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Shifts in soil organic carbon for plantation and pasture establishment in native forests and grasslands of South America

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Abstract

The replacement of native vegetation by pastures or tree plantations is increasing worldwide. Contradictory effects of these land use transitions on the direction of changes in soil organic carbon (SOC) stocks, quality, and vertical distribution have been reported, which could be explained by the characteristics of the new or prior vegetation, time since vegetation replacement, and environmental conditions. We used a series of paired-field experiments and a literature synthesis to evaluate how these factors affect SOC contents in transitions between tree- and grass-dominated (grazed) ecosystems in South America. Both our field and literature approaches showed that SOC changes (0–20 cm of depth) were independent of the initial native vegetation (forest, grassland, or savanna) but strongly dependent on the characteristics of the new vegetation (tree plantations or pastures), its age, and precipitation. Pasture establishment increased SOC contents across all our precipitation gradient and C gains were greater as pastures aged. In contrast, tree plantations increased SOC stocks in arid sites but decreased them in humid ones. However, SOC losses in humid sites were counterbalanced by the effect of plantation age, as plantations increased their SOC stocks as plantations aged. A multiple regression model including age and precipitation explained more than 50% ($p < 0.01$) of SOC changes observed after sowing pastures or planting trees. The only clear shift observed in the vertical distribution of SOC occurred when pastures replaced native forests, with SOC gains in the surface soil but losses at greater depths. The changes in SOC stocks occurred mainly in the silt+clay soil size fraction (MAOM), while SOC stocks in labile (POM) fraction remained relatively constant. Our results can be considered in designing strategies to increase SOC storage and soil fertility and highlight the importance of precipitation, soil depth, and age in determining SOC changes across a range of environments and land-use transitions.

Keywords: soil organic matter, rainforests, land use transitions, vegetation replacement, mean annual precipitation, plantation age

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Introduction

Soil organic carbon (SOC) losses after the conversion of natural ecosystems to annual cropping systems are well documented (Burke *et al.*, 1989; Harrison *et al.*, 1993; Murty *et al.*, 2002; Lal, 2004). However, there is less consensus about the net effects on SOC after replacement with perennial crops, such as pastures and tree plantations. Tree plantations accumulate significant amounts of C in their biomass, but have been shown to decrease SOC in some tropical ecosystems (Hoen & Solberg, 1994; Guo & Gifford, 2002; Berthrong *et al.*, 2009). In contrast, other studies show no losses or even increases of SOC in mature plantations (Jobbagy & Jackson, 2000; Paul *et al.*, 2002; Nosetto *et al.*, 2006; Fialho & Zinn, 2012). Pasture studies similarly provide no consensus, with some studies showing SOC increases in the top soil layers when native forests are replaced by pastures (Bonde *et al.*, 1992; Trumbore *et al.*, 1995; Moraes *et al.*, 1996) but others showing the opposite (Falesi, 1976; Desjardins *et al.*, 1994; Don *et al.*, 2011). These contradictory results could be explained in part by interactions with the type of native vegetation that

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was replaced, the age at which tree plantations or pastures were sampled, and environmental conditions, including precipitation, temperature, and soil attributes (Nepstad *et al.*, 1994; Van Dam *et al.*, 1997; Paul *et al.*, 2002; Lilienfein *et al.*, 2003; Cerri *et al.*, 2004; López-Ulloa *et al.*, 2005; Laganière *et al.*, 2010). Few studies have synthesized the effects of land use change trajectories on SOC regionally, considering the effects of climate, time since conversion, or the characteristics of the native vegetation replaced (Kirschbaum *et al.*, 2008b; Berthrong *et al.*, 2012).

The quantity, quality, and vertical distribution of SOC varies according to the vegetation type that dominates an ecosystem (Jobbagy & Jackson, 2000). Thus, land use changes involving reciprocal replacements between grass- and tree-dominated vegetation, can alter the quantity, quality, and vertical distribution of SOC. These transitions involve shifts in rates of primary productivity, biomass partitioning between above and below ground tissues, and vertical root distributions (Nepstad *et al.*, 1994; Jackson *et al.*, 2000). Such factors may in turn affect and interact with nutrient cycling, the organic matter fractions and carbon storage (Trumbore, 1997; Gill & Burke, 1999; Jobbagy & Jackson, 2000). In a global review of diverse vegetation transitions, Guo & Gifford (2002) found that replacing forests with pastures increased SOC levels by 8%, while tree plantations replacing grasslands and forests decreased SOC by 10 and 13%, respectively. Land use changes often affect SOC quality, which can be assessed by the proportion of total C present in different soil particle-size or density fractions, among other methods. Piñeiro *et al.* (2009) found that cattle grazing altered plant functional types and hence C accumulation mainly in the clay+silt fraction (C-MAOM). A detailed evaluation of the effects of reciprocal vegetation change, such as those between woody- and herbaceous-dominated systems, should help clarify the underlying mechanisms dictating SOC changes and help predict the net effects of land use conversions on SOC stocks.

Besides their association with vegetation traits, SOC changes after vegetation replacement are affected by climate and soil factors, with the time since conversion critical to interpreting SOC trends. Jobbagy & Jackson (2000) showed that SOC contents in natural ecosystems increased with precipitation and clay content and decreased with temperature. In a global review, Amundson (2001) observed that SOC inputs increased with mean annual precipitation (MAP), possibly due to increases in vegetation productivity, but SOC mean residence time decreased with higher MAP and mean annual temperature (MAT). Time is also a key factor in rates of soil formation and the time since vegetation replacement can therefore influence SOC contents and stabilization. Some authors have observed increases in SOC contents with increasing age in plantations (Guo & Gifford, 2002) and pastures (Feigl *et al.*, 1995; Moraes *et al.*, 1996; Koutika *et al.*, 1997; Cerri *et al.*, 2004; Desjardins *et al.*, 2004; Lisboa *et al.*, 2009). In addition, interactions may arise between soil texture, age, MAT and MAP, and different land use changes that could determine regional patterns of SOC accumulation (Berthrong *et al.*, 2012).

Reciprocal replacements between grass- and tree-dominated vegetation can also modify soil organic nitrogen (SON) contents, affecting SOC changes. Differences in N uptake of these vegetation types, as well as differences in litter quality and other N fluxes, will determine changes in N availability and N contents in the soil. For example, when tree plantations replace grasslands or pastures there is typically an increase in water and nutrient uptake and a decrease in soil water and nutrient contents (Nosetto *et al.*, 2005; Farley *et al.*, 2008; Guo *et al.*, 2008). In addition, in tree biomass most of the N is partitioned to lower-concentration N pools (thick roots and trunks), while in pastures, N tends to be allocated into plant pools with higher N contents, such as fine roots and leaves, speeding up N cycling (Kirschbaum *et al.*, 2008a). Some authors have observed increased N mineralization rates in forest-to-pasture transitions (Matson *et al.*, 1987; Hölscher *et al.*, 1997) while others have shown that these differences disappear as pastures age (Neill *et al.*, 1999; Verchot *et al.*, 1999). Finally, changes in N availability can potentially decrease SON contents and limit SOC accumulation (Kirschbaum *et al.*, 2008b; Piñeiro *et al.*, 2009; Paruelo *et al.*, 2010).

