



Small-scale spatial variation in soil CO₂ efflux in a Mediterranean semiarid steppe

Fernando T. Maestre*, Jordi Cortina

Departamento de Ecología, Universidad de Alicante, Apartado de Correos 99, 03080 Alicante, Spain

Received 16 October 2002; received in revised form 28 March 2003; accepted 3 April 2003

Abstract

Soil respiration is one of the main processes of loss of organic C, but few studies so far have evaluated losses from arid and semiarid soils as compared with other ecosystems. Spatial variation in CO₂ efflux is especially important in semiarid areas, where the distribution of ecological factors and organisms is markedly patchy. We have evaluated the small-scale spatial variation of soil respiration in a semiarid *Stipa tenacissima* steppe from late winter to early summer. We selected the five most frequent soil cover types in the study site: upslope and downslope of *S. tenacissima* tussocks (SU and SD surface units, respectively), patches of the perennial grass *Brachypodium retusum* (BR surface unit), biological crusts (BC surface unit), surface earthworm casts (EC surface unit) and bare ground (BG surface unit). The dynamics of soil CO₂ efflux clearly reflected the changes in soil moisture. We observed significant differences in CO₂ efflux between surface units, with BR and BG showing maximum and minimum CO₂ efflux rates, respectively. Soil temperature increased during the course of the study period, showing significant differences between the most shaded (SU and SD) and the other surface units (BC, BG, BR and EC), with higher temperatures in the latter group. Soil CO₂ efflux was poorly correlated with soil temperature, but significant non-linear relationships were found for SU, BR and BC surface units. Rainfall simulation significantly enhanced CO₂ efflux in SU, BR and EC surface units. Our results highlight the importance of the spatial variation of both vegetation and surface soil features for the estimation of CO₂ efflux in semiarid ecosystems. They also suggest that estimations based only on vegetated and bare-ground areas can be rather conservative if the sampling effort is not high enough to capture the spatial variability in CO₂ efflux in the latter areas.

© 2003 Elsevier Science B.V. All rights reserved.

Keywords: *Brachypodium retusum*; *Stipa tenacissima*; Carbon dioxide; Soil respiration; Spatial variation

1. Introduction

Soil respiration constitutes one of the main sources of CO₂ to the atmosphere, accounting for over 25% of global emissions (Bouwman and Germon, 1998). Despite the importance of this process, knowledge about the factors controlling it and its variability

across ecosystems is still quite limited (Raich and Schlesinger, 1992; Rustad et al., 2001). Soil respiration is one of the main processes of loss of C from arid and semiarid soils (Conant et al., 2000), and, because of the relatively small organic C pools that they contain, it is one of the ecosystem properties most sensitive to climate change (West et al., 1994). However, it has been less studied in these areas as compared with other ecosystems (Raich and Schlesinger, 1992).

Soil CO₂ efflux is difficult to estimate due to the high spatial variability that characterises it (Fang et al.,

* Corresponding author. Tel.: +34-965909564;
fax: +34-965903565.
E-mail address: ft.maestre@ua.es (F.T. Maestre).

1998; Stoyan et al., 2000; Xu and Qi, 2001). This variability can be especially large in semiarid areas, where the distribution of resources, conditions and organisms is markedly patchy (Schlesinger and Pilmanis, 1998). Features of the soil surface, such as the presence of rock fragments, earthworm casts and biological crusts, can have strong impacts on soil CO₂ dynamics in semiarid ecosystems (Casals et al., 2000; Romanyà et al., 2000). These properties often show complex spatial patterns in these areas (Maestre et al., 2002; Maestre and Cortina, 2002; Maestre, 2003). Thus, in addition to the effects of the patchy distribution of vegetation and belowground soil properties, heterogeneity of surface soil features can increase the spatial variation of soil CO₂ efflux in semiarid ecosystems. However, the effects of the spatial variation of both vegetation and surface soil features on soil CO₂ efflux within semiarid ecosystems are still poorly known.

In this study we aimed to characterize the small-scale spatial variation of soil respiration in a semiarid alpha grass (*Stipa tenacissima* L.) steppe during spring and early summer. *S. tenacissima* is a perennial tussock grass that dominates the landscape of large arid and semiarid areas within the Mediterranean Basin (Le Houérou, 2001). Vegetation within these steppes typically shows complex spatial patterns that influence the distribution of surface soil features—such as physical and biological crusts, earthworm casts, and rock fragments—at the plant and hillslope spatial scales (Maestre et al., 2002; Maestre and Cortina, 2002; Maestre, 2003). Our main objective was to evaluate the effects on soil CO₂ efflux promoted by the small-scale spatial variation of vegetation and surface soil features in a semiarid *S. tenacissima* steppe.

