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Research article

Reductions of plant cover induced by sheep grazing change the above-belowground partition and chemistry of organic C stocks in arid rangelands of Patagonian Monte, Argentina

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ABSTRACT

The objective of this study was to estimate the size and chemical quality of the total organic C stock and its partition between above-belowground plant parts and soil at sites with different plant cover induced by sheep grazing in the arid Patagonian Monte. This study was conducted at six representative sites with increasing signs of canopy disturbance attributed to grazing pressure. We used faeces density as a proxy of grazing pressure at each site. We assessed the total plant cover, shrub and perennial grass cover, total standing aboveground biomass (AGB), litter mass and belowground biomass (BGB) at each site. We further estimated the content of organic C, lignin and soluble phenols in plant compartments and the content of organic C, organic C in humic substances (recalcitrant C) and water soluble C (labile C) in soil at each site. Total plant cover was significantly related to grazing pressure. Standing AGB and litter mass decreased with increasing canopy disturbance while BGB did not vary across sites. Total organic C stock and the organic C stock in standing AGB increased with increasing total plant, shrub, and perennial grass cover. The organic C stock in litter mass increased with increasing total plant and shrub cover, while the organic C stock in BGB did not vary across sites. Lignin content in plant compartments increased with increasing total and shrub cover, while soluble phenols content did not change across sites. The organic C stock and the water soluble C content in soil were positively associated with perennial grass cover. Changes in total plant cover induced by grazing pressure negatively affected the size of the total organic C stock, having minor impact on the size of belowground than aboveground components. The reduction of perennial grass cover was reflected in decreasing chemical quality of the organic C stock in soil. Accordingly, plant managerial strategies should not only be focused on the amount of organic C sequestered but also on the chemical quality of organic C stocks since C chemistry could have an important impact on ecosystem functioning.

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1. Introduction

The above-belowground partitioning of organic C stocks may vary among biomes, ecosystems, environmental conditions and managerial practices (Derner and Schuman, 2007; Locatelli and Leonard, 2001; Zhao et al., 2004). Soils are the largest organic C reservoir in the biosphere in most terrestrial ecosystems (Lal, 2004, 2011; Schlesinger, 1997). Soil organic C gains and losses are strongly related to the mass and decay rates of senesced plant tissues (Costa et al., 2012; Kröpfl et al., 2013; Larreguy et al., 2014). Our ability to predict and mitigate C losses would depend on a better understanding of the distribution, amount, concentration of labile and recalcitrant compounds (chemical quality) and degradability of the organic C stocks (Chapin and Ruess, 2001).

In the arid ecosystems the scarce plant cover, life history of plants, and the rate of herbivory are main controls of the size and dynamics of C stocks (Golluscio et al., 2009; Milchunas and Lauenroth, 1993). In these ecosystems, vegetation is mostly dominated by woody species along with perennial grasses. Woody plants have high amount and diversity of chemical (e.g. soluble phenols) and/or structural (e.g. spines) defenses against desiccation, herbivory, pathogens and UV radiation. In contrast, perennial grasses have low protection against both abiotic factors and herbivory and are more affected than woody species by herbivores

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(Aerts and Chapin, 2000; Carrera et al., 2009; Hättenschwiler and Vitousek, 2000; Moreno et al., 2010). Accordingly, the amount and chemistry of above and belowground litter mass may differ between plant groups. Moreover, the relative dominance of different plant groups may have consequences on the organic matter decay and C cycling (Aerts and Chapin, 2000). In general, litter with low concentration of secondary compounds decomposes fast, and may contribute to enhance the content of soil labile C (Montané et al., 2010; Su et al., 2004). In contrast, litter with high concentration of lignin and/or soluble phenols are usually recalcitrant to decomposition leading to the formation of humic substances (Almendros et al., 2005; Schaeffer et al., 2015).

Disturbances such as those induced by grazing may cause changes in the spatial arrangement and abundance of plant species and/or plant growth forms, affecting the contribution of AGB and BGB to litter, with consequences to the size and quality of organic C stocks and the rates of biogeochemical cycles (Angassa, 2012; Oñatibia et al., 2015; Zhao et al., 2009). The most conspicuous effects of grazing disturbance in Patagonian Monte ecosystems are the reduction of plant cover and biomass, the replacement of non-woody species (mainly perennial grasses) by evergreen woody plants, and the reduction in litter amount and chemical quality (Bertiller and Ares, 2011; Bertiller and Bisigato, 1998; Carrera et al., 2008; Carrera and Bertiller, 2013). On the other hand, changes in root biomass were less noticeable (Rodríguez et al., 2007; Larreguy et al., 2014) as in other ecosystems (Costa et al., 2012; Milchunas and Lauenroth, 1993). Additionally, increasing bare soil or sparsely vegetated areas may be strongly impacted by wind and water soil erosion (Breshears et al., 2003; Tongway et al., 2003) causing losses of fine soil material and the associated organic matter (Bisigato et al., 2008; Neff et al., 2005).

