Soil respiration in Patagonian semiarid grasslands under contrasting environmental and use conditions

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ABSTRACT

Grasslands comprise 85% of Southern Patagonia land area and play a critical role in the global carbon cycle. We evaluated seasonal dynamics to identify differences in soil respiration rates between contrasting grasslands across a climate gradient (rainfall), long term grazing intensity (moderate and high stocking rates) and land uses (silvopastoral system, primary forest and grassland). Soil respiration varied from 0.09 g CO_2 h^{-1} m^{-2} in winter to a maximum of 1.43 g CO_2 h^{-1} m^{-2} in spring. We found that the soil respiration rate was 30% higher in moderately grazed grasslands than in heavily grazed grasslands. Land-use changes showed that soil respiration followed the order silvopastoral system > native forest > grassland. While almost all plant and soil variables had a significant effect on soil respiration, soil carbon concentration, litter cover and depth and bare soil cover were the main factors explaining 78−83% of the variance in soil respiration. Soil respiration rates were correlated strongly to air and soil temperatures and to a lesser extent with mean monthly rainfall and soil volumetric water content. The information provided in the present work about soil respiration is essential to estimate carbon balance for a range of important and widespread ecosystems in Patagonia.

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1. Introduction

In Santa Cruz province (area of 243,943 km², from 46° to 52° 30′S), grasslands comprise approximately 85% of the total land area, where the main activity is extensive sheep production, with stocking rates ranging from 0.13 to 0.75 head ha^{-1} yr^{-1}. In this province, deciduous *Nothofagus antarctica* forest cover 159,720 ha in a narrow (50 km wide) and long (1000 km) strip of land along the Andes Mountains, which has been historically used as silvopastoral systems, with livestock feeding on natural grasslands that grow in the understory of thinned forests (Peri et al., 2009a).

Concern about global climate change has focused attention on the stocks and flows of the global carbon cycle mainly under Article 3.4 of the Kyoto Protocol of the United Nations Framework Convention on Climate Change (IPCC, 2001). In Southern Patagonia (Santa Cruz and Tierra del Fuego provinces), mean maximum annual temperature is predicted to increase by 2−3 °C in 2080 between 46 and 52° 30′ SL (Kreps et al., 2012) and this would have

significant effects on Patagonian ecosystems. In this context, data on C storage in forests, grasslands and shrublands are essential for understanding the importance of rapidly increasing level of CO_2 in the atmosphere and its potential effect on global climate change. In Southern Patagonia, studies have estimated the C sequestration in different ecosystems (Peri and Lasagno, 2009, 2010; Peri et al., 2010; Peri, 2011). Total C storage (above- and belowground-biomass) ranged from 4.9 Mg C ha^{-1} (dominant *Jarava chrysophylla* and *Poa spiciformis* grassland with 40% bare soil) to 182.0 Mg C ha^{-1} (optimal growth stands in *N. antarctica* forest growing at good quality sites). Also, the effect of long-term livestock grazing on C content of the plant-soil grassland system (0.30 m depth) of Dry Magellanic Grass Steppe and Sub-andean Grassland areas in Southern Patagonia has been reported (Peri, 2011). On these extensively managed grasslands, grazing intensity was the main management practice that affected ecosystem C levels with values ranging from 50 Mg C ha^{-1} at a heavy stocking rate (0.70 ewe ha^{-1} yr^{-1}) to 130 Mg C ha^{-1} under low grazing intensity (0.10 ewe ha^{-1} yr^{-1}). Peri et al. (2009b) reported the aboveground and belowground C sequestration for different components of trees and pasture (green and dead leaves, pseudostem and coarse and fine roots), and the C storage in leaf litter in an

N. antarctica silvopastoral system which varied according to silviculture practice (thinning intensity) and site quality. In these Patagonian ecosystems, soil C constitutes between 79 and 90% of the total C depending on plant functional types and environmental conditions (Peri and Lasagno, 2009, 2010; Peri et al., 2010; Peri, 2011). This is important because soils contain up to three times more carbon than the global vegetation pool and atmosphere combined and this large carbon pool is vulnerable to land-use change and management (Trumbore, 2009).

However, it is necessary to quantify the net amount of C sequestration of all C pools and fluxes within an ecosystem in order to best estimate its contribution and effectiveness in mitigating atmospheric CO_2. Soil respiration, produced mainly by roots and soil organisms (mycorrhizal fungi and microbial), and to a lesser extent, chemical oxidation of carbon compounds, is the primary pathway for CO_2 fixed by plants to return to the atmosphere. Soil respiration is therefore a key process that needs to be considered to understand the terrestrial carbon cycle. Several studies in different ecosystems and land uses (grasslands, forests and agroforestry systems) have analysed the relative contribution of environmental (soil temperature and moisture, substrate availability and quality) and management (grazing, cropping) on soil respiration (Lloyd and Taylor, 1994; Raich and Tufekcioglu, 2000; Lee and Jose, 2003; Hibbard et al., 2005; Wang and Fang, 2009). Soil respiration also varies with vegetation and among major biome types (Raich and Schlesinger, 1992). Such findings indicate that environment, human activities and vegetation type are important determinants of soil respiration rate, and therefore that changes in these factors have the potential to modify the responses of soils. In this context, this study is the first to examine and compare the soil respiration within temperate and semiarid grassland ecosystems in Southern Patagonia. Our objective was to evaluate the main factors that might influence soil respiration rates in response to climate, grazing and land use. For this, we evaluated: 1. the seasonal dynamics of soil respiration rates between contrasting grasslands across a climate (precipitation and temperature) gradient; 2. the effects of long term grazing intensity on temporal variation of soil CO_2 efflux from dry and humid Magellanic grass steppe areas in Southern Patagonia and 3. soil respiration in response to land-management practices by comparing silvopastoral systems, primary forest and the adjacent open grassland site. In this context, we hypothesized that: (i) vegetation type mainly influences soil respiration rates across a climate and vegetation gradient in grasslands under low-moderate grazing intensity, (ii) high stocking rates mostly affects negatively soil respiration through its effect on plants and soil parameters and (iii) soil respiration in woody communities is higher than in grasslands.

