



# Changes in soil moisture predict soil carbon losses upon rewetting in a perennial semiarid steppe in SE Spain

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## ABSTRACT

Our understanding of the spatial and temporal dynamics of soil CO<sub>2</sub> pulses after rainfall events is still limited and thus, our capacity to predict the consequences of future changes in precipitation patterns for dryland soils. In this study we examined the response of soil CO<sub>2</sub> pulses to rainfall size and pre-rain soil moisture conditions in a semiarid grassland. In a first experiment, we manipulated the amount of rainfall in a factorial combination that included three levels of rainfall size (1, 5 and 15 mm), three soil covers: vegetated areas (VEG), biological soil crusts (BSC) and bare soil (BS) and two nearby sites: a natural grassland and a degraded grassland. We measured soil CO<sub>2</sub> efflux over 24 h to capture rainfall pulses. In a second experiment conducted at the natural grassland, we measured soil CO<sub>2</sub> efflux after manipulating soil moisture to its full range in the area by wetting the soil to: 0–10%, 10–15%, 20–25%, 30–35% water content levels. All soil covers responded to the rainfall treatments within minutes, reaching up to 120 times baseline values and shortly returning to background rates. Rainfall size had a larger impact on the response than pre-rain soil moisture conditions. Whereas in most cases rainfall amount increased soil CO<sub>2</sub> pulses, initial moisture conditions did not affect total carbon losses despite much larger CO<sub>2</sub> peaks in very dry soils. Interestingly, even extremely low rainfall events (1 mm) caused significant carbon losses. The amount of carbon lost after rainfall events ranged from 0.45 in bare soils to 1.18 g C m<sup>-2</sup> day<sup>-1</sup> in vegetated areas. Overall, rainfall had a larger impact in vegetated areas at the degraded site implying that larger carbon losses can be expected as a result of land degradation. Sudden changes in soil moisture caused by rainfall predicted 65% of total carbon losses in BS, 70% in BSC and 80% in VEG at both sites. However, the slope was significantly lower in bare soils suggesting substrate limitation. Since most of the carbon resides belowground in these grasslands, carbon losses as a result of larger rainfall events and longer dry periods in this area could have important consequences for soil carbon stocks.

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## 1. Introduction

Semiarid and arid ecosystems are characterised by irregular rainfall events that often produce what is known as rainfall pulses (Birch, 1958). These rainfall pulses wet the soil surface, where labile carbon and microbial biomass accumulate over dry periods, and become available for microbial decomposition leading to large soil CO<sub>2</sub> effluxes (e.g. Harper et al., 2005; Rey et al., 2005; Sponseller, 2007; Borken and Matzner, 2009; Williams et al., 2009; Munson et al., 2010). Abiotic processes, including carbonate dissolution (Schlesinger, 1985; Roland et al., 2013; Rey, 2015) and water physical CO<sub>2</sub> displacement from soil pore

spaces (Huxman et al., 2004; Lupascu et al., 2014) may also contribute to the observed soil CO<sub>2</sub> pulses upon rewetting.

In semiarid and arid ecosystems most of the carbon resides belowground (Burke et al., 2008) so soil CO<sub>2</sub> pulses caused by episodic precipitation events have potential important consequences for soil carbon stocks. Thus, accurately quantifying soil CO<sub>2</sub> pulses after rainfall events is essential to understand carbon balance dynamics in these belowground dominated ecosystems. Since precipitation frequency and intensity are predicted to increase (IPCC, 2013), rainfall pulses may become even more important in the near future. Furthermore, it has recently been shown that semiarid ecosystems are much more important in the global terrestrial carbon balance than previously thought, determining the interannual variation in the terrestrial carbon sink (Ahlström et al., 2015).

Several studies have tried to quantify and describe rainfall pulses (e.g. Yang et al., 2008; Munson et al., 2010; Xu and Luo, 2012). The

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**Table 1**  
Three-way ANOVA results to tests differences between rainfall size treatment, soil covers in environmental conditions: initial temperature, initial soil water content, change in SWC in Experiment I ( $n = 4$ ).

Factors		$T_0$ (°C)			SWC <sub>0</sub> (%)			$\Delta$ SWC (%)		
		F	df	P	F	df	P	F	df	P
Three-way MANOVA										
Exp. I	Site	13.635	1	<b>0.0005</b>	35.297	1	<b>0.0001</b>	21.69	1	<b>0.0001</b>
	Rainfall size	0.7894	2	0.4597	0.3958	2	0.8522	173.64	2	<b>0.0001</b>
	Soil cover	22.008	2	<b>0.0001</b>	7.4033	2	0.2582	1.258	2	0.2924
	Site x Treat	0.6185	2	0.5425	2.4438	2	0.3782	9.378	2	<b>0.0003</b>
	Site x SC	0.0003	2	0.9969	3.6977	2	0.2327	5.003	2	<b>0.0102</b>
	Treat x SC	0.0727	4	0.9901	2.1230	4	0.7882	3.3995	4	<b>0.0102</b>
	Site x Treat x SC	0.3321	4	0.8552	0.6458	4	0.9705	1.4971	4	0.2160

Bold numbers are statistically significant ( $P < 0.05$ ).

magnitude of soil carbon loss is positively correlated to rainfall event size (Cable and Huxman, 2004; Chen et al., 2008), pre-rain soil water conditions (Sponseller, 2007), plant activity (Harper et al., 2005) and soil organic matter content (Ma et al., 2012). Despite the increasing number of studies and recent advances in our understanding of rainfall pulses, several aspects need urgent attention. For instance, the spatial variability that characterises these ecosystems is rarely taken into account and the effect of soil degradation on carbon losses after rainfall events is poorly understood.

Semiarid ecosystems are characterised by highly heterogeneous sparse vegetation with patches of bare soil and presence of biological soil crusts, which are widespread across arid regions (Belnap and Lange, 2003). These communities are dominated by lichens, mosses and cyanobacteria and play an important role in water, carbon and nutrient cycles (Castillo-Monroy et al., 2011; Berdugo et al., 2014). Plants regulate soil moisture dynamics by minimising evaporative losses, intercepting rainfall water and taking up water through roots. Plants also modify soil physicochemical characteristics by providing labile carbon substrates as root exudates for heterotrophic microorganisms and litter as organic matter input (Cardon and Gage, 2006). Moreover, growth and maintenance of plant roots (autotrophic respiration) directly contribute to soil respiration, reaching up to 50% of annual soil CO<sub>2</sub> efflux in some cases (Rey et al., 2002). Microbes and biological soil crusts that live in the topsoil are capable of responding to sudden soil moisture availability much faster than roots, and are capable of withstanding extended periods of drought (Schimel et al., 1999). Given that different biotic components contribute to soil CO<sub>2</sub> efflux in different soil covers, the response to rainfall events of these highly patchy soils may differ. Despite the large spatial variability of these ecosystems, few field studies have taken into account soil cover when quantifying the dynamics of soil CO<sub>2</sub> efflux after rainfall events. Such information would be very valuable when assessing carbon losses in semi-arid ecosystems at large spatial scales.

Another important factor affecting semiarid ecosystems is land degradation. More than 20 of semiarid lands are degraded or prone to desertification, and this area is expected to increase, potentially affecting soil carbon dynamics (Reed et al., 2012; Feng and Fu, 2013). Thus, understanding how changes in vegetation cover and soil impoverishment as a result of land degradation will affect ecosystem and soil carbon fluxes is important for the prediction of ecosystem carbon dynamics to global change. Loss of vegetation cover, and shallow soils, as a result of land degradation, alter soil hydrological conditions (Rey et al., 2011) and in turn, may affect soil CO<sub>2</sub> pulses upon rewetting.

