Biogeochemistry **48:** 261–281, 2000.

CO_2 efflux from a Mediterranean semi-arid forest soil. I. Seasonality and effects of stoniness

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Received 10 June 1998; accepted 24 March 1999

Key words: drying and rewetting cycles, gravel layer, Mediterranean arid ecosystems, simulated rainstorm, soil respiration, soil temperature, soil water potential

Abstract. We studied the seasonality of total soil CO_2 efflux and labeled C-CO_2 released from ^{14}C labeled straw incubated in the H horizon of a semi-arid Mediterranean forest soil. Field measurements were carried out over 520 days in a series of reconstructed soil profiles with and without a gravel layer below the H horizon. We monitored soil climate and related this to soil CO_2 efflux. Seasonal variations in soil CO_2 efflux in a semiarid Mediterranean forest were mainly related to changes in soil temperature. In spite of drought, high respiration rates were observed in mid summer. High soil CO_2 efflux in hot and dry episodes was attributed to increases in soil biological activity. The minimum soil CO_2 efflux occurred in late summer also under dry conditions, probably related to a decrease in soil biological activity in deep horizons. Biological activity in organic layers was limited by water potential (Ψ) in summer and by temperature in winter. Rewetting a dry soil resulted in large increases in soil CO_2 efflux only at high temperatures. These large increases represented a significant contribution to the decomposition of organic matter in the uppermost horizons. Soil biological activity in the uppermost horizons was more sensitive to changes in soil Ψ and hence to summer rainstorms than the bulk soil microbial activity. The presence of a layer of gravel improved both moisture and temperature conditions for the decomposition of organic matter. As a result, soil CO_2 efflux increased in soils containing rock fragments. These effects were especially large for the organic layers.

Introduction

The amount of carbon dioxide produced in the soil is related to the lability of soil organic matter (SOM), and to the activity of the belowground part of the ecosystem. Since the early studies of Russell and Appleyard (1915; in Box & Meentemeyer 1993), measurements of soil CO_2 have been widely used to describe soil biological activity, to assess the effects of management practices and disturbances. Numerous studies have described the relationships between soil CO_2 efflux and environmental factors such as temperature and moisture. It is commonly agreed that soil biological activity may relate to temperature and water availability through monotonic or unimodal response curves, depending on the range of conditions considered (Killham 1994). Such relationships have been included in models of SOM dynamics (Andrén et al. 1992; Parton et al. 1988). However, in some cases field measurements of soil CO_2 efflux apparently deviate from these general relationships (Ewel et al. 1987; Weber 1990; see examples cited in Box & Meentemeyer 1993). These discrepancies may result from various factors such as variability of climate or soil attributes, which are not taken into account in general models.

Depending upon the scale of the study, SOM dynamics in Mediterranean forests may be especially sensitive to factors other than large seasonal changes in soil temperature and moisture. Microclimatic changes associated with the physical structure of the soil may have a significant effect on the cycling of C in forest soils. Mediterranean forest soils often contain large amounts of rock fragments on the soil surface that are associated with unusually high amounts of organic matter in the forest floor (Vallejo 1983; Van Wesemael & Veer 1992; Fons & Vallejo 1999). The latter authors hypothesized that stony surfaces can give rise to a physical and biological disconnection between organic and mineral layers. Other authors (De Vries 1963; Mehuys et al. 1975; Jury & Bellantuoni 1976; Childs & Flint 1990; Ingelmo et al. 1994) have described the effects of stones on soil temperature and moisture. In arid and semi-arid regions, soils containing rock fragments in surface horizons are more productive. That is, rock fragments decrease the ecological aridity of the area (Kadmon et al. 1989; Kosmas et al. 1994; Poesen & Lavee 1994; Van Wesemael et al. 1995).

We hypothesize that microclimatic changes associated with the presence of a gravel layer may result in large increases in soil organic matter accumulation at the soil surface. In this field study we aimed to analyze the response of how soil CO_2 efflux to the seasonal changes in soil climate under semiarid conditions, and the extent to which topsoil stony surfaces modify both soil microclimatic conditions and soil microbial activity in the mineral soil and in the organic layers.

