REGULAR ARTICLE

Temporal and spatial variability in soil CO_2 efflux in the patagonian steppe

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Abstract

Aims Soil respiration is a major flux of CO_2 to the atmosphere. Despite its significance there is a limited understanding of its magnitude, controlling factors and how it varies over time and space in arid ecosystems. We evaluated the temporal pattern of soil CO_2 efflux and their response to rain pulses in a patagonian steppe, taking into account the spatial heterogeneity (bare soil and vegetated patches).

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Materials and methods We measured soil CO_2 efflux in bare soil and vegetated patches along the year. We also analyzed physical and chemical soil traits, root density and heterotrophic bacterial count.

Results Soil water content and temperature exhibited seasonal variability and it was larger in bare soil patches than in vegetated patches. Root density, organic matter and phosphorus were higher in vegetated patches than in bare soil. CO_2 efflux was 48% higher in vegetated patches than in bare soil patches. Soil CO_2 efflux decreased from summer to winter, reaching its maximum value (about 0.6 μmol m^2 s^{-1}) in spring. In both patch types, soil CO_2 efflux was explained by the interaction between soil temperature and soil water content. Soil CO_2 efflux also was positively correlated with soil root density. Bare soil and vegetated patches exhibited distinct response to a rain pulses. Vegetated patches were highly sensitive to rainfall events, generating a large CO_2 pulse, returning to previous values after three days. Bare soil CO_2 efflux did not exhibit significant changes after a rain pulse.

Conclusions In patagonian arid ecosystems, the seasonal variation in soil respiration is explained mainly by the interaction between soil temperature and water content. Bare soil patches had higher water content but lower root density resulting in lower soil CO_2 respiration than vegetated patches. However, at ecosystem level the contribution of bare soil to total soil CO_2 efflux was similar to the contribution of vegetated patches because bare soil cover is 65% in the study area. Changes in the number of small rain events as well as changes in plant cover could have large consequences on soil ecology and biochemistry in dry and heterogeneous ecosystems.

Introduction

The carbon flux between the soil and the atmosphere takes place mainly in the form of carbon dioxide (CO_2) originating from autotrophic (roots) and heterotrophic (microbial) respiration. This process is one of the main pathways in the global carbon cycle (Bolstad et al. 2004; Borken et al. 2006; Euskirchen et al. 2006). In general, about half of the soil respiration is derived from metabolic activity for the support and root growth and associated rhizosphere organisms (Hanson et al. 2000; Högberg et al. 2001), and the rest of CO_2 efflux is associated with respiration from microbial communities (Trumbore 2000; Giardina et al. 2004). However, the proportion of soil respiration from autotrophic and heterotrophic contributions varies seasonally and spatially within an ecosystem and among ecosystems (Hanson et al. 2000; Wang et al. 2014).

The soil CO_2 efflux is generally assumed as "the soil respiration" (Xu and Shang 2016). Several factors affect soil respiration, including soil temperature (Davidson and Janssens 2006), soil moisture (Zhang et al. 2010; Bao et al. 2016), quantity and quality of litter (Han et al. 2015), salinity (Lai et al. 2012), and organic matter (Lai et al. 2013). In ecosystems without strong seasonality in precipitation, soil temperature is a good predictor of soil respiration (Fang and Moncrieff 2001; Bolstad et al. 2004), however, within certain biomes soil moisture and soil carbon emerge as dominant predictors of soil respiration (Hursh et al. 2016). Under drought conditions, the amount and distribution of precipitation has also been shown to be a key controlling factor of soil respiration (Deng et al. 2012).

Arid and semi-arid regions account for nearly one-third of the global land area and soil respiration is the main process for carbon emission in these regions (Conant et al. 2000). In general, these ecosystems are characterized by low soil respiration rates (Cable et al. 2011), and exhibit high variability in seasonal and inter-annual precipitation. During the dry period some small and erratic rain pulses occur (Reynolds et al. 2004; Collins et al. 2008). The discrete and unpredictable rainfall events drive metabolic activity of roots and microbial until available water is depleted, affecting soil CO_2 emissions (Davidson et al. 1998; Kelliher et al. 2004; Jarvis et al. 2007). The rain pulse effects on soil CO_2 are generally intensified by the dry condition of the antecedent soil, and these are less evident if the soil is wet before the rainfall event (Cable et al. 2008).

