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Impact of land degradation on soil respiration in a steppe (*Stipa tenacissima* L.) semi-arid ecosystem in the SE of Spain

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Dr. Pegoraro passed away on 21 April 2007 after a long illness. This work is dedicated to him, for his constant strength, and his energy and enthusiasm for work until the last moment.

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ABSTRACT

Climate change scenarios predict increases in temperature, changes in precipitation patterns, and longer drought periods in most semi-arid regions of the world. Ecosystems in these regions are prone to land degradation, which may be aggravated by climate change. Soil respiration is one of the main processes responsible for organic carbon losses from arid and semi-arid ecosystems. We measured soil respiration over one year in two steppe ecosystems having different degrees of land degradation under three ground-covers: with vegetation, bare soil, and an intermediate situation between plants and bare soil.

The largest differences in soil respiration rates between the sites were observed in spring, coinciding with the highest level of plant activity. The degraded site had drier and hotter soils with less soil water availability and a longer drought period. As a result, vegetation on the degraded site did not respond to spring rainfall events. Soil respiration showed a strong seasonal variability, with average annual rates of 1.1 and 0.8 μmol CO_2 m^{-2} s^{-1} in the natural and degraded sites, respectively. We did not observe significant differences in soil respiration rates associated with ground-cover i.e., the temporal variation was much larger than the spatial variation. At both sites, soil moisture was the controlling driver of soil respiration for most of the year, when temperatures were above 20 °C and constrained the response to temperature for the few months when the temperature was below 20 °C. An empirical model based on soil temperature and soil moisture explained 90% and 72% of the seasonal variability of soil respiration on the natural and degraded sites, respectively. For the first time, this study suggests that land degradation may alter the carbon balance of these ecosystems through changes in the temporal dynamics of soil respiration and plant productivity, which have important negative consequences for ecosystem functioning and sustainability.

1. Introduction

Soil respiration is a major flux of CO_2 to the atmosphere, accounting for up to 25% of global CO_2 emissions (Schimel, 1995). The rate of soil respiration varies among different ecosystems and is generally the dominant component of ecosystem respiration (Raich and Schlesinger, 1992). Notwithstanding research over the last decade (Reichstein et al., 2003; Hibbard et al., 2005), knowledge of the drivers acting on soil respiration is in general still poor by comparison with our understanding of the leaf processes of photosynthesis and respiration. Furthermore, soil respiration in arid and semi-arid ecosystems has been less intensively investigated than in other ecosystems (Raich and Potter, 1995; Subke et al., 2006; Bond-Lamberty and Thomson, 2010) and consequently rather less is known about how soil respiration varies over time and space.

Arid and semi-arid regions are characterized by erratic and random rainfall events that interact with season and with functioning of autotrophic and heterotrophic ecosystem processes. Such events have crucial impacts on soil respiration, often causing pulses of CO_2 emission to the atmosphere (Davidson et al., 1998; Rey et al., 2002, 2005; Jarvis et al., 2007). Although the importance of the timing and intensity of rainfall events has been widely recognized recently (Harper et al., 2005; Sponseller, 2007; Liu et al., 2009), the processes involved are not fully understood.

Other characteristics of arid and semi-arid ecosystems are large spatial variability and patchy distribution of resources, environmental conditions, roots and the microorganisms responsible for organic matter decomposition. Soil properties, such as the presence of rock fragments, earthworms, other micro and macro-fauna and biological crusts, can all have a strong influence on soil carbon dynamics.

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Thus, these ecosystems are also characterized by heterogeneity of surface soil characteristics, the effects of which are very poorly understood (Nadeau et al., 2007; González-Polo and Austin, 2009).

Although several models have been used to describe the relationships between soil respiration and soil environmental variables (e.g., Reichstein et al., 2002; Reth et al., 2005), it is not clear whether such models are suitable for semi-arid ecosystems, because the interactions between environmental variables, soil properties and vegetation characteristics are different. Soil respiration is a complex process resulting mainly from the biological activity of soil biota and root respiration, both of which are influenced by physiological, phenological and environmental processes that vary both in time and space, as well as with ecosystem type.

In arid and semi-arid ecosystems, the spatial and temporal fluctuations of water availability are, in general, the fundamental drivers of biological processes (Noy-Meir, 1973). It has, for example, been shown that in Mediterranean-climate ecosystems, which are subjected to prolonged summer droughts, soil moisture is the critical environmental determinant limiting the response to temperature (Reichstein et al., 2002; Rey et al., 2002, 2005; Jarvis et al., 2007). Thus, the assumption of a simple relationship with temperature in order to predict the response of soil respiration to climate change in arid and semi-arid-zone vegetation, could lead to considerable errors in the estimation of the terrestrial carbon sink.

Furthermore, arid and semi-arid ecosystems are prone to soil degradation, which may be aggravated by land use, especially grazing intensity and cropping history, and by climate change (Frank, 2002). Whether these ecosystems are sources or sinks of CO$_2$ is likely to depend on the extent to which the carbon stock in soils may change as a consequence of soil degradation.

In this study we aimed: (1) to examine the environmental variables controlling soil respiration in a semi-arid ecosystem in the Southeast of Spain, and (2) to assess the impact of land degradation on soil respiration. To achieve this we have compared soil respiration in two steppe sites with different degrees of land degradation over one year (2007). The two sites are located in the same area but differ in the degree of vegetation cover and in soil properties, as a result of land use history. Both sites are dominated by alpha grass (*Stipa tenacissima* L.), a perennial tussock grass widely distributed across the Mediterranean basin, over an area of 60 000–80 000 km^2 where annual rainfall is between 100 and 500 mm (Le Houerou, 2001).

2. Materials and methods

2.1. Study area

The study sites are located in the Cabo de Gata Natural Park (PNCG), in the province of Almería (Andalucía) in the SE of Spain (N36°56′26.0″, W2°01′58.8″). The climate in this area is subtropical, dry, and semi-arid with a mean annual precipitation of 220 mm and a mean annual temperature of approximately 18 °C, that is characterized by prolonged summer droughts (from May to September, with no rain, in general, between June and September), and infrequent and random rainfall events. Annual potential evapotranspiration is approximately 1390 mm (nearby meteorological Station, Níjar). The sites are characterized by strong inter-annual variation and random patterns of precipitation, which mostly occur in spring and in autumn. Geologically, the region is a series of alluvial fans (glacis) with gentle slopes (2–8%) with petrocalcic horizons. The dominant soils are classified as Lithic leptosols (calcaric) (WRB, 2006) (Table 1), and are thin, of variable depth (down to a maximum of *ca* 30 cm, but on average 10 cm), alkaline (pH above 8), saturated in carbonates with a moderate stone content and with common rock outcrops, particularly at the degraded site (Table 2).

Table 1
Main characteristics of the field sites.