Material and methods

Study site

This study was conducted in a 40-years-old *Pinus halepensis* Mill. stand, referred to as the Maials site, which corresponds to the drier and warmer end of a European North-South climatic transect (VAMOS-EC project). It is located in the Ebro Basin (NE Spain) (41°22′ N, 0°22′ E) at an elevation of 260 m.a.s.l., on a 26° North-facing slope. The overstorey is dominated by *Pinus halepensis* Mill. and the understorey consists mainly of the shrubs *Quercus coccifera* L. and *Pistacia lentiscus* L. The soil developed from a calcarenite and marl colluvium is 70 cm-deep, fine-textured, with a pH (H_2O) of 8.4 and 40% of carbonates. Organic carbon concentration in the 0–3 cm is 49 g kg^{-1} and total nitrogen is 3 g kg^{-1}. According to the FAO-UNESCO (1988) classification, the soil is a Calcaric Regosol. Rock fragments are usually found throughout the soil profile and are most abundant at, or near, the soil surface. Humus forms range from Vermimull to Leptomoder (according to the classification proposed in Green et al. 1993). Interannual variation in needle litterfall (kg ha^{-1} ± S.E. among litter traps, n = 8) is high and ranged from 1323±122 in 1994–1995 to 2187±234 in 1995–1996. The main needle litterfall (90%) takes place in summer with a maximum during July.

In the study area the mean annual precipitation is 388 mm (39 year average) and the mean annual temperature is 15.2 °C (29 year average). The mean annual potential evapotranspiration (PET) calculated by using the Thornthwaite approach (Palmer & Harens 1958) is 829 mm. The arid period (Bagnouls & Gaussen 1954) extends from June to October. According to the Köppen classification the Mediterranean climate is wet temperate with hot and dry summer (*Csa*).

Experimental design

To study the effects of surface stoniness on soil CO_2 efflux, we measured soil respiration in 24 reconstructed soil profiles distributed in 12 plots within the site. Each plot consisted of two cylinders with (G+) and without (G−) a gravel layer between the H horizon and the mineral soil. In each cylinder we measured soil CO_2 efflux from fresh organic matter (^{14}C-labeled wheat straw incubated in the H horizon) and from native SOM. To analyze the seasonality of soil CO_2 efflux we took measurements on 23 occasions over 520 days. To relate soil CO_2 efflux from repacked cylinders to that from the unaltered soil profile (thereafter reference-site), we measured soil respiration in 8 randomly distributed unaltered plots within the same site.

Soil preparation and cylinder repacking

Mineral (A1) and organic (L, F and H) soil horizons samples were air-dried and passed through a 2 mm mesh sieve. The mineral soil (A1 horizon) was divided into two subhorizons; A1, corresponding to the first 5 cm of mineral soil, and A2, from 5 to 25 cm depth. This experiment is part of a broader multifactorial study on the effects of soil fauna on C dynamics (Romanyà et al. 1999). For this reason, all soils were defaunated at the begining of the experiment by remoistening the air dried samples and by two subsequent deep freezing and thawing episodes (Hutha et al. 1991). Gravel of 2–4 cm in diameter was taken from a limestone quarry (bulk density 0.55 Mg m^{-3}; particle density 2.71 Mg m^{-3}). All horizons were thoroughly homogenized and used to reconstruct the soil profile in polyvinyl chloride (PVC) cylinders of 12 cm diameter and 25 cm depth. All cylinders were maintained as plant-free by carefully pulling out all germinating seeds.

Each soil horizon was repacked in the cylinders so that each cylinder contained a sequence of L, F, H, A1 and A2 layers. In the G+ cylinders, a 5 cm layer of gravel was placed on the mineral soil (A1 horizon) such that a significant part of the H horizon was intermingled with gravel. Each layer was separated by pieces of fiberglass cloth of 0.6×1 cm mesh. To enable “in situ” respiration measurements using the alkali absorption technique a 2.8 dm^3 chamber was fitted to the upper rim of each PVC cylinder.

In each cylinder we incubated 60 g of H horizon and 1.32 g of ground ^{14}C-labeled wheat straw (%C: 41.5; specific activity: 1.10 MBq g^{-1}). Labeled C was thoroughly mixed and accounted for 2.2% of the C content of the H horizon.

Simulated rainstorms (R+ treatments)

To determine the effect on soil-CO_2 efflux of sudden changes in water potential associated with rainstorms we irrigated 6 of the 12 plots with 40 mm of distilled water by using a spray system. Irrigated plots (R+) were selected at random. This rainfall simulation (R+ treatments) was applied on two occasions in the same plots: late winter (March, 1995) and summer (July, 1995). To analyze the effect of wetting and drying a second irrigation was done in August, 27 days after the last rain simulation. In this case rainfall was simulated in all plots. CO_2 efflux measurement started one hour after irrigation.