2. Materials and methods

The study was conducted in permanent plots established as part of PEBANPA network (Biodiversity and Ecological long-term plots in Southern Patagonia). In Santa Cruz province, rainfall decreases from 800-1000 mm–200 mm yr^{-1} from west to east across the Andes Mountains that act as an orographic barrier to moist winds coming from the west. The wide range of precipitation and soil characteristics in Patagonia, between the deciduous *Nothofagus* forest in the west and the steppe in the east, constitutes an outstanding vegetation gradient. The climate in this region is dry, cold and windy. Temperatures are highest from December to February, and at a minimum in June–July. Summers are short, but with long days due to latitude. The windiest season is from November until March. The predominant wind direction is from the south-southwest. Severe and frequent windstorms occur in spring and summer, with windspeeds over 120 km h^{-1} (Peri and Bloomberg, 2002).

2.1. Study sites in a vegetation and climate gradient

To identify potential differences in soil respiration rates related to contrasting grasslands across a climate gradient, three study areas of 25 km^2 (5 × 5 km) were selected representing main grassland ecosystems in the Magellanic grass steppe (centre of study area located at 51° 30′ 51″S, 70° 04′ 55″W), "mata negra" Matorral Thicket (51° 07′ 23″S, 70° 58′ 38″W) and Andean (51° 12′ 54″S, 72° 08′ 29″W) ecological areas in Santa Cruz province, southern Patagonia, Argentina. The selected study sites corresponded to a low-moderate grazing intensity. The estimation of carrying capacity was based on the biomass production of short grasses and forbs that grow in the space among tussocks of each ecological area and the requirements of 530 kg DM yr^{-1} for 1 Corriedale ewe of 49 kg of live weight which represents a "Patagonian sheep unit equivalent (PSUE)" (Borrelli, 2001). Most of the grazing plans consisted of an adaptive scheme based on year-round continuous grazing with variable animal stocking rate adjusted yearly according to herbage mass assessments.

In the Magellanic grass steppe, the vegetation is dominated by the tussock *Jarava chrysophylla* (40–60%) and associated with *Poa spiciformis*, *Carex andina*, *Rytidosperma virescens*, *Acaena* sp., dwarf-shrubs *Nardophyllum bryoides*, *Ephedra frustillata* and *Perezia recurvata*, and shrubs *Berberis microphylla* and *Junellia tridens*. The mean long term stocking rate was 0.31 ewe ha^{-1} yr^{-1}, mean annual precipitation (MAP) of 235 mm yr^{-1} and mean annual temperature (MAT) of 7.1 °C (mean of 11.9 °C in summer and 1.2 °C in winter).

The vegetation of the Matorral Thicket site is dominated by the shrub *J. tridens* (30–35%) and associated with grasses *J. chrysophylla*, *Jarava ibari*, *Bromus setifolius*, *Festuca pyrogea*, dwarf-shrubs *Clinopodium darwinii*, *Nassauvia aculeata*, *Nassauvia glomerulosa*, *N. bryoides* and herbs (*Cerastium arvense*, *Acaena poeppigiana*). The mean long term stocking rate was 0.22 ewe ha^{-1} yr^{-1}, MAP of 155 mm yr^{-1} and MAT of 6.5 °C.

The vegetation in the Andean ecological area is dominated by *Festuca pallescens* (20–30%), *Phleum alpinum*, *B. setifolius*, *Agrostis flavidula*, *Carex argentina*, *Poa pratensis* and *Azorella monantha*. The mean historical stocking rate was 0.45 ewe ha^{-1} yr^{-1}, MAP of 390 mm yr^{-1} and MAT of 4.9 °C.

2.2. Study sites for grazing intensity

Two study areas of 25 km^2 (5 × 5 km) were selected in both the dry and humid Magellanic steppe areas, to evaluate two long term grazing intensities (moderate and high stocking rates) on soil respiration. In the dry Magellanic steppe, moderate stocking rate represented 0.26 ewe ha^{-1} yr^{-1} (centre of study area located at 51° 32′ 40″S, 69° 16′ 38″W) and high stocking rate had 0.51 ewe ha^{-1} yr^{-1} (51° 31′ 01″S, 69° 30′ 31″W). The vegetation is dominated by tussocks of *Festuca gracillima* and associated with short grasses *P. spiciformis*, *B. setifolius* and *Hordeum comosum*, graminoids (*Carex* spp.), herbs (*Viola maculata*, *Calceolaria uniflora*) and dwarf-shrub (*N. bryoides*, *Nassauvia ulicina*, *Azorella fuegiana*). The MAP is 240 mm yr^{-1} and MAT of 7.7 °C (mean of 12.8 °C in summer and 1.5 °C in winter).