In this article we combine paired-field experiments and a literature synthesis to explore how the replacement of natural forest and grassland by tree plantations and pastures (1) influences SOC storage across gradients of precipitation, temperature, and plantation age, and (2) affects SOC and SON pools in different soil organic matter fractions and depths.

Materials and methods

Regional changes in SOC stocks

To assess pasture and plantation effects on SOC contents regionally, we compiled data from published studies evaluating SOC changes after plantation or pasture establishment in South America. We found 13 articles that evaluated a total of 27 sites with pastures and 22 sites with plantations established on native grasslands, forests, or savannas in Argentina, Brazil, and Uruguay (Table 1). Most studies in the literature measured SOC contents only to 20 cm depth, so we performed

Table 1 Characteristics of the pasture and tree plantation sites reviewed

Native vegetation	Species in current land use	Original SOC[a] (Mg ha^{-1})	Current SOC[a] (Mg ha^{-1})	Difference[a] (Mg ha^{-1})	MAP[b] (mm)	MAT[c] (°C)	Age (years)	Location	Source
Current land use = Pastures									
Forest	*Brachiaria humidícola*	90	93	2.60	2100	26.5	8	Brazil	(Cerri *et al*., 1991)
Forest	*Brachiaria humidícola*	29	32	3.27	2100	26.5	3	Brazil	(Desjardins *et al*., 2004)
Forest	*Brachiaria humidícola*	29	34	4.52	2100	26.5	9	Brazil	(Desjardins *et al*., 2004)
Forest	*Brachiaria humidícola*	29	34	5.13	2100	26.5	15	Brazil	(Desjardins *et al*., 2004)
Forest	*Brachiaria humidícola*	55	56	0.61	2100	26.5	4	Brazil	(Desjardins *et al*., 2004)
Forest	*Brachiaria humidícola*	55	60	4.99	2100	26.5	8	Brazil	(Desjardins *et al*., 2004)
Forest	*Brachiaria humidícola*	55	62	6.52	2100	26.5	15	Brazil	(Desjardins *et al*., 2004)
Forest	*Panicum maximum*	25	13	−12.20	1500	28	11	Brazil	(Falesi, 1976)
Forest	*Panicum maximum*	15	12	−3.10	1750	27.2	10	Brazil	(Falesi, 1976)
Forest	*Brachiaria humidícola*	48	56	7.89	1750	27.2	17	Brazil	(Koutika *et al*., 1997)
Forest	*Brachiaria brizantha*	48	49	0.18	1750	27.2	7	Brazil	(Koutika *et al*., 1997)
Forest	*Panicum máximum*	48	49	0.70	1750	27.2	12	Brazil	(Koutika *et al*., 1997)
Forest	*Brachiaria brizantha*	25	45	20.26	2200	25.6	95	Brazil	(Lisboa *et al*., 2009)
Forest	*Brachiaria brizantha*	25	39	13.92	2200	25.6	17	Brazil	(Lisboa *et al*., 2009)
Forest	*Brachiaria brizantha*	25	40	14.90	2200	25.6	34	Brazil	(Lisboa *et al*., 2009)
Forest	nd[e]	25	40	14.60	2200	25.6	81	Brazil	(Neill *et al*., 1996)
Grassland	*Brachiaria brizantha*	70	73	2.99	1600	20	15	Argentina	This study
Grassland	*Brachiaria brizantha*	45	46	0.34	1600	20	15	Argentina	This study
Grassland	*Brachiaria brizantha*	63	69	6.40	1600	20	15	Argentina	This study
Forest	*Axonopus compressus*	34	51	16.68	2000	21	55	Argentina	This study
Forest	*Axonopus compressus*	34	45	10.93	2000	21	65	Argentina	This study
Forest	*Axonopus compressus*	36	40	4.41	2000	21	25	Argentina	This study
Cerrado[d]	*Brachiaria decumbens*	29.04	33	3.96	1550	22	13	Brazil	(Lilienfein *et al*., 2003)
Cerrado	*Brachiaria decumbens*	29.04	38.88	9.84	1550	22	13	Brazil	(Lilienfein *et al*., 2003)
Cerrado	*Brachiaria sp.*	29.9	34.6	4.70	1370	19.2	20	Brazil	(Maquere *et al*., 2008)
Cerrado	*Brachiaria sp.*	29.9	37.2	7.30	1370	19.2	80	Brazil	(Maquere *et al*., 2008)
Cerrado	*Ag (9)/Bd(4)*[f]	39.5	45	5.50	1500	22.5	13	Brazil	(Marchão *et al*., 2009)
Cerrado	*Brachiaria decumbens*	37.9	40.7	2.80	1500	23.6	15	Brazil	(D'andréa *et al*., 2004)
Cerrado	*Brachiaria sp.*	44.5	50.1	5.60	1500	20	9	Brazil	(Batlle-Bayer *et al*., 2010)
Cerrado	*Brachiaria sp.*	68.7	65.8	−2.90	1500	20	11	Brazil	(Batlle-Bayer *et al*., 2010)
Cerrado	*Brachiaria sp.*	68.7	67	−1.70	1500	20	11	Brazil	(Batlle-Bayer *et al*., 2010)
Cerrado	*Brachiaria sp.*	54	53.5	−0.50	1500	20	11	Brazil	(Batlle-Bayer *et al*., 2010)
Current land use = Tree plantations									
Grassland	*Eucaliptus globulus*	19.7	17.7	−2.03	1261	18.5	12	Uruguay	(Berthrong *et al*., 2012)
Grassland	*Eucaliptus globulus*	48.4	48.9	0.45	1216	17.3	19	Uruguay	(Berthrong *et al*., 2012)
Grassland	*Eucaliptus grandis*	17.8	14.5	−3.25	1262	18.5	10	Uruguay	(Berthrong *et al*., 2012)
Grassland	*Eucaliptus camandulensis*	91.4	63.9	−27.45	1216	17.3	30	Uruguay	(Berthrong *et al*., 2012)

Table 1 (continued)