Although the importance of rainfall pulses for the ecosystem carbon balance in this biome is widely recognised (e.g. Jarvis et al., 2007; Collins et al., 2008; Jenerette et al., 2008; Yan et al., 2010), a proper understanding of the response of soil CO<sub>2</sub> efflux to rainfall events is still lacking. Despite much research on soil CO<sub>2</sub> pulses (e.g. Jenerette and Chatterjee, 2012; Collins et al., 2014), it is not yet clear which factors control the pulse effect of a single rainfall event and its implications for semiarid ecosystem functioning (Nielsen and Ball, 2015).

The overall aim of this study was to characterise how soil CO<sub>2</sub> efflux responds to rainfall pulses, and how rainfall size and soil moisture conditions affect the response of different characteristic soil covers: bare soil (mostly heterotrophic respiration), biological soil crusts and vegetated areas (that includes autotrophic respiration). Moreover, we aimed to understand whether land degradation affects rainfall pulses in different soil covers beyond changes in plant cover and soil depth, by comparing two nearby grassland sites with similar characteristics but different land use history.

We hypothesised that: (1) the response of soil CO<sub>2</sub> efflux to rainfall events and thus, the amount of carbon loss upon rewetting, will increase with both, soil dryness prior to rainfall event (that favours the accumulation of labile carbon) and the size of the event (that will increase moisture activating microbial activity) (2) the response will differ between soil covers with greater response under plant patches, given the large accumulation of labile carbon compared to bare soils, (3) land degradation will induce larger CO<sub>2</sub> pulses given that the degraded soils are subject to longer dry periods (with an altered hydrological cycle as a result of significantly lower vegetation cover and shallower soils) favouring the accumulation of labile carbon that becomes available upon rewetting.

## 2. Material and methods

To address these hypotheses we carried out a multifactorial field experiment in two nearby grassland sites differing in land use history, where we manipulated the amount of rainfall and followed rainfall pulses over 24 h in three soil covers. In another experiment carried out at the natural grassland site we manipulated the initial soil moisture conditions.

**Table 2**  
Four-way ANOVA with repeated measures (time) results of Experiment I to test differences in the response of soil respiration to different rainfall size treatments in different sites and soil covers over 24 h ( $n = 4$ ).

EXP. I		SR ( $\text{g m}^{-2} \text{day}^{-1}$ )		
Four-way ANOVA		F	df	P
Factor	Site	1.0845	1	0.3071
	Rainfall size	42,965	2	<b>0.0001</b>
	SC	18.754	2	<b>0.0001</b>
	Site × Rainfall size	1.5808	2	0.2157
	Site × SC	4.9855	2	<b>0.0108</b>
	Rain × SC	4.0638	4	<b>0.0002</b>
	Site × Rainfall size × SC	1.4212	4	0.2403
	Time	20.749	10	<b>0.0001</b>
	Time × Site	3.2822	5	<b>0.0127</b>
	Time × SC	10.971	10	<b>0.0001</b>
	Time × SC × Site	3.9080	20	<b>0.0002</b>
	Time × Site × Rainfall size	4.3398	10	<b>0.0001</b>
	Time × SC × Rainfall size	3.0953	20	<b>0.0001</b>
	Time × SC × Rainfall size × Site	1.3812	20	0.1390

Bold numbers are statistically significant ( $P < 0.05$ ).

2.1. Study sites

The study sites are located in the Cabo de Gata Natural Park, in the province of Almería (Andalucía) in the SE of Spain (N 36° 01' 26.0", W 2° 01' 58.8"). The climate in this area is semiarid with a mean annual precipitation of 250 mm and a mean annual temperature of ~18 °C (estimated from Nijar meteorological station, the nearest to the study sites) and is characterised by prolonged summer droughts (from May to September) and infrequent and random rainfall events (Rey et al., 2012). The dominant soils are classified as Lithic Leptosols (WRB, 2006) (Table 1A in Appendix A). The ecosystem is a perennial steppe of *Stipa tenacissima* characterised by open areas with vegetation cover varying between 18 and 65% of the ground surface (Table 2A in Appendix A), depending upon past human impact.

2.2. Experimental design

We selected two nearby sites (15 km apart) with the same vegetation and substrate but differing in vegetation cover and soil depth as a result of land degradation (Rey et al., 2011). The natural site (Balsablanca), is located 200 m a.s.l.; whereas the degraded site (Amoladeras), is nearer to the sea, at 50 m a.s.l., with less vegetation cover and shallower soils as a consequence of intensive grazing (Table 1A in Appendix A).

We selected these sites as representative of two distinctive degradation stages based on a previous hierarchical classification of the ecosystems present at the park (see Escribano, 2002). The sites had the same geology, topography, vegetation type, and climate. According to the soil cartography map (CMA, 1999), the soils in

