



Effects of long-term grazing disturbance on the belowground storage of organic carbon in the Patagonian Monte, Argentina



C. Larreguy^{a,*}, A.L. Carrera^{a,b}, M.B. Bertiller^{a,b}

^a Centro Nacional Patagónico – CONICET, Boulevard Brown 2915, Puerto Madryn 9120, Chubut, Argentina

^b Facultad de Ciencias Naturales – UNPSJB, Boulevard Brown 3000, Puerto Madryn 9120, Chubut, Argentina

ARTICLE INFO

Article history:

Received 13 June 2013

Received in revised form

18 December 2013

Accepted 25 December 2013

Available online

Keywords:

Arid ecosystems

Deciduous shrubs

Dwarf shrubs

Plant patches

Root biomass

Soil organic carbon

ABSTRACT

The objective of this study was to analyze the effect of grazing disturbance on the amount and the spatial distribution (vertical and horizontal) of root biomass and soil organic carbon (SOC) in order to evaluate whether grazing alters the belowground storage of organic carbon (C) in arid rangelands of the Patagonian Monte. We selected three representative sites (3 ha each) with low, moderate and high grazing disturbance located far, mid-distance and near the watering point, respectively, in rangelands submitted to sheep grazing for more than 100 years. We assessed the canopy structure and identified the four most frequent plant patch types at each site. We selected four replications of each patch type and extracted a soil sample (0–30 cm depth) underneath the canopy and in the middle of the nearest inter-patch bare soil area in winter and summer. We assessed the root and soil dry mass and the respective organic C concentration in each sample and then we estimated the total belowground organic C storage at each site. Total plant and perennial grass cover were lower with high than low grazing disturbance while the reverse occurred with dwarf shrub cover. High grazing disturbance led to the increase in total root biomass in the whole soil profile of patch areas and in the upper soil of inter-patch areas. SOC was higher in patch than in inter-patch areas at all sites but at both areas was reduced with high grazing disturbance. This was probably the result of the low total plant cover and the low and recalcitrant contribution of above and below-ground plant litter to soils at sites with high grazing disturbance. Accordingly, these changes did not result in variations in the total belowground organic C storage. We concluded that high grazing disturbance did not affect the total belowground organic C storage but led to changes in the spatial patterning of this organic C storage (i.e. shifting from soil to roots).

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

Soil is the largest storage of terrestrial organic carbon (C) in the biosphere (Lal, 2004a, 2011; Schlesinger, 1997). The total organic C storage is regulated mainly by primary production and decomposition processes which are controlled by biome type, environmental conditions, and management practices (Derner and Schuman, 2007; Zhao et al., 2004). In arid and semiarid ecosystems, these processes are strongly related to the amount and seasonal distribution of precipitation (Reynolds et al., 2004; Sala et al., 1988). Furthermore, low plant cover (<40–60%), the heterogeneous spatial distribution of plants, and the selective grazing by domestic herbivores could also control processes related to the input and output of soil organic carbon (SOC) in these ecosystems (Austin et al., 2004; Costa et al., 2012; Kröpfl et al., 2011). In these

heterogeneous environments, the soil associated with plant patches concentrates SOC, microbial activity, and nutrients (Whitford, 2002). Since these arid ecosystems occupy more than 35% of the global land area, they are considered important storages of SOC (Lal, 2004b; Muñoz-Rojas et al., 2012a, 2012b).

In the Patagonian Monte, plant patches are dominated by shrubs and perennial grasses (Ares et al., 1990; Bertiller et al., 1991). Both plant functional groups (*sensu* Körner, 1993) differ in the height of adult plants, leaf lifespan, and rooting depth (Bertiller et al., 1991; Bucci et al., 2009; Rodríguez et al., 2007; Scholz et al., 2012). Shrubs display a wide variation in morphological and functional traits related to defenses against water shortage and herbivory (Bertiller et al., 1991; Moreno et al., 2010). Evergreen tall shrubs usually have long lasting tissues and deep root systems with large accumulations of secondary metabolites, and develop vegetative and reproductive growth coupled with high temperatures, independently from water inputs (Bertiller et al., 1991; Campanella and Bertiller, 2008; Coronato and Bertiller, 1997). Deciduous shrubs usually have structural defenses against water shortage and

* Corresponding author. Tel.: +54 280 4451024; fax: +54 280 4451543.
E-mail address: larreguy@cenpat.edu.ar (C. Larreguy).

herbivory, dimorphic root system and develop vegetative and reproductive growth during periods with favorable water conditions (Bertiller et al., 1991; Campanella and Bertiller, 2008). Dwarf shrubs with shallow roots have large accumulations of secondary compounds in tissues which not only increase tolerance to water shortage but also provide resistance to herbivores (Grace, 1998). In contrast, perennial grasses are shallow-rooted species with low concentration of secondary compounds in their tissues, and display vegetative growth and reproductive activity coupled with precipitation inputs (Bertiller et al., 1991; Campanella and Bertiller, 2008). Accordingly, changes in the arrangement and abundance of plant species and/or plant functional groups induced by grazing disturbance could affect the contribution of roots and aboveground parts to litter with consequences on SOC (Angassa, 2012; Verlinden and Kruger, 2007).

In the Patagonian Monte, grazing was introduced at the beginning of the last century (Ares et al., 1990) and was typically organized in ranches of about 4 paddocks of 2500 ha each sharing a single permanent watering point. Since then, domestic herbivores have caused environmental impacts on ecosystem structure and function. The most conspicuous effects of long term grazing disturbance are the plant cover reduction and the replacement of perennial grasses by woody plants (Bertiller and Ares, 2011; Bertiller and Bisigato, 1998; Larreguy et al., 2012a). However, this notorious effect of grazing on aboveground cover is not always associated with reductions in the fine root biomass and SOC (Costa et al., 2012; Larreguy et al., 2012a; Milchunas and Lauenroth, 1993; Rodríguez et al., 2007). Some studies reported that grazing disturbance induced changes in the horizontal and vertical distribution of root biomass (Jackson et al., 2000; Schenk and Jackson, 2002), the reduction of SOC, and/or the redistribution of organic C storages from belowground towards plant canopies (Milchunas and Lauenroth, 1993). All of these changes affecting the quantity and distribution of SOC may have consequences on the total belowground organic C storage and biogeochemical cycles (Snyman, 2009; Zhao et al., 2009). These issues have been scarcely explored in grazed ecosystems although they are strongly related to ecosystem functioning. The capacity to predict and ameliorate the consequences of grazing disturbance on ecosystem function and global change depends in part on a better understanding of the distributions and controls of SOC and how vegetation changes (e.g. reduction of plant cover, plant species replacements) may affect the quantity and distribution of roots and SOC, and the total belowground organic C storage (Chapin and Ruess, 2001).

The objective of this study was to assess the total and the vertical and horizontal distribution of root biomass and SOC and quantify the total the belowground organic C storage in rangelands submitted to sheep grazing for more than 100 years in the Patagonian Monte. We hypothesized that the reduction of the total plant cover and the increase in cover of shrubs with shallow rooting depth and high concentration of chemical defenses induced by grazing disturbance lead to (1) increased amount and spatial heterogeneity of root biomass (root concentration underlying plant canopies and in the upper soil), (2) reduced concentration and spatial heterogeneity of SOC, and consequently, (3) little changes in the total belowground storage of organic C (C in root biomass + SOC).