Since arid ecosystems occupy more than 35% of the global land area, they are considered important reservoirs of soil organic C (Lal, 2004). However, the impact of grazing on the amount and chemical quality of above-belowground organic C stocks has been scarcely explored in these ecosystems. Previous studies showed positive (Reeder and Schuman, 2002), neutral (Shrestha and Stahl, 2008) or negative effects of grazing (Pei et al., 2008) on the size of soil organic C stocks (Baisden and Amundson, 2003). However, none of these studies analyzed whether these responses were associated with changes in the C partitioning or in chemical quality (recalcitrant or labile C) of organic C stocks.

Our objective was to estimate the size and chemical quality of the total organic C stock and its partition among above, belowground plant parts and soil at sites with different plant cover induced by sheep grazing in the arid Patagonian Monte. We hypothesized that the reduction of plant cover induced by sheep grazing affects C partitioning by increasing the size of belowground-C relative to aboveground C stocks and by increasing recalcitrant C in arid ecosystems.

2. Materials and methods

2.1. Study area and sampling sites

The study was carried out in northeastern Patagonia (Patagonian Monte). Mean annual temperature is 13.7 °C and mean annual precipitation is 177.6 mm (series from 1952 to 2009, CENPAT, 2014; INTA, 2014). Vegetation corresponds to the shrubland of *Larrea divaricata* Cav. and *Stipa* spp., characteristic of the southern portion of the Monte Phytogeographic Province (León et al., 1998). Soils are a complex of Typic Petrocalcids-Typic Haplocalcids in which the presence of a calcium carbonate layer approximately 35–40 cm deep (del Valle, 1998; Soil Survey Staff, 1998) with a variable degree of compaction is in many cases a physical barrier to root penetration (Súnico, 1996).

In the Patagonian Monte, sheep grazing (mainly Merino breed) was introduced at the beginning of the last century to produce mainly fine wool and was typically organized in ranches of about 4 paddocks of 2500 ha each sharing a single permanent watering point. Since then, the mean historical stocking rate has been 0.11–0.14 sheep ha^{-1} (including adults and juveniles), keeping sheep in the same paddock throughout the year. This in turn led to the formation of extended piospheres (1500–4000 m) around watering points where the spatial pattern of vegetation, the dominant plant traits, and the upper soil conditions were modified by the frequent visit of grazers (Ares et al., 2003; Bisigato and Bertiller, 1997; Bisigato et al., 2008; Larreguy et al., 2014). These domestic herbivores weigh between 40 and 60 kg and feed mainly on perennial grasses and some shrubs (Baldi et al., 2004). Accordingly, the size of shrub patches, perennial grass cover, and total plant cover decreases near the watering point (Bär Lamas et al., 2013; Bertiller et al., 2002; Bertiller and Ares, 2008; Pazos et al., 2007). In order of importance, *Pappostipa speciosa* (ex *Stipa speciosa*), *Nassella tenuis* (ex *Stipa tenuis*), and *Poa ligularis* are the dominant perennial grass species in the area. Among them, *P. speciosa* is less preferred by herbivores than the other species. Other less abundant and highly preferred perennial grass species are *Elymus patagonicus* and *Jarava neaei* (ex *Stipa neaei*) (Bisigato and Bertiller, 1997). Faeces counts and density of sheep paths (Bisigato and Bertiller, 1997; Pazos et al., 2007), vegetation structure assessed by remote sensing (Ares et al., 2003) as well as to reductions in soil organic C with increasing grazing disturbance (Carrera et al., 2008; Prieto et al., 2011) are indicators usually used to confirm the existence of areas affected by grazing disturbance around watering points (piospheres).

This study was conducted at six sites (Supplementary material Table 1) with similar soil conditions, topography and vegetation type and increasing signs of canopy disturbance attributed to grazing pressure (Bär Lamas et al., 2013; Brooks et al., 2006; Larreguy et al., 2014). The gradient of grazing disturbance used in this study is consistent with those reported for the shrubland of *Larrea divaricata* and *Stipa* spp. characterized by decreasing total, perennial grass and in some cases shrub cover, as well as reduced shrub patch size with increasing grazing disturbance in the Patagonian Monte (Bär Lamas et al., 2013; Bertiller et al., 2002; Bertiller and Ares, 2008; Bisigato and Bertiller, 1997; Bisigato et al., 2008; Carrera et al., 2008; Pazos et al., 2007, 2010). We used the total faeces density assessed for these sites by Bär Lamas et al. (2013) in 2009 as an index of grazing pressure (Lange and Willcocks, 1978).