In the humid Magellanic steppe, moderate stocking rate represented 0.40 ewe ha^{-1} yr^{-1} (centre of study area located at 51° 48′ 19″S, 69° 40′ 38″W) and high stocking rate had 0.85 ewe ha^{-1} yr^{-1} (51° 54′ 44″S, 69° 39′ 12″W). The vegetation is dominated by tussocks of *F. gracillima* (20–30%) and associated with grasses *Festuca magellanica*, *P. spiciformis*, *R. virescens*, *B. setifolium*, *Agropyron fuegianum*, graminoids (*Carex* spp.), dwarf-shrubs (*C. darwinii*, *Senecio laseguei*) and herbs (*Calceolaria polyrrhiza*). The site is characterized

by a MAP of 265 mm yr^{-1} and a MAT of 6.9 °C.

2.3. Study sites for land use

To determine potential differences in soil respiration to land-management practices, three study areas of 10 ha were selected in an *N. antarctica* forest under silvopastoral use (centre of study area located at 51° 13′ 21″S, 72° 15′ 34″W), primary forest (51° 13′ 09″S, 72° 16′ 13″W) and adjacent open grassland site. The open site corresponds to the Andean ecological area used for the study of vegetation and climate gradient (51° 12′ 54″S, 72° 08′ 29″W). Stands were characterized with three circular plots of 500 m^2. In the silvopastoral system, the stand was characterized by 410 trees ha^{-1}, mean diameter at breast height (DBH) of 28.3 cm, a total dominant height of 8.1 m, a basal area of 47.1 m^2 ha^{-1} and a crown cover of 52%. In contrast, the primary forest had 850 trees ha^{-1}, mean DBH of 21.6 cm, a total dominant height of 7.9 m, a basal area of 52.2 m^2 ha^{-1} and a crown cover of 85%. The vegetation in the silvopastoral system site is dominated by *C. andina* (20−30%), *Poa pratensis*, *Phleum commutatum*, *Dactylis glomerata*, *B. setifolius*, *Agrostis flavidula*, *Deschampsia flexuosa* and *F. pallescens*. The mean historical stocking in the silvopastoral system rate was 0.57 ewe ha^{-1} yr^{-1}. The vegetation in the primary forest site is dominated by shade tolerant herbs (*Osmorhiza chilensis*, *Phaiophleps biflora*), shrubs (*Baccharis magellanica*, *Senecio filaginoides*) and grasses (*D. flexuosa*). These study sites had a mean annual precipitation (MAP) of 420 mm yr^{-1} and a mean annual temperature (MAT) of 5.1 °C.

2.4. Soil respiration measurements

Measurements of CO_2 resulting from soil respiration (both from roots and micro-organisms) were taken from each site in spring (November), summer (January−February), autumn (April) and winter (July) during 2011−2013 using the soda lime method (Edwards, 1982). Keith and Wong (2006) determined that measurement of CO_2 efflux by soda lime absorption was quantitatively similar and unbiased in relation to the flow-through non-steady-state IRGA method. For this, five sampling stations were randomly chosen in each study site. At each point, white opaque plastic respiration chambers (10 cm height × 21 cm diameter), with a well-sealed lid, installed at a depth of 1 cm were inverted over open jars (diameter of 7 cm) containing 50 g of previously dried (105 °C, 24 h) and weighted soda lime granules. The area inside the chamber was cleaned of all green plants and any organic living matter. After 24 h, the soda lime jars were capped, transported to the laboratory, dried at 105 °C for 24 h, and reweighted. Two blanks chambers per site of the same cut-off bucket with well-sealed lid were employed by using capped jars of soda lime to account for minute gains in CO_2 that occurred during oven drying (the only time that the blanks were left uncapped). Soil respiration (g CO_2 h^{-1} m^{-2}) was calculated by multiplying field estimates by a correction factor of 1.69 to allow for loss upon drying of water produced by adsorption of CO_2 by soda lime (Keith and Wong, 2006).

2.5. Environmental and plant measurements

Air and soil temperatures, and air relative humidity were measured continuously every 2 h with a datalogging system (HOBO H8 Family, Onset Computer Corporation, USA), using sensors located at each study site. Rainfall for most sites were obtained from the WorldClim data set (Hijmans et al., 2005), but also rainfall records were obtained from the Río Gallegos and Río Turbio airports (Servicio Meteorológico Nacional, Buenos Aires, Argentina), which are located near (20−30 km) four of the study sites.

Periodically (at the same time of soil respiration measurements) measurements of gravimetric soil moisture were obtained from the first 0.3 m (n = 5) in each study site. Then, volumetric soil moisture was calculated using soil bulk density and the gravimetric measurements. To characterize soil properties, composite samples of five soil cores were taken (0.20 m depth) at random in each study site. At the same location soil litter depth was assessed. The samples were air dried and ground to pass a 2-mm sieve. For this study, soil organic carbon (C) analysis was carried out by using the traditional wet digestion method (Allison, 1960).

