



Shifting carbon pools along a plant cover gradient in woody encroached savannas of central Argentina



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ABSTRACT

Woody plant encroachment is a widespread process of land cover change driven by a combination of local land use practices and regional to global environmental changes. Increases in woody plant cover alter the distribution of carbon in the ecosystem and can affect water and nutrient cycling. Although semiarid rangelands comprise almost half of the global land surface, our understanding on the effects of woody plant encroachment on carbon stocks in these ecosystems is uncertain – studies have found both net C gains and losses. We measured, for the first time in South American semiarid savannas, ecosystem C stocks along a gradient of woody plant density across 30,000 km² of the Caldenal in central Argentina. We characterized changes in C stocks in live biomass (woody and herbaceous, above- and belowground), litter, and soil organic carbon (to 1.5 m depth) pools along a woody plant cover gradient (0–94%). We found a significant increase in ecosystem C stocks with increasing woody cover, with mean values of 4.5, 8.4, 12.4, and 16.5 kg C m⁻² for grasslands, shrublands, open and closed forests, respectively. Using dendrochronological data we estimated the average C accrual rate to be 104 g C m⁻² yr⁻¹ at the ecosystem (plant + soil) level. Woody plant cover and soil silt content were the two primary factors accounting for the variability of ecosystem C. We developed simple regression models that reliably predict soil, tree and ecosystem C stocks from basic field measurements of woody plant cover and soil silt content. These models could prove to be valuable tools for broad scale estimation if linked to regional soil maps and remotely sensed data, allowing for precise and spatially explicit estimation of C stocks and change at regional scales.

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1. Introduction

Land cover changes in terrestrial ecosystems not only generate changes locally, they also affect the global system through changes in energy fluxes and element cycles, including changes in greenhouse gas concentrations and radiation balance (Charlson et al., 2005). Rangelands comprise almost 45% of the global land surface (Bailey, 1996), and changes in their cover can significantly influence global climate (Rotenberg and Yakir, 2010). For the last 150 years, increases in woody plant cover (WPC) have been observed in arid and semiarid regions worldwide (Van Auken, 2000; Asner et al., 2004). Given current trends and potential extent of encroachment, significant shifts may be occurring in the global

carbon (C) cycle. For example, Houghton (2007) estimated that 40–70% of the net terrestrial C sink in the continental US corresponds to woody plant encroachment (WPE), especially across semiarid grasslands. However, little is known about the implications of this land cover change on ecosystem C stocks in other regions of the world, especially in the southern hemisphere.

Woody plant encroachment is the process of an increase in woody plant density, and is considered one of the most threatening forms of rangeland degradation (Briggs et al., 2005). Woody encroachment is a widespread process occurring in Australia (Fensham et al., 2005; Robinson et al., 2008), Africa (Roques et al., 2001; Augustine and McNaughton, 2004; Sankaran et al., 2005; Wigley et al., 2009), Europe (Anthelme et al., 2007), North America (Glendening, 1952; Asner et al., 2003) and South America (Cabral et al., 2003; Dumig et al., 2008; Silva and Anand, 2011). Given its worldwide occurrence, it has been suggested to be a consequence of global drivers such as the recent increases in atmospheric CO₂ (Harrell and Fuhlendorf, 2002; Wigley et al., 2010;

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Donohue et al., 2013), but local drivers, such as introduction of cattle and changes in fire regimes, seem to be important as well (Archer et al., 1995; Asner et al., 2004).

Although considerable attention has been given to the causes of woody encroachment, less is known about its consequences on ecosystem functioning. A recent meta-analysis found that it had mixed effects on ecosystem structure and functioning at global scales, and that specific shrub traits influence the functional outcome of encroachment (Eldridge et al., 2011). Despite numerous studies in North America, Australia and Africa, it is not clear if areas with higher woody plant density due to woody plant encroachment function as net carbon sinks or sources. Aboveground C stocks typically increase as a consequence of the replacement of grasses by woody species (Eldridge et al., 2011), but differences emerge when the soil component is included. In the southwestern US, wooded areas in Texas increased the rate of accumulation of soil organic C (SOC) by 100–500% as compared to grasslands (Liao et al., 2006), resulting in a significant increase in landscape-scale ecosystem C stocks (Hibbard et al., 2003). In Arizona, soils under shrubs contained twice as much C as surrounding grass sites (Cable et al., 2009). However, Hughes et al. (2006) found that although aboveground C pools increased substantially with *Prosopis* tree stand development, no such change was found in surface soil C pools (0–10 cm depth). Along a rainfall gradient in North America, Jackson et al. (2002) found that while drier sites were gaining SOC, wetter sites were losing it. Moreover, the losses of SOC at wetter sites were substantial enough to offset the increase in aboveground C. In Africa, WPE generated a low gain in ecosystem C stocks, suggesting that the process is very slow (Coetsee et al., 2013). This variability demonstrates the site- and scale-specific nature of results and the need to measure different components of the soil C pool to assess the net ecosystem effect of WPE on carbon storage. Studies of C stocks across different levels of shrub and tree density are scarce in South American savannas, which represent ~20% of the global total area occupied by this biome (Olson et al., 2001).