Native vegetation	Species in current land use	Original SOC[a] (Mg ha^{-1})	Current SOC[a] (Mg ha^{-1})	Difference[a] (Mg ha^{-1})	MAP[b] (mm)	MAT[c] (°C)	Age (years)	Location	Source
Grassland	*Eucaliptus grandis*	47.2	75.5	28.34	1248	17.3	28	Uruguay	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus camandulensis*	81.5	123.5	42.05	928	15.0	50	Argentina	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus grandis*	9.6	9.9	0.27	1278	18.5	20	Uruguay	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus grandis*	24.9	8.0	−16.83	1406	18.5	13	Uruguay	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus camandulensis*	58.0	101.0	43.00	935	15.0	100	Argentina	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus camandulensis*	50.7	50.4	−0.29	968	16.9	30	Argentina	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus camandulensis*	15.5	40.9	25.42	842	15.6	35	Argentina	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus camandulensis*	39.6	37.7	−1.88	783	15.6	15	Argentina	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus camandulensis*	29.2	51.4	22.21	772	15.6	30	Argentina	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus camandulensis*	37.3	74.4	37.08	755	16.8	45	Argentina	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus camandulensis*	81.6	93.3	11.68	1002	16.9	30	Argentina	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus globulus*	86.9	66.1	−20.80	1229	17.3	12	Uruguay	(Berthrong *et al.*, 2012)
Grassland	*Eucaliptus viminaldis*	21.9	34.7	12.80	661	15.1	35	Argentina	(Berthrong *et al.*, 2012)
Grassland	*Pinus elliottii*	62.9	56.4	−6.47	1600	20.0	15	Argentina	This study
Grassland	*Pinus elliottii*	59.2	47.6	−11.64	1600	20.0	31	Argentina	This study
Grassland	*Pinus elliottii*	41.7	33.4	−8.34	1600	20.0	25	Argentina	This study
Grassland	*Pinus taeda*	37.0	25.2	−11.80	2000	14.5	8	Brazil	(Marchão *et al.*, 2009)
Grassland	*Pinus taeda*	37.0	14.0	−23.00	2000	14.5	30	Brazil	(Marchão *et al.*, 2009)
Forest	*Pinus taeda*	41.1	34.7	−6.41	2000	20.0	14	Argentina	This study
Forest	*Pinus taeda*	52.8	32.6	−20.21	2000	20.0	30	Argentina	This study
Forest	*Pinus taeda*	46.5	28.5	−18.05	2000	20.0	7	Argentina	This study
Cerrado	*Eucaliptus saligna*	30	39	8.70	1370	19.2	60	Brazil	(Maquere *et al.*, 2008)
Cerrado	*Eucaliptus saligna*	30	37	6.90	1370	19.2	60	Brazil	(Maquere *et al.*, 2008)
Cerrado	*Pinus caribaea*	55	49	−6.00	1550	22.0	20	Brazil	(Lilienfein *et al.*, 2003)

[a] SOC stocks in the first 20 cm of the soil.

[b] MAP: mean annual precipitation.

[c] MAT: mean annual temperature.

[d] The "Cerrado" is a tropical savanna of Brazil.

[e] nd: no data.

[f] Ag (9)/Bd(4): 9 years *Andropogon giganteum*/4 years *Brachiaria decumbens* rotation.

our analysis on topsoil SOC stocks, transforming SOC concentrations where needed to stocks using reported bulk density. The percentage of SOC change was estimated according to the Eqn 1:

$$\text{SOC change}\,(\%) = \left(\frac{\text{SOC current} - \text{SOC original}}{\text{SOC original}}\right) \times 100 \quad (1)$$

where SOC change is the percentage change in SOC after vegetation replacement, SOC current is the SOC content (Mg ha^{-1}) in the soil under the new vegetation, and SOC original is the SOC content (Mg ha^{-1}) of the native ecosystem.

In addition to obtaining SOC contents, we also retrieved data for mean annual precipitation (MAP), mean annual temperature (MAT), and time elapsed since the replacement of the native vegetation with pastures or tree plantations (age) for each site (Table 1). If MAP or MAT data were not reported in the article, we searched for the nearest weather station to the study site in the FAO climate database (Fao, 1985). Surprisingly, soil texture data was missing in most papers and was therefore not included in our literature analysis.

Field Experiments

To evaluate SOC and SON content in original and transformed vegetation, we selected 11 sites in Argentina (27°S, 54°W), focusing on the provinces of Misiones and Corrientes in the northeast part of the country where vegetation change is currently rapid. In northern Misiones, grazed pastures and tree plantations have replaced native forest, while in southern Misiones and northeastern Corrientes they have replaced native grasslands that were grazed. The climate is subtropical humid without a dry season. The mean annual temperature is 20 °C and mean annual rainfall increases from 1600 mm in the south to 2000 mm in the north (Ligier *et al.*, 1988). Landscape relief is rolling with average slopes around 5% and soils are mostly deep-dusky red soils classified as Ultisols and Alfisols, with clayey texture (20–40% silt, 50–80% clay, 3–20% sand) and its parent rock is basalt (Ligier *et al.*, 1988).

The native forests of Misiones includes diverse tree species, usually covered with lianas and epiphytes, mixed with shrubs, bamboos, and grasses (Parodi, 1964). The main tree species are: *Araucaria angustifolia*, *Aspidosperma australe*, *Nectandra lanceolata*, *N. megapotamica*, *Aspidosperma polyneuron*, *Parapiptadenia rigida*, *Myrocarpus frondosus*, *Enterolobium cortortisiliquum*, *Peltophorum dubium*, *Cedrela fissilis*, *Cabralea canjerana*, *Cordia trichotoma*, and *Handroanthus heptaphyllus* (Ifona, 1988; Erize *et al.*, 1997). The natural grassland region studied belongs to the district of Northern Campos of Rio de la Plata grasslands (Soriano *et al.*, 1992). The most common grassland species are grasses such as: *Axonopus compressus*, *Paspalum notatum*, *Paspalum paniculatum*, accompanied by other grasses such as *Schizachyrium sp.*, *Chloris sp.*, *Andropogon lateralis*, *Elionurus muticus*, *Aristida jubata*, *Sorghastrum pellitum*, and *Paspalum coryphaeum* (Soriano *et al.*, 1992; Carnevali, 1994; Lacorte & Goldfarb, 1996).

In each of the 11 study sites, we sampled adjacent stands of natural vegetation and either tree plantation or pastures, substituting time for space in our analysis of SOC changes. In northern sites, where the vegetation was originally native forest, we sampled three locations with paired stands of native forest and pine plantations (*Pinus taeda*) and three sites with stands of native forest and planted pastures (*A. compressus*, a C_4 species). At the southern sites, where the native vegetation is grassland, samples were taken in three sites that had adjacent stands of native grassland and pine plantations (*Pinus elliottii*) and in three sites that had stands of native grassland and C4 pastures (*Brachiaria brizantha*, a C_4 species) (Table 2; Fig. 1). For analyzing SOC changes, we evaluated four different vegetation transitions: native forest to pasture (F-P), native forest to tree plantations (F-T), native grasslands to tree plantations (G-T), and native grasslands to pastures (G-P), each with three replicates (see Fig. 1). For site selection, we reconstructed land use and management practices with land owners, and selected only sites where either pastures or tree plantations had been the first land use planted after replacement of the native vegetation. At all sites, pastures and grasslands were grazed by livestock at a density of 0.7 cows ha^{-1}. Because some of the tree plantations were old enough to have been thinned once, the tree density at the time of sampling ranged from 1000 to 700 plants ha^{-1} in the younger and older sites, respectively. At all plantations sites, initial management consisted of clear-cutting the forest and burning of forest residues.