2. Materials and methods

2.1. Study area

The study site is a steppe located close to Aigües de Busot, in SE Spain (38°31'N, 0°21'W; 460 m a.s.l.; 12° slope facing SE). The climate is semiarid, with a 1960–1990 mean annual rainfall and temperature of 388 mm and 16 °C, respectively (Pérez, 1994). Annual evapotranspiration is 819 mm, and within-year coefficients of variation for monthly rainfall and tem-

perature are 49 and 38%, respectively. The soil is a *Lithic Calciorthid* (Soil Survey Staff, 1994). Soil texture (0–20 cm depth) is silty, with 20% sand, 52% silt and 28% clay for the soil under the canopy of *S. tenacissima*, and 20% sand, 55% silt and 25% clay for the soil in bare-ground areas (Maestre et al., 2001). Species composition and vegetation structure of this site is representative of *S. tenacissima* steppes in SE Spain (Fig. 1). Vegetation is 45%, and is dominated by the perennial grasses *S. tenacissima* (typical height 50–150 cm) and *Brachypodium retusum* (Pers.) P. Beauv (typical height: 10–30 cm), which account for more than 73% of the total plant cover. Dispersed shrubs such as *Globularia alypum* L. and *Anthyllis cytisoides* L. are also present. Earthworm casts, biological crusts and mosses are common features of the soil surface (Maestre and Cortina, 2002).

2.2. Experimental design and field measurements

We selected the five most frequent soil cover types (hereafter called surface units) in the study area (Fig. 1): *B. retusum* patches (BR), biological crusts (BC), earthworm casts (EC), bare ground (BG), and *S. tenacissima* tussocks. There are important differences in the characteristics of the soil surface between the upslope (SU) and downslope parts (SD) of *S. tenacissima* tussocks (24% of total surface cover), due to the accumulation of runoff water and sediments in the former (Puigdefábregas et al., 1999). Thus, we considered these two situations as different surface units. Measurements of soil CO₂ efflux were taken according to a stratified random design. On February 2001, we randomly selected 10 permanent circular plots (78 cm²) per surface unit. During plot establishment, each plot falling within distances less than 2 m of an existing replicate was discarded and reallocated to ensure a minimum distance of 2 m between replicates.

The SU surface unit is characterised by permanent shade conditions, high litter accumulation, and the presence of mosses (*Weissia* sp.; Maestre et al., 2002) on the soil surface. The SD surface unit has similar features, but the biological crusts are dominated by cyanobacteria (*Nostoc* sp. and *Microcoleus* sp.; Maestre et al., 2002). Both SU and SD are located less than 3 cm from the upslope and downslope edges of *S. tenacissima* tussocks, respectively. The BR surface unit (11% of total surface cover) is located

(A)



(B)



(C)



(D)



(E)



(F)



(G)



Fig. 1. View of the study area (A) and of the different surface units (B–G). Arrows in (A) show the location of some *Stipa tenacissima* tussocks; the scale in it refers to the large and dark shrub patch located in the middle of the image. B: upslope of *S. tenacissima*, C: downslope of *S. tenacissima*, D: *Brachypodium retusum*, E: biological crusts, F: earthworm casts, and G: bare ground.

within patches of *B. retusum*, and is characterised by moderate shade conditions (photosynthetically active radiation is over 15–30% of that found in open areas), high litter content, and the occasional presence of earthworm casts. The BC surface unit (7% of total surface cover) is located in open areas with no above-ground parts of vascular plants, and is characterised by the lack of shade and the presence of a biological crust dominated by cyanobacteria and lichens (mainly *Psora crenata* [Th. Tayl.] Reinke and *Collema* sp.; Maestre et al., 2002). The EC surface unit (20% of total surface cover) is located in open areas where the soil surface is completely covered by earthworm casts, sometimes weakly colonised by cyanobacteria. The dry mass of casts per unit area in this surface unit, in the upper 1.2 cm, is $1.01 \pm 0.10 \text{ g cm}^{-2}$ (mean \pm S.D., $n = 10$). The BG surface unit (19% of total surface cover) is located in open areas with no vascular plant cover or earthworm casts, and is characterised by the presence of a physical crust and some colonisation of the soil surface by cyanobacteria.

Soil CO₂ efflux was measured in situ using an infrared gas analyzer system (model CIRAS-1, PP Systems, Hitchin, UK) equipped with a flow-through closed chamber (model STP-1, same manufacturer). At the time of measurements, the chamber, which had an area of 78 cm² and a volume of 1170 cm³, was inserted 3 cm into the soil. Measurements at each sampling point took 120 s, a sampling interval long enough to get reliable estimates of CO₂ efflux with the equipment used (PP Systems, 1993). They were performed monthly between March and July 2001. We selected this period because this is the period of maximum vegetation activity in *S. tenacissima* grasslands (Haase et al., 1999). Measurements were performed between 10:00 and 13:00 h (local time, GMT + 1). We selected this time of the day for measurements because it has been shown that midday values of CO₂ efflux are representative of daily averages in grasslands (Mielnick and Dugas, 2000). In addition, we performed a rainfall simulation on 26 June 2001, with the aim of evaluating short-term changes in soil CO₂ efflux after a rainfall event. On that day we measured CO₂ efflux following our usual protocol. Immediately after each measurement, we added water over the whole surface of the plots in an amount equivalent to a 24 mm rainfall event. This amount is representative of late-spring storms in the study area (Pérez, 1994).

We took special care to avoid runoff generation during the addition of water. After this, new measurements of CO₂ efflux were performed 3 h after watering.

We measured soil temperature during CO₂ efflux measurements with protected diodes buried at 5 cm depths. Diodes were placed adjacent to CO₂ measurement plots in five randomly selected plots per surface unit. In addition, we measured soil moisture in an adjacent site on SU and BG surface units by using time-domain reflectometry (TDR; Topp and Davis, 1985). We installed 20 cm length TDR probes vertically in 12 randomly selected SU and BG surface units. Measurements were taken with a Tektronix 1502C metallic TDR cable tester (Tektronix, Beaverton, OR, USA) at 1–2-week intervals between March and June 2001. For the estimation of volumetric soil moisture, we used a site-specific calibration factor for the soils of the study area.