Variable	Site	
	Balsablanca (BB)	Amoladeras (AMO)
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)	220	220
Mean PPFD (μmol mol^{-1})	1549	1549
Mean annual atmospheric pressure (kPa)	99	101
Maximum VPD (kP)	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
Bulk density (g cm^{-3})	1.25	1.11
Maximum soil depth (cm)	20	10
Mean annual soil temperature (°C)	21.9	25.1
Mean annual soil water content (%)	13.8	8.3

The vegetation of these sites is dominated by *S. tenacissima* (with an average height between 60 and 100 cm), but there are a large number of other shorter grass species with low soil coverage, such as: *Chamaerops humilis*, *Rhamnus lycioides*, *Asparagus horridus*, *Olea europea* var. *sylvestris*, *Pistacia lentiscus*, and *Rubia peregrina*.

S. tenacissima L. is a rhizomatous, perennial tussock grass, highly adapted to water stress conditions and has long, narrow leaves, a large root:shoot ratio, and shallow roots that spread from both seeds and stolons. *S. tenacissima* L. can be considered as a drought-tolerant species since it has developed several strategies to endure the extreme conditions, such as minimizing light interception and photoinhibition (Valladares and Pugnaire, 1999), non-rainfall water gains (Ramírez et al., 2007), and a rapid photosynthetic response to rainfall (Balaguer et al., 2002). The ecosystem is characterized by open, vegetation-free areas, with vegetation cover varying between 18 and 65% of the ground surface, depending upon past human impact (Maestre, 2004), and by complex patterns of vegetation that influence soil surface properties, such as physical and biological crusts and rock fragments (Maestre and Cortina, 2002).

The two sites are located approximately 15 km apart. Both sites are equipped with meteorological and eddy-covariance towers designed to measure the exchange of carbon, water, and energy between the vegetation and the atmosphere (a part of the CARBOEUROPE network of flux sites). Both sites are located on a flat area. The main site, Balsablanca (the "non-degraded" site), is a natural alpha grassland location, in terrain 200 m asl; whereas the more degraded site, Amoladeras (the "degraded" site), is nearer to the sea, at 50 m asl, with less vegetation cover and shallower soils as a consequence of intensive grazing. Despite these differences, the climatic conditions during the time period of the study were not significantly different between the sites. The main characteristics for the sites are presented in Table 1.

We selected these sites as representative of two distinctive degradation stages based on a previous hierarchical classification of the ecosystems present in the PNCG (see Escribano, 2002). We made sure that both sites were comparable with the same geology, topography, vegetation type, climate, etc., and consistent with a soil cartography map (CMA, 1999), which indicates that in Amoladeras

Table 2
Ground-cover (in percentage) for the two sites: Balsablanca (BB) and Amoladeras (AMO) measured in summer 2007. Values are the mean ± 1 SE ($n = 6$). Numbers with different letters are significantly different (ANOVA, $P < 0.05$).

Site	Vegetation cover	Litter	Biological crust	Bare soil	Gravel	Rock
BB	63.2 ± 5.2a	8.1 ± 1.9a	18.2 ± 3.8a	0.3 ± 0.3a	8.6 ± 2.5a	1.5 ± 0.5a
AMO	23.1 ± 2.4b	10.5 ± 2.0a	23.1 ± 2.8a	8.1 ± 0.1b	21.1 ± 0.1b	14.0 ± 1.2b

(the “degraded” area), the soils have characteristics typical of degradation processes, in comparison to soils in the reference site, Balsablanca (the “non-degraded” area). Other degradation indicators were also used, such as the percentage of vegetation cover, the percentage of rock outcrops, and surface coarse fragments (Cammeraat, 1996; Dregne, 2002; LADA-L, 2009).

2.2. Experimental design

In December 2006, we selected six permanent, replicated plots at both sites within a 100 m fetch of the tower. Plots measured 10 m by 10 m and were at least 5 m apart. The distribution of vegetation was mainly patchy, with different proportions of plant cover at each site. In each plot we selected three areas with *Stipa* plants and placed soil collars at three different locations: *under the plant cover* (P), at 40–50 cm from the plants on *bare soil* (S), and in an *intermediate* location approximately half way between P and S (I). Other common ground-covers included soil crust (both biological and physical crusts), and rock and gravel (see Table 2). The experimental design was a *randomized block design* with a replication number of six.

2.3. Soil respiration measurements

At both sites, measurements of soil respiration (R_s) were made during 2007 at a frequency of approximately two weeks, depending upon the time of year. Measurements began in February 2007 and continued until February 2008. At the beginning of the year soil collars (15 cm in diameter and 7 cm in height) were inserted 3.5 cm into the soil where they remained for the duration of the experiment. Small plants, litter, insects, and grasses were regularly and carefully removed from each collar. To avoid strong diurnal fluctuations, measurements were made between 10:00 and 13:00 h at both sites on alternative consecutive days. The midday period was considered to provide rates of respiration that were representative of the *average daily value* in grasslands (Mielnick and Dugas, 2000). We measured diurnal courses of R_s at different times of the year in order to make sure that this was the case (data not shown). Plots were measured in random order on each date to avoid biased estimates. A portable, closed chamber, soil respiration system (EGM-4, PP-systems, Hitchin, UK) was used to measure R_s rates *in situ*. The chamber covered an area of 78 cm^2 and had a volume of 1170 cm^3. Because of the low rates of R_s, each measurement period was 120 s to ensure reliable measurements. Soil temperature was measured at a 3.5 cm depth with a digital thermometer, and the soil volumetric water content (W) was measured with a portable theta probe (ML2x, Devices Ltd., Cambridge, UK) adjacent to the soil collars at the time of each R_s measurement.

2.4. Modelling soil respiration

We considered soil respiration (R_s) to be dependent on the soil temperature (T) and the soil moisture content (W) according to the following relationship:

$$R_s = f(T)^* f(W), \tag{1}$$

and,

$$f(T) = R_{\text{basal}} e^{bT} \tag{2}$$

where R_s is the CO_2 emission flux density resulting from soil respiration (μmol m^{-2} s^{-1}), T is soil temperature (°C) measured at a depth of 3.5 cm, and R_{basal} (the basal respiration rate) and b are fitted parameters. The Q_{10} (the increase in the flux rate for a 10 °C increase in temperature) was calculated as follows:

$$Q_{10} = e^{10b} \tag{3}$$

The relationship between R_s and soil volumetric water content (W) was determined by fitting a non-linear relationship to the mean plot values ($n = 6$) using the following equation:

$$f(W) = (c^* W)/(d + W) \tag{4}$$

where W is the soil volumetric water content (m^3 m^{-3}) measured at the depth of 3.5 cm, and c and d are fitted parameters.