2. Materials and methods

2.1. Study area

The study area is located in the Patagonian Monte. Mean annual temperature is 13 °C and mean annual precipitation is 188 mm (Barros and Rivero, 1982). Soils are a complex of Typic Petrocalcids-Typic Haplocalcids (del Valle, 1998; Soil Survey Staff, 1998) and

vegetation is representative of the shrubland of *Larrea divaricata* Cav. and *Stipa* spp., characteristic of the southern portion of the Monte Phytogeographic Province, Argentina (León et al., 1998). Plant cover has a patchy structure dominated by shrubs and perennial grasses (Bisigato and Bertiller, 1997). The typical organization of ranches in paddocks led to the formation of extended piospheres of more than 1500 m around watering points where the spatial pattern and traits of plant species, and upper soil properties are modified by the frequent visit of grazers (Ares et al., 2003; Bertiller and Ares, 2011; Bisigato and Bertiller, 1997; Carrera et al., 2008; Larreguy et al., 2012b; Prieto et al., 2011; Bär Lamas et al., 2013). This study was conducted in La Esperanza wildlife refuge (42° 12' 13.7"S, 64° 58' 55.6"W; 92 m a.s.l.) of about 6.000 ha submitted to sheep grazing with a stocking rate of 0.11–0.14 sheep ha⁻¹ since the beginning of the last century up to the year 2003 when this area was converted to a wildlife refuge and the stocking rate was gradually reduced (0.01 sheep ha⁻¹ per year). In 2008, all domestic herbivores were removed.

Within La Esperanza, we identified an extended piosphere of about 2500 ha in which the site near the watering point had higher faeces count and plant and soil indicators of grazing disturbance than that far the watering point (Bär Lamas et al., 2013). In this piosphere, we delimited three sites (3 ha each, minimal area *sensu* Mueller-Dombois and Ellenberg, 1974) with low, moderate and high grazing disturbance located at far, mid, and near distances from the single permanent watering point, respectively (Ares et al., 2003; Bertiller and Ares, 2011). These sites were separated at least 1500 m from each other.

2.2. Climatic conditions in the study area

We registered the mean monthly air temperature and the daily precipitation with an automatic data recorder (21X Micrologger, Campbell Scientific) during the period March 2010–February 2011 located at the site with moderate grazing disturbance (42° 12' 27.8"S, 64° 59' 34.5"W; 94 m a.s.l.).

2.3. Canopy structure

Total and species plant cover were assessed at four randomly located 25-m linear transects by the line intercept method (Mueller-Dombois and Ellenberg, 1974) at each site (low, moderate and high grazing disturbance) in autumn 2010. We further assigned each species to one of the following plant functional groups: evergreen tall shrubs (ETS), shrubs more than 30 cm tall with evergreen leaves; deciduous shrubs (DES) shrubs more than 30 cm tall with drought deciduous leaves; dwarf shrubs (DS), shrubs less than 30 cm tall; and perennial grasses (PG) (Supplementary data Table 1). Perennial herbs (i.e. plants with leaves and aboveground stems dying at the end of the growing season but underground stems laying dormant until the next growing season) and annuals were present with a very low cover (<0.01%) at all sites and they were not included in the analysis. Additionally, at each transect, we assessed the number, the area, the height and the plant functional group composition of each intercepted patch (Mueller-Dombois and Ellenberg, 1974). These attributes were used to identify the 4 most frequent patch types at each site (Larreguy et al., 2012b). 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).

2.4. Soil sampling

Sampling was carried out in two contrasting seasons: winter 2010 and summer 2011. We randomly selected 4 plant patches of

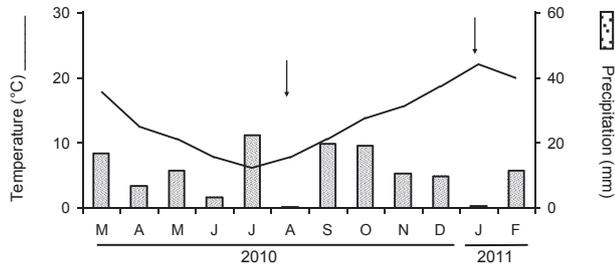


Fig. 1. Mean monthly temperature and monthly precipitation at the study area during the period March 2010–February 2011. Arrows indicate the sampling months.

each patch type per site (low, moderate and high grazing disturbance) and season (16 plant patches per site and season) and we collected a soil sample (0–30 cm depth) under the south-eastern part of the canopy (between the basal insertion of the branches and the edge of the patch crown) and another in the middle of the nearest inter-patch area with a metallic tube (5 cm in diameter, 45 cm depth, [Supplementary data Fig. 1](#)) per selected plant patch (16 plant patches and 16 inter-patch areas per site and season = 192 soil cores). After each extraction, we divided each soil core into six subsamples of 5 cm deep (0–5, 5–10, 10–15, 15–20, 20–25, 25–30 cm). Each soil subsample was air-dried to constant weight ([Walworth, 2006](#)) and weighed. Roots were separated from each subsample (192 soil core \times 6 depths = 1152 sub-samples), briefly washed with tap water to remove the adhered soil particles, dried at 45 °C for 48 h and weighed. Root biomass at each depth was expressed as mass per unit area. We assessed the organic C concentration in root biomass through the oxidation of organic matter by dry combustion at 550 °C ([Schlesinger and Hasey, 1981](#)). In this procedure, we assumed that one-half the ash-free mass is considered carbon mass ([Schlesinger and Hasey, 1981](#)). Soil from each subsample was air-dried to constant weight ([Walworth, 2006](#)), sieved to 2 mm mesh and weighed. Soil organic carbon (SOC) at the different depths was assessed by the $K_2Cr_2O_7-H_2SO_4$ oxidation method of Walkey and Black ([Nelson and Sommers, 1982](#)) in soil samples from one randomly selected patch of each patch type and from the corresponding inter-patch area of each site and season [3 sites \times (4 plant patches + 4 inter-patch areas) \times 2

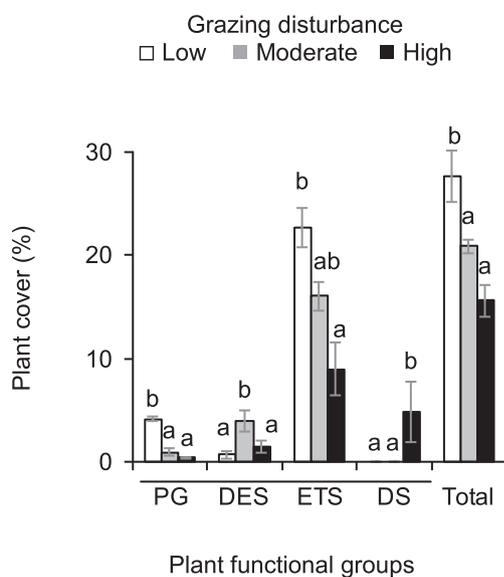


Fig. 2. Plant cover (%) at sites with low, moderate and high grazing disturbance. PG: perennial grasses, DES: deciduous shrubs, ETS: evergreen tall shrubs, and DS: dwarf shrubs. Vertical lines indicate one standard error. Different letters indicate significant differences in total and within each plant functional group cover among sites.

seasons \times 6 depths = 288 sub-samples]. Soil bulk density was determined using the core method in each patch and inter-patch area at each site ([Blake, 1965](#)). To assess bulk density, discounted the weight of roots and gravels from the total soil weight of each subsample and divided this mass by the volume of soil core (5 cm in diameter, 5 cm height).