We evaluated the root content of all surface units sampled for soil respiration during spring 2002. A 0–10 cm depth soil core (90 cm³) per surface unit was extracted and transported to the laboratory. Roots were manually separated from the soil, dried at 60 °C to constant weight, and weighed thereafter. After extracting the roots, we determined the soil organic matter content following the loss-on-ignition method, by burning soil samples in a furnace at 550 °C for 2 h.

2.3. Statistical analyses

We used repeated measures ANOVA to test for differences between surface units in soil CO₂ efflux, temperature and moisture. Changes in CO₂ efflux after irrigation were analysed separately for each surface unit using *t*-tests for paired samples. The magnitude of these differences was analysed by using one-way ANOVA. The relationship between CO₂ efflux and soil temperature was analysed using linear and non-linear regressions. Differences between surface units in root biomass and soil organic content were evaluated with one-way ANOVA. In all ANOVA analyses, differences between surface units ($P < 0.05$) were analysed with the Student–Newman–Keuls (SNK) test when appropriate. Data were tested prior to analyses for assumptions of normality and homogeneity of variances, and were log-transformed when necessary. All statistical analyses were performed by using the SPSS 9.0 package (SPSS, Chicago, IL, USA).

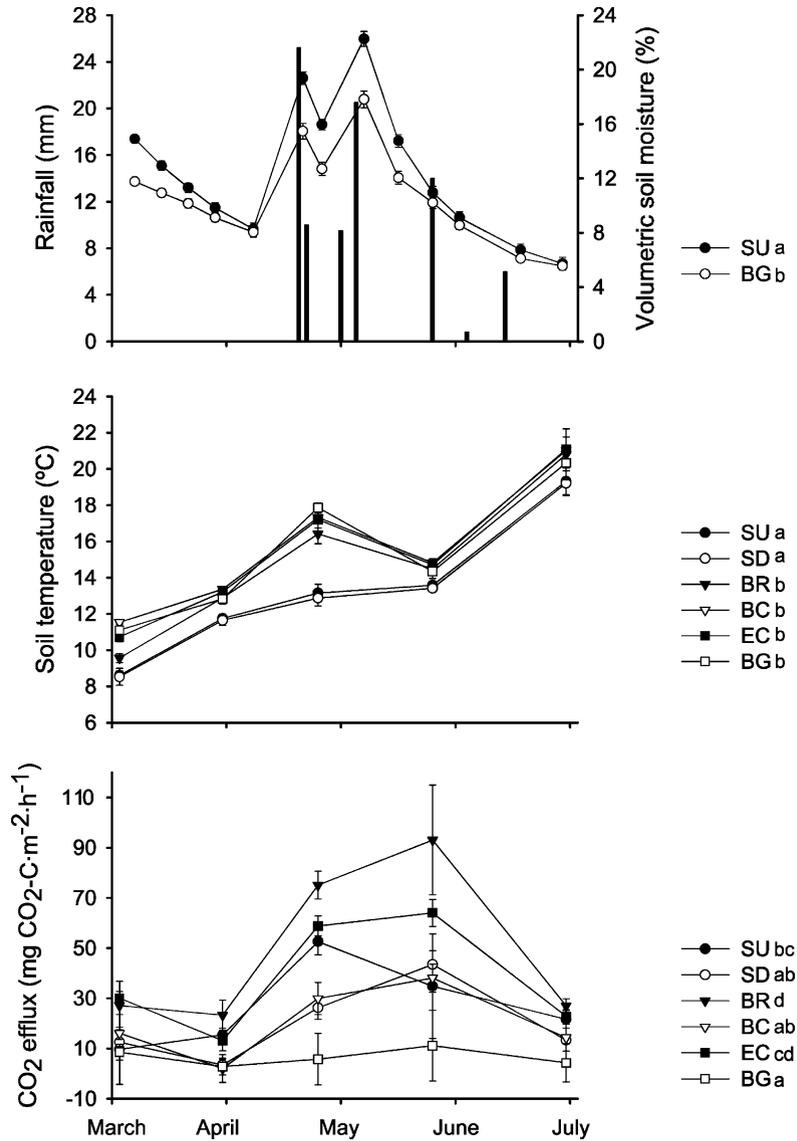


Fig. 2. Rainfall and soil moisture (upper graph), soil temperature at 5 cm depth (middle graph), and soil CO₂ efflux (bottom graph) between March and July 2001. Data represent means ± S.E. ($n = 10$ for soil CO₂ efflux and temperature; $n = 12$ for soil moisture). Different lower case letters close to the legend indicate significant differences between surface units after repeated measures ANOVA ($P < 0.05$). SU: upslope of *Stipa tenacissima*, SD: downslope of *S. tenacissima*, BR: *Brachypodium retusum*, BC: biological crusts, EC: earthworm casts, and BG: bare ground.