2.5. Soil chemical determinations

In each plot, we made a number of measurements on soil samples taken adjacent to each soil collar. Samples were pooled for each plot ($n = 6$) and site for pH, for carbonate content, and for total N determinations. Composite samples were passed through a 2 mm sieve and labelled as the fine-earth fraction. The methods described in Klute (1986) were followed for these analyses. The particle-size distribution was determined on samples taken from bare soil by the pipette method after the removal of organic matter with H_2O_2 and dispersion using Na-hexametaphosphate. The organic carbon content was determined by the Tyurin method using wet combustion and a mixture of $K_2Cr_2O_7$ and H_2SO_4, and by titrating the residual dichromate with ferrous sulphate. Organic nitrogen was mineralized with H_2SO_4 and selenium to NH_4SO_4, distilled in the form of NH_4OH, and titrated with diluted H_2SO_4 by the Kjeldahl method. The pH (1:1 fine-earth: distilled water suspension) was measured by the potentiometric method. The $CaCO_3$ equivalent was measured by Bernard’s calcimeter. A soil core taken with a cylindrical metal corer was used to determine the bulk density adjacent to each soil collar. For dry mass determinations, samples were oven-dried at 105 °C.

2.6. Fine root biomass

At the end of the measurement period, the fine root biomass beneath each type of ground-cover was determined by taking three soil cores of 4.8 cm diameter surrounding each soil collar. The cores were pooled and the roots were carefully extracted at the laboratory. Fresh soil was carefully separated from the roots by sieving the soil through a 2 mm mesh. Fine roots were then oven-dried at 105 °C. The fine root density for each type of ground-cover type was expressed as root dry mass per unit volume of soil.

2.7. Determination of the different types of ground-cover

The main ground-cover components were as follows: live vegetation, litter (all dead material), biological crust, bare soil, and gravel and rock outcrops. To quantify the proportions of each type of ground-cover component, we followed the transect method proposed by Tongway and Hindley (1995), utilizing the same 10 m by

10 m plots as described earlier. Four 10 m transects, running in two different directions, were selected in each plot, and the extension (cm) of each type of ground-cover component was measured along each transect. Components of ground-cover type occupying 1 cm or more were considered. An average value for each type of ground-cover was obtained from the four transects on each plot, in order to obtain the overall percentage of ground-cover at each site.

2.8. Vegetation index

As a proxy for vegetation activity we used the radiometric index EVI (Enhanced Vegetation Index), that were calculated from MODIS images which combined medium spatial and high temporal resolution. For the exact period of the study, February 2007 through February 2008, images (C5) were obtained from the internet (http://LPDAAC.usgs.gov). A detailed treatment of the images and the algorithms applied are described in detail in the website given above. The 16 day components (MODQ3Q1) were downloaded and filters were applied in order to select high spectral quality data. The information was transformed to datum ED50 and geo-referenced at UTM 30N. We then selected the series of images corresponding to the 250 m × 250 m pixels that included each site.

2.9. Statistical analyses

The data were analyzed as a randomized block design with the ground-cover and the plot as factors. Since we used the same collars to follow the temporal variability of R_s and since the measurements were done at regular intervals, a repeated-measures analysis of variance was used to test for differences between the sites and the ground-cover types within each site for soil temperature, soil water content, and R_s rates over the entire experimental period. We used repeated-measures analysis of variance utilizing general linear models in the statistical software SAS (proc MIXED, repeated option).

Based on soil temperature, three distinctive periods were identified, as follows: **Period I** (temperature less than 20 °C), **Period II** (temperature above 20 °C), and **Period III** (“spring”), for which the equations described in Section 2.4 were applied and then the relationships fitted separately. The relationships between soil respiration, soil temperature, and soil volumetric water content were analyzed using non-linear regressions (proc NLIN). All of the data were tested for a normal distribution before the statistical analyses were made using a Hartley’s Test (Sokal and Rohlf, 1995).

By assuming that (1) morning measurements are reasonable estimates of the daily means of R_s, and by (2) interpolating between the measurement dates, we estimated the mean flux each day of the year and then computed, for each ground-cover type and site, the amount of carbon respired annually.

Differences in soil chemical properties and fine root density between the different ground-cover types and between the sites were analyzed using a nested analysis of variance (proc GLM), with ground-cover nested within the site. When the analysis was significant, a comparison of means was done with the *Least-significant differences* test (LSD). Step-wise multiple regressions were used to investigate which environmental variables and soil properties had the largest effects on annual soil respiration, as well as for the relationship between soil respiration and soil biochemical properties (proc REG). Mean annual soil temperature, mean annual soil moisture, soil pH, soil organic carbon, sand content, carbonate content, etc., were used as independent variables. Differences were considered to be significant at the 5% level of probability. All of the statistical analyses were performed with the SAS statistical package (SAS 9.1, SAS Institute, Cary, NC, USA).

3. Results

3.1. Site characteristics

Given the proximity of the study sites, total annual rainfall was essentially the same, 263 and 259 mm for the year of the study (February 2007–February 2008) on the non-degraded and degraded sites, respectively. The sites did not differ significantly in micro-meteorological conditions (Table 1, measured using the meteorological tower installed at the sites through 2007). The largest differences among the sites were found in the percentages of vegetation and ground-cover (Table 2). The sites also differed in soil properties (Table 1), with a significantly higher C/N, a lower pH, and a lower carbonate content in the “non-degraded” than in the “degraded” site (see also Fig. 6). The soils were of similar texture and bulk density but were shallower in the “degraded” site than in the “non-degraded” site (Table 1).

3.2. Seasonal dynamics of soil environmental conditions and soil respiration

The seasonal patterns of environmental variables were similar at both sites (Fig. 1). Soil temperature changed markedly over time ($P < 0.001$), but was consistently higher at the “degraded” site than in the “non-degraded” site ($P < 0.001$). Soil temperature measured at 3.5 cm depth was significantly lower (repeated-measures analysis of variance, $P < 0.0001$) under plant cover (P) than for the other two ground-covers (I, S) at both sites. Annual mean soil temperatures (°C) were: 19.5 ± 1.7 (P), 22.2 ± 2.1 (I), 23.3 ± 2.1 (S), and 22.1 ± 1.4 (P), 24.4 ± 1.7 (I), 26.0 ± 1.7 (S), for the “non-degraded” and “degraded” sites, respectively. Values increased from 10 °C at the beginning of the year to 40 °C on DOY 210 in the middle of summer at the “non-degraded” site, and from 15 to 50 °C on DOY 240 at the “degraded” site.

There were no significant differences in soil water content between the ground-cover types at any site ($P > 0.05$ in all cases). The mean annual percentages were: 15.2 ± 2.0 (P), 14.4 ± 2.9 (I), and 14.5 ± 2.1 (S) at the “non-degraded” site and; 7.4 ± 2.0 (P), 8.3 ± 2.2 (I), and 8.7 ± 2.0 (S) at the “degraded” site. Differences between the sites were not significant ($P > 0.05$) although the “degraded” site had consistently drier soil than the “non-degraded” site.