2.2. Plant cover

Total plant cover and the cover of dominant plant growth forms (shrubs and perennial grasses) were assessed at four randomly located 25-m linear transects by the line intercept method (Muller-Dombois and Ellenberg, 1974) at representative areas (3 ha each, minimal area *sensu* Muller-Dombois and Ellenberg, 1974) of each site in autumn 2010. We further calculated the absolute total plant cover and the relative shrub and grass cover. We estimated the grazing disturbance level at each site by comparing the perennial grass cover at each site with those reported in other areas of the Patagonian Monte. These areas encompassed a site excluded from domestic herbivores for 12 years, and sites with low, moderate and high grazing disturbance (>3000 m far from the watering point, ca. 600 m and <300 m from the watering point, respectively) (Bisigato and Bertiller, 1997; Carrera et al., 2008; Larreguy et al., 2012; Pazos et al., 2007; Prieto et al., 2011). Additionally, at each transect, we assessed the number of plant patches and the area, maximum height, plant growth form composition of each intercepted patch

(Muller-Dombois and Ellenberg, 1974). These attributes were used to identify the 4 most frequent patch types at each site (Larreguy et al., 2014). Plant patches were defined as discrete units of the spatial pattern of vegetation surrounded by bare soil, at least 20 cm from the nearest neighbor patch (Bisigato and Bertiller, 1997). The most frequent patch types varied from small patches with few plant species to large patches with numerous plant species with different relative contribution of plant growth forms to the total patch cover in the six sites (Supplementary material Table 1).

2.3. Aboveground biomass, litter mass, belowground biomass and soil samples

Sampling was carried out in two seasons (winter and summer) and in two consecutive years 2011–2012 in order to include eventual inter -seasonal and inter-annual variations in the studied variables. At each sampling date, we randomly selected four plant patches of each patch type at each site (16 plant patches per site). The plant biomass at each plant patch was assessed by the reference unit technique (Davis and Roberts, 2000). To this purpose, we harvested a representative unit of reference of each species by patch type and counted the number of times that this unit was contained in the canopy of the respective species and patch type. Then, each unit was dried at 45 °C during 48 h and weighed (Davis and Roberts, 2000). The dry mass of each unit was used to calculate the total AGB (g m^{-2}) per species. Further, we calculated the total AGB per patch by adding the AGB of all species present in the patch. Total plant biomass, standing AGB, litter mass, and BGB were expressed as mass per unit area.

Additionally, we collected the litter accumulated on the soil within 1 rectangular plot of 10 × 20 cm located under the south-eastern part of the canopy (plant patch microsite) of each plant patch (between the basal insertion of the branches and the edge of the patch crown) and in the middle of the nearest inter-patch area (inter-patch microsite) per selected plant patch (16 plant patches and 16 inter-patch areas per site and sampling date; n = 384, plant patches: 16 plant patches x 2 season × 2 years x 6 sites; and n = 384 inter-patch areas: 16 inter-patch areas x 2 seasons x 2 years × 6 sites). Litter samples were cleaned of attached soil particles with a brush (Carrera et al., 2008), dried at 45 °C for 48 h and weighed. Next to each litter sample at both plant patch and inter-patch microsites (16 plant patches and 16 inter-patch areas per site and sampling date, n = 384 per microsite), we collected a soil sample (0–30 cm depth) with a metallic tube (5 cm in diameter, 45 cm depth). The soil from each sample was air-dried to constant weight (Walworth, 2006), sieved to 2 mm mesh and weighed. Roots were separated from each sample, briefly washed with tap water to remove the adhered soil particles, dried at 45 °C for 48 h and weighed. We selected this soil depth based on previous studies in the Patagonian Monte indicating that grasses have the highest concentration of roots in the upper soil and several shrubs may develop deep/dimorphic root systems with high concentration of fine roots in the upper soil and a pivotal woody root reaching 2–3 m depth (Bertiller et al., 1991; Rodríguez et al., 2007). Besides, some studies in arid and semi-arid ecosystems of the world, including the Patagonian Monte, reported that between 50 and 70% of root biomass is concentrated in the first 30 cm of soil depth (Jafari, 2013; Pavón, 2007; Rodríguez et al., 2007; Schenk and Jackson, 2002). This was associated with the higher nutrient concentration (e.g. N) and lower oxygen deficiency in the upper than in deep soil (Schenk and Jackson, 2002) and with a more or less compact caliche layer at ca. 35–40 cm below the soil surface (del Valle, 1998). Moreover, grazing disturbance affects mainly perennial grasses (Bisigato and Bertiller, 1997) with roots concentrated in the upper soil. Accordingly, root biomass and soil organic matter of this soil fraction may be the most affected by grazing disturbance.

2.4. Concentration of organic C in plant and soil

We assessed the organic C concentration of the standing AGB, litter mass and BGB from each plant patch type at each site and sampling date by dry combustion at 550 °C (Schlesinger and Hasey, 1981) and the soil organic C concentration by the $K_2Cr_2O_7$-H_2SO_4 oxidation method of Walkey and Black (Page et al., 1982).

2.5. Concentration of lignin and soluble phenols in standing AGB, litter mass and BGB, and water soluble C and C in humic substances in soil

We assessed the concentration of lignin and soluble phenols in the standing AGB, litter mass and BGB from each plant patch type at each site and sampling date. Lignin was assessed by van Soest (1963) method and soluble phenols by Folin-Ciocalteu method using tannic acid as standard (Waterman and Mole, 1994).