3. Results

Rainfall during the study period was 86 mm, corresponding to 65% of the 30-year average (Pérez, 1994). It was mainly concentrated between 18 April and 23 May (Fig. 2). Soil moisture was higher in SU than in

BG surface units during most of the study period, but especially after rainfall events (Fig. 2); these differences were significant (repeated measures ANOVA, $F_{\text{surface unit}} = 17.279$, d.f. = 1, 22, $P < 0.001$). Dynamics of soil CO₂ efflux followed changes in soil moisture, rather than those of soil temperature, and

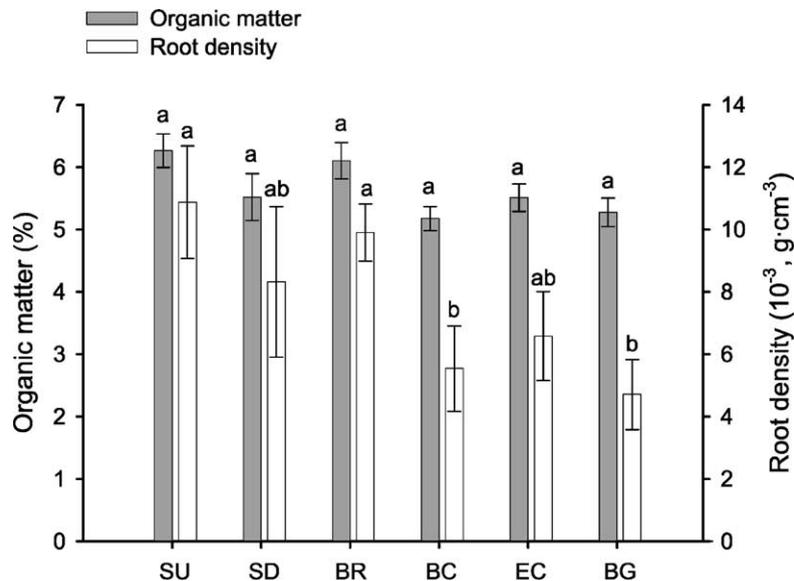


Fig. 3. Soil organic matter content and root density of the surface units sampled for soil CO_2 efflux. Data represent means \pm S.E. ($n = 10$). Different lower case letters indicate significant differences between surface units after one-way ANOVA ($P < 0.05$, SNK test). SU: upslope of *Stipa tenacissima*, SD: downslope of *S. tenacissima*, BR: *Brachypodium retusum*, BC: biological crusts, EC: earthworm casts, and BG: bare ground.

substantially increased after rainfall events (Fig. 2). We found significant differences in soil CO_2 efflux between surface units, with BR and BG surface units showing the maximum and minimum amounts, respectively (mean and standard error over the study period of $49.1 \pm 6.4 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ versus $6.5 \pm 3.8 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$). These differences were especially evident after rainfalls, and diminished as soil moisture declined. Soil temperature increased during the course of measurements, and showed significant differences between the most shaded surface units (SU and SD) and the rest of surface units (BC, BG, BR and EC), with higher temperatures in the latter group (Fig. 2). Root density differed significantly between surface units (Fig. 3). It was significantly higher in SU and BR surface units as compared with BC and BG surface units. Soil organic matter showed slight differences between surface units, but they were not significant (Fig. 2). In general, CO_2 efflux was poorly correlated with soil temperature, and no linear relationship was observed for any surface unit evaluated (Fig. 4). However, significant non-linear relationships were found for SU, BR and EC surface units. The addition of water significantly enhanced CO_2 efflux in

SU, BR and EC surface units (Fig. 5). The magnitude of the change in CO_2 efflux showed significant differences between surface units, with the highest increase in BR followed by EC and SU surface units, and a decrease in the CO_2 efflux in BC surface unit (Fig. 5). In contrast to all other surface units, mean CO_2 efflux decreased in the BC surface unit after rainfall simulation.

4. Discussion

Our results show the presence of large small-scale differences in soil CO_2 efflux. Small-scale spatial variation of soil CO_2 efflux has been described in a wide variety of ecosystems, including crops (Robertson et al., 1997; Stoyan et al., 2000), tropical bare soils (La et al., 2000), temperate coniferous forests (Buchmann, 2000; Rayment and Jarvis, 2000) and afforestations (Stoyan et al., 2000; Xu and Qi, 2001). However, it has rarely been reported in semiarid ecosystems (Billes et al., 1971), despite the inherent heterogeneity in soil resources and plant cover that characterize them (Schlesinger and Pilmanis, 1998).