Soil respiration was significantly higher in the “non-degraded” site than in the “degraded” site ($P < 0.001$), for all ground-covers (Figs. 1 and 2). There were no differences in soil respiration between ground-cover types over time at any site ($P > 0.05$ in all cases). However, when analyzed by period, rates measured under bare soil were significantly higher than those measured under plant during **Period II** ($P < 0.05$ in both sites). The annual mean values were: 1.01 ± 0.10 (P), 1.16 ± 0.12 (I), and 1.24 ± 0.09 (S) μmol m^{-2} s^{-1} at the “non-degraded” site, and 0.77 ± 0.10 (P), 0.89 ± 0.11 (I), and 0.72 ± 0.09 (S) μmol m^{-2} s^{-1} at the “degraded” site. Soil respiration varied markedly over the year (Fig. 1). Peak maximum respiration rates were measured in spring and in autumn, and minimum rates were measured in the summer in the “non-degraded” site, whereas maximum rates were measured in autumn at the “degraded” site, coinciding with higher photosynthetic activity and rainfall events (Fig. 2).

In general, in addition to soil temperature and soil water content, R_s followed plant activity (measured as the vegetation index) at both sites (Fig. 2). Maximum rates for the vegetation index were observed in autumn coinciding with higher soil water content following rainfall events and with optimal temperatures. Soil respiration in the “degraded” site seemed to be more responsive to rainfall events. After the dry summer there was a larger rainfall event on DOY 270, which led to a large increase in R_s at both sites.

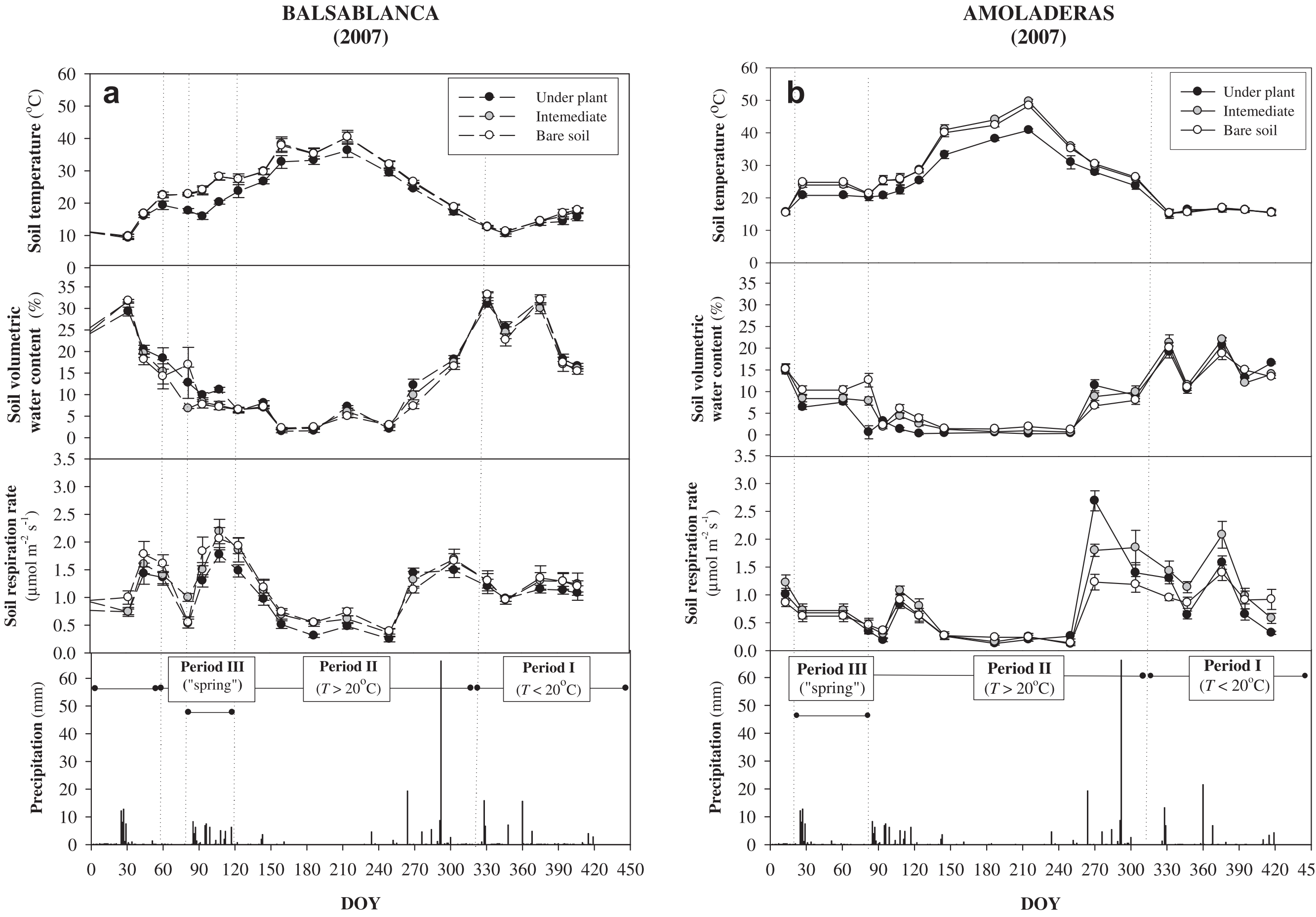

Fig. 1. The seasonal variability in soil temperature (°C) and soil volumetric water content (%) measured at 3.5 cm depth, the soil respiration rate (μmol m^{-2} s^{-1}) for each ground-cover (under plant cover, intermediate, and bare soil) type, and the precipitation (mm) spanning the study period (February 2007–February 2008) in (a) Balsablanca (the natural site) and in (b) Amoladeras (the degraded site). Symbols represent the mean ± 1 SE ($n = 6$).

Other rainfall events occurred in autumn, and although they all stimulated R_s (and plant activity), the increase in R_s was less pronounced than the response to the first rain after the drought period. Soil respiration measured under plant cover seemed to be more responsive to rainfall events than for bare soil.