In the soil samples, we assessed the concentration of organic C in humic substances (recalcitrant carbon) by extraction with 0.1 M sodium pyrophosphate (1: 3 soil: solution) and subsequent $K_2Cr_2O_7$-H_2SO_4 oxidation method of Walkey and Black (Moreno et al., 1999; Sims and Haby, 1971), and the concentration of water soluble C (labile carbon) in an aqueous extract of soil (1: 3 soil: water) by the $K_2Cr_2O_7$-H_2SO_4 oxidation method of Walkey and Black (Pascual et al., 2000; Sims and Haby, 1971).

2.6. Data analysis

We used (i) the standing AGB, litter mass and BGB (30 cm depth) per m^2 and the respective concentration of organic C, soluble phenols and lignin to estimate the organic C stocks (OC_{stock}) of each plant compartment and the respective soluble phenolic and lignin contents (Ellert et al., 2001) at each site and sampling date; and (ii) the soil mass and the concentrations of organic C, C in humic substances and water soluble C to calculate the OC_{stock} in soil (depth 30 cm) and the respective water soluble C, and C in humic substances (recalcitrant C) contents (Ellert et al., 2001) at each site, sampling date and microsite (plant patch or inter-patch) as:

$$OC_{stock}/\text{chemical content of soil or plant compartments (j)} = \left[\left(\sum_{i=1}^{4} C_{ij} * Mij * ni \right) \Big/ N \right] * pcov$$

where, j is the compartment (standing AGB, litter mass, BGB or soil), i is the patch type or inter-patch associated (1, 2, 3, 4), C_{ij} is the mean value of organic C, soluble phenols or lignin concentration (mg per gram of biomass) in the standing AGB, litter mass or BGB, or in soil (mean value of organic C, water soluble C or C in humic substance concentration (mg per gram of soil) at each plant patch or inter-patch i; Mij is the mean value of standing biomass, litter mass, BGB or soil mass at each patch type or inter-patch i, ni is the number of patch types or inter-patches i; N is number of patches or inter-patches; pcov is the proportion of plant patches or inter-patch areas cover at each site.

The total of organic C stock (total OC_{stock}) at each site and sampling date was calculated as the sum of OC_{stock} in vegetation compartment and soil. We used ANOVA to test for significant differences in above and BGB, litter mass and total plant mass and in the concentration of organic C, soluble phenols and lignin in standing AGB, litter mass and BGB, and in the concentration of organic C, C in humic substances and water soluble C in soil among sites with different plant cover induced by grazing disturbance. In those cases where normality and/or homogeneity of variances could not be achieved, data were log-transformed and the assumptions of normality and homoscedasticity were again checked before applying parametric data analyses (Sokal and Rohlf, 1981). Samples from both seasons (winter and summer) and years (2011–2012) were combined for the analyses since we did not find significant differences between years.

We analyzed the relationship among total plant cover, plant cover by growth form (perennial grasses and shrubs), total OC $_{stock}$, OC $_{stock}$ in BGB, OC $_{stock}$ in standing AGB, OC $_{stock}$ in litter mass, OC $_{stock}$ in soil, total contents of water soluble C and C in humic substances in soil, and total contents of soluble phenols and lignin in plant compartments at each site by principal components analysis and Pearson correlation analysis (Norusis, 1997). The relationship between organic C stocks or chemical contents and plant cover was quantified by regression analysis. All statistical analyzes were performed using SPSS for Windows (Norusis, 1997). The significance level used throughout this study was $p \leq 0.05$.

3. Results

3.1. Absolute total plant cover and relative shrub and perennial grass cover

Total plant cover was negatively related to faeces density ($R^2 = 0.76$, $p = 0.02$) and varied from ca. 8% in the most disturbed site to ca. 30% in the less disturbed site (Fig. 1a). Based on the perennial grass cover these sites have different grazing disturbance levels (Supplementary material Table 2). Accordingly the selected sites could be arranged across a gradient of decreasing canopy signs of grazing disturbance from 1 to 6 (henceforth grazing disturbance). The contribution of shrub cover was variable among sites having sites 2 and 4 the largest shrub contribution and sites 3 and 6 the lowest one (Fig. 1b).

3.2. Above and below-ground biomass, litter mass and total plant mass

Standing AGB and litter mass decreased with increasing grazing disturbance ($R^2 = 0.87$, $p < 0.01$; and $R^2 = 0.77$, $p = 0.02$), while BGB did not vary across sites ($R^2 = 0.07$, $p = 0.63$). This resulted in decreasing total mass with increasing grazing disturbance ($R^2 = 0.89$, $p < 0.01$) (Supplementary material Table 3).