We analyzed the relative distribution of root biomass (RB) and SOC across the soil profile (0–30 cm) among sites, and patch and inter-patch areas in both seasons:

Relative distribution of RB or SOC in soil profile (%)

$$= \frac{RB \text{ or } SOC_i}{\text{total RB or SOC}} * 100$$

where RB or SOC_{*i*} is the biomass of roots or SOC at soil depth *i* (0–5, 5–10, 10–15, 15–20, 20–25, 25–30 cm), and total RB or SOC is the total root biomass or SOC in soil profile (0–30 cm) at each plant patch and inter-patch area and site.

Total belowground storage of organic C (0–30 cm depth) was calculated as the sum of the organic C content in soil and in root biomass and expressed as grams of C per soil volume (cubic meter).

2.5. Statistical analysis

The significance of the differences in root biomass and SOC among sites (low, moderate and high grazing disturbance), areas (patch and inter-patch areas), season (winter and summer), and depths (0–5, 5–10, 10–15, 15–20, 20–25, 25–30 cm) were analyzed by ANOVA. The significance of the differences in soil bulk density and in the total belowground storage of organic C (C in root biomass + SOC from 0 to 30 cm depth) among sites was also analyzed by ANOVA. Least significant difference test was used for multiple comparisons among sites at each plant functional group, season and area (patch and inter-patch). In those cases where normality and 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](#)). The significance of the differences in the relative distribution of root biomass and SOC across the soil profile (0–30 cm) among sites, and areas in both seasons were assessed by chi-square test. Regression analysis was used to evaluate the relationship between root biomass and SOC. The best least squares fit between a linear and a nonlinear saturation function was selected depending on the shape of the variable response. The level of significance was always $p \leq 0.05$. All statistical analyses were performed with the SPSS 7.5 package for windows ([Norusis, 1997](#)).

3. Results

3.1. Climatic conditions

During the study period (March 2010–February 2011), total precipitation was 132.2 mm ([Fig. 1](#)). The largest daily precipitation event occurred at the end of the summer (11.7 mm) along with intermediate temperature (15.2 °C) but also large daily precipitation events were concentrated in autumn (10.0 mm) and spring (8.6 mm) associated also with intermediate temperatures (10.1 and 8.2 °C). The maximum and minimum daily temperatures were in January (27.5 °C) and August (−1.3 °C), respectively.

3.2. Canopy structure

Total plant cover decreased ($p < 0.01$) with increasing grazing disturbance ([Fig. 2](#)). The cover of evergreen tall shrubs (ETS) and perennial grasses (PG) was higher at the site with low than at those

with moderate and high grazing disturbance, while the opposite occurred with dwarf shrub (DS) cover. The highest cover of deciduous shrubs (DES) occurred at the site with moderate grazing disturbance (Fig. 2).

The most frequent patch types varied from small patches with few species to large patches with numerous species at the three sites. However, the relative dominance of plant functional groups at patch types changed with grazing disturbance (supplementary data Table 2). Most plant patches were dominated by ETS at all sites, except for the site with low grazing disturbance in which one type

of plant patch was exclusively dominated by PG. The relative dominance of PG in plant patches decreased with increasing grazing disturbance, while the opposite occurred with the relative dominance of DS.

3.3. Root biomass

Total root biomass was lower with low than high grazing disturbance ($p < 0.01$) and it did not differ significantly between seasons (low: $p = 0.12$; high: $p = 0.92$). The site with moderate