Root, soil, and litter samples were taken at all sites ~5 m away from any fence lines to reduce any edge effects. The top 100 cm of the mineral soil was sampled (previously removing the litter and OH layer) using a 2 cm wide soil corer, with 4–6 subsamples pooled in each stand. Samples were separated into 0–5, 5–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm depth intervals. All samples were passed through a 2 mm sieve and were oven dried at 60 °C. The SOC partition throughout particle-size fractions was determined according to Cambardella & Elliott (1992). Briefly, 10 g of 2 mm sieved soil was shaken overnight (18 h) in 30 ml of 5% hexametaphosphate dispersant solution. The dispersed soil was sieved using a 53 μm mesh sieve and washed with approximately 600 ml of distilled water. The material left on the sieve constituted the particulate fraction of organic matter (POM) and the material that went through the sieve constituted the mineral-associated organic matter (MAOM) fraction. Both fractions were collected separately and oven dried at 60 °C until they reached a constant weight. The MAOM fraction was ground with a mill (IKA, Model M20) and the sand fraction was ground to dust with a manual mortar. The C and N concentrations were determined with an elemental analyzer (Carlo Erba) in the Stable Isotope Laboratory at Duke University, USA. Carbon and N concentrations from the sand fraction constituted the C and N of the particulate organic matter (C- POM and N-POM), and the C and N present in the MAOM fraction were denominated as C-MAOM and N-MAOM, respectively. Soil pH was measured in distilled water (15 g of soil in 30 ml) with a pH meter (Elliot *et al.*, 1999). Bulk density samples were taken to 30 cm depth using a soil cylinder core sampler with 6 cm of diameter, at the same intervals as for the C and N analysis. Soil bulk density from deeper depths (30–100 cm) was obtained from published soil profiles

Table 2 Location and description of our field sites

Site	Lat-Long	Department-province	Land use	Age (years)	Clay+silt content (%)[a]
La Península	28º17′11,4″ S	Santo Tomé	Native grassland	15	92.47
	55º50′54,6′′ WO	(Corrientes)	Tree plantation	15	93.42
			Pasture		93.41
Santa Cecilia	27º28′14,9″ S	Candelaria	Native grassland		89.01
	55º41′13,1′′ WO	(Misiones)	Tree plantation	25	88.76
Santo Tomás	27º35′44,8″ S	Ituzaingó	Native grassland		95.03
	55º57′25,4″ WO	(Corrientes)	Tree plantation	31	94.96
Itambé norte	27º26′56″ S	Capital	Native grassland		93.65
	55º59′14,0″ WO	(Misiones)	Pasture	15	93.76
San Francisco	27º54′59,7″ S	Santo Tomé	Native grassland		84.1
	56º05′00,7″ WO	(Corrientes)	Pasture	15	86.04
Robicué I	26° 05′07,6″ S	Iguazú	Native forest		97.91
	54° 24′ 52,6″ W	(Misiones)	Pasture	25	93.36
Eto. Vilm	26° 00′ 28,4″ S	Iguazú	Native forest		94.70
Ricardo	54°30′40,7″ WO	(Misiones)	Pasture	55	93.38
Robicué II	26° 05′07,6″ S	Iguazú	Native forest		97.91
	54° 24′ 52,6″ W	(Misiones)	Pasture	65	93.74
San Gabriel	26º 01′ 55,37″ S	Iguazú	Native forest		90.80
	54º 33′ 25,21″O	(Misiones)	Tree plantation	7	88.27
Sajonia	26º01′48,2″ S	Iguazú	Native forest		78.49
	54º39′24,6″ WO	(Misiones)	Tree plantation	14	81.95
La Paulina	26° 1′51.59″S	Iguazú	Native forest		89.12
	54°24′30.72″O	(Misiones)	Tree plantation	30	89.33

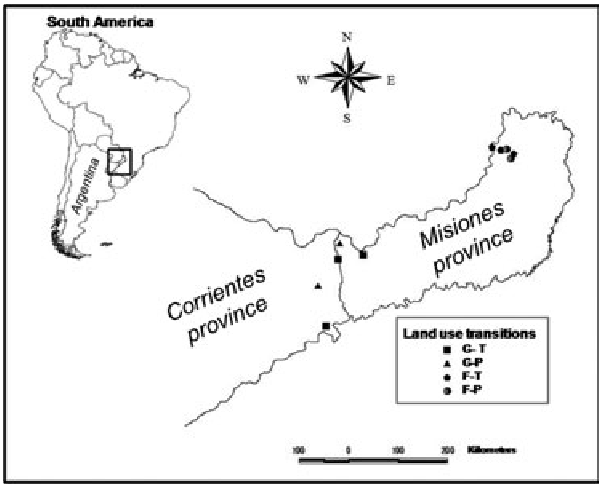

Fig. 1 Map showing the location of our field experiments. Land use changes included transitions from native forest to pasture (F-P), native forest to tree plantations (F-T) in the north, and native grasslands to tree plantations (G-T) and native grasslands to pastures (G-P) in the southern part of the study region.

measured for the same soils in nearby areas (Morrás & Piccolo, 1998). The similarity of soils between stands and therefore the correct selection of sampling sites was evaluated by comparing soil texture data between paired stands (Table 2). Observed differences in silt+clay contents between paired stands were always less than 5%.

Fine roots samples were sampled randomly in tree plantations and forests to a depth of 30 cm. Coarse and fine roots where separated by hand in the laboratory and only root diameters <5 mm where included in our analyses. In grasslands and pastures, root samples were taken using a 7 cm wide soil core down to 30 cm depth, at intervals from 0 to 10, 10 to 20, and 20 to 30 cm, three subsamples per stand. In all stands, three litter (plant material deposited on the soil surface, being visibly separately of mineral soil) subsamples were taken using a 25.5 cm wide ring. In forest and tree plantations, litter samples were collected excluding coarse-woody debris, but including the OH horizon. Roots and litter were separated from the soil by hand and oven dried at 60 °C for 24 h, and homogenized and ground to fine powder for chemical analysis. Carbon and N contents in roots and litter were also analyzed by dry combustion in a Carlo Erba Elemental Analyzer at Duke University.

Soil organic C and N contents in each fraction and depth were corrected to an equivalent soil mass to avoid overestimates of carbon stocks in compacted sites (Davidson & Ackerman, 1993; Henderson, 1995). The SOC contents (Mg ha^{-1}) for each soil fraction were estimated using the following equation:

$$\text{SOC} = \frac{\text{Wf} \times \text{CP} \times \text{BD} \times \text{Z} \times 100}{\text{Ws}} \tag{2}$$

where Wf is weight (g) of fraction (POM or MAOM), CP is C percentage for each fraction, BD is bulk density (Mg m^{-3}), Z is corrected depth (m), and Ws is total soil weight, prior to fractionation (g) (Sollins *et al.*, 1999; Solomon *et al.*, 2002). To isolate the soil compaction effect, the sampling depth of human modified systems (pasture or tree plantations) were corrected using the following equation:

$$Z = \left(\frac{\mathrm{BDn}}{\mathrm{BDp}}\right) \times X \tag{3}$$

where BDp is bulk density (Mg m^{-3}) of soils in planted systems, BDn is bulk density (Mg m^{-3}) of soils natural systems (grassland or forest) and X is the soil sampling depth (m) (Davidson & Ackerman, 1993; Solomon *et al.*, 2002).

Statistical Analysis

To analyze the effects of different factors (MAP, MAT, and plantation age) on SOC changes after the conversion of natural ecosystems to pastures or tree plantations at regional scale based on data published in literature, we constructed simple and multiple regressions models (see Table 3). To compare SOC, SON, and C : N ratios that occurred at different depths between grassland to pasture (G-P), grassland to tree plantation (G-T), forest to pasture (F-P), and forest to tree plantation (F-T) transitions (see Fig. 1), we used a paired design to consider the paired observations with different land uses (native vs. plantation or pasture). Statistical analyses were performed using a mixed model with spatial autocorrelation in depth to account for correlations between soil samples taken at consecutive depths in the same soil core. A spatial power structure was selected to define unequal intervals between successive depths (Sas Institute Inc., 1999). To correct the degrees of freedom we used the Kenward-Roger correction in the denominator (Spilke *et al.*, 2005). Significant differences were indicated with standard statistical nomenclature (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$ and †$p < 0.1$).