Most studies assessing C stocks for different levels of woody plant density have been measured at relatively fine scales, ranging from hectares to a few square km. To complement such studies, regional assessments are needed to evaluate the effects of WPE at broad scales. In this study, we assessed C stocks along a woody cover gradient in central Argentina (30,000 km²) by assessing woody and non-woody vegetation, litter and soils. Our objective was to examine regional C patterns in order to increase our understanding of WPE consequences in semiarid savannas and to develop models that could be used by managers to estimate C stocks at the local or regional levels.

2. Materials and methods

2.1. Study area

The 30,000 km² study area is located in the northern section of the Caldenal savannas of central Argentina (Fig. 1). The Caldenal is a semiarid savanna ecosystem dominated by the *caldén* tree (*Prosopis caldenia*) with an understory of perennial grasses frequently interspersed with dunes, wetlands and lagoons (Cabrera, 1994). The climate is temperate with mean annual temperature of 15 °C; mean monthly temperature of the hottest and coldest month is 24 °C and 8 °C, respectively (Cano et al., 1980). The region is flat or slightly rolling and is formed mainly of a deep mantle of loessic sediments (Soriano et al., 1991). Edaphic great groups found in this region are Entic Haplustolls towards the east and Ustic Torripsamments towards the west (INTA, 2014). The area is characterized by a SW–NE rainfall gradient ranging from 400 to 700 mm/yr

across 150 km. Rainfall is concentrated in summer months, but it is not enough to compensate atmospheric demands, resulting in year-round water deficits (Cano et al., 1980).

Major changes occurred in the area with the arrival of settlers at the end of the 19th century and have intensified since then (Alonso, 2009). These changes include replacement of natural systems with agriculture, extractive logging, introduction of non-native species, overgrazing by livestock, and alteration of fire regimes (Amieva, 1993; Mendez, 2007). In areas not converted to agriculture, native woody plants have been documented to encroach both in savannas, where woody plant density increases (Lell, 2004; González-Roglich et al., 2012b), and in grasslands (Echeverria and Giulietti, 2002; González-Roglich et al., 2012a), where woody plants had been absent, at least at end of the 19th century when European settlers arrived. *Caldén* woodlands have encroached in ~12,000 km² of grasslands (14% of the area) in the last 120 years, and in the last 60 years the spatial pattern of the originally open savannas has changed to a mosaic of agriculture and dense woodlands (González-Roglich et al., Unpublished). The increase in woody plant cover has been mostly attributed to local management, mainly due to changes in fire regime and grazing (Dussart et al., 1998; Esterlich et al., 2005; Medina, 2007). It is necessary then to understand the consequences of such an extended structural change in these semiarid savannas have on ecosystem C stocks at the regional level.

2.2. Study design

To determine the effect of WPE on ecosystem C stocks, 35 50 × 50-m sites representing a gradient in WPC from grassland to closed forest were surveyed in the 2012–2013 Summer months. Sites were grouped in clusters of five with distances <10 km among the sites within a cluster (Fig. 1). Clusters were distributed within the study area to maximize representation. Each cluster contained at least one grassland, shrubland, open and closed forest site. Since management is an important factor influencing WPE (Naito and Cairns, 2011), sites within a cluster were located, in most cases, in the same ranch (mean ranch size = 49.5 km², standard deviation = 25.6 km²) in an effort to control for the effect of different cattle and fire management regimes, which were assumed to be more constant within each individual property than among different ranches.