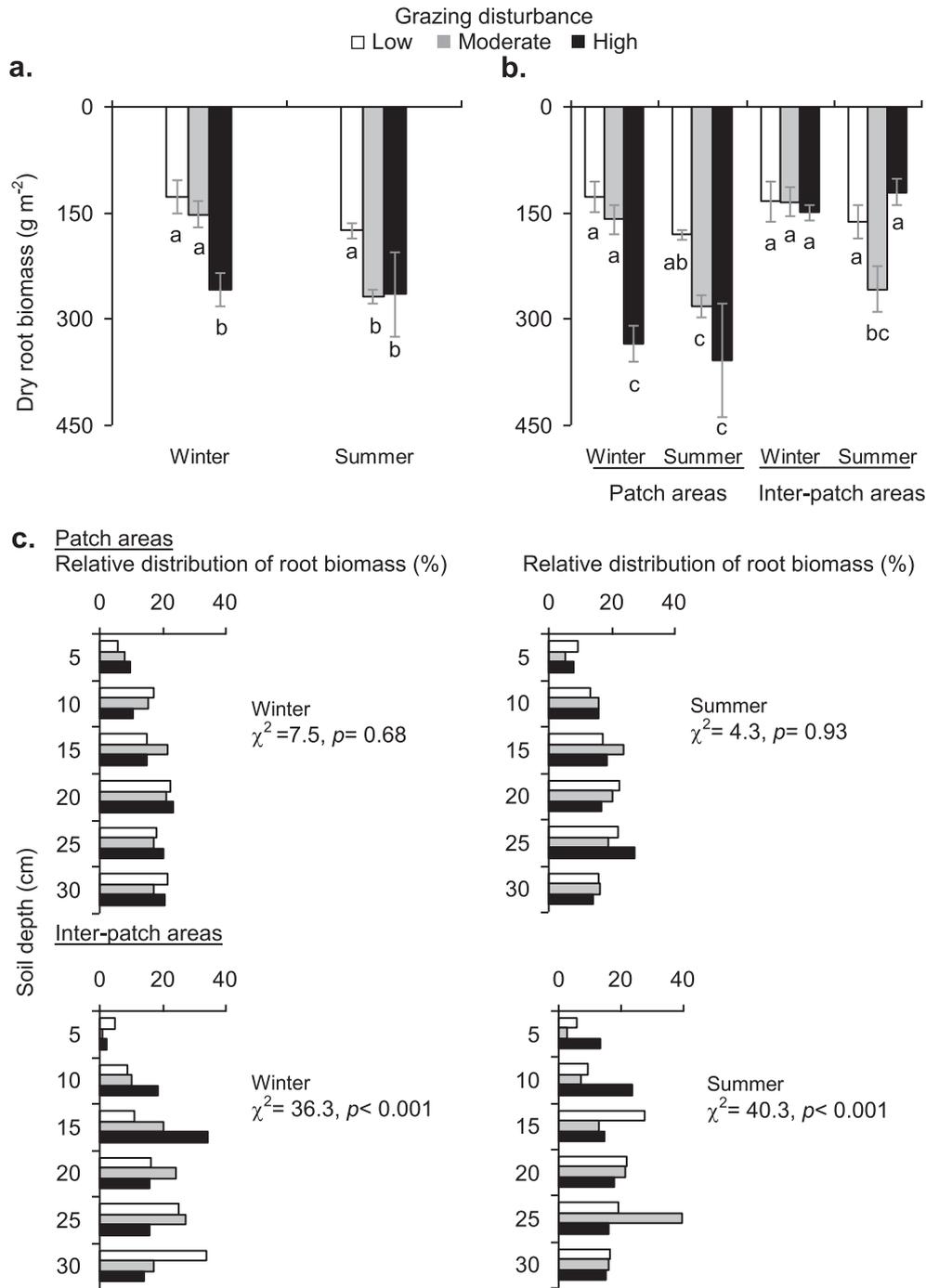


Fig. 3. a. Mean root biomass (g C m⁻², 0–30 cm), b. root biomass in patch and inter-patch areas, and c. relative distribution of root biomass in the soil profile of patch- and inter-patch areas at sites with low, moderate and high grazing disturbance. Vertical lines indicate one standard error. Different letters indicate significant differences among sites and seasons (winter and summer). Chi square values (χ^2) resulting from comparisons of the relative root distribution in the soil profile among sites at patch and inter-patch areas and seasons.

grazing disturbance had lower total root biomass in winter than in summer ($p = 0.02$) (Fig. 3a). Moreover, total root biomass at the site with moderate grazing disturbance did not differ from those with low grazing disturbance in winter and with high grazing disturbance in summer.

Root biomass differed between patch and inter-patch areas depending on the sites ($p < 0.01$) and season ($p < 0.01$) (Fig. 3b). The variability in root biomass between patch and inter-patch areas was larger at the site with high disturbance rather than at those with moderate and low grazing disturbance. Moreover, the root biomass was higher in patch than in inter-patch areas ($p < 0.01$) only at the site with high grazing disturbance. Patch areas exhibited the lowest root biomass under low grazing disturbance and the highest under high grazing disturbance ($p < 0.05$) in both seasons (Fig. 3b). Patch areas with moderate grazing disturbance had lower dry root biomass in winter than in summer (Fig. 3b). Root biomass in the inter-patch areas did not differ between the sites with low and high grazing disturbance and between seasons, while with moderate grazing disturbance, root biomass was higher in summer than in winter. Moreover, in both seasons, root biomass in the inter-patch areas with moderate grazing disturbance did not differ from that in patch areas (Fig. 3b).

The relative distribution of root biomass in the soil profile of patch areas did not vary among sites in both seasons (Fig. 3c). In contrast, the relative distribution of root biomass in the soil profile in the inter-patch areas differed among sites in both seasons (Fig. 3c). In general, root biomass in the inter-patch areas with low grazing disturbance was concentrated below 15 cm of soil depth ($p < 0.05$) while at the site with high grazing disturbance root biomass was concentrated above 15 cm of soil depth ($p < 0.05$). Inter-patch areas with moderate grazing disturbance exhibited the highest values of root biomass at 20–25 cm depth (Fig. 3c).

3.4. Concentration of organic carbon in root biomass

Organic C concentration in root biomass differed among sites depending on the season ($p < 0.001$). Organic C concentration in roots was higher in winter than in summer at sites with low and moderate grazing disturbance, while the reverse occurred at the site with high grazing disturbance (Fig. 4).

3.5. Soil bulk density

Soil bulk density was lower ($p < 0.001$) in patch than inter-patch areas at sites with low and moderate grazing disturbance while it

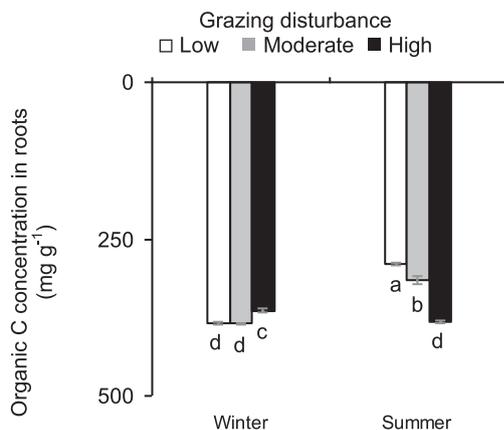


Fig. 4. Organic C concentration in root biomass (mg C g^{-1} roots, 0–30 cm) at sites with low, moderate and high grazing disturbance. Vertical lines indicate one standard error. Different letters indicate significant differences among sites and seasons (winter and summer).

Table 1

Mean \pm one standard error of the soil bulk density (g cm^{-3}) in patch and inter-patch areas at sites with low, moderate and high grazing disturbance. Different letters indicate significant differences among sites at patch and inter-patch areas.

	Soil bulk density (g cm^{-3})	
	Patch area	Inter-patch area
Grazing disturbance		
Low	1.11 \pm 0.03 a	1.19 \pm 0.03 ab
Moderate	1.04 \pm 0.02 a	1.13 \pm 0.03 a
High	1.20 \pm 0.04 b	1.26 \pm 0.04 b

did not differ between areas at site with high grazing disturbance. In both areas, the highest values of soil bulk density were found at the site with high grazing (Table 1).

3.6. Concentration of soil organic carbon (SOC)

SOC differed among sites ($p < 0.01$), showing the lowest values at the site with high grazing disturbance in both seasons (Fig. 5a). SOC was higher in summer than in winter at all sites ($p = 0.04$; Fig. 5a).

SOC was higher in patch than in inter-patch areas at all sites ($p < 0.01$). Both, patch and inter-patch areas, exhibited higher SOC in summer than in winter ($p < 0.01$, Fig. 5b). Patch areas with low grazing disturbance had the highest SOC in winter, while patch areas with moderate grazing disturbance showed the highest SOC in summer (Fig. 5b). Inter-patch areas with high grazing disturbance showed the lowest SOC in winter, while SOC did not differ among sites in summer (Fig. 5b).

SOC decreased with soil depth in both seasons at all sites ($p < 0.05$, Fig. 5c). The relative distribution of SOC in the soil profile did not vary among sites, seasons, and areas ($p > 0.05$, Fig. 5c).

3.7. Relationship between root biomass and soil organic carbon (SOC) across the soil profile

The distribution of root biomass in the soil profile was negatively related to SOC in both patch and inter-patch areas (Fig. 6a and b, respectively). This relationship was stronger in patch than in inter-patch areas.

3.8. Total belowground storage of organic C (C in root biomass + SOC)

The total belowground storage of organic C did not differ among sites ($p = 0.40$), and was higher in summer ($7655.00 \pm 152.55 \text{ g C m}^{-3}$) than in winter ($6176.78 \pm 202.90 \text{ g C m}^{-3}$) ($p < 0.001$, Fig. 7).