Measurement of CO_2 efflux

After installation in the field (August, 1994), cylinders were left to settle for 3 months. Soil respiration was then measured periodically during 23 periods of 24 h each, from November 94 to February 96, by the alkali (0.25 M NaOH) absorption technique (Anderson 1982). The cylinders were sealed for 24 h using a closed chamber with an alkali trap inside and left open the rest of period. Following the recommendation of Raich and Schlesinger (1992), the ratio between the surface area of absorbent alkali was 17%of the surface of covered ground. Reference-site measurements started in mid-winter (February, 1995). In this case, the closed chambers were inserted directly on the soil. Total C-CO_2 was determined by titration using 0.5 M HCl and phenolphthalein as an indicator. The precision of titration was equivalent to 0.55 mg C m^{-2} h^{-1}. We measured ^{14}C release from cylinders by scintillation counting. Prior to incubations we also measured straw ^{14}C enrichment by scintillation counting. Then we calculated the efflux of labelled-C that will be refered in the text as ^{14}C efflux. To correct for the absorption of atmospheric CO_2 at each sampling, we incubated 8 blanks (i.e. closed chambers with alkali traps which were not exposed to soil) in the site.

Monitoring of meteorological and soil climatic data

Daily meteorological data were obtained from the nearby station of Seròs (Spanish National Meteorological Service). On each day of measurement of soil CO_2 efflux, six samples of H and A1 (0–10 cm) were randomly collected at the site to determine gravimetric soil water content. Soil water potential (Ψ) and temperature were measured with screen shield Wescor psychrometric thermocouple hygrometers (PST-55-15-SF). Fourteen psychrometric probes were installed in the lower part of the H and A1 horizons in 7 PVC cylinders with the same characteristics as those used for the incubations. Four of these cylinders contained a gravel (G+) layer and three did not (G−). To avoid interference between site heterogeneity and the effects of gravel on soil water potential, we alternated G− cylinders with G+ in one plot.

Psychrometer probes were installed horizontally to minimize diurnal variations in microvolt output (Merrill & Rawlins 1972). In each cylinder a hole was drilled in the H horizon (3 cm depth) and A1 horizon (8 cm in G− and 11 cm in G+) and an 8 mm diameter steel rod was driven 60 mm into the tubes. Psychrometer probes were then inserted into the cavities thus formed and at least 50 cm of cable was covered by soil to maintain the depth of the probe. Soil water potential and temperature were monitored using a datalogger (CR7 Datalogger Campbell Scientific, Inc., Logan) installed in the study area. Because temperature gradients are a major source of error in water potential measurements by thermocouples (Rawlins & Campbell 1986), data were collected daily at 6 a.m. and 6 p.m. when soil temperature is expected to be more stable. Field measurements with a microvoltmeter were converted to water potential values using the psychrometer-specific linear regressions between microvolts and water potential provided by Wescor with each thermocouple (Briscoe 1986). Before installing thermocouple probes in the field, each probe was tested by immersing it in a solution of NaCl (0.5 M). Afterwards, each probe was rinsed with distilled water and air-dried. Psychrometers in the H horizon were exposed to steep temperature gradients. Such gradients make readings meaningless (Rundell & Jarrell 1989). In addition when soil water potential was out of the below range of measurement ($\psi < -6$ MPa), datalogger recorded values close to zero despite that the soil was clearly dry. These data were thus eliminated from the data set.

Statistical analyses

Coinciding with soil CO_2 efflux measuring dates, soil temperature was recorded on an hourly basis. Average, maximum and minimum annual temperature were obtained from this database. We tested for differences in soil temperature with a two-way ANOVA with interactions with depth (soil horizon) and gravels as fixed factors. To test for differences in total and labeled soil CO_2 efflux between G+ and G− cylinders we used a paired *t* test for each plot and sampling date. We used a stepwise multiple regression to select the microclimatic variables that best explained the variation in total soil CO_2 and ^{14}C efflux. For this purpose, we used the means of microclimatic variables (organic or mineral horizon temperature, organic or mineral horizon ψ) for each day of soil CO_2 efflux measurements. The significance level for the introduction or removal of variables in the model was 0.05 and 0.1, respectively. To achieve homogeneity of variance and avoid residual correlation ^{14}C data were transformed using a log natural function. Cumulative soil CO_2 efflux was calculated for each cylinder by integrating the 23 measurements over time. Except for the rainfall simulation days, the periods of time between measurements were assigned the value of the previous measurement for the first half of the period and the latter for the second half. The mean annual efflux was calculated from cumulative values. All statistical analyses were performed by using SPSS 6.0.