3.3. *Control of soil temperature and soil moisture on soil respiration*

Since no significant differences were observed between the ground-cover types at any site ($P > 0.05$ in all cases), R_s was modelled as a function of soil temperature and soil moisture using all of the data together. As explained in the Method section, the year was separated into three periods based upon a threshold value for soil temperature of 20 °C found at the “non-degraded” site (Fig. 3). **Period I** (below 20 °C, “*winter*”). **Period II** (above 20 °C, “*summer*”) and, **Period III** (“*spring*”) was identified as a short period when R_s was higher (the “non-degraded” site) or lower (the “degraded” site) than expected based upon the soil temperature and the soil water content. We first used the data from the “non-degraded” site to obtain a model and then applied the model to the “degraded” site. During **Period I** we used the multiplicative model in Equation (1), where R_s was explained by both soil temperature and soil moisture, since the inclusion of soil moisture significantly improved the prediction ($R^2 = 0.71$). The Q_{10} value for this period was 3.32. In **Period II**, we found that R_s responded solely to soil moisture ($R^2 = 0.90$) (Fig. 4). The threshold value of 20 °C corresponded to a soil water content of 0.15 m^3 m^{-3} and 0.12 m^3 m^{-3} in the “non-degraded” and the “degraded” site, respectively. The model successfully predicted R_s at both sites (Fig. 5), with the exception of at the “non-degraded” site in **Period III**. Soil environmental conditions and R_s for each period are given in Table 3 together with the model estimated parameters.

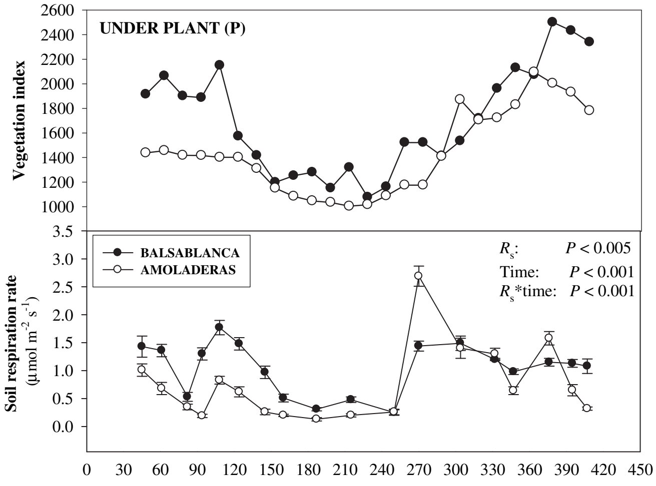

Fig. 2. The seasonal course of soil respiration measured under plant cover and for the vegetation index at the Balsablanca (black) and Amoladeras (white) sites. The symbols represent the mean ± 1 SE ($n = 6$). The statistics refer to results obtained from a repeated-measures analysis of variance for testing the differences between sites over time ($P < 0.05$).

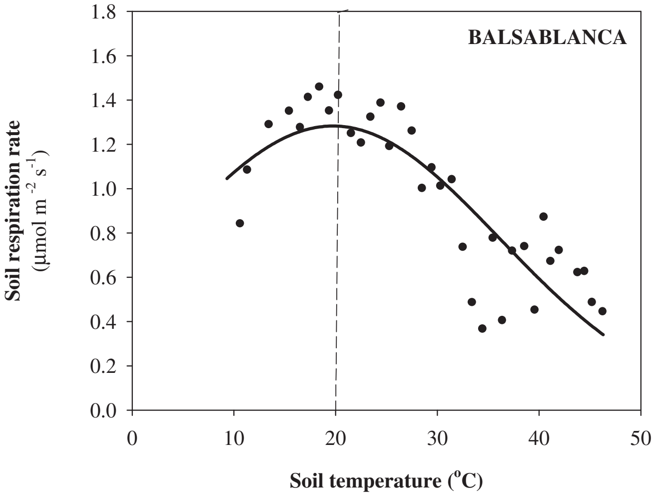

Fig. 3. Relationship between soil temperature and soil respiration using averaged values for each temperature degree for all ground-cover types in Balsablanca.

Annual respired carbon ranged from 260.8 g C m^{-2} yr^{-1} for bare soil at the "degraded" site, to 430.3 g C m^{-2} yr^{-1} for bare soil at the "non-degraded" site. The cumulative amount of carbon respired over the year was the largest for bare soil at the "non-degraded" site. The total amount of carbon respired for the other ground-cover types were, as follows: 366.5 (P), 418.4 (I), and 300.3 (P) and 320.5 (I) g C m^{-2} yr^{-1}, in the "non-degraded" and the "degraded" sites, respectively.

3.4. Relationship with chemical properties

Soils in the "non-degraded" site had a significantly lower pH ($P < 0.001$), a higher C:N ratio ($P < 0.001$), and a lower carbonate content than soils at the "degraded" site ($P < 0.001$) (Fig. 6). Also, the pH was significantly lower ($P < 0.001$) and total N and C were significantly higher ($P < 0.001$) under plant cover than under the other two ground-cover types. However, no significant differences ($P > 0.05$) in the carbonate content between the ground-cover types were found. Soil texture was also significantly different among the sites, with significantly more clay, less silt, and a larger bulk density ($P < 0.05$ for all cases) at the "non-degraded" than at the "degraded" sites. Although we found that the soil volumetric water content was the main variable driving the R_S for all ground-cover types at both sites in the multiple regression analysis, soil properties related to the water holding capacity, such as bulk density, were positively correlated with the mean annual respiration rate measured over bare soil ($R^2 = 0.69, P < 0.001$). The soil volumetric water content ($P < 0.0001$) and the soil temperature ($P < 0.005$) were the only two variables that explained R_S at the "non-degraded" site (63%), whereas the carbonate content ($P < 0.04$) was also an explanatory variable at the "degraded" site (the model explained 43%). When analyzed by ground-cover type, the step-wise multiple regression revealed that the soil water content (89%), the temperature (6%), and the carbonate content (1.8%) explained 97% of the mean annual respiration rate in S, and 83% in I, whereas soil water content was the sole significant variable explaining 50% of R_S in P.

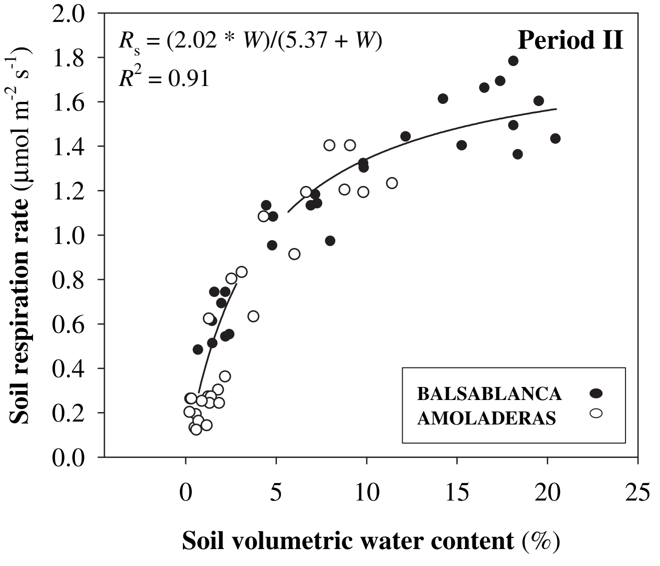

Fig. 4. The relationship between soil volumetric water content and soil respiration for the Balsablanca (black circles) and Amoladeras (white circles) sites. The values are the mean of each measurement date and soil cover during **Period II** ($T > 20$ °C).