In arid and semiarid environments the vegetation is patchy, with patches of bare soil and patches of vegetation. This vegetation pattern generates heterogeneity in resources availability and root and microbial density which can have relevant effects on soil respiration (Helmuth et al. 2005; Cable et al. 2008; Martin and Bolstad 2009; Han et al. 2014b, 2017). Therefore, increasing the temporal and spatial resolution of soil respiration estimates may help in reducing uncertainly when quantifying ecosystem carbon fluxes (Martin and Bolstad 2009). Dry environments have received less attention in the study of soil respiration than other ecosystems worldwide (Xu and Shang 2016). Particularly for Patagonian steppe, a large desert in southern Argentina, the CO_2 fluxes are unknown (but see Peri et al. 2015 for magallanic steppes). Patagonian steppe is a cold and arid-semiarid region with an asynchronism between water availability and favorable temperatures for biotic activity (Austin et al. 2004; Bertiller et al. 2006; Scholz et al. 2012). Further, these are very heterogeneous environments where shrubs and grasses are grouped forming islands of fertility (Soriano et al. 1994; Mazzarino et al. 1998). Soils in these vegetated patches contain more moisture and nutrients than bare soil patches around them (Austin et al. 2004). Therefore, soil respiration rate is expected to have a strong spatial pattern. In this study we evaluated the seasonal pattern of soil CO_2 efflux in the Patagonian steppe, taking into account the spatial heterogeneity of this environment. We analyzed also the effects of soil temperature, soil moisture and root density on soil respiration. In addition, we studied the response of a small rain pulse on CO_2 fluxes from soil during the dry season. We hypothesized that seasonal variability in soil respiration is attributed to variation in soil temperature and moisture. Further, we hypothesized bare soil patches release lower amount of CO_2 than vegetated patches. Given that water is one of the main driving factors of biological activity in arid and semiarid ecosystems, we expected to observe an increase in soil respiration after a rain pulse in both patch types.

Materials and methods

Study site

The study area is located at the Rio Mayo Experimental Station, Instituto Nacional de Tecnología Agropecuaria (INTA, 45°24'11″S 70°17'37″W) near Río Mayo town, southwest of Chubut Province, Argentina. The vegetation is a typical patagonian semiarid steppe dominated by few shrubs and grasses species, which are distributed in patches with same individuals surrounded by bare soil. The dominant shrub species are *Azorella prolifera* (Cav.) G.M. Plunkett & A.N. Nicolas (ex. *Mulinum spinosum*), *Adesmia volckmannii* Phil. and *Senecio filaginoides* DC. The dominant grass species are *Pappostipa speciosa* (Trin. & Rupr.) Romasch., *Pappostipa humilis* (Cav.) Romasch. and *Poa ligularis* Nees ex Steud. Shrubs have dimorphic root systems with lateral roots and one tap root (Bucci et al. 2009). Grasses have fibrous root systems and root biomass decreases from center to the periphery of tussock. Some grass roots expand outside the basal area of tussock (Soriano et al. 1987), thus the zone of influence of a grass is colonized by roots of neighboring grass species (Reyes and Aguiar 2017).

Soils are of coarse texture (sandy), with a high content of pebbles of varying diameter (Paruelo et al. 1988). Mean annual precipitation in the site is about 150 mm, 70% of which falls during winter, with isolated and unpredictable short rain events in summer. The evapotranspiration measured with an open top chamber were within 78 and 92% of total annual precipitation (Pereyra et al. 2017). Mean monthly temperature varies from 1 °C in July to 15 °C in January.

The principal economic activity of the region since the end of the nineteenth century is the livestock (Golluscio et al. 1998). Until 2013, the livestock management practice in the study site consisted in a stocking rate of 0.14 sheep per hectare only from May to October. During the rest of the year the animals were moved to sites with abundant forage. In 2013 three plots of 625 m^2 each were established separated from each other by 15 m within a 4 ha closure. The study was carried out from June 2015 to May 2016, except the evaluation of responses of soil CO_2 efflux to rain pulse which was carried out in January 2015.

Soil chemical properties

In November 2015, three cores (5 cm diameter, 5 cm deep) from the upper soil layers were taken randomly in two patch types (vegetated and bare soil) and in each plot, and mixed well to produce one composite sample ($n = 3$, one per plot and patch type). We defined vegetated patches as the sites that have a mix of shrubs and grasses representative of the study area. We defined bare soil patches as the sites as far away as possible (at least 50 cm) from the vegetated patches or any single plant. All soil samples were analyzed for pH, electrical conductivity, organic matter, total nitrogen and available phosphorus. Electrical conductivity was determined in a saturated extract, and corrected for temperature (Richards 1954). The values were reported in dS m^{-1} at 25 °C. Soil pH was determined in a solution 1:2.5 of distilled and deionized H$_2$O. Soil organic matter, total Nitrogen and available Phosphorous were analyzed in the Soil Laboratory (INTA Chubut, Argentina). Soil organic matter was determined using the wet oxidation method (Walkley and Black 1934). Soil total Nitrogen was determined with the Kjeldahl method (Bremner 1996). Available Phosphorus was measured using the Olsen method (Olsen et al. 1954).