Results

Soil microclimate

The mean annual soil temperature was 15.5 °C in the H horizon and 15.2 °C in the A1 horizon. The lowest temperature recorded was −1.4 °C in the H, and 0.6 °C in the A1 horizon. The highest temperatures were 38.7 °C and 31.2 °C in the same horizons. The gravimetric soil moisture ranged from 3% (dry weight) in both horizons to 91% in the H and 33% in the A1 horizon (Figure 1(a)). During the rainy season (autumn-1994), soil moisture increased from 5% to 91% in the H horizon and from 4% to 33% in the A1 horizon. In the dry season, the water content of the H and A1 horizons was 4% and 3% respectively. The gravimetric moisture content of soils from the site showed an exponential relationship with Ψ in the cylinders on days of CO_2 efflux measurements ($r^2 = 0.36$, $p < 0.02$ for H horizon; $r^2 = 0.52$, $p < 0.003$ for A1 horizon). In autumn, after the first rainfall, Ψ in A1 ranged between −1.5 MPa and −3 MPa. In winter, Ψ increased slowly whereas in spring all soils started to dry. In summer there was a long period in which soil Ψ was below the limit of detection of the psychrometers (−6 MPa). The Ψ in the H horizon showed a highly irregular pattern with several breaks in continuity.

Effects of surface stoniness and rainstorms on soil temperature and water potential

In winter both the H and A1 horizons in the G+ cylinders showed the highest minimum temperatures, whilst in summer these horizons showed the lowest maximum temperatures. The daily maximum ranges were recorded in summer. In the H horizon they were 13.2 °C in the G+ cylinders and 14.9 °C in G−. In the A1 horizon they were 5.9 °C for G+ and 7.2 °C for G− (Table 1). In autumn 1994, after successive rainfall events (241 mm), and in summer 1995, after rainfall simulations (40 mm), Ψ in the A1 horizon was higher in G+ than in G− cylinders (Figure 1(c)). When rainfall events were less intense and infrequent (autumn-95), increases in soil Ψ were not affected by gravels. In summer and spring, when the soil had begun to dry, Ψ rapidly decreased and the mineral soil below the gravel layer remained wetter than the soil in the G− cylinders for some weeks. The effect of the gravel layer on the H horizon Ψ was less evident (Figure 1(b)), perhaps as a result of the high variability in the measurements of Ψ in this horizon. Only in autumn 1994 the Ψ in the H horizon was higher in the G+ treatments.