The characteristics of the vegetation were estimated in three randomly selected linear transects of 20 m in each study site using the point contact method (Levy and Madden, 1933). Each transect was divided into 20-cm intervals. The percentage of the ground covered by vegetation (plant life forms), bare soil, and litter was obtained from the 100 recording points. The annual aboveground net primary production (ANPP) of grasses and graminoids (expressed as g C m^{-2} yr^{-1}) was estimated by clipping vegetation within a 0.2 m^2 quadrat during maximum biomass accumulation (December−January) in three enclosures (1.5 × 1.2 m) randomly distributed in each site. The samples were dried in an oven at 60 °C for at least 24 h and then weighed for aboveground biomass.

2.6. Data analysis

Soil respiration data were analysed using ANOVA for repeated measures with vegetation gradient and long term grazing intensity in steppe grasslands and land use (primary forest, silvopastoral system and open), as factors and each sampling date as sub factor. This analysis was done because the values are not independent of time. Tukey tests were performed when F-values were significant ($P < 0.05$). Linear and nonlinear regressions were made to find the best model explaining the relationship between the soil variables and the annual average soil respiration in all studied sites. Similarly, these types of regressions were performed to relate climatic variables to soil respiration.

3. Results

Main characteristics of study sites where soil respiration measurements were carried out are presented in Table 1. For the vegetation and climate gradient sites, the grass and litter cover, litter depth, the annual ANPP, soil carbon concentration (C%) and mean soil volumetric water content (VWC) (depth 0.20 m) followed the order Andean grassland > Magellanic grass steppe > Matorral Thicket. For the same variables, the dry and humid Magellanic steppe areas with high long term stocking rates had lower values than those with moderate grazing intensity. Also, we found contrasting patterns between land uses where primary forest showed lower values of grass cover, annual ANPP and mean soil VWC than open and silvopastoral sites. Overall we found contrasting vegetation and environmental conditions between study sites. For example, soil C% varied from 2.1 to 6.5%, annual ANPP ranged between 4.1 and 40.5 g C m^{-2} and bare soil cover from 2 to 31% (Table 1). While mean seasonal soil temperature (5 cm depth) varied between 5.9 and 11.4 °C, soil temperature reached the lowest values, between 3 and -1.7 °C in July (data not shown).
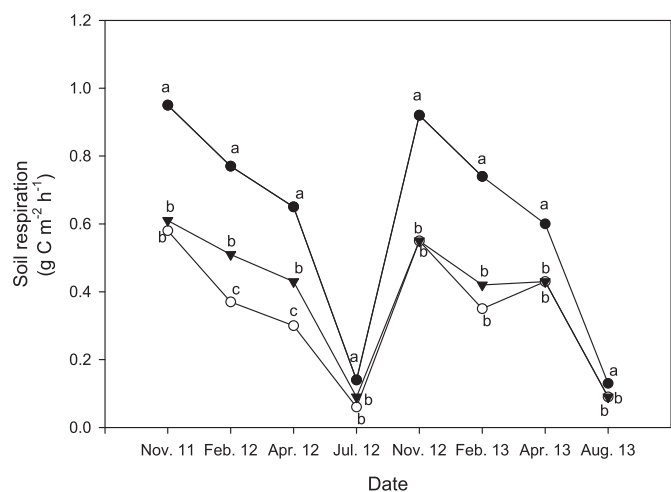
3.1. Soil respiration in a vegetation and climate gradient

Seasonal patterns of soil respiration for the three sites representing the vegetation and climate gradient are shown in Fig. 1. Soil respiration varied from 0.09 g CO_2 h^{-1} m^{-2} in winter (July) to a maximum of 0.95 g CO_2 h^{-1} m^{-2} in spring (November) in the Andean grassland. There was significant ($F = 13.85$, p < 0.01, $df = 95$)

Table 1
Main characteristics of the study sites (mean ± standard deviation) where soil respiration measurements were taken in grasslands ecosystems in Southern Patagonia, Argentina. ANPP = annual aboveground net primary production; C% = soil carbon concentration; VWC = mean soil volumetric water content (depth 0.20 m) at soil respiration measurements over seasons (summer, autumn, winter and spring); ST = mean seasonal soil temperature (5 cm depth).

Ecological area	Grass cover (%)	Bare soil (%)	Litter cover (%)	Litter depth (cm)	ANPP (g C m^{-2})	C (%)	VWC (%)	ST (°C)
Study sites for vegetation gradient								
Magellanic grass steppe	58 ± 4.4	20 ± 5.7	8.1 ± 3.2	0.2 ± 0.08	8.4 ± 1.3	3.2 ± 0.4	24.8 ± 6.5	7.3 ± 6.8
Matorral thicket	16 ± 7.2	31 ± 6.5	4.4 ± 4.1	0.1 ± 0.05	4.1 ± 0.8	2.1 ± 0.3	19.3 ± 7.2	6.2 ± 6.7
Andean grassland	78 ± 8.1	2 ± 5.2	18.2 ± 8.8	0.5 ± 0.09	40.5 ± 5.6	4.8 ± 0.7	27.5 ± 11.2	5.9 ± 5.4
Study sites for grazing intensity								
Dry magellanic steppe, moderate stocking rate	58 ± 4.3	8 ± 2.9	9.8 ± 2.8	0.3 ± 0.05	14.8 ± 2.7	4.2 ± 0.2	22.0 ± 5.3	10.5 ± 4.9
Dry magellanic steppe, high stocking rate	45 ± 3.2	17 ± 3.7	5.4 ± 3.4	0.2 ± 0.03	9.5 ± 1.5	3.5 ± 0.3	19.7 ± 4.7	11.4 ± 5.8
Humid magellanic steppe, moderate stocking rate	72 ± 4.8	10 ± 3.2	10.2 ± 5.1	0.4 ± 0.04	19.5 ± 3.3	5.7 ± 0.8	24.2 ± 6.2	9.1 ± 5.2
Humid magellanic steppe, high stocking rate	57 ± 6.1	2 ± 2.7	6.5 ± 2.3	0.2 ± 0.05	7.9 ± 1.8	3.9 ± 0.4	22.3 ± 5.6	9.8 ± 6.3
Study sites for land use[a]								
Silvopastoral system	79.8 ± 3.7	4 ± 2.2	21 ± 3.6	0.4 ± 0.06	32.3 ± 3.8	5.8 ± 0.2	23.3 ± 13.5	6.5 ± 4.3
Primary forest	12.0 ± 4.2	2 ± 1.8	65 ± 5.7	0.5 ± 0.10	7.8 ± 0.9	6.5 ± 0.1	20.5 ± 14.0	7.1 ± 3.8