EXPERIMENT I:  
Rainfall size

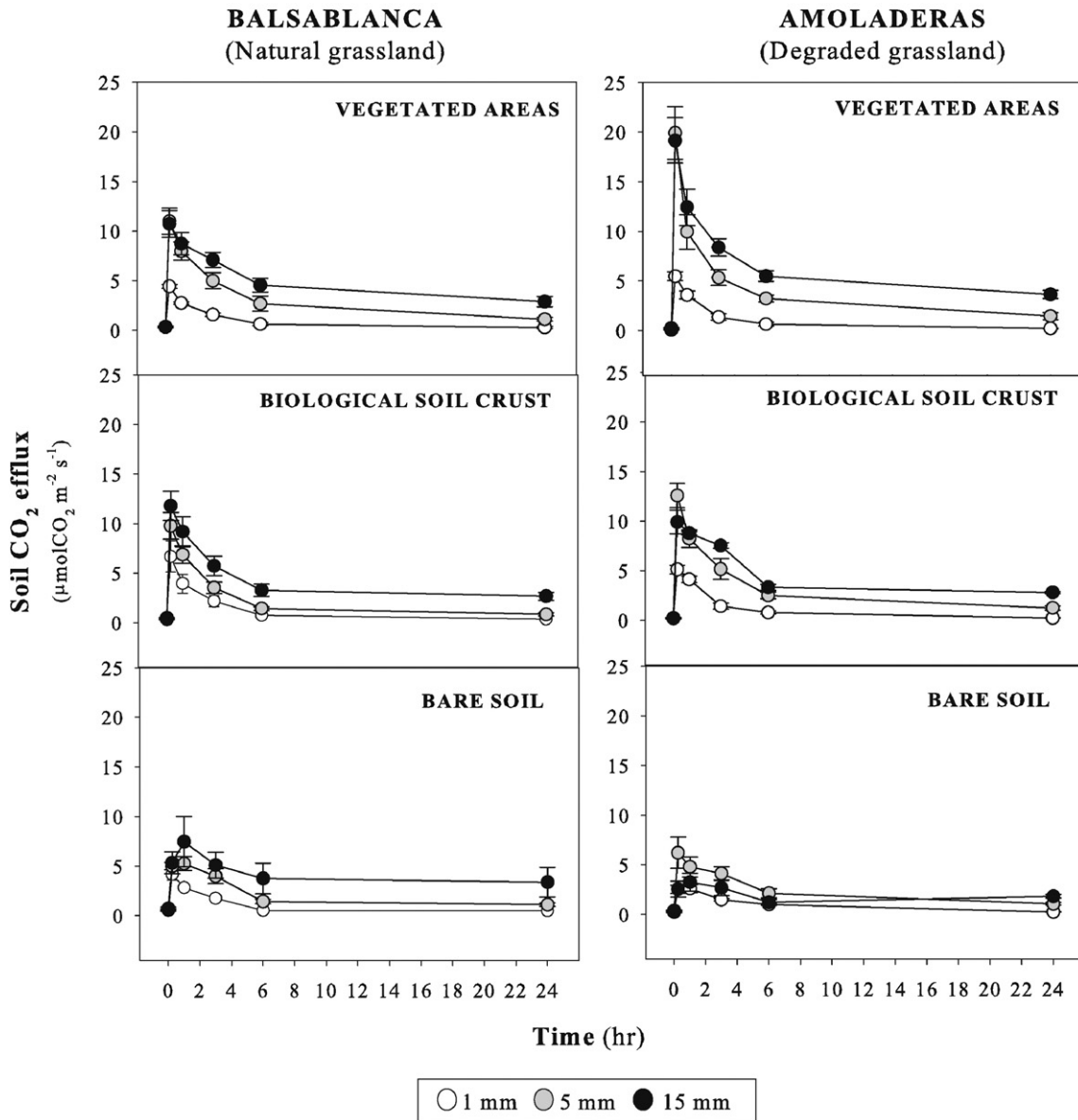


Fig. 1. Response of soil CO<sub>2</sub> pulses to rainfall size (EXPERIMENT I) over 24 h in the different soil covers (vegetated areas, biological soil crusts and bare soils) at the natural and degraded grassland sites. Values are the mean (n = 4) ± 1 SE.

Amoladeras, has physico-chemical characteristics typical of degradation processes in comparison to soils in Balsablanca (Table 2A in Appendix A). Further details of the sites are given elsewhere (Rey et al., 2011).

At each site, we selected a 10 m<sup>2</sup> plot that was located at least 100 m from the edge of the field and was representative of the entire field site. We randomly assigned four subplots where we placed three soil collars, one in each soil cover: bare soil (BS), biological soil crust (BSC) and under a *Stipa* sp. plant (VEG) per rainfall treatment.

### 2.3. Manipulative experiments

In August 2009, we carried out a manipulative experiment at both field sites:

In Experiment I, we added water as a single uniform event in each subplot to each soil collar (one per rainfall size treatment). We used a sprayer to simulate the following rainfall size treatments often observed at the site: 1, 5, and 15 mm. All measurements were taken at random between 15 and 17 August, the middle of the dry season. Field soil

## EXPERIMENT I: Rainfall size

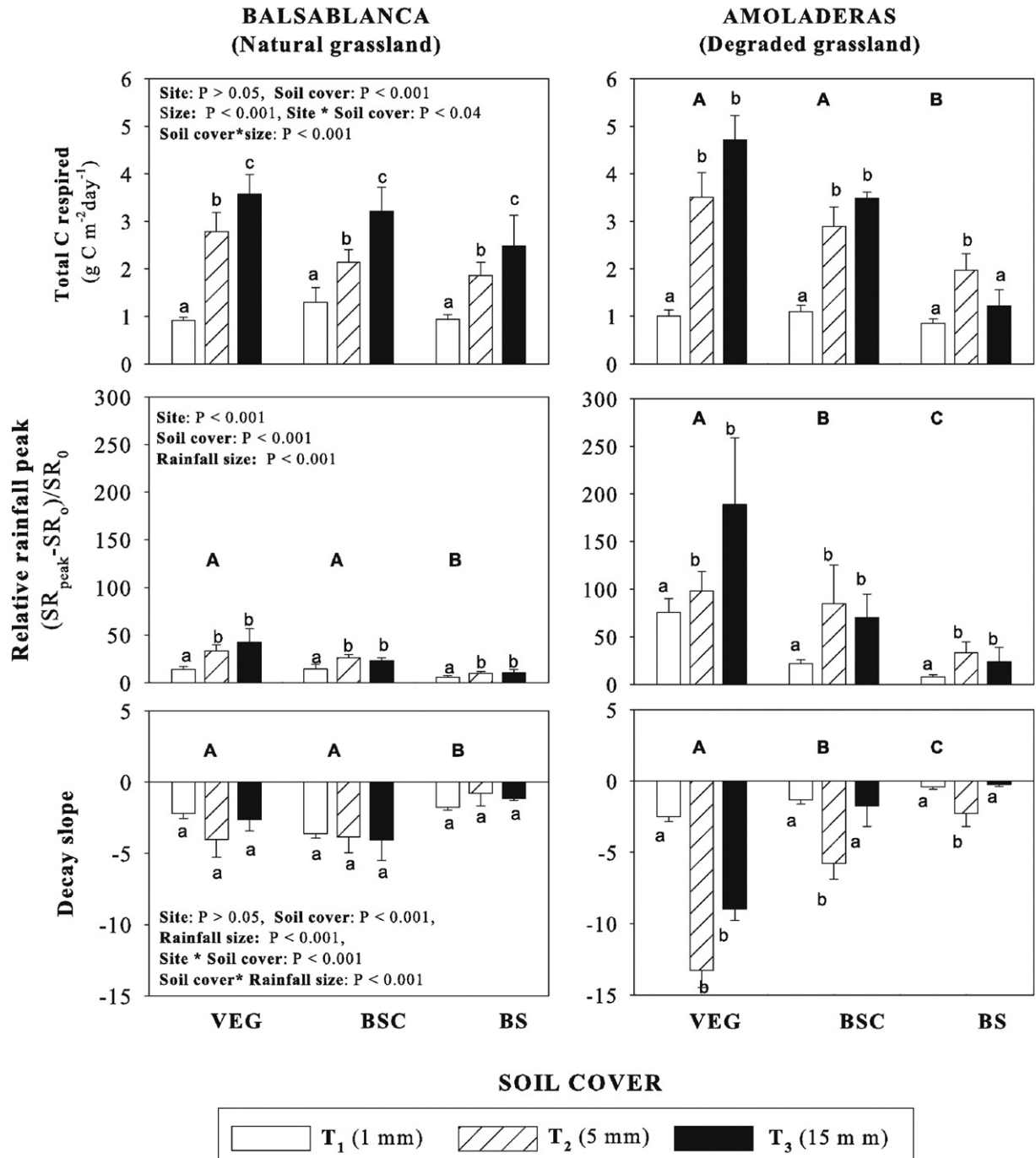


Fig. 2. Total carbon respired over 24 h, relative peak and decay slope in response to rainfall size for different soil covers and sites. Values are the mean ( $n = 4$ )  $\pm$  1 SE.

**Table 3**

Three-way ANOVA results of Experiment I to tests differences between total amount of carbon respired, relative peak after rainfall event, relative change in soil CO<sub>2</sub> efflux rate after 24 h and slope of the peak for soil cover, rainfall size treatment and site ( $n = 4$ ).

Factors		Total C respired (g C m <sup>-2</sup> day <sup>-1</sup> )			Relative peak			Relative change after 24 h.			Slope (μmol CO <sub>2</sub> μmol CO <sub>2</sub> <sup>-1</sup> h <sup>-1</sup> )		
Three-way MANOVA		F	df	P	F	df	P	F	df	P	F	df	P
Exp. I	Site	1.0588	1	0.3081	21.633	1	<b>0.0001</b>	10.921	1	<b>0.0017</b>	17.074	1	<b>0.0001</b>
	Rainfall intensity	55.775	2	<b>0.0001</b>	4.3621	2	<b>0.0175</b>	15.628	2	<b>0.0001</b>	25.074	2	<b>0.0001</b>
	Soil cover	17.859	2	<b>0.0001</b>	11.845	2	<b>0.0001</b>	3.0703	2	0.0546	57.016	2	<b>0.0001</b>
	Site × Treat	1.1585	2	0.3216	1.8839	2	0.1990	4.8636	2	<b>0.0114</b>	19.093	2	<b>0.0001</b>
	Site × SC	3.5130	2	<b>0.0368</b>	5.0386	2	<b>0.0099</b>	1.0668	2	0.3512	29.344	2	<b>0.0001</b>
	Treat × SC	5.1530	4	<b>0.0014</b>	1.5736	4	0.1146	2.1010	4	0.0933	8.4247	4	<b>0.0001</b>
	Site × Treat × SC	1.5110	4	0.2116	0.8371	4	0.5077	0.7952	4	0.5335	3.2414	4	<b>0.0167</b>

Bold numbers are statistically significant ( $P < 0.05$ ).

water content was very low at the time (*ca.* 5%) and vegetation was inactive. These rainfall sizes are representative of those encountered at the study area. Over a three-year period (2007–2009), 55% of the rainfall events were <1 mm, 20% <5 mm, 11% up to 15 mm and the rest 2% larger than 15 mm.