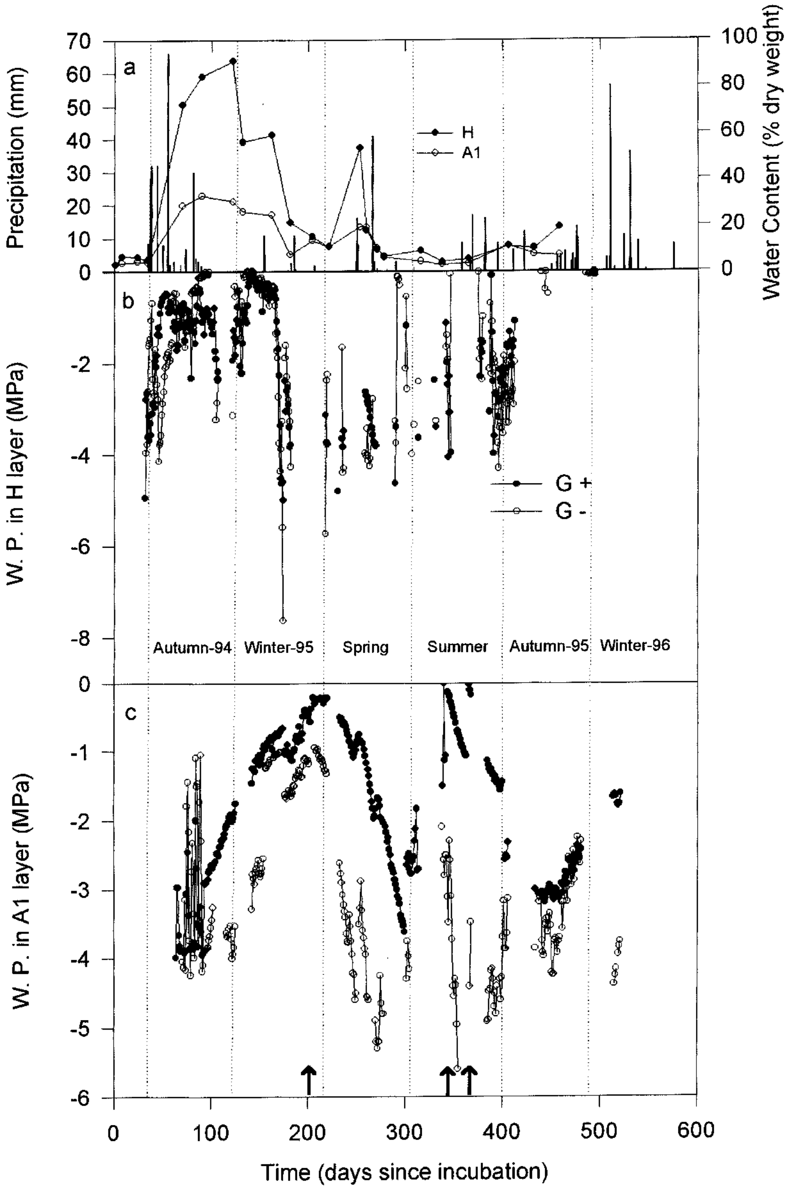

Figure 1. Precipitation and water content of the organic and mineral soil in an Aleppo pine forest (a). Water potential (MPa) in the organic (b) and mineral (c) horizons (0–10 cm) from cylinders with gravel (G+) and without gravel (G−) during the experimental period (from August-94 to February 1996). Arrows indicate simulated rainstorms (40 mm).

Table 1. Mean, maximum and minimum soil temperatures in organic (H) and mineral (A1) horizons in cylinders with (G+) and without (G−) the gravel layer. The data correspond to the days of measurement of CO_2 efflux. Error of the mean in brackets (n = 4 for G+ and n = 3 for G−). Significant differences from an two-factor ANOVA are indicated by: (*) $p < 0.05$, (**) $p < 0.01$, (***) $p < 0.001$ and (n.s.) $p > 0.05$.

	Organic layer (H)		Mineral layer (A1)		Significance factor	
	G+	G−	G+	G−	Horizons	Gravel
Mean	13.11 (0.10)	13.14 (0.03)	12.86 (0.06)	12.83 (0.04)	**	n.s.
Maximum	35.04 (1.52)	37.14 (0.22)	27.22 (0.26)	29.07 (0.09)	***	*
Minimum	−0.52 (0.40)	−1.44 (0.31)	2.90 (0.15)	1.54 (0.13)	***	**

Total and labeled soil CO_2 efflux

Soil CO_2 efflux took place mainly in autumn of 1994 and in summer, while in winter and autumn 1995 CO_2 release was very low (Figure 2(a)). During arid months (from June to October), the mean soil CO_2 efflux (mg C-CO_2 m^{-2} h^{-1} $\pm$ S.E.) was 44.6$\pm$6.0 while for the rest of the year it was 35.5$\pm$3.3. Higher values were observed in early summer (60–70 mg C-CO_2 m^{-2} h^{-1}). The highest measured value (112 mg C-CO_2 m^{-2} h^{-1}) followed the mid summer rainfall simulation (day 338). The total soil CO_2 efflux from the cylinders and site-reference measurements were similar in magnitude and well correlated (r = 0.84, $p < 0.001$; Figure 2(a)). Towards the end of summer, despite the high temperature there was a decrease in CO_2 efflux from the site-reference. Efflux from the cylinders did not show a similar decrease because they were exposed to rainfall simulation during that period.

^{14}C release steadily decreased during the incubation, following a negative exponential function (Figure 2(b)). An exponential regression between ^{14}C efflux in the R− cylinders and time of incubation explained 27% of the variability (Table 2). From late winter (after day 177) to summer, we observed several increases in ^{14}C efflux that separated from the negative exponential model and coincided with increases in soil temperature, and with natural and simulated rainfall events.