Soil CO_2 efflux, temperature and water content

Soil CO_2 efflux was determined in both patch types, monthly or bimonthly throughout the year from June 2015 to May 2016 in the three plots. A portable closed chamber to determined soil respiration (6400–09, LI-COR), connected to a gas exchange system (LI-6400, LI-COR) was used. The chamber covers an area of 80 cm^2. The chamber in vegetated patches was placed as near possible to the base of the shrubs under the crown. Soil PVC collars (10 cm in diameter and 4.4 cm in height) were inserted into the soil at 2.2 cm depth one day before each measurement date to allow stabilization of the CO_2 efflux before the measurements. Each measurement date new collars were installed in other sites of each plot. Each measurement took between 5 to 20 min, depending on the time of year (in winter the measurements took longer because the rates were relatively low), and included three averaged consecutive cycles. To avoid the effects of strong diurnal fluctuations in air temperature on soil respiration, measurements were done between 11:00 and 15:00 h on two consecutive days with similar climatic conditions in each study period.

At the time of each soil respiration measurement, soil temperature was measured at 0–10 cm depth with a soil temperature probe from the LI-6400. Similarly, soil volumetric water content (%) was measured at 0–10 cm depth, close to the soil collars using ECH2O probes (Decagon Devices, Inc.). The probes have an accuracy of 0.03 m^3/m^3 and a maximum temperature sensitivity of 0.003 m^3/m^3 per 1 °C. The probes were calibrated in the laboratory with soil samples obtained from the study site (Pereyra et al. 2017).

Responses of soil CO_2 efflux to a rain pulse

In January 2015, within the framework of another study in the same study site, soil CO_2 efflux was determined previous to a rain event of 3.5 mm, one day and three days after the event. The measurements of soil CO_2 efflux were taken as it was explained above, in three plots and 4 measurements per plot. Likewise, soil water content was measured at 0–10 cm depth, close to the soil collars, using the same ECH2O probes mentioned above.

Root biomass and soil bacterial count

At the end of the each soil respiration measurement, soil cores of 10 cm diameter and 10 cm depth inside each soil collar were collected and were transported to the laboratory. Fresh soil was carefully separated from the roots by sieving the soil through a mesh of 0.5 mm. Roots were washed and oven-dried at 70 °C until constant weight. Root density was determined as root dry mass per unit volume of soil.

Cultivable heterotrophic bacteria from superficial soil (0–5 cm) were determined in November 2015 by the dilution plate count method (see Pepper and Gerba 2015). One soil sample (each was a pool of 3 sub-samples) were collected in the two patch types in each plot. For each sample, 1 g of soil was weighed and placed in dilution bottles containing 20 ml of sterile saline solution. Bottles were shaken at 1000 rpm for 5 min, and then 1 ml of the suspension was serially diluted and 0.1 ml spread-plated onto nutritive agar. Plates were incubated at 25 °C during 4 days. After, colonies were counted and colony-forming units (CFUs) were determined. Only plates containing between 30 and 300 colonies were considered for counting.

Statistical analyses

Statistical analyses were performed using the software R version 3.4.4 (R Development Core Team 2018). We used linear models (LMs) with F-test to evaluate the effects of the patch type (explanatory variable) on soil chemical characteristics and soil bacterial count (dependent variables). Generalized least squares fitted linear models (GLSs) with F-test were used to evaluate the effects of the patch type (explanatory variable) on root density and soil respiration (dependent variables), with temporal correlation structure (corAR1). We also used GLSs to evaluate the effect of the interaction between patch type and month (explanatory variables) on soil water content, soil temperature, root density and soil respiration (dependent variables), using corAR1. To evaluate the effect of rain pulse on soil water content and soil CO_2 efflux, we performed GLSs with the time factor with three categories (before rain, 1 day after rain and 3 days after rain) and the patch type factor and their interaction as explanatory variables. In both GLSs we used the compound symmetry correlation structure (corCompSym), but this factor was not significant (test REML: chi-squared = 0.029, df = 1, p = 0.86 for GLS with soil water content as dependent variable, and chi-squared = 0.2, df = 1, p = 0.65 for GLS with soil CO_2 efflux as dependent variable) and thus it was removed from the models. Tukey's post-hoc analysis was used to evaluate differences in soil water content and soil CO_2 efflux after rain with respect to before rain. We performed a multiple regression analysis, using GLSs, to evaluate the effect of the interaction between soil temperature and soil water content (explanatory variables), with patch type as a covariable, on soil CO_2 efflux (dependent variable), using corAR1. And we tested a linear regression between root density (explanatory variable), with patch type as a covariable, and soil CO_2 efflux (dependent variable), using corAR1. Cox and Snell's R^2 (Cox and Snell 1989) was calculated with the function "nagelkerke" of the R package "rcompanion" version 2.1.7 (Mangiafico 2015). The GLSs were carried out using the function "gls" from the R package "nlme" version 3.1–131.1 (Pinheiro and Bates 2000). When necessary, all models were adjusted by variance modeling; model selection was based on Akaike's information criterion (AIC; Burnham and Anderson 2002). The simplification of the fixed effects of all models to reach the adequate minimum model was carried out by hypothesis test (F-value). Tukey's post-

hoc analysis was used for multiple comparisons in all models when F-test was significant, using the function "glht" of the R package "multcomp" version 1.4–8 (Bretz et al. 2010). To graph the results of the best fitted model we used the R package "visreg" version 2.5–0 (Breheny and Burchett 2017).