For woody plants, two 50 × 5-m belt transects were established per site. All woody plant material, alive and standing dead, whose stems emerged within the belt were surveyed, recording species, diameter at the base of the main trunk (defined as the tallest), diameter at ground level of the group of stems when more than one were present, height and crown radii (the longest radius and its perpendicular). Each site was later assigned to a specific woody cover type based on indices derived from field data. Mean crown area (m²) was multiplied by plant density (number per m²) to compute shrub (SCI) and tree cover (TCI) indices, defining classes as follows: grassland (TCI < 0.3 and SCI < 0.2), shrubland (TCI < 0.3 and SCI > 0.2), open forest (0.3 < TCI < 0.6), and closed forest (TCI > 0.6).

Woody plants <3.2 m in height were considered shrubs, and >3.2, trees. Species-, genus- or plant form-specific allometric equations were used to estimate above ground biomass per plant (Hierro et al., 2000; Belmonte Serrato and Lopez-Bermudez, 2003; Iglesias and Barchuk, 2010; Risio Allione, 2012; Conti et al., 2013). For *P. caldenia*, the most common species encountered, we produced a revised allometric equation, based on two existing models: (1) a species-specific model for small to medium sized trees (Risio Allione, 2012), and (2) a general equation for larger mesquite trees (Jenkins et al., 2003). Below ground biomass was estimated as 35% of above ground woody plant biomass, as has been determined for *P. caldenia* in this region (Risio Allione, 2012). Fine roots (<2 mm) were not accounted for in this study.

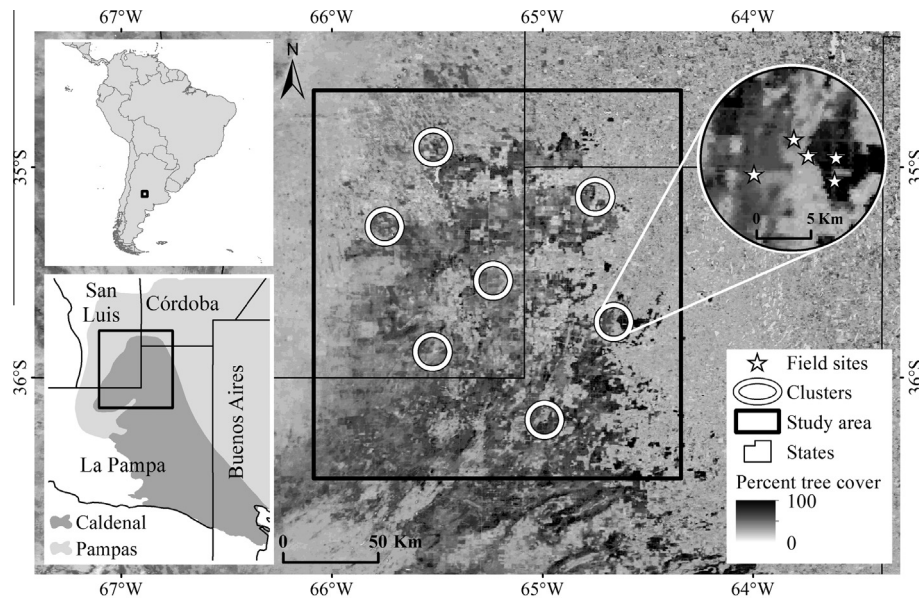


Fig. 1. Seven clusters were established in the study area in the semiarid savannas of central Argentina. Each cluster contained five sites representing a woody cover gradient, ranging from grassland to closed forest. The two clusters to the northwest of the study area are located on Ustic Torripsaments while the other five are on Entic haplustolls. Percent tree cover was derived from the MODIS Vegetation Continuous Fields product Collection 5 version 1 from 2009.

Based on biomass distribution among the different structural components of *P. caldenia* (Risio Allione, 2012) we assumed biomass of standing dead woody plants to be 25% of that of the alive above-ground biomass for the same species. Given the uncertainty on its estimation and the relatively small size of the pool, we did not estimate belowground biomass of dead trees. To estimate carbon content from biomass, we used conversion factors for closely related species (de Petre et al., 2005; Northup et al., 2005), which ranged from 0.44 to 0.48 g of C per g of dry biomass.

Grass, herb and fine litter biomass were estimated in three 0.6 m² (0.3 m by 2.0 m) randomly located quadrats per site. Above-ground biomass of grasses and herbs was collected by clipping at ground level the standing component. Plant tissues easily identifiable as leaves and twigs lying on the floor were collected as the fine litter component. Samples were oven dried to constant weight. Below ground biomass for grasses was estimated using a 7:1 root to shoot ratio developed for central Argentine rangelands (Busso, 1997). Conversion factors of 0.41, 0.42 and 0.41 g of C per g dry biomass were used for aboveground, belowground and litter biomass, respectively (Andrioli and Distel, 2008).