The pulse-event sizes were also randomised with respect to time of the day to minimise the effects of diurnal variation in soil temperature (all soil CO<sub>2</sub> efflux measurements between 10 and 14:00 h). We measured soil temperature and soil water content at 3 cm at each measuring time with a soil thermistor and a portable soil moisture sensor (ML2x, Devices Ltd., Cambridge, UK), respectively. Soil CO<sub>2</sub> efflux was measured before and right after the event and for 24 h with a portable gas analyser (EGM-4, PP-Systems, USA) at times 15 min, 1 h, 2 h, 4 h and 24 h to capture the short-term temporal dynamics and characterise the response to rainfall events of each soil cover.

In a subsequent experiment, Experiment II, we tested the influence of precedent soil moisture conditions by slowly wetting the soil prior to simulating a rainfall event up to 0–5, 10–15, 20–25 and 30–35% soil volumetric water content at 3 cm and applied 5 mm of water by spraying evenly this amount on the soil surface of each soil collar. This event size was chosen because in the study area a large proportion of the rainfall events that wet the soil are of this magnitude (20% of the total over three year period). We carried out the second experiment only in the natural site, assuming that the response to initial soil moisture conditions was the same at both sites (based on previous results). The range of soil moisture conditions represents the full range of soil moisture contents measured at the sites (Rey et al., 2011, 2012).

In this case, we measured soil CO<sub>2</sub> efflux at time 0, 25 min, 1 h, 2 h, 4 h and 24 h after the rainfall event. Soil moisture was monitored throughout the 24 h, reached a maximum after 25 min of applying water and then progressively declined. This experiment was carried out the subsequent week (23–26 August) with the same experimental design by moving the soil collars to a different position in the same subplots as Experiment I. To avoid rainfall pulses caused by the rewetting of soils, we waited for a couple of days before carrying out this experiment. Soil moisture was

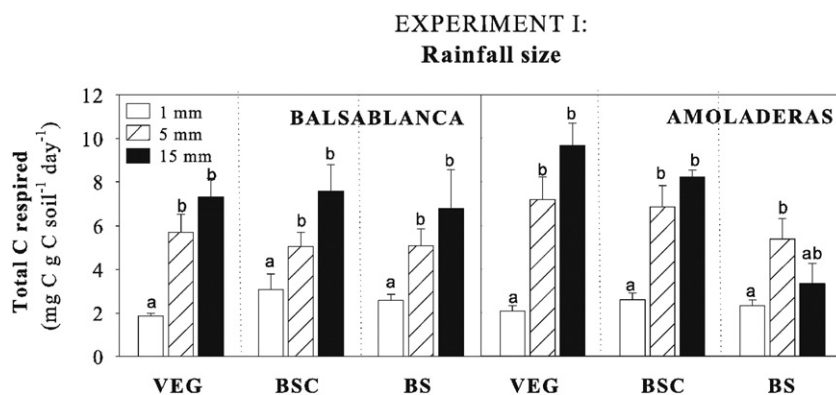
monitored to ensure it was kept at target levels. The last rainfall event prior to the experiment was on day 161 (June) with 1 mm of rain.

#### 2.4. Statistical analyses

Experiment I: We analysed differences in rainfall CO<sub>2</sub> pulses in response to rainfall size using a three-way analysis of variance. Main fixed factors were: *site* (natural, degraded), *soil cover* (VEG, BSC, BS) and *rainfall treatment* (1, 5, 15 mm). We first analysed the evolution of soil CO<sub>2</sub> efflux (μmol m<sup>-2</sup> s<sup>-1</sup>) over 24 h period for both sites, rainfall treatments and soil covers with a four-way ANOVA with repeated measures on one factor (time). Then, we obtained several parameters to characterise the response curves: total amount of carbon respired (by interpolating soil CO<sub>2</sub> efflux rates between measuring times for each curve) (TC<sub>respired</sub>), relative CO<sub>2</sub> peak (to the pre-rain soil CO<sub>2</sub> efflux rate) (SR<sub>peak</sub>), relative change in SR after 24 h period as a proxy of duration of the rainfall pulse (SR<sub>24</sub>) and slope of the decay after the peak (differences between the peak respiration rate and the soil CO<sub>2</sub> efflux rate after the peak) (slope). The total amount of carbon respired was calculated per area and on carbon basis using bulk density and total organic carbon content for each soil cover and site. We performed a three-way ANOVA to test if *site*, *soil cover* and *rainfall size* affected these response curve parameters. When factors were significant ( $P < 0.05$ ), post hoc tests were done using a Tukey's test.

To assess if differences between treatments were related to environmental conditions, we calculated mean soil temperature (°C) and soil water content (%) at the time of the event, and the change in soil water content with rainfall treatment (ΔSWC). We then performed a three-way ANOVA to test if *site*, *soil cover* or *rainfall size* affected these environmental parameters. Again, when factors were significant ( $P < 0.05$ ), post hoc tests were done using a Tukey's test.

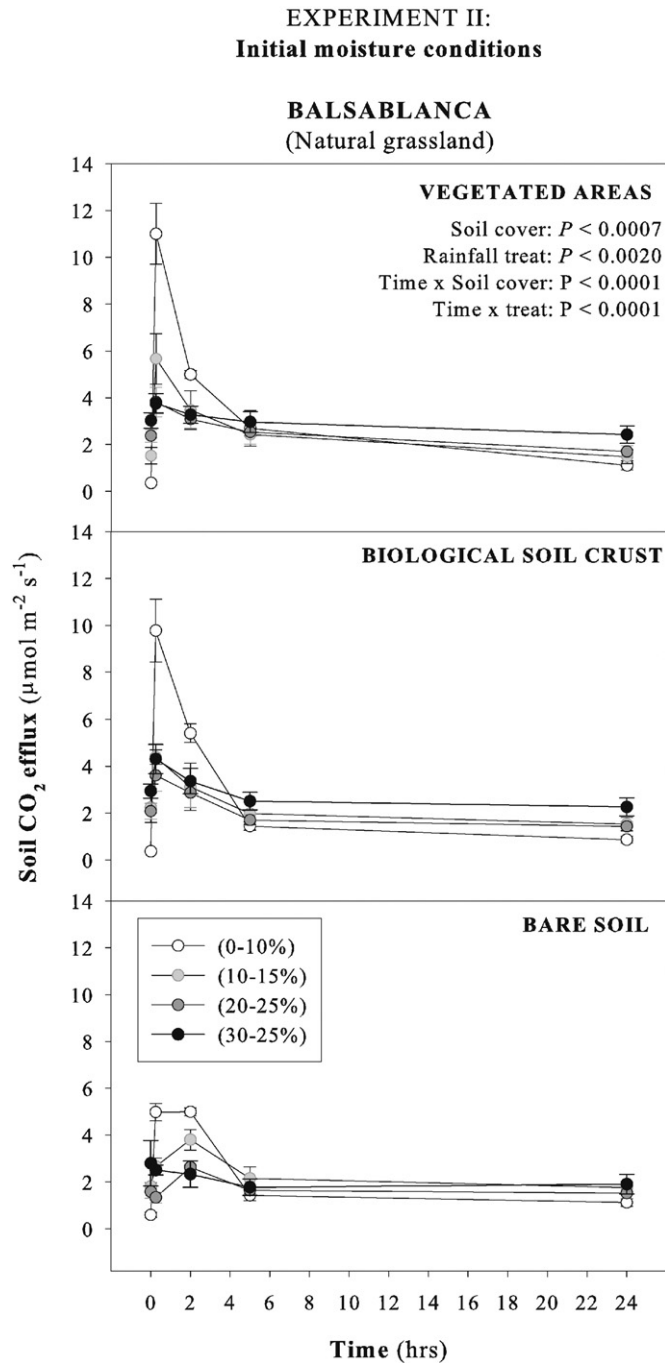
In Experiment II, soil cover (VEG, BSC, BS) and soil moisture treatments (0–5, 10–15, 20–25 and 30–35% soil volumetric water content) were fixed factors in a three-way ANOVA. Similarly, we first analysed the response over time by using a three-way ANOVA with repeated