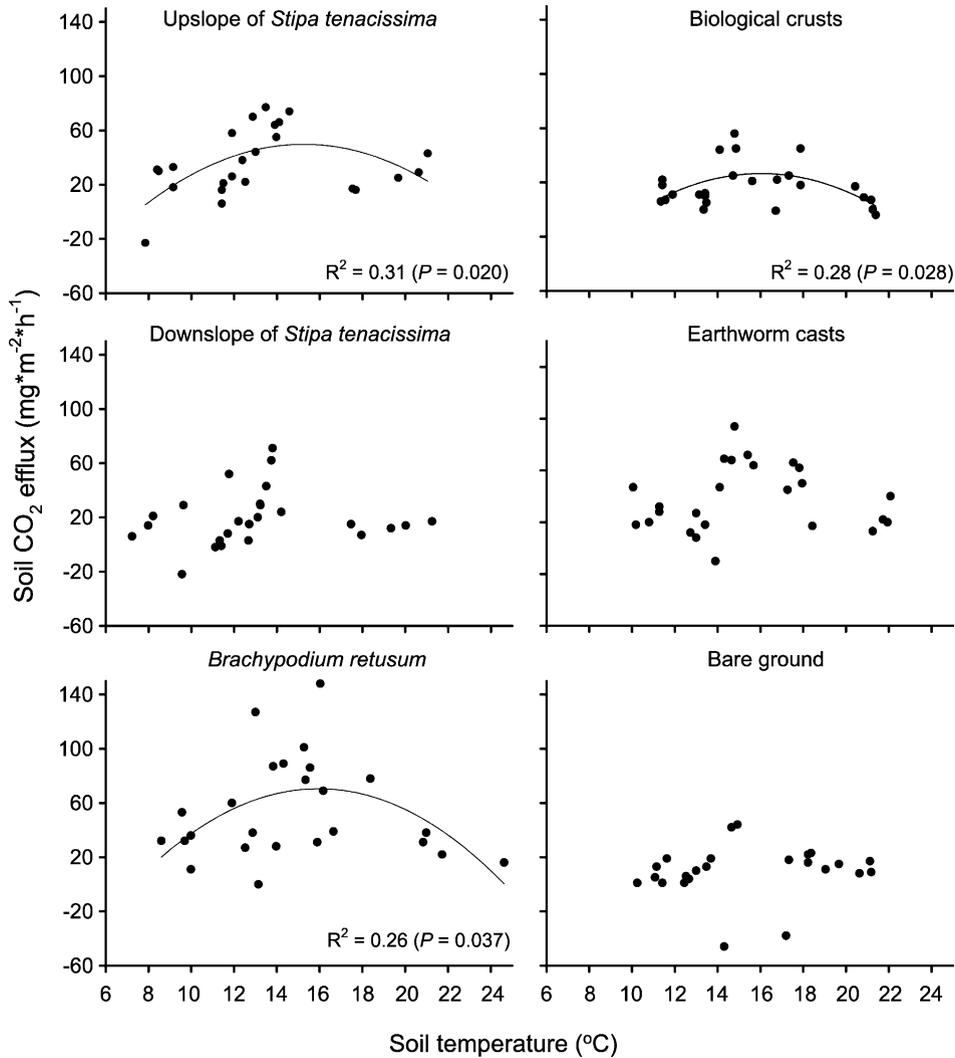


Fig. 4. Relationships between soil CO₂ efflux and temperature during the study period. Only significant non-linear regressions ($P < 0.05$) are shown.

The magnitude of soil CO₂ efflux obtained in this study is similar to that reported for global grasslands (46–57 mg m⁻² h⁻¹; Raich and Schlesinger, 1992), and to that reported for a semiarid *Pinus halepensis* forest in Spain (36–70 mg m⁻² h⁻¹; Casals et al., 2000), for three semiarid ecosystems (desert scrub, pinyon–juniper woodland and *Pinus ponderosa* forest) in Arizona (20–125 mg m⁻² h⁻¹; Conant et al., 2000), and for a tallgrass prairie in Nebraska (52 mg m⁻² h⁻¹; Norman et al., 1992). However, it is lower than that reported for semiarid grasslands of the North-

ern Great Plains (145–179 mg m⁻² h⁻¹; Frank et al., 2002).

Increased CO₂ efflux in vegetated versus bare patches was expected due to the differences in soil properties, root density and microbial activity promoted by vascular plants. Soil CO₂ efflux is often positively related with variables such as moisture, temperature, soil organic matter (SOM) and microbial activity (Conant et al., 2000; Stoyan et al., 2000; Xu and Qi, 2001). With the exception of temperature, these properties usually present higher values