Woody plant cover was estimated using a spherical densiometer (Lemmon, 1956) at 1.2 m above ground level. Densiometer readings were converted to percent woody plant cover, and averaged at the site level. To estimate the age of the presumably oldest trees in the site, increment core samples were taken from the five trees with largest diameter at breast height. Samples were mounted on wood supports, sanded, scanned to a resolution of 1200 dpi and then rings were counted on screen. The age of the plant was estimated as the number of rings plus 5 years, time estimated for *P. caldenia* to achieve that height. The age of the oldest tree in each site was assumed to indicate the beginning of the encroachment process, and used to estimate the annual rate of C accrual for SOC, biomass C and total ecosystem C.

Soil samples were collected from three locations per site positioned at 20 m from the center of the site, oriented at 90, 210 and 330 degrees clockwise from the magnetic north. At each location, a 70 cm wide and 70 cm deep pit was dug. Soil organic horizon (SOH), 0–10 cm, 10–30 cm, and 30–50 cm soil samples were collected from the south facing wall of the pit to estimate SOC. A manual auger of 10 cm diameter was used take samples at

85–100 cm and 135–150 cm depths. At the first three depths, another set of samples were collected using a metal frame of known capacity to estimate bulk density air drying soil samples for a week at room temperature, and then at 100 C until constant weight (48–72 h). Soil texture was determined for each site from the 0–10 and 30–50 cm deep samples (Bouyoucos, 1962). Samples for C estimation were air dried, sieved using a 2 mm mesh, pooled at the site level for each depth and analyzed with a CE Instruments NC2100 elemental analyzer (ThermoQuest Italia, Milan, Italy). Carbon concentrations and bulk density were used to estimate organic C mass per unit area (kg C m⁻²). Regression models were built for each site to interpolate C content for unsampled sections of the soil profile (50–85 and 100–135 cm deep). Total ecosystem C stock for each site was estimated by aggregation of each of the individual components.

ANOVA tests were used to assess the similarity in environmental conditions (i.e., mean annual rainfall, elevation, slope, soil texture, latitude and longitude) among land cover classes. When variables did not meet normality assumptions, natural log transformations were applied. To assess the effect of WPC on the different components of ecosystem C stocks, ANOVA tests were used. Two groups of tests were performed, one using the absolute C stocks of each component, and the other using the difference between each C stock along the woody cover gradient and its reference condition (i.e. the grassland site within the same cluster). Linear regression models were used to determine the effect of woody plant cover on the different C pools. Multiple linear regression models were built to predict the stocks in the larger C pools along the woody cover gradient (i.e. soil organic C, tree C and ecosystem C). We used Akaike's Information Criterion (Akaike, 1974) with small-sample bias adjustment (AICc) and respective AIC weights for model selection. When the selected best model had multiple variables, we also present individual models to better understand the individual contribution of each variable and their interactions.

3. Results

Closed forests have on average 12.0 kg m⁻² additional C than grasslands, 8.5 kg C m⁻² more than shrublands and 4.6 kg C m⁻²

more than open forests, with the difference between forest types not significant (Fig. 2). The increment in total ecosystem C was positively correlated with SOC, tree C, SOH and fine litter ($r > 0.6$ in all cases). Of the total C stock increment observed along the wood cover gradient, most of the change was due to increases in SOC and tree C. Structurally, grasslands were characterized by low density of woody plants, shrublands by the dominance of woody plants shorter than 3.2 m, and forests by the abundance of trees, present at higher densities in closed forests than in open forests (Table 1). By design, woody plant cover, our proxy for encroachment progression, was significantly different between the four cover classes ($P < 0.01$) with mean values of 74.2% for closed forest, 39.5% for open forests, 13.1% for shrublands, and 0.1% for grasslands. The mean age of the largest trees in open and closed forests were 85–90 years respectively (difference not significant). Using the ages of the oldest trees in each site we estimated mean annual C accrual rates of $65.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ for SOC (± 62.3 st. dev.), 34.4 for biomass C (± 21.1 st. dev.), and $104.2 \text{ g C m}^{-2} \text{ yr}^{-1}$ for total ecosystem C (± 79.5 st. dev.).