Table 3 Simple and multiple regression parameters of models relating SOC changes that occurred after converting native vegetation to pastures or plantations as a function of time since conversion (age), mean annual precipitation (MAP), and mean annual temperature (MAT)

	Model	Parameter	Values	Significance p value
Tree plantations	Simple regression models	Intercept	122	<0.001
		MAP (mm)	−0.08	<0.001
		r^2	0.48	
		Intercept	−31.2	0.049
		Age (years)	1.38	0.003
		r^2	0.28	
		Intercept	186	0.03
		MAT (ºC)	−10.0	0.03
		r^2	0.15	
	Multiple regression model	Intercept	78.74	0.013
		Age (years)	0.83	0.032
		MAP (mm)	−0.07	<0.001
		r^2 adjusted	0.54	
Pastures	Simple regression models	Intercept	−62.9	0.01
		MAP (mm)	0.04	0.002
		r^2	0.26	
		Intercept	−0.67	0.88
		Age (years)	0.70	<0.001
		r^2	0.47	
		Intercept	24.1	0.49
		MAT (ºC)	−0.37	0.80
		r^2	0.002	
	Multiple regression model	Intercept	−55.08	0.005
		Age (years)	0.62	<0.001
		MAP (mm)	0.03	0.005
		r^2 adjusted	0.57	

All models were significant ($p < 0.05$)

Results

Regional changes in SOC contents

Changes in surface SOC contents (0–20 cm depth) after plantation or pasture establishment varied with MAP and plantation age, but not with MAT (Fig. 2). Along MAP and plantation age gradients, tree plantation and pastures effects on surface SOC contents followed the same trend for all native vegetation types of native vegetation replaced (forest, grasslands, or savannas). Therefore, tree plantation and pastures effects on SOC were analyzed independently of the native vegetation replaced.

Changes in soil organic carbon were negatively associated with MAP in plantations but positively associated with MAP in pastures (Fig. 2a and c). All tree plantations lost SOC in sites where MAP was higher than 1200 mm, while only a few sites lost SOC in the first 20 cm of soil profiles under pastures across the precipitation gradient. Changes in SOC contents were positively associated with plantation age in tree plantations and pastures (Fig. 2b and d). All plantations younger than 20 years of age lost SOC whereas most of the older ones showed SOC gains, regardless of the native vegetation they replaced. Increases in SOC contents after vegetation replacement occurred earlier in pastures than in tree plantations, and only plantations older than 30 years showed similar or higher SOC contents than the native ecosystems (Fig. 2d). Nevertheless, the slope of the simple regression between age and percentage of SOC changes in pastures was 0.7% yr^{-1} while in plantations it was 1.4% yr^{-1} suggesting a greater and faster effect of age in tree plantations (Table 3).

Mean annual precipitation and time since conversion accounted for more than 50% of reported SOC changes under tree plantations or pastures (Table 3). Using a multiple regression analysis we estimated the age at which tree plantations or pastures reached native SOC contents for a given level of MAP

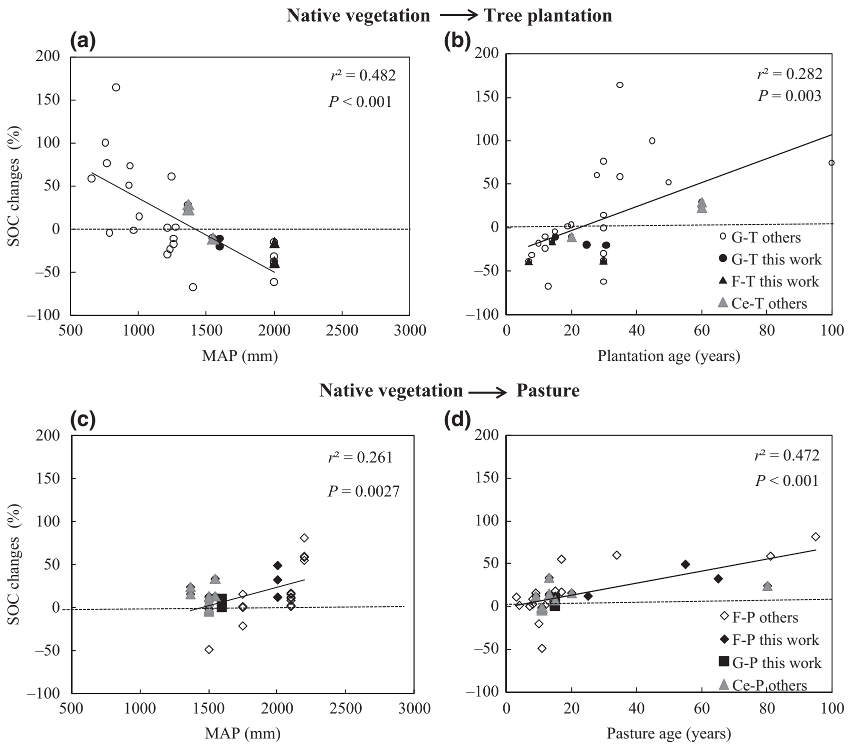

Fig. 2 Relationship between changes in SOC contents with mean annual precipitation (MAP) and with time elapsed (age) since the native vegetation was replaced by tree plantations (panels a and b) or pastures (panels c and d), for the first 20 cm of soil. G is grassland, F is forest, Ce is Cerrado a savanna ecoregion of Brazil, P is pasture, and T is tree plantation.

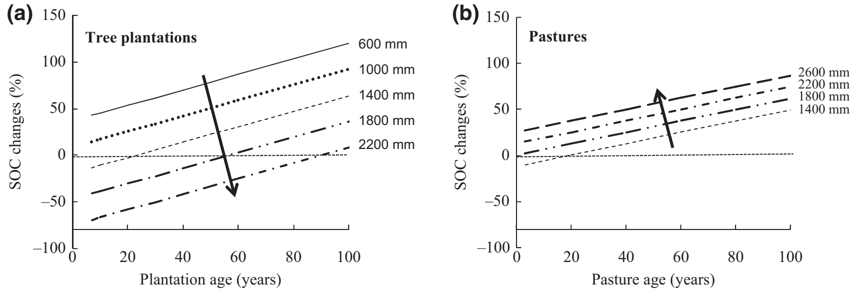

Fig. 3 Relationship between changes in SOC contents at different levels of mean annual precipitation (MAP) with age for (a) tree plantations and (b) pastures. Lines were constructed based on the multiple regression models presented in Table 3. The arrows indicate the direction in which MAP isohyets increase.