The analysis of single cylinder data showed that during most of the period of study, ^{14}C release did not correlate with total CO_2 efflux. However, on a few occasions these two parameters showed significant correlations (Figure 2(c)). In winter, ^{14}C release was not related to soil CO_2 efflux, irrespective of rainfall or irrigation events. In summer and sometimes in spring, when the uppermost horizons were dry, no relationship was observed between total CO_2 efflux and the release of ^{14}C incubated in the H horizon. A significant

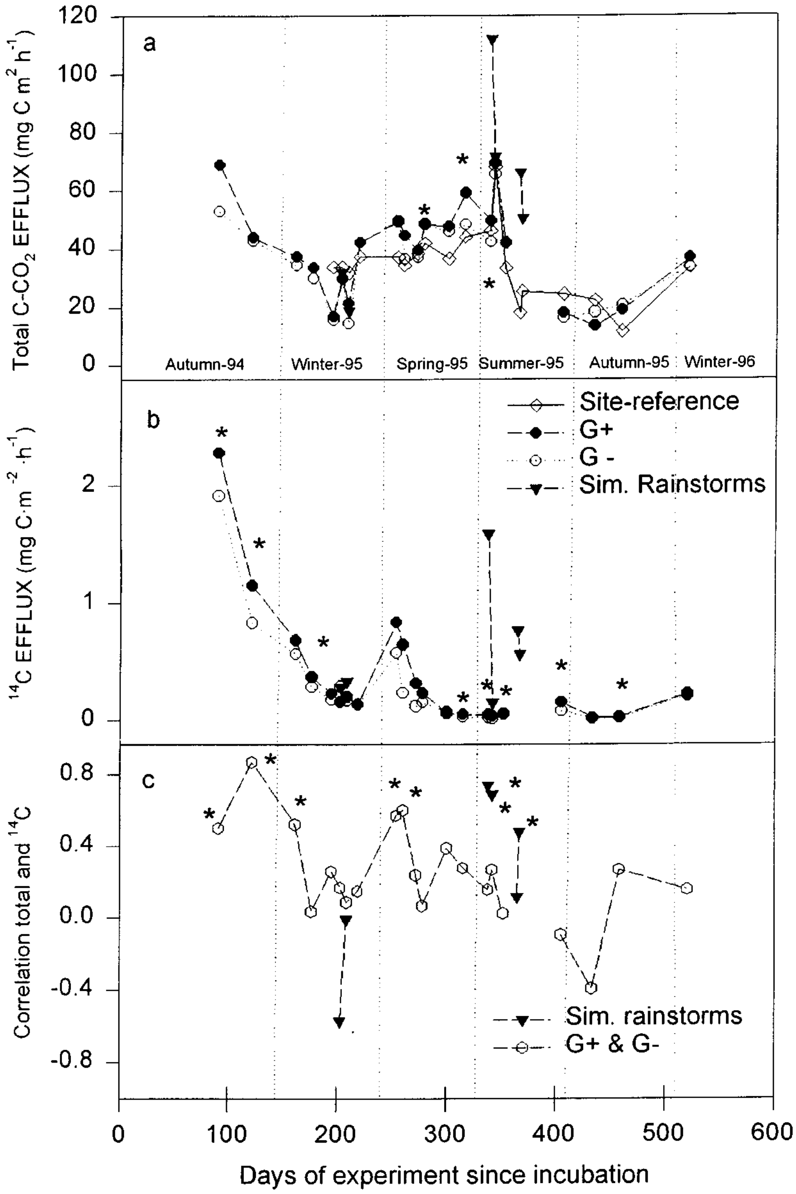

Figure 2. Yearly patterns of CO_2 efflux from a Mediterranean Aleppo pine forest soil as affected by a gravel layer and by simulated rainstorms. (a) Seasonal variations in total CO_2 efflux. (b) Seasonal variations in labeled CO_2 efflux. (c) Correlation between ^{14}C and total-C efflux. The effects of rainfall simulation are only plotted when significantly different from control plots. During rainfall simulation we did not observe any effect of gravel, so simulated rainstorms refer to the mean of the G+ and G− treatments. $*$ in (a) and (b) refers to significant differences between G+ and G− cylinders ($p < 0.05$, $n = 12$). $*$ in (c) refers to significant correlation coeficient ($p < 0.05$, $n = 24$ for each data of measurement except for data of rainstorms simulation where $n = 12$).