3.3. Concentration of organic C, soluble phenols and lignin in plant compartments, and concentration of organic C, C in humic substances and water soluble C in soil

Concentration of organic C, soluble phenols and lignin in standing AGB and litter mass increased with decreasing grazing

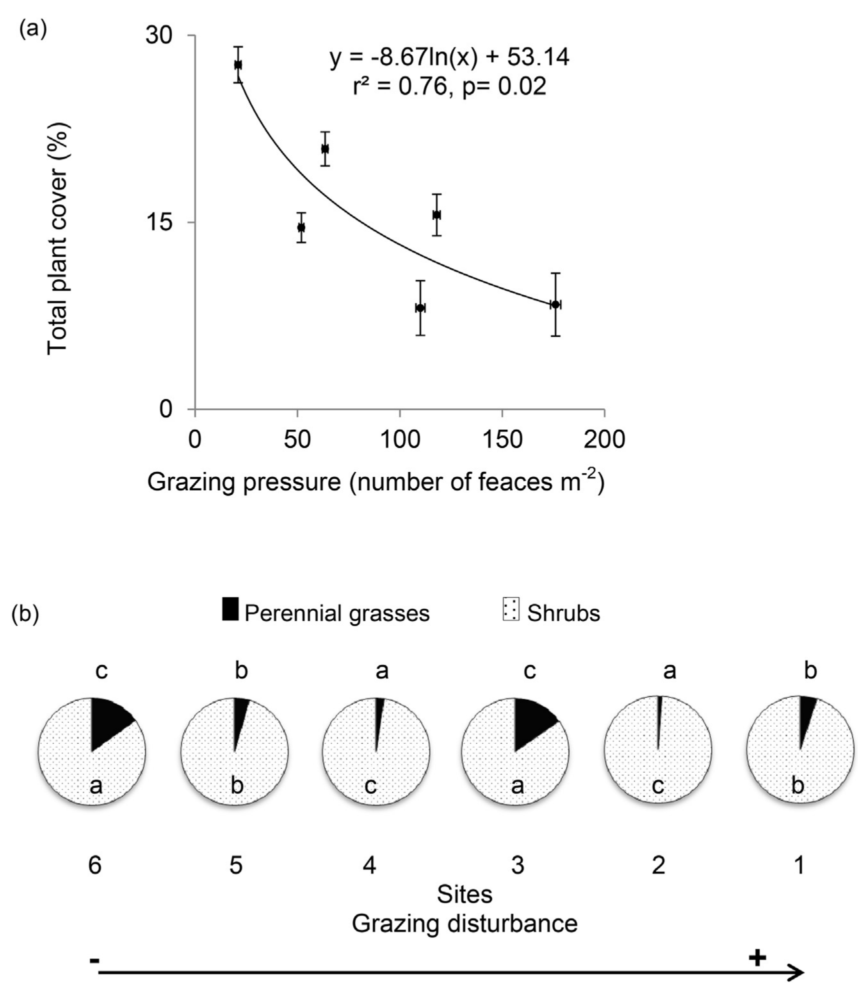

Fig. 1. (a) Absolute total plant cover, and (b) relative shrub and perennial grass cover at each site. Different letters indicate significant differences in the relative plant cover within each plant growth form (shrubs, perennial grasses) among sites.

disturbance ($R^2 = 0.82$, $p = 0.10$; $R^2 = 0.71$, $p = 0.04$; $R^2 = 0.82$, $p = 0.01$; and $R^2 = 0.95$, $p < 0.01$; $R^2 = 0.83$, $p = 0.01$; $R^2 = 0.72$, $p = 0.03$ respectively) while these chemical variables in BGB did not vary among sites ($p > 0.05$) (Supplementary material Table 4). On the other hand, concentrations of organic C and C in humic substances in soil were more variable across the grazing disturbance gradient, and the highest values were found at sites with less grazing disturbance. In contrast, water soluble C concentration in soil showed the highest values at sites with low and high grazing disturbance across the gradient (Supplementary material Table 4).

3.4. Relationship between plant cover induced by grazing disturbance and organic C stocks (OC_{stocks}) and chemical contents in plant and soil

The total organic C stock (total OC_{stock}) increased with increasing total plant, perennial grass and shrub cover (Fig. 2). Although the three relationships were statistically significant the total plant cover was the variable explaining the greatest variance in total OC_{stock} ($R^2 = 0.80$, $p = 0.02$).

The OC_{stock} in standing AGB increased with increasing total plant, perennial grass and shrub cover (Fig. 3a). Also, OC_{stock} in litter mass increased with increasing total plant and shrub cover (Fig. 3b). In contrast, OC_{stock} in BGB was not related to total plant and by growth form cover (Fig. 3c).

The OC_{stock} in soil was positively associated only with perennial grass cover (Fig. 4).

The total content of lignin increased with increasing total plant and shrub cover (Fig. 5a). Neither the total content of soluble phenols in plant compartments (Fig. 5b) nor the content of soil organic C in the humic substances (Fig. 6a) were significantly associated with plant cover. On the other hand, the content of water soluble C in soil increased with increasing perennial grass cover (Fig. 6b).

The principal component analysis (PCA) grouped the total OC_{stock} with total plant cover ($r = 0.89$, $p = 0.02$) and shrub cover ($r = 0.83$, $p = 0.04$) on positive values of PCA axis 1 (67.3% of the total variance, Fig. 7) and sites 4, 5, 6 (low grazing disturbance). Also, total plant cover and shrub cover were closely related to lignin content and sites 4 and 5 (positive values of axis 2). In contrast, site 6 (site with the lowest grazing disturbance) was clustered with high content of water soluble C and high cover of perennial grasses on negative values of PCA axis 2 (20.0% of the total variance) (Fig. 7).