**Fig. 3.** Total carbon respired per unit of soil carbon over 24 h, in response to rainfall size for different soil covers and sites. Values are the mean ( $n = 4$ ) ± 1 SE.

measures on one factor (time). Besides, differences between response curve parameters ( $TC_{\text{respired}}$ ,  $SR_{\text{peak}}$ , etc.) and environmental variables (temperature, SWC, etc.) were tested with a two-way ANOVA. When factors were significant ( $P < 0.05$ ), post hoc tests were done using a Tukey's test.

In our experimental design we assumed that soil  $CO_2$  pulses during the dry period are a function of rainfall intensity and pre-rain soil moisture conditions. To understand whether differences in the response between soil covers could be attributed to differences in soil carbon content we expressed the total amount of carbon respired on a carbon basis. Then, to test whether the total amount of carbon respired was related to changes in soil water content ( $\Delta SWC$ , %) at different soil covers, we compared regression slopes across soil cover types using the



**Fig. 4.** Effect of initial moisture conditions on soil  $CO_2$  pulses (EXPERIMENT II) over 24 h in the different soil covers (vegetated areas, biological soil crusts and bare soils) at the natural grassland. Values are the mean ( $n = 4$ )  $\pm$  1 SE.

interaction term *covariate by factor* in an ANCOVA model (i.e., parallelism test). All analyses were performed using JMP 9.0 software from SAS (2010 SAS Institute Inc., USA).

### 3. Results

#### 3.1. Environmental conditions

Mean daily air temperature during the study period was  $27.5^\circ\text{C}$  (minimum:  $15.6^\circ\text{C}$ , maximum:  $34.5^\circ\text{C}$ ) with minimum variation in mean, maximum, and minimum daily air temperatures over the 10-day study period. There was no precipitation prior (one event of  $< 1$  mm occurred on 20th June) or during the study period. Initial soil temperature differed between sites ( $P < 0.0005$ ) and soil covers ( $P < 0.0001$ ) (Table 1). Soil temperature and soil water content were significantly lower under plant than in the other two soil cover types at both sites. The degraded site was consistently warmer ( $2^\circ\text{C}$  on average) and slightly drier (6%) than the natural grassland. Despite such small differences in soil environmental conditions, soil  $CO_2$  efflux rates in the natural site were more than two-fold those measured in the degraded site prior to the rainfall experiments ( $0.48$  and  $0.22 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively).

#### 3.2. Impact of rainfall size

In Experiment I where we manipulated rainfall size between 1 and 15 mm, all rainfall treatments resulted in a  $CO_2$  peak after 15 min of rainfall application after which soil  $CO_2$  efflux declined over the 24 h. (Time,  $P < 0.0001$ ). Overall, soil  $CO_2$  efflux positively responded to rainfall size ( $P < 0.0001$ , Table 2) and soils under vegetated areas were more responsive than soils under biological soil crust or bare soil (Time  $\times$  soil cover,  $P < 0.0001$ ) (Fig. 1). However, soil covers responded differently between sites (Time  $\times$  soil cover  $\times$  Site,  $P = 0.002$ ). At the natural site, increased rainfall size resulted in higher soil  $CO_2$  efflux rates in all soil covers. Moreover, soils under vegetated areas and biological soil crust showed similar response (Fig. 1). At the degraded site, the response was larger than at the natural site (Time  $\times$  Site,  $P = 0.012$ ). However, soils responded positively to rainfall size only under plant, where peak soil  $CO_2$  efflux rates were two times higher than at the natural site at rainfall treatments of 10 and 15 mm (Fig. 1). Finally, the response of biological soil crusts and bare soils seemed to saturate at 5 mm when, although not significantly, maximum soil  $CO_2$  efflux rates were measured.

The total amount of carbon respired over the 24 h. period after rainfall events differed significantly between soil covers ( $P < 0.001$ ) and rainfall size ( $P < 0.0001$ ). Although total carbon respired was on average similar between sites ( $P = 0.31$ ) and the trend between soil covers was similar, soil cover were more responsive at the degraded site ( $P = 0.03$ ) (Fig. 2, Table 3). In general, the largest carbon losses after rainfall events were found under vegetated areas, then biological soil crusts and last, bare soil. However, this trend was significant only at the degraded site, where bare soils released significantly less carbon after rainfall events than under the other soil covers (three times less

**Table 4**

Three-way ANOVA results for Experiment II to test differences in the response of soil respiration to rainfall treatments (initial soil water content conditions) in different soil covers over 24 h ( $n = 4$ ).

Three-way ANOVA		SR ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )		
		F	df	P
Exp II	Treat	5.9811	3	<b>0.0020</b>
	SC	8.9783	2	<b>0.0007</b>
	Treat $\times$ SC	0.4825	6	0.8169
	Time	117.02	4	<b>0.0001</b>
	Time $\times$ Treat	11.285	10	<b>0.0001</b>
	Time $\times$ SC	6.8892	8	<b>0.0001</b>
	Time $\times$ Treat $\times$ SC	0.8434	24	0.6754

Bold numbers are statistically significant ( $P < 0.05$ ).

than the amount of carbon released in vegetated areas). Besides, although at both sites the total amount of carbon released increased with rainfall size (*Site* × *rainfall size*,  $P = 0.32$ ), maximum carbon losses were reached after 15 mm events at the natural site while at 5 mm events at the degraded site. When rates were expressed on a carbon basis, differences between soil covers disappeared at the natural grassland site (Fig. 3).

Regarding the relative peak (compared with initial soil CO<sub>2</sub> efflux rates prior to rainfall events) and decay afterwards, both responses were much higher with differences among soil covers more pronounced at the degraded site (Table 3, Fig. 2). There, the response between soil covers significantly differed while at the natural site, soils under plant and biological soil crust showed similar responses.

### 3.3. Influence of initial soil moisture conditions

In Experiment II, the same amount of rainfall (5 mm) was applied to soils in the natural site with varying soil water content to assess the importance of initial soil moisture conditions.

As expected, soil moisture treatment resulted in significant differences in soil temperature as well as soil water content (SWC) (Table 5). Although all soil moisture treatments led to a rainfall pulse in all soil covers (*Time*,  $P < 0.001$ ), not all soil covers responded immediately to the rainfall event (*Time* × *soil cover*,  $P < 0.0001$ ) (Fig. 4). Soils under plant and biological soil crusts were significantly more responsive than bare soils (Table 4). However, all soil covers responded similarly to soil moisture conditions (*Treat* × *soil cover*,  $P = 0.82$ ). In all cases, increased aridity led to higher responses (soil moisture conditions,  $P < 0.002$ ) and soils were most responsive when very dry (<10%) (*Time* × *treat*,  $P < 0.0001$ ) (Fig. 4).