4. Discussion

Our findings supported our first hypothesis that the reduction in total plant cover and increased cover of shrubs with shallow rooting depth and high concentration of chemical defenses induced by high grazing disturbance lead to increased total root biomass and spatial heterogeneity of root biomass (concentration of root biomass in patch areas and in the upper soil in the inter-patch areas). These results are consistent with previous studies indicating that grazing disturbance did not affect negatively the allocation of carbon to root biomass in the first 30 cm of soil depth (Larreguy et al., 2012a; Rodríguez et al., 2007). This could be partially associated with the shifting of plant functional groups, varying in rooting depth and aboveground phenological timing induced by grazing (Bertiller et al., 1991; Campanella and Bertiller,

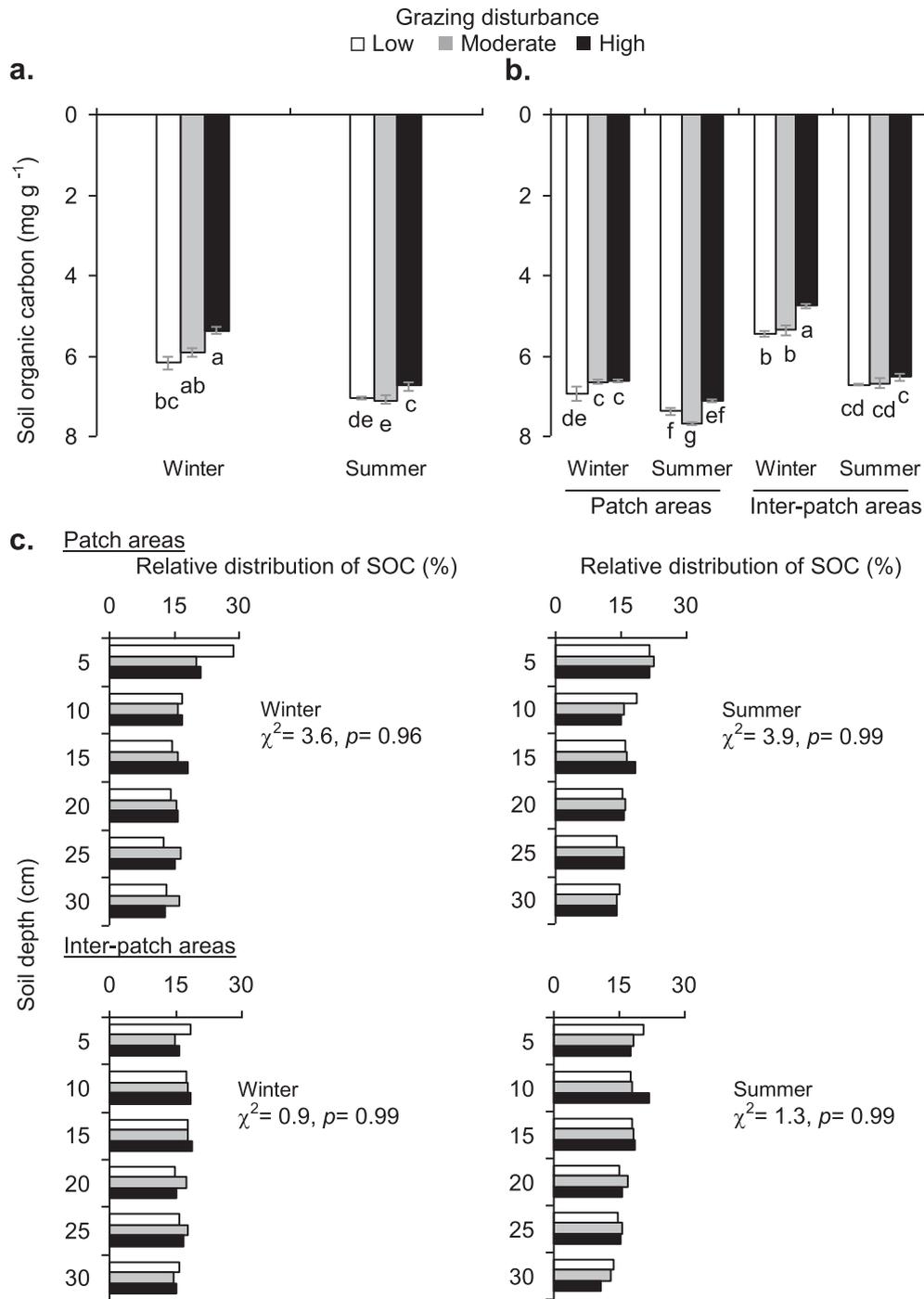


Fig. 5. a. Mean soil organic carbon concentration (SOC, mg C g⁻¹ dry soil) at sites with low, moderate and high grazing disturbance, b. SOC in patch and inter-patch areas at the three sites, and c. relative distribution of SOC (%) in the soil profile of patch- and inter-patch areas at the three sites. Vertical lines indicate one standard error. Different letters indicate significant differences among sites and seasons (winter and summer). Chi square values (χ^2) resulting from comparisons of relative SOC distribution in the soil profile among sites at patch and inter-patch areas and seasons.

2008). Aboveground phenological timing could also be associated with the seasonal variation in root biomass at the site with moderate grazing disturbance (summer > winter), which showed the highest cover of deciduous shrubs (DES). DES species have dimorphic root systems and display a dormancy period from mid-end summer up to the end of winter and vegetative and reproductive growth from spring to mid-end summer (Bertiller et al., 1991; Bucci et al., 2009; Campanella and Bertiller, 2008; Kummerow et al., 1983).

In contrast, the site with low grazing disturbance was mostly dominated by evergreen tall shrubs (ETS) and perennial grasses (PG). ETS may develop vegetative growth independently from water inputs during spring-summer or throughout the year due to their deep or dimorphic root systems (more than 300 cm) reaching more stable water sources stored in deep soil (Casper and Jackson, 1997; Rodríguez et al., 2007). Conversely, PG have shallow root systems and develop vegetative growth coupled with precipitation inputs (Bertiller et al., 1991; Campanella and Bertiller,

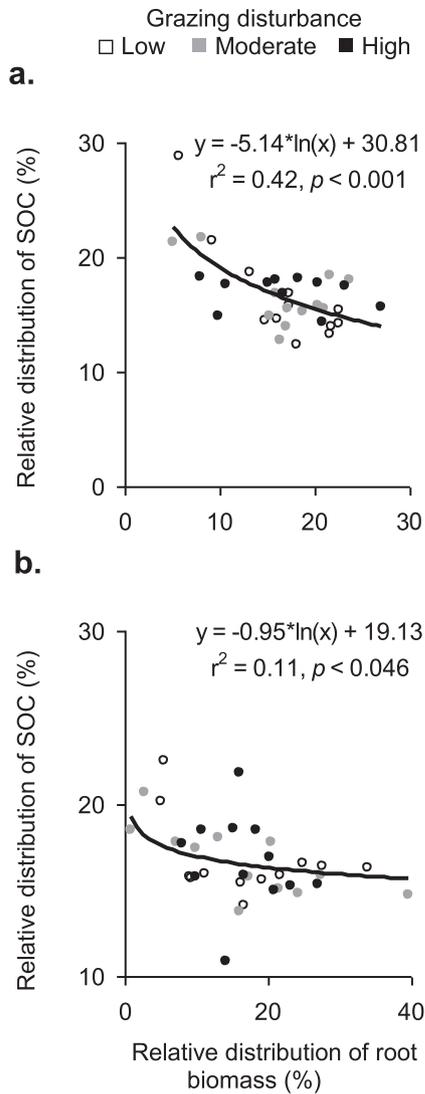


Fig. 6. Relationship between the relative distribution of root biomass and soil organic carbon (SOC, mg C g⁻¹ dry soil) in the soil profile (0–30 cm) at a. patch and b. inter-patch areas.