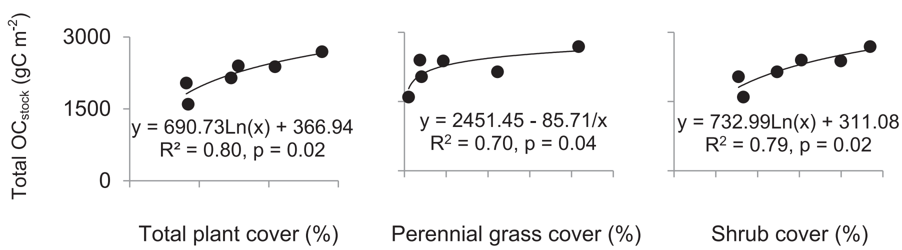

Fig. 2. Relationship between mean values of total plant cover, perennial grass and shrub cover and total organic C stock (total OC_{stock}).

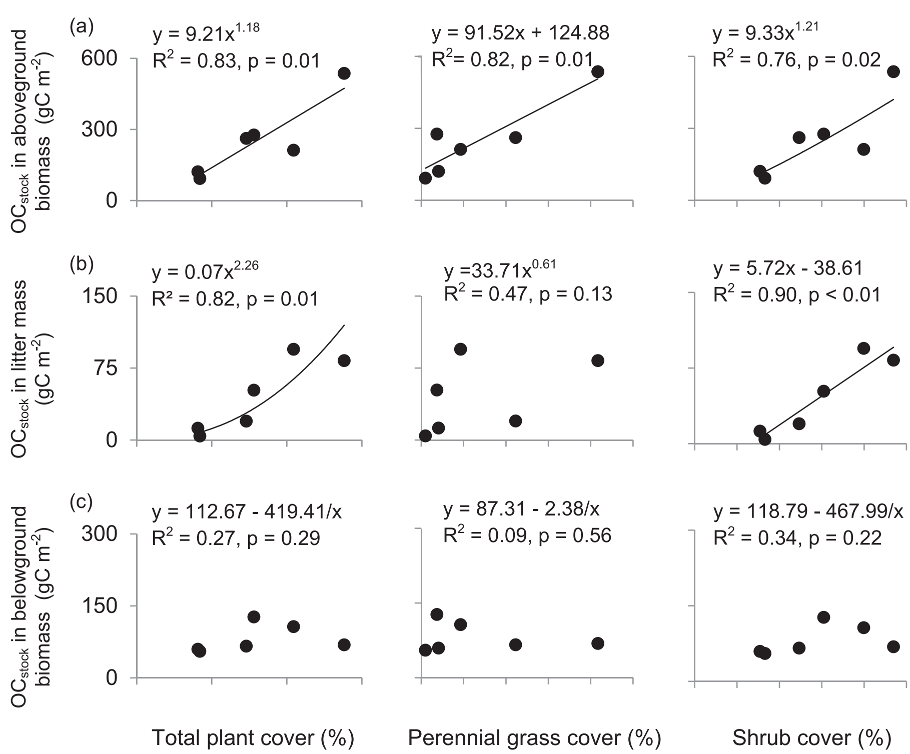

Fig. 3. Relationship between mean values of total plant cover, perennial grass and shrub cover and (a) the organic C stock in standing AGB, (b) the organic C stock in litter, and (c) the organic C stock in BGB.

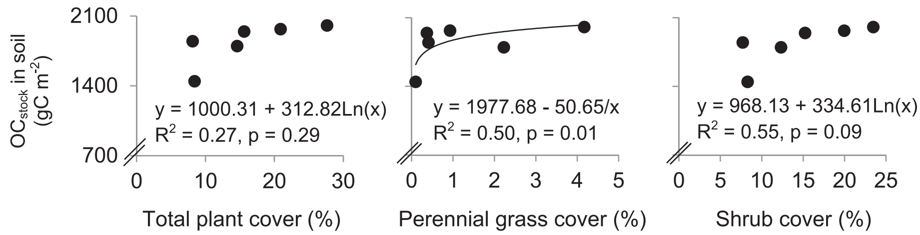

Fig. 4. Relationship between mean values of total plant cover, perennial grass and shrub cover and the organic C stock in soil.