The total amount of carbon lost was not significantly different between soil moisture treatments ( $P > 0.05$ ) but significantly differed between soil covers ( $P < 0.02$ ), with largest carbon losses under vegetated areas and smallest in bare soil (Fig. 4). However, the relative CO<sub>2</sub> peak was highly significantly larger than in other treatments (7–100 fold) when soils were driest (0–10%) and smallest when soils were wettest (30–35%). Moreover, rainfall pulses significantly differed between soil covers ( $P < 0.01$ ) with the largest peaks under plant, biological soil crusts and bare soils, respectively. The slope after the peak generally decreased with increasing initial soil moisture conditions and was significantly larger at the driest soil treatment in all soil covers (Fig. 5). After 24 h soil CO<sub>2</sub> efflux rates have returned mostly to their initial values. Although not significantly, soils under plant and biological soil crust responded faster than bare soils in all soil moisture treatments (Fig. 5).

The total amount of carbon loss after rainfall events in both sites and all soil covers was linearly related to the change in soil water content with rainfall, explaining 80, 70 and 65% of the variance observed in VEG, BSC and BS, respectively (Fig. 6). The parallelism test of the effect change in SWC across soil types reached the significance level ( $P =$

0.005), showing an increase of the regression slope from BS to VEG, with an intermediate value in BSC. An *a posteriori* test of the differences among the slopes of total carbon respired on change in SWC showed that only the regression slopes in BS and VEG were significantly different ( $P = 0.004$ , after applying the Bonferroni sequential correction).

## 4. Discussion

### 4.1. Impact of rainfall size

Our results are consistent with previous studies conducted in semi-arid grasslands where rewetting triggers rapid increases in soil respiration within minutes (e.g. Sponseller, 2007; Chen et al., 2008; Munson et al., 2010; Wang et al., 2016). In most of the studies that have measured the response of soil CO<sub>2</sub> efflux on an hourly basis, rates returned to pre-rain values within two days (e.g., Borken et al., 2003; Sponseller, 2007; Chen et al., 2008). Despite the transient nature of these pulses, soil carbon losses resulting from rainfall events can be important at ecosystem level (Jarvis et al., 2007). López-Ballesteros et al. (2015) estimated that rainfall CO<sub>2</sub> pulses contribute as much as 40% of the ecosystem carbon losses over the dry season at the same natural grassland studied here, and that soil CO<sub>2</sub> efflux was the only component significantly affected by rainfall pulses. Interestingly, we found that rainfall events of only 1 mm, which represent more than half of rainfall events in our study area (55% average over three years), caused carbon losses that would amount to 50 g C m<sup>-2</sup> yr<sup>-1</sup> which is a considerable amount of carbon given that the ecosystem is a net sink of carbon of around 100–124 g C yr<sup>-1</sup> (Rey et al., 2014). This suggests that, light but frequent rainfall events, may represent a significant carbon loss for these ecosystems. Moreover, given the increasing carbon losses with increasing rainfall size, this study suggests that the predicted increase in extreme rainfall events in the near future (IPCC, 2013) may have profound impacts on the carbon stocks of these semiarid ecosystems. The dynamic nature of these rainfall pulses together with the fact that they can contribute as much as 40% of the ecosystem carbon losses over the dry season (López-Ballesteros et al., 2015) emphasises the need of intensive temporal monitoring programs to accurately characterise carbon cycle dynamics in semiarid ecosystems.

Since the magnitude of the response differed among soil covers, this study also highlights the importance of considering the spatial heterogeneity of these ecosystems. As expected, soils under vegetated areas and biological soil crusts were more responsive to increases in rainfall size than bare soils. In this study, root respiration can be considered negligible as plants were inactive and roots take longer to respond to rainfall and require larger rainfall amounts to become active (López-Ballesteros et al., 2015). Soils under vegetated areas had significantly more carbon and nitrogen than bare soils (25%), i.e. greater substrate availability, which explains larger soil CO<sub>2</sub> pulses under vegetated areas. Most of the studies undertaken in similar climates have found

**Table 5**

Two-way ANOVA results of Experiment II to tests differences between environmental variables and total amount of carbon respired, relative peak after rainfall event, relative change in soil respiration rate after 24 h and slope of the peak for soil cover (SC) and rainfall size (Treat) ( $n = 4$ ).

Factors	T <sub>0</sub> (°C)			SWC <sub>0</sub> (%)			ΔSWC(%)						
	F	df	P	F	df	P	F	df	P				
Exp. II	Treat	25.814	3	<b>0.0001</b>	361.88	3	<b>0.0001</b>	30.108	3	<b>0.0001</b>			
	SC	2.6854	2	0.0818	0.2557	2	0.7727	4.4035	2	<b>0.0195</b>			
	Treat × SC	1.1997	6	0.3288	0.8241	6	0.8241	3.1413	6	<b>0.0195</b>			
Factors	Total C respired (g C m <sup>-2</sup> day <sup>-1</sup> )			Relative peak			Relative change after 24 h.			Slope (μmol CO <sub>2</sub> μmol CO <sub>2</sub> <sup>-1</sup> h <sup>-1</sup> )			
	F	df	P	F	df	P	F	df	P	F	df	P	
Exp. II	Treat	1.2951	3	0.2910	69.71	3	<b>0.0001</b>	23.330	3	0.0001	8.9102	3	0.0002
	SC	4.3435	2	<b>0.0204</b>	8.88	2	<b>0.0007</b>	1.1121	2	0.33	1.0598	2	0.3572
	Treat × SC	0.5635	6	0.7534	7.176	6	<b>0.0001</b>	1.7134	6	0.14	0.9317	6	0.4943

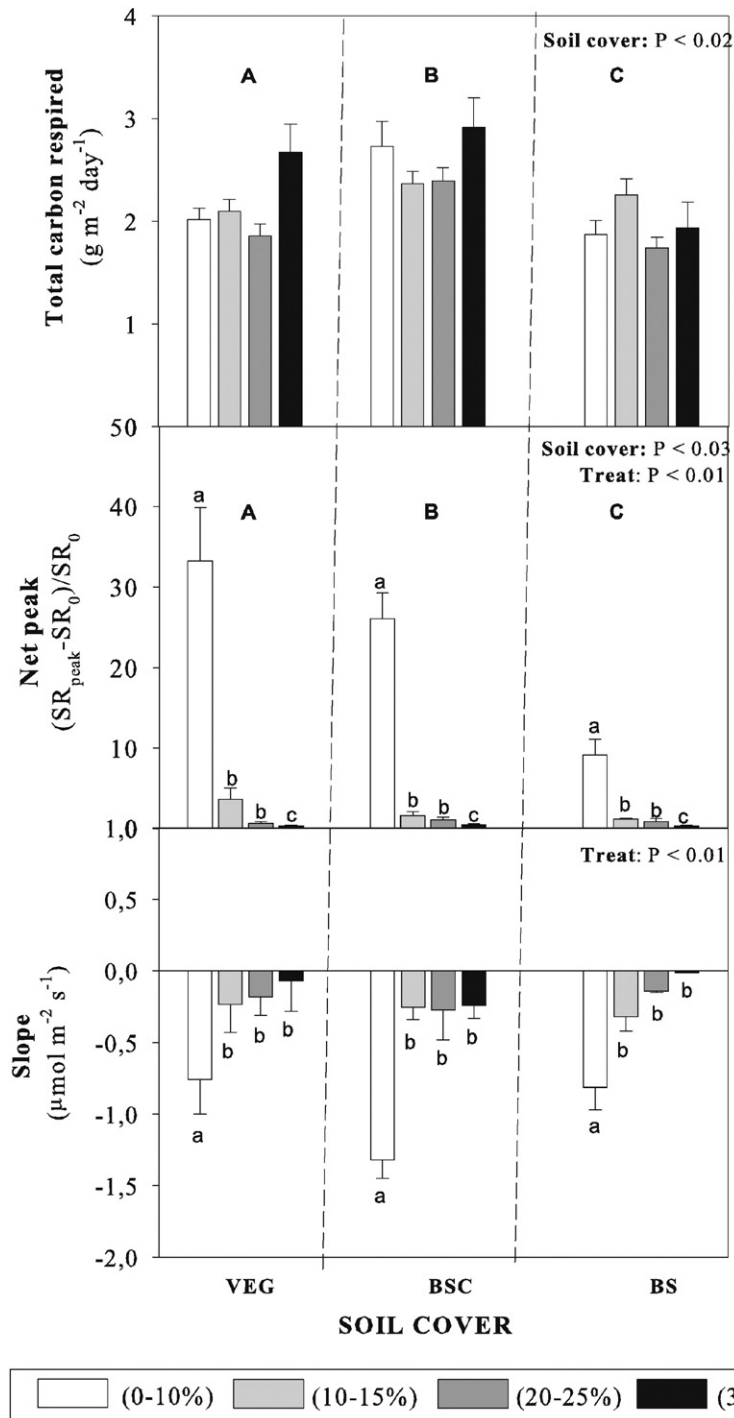
Bold numbers are statistically significant ( $P < 0.05$ ).