2008; Casper and Jackson, 1997). The aboveground phenological asynchronism between both plant functional groups and probably differences in root turnover due to differences in root chemistry between them (Rodríguez et al., 2007) could explain the lack of differences in root biomass between seasons.

At the site with high grazing disturbance, ETS and shallow-rooted dwarf shrub (DS) could eventually occupy the upper soil spaces freed by roots of PG with roots with low turnover due to the high concentration of secondary metabolites (Lynch, 2005; Rodríguez et al., 2007). This in turn could decelerate root-mass decay and C input to soil from decomposing tissues (Carrera and Bertiller, 2013; Hoorens et al., 2003). However, this pattern could be different in other ecosystems since the magnitude of the grazing effect on SOC assessed at different spatial scales has not been consistent among studies (Milchunas and Lauenroth, 1993). This in turn, may be attributable to multiple and complex interactions among chemical, physical and biological soil characteristics, plant species composition, management type and climate (Costa et al., 2012; Haferkamp and MacNeil, 2004). The study of these interactions at different scales is necessary to understand the distributions and controls of SOC in different ecosystems and eventually

to use this knowledge in managerial tools oriented to ameliorate the consequences of grazing disturbance on ecosystem function and climate global change.

In accordance with several studies in arid and semiarid ecosystems (Rango et al., 2006; Reynolds et al., 1999), we found that the SOC concentration was higher in plant patch areas than in inter-patch areas at all sites. It is well known the effect of plant canopies on the generation and maintenance of “fertility islands” through the accumulation of plant litter and soil microorganism activity (Burke et al., 1995; Li et al., 2005; Prieto et al., 2011). In contrast inter-patch areas receive less litter and are more exposed to wind and water erosion and more prone to lose litter and soil organic matter than patch areas (Rostagno et al., 1991; Vásquez-Méndez et al., 2011). Also, decreased SOC with soil depth at both patch and inter-patch areas could be explained by the input of organic C from aboveground litter and/or the high fine root turnover rate in the upper soil due to the frequent changes in soil water conditions (Jobbágy and Jackson, 2000; Larreguy et al., 2012b; Parras-Alcántara et al., 2013). Grazing disturbance led to reduced amount of SOC probably in relation to reduced total plant cover, lower litterfall, and higher above and below-ground plant litter recalcitrance (Carrera et al., 2008; Larreguy et al., 2012b). These findings partially supported our second hypothesis that vegetation changes induced by grazing, probably associated with increased soil exposure to water and wind erosion, led to decreasing SOC (e.g. Bisigato et al., 2008; Schlesinger et al., 1990). Additionally, increasing grazing disturbance led to the increase in soil bulk density probably due to increasing effect of trampling (Prieto et al., 2011; Steffens et al., 2008). Mean values of soil bulk density assessed in this study (1.04–1.26 g cm⁻³) were within the range values or slightly lower than those reported for other arid ecosystems (1.15–1.56 g cm⁻³, Rostagno et al., 1991; Wang et al., 2010).

SOC values at the three sites were within the range of values reported for shrublands (2800–8700 g m⁻³, Carrera et al., 2007; Conti and Díaz, 2013; Jobbágy and Jackson, 2000). However, the spatial (vertical and horizontal) heterogeneity of SOC did not change with grazing disturbance. The contrasting patterns in the spatial distribution of root biomass and SOC could indicate that the spatial distribution of SOC is less affected by belowground litter than by the amount and recalcitrance of aboveground litter (Jobbágy and Jackson, 2000). These results provided evidence in relation to hypothesis 3 indicating that the reductions in SOC were compensated with increasing C in roots under high grazing disturbance resulting in low or null changes in total belowground

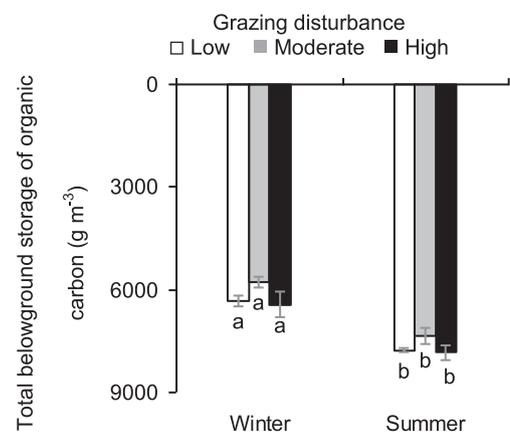


Fig. 7. Total belowground storage of organic C (g C m⁻³) at sites with low, moderate and high grazing disturbance. Vertical lines indicate one standard error. Different letters indicate significant differences among sites and seasons (winter and summer).

stocks of organic C. However, long-term simulation models of C dynamic predicted a slight increase in SOC during the current century in degraded lands and under grazing disturbance (Carrera et al., 2007; Derner and Schuman, 2007). These studies suggested that accumulations of soil organic matter could occur when other factors such as temperature, moisture, and litter quality would limit the activity of decomposer organisms (Schlesinger and Andrews, 2000). Our results showing increasing SOC in summer could further provide some evidence in relation to the long term effect of increasing temperature on SOC.

5. Conclusion

High grazing disturbance lead to increased total root biomass, concentration of root biomass in patch areas, concentration of root biomass in the upper soil of inter-patch areas, and decreased SOC. We associated root biomass changes with increasing abundance of woody plants with shallow or dimorphic root systems. We speculated that the reduction in SOC under high grazing disturbance could be the effect of reduced amount and increased recalcitrance mainly of aboveground litter inputs decelerating litter decomposition and organic matter inputs to soils. Contrasting variation patterns of root biomass and SOC resulted in no changes in the total belowground C storage with grazing disturbance. These results are important to enhance our capacity to predict and ameliorate the consequences of grazing disturbance on ecosystem function and global change.

Acknowledgments

This research was funded by ANPCYT-FONCYT (PICTs 02-02192, 08-1349), CONICET (PIP-112-200801-01664) and Chubut Province (PID 08-18) of Argentina. C. Larreguy's fellowship is supported by CONICET (National Research Council of Argentina). Recognition is also given to Fundación Patagonia Natural who allowed access to the study area in Refugio de Vida Silvestre La Esperanza.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jenvman.2013.12.024>