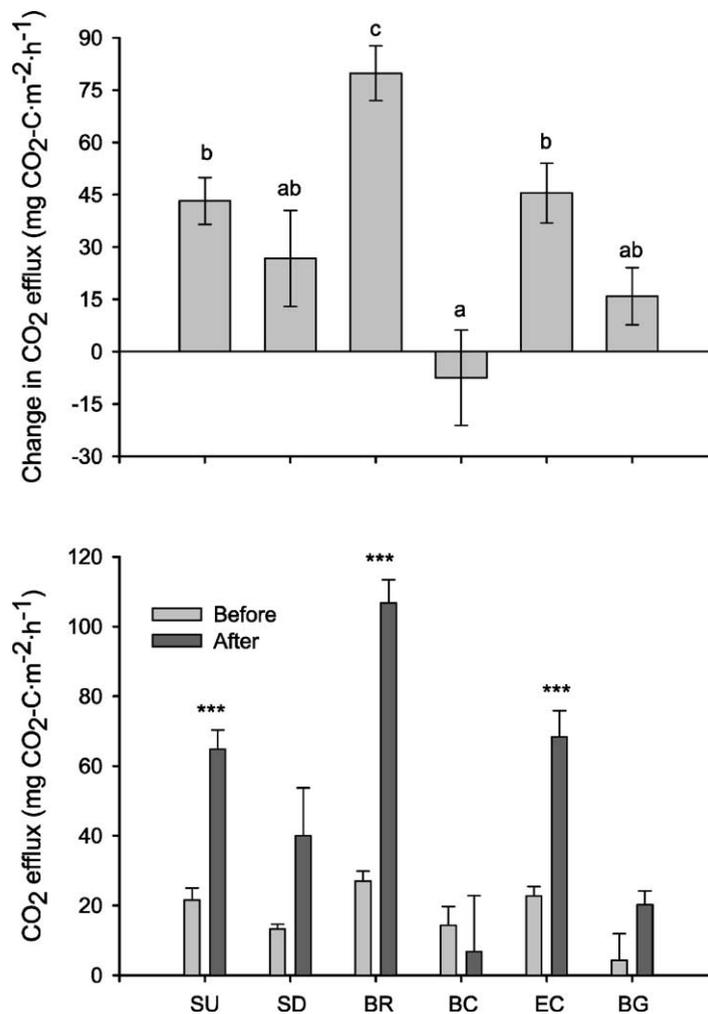


Fig. 5. Changes (upper graph) and values (lower graph) of CO₂ efflux before and after a 24 mm rainfall simulated on 26 June 2001. Data represent means and SE ($n = 10$). In the upper graph, different letters indicate significant differences between surface units after one-way ANOVA ($P < 0.05$). In the lower graph, differences between periods within each surface unit (after paired t -tests) are denoted by asterisks: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. SU: upslope of *Stipa tenacissima*, SD: downslope of *S. tenacissima*, BR: *Brachypodium retusum*, BC: biological crusts, EC: earthworm casts, and BG: bare ground.

under the canopy of vegetated patches in semiarid areas (Schlesinger and Pilmanis, 1998; Maestre et al., 2001). The higher soil moisture found in SU as compared with BS surface units after rainfall events may be promoted by run-on water inputs and higher infiltration in the former (Puigdefábregas et al., 1999; Maestre et al., 2002). This status can be maintained for some weeks after rainfalls, because the reduction in incoming radiation in SU can overcome water uptake by *S. tenacissima* tussocks (Maestre et al.,

unpublished data). Root density was, overall, higher in vegetated than in open surface units, but we found no significant differences in SOM between surface units. The latter result was unexpected, and may suggest that belowground carbon inputs by roots may be enough to maintain soil organic matter levels in open areas (Maestre et al., 2001). We also found a positive relationship between the average values of root density and SOM, and between these variables and soil CO₂ efflux, although in the latter case it was not

significant (data not shown). These results suggest that small-scale differences in soil moisture and temperature may be more relevant to explain small-scale differences in soil CO₂ efflux than SOM and root density. Further studies are needed to understand the relative importance of soil versus microclimatic factors, as well as the role of soil variables not measured in this study, such as microbial activity and the quality of carbon, in the patterns of CO₂ efflux found.

It is interesting to note the strong differences in CO₂ efflux between EC and BG surface units, despite both surface units being devoid of vascular plants. Our observations agree with studies reporting an increase in soil CO₂ efflux in the presence of earthworm casts (Wolters and Ekschmitt, 1995; Hendriksen, 1997; Romanyà et al., 2000). Earthworm casts frequently show higher contents of organic C, nutrients and microbial activity than adjacent soil (Wolters and Schaeffer, 1991; Kang and Ojo, 1996). However, we found no significant differences in the organic matter content or in root density between EC and BG surface units. Thus, it is possible that the differences observed may be promoted by higher microbial activity in the EC surface unit (Stoyan et al., 2000), as well as by differences in the quality of carbon. However, our results cannot provide direct evidence for this. Within the vegetated surface units, soil organic matter and fine root density were very similar in BR and SU surface units. But still CO₂ efflux from BR surface units was substantially higher than in SU surface units (mean and standard error over the study period of $49.1 \pm 6.4 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ versus $26.8 \pm 6.3 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$). Furthermore, the magnitude of the increase in soil CO₂ efflux after irrigation was higher in BR than in SU surface units. These results suggest that the increased soil CO₂ efflux found in BR could be mainly related to the higher temperatures found in this surface unit. However, the role of other soil properties, such as root microbial activity, fine root turnover, and soil carbon quality in the differences found should be assessed in future studies.

Soil temperature and moisture are the main factors driving soil respiration in semiarid ecosystems, but their relative importance is still controversial (Wildung et al., 1975; Conant et al., 2000; Casals et al., 2000; Frank et al., 2002). Conant et al. (2000) found that soil moisture was the main factor influencing soil CO₂ efflux in three semiarid ecosystems in Arizona. How-

ever, Casals et al. (2000) and Frank et al. (2002) suggested that the relative importance of soil temperature was higher than that of soil moisture in a semiarid *P. halepensis* forest in Spain and in semiarid grasslands in the Northern Great Plain (USA), respectively. The non-linear relationships found between soil temperature and CO₂ efflux indicate a decrease in soil CO₂ efflux at the highest temperatures, which were registered when soil moisture values were lowest. Furthermore, irrigation promoted a strong increase in soil CO₂ efflux when soil temperatures were highest. These results indirectly support the hypothesis that the response of soil respiration to increased temperature is constrained by soil moisture in the studied steppe.