[a] The open site corresponds to the Andean grassland site.

Fig. 1. Seasonal variation of soil respiration for the three sites representing the vegetation and climate gradient in Santa Cruz province (Southern Patagonia, Argentina): main grassland ecosystems in the Magellanic grass steppe (▼), "mata negra" Matorral Thicket (○) and Andean (●) grasslands. Within dates, different lower-case letters indicate significant (p < 0.05) differences among ecosystems.

differences in soil respiration rates between grasslands in the studied ecological areas across the climate gradient being higher in the Andean ecological grasslands than in all other ecosystems. Mean annual soil respiration values (average of the four seasons measured over two years) were 0.34, 0.40 and 0.61 g CO_2 h^{-1} m^{-2} in the Matorral Thicket, Magellanic grass steppe and Andean grassland, respectively. Also, there was an interaction (p < 0.001) between grasslands and time because of seasonal fluctuations in soil respiration.

3.2. Soil respiration at contrasting grazing intensity

We found contrasting seasonal patterns of soil respiration between two long term grazing intensities in both the dry and humid Magellanic steppe areas being higher (F = 22.95, p < 0.01, df = 111) in moderate than high stocking rates (Fig. 2). There was a significant (p < 0.01) interaction between grazing intensity and season. In both sites, CO_2 efflux reached its maximum in November with values of 0.71 and 0.84 g CO_2 h^{-1} m^{-2} for the moderate grazing intensity in the Dry and Humid Magellanic grass steppe, respectively (Fig. 2). In contrast, no significant differences were detected between grazing intensities in winter at any site. Mean annual soil respiration values

(average of the four seasons measured over two years) for long term moderate and high stocking rate were 0.58 and 0.41 g CO_2 h^{-1} m^{-2}, respectively.

3.3. Soil respiration and different land uses

Soil respiration rates in the silvopastoral system and primary forest were higher (F = 12.73, p < 0.01, df = 95) than in grassland in the adjacent open site (Fig. 3). Soil respiration ranged from 0.11 g CO_2 h^{-1} m^{-2} in winter to a maximum of 1.43 g CO_2 h^{-1} m^{-2} in spring in the silvopastoral system. There was an interaction (p < 0.001) between land uses and time due to seasonal fluctuations in soil respiration, with no differences in soil respiration among sites during winter (July–August).

3.4. Factors affecting soil respiration

Almost all plant and soil variables were significantly correlated (p < 0.05) to soil respiration (except grass and graminoid cover). Soil carbon concentration (depth 0.2 m), litter cover and depth and bare soil cover were the main factors explaining 78 and 83% of soil respiration in the contrasting grasslands evaluated (Table 2).

Analysing the environmental factors, soil respiration rates were correlated positively to air and soil temperatures and to a lesser extent with mean monthly rainfall (Fig. 4). Soil volumetric water content showed a weak correlation with soil respiration.