We found SOC to be the single largest C pool along the woody cover gradient, representing between 63% (closed forests) and 71% (shrublands) of the total ecosystem C stocks. Mean SOC content (to 1.5 m depth) increased along the woody cover gradient, from 3.0 kg C m^{-2} in grasslands up to 10.4 kg C m^{-2} in closed forests (Table 2). The soil organic horizon was absent in grasslands, and the significance of its C content increased with WPC representing

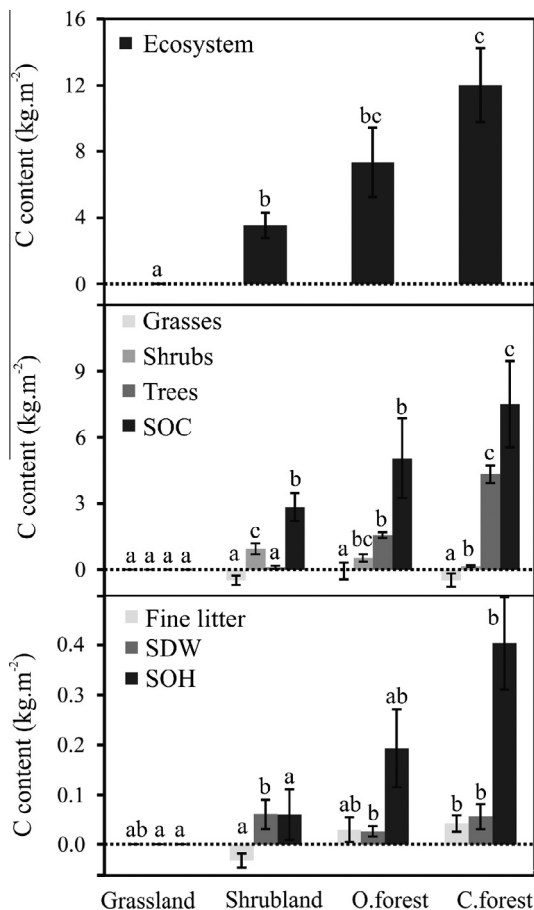


Fig. 2. Mean change in C stocks along the woody cover gradient. Grasslands represent the reference condition for each cluster (i.e. zero value for each C stock in each cluster). Values represent means and error bars standard errors of the mean. Different letters at the top of each bar indicate statistically significant differences in C stocks among land cover classes.

Table 1

Structural characteristics of the woody plants (i.e., shrubs and trees) along the woody cover gradient. Values represent means \pm standard deviations.

		Grassland	Shrubland	Open forest	Closed forest
Shrubs	Plants/ha	92 \pm 98	2180 \pm 1521	1475 \pm 1050	1131 \pm 1099
	Height (m)	1.1 \pm 0.4	1.5 \pm 0.2	1.6 \pm 0.2	1.5 \pm 0.3
Trees	Plants/ha	7 \pm 15	65 \pm 127	239 \pm 213	710 \pm 571
	Height (m)	3.6 \pm 0.3	4.1 \pm 0.5	5.7 \pm 1.2	6.1 \pm 1.5

on average 2.5% of the total ecosystem C pool in closed forest. The mean absolute amount of C in grasses decreased on average almost 30% from grasslands to closed forests, but differences were not statistically significant. In relative terms the importance of grasses also decreased, from 30% of the total ecosystem C stock in grasslands to 6% in closed forests. Fine litter and standing dead woody plants were minor components ($< 3\%$) in all land cover classes. Both in absolute and relative terms, C content of woody plants in shrubby forms was highest in shrublands (0.9 kg C m^{-2} , representing 11% of the total ecosystem C stock). Tree C stocks increased along the woody cover gradient, to a maximum of 4.3 kg C m^{-2} in closed forest. Total ecosystem C stocks on average increased fourfold along the woody cover gradient, from 4.5 kg C m^{-2} in grasslands to 16.5 in closed forests.

Along the woody cover gradient, we found that over 80% of the variability in ecosystem C and SOC was explained with field measured WPC and soil silt content in the first 10 cm of the mineral soil horizon (Table 3). Interactions between the variables did not add significant explanatory power to the models. Tree C was mostly explained by WPC, accounting for 65% of the variability. At the regional level, we found positive and significant relationships between soil silt content and total ecosystem C for the four land cover types (Fig. 3). Moreover, for each given level of soil silt content, there was higher ecosystem C content in closed forests, decreasing the C content along the woody cover gradient, with the lowest values in grasslands. For rainfall, we found a general positive trend with increasing ecosystem C at wetter sites, but the relationship was only statistically significant for shrublands and open forest, with grasslands and closed forest showing low and insignificant regression coefficients.