References

- Angassa, A., 2012. Effects of grazing intensity and bush encroachment on herbaceous species and rangeland condition in southern Ethiopia. *Land Degrad. Dev.* <http://dx.doi.org/10.1002/ldr.2160>.
- Ares, J.O., Beeskow, A.M., Bertiller, M.B., Rostagno, C.M., Irisarri, M., Anchorena, J., Defossé, G., Merino, C., 1990. Structural and dynamic characteristics of overgrazed lands of northern Patagonia, Argentina. In: Breymer, A. (Ed.), *Managed Grasslands*. Elsevier Science, Amsterdam, pp. 149–175.
- Ares, J., Bertiller, M., Bisigato, A., 2003. Modeling and measurement of structural changes at a landscape scale in dryland areas. *Environ. Model. Assess.* 8, 1–13.
- Austin, A.T., Yahdjian, L., Stara, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A., Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141, 221–235.
- Bär Lamas, M.I., Larreguy, C., Carrera, A.L., Bertiller, M.B., 2013. Changes in plant cover and functional traits induced by grazing in the arid Patagonian Monte. *Acta Oecol.* 51, 66–73.
- Barros, V., Rivero, M., 1982. Mapas de probabilidad de precipitación de la Provincia del Chubut. In: *Monografía*, vol. 54. Centro Nacional Patagónico, Puerto Madryn, Chubut.
- Bertiller, M.B., Bisigato, A.J., 1998. Vegetation dynamics under grazing disturbance. The state- and- transition model for the Patagonian steppes. *Ecol. Austral.* 8, 191–199.
- Bertiller, M.B., Beeskow, A.M., Coronato, F., 1991. Seasonal environmental variation and plant phenology in arid Patagonia (Argentina). *J. Arid. Environ.* 21, 1–11.
- Bertiller, M.B., Ares, J.O., 2011. Does sheep selectivity along grazing paths negatively affect biological crusts and soil seed banks in arid shrublands? A case study in the Patagonian Monte, Argentina. *J. Environ. Manage.* 92, 2091–2096.
- Bisigato, A.J., Bertiller, M.B., 1997. Grazing effects on patchy dryland vegetation in northern Patagonia. *J. Arid. Environ.* 36, 639–653.
- Bisigato, A., Lopez Laphitz, R., Carrera, A., 2008. Non-linear relationships between grazing pressure and conservation of soil resources in Patagonian Monte shrublands. *J. Arid. Environ.* 72, 1464–1475.
- Blake, G.R., 1965. Bulk density. In: Black, C.A., Evans, D.D., White, J.L., Ensminger, L.E., Clark, F.E. (Eds.), *Methods of Soil Analysis. Physical and Mineralogical Properties, Including Statistics of Measurement and Sampling*. American Society of Agronomy, Madison, pp. 374–390.
- Bucci, S., Scholz, F.G., Goldstein, G., Meinzer, F.C., Arce, M.E., 2009. Soil water availability and rooting depth as determinants of hydraulic architecture of Patagonian woody species. *Oecologia* 160, 631–641.
- Burke, I.C., Lauenroth, W.K., Coffin, D.P., 1995. Soil organic matter recovery in semiarid grasslands: implications for the conservation Reserve Program. *Ecol. Appl.* 5, 793–801.
- Campanella, M.V., Bertiller, M.B., 2008. Plant phenology, leaf traits, and leaf litterfall of contrasting life forms in arid Patagonian Monte, Argentina. *J. Veg. Sci.* 19, 75–85.
- Carrera, A., Bertiller, M.B., Larreguy, C., 2008. Leaf litterfall, fine-root production, and decomposition in shrublands with different canopy structure induced by grazing in the Patagonian Monte, Argentina. *Plant Soil* 311, 39–50.
- Carrera, A., Ares, J., Labraga, J., Thurner, S., Bertiller, M., 2007. Scenarios of future climate and land management forcing on carbon stocks in northern Patagonian shrublands. *Environ. Manage.* 40, 944–957.
- Carrera, A.L., Bertiller, M.B., 2013. Combined effects of leaf litter and soil microsite on decomposition process in arid rangelands. *J. Environ. Manage.* 114, 505–511.
- Casper, B., Jackson, R.B., 1997. Plant competition underground. *Annu. Rev. Ecol. Syst.* 28, 545–570.
- Chapin, F.S., Ruess, R.W., 2001. The roots of the matter. *Nature* 411, 749–752.
- Coronato, F.R., Bertiller, M.B., 1997. Climatic of soil moisture dynamics in an arid steppe of northern Patagonia, Argentina. *Arid. Soil. Res. Rehab.* 11, 277–288.
- Conti, G., Diaz, S., 2013. Plant functional diversity and carbon storage – an empirical test in semi-arid forest ecosystems. *J. Ecol.* 101, 18–28.
- Costa, C., Papatheodorou, E.M., Monokrousos, N., Stamou, G.P., 2012. Spatial variability of soil organic C, inorganic N and extractable P in a Mediterranean grazed area. *Land Degrad. Dev.* <http://dx.doi.org/10.1002/ldr.2188>.
- del Valle, H.F., 1998. Patagonian soils: a regional synthesis. *Ecol. Austral.* 8, 103–123.
- Derner, J.D., Schuman, G.E., 2007. Carbon sequestration and rangelands: a synthesis of land management and precipitation effects. *J. Soil. Water Conserv.* 62, 77–85.
- Grace, J., 1998. Plant water relations. In: Crawley, M.J. (Ed.), *Plant Ecology*. Blackwell Science, Oxford, pp. 28–50.
- Haferkamp, M.R., MacNeil, M.D., 2004. Grazing effects on carbon dynamics in the Northern Mixed-Grass Prairie. *Env. Manag.* 33, 462–474.
- Hoorens, B., Aerts, R., Stroetenga, M., 2003. Does initial litter chemistry explain litter mixture effects on decomposition? *Oecologia* 142, 578–586.
- Jackson, R.B., Schenk, H.J., Jobbágy, E.G., Canadell, J., Colello, G.D., Dickinson, R.E., Field, D.B., Friedlingstein, P., Heimann, M., Hibbard, K., Kicklighter, D.W., Kleidon, A., Neilson, R.P., Parton, W.J., Sala, O.E., Sykes, M.T., 2000. Belowground consequences of vegetation change and their treatment in models. *Ecol. Appl.* 10, 70–483.
- Jobbágy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.* 10, 423–436.
- Körner, C., 1993. Scaling from species to vegetation: the usefulness of functional groups. In: Schulze, E.D., Mooney, H.A. (Eds.), *Biodiversity and Ecosystem Function*. Springer-Verlag, New York, pp. 117–140.
- Kröpfl, A.I., Cecchi, G.A., Villasuso, N.M., Distel, R.A., 2011. Degradation and recovery processes in semi-arid patchy rangelands of northern Patagonia, Argentina. *Land Degrad. Dev.* 24, 393–399.
- Kummerow, J., Ellis, B.A., Kummerow, S., Chapin, F.S., 1983. Spring growth of Shoots and roots in shrubs of an Alaskan Muskog. *Am. J. Bot.* 70, 1509–1515. <http://www.jstor.org/action/showPublicationInfo?journalCode=americanbotany>.
- Lal, R., 2004a. Soil carbon sequestration to mitigate climate change. *Geoderma* 123, 1–22.
- Lal, R., 2004b. Soil carbon sequestration impacts on global climate change and food security. *Science* 304, 1623–1627.
- Lal, R., 2011. Sequestering carbon in soils of agro-ecosystems. *Food Policy* 36, 533–539.
- Larreguy, C., Carrera, A.L., Bertiller, M.B., 2012a. Production and turnover rates of shallow fine roots in rangelands of the Patagonian Monte, Argentina. *Ecol. Res.* 27, 61–68.
- Larreguy, C., Carrera, A.L., Bertiller, M., 2012b. Biomasa radical y carbono orgánico del suelo en el noreste de Chubut. In: *Actas del XIX Congreso Latinoamericano de la Ciencia del Suelo y XXIII Congreso Argentino de la Ciencia del Suelo*. Mar del Plata, Buenos Aires, p. 5.
- León, R.J.C., Bran, D., Collantes, M., Paruelo, J.M., Soriano, A., 1998. Grandes unidades de vegetación de la Patagonia extra andina. *Ecol. Austral.* 8, 125–144.
- Li, Q., Mayzlish, E., Shamir, I., Pen-Mouratov, S., Sternberg, M., Steinberger, Y., 2005. Impact of grazing on soil biota in a Mediterranean grassland. *Land Degrad. Dev.* 16, 581–592.
- Lynch, J.P., 2005. Root architecture and nutrient acquisition. In: BassiriRad, H. (Ed.), *Nutrient Acquisition by Plants*. Springer, Berlin Heidelberg, pp. 147–183.
- Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol. Monogr.* 63, 327–366.
- Moreno, L., Bertiller, M.B., Carrera, A.L., 2010. Changes in traits of shrub canopies across an aridity gradient in northern Patagonia, Argentina. *Basic Appl. Ecol.* 11, 693–701.
- Mueller-Dombois, D., Ellenberg, H., 1974. *Aims and Methods of Vegetation Ecology*. John Wiley and Sons, New York.