(Fig. 3). For example, at sites with 1400 mm of MAP, tree plantations reached native SOC contents 20 years after conversion, while at sites with 2200 mm MAP native SOC contents were reached after 100 years. In contrast, in sites with MAP lower than 1000 mm, SOC contents under tree plantations were greater than under native vegetation. Pasture responses were even greater across the precipitation gradient. In sites with 1400 mm of MAP, pastures reached native SOC contents after 20 years, as observed for plantations, but native SOC stocks were recovered earlier than 20 years in sites with MAP higher than 1400 mm, and SOC stocks under pastures were always greater than under native vegetation in sites with MAP 1800 mm or more.

Field Experiments

SOC and SON change after replacement of native forests or grasslands with tree plantations. In agreement with our regional literature review, SOC and SON contents in the first meter of the soil decreased after conversion of

Table 4 Total carbon and nitrogen contents and their changes under different land use trajectories for the first meter of the soil

	Native vegetation	Tree plantation	Difference	Rate of change (Mg ha^{-1} yr^{-1})	Native vegetation	Pasture	Difference	Rate of change (Mg ha^{-1} yr^{-1})
Sites with grasslands as native vegetation								
C-POM (Mg ha^{-1})	8.18	8.01	−0.17 ns	0.003 ns	9.35	12.27	2.92 ns	0.194 ns
C-MAOM (Mg ha^{-1})	164	145	-18.9^{*}	-0.789^{*}	157	159	1.98 ns	0.132 ns
SOC (Mg.ha^{-1})	172	153	$-19.0^{\dagger}$	$-0.786^{\dagger}$	166	171	4.89 ns	0.326 ns
N-POM (Mg ha^{-1})	0.30	0.32	0.02 ns	0.001 ns	0.45	0.47	0.02 ns	0.001 ns
N-MAOM (Mg ha^{-1})	13.7	12.4	$-1.3^{\dagger}$	$-0.051^{\dagger}$	13.4	13.6	0.2 ns	0.013 ns
SON (Mg ha^{-1})	13.9	12.7	$-1.2^{\dagger}$	$-0.050^{\dagger}$	13.9	14.1	0.2 ns	0.014 ns
C : N - POM	26.5	24.3	−2.22 ns		23.6	29.4	5.80 ns	
C : N -MAOM	12.1	11.9	−0.17 ns		11.6	11.5	−0.15 ns	
C : N SOM	13.1	12.8	−0.22 ns		12.3	12.7	0.44 ns	
Sites with forest as native vegetation								
C-POM (Mg ha^{-1})	17.5	8.1	−9.5 ns	−0.592 ns	7.5	9.7	2.2 ns	0.065 ns
C-MAOM (Mg ha^{-1})	163	140	-23^{*}	-1.975^{*}	134	124	−10 ns	−0.129 ns
SOC (Mg ha^{-1})	181	148	$-32^{\dagger}$	$-2.567^{\dagger}$	142	134	−7.8 ns	−0.064 ns
N-POM (Mg ha^{-1})	1.03	0.38	−0.65 ns	−0.039 ns	0.34	0.40	0.06 ns	0.002 ns
N-MAOM (Mg ha^{-1})	20.0	16.7	-3.3^{*}	-0.270^{*}	13.6	12.8	−0.84 ns	−0.011 ns
SON (Mg ha^{-1})	21.5	17.6	-4.0^{*}	-0.309^{*}	13.9	13.2	−0.8 ns	−0.009 ns
C : N - POM	17.4	21.1	3.64 ns		20.2	23.6	3.42 ns	
C : N -MAOM	8.15	8.51	$0.37^{\dagger}$		9.63	9.73	0.10 ns	
C : N SOM	9.03	9.20	0.17 ns		10.2	10.7	0.47 ns	

The symbols indicate the statistical nomenclature ($^{*}p < 0.05$, $^{\dagger}p < 0.1$ and ns: not significant). (see M&M)

the native vegetation to tree plantations, given that our study sites were on average 35 years old and that MAP was >1600 mm (Table 4). Unlike the regional review, SOC and SON losses were higher in tree plantations that replaced native forests than for those planted on native grasslands (Table 4). In both transitions, SOC losses occurred mainly in the MAOM fraction, which represented the largest contributor to total SOC (Fig. 4). The losses were 12 and 9% for C- and N-MAOM, respectively, when the previous land use was native grassland and 14 and 19% for C- and N-MAOM, respectively, in tree plantations that replaced native forest (see Table 4). In contrast, we found no major changes in the POM fraction when plantations replaced native grasslands. However, POM in the surface soils decreased by about half (54% C-POM and 63% N-POM, Table 4) when plantations replaced native forests (Fig. 4b). These results may in part be explained by initial C and N contents under native vegetation, as C-POM contents were greater under native forest (17 Mg ha^{-1}) than in native grasslands (8 Mg ha^{-1}), while C-MAOM contents were similar under both native vegetations (~160 Mg ha^{-1}) (Table 4). Finally, POM C : N ratios tended to increase in tree plantations established on native forests but decrease in tree plantations established on native grasslands (Table 4), although these results were only significant in the surface soil at native forest sites (Fig. 4). A similar but weaker pattern was observed in C : N of the MAOM fraction (Table 4 and Fig. 4).

SOC and SON changes after pasture replacement of forest or grasslands. Similar to our literature review, our field experiments showed that pastures increased or maintained SOC and SON contents in the surface soil layers when replacing either native grasslands or forests (Table 4). However, our field observations also revealed that deep (>30 cm) SOC and SON contents not analyzed in our literature review decreased when pastures replaced native forests (Fig. 5). Thus, when pastures replaced native forest, SOC contents increased in the surface soil but decreased below 30 cm, mainly in the MAOM fraction (Fig. 5). These opposite changes counterbalanced within the first meter of soil and therefore total SOC contents remained unchanged. Changes in SON followed the same trend as SOC in both soil fractions and when replacing both types of native vegetation, but N-POM changes were proportionally smal-