Despite great variability between sites and species, typical responses of biological crusts after rewetting are characterised by a quick increase in CO₂ efflux that begins almost immediately after wetting (Lange, 2001). This increase is followed by a decrease caused by the activation of photosynthesis, which may reach full activity after 30 min (Lange, 2001). We found a clear trend for lower soil CO₂ efflux after irrigation in the BC surface unit. Net photosynthesis of biological crusts in arid and semiarid ecosystems is typically higher than the soil CO₂ efflux measured in the BC surface unit, but it is often limited by low moisture content (Lange, 2001). Thus, the observed response may be caused by an increase in the CO₂ fixation activity by the photosynthetically active organisms of biological crusts. But it is also likely that the observed response may be promoted by impeded diffusion of CO₂ out of soils when their porespace are filled with water, and by the tendency for CO₂ to dissolve in soil water during wet periods.

Our results show the presence of small-scale spatial variation of soil CO₂ efflux in an *S. tenacissima* steppe during the main growing season. They also suggest that the spatial variation of both vegetation and surface soil features may be relevant for the accurate estimation of CO₂ efflux in this ecosystem. Estimations based only on vegetated and bare-ground areas have been used to predict carbon budgets in temperate grasslands (Kim et al., 1992). The large differences found in soil CO₂ efflux within the non-vegetated areas (note the strong differences between BG and EC surface units, which were often greater than those found between BG and SU surface units) suggest that such approaches can largely underestimate soil CO₂ efflux in heterogeneous

semiarid areas. Since arid and semiarid ecosystems occupy over two fifths of the Earth's total surface (Reynolds, 2001), small-scale spatial variation in soil CO₂ efflux may be relevant for accurately estimating global carbon budgets. Regional estimates of net CO₂ efflux, which are commonly obtained with models designed for scaling plot measurements (Vourlitis et al., 2000), are required to assess the contribution of a given ecosystem to global carbon budgets (Baldocchi et al., 1996). Differences in the composition of soil surface features may introduce uncertainties in the estimates of these models (Vourlitis et al., 2000). The incorporation of small-scale spatial variation in vegetation and surface soil features into these models will undoubtedly lead to an improvement in their predictive capabilities, and remains a challenging yet critical area for future research.

Acknowledgements

We thank José Huesca, Vicent Lluís Seguí, Alberto Pastor and Tatiana Espinosa for their help during fieldwork. William H. Schlesinger provided us with useful comments and improvements on an earlier version of the manuscript. This work was supported by a FPU fellowship of the Ministerio de Educación, Cultura y Deporte awarded to F.T. Maestre, and by the research projects REDMED (ENV4-CT97-0682) and FANCB (REN2001-0424-C02-01/GLO), funded by the European Commission and the Spanish CICYT, respectively.

References

- Baldocchi, D., Valentini, R., Running, S., Oechel, W., Dahlman, R., 1996. Strategies for measuring and modeling carbon dioxide and water vapor fluxes over terrestrial ecosystems. *Global Change Biol.* 2, 101–110.
- Billes, G., Cortez, J., Lossaint, P., 1971. L'activité biologique des sols dans les écosystèmes méditerranéens. I. Minéralisation de carbone. *Rev. Ecol. Biol. Sol.* 3, 375–395.
- Bouwman, A.F., Germon, J.C., 1998. Introduction. *Biol. Fertil. Soil* 27, 219.
- Buchmann, N., 2000. Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. *Soil Biol. Biochem.* 32, 1625–1635.
- Casals, P., Romanyà, J., Cortina, J., Bottner, P., Couteaux, M.M., Vallejo, V.R., 2000. CO₂ efflux from a Mediterranean semi-arid forest soil. I. Seasonality and effects of stoniness. *Biogeochemistry* 48, 261–281.
- Conant, R.T., Klopatek, J.M., Klopatek, C.C., 2000. Environmental factors controlling soil respiration in three semiarid ecosystems. *Soil Sci. Soc. Am. J.* 64, 383–390.
- Fang, C., Moncrief, J.B., Gholz, H.L., Clark, K.L., 1998. Soil CO₂ efflux and its spatial variation in a Florida slash pine plantation. *Plant Soil* 205, 135–146.
- Frank, A.B., Liebig, M.A., Hanson, J.D., 2002. Soil carbon dioxide fluxes in northern semiarid grasslands. *Soil Biol. Biochem.* 34, 1235–1241.
- Haase, P., Pugnaire, F., Clarck, S.C., Incoll, L.D., 1999. Environmental control of canopy dynamics and photosynthetic rate in the evergreen tussock grass *Stipa tenacissima*. *Plant Ecol.* 145, 327–339.
- Hendriksen, N.B., 1997. Earthworm effects on respiratory activity in a dung-soil system. *Soil Biol. Biochem.* 29, 347–351.
- Kang, B.T., Ojo, A., 1996. Nutrient availability of earthworm casts collected from under selected woody agroforestry species. *Plant Soil* 178, 113–119.
- Kim, J., Verma, S.B., Clements, R.J., 1992. Carbon dioxide budget in a temperate grassland ecosystem. *J. Geophys. Res.* 97, 6057–6063.
- La, S., Marques Jr., J., Pereira, G.T., Cora, J.E., 2000. Short-term temporal changes in the spatial variability model of CO₂ emissions from a Brazilian bare soil. *Soil Biol. Biochem.* 32, 1459–1462.
- Lange, O.L., 2001. Photosynthesis of soil-crust biota as dependent on environmental factors. In: Belnap, J., Lange, O.L. (Eds.), *Biological Soil Crusts: Structure, Function, and Management*. Springer, Berlin, Germany, pp. 217–240.
- Le Houérou, H.N., 2001. Biogeography of the arid steppeland north of the Sahara. *J. Arid Environ.* 48, 103–128.
- Maestre, F.T., 2003. Small-scale spatial patterns of two soil lichens in semi-arid Mediterranean steppe. *Lichenologist* 35, 71–81.
- Maestre, F.T., Cortina, J., 2002. Spatial pattern of soil properties and vegetation in a Mediterranean semi-arid steppe. *Plant Soil* 241, 279–291.
- Maestre, F.T., Bautista, S., Cortina, J., Bellot, J., 2001. Potential of using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecol. Appl.* 11, 1641–1645.
- Maestre, F.T., Huesca, M.T., Zaady, E., Bautista, S., Cortina, J., 2002. Infiltration, penetration resistance and microphytic crust composition in contrasted microsites within a Mediterranean semi-arid steppe. *Soil Biol. Biochem.* 34, 895–898.
- Mielnick, P.C., Dugas, W.A., 2000. Soil CO₂ flux in a tallgrass prairie. *Soil Biol. Biochem.* 32, 221–228.
- Norman, J.M., Garica, R., Verma, S.B., 1992. Soil surface CO₂ fluxes and the carbon budget of a grassland. *J. Geophys. Res.* 97, 18845–18853.
- Pérez, J.A., 1994. Atlas climático de la Comunidad Valenciana. Conselleria de Obras Públicas, Urbanismo y Transportes, Valencia, 205 pp.
- PP Systems, 1993. SRC-1 soil respiration system. Operator's Manual, Version 3.0. PP Systems, Hitchin, 28 pp.
- Puigdefàbregas, J., Solé-Benet, A., Gutierrez, L., Del Barrio, G., Boer, M., 1999. Scales and processes of water and sediment

