residue management, conservation tillage and soil restoration for mitigating greenhouse effect by CO_2 -enrichment. *Soil and Tillage Research* 43, 81–107.
- Larionova, A., Zolotareva, B., Yevdokimov, I., Bykhovets, S., Kuzyakov, Y., Buegger, F., 2011. Identification of labile and stable pools of organic matter in an agrogray soil. *Eurasian Soil Science* 44, 628–640.
- Manzoni, S., Jackson, R.B., Trofymow, J.A., Porporato, A., 2008. The global stoichiometry of litter nitrogen mineralization. *Science* 321, 684–686.
- Martin, A., Mariotti, A., Balesdent, J., Lavelle, P., Vuattoux, R., 1990. Estimate of organic matter turnover rate in a savanna soil by ^{13}C natural abundance measurements. *Soil Biology and Biochemistry* 22, 517–523.
- Nottingham, A.T., Griffiths, H., Chamberlain, P.M., Stott, A.W., Tanner, E.V., 2009. Soil priming by sugar and leaf-litter substrates: a link to microbial groups. *Applied Soil Ecology* 42, 183–190.
- Parton, W., Stewart, J., Cole, C., 1988. Dynamics of C, N, P and S in grassland soils: a model. *Biogeochemistry* 5, 109–131.
- Paterson, E., Sim, A., 2013. Soil-specific response functions of organic matter mineralization to the availability of labile carbon. *Global Change Biology* 19, 1562–1571.
- Power, J.F., Wilhelm, W.W., Doran, J.W., 1986. Crop residue effects on soil environment and dryland maize and soya bean production. *Soil and Tillage Research* 8, 101–111.
- Rasmussen, P.E., Parton, W.J., 1994. Long-term effects of residue management in wheat-fallow: I. Inputs, yield, and soil organic matter. *Soil Science Society of America Journal* 58, 523–530.
- Rasmussen, P.E., Smiley, R.W., 1997. Soil carbon and nitrogen change in long-term agricultural experiments at Pendleton, Oregon. In: Paul, E.A., Paustian, K., Elliot, E.T., Cole, V.V. (Eds.), *Soil Organic Matter in Temperate Agroecosystems: Long-term Experiments in North America*. CRC Press, Boca Raton, FL, USA, pp. 353–360.
- Reeves, D.W., 1997. The role of soil organic matter in maintaining soil quality in continuous cropping systems. *Soil and Tillage Research* 43, 131–167.
- Sayer, E.J., Heard, M.S., Grant, H.K., Marthews, T.R., Tanner, E.V.J., 2011. Soil carbon release enhanced by increased tropical forest litterfall. *Nature Climate Change* 1, 304–307.
- Schimel, D.S., 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biology* 1, 77–91.
- Schmidt, M.W., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kogel-Knabner, I., Lehmann, J., Manning, D.A., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478, 49–56.
- Shahzad, T., Chenu, C., Repinçay, C., Mougin, C., Ollier, J.L., Fontaine, S., 2012. Plant clipping decelerates the mineralization of recalcitrant soil organic matter under multiple grassland species. *Soil Biology and Biochemistry* 51, 73–80.
- Soriano, A., 1992. Rio de La Plata grasslands. In: Coupland, R.T. (Ed.), *Natural Grasslands. Ecosystems of the World 8A. Introduction and Western Hemisphere*. Elsevier, Amsterdam, pp. 367–407.
- Stewart, C.E., Plante, A.F., Paustian, K., Conant, R.T., Six, J., 2008. Soil carbon saturation: linking concept and measurable carbon pools. *Soil Science Society of America Journal* 72, 379–392.
- Sulzman, E.W., Brant, J.B., Bowden, R.D., Lajtha, K., 2005. Contribution of above-ground litter, belowground litter, and rhizosphere respiration to total soil CO_2 efflux in an old growth coniferous forest. *Biogeochemistry* 73, 231–256.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. In: *Studies in Ecology*, vol. 5. Blackwell Scientific Publications, Oxford.
- Talbot, J.M., Allison, S.D., Treseder, K.K., 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. *Functional Ecology* 22, 955–963.
- Wildung, R.E., Garland, T.R., Buschbom, R.L., 1975. The interdependent effects of soil temperature and water content on soil respiration rate and plant root decomposition in arid grassland soils. *Soil Biology and Biochemistry* 7, 373–378.
- Zhu, B., Cheng, W., 2011. Rhizosphere priming effect increases the temperature sensitivity of soil organic matter decomposition. *Global Change Biology* 17, 2172–2183.
- Zhu, B., Cheng, W., 2012. Nodulated soybean enhances rhizosphere priming on soil organic matter decomposition more than non-nodulated soybean. *Soil Biology and Biochemistry* 51, 56–65.