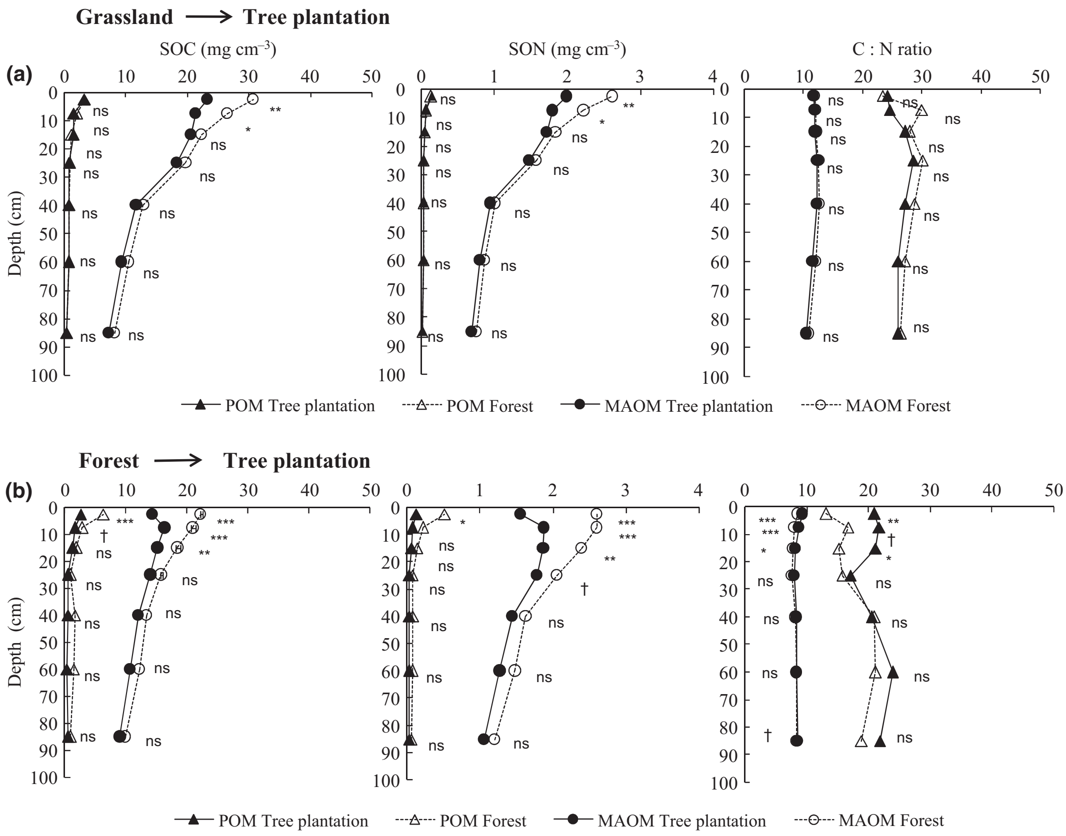

Fig. 4 Carbon and nitrogen contents and C : N ratios of two soil organic matter fractions (POM and MAOM) at different depths in adjacent stands of (a) native grassland vs. tree plantations (n = 3) and (b) Native forest vs. tree plantations (n = 3). Values for adjacent stands were compared for each depth interval using a mixed model (see M&M).

ler producing increases in the soil C : N ratios, particularly in the POM fraction (Fig. 5 and Table 4).

Changes in C : N ratios of litter and fine roots. The C : N ratio of fine roots and litter pools was equal or higher in pastures and tree plantations compared with the native vegetation they replaced, except for fine roots when tree plantations replaced native grassland (Table 5). The C : N ratios of litter and fine roots were lower in the northern portion of our study region (dominated by native forests), compared with the southern part (dominated by native grasslands), for both native and exotic vegetation. Fine root C : N ratios of tree plantations were similar to native forests and relatively low as in other tropical forests (Table 5). Grass-dominated ecosystems (grasslands and pastures) had always higher root C : N ratios than tree-dominated ecosystems (Forest and tree plantations), while litter C : N ratios were fairly similar among all ecosystems (except for native forest that showed lower values around 17) (Table 5). It is important to remind that both roots and litter were collected without coarse-woody debris to represent the C : N ratios of readily decomposable material.

Discussion

Our results show that the changes in surface soil organic carbon contents that occurred after replacing native ecosystems with tree plantations or pastures significantly varied with time since conversion, and mean annual precipitation. The SOC and SON stocks change after a land conversion only if either the inputs or outputs (or both) change during vegetation removal and establishment of the new vegetation. After a period of time, and in the absence of new disturbances, these fluxes reach a new equilibrium in which both inputs and outputs become equal and soil C and N stocks reach an approximately new steady state (Six *et al.*, 2002; Piñeiro *et al.*, 2006; Stewart *et al.*, 2008). Thus, C and N inputs or outputs to the soil most likely varied along the precipitation gradient studied and during the establishment of the new vegetation. Quantification of the relative importance of these two mechanisms

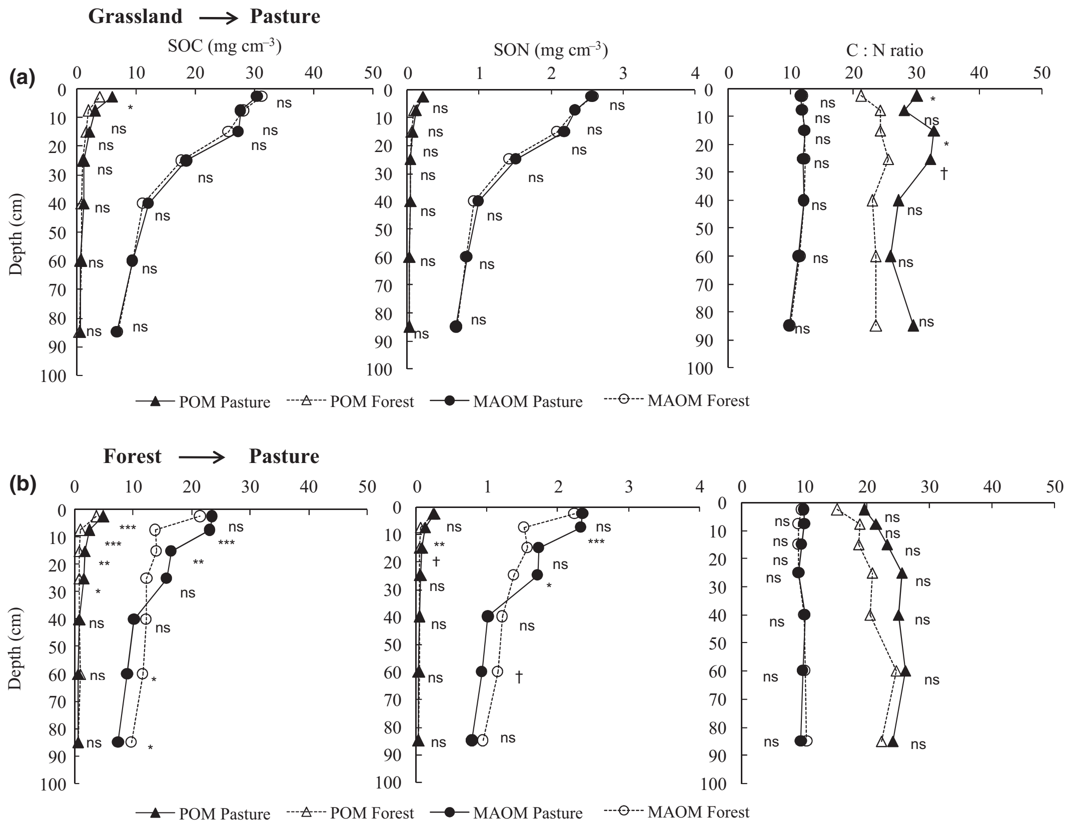

Fig. 5 Carbon and nitrogen contents and C : N ratios of two soil organic matter fractions (POM and MAOM) at different depths in adjacent stands of (a) native grassland vs. pastures (n = 3) and (b) native forest vs. pastures (n = 3). Values for adjacent stands were compared for each depth interval using a mixed model (see M&M).

Table 5 C : N ratios of litter and fine roots (<5 mm) in the different ecosystems studied

Zone	Ecosystems	C/N root	C/N litter
North	Native forest	29.2a	17.5a
	Tree plantation (*Pinus taeda*)	37.3a	42.6b
	Pasture (*Axonopus compressus*)	67.8ab	30.8ab
South	Native grassland	93.3b	40.2ab
	Tree plantation (*Pinus elliotii*)	67.8ab	50.7b
	Pasture (*Brachiaria brizantha*)	142c	49.5b

Different letters indicate significant differences ($p < 0.05$) between C : N ratios of fine roots and C : N ratios of litter between vegetation types.