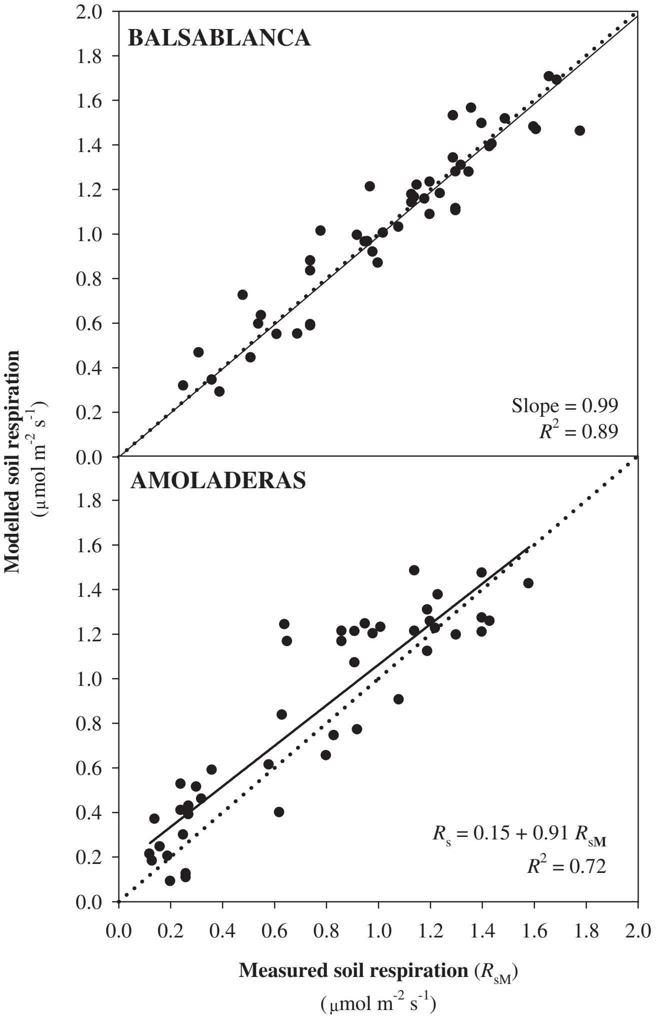

Fig. 5. Actual values measured against the modelled soil respiration in Balsablanca and Amoladeras, using the same model. In the model, soil respiration is a function of the following: soil temperature and soil moisture for **Period I** when $T < 20$ °C, and soil moisture for **Period II**, when $T > 20$ °C. The values are the mean ($n = 6$) for each measurement date and ground-cover type. The dotted line represents the 1:1 line.

3.5. Fine roots

Fine root density was significantly higher under plant cover than for the other two ground-cover types ($P < 0.001$) at both sites,

Table 3
Mean soil respiration rate (µmol m^{-2} s^{-1}), soil temperature (°C), soil volumetric water content (%), precipitation (mm) and number of events (>5 mm) of the three periods in which the year of study was separated at the two sites: Balsablanca (BB) and Amoladeras (AMO). Periods were defined based on a threshold value of soil temperature of 20 °C and thus they do not correspond to the same days at both sites. **Period III** was called "*spring*" and did not fir the predictive model based on soil temperature and soil moisture. Model parameters for the different Periods and Sites are also given.

Period		Mean	Site	
			BB	AMO
I "*Winter*"	$T < 20$ °C	R_s (µmol m^{-2} s^{-1})	1.21	1.04
		T (°C)	14.1	15.8
		W (%)	21.8	15.0
		P (mm)	120.4	104.3
		Number events	7	7
SR = (SR_{basal} e^{bT})*(SWC)/(c + SWC)		SR_{basal}	0.43 ± 0.04	
		b	0.08 ± 0.008	
		d	2.13 ± 0.65	
II "*Summer*"	$T > 20$ °C	R_s (µmol m^{-2} s^{-1})	0.84	0.67
	SR = f (SWC)	T (°C)	30.1	32.2
SR = (c*SWC)/(d + SWC)		W (%)	5.8	3.4
		P (mm)	130.2	191.5
		Number of events	4	11
		c	1.78 ± 0.11	
		d	3.84 ± 0.68	
III "*Spring*"		R_s (µmol m^{-2} s^{-1})	1.77	0.56
		T (°C)	23.5	21.8
		W (%)	9.0	8.5
		P (mm)	63.0	14.1
		Number of events	7	1

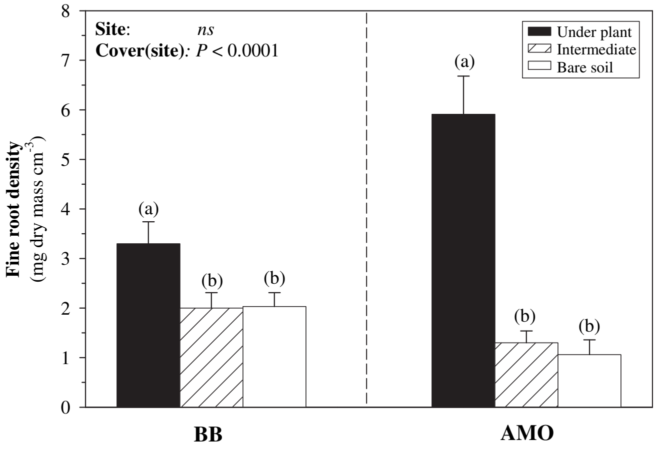

Fig. 7. Fine root density (mg dry mass cm^{-3}) for each ground-cover type at both sites ($n = 6$). Samples were taken adjacent to the measurement points of soil respiration in November 2008.

although the differences between the ground-cover types were larger at the "degraded" than at the "non-degraded" site (Fig. 7). The fine root density under plant cover was 80% higher in the "degraded" than in the "non-degraded" site, although the differences were not significant ($P > 0.05$). For the other two ground-cover types, the density of fine roots was higher in the "non-degraded" than in the "degraded" site (65 and 100% for the intermediate and bare soil, respectively).

4. Discussion

4.1. The magnitude and the seasonal dynamics of soil respiration

Soil respiration rates were generally lower than those reported from other ecosystems, but similar to those reported in other arid and semi-arid ecosystem studies (Maestre and Cortina, 2003; Carbone et al., 2008).