We found no statistically significant difference among cover classes in elevation, soil texture, latitude, longitude or mean annual rainfall. However, grasslands were located on average on sites with steeper inclination ($2.4 \pm 1.7\%$ for grasslands and $1.0 \pm 0.6\%$ for woodlands, $P = 0.01$). Even when sites on steeper inclination have been found to contain less SOC (Ritchie et al., 2007), we found no statistically significant relationship between slope and SOC ($P = 0.47$).

4. Discussion

In this study, the first of its kind for South American semiarid savannahs, we found that closed woodlands have three times more total ecosystem C than grasslands. Given the widespread occurrence of woody plant encroachment in this region and globally, this could have important implications for the global terrestrial C balance. This gain was $\sim 12 \text{ kg C m}^{-2}$ from grasslands to dense woodlands, similar to values found in encroached areas of central Brazil (Pellegriani et al., 2014) and South Africa (Coetsee et al., 2013). The rate of ecosystem C accrual we found, of approximately $100 \text{ g C m}^{-2} \text{ yr}^{-1}$, is also similar to those found for North American ecosystems similarly encroached by another *Prosopis* species (Barger et al., 2011), indicating a consistency across regions. We found that the increase in ecosystem C stocks was driven primarily by an increase in SOC and woody plant biomass. Carbon stored in the woody components of shrubs and trees increased significantly

Table 2

Carbon stocks (mean \pm standard deviation, kg C m⁻²) in the different pools: soil organic carbon (SOC), soil organic horizon (SOH), grasses, fine litter, standing dead woody plants (SDW), shrubs, trees, and total ecosystem C stock. The contribution (%) of a given pool to the ecosystem total is presented in brackets for each land cover class.

	Grassland		Shrubland		Open forest		Closed forest	
SOC	3.05 \pm 2.06	(67.5)	5.96 \pm 2.91	(71.0)	8.73 \pm 6.57	(70.1)	10.37 \pm 7.26	(63.0)
SOH	0.00 \pm 0.00	(0.0)	0.06 \pm 0.14	(0.7)	0.19 \pm 0.23	(1.6)	0.40 \pm 0.31	(2.5)
Grasses	1.37 \pm 0.73	(30.2)	1.17 \pm 0.49	(14.0)	1.28 \pm 0.67	(10.3)	1.00 \pm 0.61	(6.1)
Fine litter	0.07 \pm 0.03	(1.5)	0.05 \pm 0.02	(0.6)	0.10 \pm 0.06	(0.8)	0.10 \pm 0.05	(0.6)
SDW	0.00 \pm 0.00	(0.0)	0.06 \pm 0.08	(0.7)	0.03 \pm 0.03	(0.2)	0.06 \pm 0.08	(0.3)
Shrubs	0.01 \pm 0.02	(0.3)	0.94 \pm 0.65	(11.3)	0.53 \pm 0.50	(4.3)	0.16 \pm 0.15	(1.0)
Trees	0.02 \pm 0.04	(0.4)	0.10 \pm 0.22	(1.2)	1.56 \pm 0.38	(12.6)	4.32 \pm 1.36	(26.3)
Ecosystem	4.52 \pm 2.34		8.33 \pm 3.16		12.42 \pm 6.92		16.42 \pm 8.06	

Table 3

Best models (in bold) predicting SOC, tree C and ecosystem C for the pooled data across land cover types, based on Akaike's Information Criterion with small-sample bias adjustment (AIC_c) and AIC weights (AIC_cWt). When the best model included more than one variable, individual models and interactions are also presented.

Response	WPC	Silt	WPC * Silt	Int	Adj R ²	K	AIC _c	ΔAIC _c	AIC _c Wt
ln.soilC	1.073	0.049		0.261	0.81	4	33.53	0.00	0.77
ln.soilC	1.139	0.050	-0.003	0.239	0.80	5	36.23	2.70	0.20
ln.soilC		0.055		0.530	0.64	3	53.51	19.97	0.00
ln.soilC	1.449			1.162	0.29	3	77.24	43.70	0.00
ln.treeC	2.561			-0.582	0.65	3	25.64	0.00	0.41
ln.ecosC	1.785	0.041	-0.021	0.848	0.86	5	12.33	0.00	0.56
ln.ecosC	1.340	0.033		0.997	0.85	4	12.99	0.66	0.40
ln.ecosC	1.594			1.607	0.52	3	51.84	39.51	0.00
ln.ecosC		0.040		1.333	0.48	3	54.62	42.29	0.00

ln.soilC: natural logarithm of SOC in kg C m⁻².

ln.treeC: natural logarithm of tree C in kg C m⁻².

ln.ecosC: natural logarithm of ecosystem C in kg C m⁻².