4. Discussion

4.1. Soil respiration in a vegetation and climate gradient

We found significant differences in soil respiration rates between contrasting grasslands of three studied ecological areas across a climate and vegetation gradient in Southern Patagonia. This is consistent with Raich and Tufekcioglu (2000) who reported that soil respiration rates vary significantly among major plant biomes, suggesting that vegetation type influences the rate of soil respiration. In our study, soil respiration under moderate grazing in the Andean grassland was ~45% higher than the Matorral Thicket ecological area and ~35% higher than Magellanic grass steppe. Vegetation may affect soil respiration by influencing soil microclimate and soil structure, and the quantity and quality of detritus supplied to the soil (Seto and Yanagiya, 1983; Bowden et al., 1993). Thus, the results provide evidence that vegetation type (differences in species composition of a particular ecological area) substantially influence soil respiration rates together with other factors such as
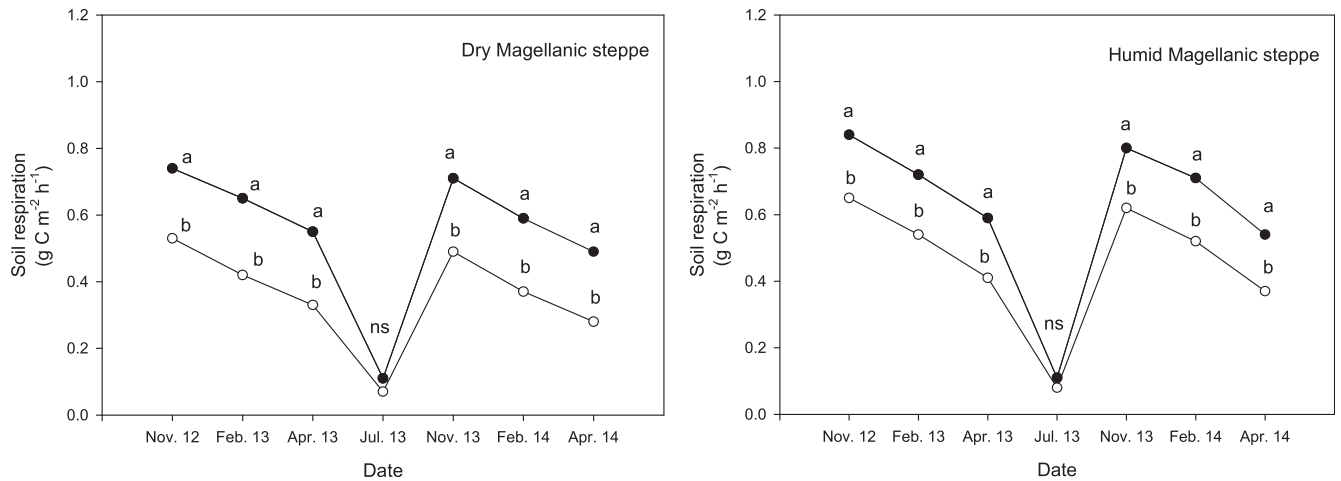
Fig. 2. Seasonal variation of soil respiration for moderate (●) and high (○) long term stocking rates in Dry and Humid Magellanic grass steppe in Santa Cruz province (Southern Patagonia, Argentina) Within dates, different lower-case letters indicate significant (p < 0.05) differences between sites with moderate and high grazing intensity.
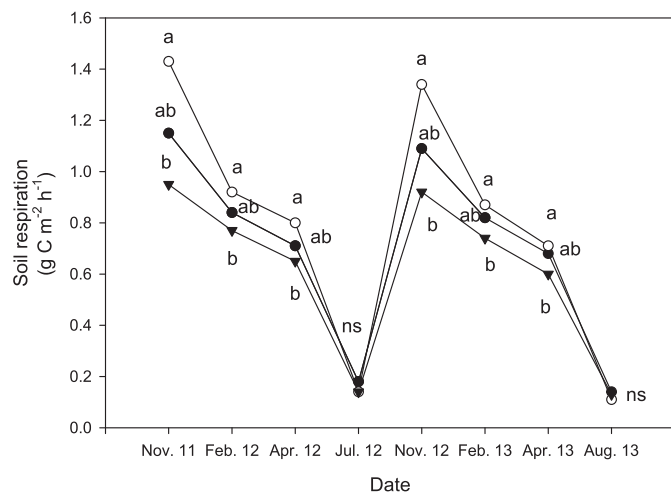
Fig. 3. Seasonal variation of soil respiration for primary forest understorey (●), silvopastoral system (○) and open grassland (▼) in Santa Cruz province (Southern Patagonia, Argentina) Within dates, different lower-case letters indicate significant (p < 0.05) differences among land uses.

temperature, moisture availability (precipitation) and carbon concentration of the substrate that simultaneously influence the production and consumption of organic matter. In this context, Wang et al. (2013) reported that the variation in soil respiration among different vegetation types in a forest-steppe ecotone of temperate China (grassland, shrubland, evergreen coniferous, deciduous coniferous and deciduous broadleaved forest) could be well

Table 2
Simple linear and nonlinear regressions between soil respiration (annual average) and main soil variables in the different studied grasslands in Southern Patagonia (n = 9).

	Significance	R^2	Equation
Soil carbon concentration (%)	$P = 0.01$	0.83	$Y = 0.091x \pm 0.163$
ANPP (g C m^2 year^{-1})	$P = 0.031$	0.51	$Y = (1/-1.49x) \pm 0.708$
Litter (cm)	$P = 0.01$	0.79	$Y = 1.015x \pm 0.259$
Litter cover (%)	$P = 0.011$	0.78	$Y = 0.0001x^2 + 0.031x + 0.274$
Bare soil (%)	$P = 0.02$	0.78	$Y = -0.013x \pm 0.704$
Grass-graminoids cover (%)	Ns	0.06	Ns

explained by soil organic carbon. However, distinguishing vegetation from climatic and soil factors over soil respiration is problematic, and further research is needed.