(inputs vs. outputs) in SOC accumulation is a key factor to investigate but requires further research. In the following paragraphs, we will attempt to explain the potential factors that may have altered inputs and outputs of C and N to soil generating the observed changes in SOC and SON stocks.

Observed changes in SOC stocks along the precipitation gradient occurred following tree plantation establishment can be attributed to changes in C inputs to the soil due to changes in C uptake by the vegetation (the net primary production -NPP- of an ecosystem). Carbon inputs to the soil from native vegetation in arid sites are lower than in humid sites because productivity strongly increases with MAP (Burke *et al.*, 1997; Paruelo *et al.*, 1999). Productivity of tree plantations relative to the native vegetation they replace, are expected to be higher in arid rather than humid areas, as tree evapotranspiration is higher than in grazed grasslands producing large differences in productivity not so evident in humid sites where tree plantations replace native forest (Nosetto *et al.*, 2005, 2012). In addition, in arid sites where trees replace grazed grasslands, a big proportion of grasslands productivity is respired by grazers not reaching the soil (Paruelo *et al.*, 2010). These facts could explain our observed increases in SOC stocks in arid sites when plantations replaced low productivity grasslands and shrublands, and initial decreases in SOC stocks in humid sites where plantations replaced highly productive native forests with high initial SOC stocks.

The SOC increases observed with increasing plantation age can be explained by changes in tree productivity and C allocation with time. Several studies have found that aboveground net primary productivity in pine plantations peaks and then decreases at around 30 years, while belowground net primary production follows the same trend, but its reduction after 30 years is smaller than aboveground net primary productivity, increasing the relative proportion of C allocated to roots (Gholz & Fisher, 1982; Gower *et al.*, 1996; Ryan *et al.*, 1997). In addition, during initial stages of tree growth a large proportion of net primary production is accumulated in tree biomass and only a small proportion of net primary production reaches the soil and feeds soil biota (Odum, 1969; Gholz & Fisher, 1982). Overall, as trees age they increase their net primary production, the relative proportion of C allocated to roots, and the proportion of net primary production that reaches the soil, all factors that increase C inputs to the soil potentially increasing soil stocks. In agreement, several authors have observed positive trends in SOC stocks with increasing plantation age (Lugo & Brown, 1993; Guo & Gifford, 2002; Paul *et al.*, 2002).

Finally, some studies suggest that SON is the primary control of SOC losses, although its mechanisms are still under debate (Kirschbaum *et al.*, 2008a,b; Parfitt & Ross, 2011). Thus, in humid areas, N losses by decomposition and leaching may limit SOC accumulation in tree plantations (Kirschbaum *et al.*, 2008b). The SON present in labile fractions (N-POM) can be easily mineralized (Alvarez & Alvarez, 2000), and therefore, is likely to be lost through leaching. Consistent with this hypothesis, our results showed a decrease in C-POM and N-POM, and increases in C/N-POM in tree plantations that replaced native forests in humid sites, and we did not observe this trend in tree plantations established on drier grasslands as N leaching is probably less important there.

Our results show that surface SOC contents increased after sowing pastures regardless of the native vegetation replaced, probably associated with pasture's higher surface root production. The positive correlation of precipitation with SOC after planting pastures found in our regional review may be due to an increase in pasture productivity with MAP (Le Houerou & Hoste, 1977) or to changes in C allocation to roots that may increase SOC formation. Trumbore *et al.* (2006) found greater amounts of roots in the top 10 cm of soil, and also higher fine root production, in pastures (25–91 g C m^{-2} yr^{-1}) than in native forests (16–53 g C m^{-2} yr^{-1}). However, Guo & Gifford (2002) observed in a global review that pastures decreased SOC contents when replacing tropical forests with MAP between 2000 and 3000 mm. These MAP values are on the wet end or outside our MAP range but suggest a potential decrease in SOC contents under pastures sown in sites with very high precipitation.

While pastures increased surface SOC contents in most sites that we reviewed, our field studies also showed that pastures lose SOC in deep soil layers when planted on native forests, offsetting surface gains and thus maintaining SOC contents summed to one meter depth. Consistent with our results, the few studies that have evaluated SOC contents in both shallow and deep soil layers (up to 1 m of soil) found no differences between pasture and forest sites (Koutika *et al.*, 1997; Roscoe *et al.*, 2001; Richards *et al.*, 2007). These authors suggest that decreases in C allocation to deep roots under pastures relative to native forests may decrease SOC and SON contents in deep soil layers. In contrast, Fisher *et al.* (1994) suggested that the elevated production of deep roots in pastures increased SOC accumulation under pastures compared with native savannas of the Brazilian Cerrado. These opposite trends in deep soil layers may be associated with differences in soil types that determine C cycling and C retention by clay and silt particles or to differences in belowground production between different pasture species or native vegetation types (Paul *et al.*, 1997; Jobbagy & Jackson, 2000; Trumbore, 2000).

Finally, our detailed field analysis suggests that SOC gains that occurred early after sowing pastures were associated with changes in POM fraction, while further increases in SOC are associated with C stabilization in MAOM fraction. Cerri *et al.* (1991) observed that initial SOC losses caused by plowing and sowing pastures are usually restored in about 8 years. Several studies have observed increases in SOC contents with pasture age, but the causes of this trend are not yet clear (Feigl *et al.*, 1995; Moraes *et al.*, 1996; Koutika *et al.*, 1997; Cerri *et al.*, 2004; Desjardins *et al.*, 2004; Lisboa *et al.*, 2009). Our results show that long-term SOC accumulation occurred in the MAOM fraction and suggest that pastures rapidly come to a balance between C inputs and C outputs in POM fraction, while C continues to accumulate in old pastures until an equilibrium is reached in the MAOM fraction in longer time frames. Interestingly, changes in plant C : N ratios (fine roots and litter) were mirrored by POM- C : N ratios, but not by the MAOM fraction, where C : N ratios remained unchanged after vegetation replacement, suggesting the relative constant stoichiometry of C and N in this fraction.

Our results highlight the importance of precipitation, age, and soil depth in controlling the magnitude and direction of soil changes after replacing natural vegetation with tree plantation or pastures in southern South America. Our main findings are:

1. Mean annual precipitation had opposite effects on SOC changes, increasing SOC gains after sowing pastures but increasing SOC losses after planting trees.
2. As pastures and tree plantation aged SOC stocks increased.
3. Soil depth was important for assessing soil carbon changes only when natural forest were replaced by pastures, since C losses were observed in deep soil layers that counterbalanced C gains in surface soil layers.
4. Decadal changes in SOC stocks occurred mainly in the silt and clay size fraction (C-MAOM).

These results can help aid the design of sustainable management practices at sites with different precipitation regimes, particularly in the case of afforestation expansion in the region. For example, our results suggest that clear-cut rotations should be longer in sites with higher annual rainfall to gain back the SOC lost with planting. In addition, pasture establishment typically increased SOC contents in surface horizons but the balance in deeper soil layers is strongly affected by the native vegetation being replaced and the vertical distribution of roots, which could result in SOC losses in deep soil layers when converting native forests to pastures.

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