Differences in the seasonal dynamics of soil respiration between the sites could largely be explained by variation in the vegetation

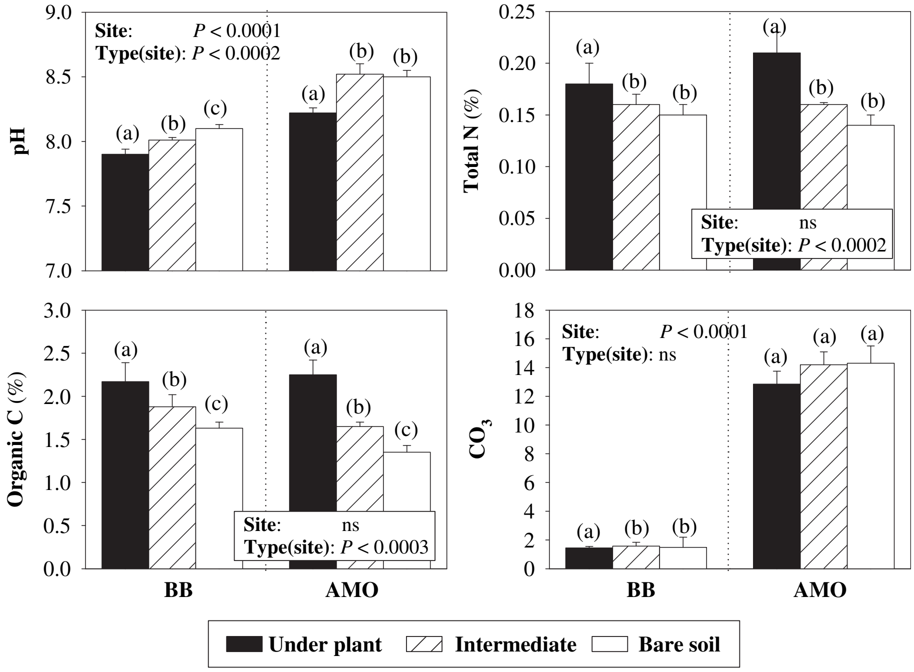

Fig. 6. The pH, total nitrogen (%), total organic carbon (%), and carbonate (%) content for the soils of each ground-cover (adjacent to the measurements points for soil respiration) type at both sites (BB = Balsablanca, AMO = Amoladeras). Bars represent the mean ± 1 SE ($n = 6$). Bars with different letters within each site are significantly different at 5% (Nested design ANOVA).

activity. Soil respiration was coupled to plant activity, suggesting that the major component of soil respiration is derived from plant assimilation in these carbon poor soils. Although the vegetation index used here can be difficult to translate directly into photosynthesis, the seasonal patterns should be good indicators for changes in plant activity in the alpha grass tussocks. For example, the vegetation index EVI has successfully been used to estimate seasonal variation in gross primary productivity, particularly in sites subjected to summer drought (Sims et al., 2006). Several studies in different vegetation types have established a connection between photosynthesis and soil respiration (e.g., Högberg et al., 2001; Sampson et al., 2007; Liu et al., 2009).

The timing of rainfall was also crucial in determining the CO_2 efflux, as widely observed in other arid ecosystems (e.g., Shen et al., 2008). The time interval between rainfall events (Reichstein et al., 2002; Huxman et al., 2004), the soil moisture at the time of the event, and the magnitude of the rainfall event are important in determining the magnitude of the response (Rey et al., 2005; Jarvis et al., 2007; Sponseller, 2007; Cable et al., 2008). Indeed, we found that small events after dry periods were much more important in stimulating soil respiration at both sites than later larger events. We also found that the “degraded” site, which suffered a much longer drought period, was much more responsive to the same rainfall event than the “non-degraded” site.

Three major processes may contribute to the rapid apparent stimulation of soil respiration following rainfall. First, large amounts of CO_2 stored in the air spaces resulting from inorganic sources and soil microbial activity during the dry period are physically displaced and released (Huxman et al., 2004). Second, precipitation pulses can liberate carbon held in large soil pools of soil carbonates (Emmerich, 2003; Inglima et al., 2009). Third, soil rewetting rapidly increases decomposition processes of readily available carbon accumulated during the previous dry period (Kieft et al., 1998), particularly in dry ecosystems, where photodegradation has been shown to play an important role in breaking down organic matter which is later available for microbial activity (Gallo et al., 2009).

4.2. Spatial variability of soil respiration

The availability of SOM varies greatly between vegetated and bare soil patches (e.g., Schlesinger and Pilmanis, 1998; Ludwig et al., 2005). In particular, alpha grass tussocks are known to create rich islands of SOM beneath them (Reynolds et al., 1999; Maestre et al., 2001), as well as less compacted soils (Bochet et al., 1999), and higher C:N ratios than bare soils. Such a finding was mostly confirmed by our soil analyses that displayed significant differences in soil chemical properties between different ground-cover types. However, in contrast with other studies where soil respiration was much larger from the soil beneath plant cover than from bare soil (Sponseller, 2007; Cable et al., 2008), we found no significant differences among the soil respiration rates measured under plant cover in the intermediate situation and in bare soil over time.

Several hypotheses may have contributed to this lack of difference. Photodegradation has recently been shown to be a major factor controlling decomposition in these water-limited ecosystems (Austin and Vivanco, 2006; Brandt et al., 2009; Gallo et al., 2009). In this process solar radiation breaks down organic matter either directly into CO_2 (photochemical mineralization) or by microbial facilitation (Brandt et al., 2009). The exposure of soil to the sun may favour microbial populations that can tolerate higher temperatures, lower moisture, and higher UV-radiation (Caldwell et al., 2007). Since the intermediate and bare soils were permanently exposed to full solar radiation, whereas the soils beneath the plant cover were mostly shaded, levels of radiation may partly explain the differences in respiration. Besides, during the summer months (when photodegradation is most important), the rates of soil respiration under plant cover during the daytime were consistently and often significantly lower than the rates measured in the intermediate and bare soils. In contrast, night-time measurements were the reverse, with higher rates under plant cover than under bare soil (data not shown), consistent with this hypothesis.

Although we could not detect significant differences between soil cover and soil moisture, it is likely that microbes located on or just beneath the soil surface are hydrated more frequently not only with very small rainfall events but also with high relative humidity and the dew generated in the early morning (Luo and Zhou, 2006). The vertical distribution of soil moisture has also been recognized to exert strong control on patterns of soil respiration and ecosystem exchange (e.g., Schwinning et al., 2004). This “hidden” input of water may not even be detectable with standard soil moisture sensors, but may likely exert enough control to stimulate soil microbial activity at the soil surface, particularly in intermediate (which includes biological soil crust) and bare soil covers. Likely is that these small differences in water availability may have been more important than differences in soil organic carbon and fine root density.