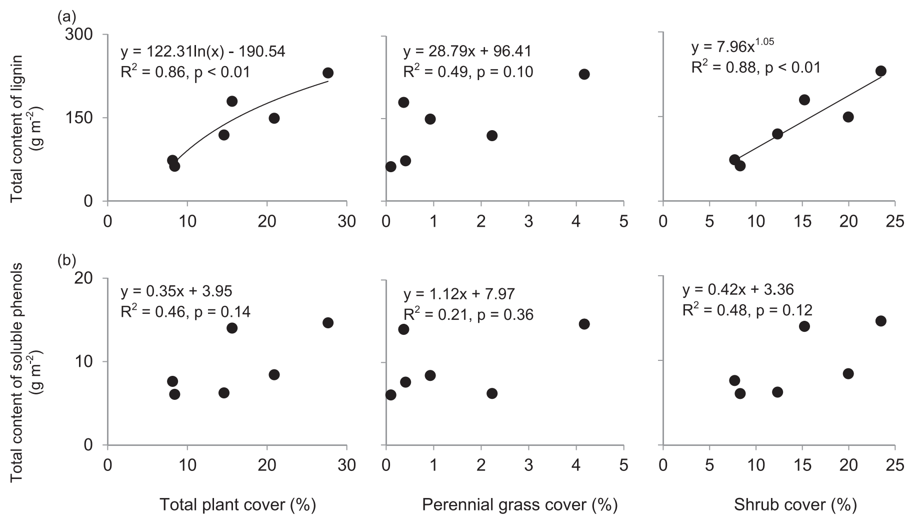

Fig. 5. Relationship between mean values of total plant cover, perennial grass and shrub cover and the content of lignin and soluble phenols (standing AGB + litter mass + BGB).

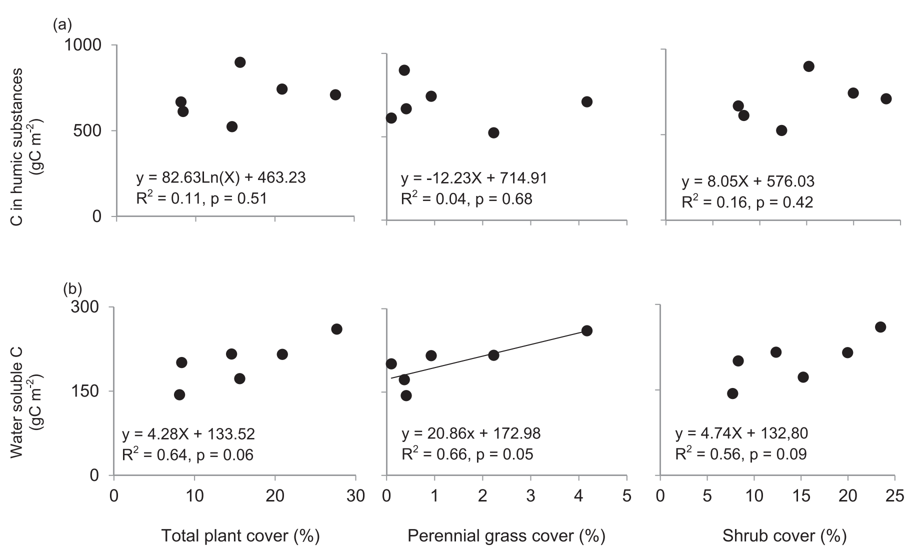

Fig. 6. Relationship between the mean values of total plant cover, perennial grass and shrub cover and the content of C in humic substances and water soluble C in soil.

4. Discussion

Our results showed that plant cover reduction and changes in growth form composition (proportion of perennial grasses and shrubs) induced by sheep grazing affected the size, chemical quality, and the above-belowground partition of the organic C stocks in arid ecosystems of the Patagonian Monte. The size of the total organic C stock (1549–2762 g C m^{-2}) in this study was within the range of values (909–5793 g m^{-2}) reported for other arid and semiarid ecosystems of the world (Nosetto et al., 2006; Woomer et al., 2004). Although this study included only one grazing gradient, the selected sites were representative of sites with low (Bisigato and Bertiller, 1997; Prieto et al., 2011), moderate (Bisigato and Bertiller, 1997; Bisigato et al., 2008) and high (Bisigato and Bertiller, 1997; Prieto et al., 2011; Larreguy et al., 2012) grazing disturbance characteristic of the Patagonian Monte. Changes in