Results

Total precipitation from June 2015 to May 2016 in the study site was 101.9 mm. Around 70% of the precipitation occurred from June to September (winter) (Fig. 1a). Mean monthly air temperature varied between 3 °C in winter to 16 °C in summer (Fig. 1b).

Soil chemical properties varied between patch types, except pH (Table 1). Organic matter and available P were significantly higher in vegetated patches than in bare soil ($p = 0.005$ and $p = 0.006$, respectively). Soil electric conductivity and N content were marginally significant ($p = 0.087$ and $p = 0.07$, respectively) higher in vegetated patches than in bare soil.

Soil water content (Fig. 2a) varied seasonally in the study area ($F_{(8,75)} = 77.7$, $p < 0.0001$) and between patch types ($F_{1,75} = 14.3$, $p = 0.0003$), without significant interaction between months and patch types ($F_{(8,67)} = 1.76$, $p = 0.1$). Soil water content reached 30% in September (end of winter) and close to 10% from January to May (summer to autumn). In the bare soil patches the soil water content was 6.5% higher than in the vegetated patches. Soil temperature and soil water content showed opposite seasonal patterns (Fig. 2 a, b). The interaction between months and patch types was significant ($F_{(8,67)} = 2.32$, $p = 0.03$) for soil temperature. Soil temperature was low during winter and reached its maximum value in January (Fig. 2b). There were no substantial differences in soil temperature between patch types.

Root density varied also seasonally and between patch types ($F_{(7,64)} = 2.46$, $p = 0.03$ and $F_{(1,64)} = 27.4$, $p < 0.0001$, respectively; Fig. 2c), without significant interaction between months and patch types ($F_{(7,57)} = .44$, $p = 0.87$). Root density was higher in spring in both patch types (Fig. 2c). Root density was more than two-folds higher in vegetated patches than in bare soil throughout the year (Fig. 2c). The mean annual root density was about twice as high in the vegetated patches compared to bare soil (Table 1). Heterotrophic

bacterial count did not show significant differences between patch types (Table 1).

Soil CO_2 efflux in both patch types exhibited a strong seasonal pattern ($F_{(8,75)} = 33.5$, $p < 0.0001$) (Fig. 3). The values were low (below 0.3 µmol m^{-2} s^{-1}) in winter, summer and autumn. Soil CO_2 efflux increased during the late winter (September), reaching its maximum value in November and then started to decrease in early summer (January). The maximum values were close to 0.6 µmol m^{-2} s^{-1}. CO_2 efflux from vegetated patches was higher than bare soil CO_2 efflux throughout the year ($F_{(1,75)} = 22.1$, $p < 0.0001$). There was not significant interaction between months and patch types ($F_{(8,67)} = 22.1$, $p = 0.55$). The annual mean soil CO_2 efflux from vegetated patches was about 48% higher than from bare soil patches ($p = 0.0004$; Table 1).
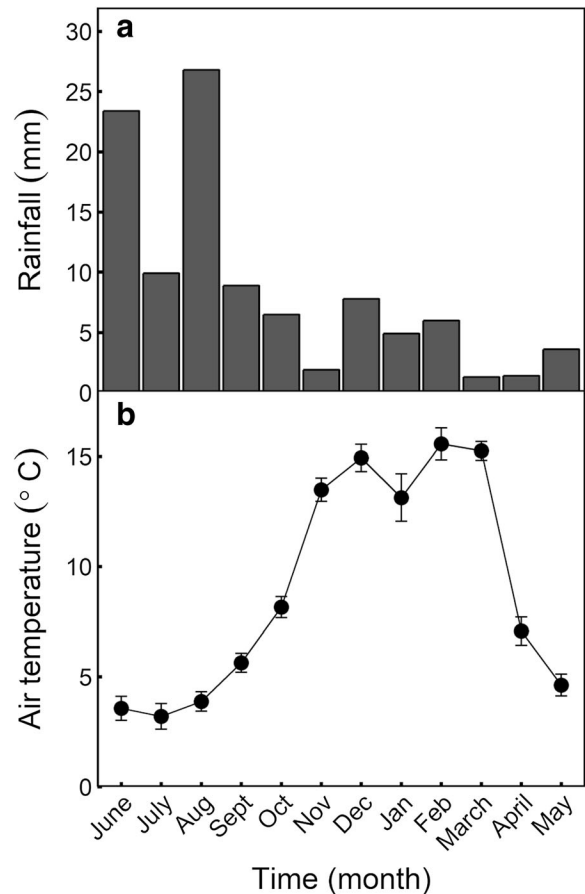