greater responses in vegetated areas than in bare soils (Sponseller, 2007; Jenerette and Chatterjee, 2012; Su et al., 2013). However, it is noteworthy that biological soil crusts showed a similar response to vegetated areas, despite having lower total organic carbon, and responded

even more to small rainfall events. Previous studies have shown the important contribution of biological soil crusts to rainfall pulses (Cable and Huxman, 2004; Thomas et al., 2011; Chamizo et al., 2012; Zhao et al., 2014) and soil moisture dynamics (Berdugo et al., 2014). Greater soil

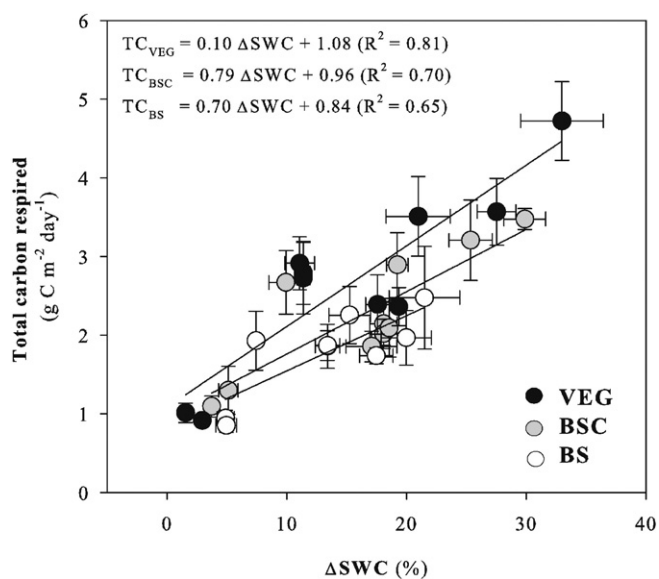
**EXPERIMENT II: Prerain soil moisture conditions**

**BALSABLANCA  
(Natural grassland)**



**Fig. 5.** Effect of initial soil moisture conditions on total carbon respired over 24 h, relative peak and decay slope for different soil covers at the natural grassland site. Values are the mean ( $n = 4$ )  $\pm$  1 SE.





**Fig. 6.** Relationship between change in soil moisture (%) upon rewetting and total carbon respired ( $\text{g C m}^{-2} \text{ day}^{-1}$ ) for the different soil covers: vegetated areas, biological soil crusts and bare soils for both Experiments. Each point represents the mean ( $n = 4$ )  $\pm 1$  SE. The regression lines were calculated for each soil cover.

water content with increasing rainfall size increases penetration of water into the soil profile (Sala and Lauenroth, 1985), and probably extends the duration of microbial activity in vegetated and biological soil crust areas where more carbon is stored with higher water retention (Berdugo et al., 2014). Furthermore, several studies have observed an increase in microbial biomass in response to increasing rainfall size (e.g., Liu et al., 2009; Zhang et al., 2013; Bell et al., 2014). For example, in a steppe in Colorado, microbial biomass increased rapidly and positively to rainfall size (Dijkstra et al., 2012).

Given that these ecosystems are characterised by a patchy environment with islands of resource concentrated under vegetated areas, such spatial heterogeneity needs to be taken into account when assessing carbon losses driven by rainfall events.

#### 4.2. Influence of initial moisture conditions

As expected, pre-rain soil moisture conditions affected soil  $\text{CO}_2$  pulses, but contrary to our hypothesis, only the short-term temporal dynamics over 24 h. Despite much larger soil  $\text{CO}_2$  pulses in very dry soils, initial soil moisture conditions had no effect on the total amount of carbon lost upon rewetting. Some studies have observed that the same rainfall size had greater effects on soil respiration under drier antecedent soil conditions (Cable et al., 2008; Yan et al., 2010; Wu and Lee, 2011). In our study, rainfall size (i.e. sudden changes in water availability) had a larger impact than initial soil moisture conditions (available soil water) for the net response of soils to rainfall events, suggesting that sudden changes in soil moisture rather than soil moisture itself are the main driver of soil carbon mineralisation (see Borken and Matzner, 2009; Unger et al., 2010 for similar results). Mechanisms proposed to explain these mineralisation pulses (see Unger et al., 2010) involve a rapid increase in microbial biomass and/or substrate availability. This study suggests that sudden changes in soil moisture lead to an immediate increase in substrate availability. This probably results from the physical disruption of macro-aggregates, which exposes previously unavailable organic substrates for decomposition (e.g. Deneff et al., 2001) and from the release of hypo-osmotic substances by soil microbes (Fierer et al., 2003; Unger et al., 2010).

In accordance to previous studies, our results show that soils in vegetated areas respond more to rainfall events regardless of initial soil moisture conditions (Sponseller, 2007; Jenerette and Chatterjee,

2012). Although we did observe much larger  $\text{CO}_2$  pulses in dry soils (<10%), this response was only significant in vegetated areas and biological soil crusts, suggesting strong carbon limitation in bare soils. In this case, differences between soil covers were also explained by differences in available substrate, as suggested by the fact that total carbon losses were expressed on a carbon basis, all soil covers lost similar amounts of carbon. The amount of carbon lost after a 5 mm rainfall event ranged between 0.45 in bare soils to  $0.75 \text{ g C m}^{-2} \text{ day}^{-1}$ , which are comparable with fluxes from vegetated and bare soils spaces of a steppe after pulses of the same size ( $0.3\text{--}3 \text{ g C m}^{-2}$ ; Munson et al., 2010).

Our results of Experiment II show that although dry soils lead to large rapid soil  $\text{CO}_2$  peaks, this response is very transient and rates return immediately to background values, so the overall carbon losses over 24 h were not affected by pre-rain soil moisture conditions.