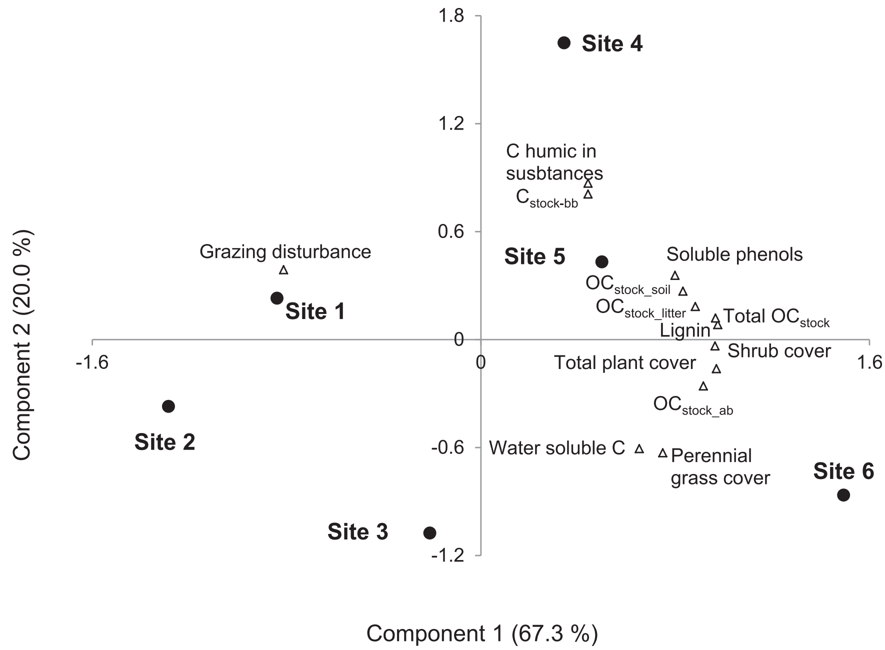

Fig. 7. Ordination of sites with respect to the two first principal component analysis of the correlation matrix among total plant cover, shrub cover, perennial grass cover, total organic C stock (Total OC_{stock}), OC_{stock} in standing AGB ($OC_{stock-ab}$), OC_{stock} in litter mass, OC_{stock} in BGB ($OC_{stock-bb}$), OC_{stock} in soil, contents of soluble phenols and lignin content in plant compartment, contents of water soluble C and C in humic substances in soil and grazing disturbance at each site.

total plant, perennial grass and shrub cover were associated with changes in the total organic C stock. The most conspicuous change was the reduction in the organic C stock in standing AGB with decreasing total, perennial grass and shrub cover induced by grazing disturbance. This could be associated with the direct effect of sheep on aboveground plant parts by the removal of preferred fast-growing species with high leaf turnover rate (e.g. perennial grasses and some shrubs) and their replacement by slow-growing woody species with low annual leaf turnover rate (e.g. evergreen shrubs). In contrast, C stock in BGB did not vary with changes in plant cover. This is probably associated with the ability of some shrubs to develop dimorphic root systems increasing the volume of soil explored and occupying the soil surface released by perennial grass roots in sites with high grazing disturbance (Gebauer et al., 2002; Hofstede and Rossenaar, 1995; Rodríguez et al., 2007; Larreguy et al., 2014). These results were consistent with those observed in other areas of the Patagonia (Bär Lamas et al., 2013; Bisigato and Bertiller, 1997; Campanella and Bertiller, 2008; Larreguy et al., 2014; Oñatibia et al., 2015) and other arid ecosystems of the world (Raiesi and Asadi, 2006; Smith et al., 2014) and support our hypothesis that reductions in plant cover induced by grazing disturbance have higher negatively effects on aboveground (standing biomass and litter mass) than on belowground components (root biomass and soil) of organic C stocks.

A relevant finding in this study was the positive association between the cover of perennial grasses and the organic C stock in soil and its content of water soluble C. Particularly, the organic C stock in soil decreased with decreasing perennial grass cover. Probably, other factors also contributed to the reduction in the size of the organic C stock in soil under grazing disturbance such as the increase in litter recalcitrance slowing down organic matter decomposition at ecosystem level and reducing the input of organic C into the soil (Breshears et al., 2003; Carrera and Bertiller, 2013; Carrera et al., 2008; Golluscio et al., 2009; Tongway et al., 2003). On the other hand, increased content of water soluble C could be related to the fact that perennial grasses produce litter with lower protection against herbivores and environmental stress than shrubs (Carrera et al., 2009; Moreno et al., 2010; Saraví Cisneros et al., 2013; Wright and Westoby, 2003). In general, litter produced by perennial grasses has labile compounds, readily available as an energy source for soil microorganisms, enhancing the input of organic matter into the soil (Cook and Allen, 1992; Haynes, 2000). Water soluble C is a labile fraction of the soil organic matter and has higher recycling rates than C in humic substances (Derner et al., 2006; Ghani et al., 2003; Oyonarte et al., 2007). Accordingly, labile C in soil is a main variable related to ecosystem functioning and soil degradation induced by grazing disturbance, and perennial grass cover could be used as an indicator of the state of organic C stocks in soil. Although, the content of C in humic substances did no change consistently with plant cover, it was closely related to BGB. In general, the content of C in humic substances is related to plant and litter chemistry, being high in those soils receiving litter with high content of recalcitrant compounds (Almendros et al., 2005). Increasing recalcitrance of organic C stocks could increase the residence time of the organic C in above and belowground components (Lambers et al., 2006). This in turn could decelerate ecosystem processes such as organic matter decomposition and nutrient release affecting primary productivity in these ecosystems (Lambers et al., 2006; Lorenz and Lal, 2005).

In conclusion, changes in total plant cover induced by grazing disturbance negatively affected the size of the organic C stock, having minor impact on the size of belowground compared to aboveground components. Moreover, the size of aboveground organic C stocks was associated with shrub cover while organic C stocks in soil were related to perennial grass cover. Particularly, the reduction of perennial grass cover was reflected in a decrease in the chemical quality of the organic C stock in soil (reduction of water soluble C). Our results highlighted that perennial grass cover could be used as an indicator of main changes in soil OC stock. Accordingly, plant managerial strategies should not only be focused on the amount of organic C sequestered but also on the chemical quality organic C stocks since C chemistry could have an important impact on ecosystem functioning.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jenvman.2017.04.086.

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