Fig. 1 **a** Monthly rainfall (mm) and (**b**) mean air temperature (°C) during the study period (June 2015 to May 2016) in a patagonian steppe. Data were obtained from a meteorological station located at 2 Km. from the study site (http://sipas.inta.gob.ar/)

A rain pulse (3.5 mm) during the dry season enhanced three times the soil water content immediately after the event, but it returned to values recorded before the rain pulse three days later ($F_{(2,69)} = 62.1$, $p < 0.0001$ for factor time) (Fig. 4a). There were not significant differences between patch types ($F_{(1,68)} = 0.71$, $p = 0.4$) nor significant interaction between time and patch type ($F_{(2,66)} = 0.35$, $p = 0.71$) for soil water content. There was significant interaction between time and patch type ($F_{(2,66)} = 3.19$, $p = 0.048$) for soil CO_2 efflux. Soil CO_2 efflux showed a differential response to the water pulse depending on the patch type (Fig. 4b). There was a significant increment in soil CO_2 efflux from vegetated patches immediately after the pulse respect to the values observed before the rain event (Fig. 4b). Nevertheless, bare soil CO_2 efflux did not exhibit substantial responses to the water pulse. After three days of the rain pulse soil CO_2 efflux values were relatively similar to those observed before the rain event in both patch types.

Soil CO_2 efflux was correlated with soil temperature and soil water content, with significant interaction between both factors ($R^2 = 0.25$, $F_{(1,80)} = 10.6$, $p = 0.002$) and significant effect of the patch type ($F_{(1,80)} = 15.2$, $p = 0.0002$). The contour plots (Fig. 5a, b) showed that higher values of soil respiration were observed when soil temperature and soil water content were high. At the same soil temperature and soil water content, soil respiration from vegetated patches was higher than from bare soil patches. Soil CO_2 efflux also was linearly and positively correlated with root density ($R^2 = 0.36$, $F_{(1,71)} = 19.5$, $p < 0.0001$) (Fig. 6), without statistically significant differences between patch types ($F_{(1,70)} = 0.95$, $p = 0.33$).

Discussion

Seasonal dynamic of soil respiration

Soil CO_2 efflux in the patagonian steppe (mean annual value was 0.28 μmol m^2 s^{-1}) fell within the range reported for other arid and semi-arid ecosystems (Maestre and Cortina 2003; Carbone et al. 2008; Cable et al. 2011; Peri et al. 2015; Xu and Shang 2016). For example, mean annual soil CO_2 efflux in the Mohave desert is 0.33 μmol m^2 s^{-1} and in the Great Basin, a cold desert with similar functional attributes to the patagonian steppe, is 0.97 μmol m^2 s^{-1} (Cable et al. 2011). The large CO_2 fluxes from soil for short-time periods after rain events were not well captured because we lacked continuous measurements, which could result in an underestimation of the total soil CO_2 efflux. Soil CO_2 efflux showed a pronounced seasonality indicating that it was sensitive to seasonal changes in soil environmental conditions. A similar seasonal dynamic in soil respiration was observed by Peri (2011) in semiarid grasslands in the southern portion of Patagonia.

For several ecosystems, CO_2 fluxes from soil increase exponentially with temperature and often are limited by available soil moisture (Carlyle and Than 1988; Fang and Moncrieff 2001; Xu and Shang 2016). Nevertheless, as Davidson et al. (1998) suggest, it is difficult and perhaps impossible to distinguish the effect of soil temperature and soil moisture separately. In our study site soil CO_2 efflux exhibited a significant relationship with the interaction between soil temperature and soil water content. Consistent with other studies (Curiel Yuste et al. 2003), soil CO_2 efflux, both from bare soil and vegetated patches, was highly correlated

Table 1 Soil pH, electric conductivity (dS m^{-1}), organic matter (%), total nitrogen (%), available phosphorous (ppm), mean annual root density (mg cm^{-3}), mean annual CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) and total heterotrophic bacteria (CFU $\times$ 10^5 g^{-1} soil) in bare soil and vegetated patches. Each value represents the mean $\pm$ CI ($n = 3$). The F-statistic value, degrees of freedom (df) and p value are showed