Table 2. Relationship between soil microclimatic parameters, time of incubation and total and labeled soil CO_2 efflux (n = 27). Significant correlations are indicated by: (*) $p < 0.05$, (**) $p < 0.01$, (***) $p < 0.001$.

		Temperature		Water potential		Time
		H	A1	H	A1	
Total-C	G+	0.66***	0.65***	0.31	−0.31	0.00
	G−	0.67***	0.66***	0.29	−0.36	0.04
ln (^{14}C)	G+	−0.31	−0.30	0.36	0.46**	−0.54**
	G−	−0.38*	−0.37*	0.26	0.29	−0.56**

relationship between these two parameters was observed only in spring after rainfall events and in summer only in R+ cylinders, coinciding with high temperatures and high water potential in the H horizon. In order to explore the effects of the availability of water on soil CO_2 efflux, measurements from all cylinders were split into two groups as a function of Ψ in the H layer (Figure 3). When the Ψ of the H layer was higher than -3 MPa, the correlation between ^{14}C and total CO_2 efflux accounted for 51% of the variance in the G+ and G− cylinders. When the Ψ in the H layer was lower than -3 MPa, correlation was not significant.

Relationship between CO_2 efflux and microclimate

The total soil CO_2 efflux was positively correlated with temperature in the H and A1 horizons and not with soil Ψ (Table 2). The ^{14}C efflux was positively correlated with Ψ and negatively correlated with soil temperature. During the first 177 days of incubation (autumn 1994), both total and labeled CO_2 efflux were high, probably as a result of the effects of repacking the cylinders and the rapid decomposition of fresh ^{14}C. Thus, in order to determine the separate effects of soil climate on soil CO_2 efflux, stepwise multiple regressions between soil CO_2 efflux (total and ^{14}C) and the microclimatic parameters were carried out only with the measurements taken after day 177. Seasonal variation in total soil CO_2 efflux was primarily related to soil temperature and secondly to Ψ (Table 3). In contrast, ^{14}C release was related to Ψ or to its combined effect with soil temperature.

Effects of rainstorm simulation and surface stoniness

The increases in ^{14}C release resulting from summer rainstorm simulations were proportionally larger than increases in total soil CO_2 efflux (Figure 4).

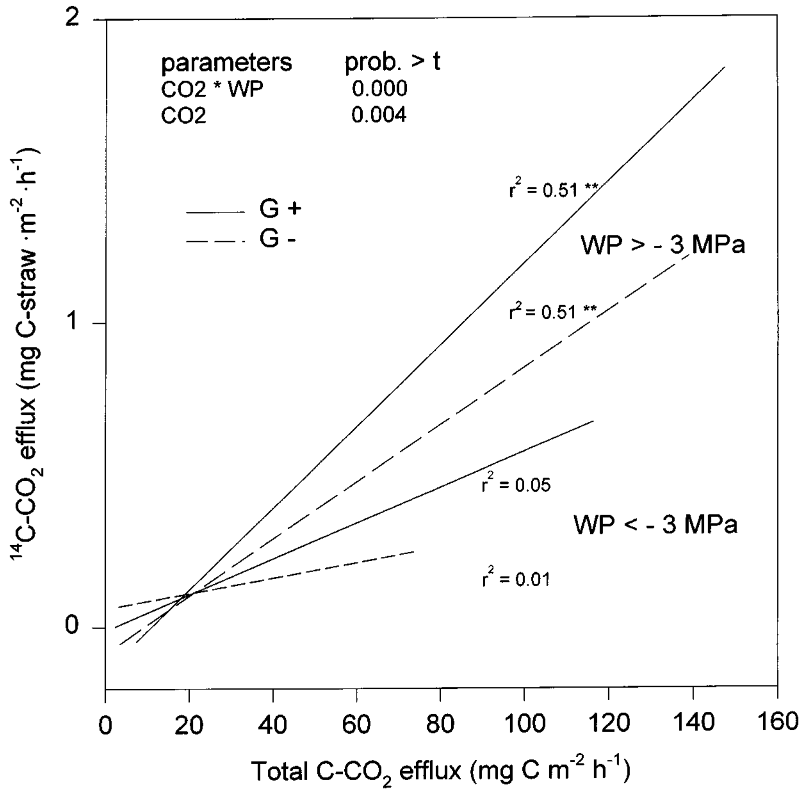

Figure 3. Regression between ^{14}C and total C-CO_2 efflux as calculated for all cylinders and measurement dates, grouped by presence (G+) or absence (G−) of the gravel layer, and by two ranges of H-horizon water potential (Ψ). Model adjustment and the level of significance of parameter estimates are indicated.