4.3. Control on the seasonal dynamics of soil respiration

By combining all of the data for all of the dates, the model, based solely on soil temperature and soil moisture, could account for more than 90% of the seasonal variability in soil respiration. In contrast with other types of ecosystems (e.g., I Rey et al., 2002; Reichstein et al., 2003), soil moisture was the single best predicting variable for most of the year at both sites. In contrast, temperature controlled soil respiration only during the short “winter” period (to the end of February in the “non-degraded” site) when temperatures fell below 20 °C. An overriding control of soil moisture on soil respiration has commonly been observed in other semi-arid ecosystems (Rey et al., 2005; Jia et al., 2006; Almagro et al., 2009; Liu et al., 2009). At both sites, soil respiration fell when the soil water content decreased below 12–15%, with the consequence that the more degraded site was subjected to a longer drought period. Similar soil water content threshold values have been reported in other ecosystems (Davidson et al., 1998). However, the model failed to adequately predict both the respiration rates in “spring” and the peaks immediately following rainfall events.

The apparent responses over the year to soil temperature and soil moisture may mask the phenological control of soil respiration (Rey et al., 2002; Curiel-Yuste et al., 2003). The largest amount of root growth in surface soil layers occurs in spring in these ecosystems (e.g., Carbone et al., 2008). The autumn period coincided with rains that likely also favoured the development of fine roots and, thus, high root activity. Therefore, it is likely that soil respiration was stimulated not only by optimal soil temperature and soil moisture conditions, but also by the increase in microbial populations, root biomass, and root activity at these times (e.g., Xu et al., 2004).

Contrary to expectation, the total CO_2 respired from bare soil was greater than from the soil under plant cover at the natural alpha grass site, whereas at the more degraded site, the opposite occurred. However, it is possible that we overestimated the amount of carbon respired under plant cover since it responded more than the bare soil to rainfall events. Total amounts of respired CO_2 under each land cover type for both sites were lower than reported for forest soils (Mielnick and Dugas, 2000; Davidson et al., 1998). Although we did not measure soil respiration *immediately* after the rainfall events when most of the response occurs (Rey et al., 2005), large soil respiration rates were always measured shortly after rainfall and contributed considerably to the total amount of carbon respired during the year. Other studies carried out in semi-arid climates have found that precipitation pulses during the dry season can contribute significantly to the total amount of carbon respired over the year (Jarvis et al., 2007; Huxman et al., 2004; Xu et al., 2004; Misson et al., 2006), although this has not always been the case (Carbone et al., 2008).

4.4. Impact of land degradation

The two sites experienced similar temperature and precipitation events, but between them the soil environmental conditions differed significantly. The main differences between the natural and the "degraded" site (attributable mostly to their different degree of degradation) were vegetation cover, soil depth, soil microclimate, carbonate content, and pH. A much larger proportion of the ground surface was uncovered at the more degraded site, so the ground surface was more exposed to solar radiation and wind, without the interception of precipitation by vegetation. As a result, the "degraded" site had hotter and drier soils, associated larger evaporation losses, a lower water storage capacity, and a larger area of soil exposure to solar radiation than the "non-degraded" site. Therefore, the main attributes of soil degradation were changes in the soil thermal and hydrological properties, which, in turn, may have caused the loss of vegetation cover and a lower vegetation activity, as a result of strong water limitation.

Differences in soil texture were detected with higher clay and less silt in the "non-degraded" than in the "degraded" site. Soil texture modifies the hydrological characteristics of arid soils by controlling the infiltration depth, the water holding capacity, and the hydraulic conductivity for water (Cable et al., 2008), all of which can influence other soil processes. Soil respiration rate, for example, was 25% lower in the "degraded" than in the natural site. These differences were largest in spring and were largely attributable to differences in soil water availability and thus in plant activity. Despite lower carbon loss, the relative contribution of this loss to the total net carbon balance may have been larger given that the "degraded" site had one third of the vegetation cover present in the "non-degraded" site.

Another important difference between the sites was the seasonal variation in soil respiration, particularly during spring. Productivity in arid ecosystems is not directly responsive to rainfall, but rather to water availability. Therefore it is important to understand water recharge since antecedent moisture conditions may be just as important as the sum of small rainfall events in determining productivity. During the winter prior to this study, little rain fell at both sites which may have influenced both of the ecosystems differently. Spring precipitation has also been identified as a crucial factor for determining productivity in semi-arid regions (Knapp et al., 2002; Fay et al., 2003; Huxman et al., 2004). One possibility for the lack of response of soil respiration to spring rainfall, and for the lack of productivity at the "degraded" site, is that it was insufficient to activate the roots and photosynthesis (Fernández, 2007) (since at the "degraded" site the drought time period began much earlier in the year). Seed production, tiller density, and leaf area or root biomass may be reduced after a year with low precipitation and this may constrain plant productivity the following spring. A strong dependence of the alpha grass growth rate on plant and soil water status has also been reported (Pugnaire et al., 1996; Balaguer et al., 2002). Balaguer et al. (2002) indicated that below a certain threshold value of soil water content, the roots may not respond. Therefore, differences in soil surface characteristics may have modified surface infiltration, the depth of soil water storage, and therefore, the temporal duration of biologically available water (McAuliffe, 2003). The importance of soil depth and an access to water has been shown to alter the seasonality of carbon fluxes in semi-arid shrublands (Potts et al., 2008).

Another important difference between the sites was the carbonate content, which has been shown to be involved in the soil carbon dynamics of these types of ecosystems (Inglima et al., 2009) and to even alter the seasonal dynamics of ecosystem carbon fluxes (Emmerich, 2003). Therefore, since the "degraded" site had higher carbonate content than the "non-degraded" site, it is possible that inorganic carbon contributed to the total amount of carbon loss during soil respiration particularly after rainfall events (Inglima et al., 2009).

5. Conclusions

(1) Soil water content was the main driving variable of soil respiration at both sites, particularly when the soil volumetric water content (at 3.5 cm) was below the threshold value of 13%. Even during the winter months when soil moisture was above 13%, the impact of temperature on soil respiration was mediated by soil moisture.
(2) At both sites, the temporal variability in soil respiration rates was much larger than the spatial variability. No differences in soil respiration rates between soil cover types were observed.
(3) The temporal dynamics of soil respiration were affected by the degree of land degradation at the two sites. As a consequence of thinner soils and lower vegetation cover, the dry period was much longer on the more degraded site than on the reference site. Neither plant activity nor soil respiration responded to increases in soil moisture and an optimal temperature during spring at the degraded site.
(4) Land degradation altered the hydrological cycle and, in turn, the seasonal dynamics of vegetation and soil activity, further reducing plant productivity. Such a phenomenon is clearly likely to impact the sustainability of these steppe ecosystems in the future.
(5) Although arid regions comprise the most extensive biome in the world, there are few current studies of vegetation processes in this biome. This work demonstrates the different drivers and mechanisms that may be in place, and that may alter the carbon balance of arid-zone ecosystems, through degradation leading to changes in plant productivity, soil respiration, and hydrological dynamics.

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