4.2. Soil respiration at contrasting grazing intensity

We found also that long term grazing intensity altered the soil respiration rate in grassland ecosystems. Thus, mean annual soil respiration values for long term moderate grazing was up to ~30% higher than for grasslands under high stocking rates and this response was similar between dry and humid Magellanic steppe areas. Similarly, Cao et al. (2004) reported that soil respiration was almost double at a site with light grazing (2.5 sheep ha^{-1}) compared with a heavily grazed (5.3 sheep ha^{-1}) during the growing season in alpine meadow on the northeastern Tibetan Plateau, but with similar seasonal patterns. However, according to Frank et al. (2002) grazed prairies showed a higher soil CO_2 flux than non-grazed prairies. Although comprehensive mechanisms involved in the effect of grazing on soil respiration must be studied, we believe that the low soil respiration rate at the long term high stocking rate in both evaluated sites may be mainly due to both the low vegetation cover (or high bare soil cover) and low ANPP. Vegetation cover and ANPP may be key factors that affect soil respiration by influencing the overall rate of root respiration. The proportion of the total soil respiration flux that is attributable to live root respiration (related to plant cover) appears to be very high in cold biomes, with values up to 93% in arctic tundra (Chapin et al., 1980) and ~40% in grasslands (Kucera and Kirkham, 1971; Coleman, 1973; Herman, 1977; Buyanovsky et al., 1987). Also, it was demonstrated that the reduction of perennial grass cover induced by grazing intensity in northern Patagonia (Argentina) affected negatively soil enzyme and microbial activities related with C cycling (Prieto et al., 2011). The mean rates of soil respiration were positively correlated with ANPP in the different grassland ecosystems evaluated which indicates a linkage between plant net biomass production and of CO_2 efflux. This is expected because ANPP provides the organic substrate that drives soil microorganism activity (Bahn et al., 2008). Flanagan and Johnson (2005) suggested that plant aboveground biomass was good proxy for accounting for variations in both autotrophic and heterotrophic capacity for soil respiration in a native Canadian grassland ecosystem. However, estimates of site productivity from aboveground biomass may be strongly biased as belowground
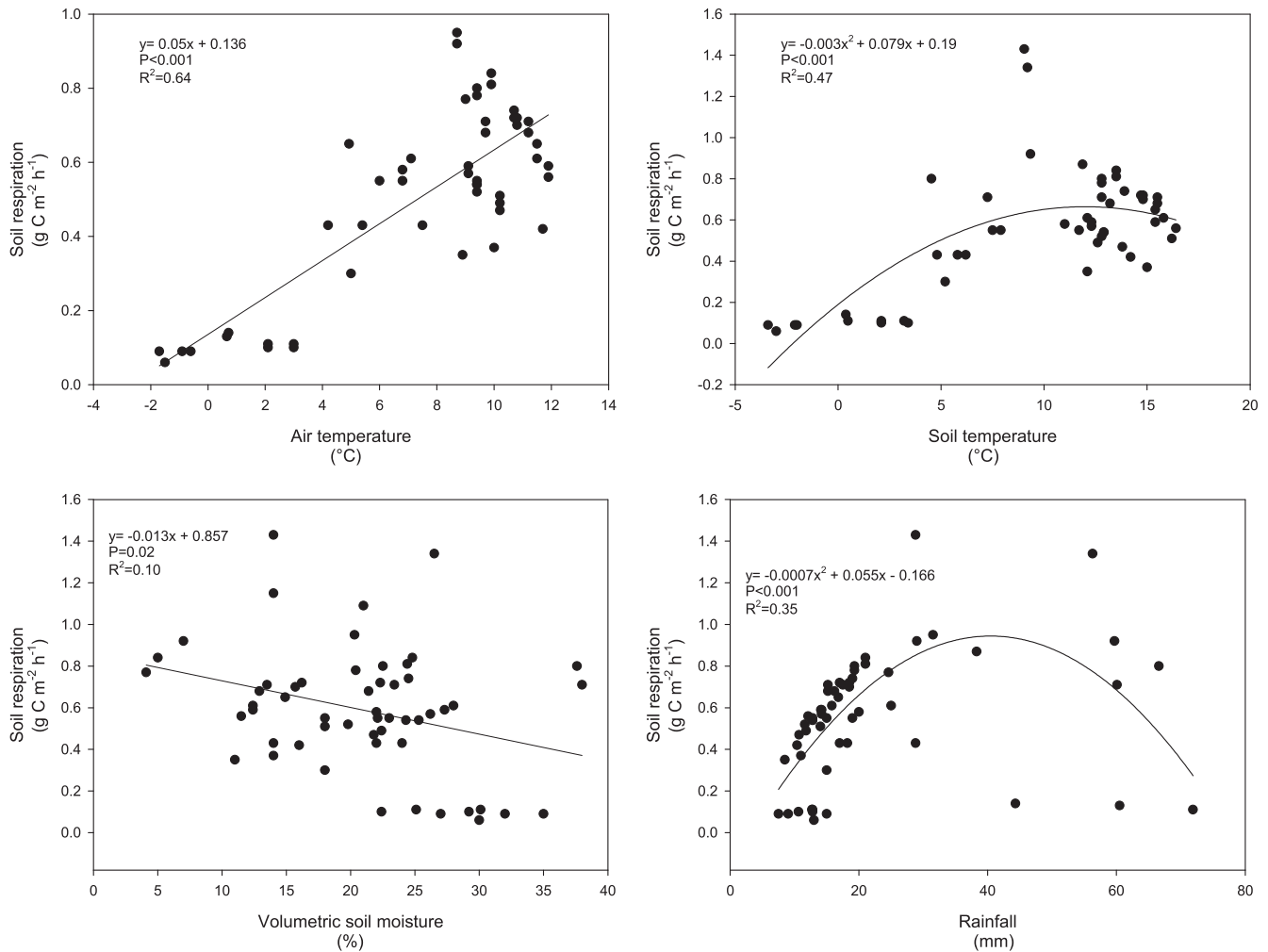
Fig. 4. Relationship between soil respiration and environmental variables (showing the best fitted regression models) for grasslands of Southern Patagonia, Argentina.