- redistribution in drylands: results from the Rambla Honda field site in Southeast Spain. *Earth-Sci. Rev.* 48, 39–70.
- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B, 81–99.
- Rayment, M.B., Jarvis, P.G., 2000. Temporal and spatial variation of soil CO₂ efflux in a Canadian boreal forest. *Soil Biol. Biochem.* 32, 35–45.
- Reynolds, J.F., 2001. Desertification. In: Levin, S.A. (Ed.), *Encyclopedia of Biodiversity*, vol. 2. Academic Press, San Diego, USA, pp. 61–78.
- Robertson, G.P., Klingensmith, K.M., Klug, M.J., Paul, E.A., Crum, J.R., Ellis, B.G., 1997. Soil resources, microbial activity, and primary production across an agricultural ecosystem. *Ecol. Appl.* 7, 158–170.
- Romanyà, J., Casals, P., Cortina, J., Bottner, P., Couteaux, M.M., Vallejo, V.R., 2000. CO₂ efflux from a Mediterranean semi-arid forest soil. II. Effects of soil fauna and surface stoniness. *Biogeochemistry* 48, 283–306.
- Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C., Gurevitch, J., GCTE-NEWS, 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralisation and above-ground plant growth to experimental ecosystem warming. *Oecologia* 126, 543–562.
- Schlesinger, W.H., Pilmanis, A.M., 1998. Plant–soil interactions in desert. *Biogeochemistry* 42, 169–187.
- Soil Survey Staff, 1994. *Keys to Soil Taxonomy*, fourth ed. SMSS Technical Monograph No. 6, Blacksburg, Virginia, 524 pp.
- Stoyan, H., De-Polli, H., Bohm, S., Robertson, G.P., Paul, E.A., 2000. Spatial heterogeneity of soil respiration and related properties at the plant scale. *Plant Soil* 222, 203–214.
- Topp, G.C., Davis, J.L., 1985. Measurement of soil water content using time-domain reflectometry (TDR): a field evaluation. *Soil Sci. Soc. Am. J.* 49, 19–24.
- Vourlitis, G.L., Oechel, W.C., Hope, A., Stow, D., Boynton, B., Verfaillie, J.J., Zulueta, R., Hastings, S.J., 2000. Physiological models for scaling plot measurements of CO₂ flux across an arctic tundra landscape. *Ecol. Appl.* 10, 60–72.
- West, N.E., Stark, J.M., Johnson, D.W., Abrams, M.M., Wright, J.R., Heggem, D., Peck, S., 1994. Effects of climatic change on the edaphic features of arid and semiarid lands of western North America. *Arid Soil Res. Rehab.* 8, 307–351.
- Wildung, R.E., Garland, T.R., Buschbom, B.L., 1975. The interdependent effects of soil temperature and water content on soil respiration rate and plant root decomposition in arid grassland soils. *Soil Biol. Biochem.* 7, 373–378.
- Wolters, V., Ekschmitt, K., 1995. Earthworm effects on the use of C sources by micro-organisms: non-linear response to temperature alteration. *Biol. Fertil. Soils* 19, 109–114.
- Wolters, V., Schaeffer, M., 1991. Effects of burrowing by the earthworm *Aporrectodea caliginosa* (Savigny) on beech litter decomposition in an agricultural and in a forest soil. *Geoderma* 56, 627–632.
- Xu, M., Qi, Y., 2001. Soil-surface CO₂ efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biol.* 7, 667–677.