	Bare soil patch	Vegetated patch	F	DF	p
pH	7.17 ± 0.24	7.13 ± 0.24	0.07	(1, 4)	0.8
Electric conductivity (dS m^{-1})	0.14 ± 0.08	0.24 ± 0.08	5.08	(1, 4)	0.087
Organic matter (%)	0.48 ± 0.18	1.01 ± 0.18	32.3	(1, 4)	0.005
Total nitrogen (%)	0.021 ± 0.04	0.067 ± 0.04	5.97	(1, 4)	0.07
Available phosphorous (ppm)	11.5 ± 2.4	18.1 ± 2.4	28.4	(1, 4)	0.006
Mean annual root density (mg cm^{-3})	1.14 ± 0.25	2.31 ± 0.42	30.6	(1, 71)	<0.0001
Mean annual CO_2 efflux (μmol CO_2 m^{-2} s^{-1})	0.21 ± 0.05	0.31 ± 0.08	13.4	(1, 83)	0.0004
Total heterotrophic bacteria (CFU × 10^5 g^{-1} soil)	19.8 ± 23.6	21.0 ± 23.6	0.01	(1, 4)	0.93

with changes in soil temperature only when water was not limited. In ecosystems subject to seasonal drought such as the patagonian steppe, the exponential relationship between soil respiration and soil temperature would no longer apply (Manzoni et al. 2012). High temperatures combined with low soil water content may limit the increase in soil CO_2 fluxes from soil respiration such as it was observed during summer in our study. Soil water content at 0–10 cm depth decreased to 10%, probably resulting in very low root and microbial

Fig. 3 Temporal dynamic in soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) in bare soil patches (white symbols) and in vegetated patches (black symbols), during the study period (June 2015 to May 2016) in a patagonian steppe. Symbols represent the mean $\pm$ CI (n = 3)
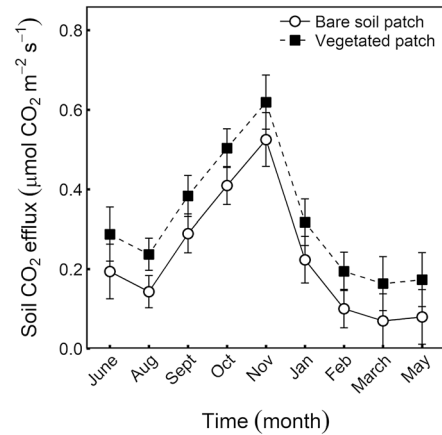
activity. The decrease in soil water availability during the dry season affects several physiological processes leading to plant dehydration and a substantial loss of

Fig. 2 a Temporal dynamic in soil volumetric water content at 0–10 cm depth (%), (b) soil temperature at 0–10 cm depth (°C) and (C) root density at 0–10 cm depth (mg dry mass cm^{-3}) in bare soil patches (white symbols) and in vegetated patches (black symbols) during the study period (June 2015 to May 2016) in a patagonian steppe. Symbols represent the mean $\pm$ CI (n = 3)
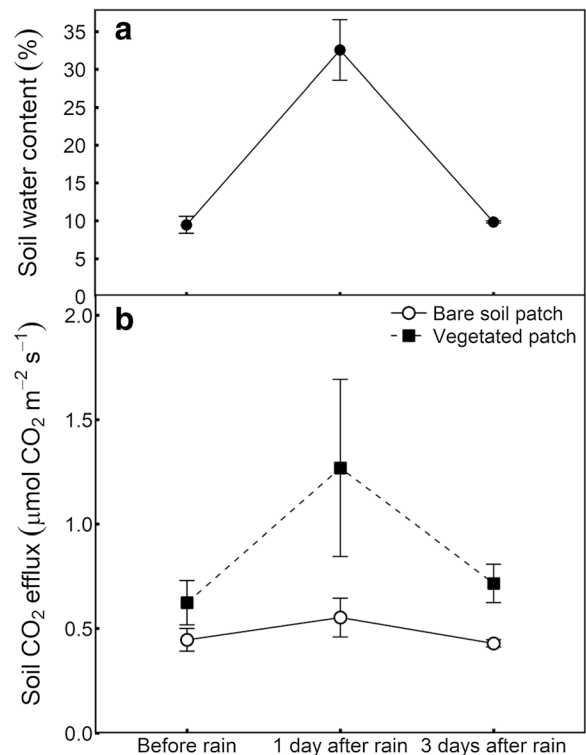

Fig. 4 a Soil volumetric water content at 0–10 cm depth (%) before, the next day and three days after a short rain event (3.5 mm) during summer. b Soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) from bare soil patches and vegetated patches before, the next day and three days after rain. Symbols represent the mean $\pm$ CI (n = 3)

root functionality in this ecosystem (Scholz et al. 2012; Bucci et al. 2013). For example, shallow roots of *S. filaginodes* and *A. prolifera*, two of the three dominant shrub species in this steppe, loss up to 70% of its water uptake capacity during the day (Bucci et al. 2013). This is also reflected in a decrease in plant transpiration during the drought period (Pereyra et al. 2017), therefore decreasing CO_2 capture. Likewise it is highly probable that during the summer drought a portion of microbial biomass die and other fraction of soil microorganism could have dormancy or spore formation (Schimel et al. 2007; Liu et al. 2009), resulting in a lower CO_2 released by heterotrophic respiration. Consistent with low summer respiration rates found in our study, Gonzalez-Polo and Austin (2009) observed a decrease of microbial biomass-C and beta-glucosidase activity and extracellular organic carbon increases during summer respect to spring in the patagonian steppe.