productivity is not taken into account. This became more relevant in the Patagonian Monte arid environment where 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 (Larreguy et al., 2014). Also, in the present work, litter cover, litter depth and soil carbon concentration (C%) in the uppermost soil layers, in both the dry and humid Magellanic steppe areas, were lower under heavy long term stocking rates than sites under moderate grazing intensity. This is consistent with Peri (2011) who reported that long term grazing intensity affects total C in Patagonian grasslands being lower at a heavy stocking rate. Bahn et al. (2008) indicated that the degree to which soil CO_2 efflux is coupled to soil C content may be largely determined by the reductions of supply by removal of aboveground biomass through grazing. Grassland ecosystems with high soil organic matter may promote organic matter decomposition (microbial activity) by continuous addition of litter and root turnover, thereby increasing soil respiration rates. This is consistent with Mallik and Hu (1997) who established a strong relationship between soil organic matter and soil respiration with exclusion of root respiration in an incubation study. However, little evidence is currently available to understand the possible mechanism involved in soil respiration under different long term grazing intensities. For this, further studies are required.

4.3. Soil respiration and different land uses

We found differences in soil respiration between land uses. The likely reason for higher soil respiration within the silvopastoral system and primary forest (mean annual soil respiration up to 0.75 g CO_2 h^{-1} m^{-2}) compared to the grasslands (0.60 g CO_2 h^{-1} m^{-2}) is the presence of the trees in the system. This has been demonstrated previously by Raich and Schlesinger (1992) who reported, from a review of several studies, that soil respiration from forested land compared to conventional agricultural land was up to three times higher. Similarly, Peichl et al. (2006) measured that soil respiration in a poplar intercropping system in southern Ontario (Canada) was higher than in a barley monoculture. Probably, the higher C input in the form of litterfall in ecosystems with trees creates favourable conditions for soil microorganisms leading to enhanced microbial activity and CO_2 evolution or higher tree root respiration (Matteucci et al., 2000). However, the conversion from forests to grasslands may modify soil respiration rates depending on site conditions. For example, Wang and Fang (2009) report that transformation from grasslands to woodlands led to a 22% increase in soil respiration rates in subtropical grasslands, while in a pasture of Canada, the conversion of pasture to forests decreased soil respiration rates by 41%. Also, in a humid temperate region of southern Europe soil respiration

followed the order pasture > oak forest > cropland (Merino et al., 2004). The CO_2 efflux from soils in woody communities was higher than that in subtropical savanna grasslands of southern Texas, USA (McCulley et al., 2007). This highlights the importance of environmental conditions (mainly soil water availability and temperature), input of organic residues, soil microbial biomass and soil properties on the magnitude on soil respiration among different ecosystems and land uses.

The trend of higher soil respiration in silvopastoral system compared with primary forest may be due to an improvement of microclimate (soil temperature, incoming radiation and moisture regime) that enhanced organic matter decomposition. This has been confirmed by Bahamonde et al. (2012) who determined that total transmitted radiation, soil and air temperatures were the main environmental factors explaining 61 and 40% of the variation of litter (grasses and tree leaves) decomposition in *N. antarctica* forest in Patagonia under silvopastoral use. Similarly, Lee and Jose (2003) reported that soil respiration increased in a pecan - cotton alley cropping system compared with pecan orchards and a cotton monoculture in Southern USA due to better soil temperature conditions, and higher microbial biomass, organic matter and fine root biomass.

4.4. Factor affecting soil respiration

Furthermore, we found a strong seasonal variation in soil respiration in all studied sites. Soil respiration, regardless of site, was higher in spring (November) when soil moisture is not limiting and temperature are favourable to biological activity, and declined in summer due to water stress and in winter due to low temperatures. It is known with some certainty that both fluctuations in moisture content and temperature influence soil respiration accounting for more than 50% the annual and seasonal variation in CO_2 levels in agricultural and forest soils (Buyanovsky and Wagner, 1983; Gordon et al., 1987). In our study, air and soil temperatures were correlated positively with soil respiration rates and appear more important than soil moisture and precipitation (Table 2, Fig. 4). Similarly, Raich and Schlesinger (1992) reported that on a global scale, temperature was the single best predictor of annual soil respiration accounting for 42% of the variation in a linear model. Also, Cao et al. (2004) showed that soil temperature was the main environmental factor controlling soil respiration of a grazed alpine meadow on the northeastern Tibetan Plateau. In contrast, Liu et al. (2009) suggested that soil water availability was more important than temperature in regulating soil and microbial respiratory processes, microbial biomass and their responses to climate change in the semiarid temperate steppe in northern China. These authors found after 3 years of measurements, that while soil moisture content accounted for 34.0–41.4% of the seasonal variations in soil respiration, soil temperature and moisture together accounted for 65.0–96.1% of this variation. Our results agree with Lloyd and Taylor (1994) who stated that for biomes in areas where soil temperatures are low (like Southern Patagonia), soil respiration rate is most sensitive to fluctuations in temperature. Soil respiration is controlled by the complex interaction of environmental and biotic factors. The knowledge provided in the present study together with C pools data from different components of Patagonian grasslands (Peri, 2011) provides a framework to estimate net CO_2 emissions at ecosystem level for the studied vegetation types growing across a climate gradient, under a range of grazing intensities and diverse land uses.

Acknowledgements

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