WPC: percent woody plant cover.

Silt: soil percent silt content.

Int: intercept.

K: number of parameters in the model, including intercept.

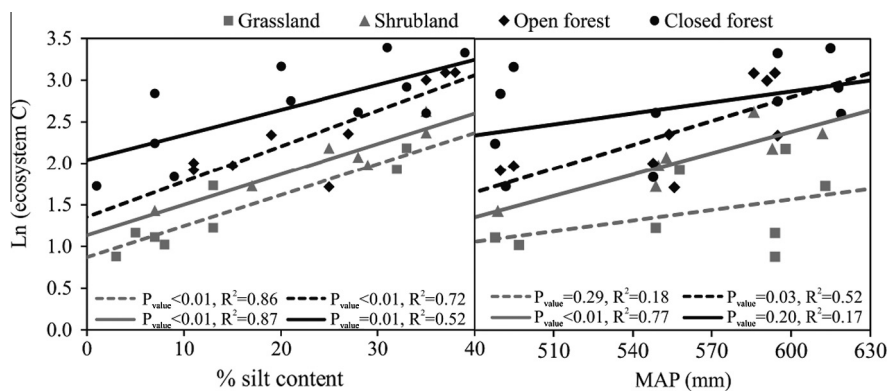


Fig. 3. Relationship between ecosystem carbon stocks and soil silt content (left panel), and mean annual rainfall (right panel). The effect of woody plant cover on ecosystem C stocks is depicted by the regression lines, presenting similar slopes for the different land covers, but being shifted upward (i.e. more C content) as grasslands are replaced by shrublands, and finally shrublands by forest stands.

with woody plant cover, but never represented more than 30% of the total ecosystem C stock, most of which was in the soil C pool (range 63–71%), as expected for semiarid ecosystems (Blanco and Lal, 2010).

Total ecosystem C stocks have been found to depend on four main factors: precipitation, soil properties, vegetation type and management, (Derner and Schuman, 2007). The clustered design allowed us to assess the effect of woody plant cover on ecosystem C stocks in semiarid savannas while minimizing the effect of the other three factors. We consider that by selecting clustered sites as close as possible to each other (<10 km), and when possible in the same rural property, the effect of differential management within each cluster was minimized. We acknowledge that this

assumption could be violated, but there are few options when designing a regional scale study in an area with high levels of turnover in ownership and management of the privately owned rural enterprises like this region.

Our results indicate a net gain in ecosystem level C stocks along the woody cover gradient, and a significant proportion of that gain is due to increases in SOC. Field data from North America indicate that the increase in SOC in encroached sites is a function of woody patch age (Archer et al., 2004). If we consider the woody cover gradient as a proxy for encroachment gradient, then the increase SOC we found for this region with changing woody cover would support this notion. However, given that we did not find significant differences in the age of the largest trees between open and closed

forests, we cannot confirm this temporal trend. There are at least three important mechanisms driving SOC accumulation following WPE into grasslands that have previously been hypothesized (Boutton et al., 2009): (i) higher rates of net primary productivity (NPP) in wooded areas relative to grasslands; (ii) increased biochemical recalcitrance of litter inputs in wooded areas; and (iii) physical protection of organic matter inputs within the soil structure. Changes from grasslands to woodlands often increase above-ground NPP (Barger et al., 2011), augmenting the litter fall input to the soil and potentially making the SOC stock larger over time (Knapp et al., 2008; Strand et al., 2008; Throop and Archer, 2008). We did not directly measure NPP in this study, but both the increase in total plant biomass present in the ecosystem, and in the soil organic horizon along the woody cover gradient, suggest that the increase in NPP is a likely mechanism driving the increase found in SOC. The recalcitrance of the organic matter depends on the lignin and aliphatic biopolymers content in the original plant tissue (Kogel-Knabner, 2002). Recent studies in subtropical savannas of North America found that in wooded areas the content of substituted fatty acids (a proxy for the relatively resistant biopolymers) was 4–7 times higher than in grassland litter (Boutton et al., 2009), providing evidence for this mechanism as a driver of increased SOC after WPE.