On the other hand, low temperatures during winter affect the physiological plant activity. During winter several species from the steppe exhibited tissue damage (Scholz et al. 2012; Zhang et al. 2016) modifying the metabolic activity. Similarly, during winter Gonzalez-Polo and Austin (2009) observed a decrease of microbial biomass and beta-glucosidase activity in the patagonian steppe.

Patch traits and spatial variability of soil CO_2 efflux

Bare soil and vegetated patches in the patagonian steppe had different physicochemical and biological properties. Shrubs in arid and semiarid ecosystems are known to be "fertility islands" with higher water and nutrient resources than in bare soil (Schlesinger et al. 1996; Aguiar and Sala 1999; Austin et al. 2004; Gonzalez-Polo and Austin 2009). In our study, there was less organic matter, P, N and root biomass in the bare soil patches than in the vegetated patches, although soil water content was significantly higher in bare soil than in vegetated patches. This pattern in the soil water content spatial variability was expected for us. In a previous study in this same area we determined higher root water uptake and higher water loss in the vegetated patches than water loss to atmosphere by direct evaporation from bare soil (Pereyra et al. 2017). Consequently bare soil could maintain more water than vegetated patches.

In spite of the method of plate count with agar as a nutrient medium has limitation because only a small fraction of the heterotrophic population can be counted, we used this technique for comparative purposes. It is known that microbial biomass is heterogeneous, being
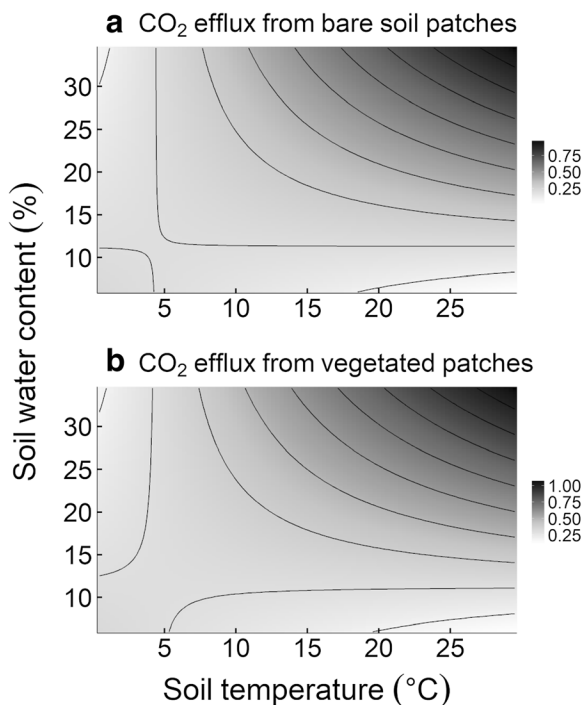

Fig. 5 Contour plots of soil CO_2 effluxes ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) relative to soil volumetric water content at 0–10 cm depth (%) and soil temperature at 0–10 cm depth (°C) from (**a**) bare soil patches and (**b**) vegetated patches. The values on the right side indicate the magnitude of CO_2 efflux
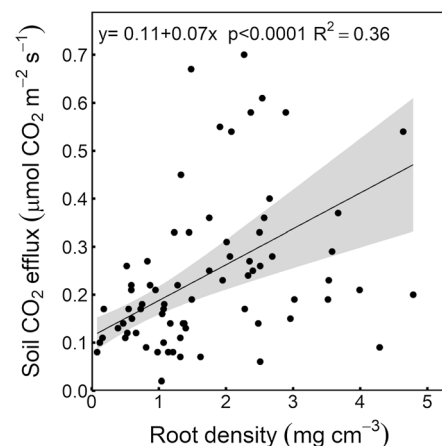

Fig. 6 Relationship between soil CO_2 effluxes ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) and root density (mg cm^{-3}). Each dot represents one measurement during the study period (June 2015 to May 2016). The solid line is the linear regression fitted to all data and the gray band is the 95% confidence interval

higher in vegetated patches than in bare soil (Rousk and Bengtson [2014]). Nevertheless, we did not find significant differences in heterotrophic bacterial count between patch types during the spring, similar to finding by Prieto et al. ([2011]) for other semiarid Patagonian ecosystems. We did not determine microbial biomass, however other studies have observed substantially higher microbial biomass, beta-glucosidase activity and dehydrogenase activity (a measure of the overall soil microbial activity) in vegetated patches than in bare soil of arid patagonian environments (Gonzalez-Polo and Austin [2009]; Prieto et al. [2011]). These results suggest that autotrophic respiration is the main driver of the spatial variation in soil CO_2 emission.