#### 4.3. Impact of land degradation

Previous work at the study area found that degraded soils with less vegetation cover and shallower soils, were hotter and drier than natural grassland soils, resulting in less water availability and longer drought periods (Rey et al., 2011, 2012). In this study, we further show that soil degradation also affects soil  $\text{CO}_2$  pulses during the dry period. Overall, soils in vegetated areas at the degraded site were much more responsive to the same rainfall amount than in the natural grassland releasing 30% more carbon than soils in the natural grassland. Higher carbon availability resulting from the accumulation over longer dry periods and drier soil conditions may explain these differences. As it has been suggested and discussed above, rapid changes in soil moisture may influence the availability of carbon substrates and the stability and formation of soil aggregates (Deneff et al., 2001). Since the degraded site is subject to longer dry periods, providing that there is carbon substrate as occurs under vegetated areas, this carbon becomes available for microbial decomposition after rains.

It is also likely that different microbial communities with different historical water regimes may have contributed to the observed difference between sites (see Wang et al., 2016). The fact that the degraded site is subject to longer drought periods because of an altered hydrological cycle with less capacity to retain water (Rey et al., 2011, 2012) may have affected microbial populations at this site favouring microbial species that are more tolerant to drought stress. These changes may help explain the difference observed between sites. Selection for stress tolerant microbial species may occur with even a single drying–rewetting event and may persist for long periods (Evans and Wallenstein, 2011) and is related to disturbance history (Evans and Wallenstein, 2014). Differing sensitivities of microbial populations to drying–rewetting has also been suggested by other studies (Fierer et al., 2003; Gordon et al., 2008; Hawkes et al., 2010; Yuste et al., 2010).

Interestingly, soil degradation leads to saturation-like responses at intermediate rainfall sizes (5 mm), which suggest strong carbon limitation (Sponseller, 2007; Chen et al., 2008; Casals et al., 2011). Besides, degradation resulted in lower responsiveness of biological soil crusts to rainfall events. Both results have important consequences when scaling up annual carbon balance at degraded areas.

Our results indicate enhanced carbon losses from vegetated areas in degraded soils, compared with those from natural grasslands. High temporal monitoring programs able to capture rapid responses of degraded soils, together with latest molecular techniques (like pyrosequencing) will help to better understand how soil degradation affects carbon cycle through changes in microbial community structures and to predict future impacts of climate change on semiarid grasslands.

#### 4.4. Factors determining soil $\text{CO}_2$ pulses

The amount of carbon lost after rewetting depends on the amount of carbon in soils and the availability of that carbon for microbial decomposition, which increases with changes in soil moisture. Both experiments in

this study show that the amount of carbon was the most limiting factor for soil CO<sub>2</sub> pulses after rainfall events and indicate that the availability of that substrate is proportional to changes in soil moisture. Our estimates of total carbon lost from vegetated, biological soil crusts and bare soil in these semiarid grasslands ranged from 0.1–1.2 g C m<sup>2</sup> day<sup>-1</sup>, which are similar to fluxes observed by López-Ballesteros et al. (2015) at the same site and in other semiarid grasslands following pulses of the same size (Sponseller, 2007; Munson et al., 2010). The smallest rainfall events (1 and 5 mm) caused a flux response that lasted less than largest event (15 mm), so carbon flux returned before to the baseline. This suggests that water is the most limiting factor to soil carbon flux rates for the smallest events, but may be less limiting for events above 5 mm. Other limitations, such as the soil organic carbon availability may limit flux above this event size (Huxman et al., 2004). Soil organic carbon may be necessary for a sustained response to large precipitation events.

Since soil CO<sub>2</sub> efflux is more sensitive to immediate water availability than plant productivity at this site (López-Ballesteros et al., 2015), one may predict that soil carbon losses would increase with increasing frequency of rain events during dry summers. The amounts of carbon lost after rainfall events were explained by the change in soil moisture caused by the rewetting for both sites in all soil covers. The larger the change in soil moisture, the larger the amount of carbon lost upon rewetting. This suggests that the response is stimulated by sudden changes in soil moisture that make available accumulated carbon substrates over dry periods.

## 5. Conclusions

Our work underscores the need of high temporal and spatial resolution monitoring of soil CO<sub>2</sub> pulses to accurately estimate carbon losses. Even small rainfall events can have substantial consequences for soil

carbon losses in semiarid ecosystems. We have identified a simple factor, sudden changes in soil moisture caused by rainfall that explained soil CO<sub>2</sub> pulses in all soil covers and in both grassland ecosystems. This suggests that both, the amount and the availability of carbon substrates, control the response of soil CO<sub>2</sub> pulses to rainfall events.

These findings have important implications for predicting soil CO<sub>2</sub> dynamics because the magnitude and timing of rainfall are expected to become increasingly variable in many semiarid areas under future climate change scenarios. A recent study at this site (López-Ballesteros et al., 2015) quantified that soil CO<sub>2</sub> pulses over the dry season can account for up to 40% of the carbon balance of this natural grassland. Annual net primary production is low in this ecosystem and most semiarid ecosystems ranging from 100 to 150 g C m<sup>-2</sup> yr<sup>-1</sup> (Rey et al., 2014). Since most of the carbon resides belowground, carbon losses as a result of longer dry periods and heavier rains could have important consequences for land degradation potentially increasing soil carbon losses in this area.

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## Appendix A

**Table 1A**  
Main characteristics of the field sites.

Variable	SITE	
	Natural grassland	Degraded grassland
Longitude	2°1'58"W	2°15'1"W
Latitude	36°56'30"N	36°50'5"N
Altitude (m)	208	65
Orientation	NW	SW
Slope (%)	2–6	2–6
Average annual temperature (°C)	18	18
Maximum summer temperature (°C)	34	36
Average annual rainfall (mm)	200	200
Mean PPFD (μmol mol <sup>-1</sup> )	1549	1549
Mean annual atmospheric pressure (kPa)	99	101
Maximum VPD (kPa)	4.3	4.6
Mean annual relative humidity (%)	69.3	68.7
Vegetation	Steppe alpha grass	Steppe alpha grass
Soil type WRB, (2006)	Mollic Lithic Leptosol (Calcaric)	Lithic Leptosol (Calcaric)
Soil texture class	Sandy loam	Sandy loam
Clay (%)	16.1	14.6
Silt (%)	22.8	27.0
Sand (%)	61.1	58.4
Soil organic carbon (%)	UP: 2.17(0.14) BSC: 1.77(0.14) BS: 1.63(0.14)	UP: 2.14 (0.08) BSC: 1.46(0.14) BS: 1.33 (0.08)
Total nitrogen (%)	UP: 0.19(0.01) BSC: 0.15(0.01) BS: 0.16 (0.01)	UP: 0.21(0.09) BSC: 0.15(0.01) BS: 0.14 (0.01)
pH	8.0	8.4
Bulk density (g cm <sup>-3</sup> )	UP: 1.20(0.03) BSC: 1.23(0.04) BS: 1.32(0.04)	UP: 1.21(0.02) BSC: 1.36(0.02) BS: 1.34(0.02)
Maximum soil depth (cm)	20	10
Mean annual soil temperature (°C)	21.9	25.1
Mean annual soil water content (%)	13.8	8.3

**Table 2A**

Ground cover (in percentage) for the two sites: natural site and degraded site measured in summer 2007. Values are the mean  $\pm$  1SE ( $n = 6$ ). Numbers with different letters are significantly different (ANOVA,  $P < 0.05$ ).

SITE	Vegetation cover	Litter	Biological crust	Bare soil	Gravel	Rock
Natural	63.2 $\pm$ 5.2a	8.1 $\pm$ 1.9a	18.2 $\pm$ 3.8a	0.3 $\pm$ 0.3a	8.6 $\pm$ 2.5a	1.5 $\pm$ 0.5a
Degraded	23.1 $\pm$ 2.4b	10.5 $\pm$ 2.0a	23.1 $\pm$ 2.8a	8.1 $\pm$ 0.1b	21.1 $\pm$ 0.1b	14.0 $\pm$ 1.2b

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