The accumulation of SOC is due to both increased inputs of newer woodland-derived C and the retention of older, stabilized grassland-derived C. Approximately 30–55% of the SOC that accumulates following WPE is stabilized by physical protection in macro- and micro-aggregates, and by association with silt and clay (Boutton et al., 2009). Given that clay content in this region is very low and has little variability (between 2% and 5% for all sites), we used silt content in the first 10 cm of the profile as an indicator of soil properties (no major textural differences were found along the soil profile in any of the sites). Even though we did not directly measure the forms of stabilization of organic matter in the soil, we did find significant and positive relationships between soil silt content and SOC (Fig. 3), which could indicate that this type of structural stabilization is occurring. However, if we are interested in developing land management practices which favor C accumulation in the form of SOC, it is important to consider stability over long periods of time. Soil C storage is slow after woody plant invasion, and in some cases it is stored in the fractions with short residence time (<20 years) (Neff et al., 2009). In La Pampa, previous studies provide evidence for rapid C losses after clearing, with C half-lives just above 10 years and no evidence for long-term stabilized C in any soil fractions (Zach et al., 2006). Therefore, carbon accumulation in these sandy loam soils which experienced woody plant encroachment should not be assumed stable (Creamer et al., 2011). This should be considered when planning management decisions to optimize carbon storage.

The effect of WPE on ecosystem C stocks has been shown to vary depending on the amount of water available in the system, usually measured in the form of MAP. Several studies in North America and Europe, have found that in drier sites WPE increase the amount of total C in the system, while at wetter sites the changes become negative (Jackson et al., 2002; Alberti et al., 2011; Barger et al., 2011). Our study area in the Caldenal savannas, with a MAP of 480–630 mm, falls on the drier side of that spectrum, and the increase in ecosystem C stocks found on average along the woody cover gradient agrees with previous studies. When we pooled all land cover classes in order to model the different ecosystem pools along the woody cover gradient, MAP was not found in any case a major factor affecting the C stocks, as were woody plant cover and soil silt content. When assessing the effect of MAP on total ecosystem C (Fig. 3), we found that for all the land cover classes considered, C stocks increase with MAP, but those relationships were only significant for shrublands and open forests, while the relationship for

grasslands and closed forests rainfall was weak. It is possible that there are other factors not controlled for in the study design, like grazing and fire history, which could affect the relationship between MAP and ecosystem C stocks in the Caldenal savannas.

The predictive models developed to predict tree, soil and total ecosystem C for this region are simple and effective, and could be incorporated into predictive models of ecosystem C globally. Within ecoregions, the use of simple, linear regression models in conjunction with precipitation and soils maps has been proposed to generalize the constrained site-level C estimates (Barger et al., 2011). Of the models tested here, which are restricted only to natural grasslands and *P. caldenia* woodlands in central Argentina, we were surprised to find the most successful ones to be the most parsimonious, relying only on woody plant cover and soil silt content, but having no significant relationship with MAP. This result highlights the importance of woody plant cover and soil characteristics as drivers of ecosystem C accumulation in central Argentina. The simplicity of the models combined with the ability to easily measure explanatory variables in the field, opens the possibility for regional estimates of ecosystem C stocks. Woody plant cover could be estimated from remotely sensed products, and soil silt content could be gathered from regional soil maps, to generate regional estimates of higher precision than those currently available.

5. Conclusion

We assessed the magnitude of the most important ecosystem C stocks along a woody cover gradient in the Caldenal savannas of central Argentina in a effort to better understand the potential implications of woody plant encroachment on ecosystem C storage. We found a significant increase in total ecosystem C stocks along the woody cover gradient, with four times more C in closed forests than in grasslands. In all cases soil organic C was the largest pool, representing over 60% of the total ecosystem stock. A set of simple equations were also developed to predict soil, tree and ecosystem C using only soil silt content and woody plant cover measured in the field. The results offer an approximation to the potential effect of woody plant encroachment in the Caldenal savannas of central Argentina, but only a spatially explicit analysis assessing the area affected by this phenomenon over time will determine the real effect of the increase in woody plant density on the C budget of this region. The models created here offer a valuable tool, which linked to remotely sensed data and regional soil maps could address this need.

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