- Muñoz-Rojas, M., Jordán, A., Zavala, L.M., De la Rosa, D., Abd-Elmabod, S.K., Anaya-Romero, M., 2012a. Organic carbon stocks in Mediterranean soil types under different land uses (Southern Spain). *Solid Earth* 3, 375–386.
- Muñoz-Rojas, M., Jordán, A., Zavala, L.M., De la Rosa, D., Abd-Elmabod, S.K., Anaya-Romero, M., 2012b. Impact of land use and land cover changes on organic carbon stocks in Mediterranean soils (1956–2007). *Land Degrad. Dev.* <http://dx.doi.org/10.1002/ldr.2194>.
- Nelson, D.W., Sommers, L.E., 1982. Total carbon, organic carbon and organic matter. In: Page, A.L., Miller, D.H., Keeney, D.R. (Eds.), *Methods of Soil Analysis*. ASA, SSSA, Madison, Wis, pp. 539–579.
- Norusis, M.J., 1997. *SPSS Advanced Statistics 7.5*. SPSS, Inc., Chicago.
- Parras-Alcántara, L., Martín-Carrillo, M., Lozano-García, B., 2013. Impacts of land use change in soil carbon and nitrogen in a Mediterranean agricultural area (Southern Spain). *Solid Earth* 4, 167–177.
- Prieto, L.H., Bertiller, M.B., Carrera, A.L., Olivera, N.L., 2011. Soil enzyme and microbial activities in a grazing ecosystem of Patagonian Monte, Argentina. *Geoderma* 162, 281–287.
- Rango, A., Tartowski, S.L., Laliberte, A., Wainwright, J., Parsons, A., 2006. Islands of hydrologically enhanced biotic productivity in natural and managed arid ecosystems. *J. Arid. Environ.* 65, 235–252.
- Reynolds, J.F., Kemp, P.R., Ogle, K., Fernandez, R.J., 2004. Modifying the “pulse-reserve” paradigm for deserts of North America: precipitation pulses, soil water and plant responses. *Oecologia* 141, 194–210.
- Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soya, A.G., Tremmel, D.C., 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecol. Monogr.* 69, 69–106.
- Rodríguez, M.V., Bertiller, M.B., Sain, C.L., 2007. Spatial patterns and chemical characteristics of root biomass in ecosystems of the Patagonian Monte disturbed by grazing. *J. Arid. Environ.* 70, 137–151.
- Rostagno, C.M., del Valle, H.F., Videla, L., 1991. The influence of shrubs on some chemical and physical properties of an aridic soil in north-eastern Patagonia, Argentina. *J. Arid. Environ.* 20, 1–10.
- Sala, O.E., Parton, W.J., Joyce, L.A., Lauenroth, W.K., 1988. Primary production of the central grassland region of the United States. *J. Ecol.* 69, 40–45.
- Schenk, H.J., Jackson, R.B., 2002. The global biogeography of roots. *Ecol. Monogr.* 72, 311–328.
- Schlesinger, W.H., Andrews, J.A., 2000. Soil respiration and the global carbon cycle. *Biogeochemistry* 48, 7–20.
- Schlesinger, W.H., 1997. *Biogeochemistry: an Analysis of Global Change*. National Academic Press, New York.
- Schlesinger, W.H., Hasey, M.M., 1981. Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. *Ecology* 62, 762–774.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification. *Science* 27, 1043–1048.
- Scholz, F.G., Bucci, S.J., Arias, N., Meinzer, F.C., Goldstein, G., 2012. Osmotic and elastic adjustments in cold desert shrubs differing in rooting depth: coping with drought and subzero temperatures. *Oecologia* 170, 885–897.
- Snyman, H.A., 2009. Root studies on grass species in a semi-arid South Africa along a degradation gradient. *Agric. Ecosyst. Environ.* 130, 100–108.
- Soil Survey Staff, 1998. *Keys to Soil Taxonomy*. USDA, Washington.
- Sokal, R.R., Rohlf, F.J., 1981. *Biometry*. Freeman, San Francisco, C A.
- Steffens, M., Kölbl, A., Totsche, K.U., Kögel-Knabner, I., 2008. Grazing effects on soil chemical and physical properties in semiarid steppe of Inner Mongolia (P.R. China). *Geoderma* 143, 63–72.
- Vásquez-Méndez, R., Ventura-Ramos, E., Oleschko, K., Hernández-Sandoval, L., Domínguez-Cortázar, M.A., 2011. Soil erosion processes in semiarid areas: the importance of native vegetation. In: Godone, D., Stanchi, S. (Eds.), *Soil Erosion Studies*. Intech, pp. 26–40.
- Verlinden, A., Kruger, A.S., 2007. Changing grazing systems in central north Namibia. *Land Degrad. Dev.* 18, 179–197.
- Walworth, J.L., 2006. *Soil Sampling and Analysis*. In: *Laboratories Conducting Soil, Plant, Feed or Water Testing*. The University of Arizona Publication, p. AZ1111. <http://cals.arizona.edu/pubs/garden/az1111.pdf>.
- Wang, Y., Li, Y., Ye, X., Chu, Y., Wang, X., 2010. Profile storage of organic/inorganic carbon in soil: from forest to desert. *Sci. Total Environ.* 408, 1925–1931.
- Whitford, W., 2002. Decomposition and nutrient cycling. In: Whitford, W. (Ed.), *Ecology of Desert Systems*. Academic Press, San Diego, CA, pp. 235–274.
- Zhao, T., Sakai, K., Higashi, T., Komatsuzaki, M., 2004. Assessing soil organic carbon using portable hyper-spectral camera in Andisols. *J. Agric. Sci. Appl.* 1, 132–138.
- Zhao, W., Chen, S.P., Han, X.G., Lin, G.H., 2009. Effects of long-term grazing on the morphological and functional traits of *Leymus chinensis* in the semiarid grassland of Inner Mongolia, China. *Ecol. Res.* 24, 99–108.