In addition of temporal variation in soil CO_2 efflux we observed small-scale spatial variation, being higher CO_2 fluxes from vegetated patches compared to the fluxes from bare soil patches. Our finding is consistent with results from other studies in arid ecosystems (Sponseller [2007]; Cable et al. [2008]), although contrary to the results of Rey et al. ([2011]) who observed higher effluxes from vegetation-free areas than from vegetated areas in a semi-arid steppe in Spain. Usually this spatial variability within a site is not taking into account when quantifying soil respiration at large spatial scales. It should be noted that we performed the measurements during midday, when there is usually a peak in the daily soil respiration due to the higher temperature. This is a common limitation of studies with manual measurements, but since we are comparing patches all measured at midday, this limitation does not compromise our results.

Responses of soil CO_2 efflux to rain pulses

In arid and semiarid ecosystems precipitation pulses are important triggers of biological activity. Approximately 40 events of <5 mm are recorded per year in the Patagonian steppe (Golluscio et al. [1998]). Although some shrub species have deep roots and take up most of the water from deep soil layers (Bucci et al. [2009]; Pereyra et al. [2017]), others shrubs and grasses have shallow roots and take up most of the water from the upper layers and utilize frequent short- pulses of water (Golluscio et al. [2009]), so they tend to grow quickly during the transient increasing in soil water. Similarly, microbial community in these patagonian soils is able to respond rapidly to increase in soil water availability (Austin et al. [2004]). A rapid and short-time period increase in autotrophic and/or heterotrophic physiological activity was observed after a small rain in our study. This short-term enhancement of soil CO_2 efflux following moisture pulse, often called the "Birch effect", is a general phenomenon in most dry ecosystems (Sponseller [2007]; Yan et al. [2014]). The magnitude of CO_2 pulse released from vegetated patches, which doubled the maximum value measured during the year, suggests that this large efflux could result from accumulated microbial and plant necromass, or lysis of living microbial cells, increasing the amount of substrate for microbial activity (Schimel et al. [2007]). Although it is considered that small rain events only favor the activity of microorganisms (Austin et al. [2004]), we think that root respiration could increase as well. Root biomass at 0–10 cm soil depth represents more than 50% of the entire root profile in the study site (Pereyra et al. [2017]) and further, dominant grass species exhibit water absorption from leaf surface after water pulse during the dry season, improving plant water status (Cavallaro et al. unpublished data) and probably the photosynthetic rate. Fresh input of photo-assimilates may increase root respiration or microbial activity (free-living or root symbionts) in response to root exudation during a few hours (Han et al. [2014a]).

Differently from vegetated patches, there were not substantial increases in CO_2 efflux following sporadic wetting of top soil in the bare soil patches. Although bare soil patches had lower root density than vegetated patches, they had roots, and in addition, these patches exhibit similar amount of heterotrophic bacteria than vegetated patches. Therefore, we expected an increase in CO_2 efflux following the rain event. Different results were found in other arid ecosystems where bare soil patches have similar or even higher response to rain events than vegetated patches (Cable et al. [2008]; Song et al. [2012]).

Conclusions

Soil CO_2 efflux in the patagonian steppe exhibited a strong seasonal pattern, reaching its maximum peak in spring. Our results indicate that on a seasonal scale the driving force for soil CO_2 efflux are the soil temperature and soil water content, being soil respiration limited by low values of both factors. Considering the proportion of each patch type in the study site (plant cover 45% and bare soil 65%; Pereyra et al. [2017]), the contribution of

bare soil to total soil CO_2 efflux is similar to the contribution of vegetated patches in rain-free periods (0.136 and 0.139 μmol m^{-2} s^{-1}, respectively). In this study we highlight the importance of considering the vegetation patchiness in the estimation of the soil CO_2 efflux at ecosystem level.

The dominant shrubs and grass species of the patagonian steppe have relatively high net assimilation rate (average 14.2 μmol m^{-2} s^{-1}, Carbonell Silletta et al. unpublished data) during the morning of the growing season. Taking into account the mean ecosystem leaf area index (0.71; Pereyra et al. 2017), the carbon capture during the growing season would be 10.1 μmol m^{-2} ground area s^{-1}. It is likely that the patagonian steppe can function as a carbon sink during a part of the year. If further studies show that carbon fixation is larger than CO_2 efflux from soil and vegetation during the whole year, then this arid ecosystem could contribute substantially to global CO_2 uptake due to its large geographical extension (about 670,000 km^2). The same phenomenon has been observed for other arid and semiarid ecosystems around the world (Ahlström et al. 2015).

In addition, our results, as well as other studies, suggest that rainfall pulses during dry periods can result in a quick and disproportional soil CO_2 efflux immediately after a rain event in the vegetated patches, which may significantly contribute to the annual ecosystem carbon balance. Thus, this finding revels that changes in the number of small rain events as well as changes in plant cover could have substantial consequences on soil ecology and biochemistry in dry and heterogeneous ecosystems.

Compliance with ethical standards

Conflict of interest   The authors have no conflict of interest.

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