Table 3. Best fitting equations ($Y = ax_1 + bx_2 + c$) obtained by stepwise multiple regressions between total and labeled CO_2 efflux and soil temperature, water potential and their interaction ($p < 0.05$; $n = 25$). Standard error of each parameter is shown in parenthesis. The statistical significance of parameters and adjusted coefficient of regression (r^2a) are indicated by: (∗) $p < 0.05$, (**) $p < 0.01$, (***) $p < 0.001$, (n.s.) $p > 0.05$. H and A indicate the organic and mineral layer, respectively. T indicates temperature and ψ water potential.

Gravel layer	Dependent variable (Y)	Coefficients of regression and independent variables			r^2 a
		ax_1	bx_2	c	
G+	Total-C	2.49 (0.39)·HT***	5.82 (2.15)·Aψ*	16.00 (5.00)**	0.66**
G−	Total-C	1.59 (0.31)·HT***		15.78 (5.25)**	0.54**
G+	ln (^{14}C)	0.76 (0.14)·Aψ***	0.07 (0.03)·AT*	−1.52 (0.36)***	0.55**
G−	ln (^{14}C)	0.01 (0.01)HT·Hψ***		−1.47 (0.38)***	0.13*

In summer, simulated rainstorms increased soil CO_2 efflux by a factor of 2.3 while ^{14}C efflux increased by a factor of 36 (Figure 2). The magnitude of these effects decreased rapidly, but the effects lasted more than five days and less than fourteen days. The second rainstorm simulation was carried out in all cylinders twenty-seven days later. Compared to the site-reference respiration, the magnitude of the response to rainfall was similar to the response of the first summer irrigation. However, the absolute values of respiration were lower for both total CO_2 efflux and for ^{14}C release. No significant differences were found between the cylinders that were irrigated 27 days earlier and those that were not. The only effect of rainfall simulation in winter was the increase in ^{14}C efflux by a factor of 1.4. After rainfall simulation, Ψ in the A1 horizon in the G− treatment remained lower than in the G+ treatment. In spite of this, no significant differences in total soil CO_2 efflux were observed between the G+ and G− cylinders. The presence of the gravel layer increased both total soil CO_2 and ^{14}C efflux (Figure 2). This effect was larger during spring and summer, diminished during wet periods, and disappeared following rainfall simulations. The consistent effect of the gravel layer during the study period resulted in a higher cumulative total and ^{14}C efflux in the G+ treatment ($p <$ 0.01). In the no rainstorm simulation treatment (R−), the cumulative efflux of ^{14}C and total-CO_2 in the G+ cylinders was 34% and 10% higher than in the G− cylinders. The mean annual soil CO_2 efflux (mg C-CO_2 m^{-2} h^{-1} $\pm$ SE among plots) was 43.1$\pm$4 and 38.7$\pm$3 in the G+ and G− cylinders in the R− treatment. Two summer and one winter rainstorm simulations caused an increase in mean annual total-CO_2 efflux of 6% in the G+ and 10% in the G− treatment, and an increase in ^{14}C efflux of 20% and 17% for the G+ and G− treatment respectively. For the reference-site, the mean annual soil CO_2 efflux (22.4$\pm$0.8) was lower than in the cylinders.

Discussion

The seasonal pattern of total soil CO_2 efflux showed two peaks and two depressions. Despite the summer drought, the highest CO_2 efflux was observed in July. The lowest CO_2 efflux was observed in winter. High respiration rates in summer and low rates in winter have been reported by other authors in Mediterranean and temperate dry ecosystems (Lossaint 1973; Fouseki & Margaris 1981; Piñol et al. 1995). Multiple regression analysis of our soil respiration data indicates that even in semiarid conditions soil temperature has a greater effect on total soil CO_2 efflux than soil moisture. Except for summer drying and rewetting cycles, the changes in soil CO_2 efflux associated with Ψ were smaller than those associated with changes in temperature. Low respiration rates were observed in winter despite a high Ψ.

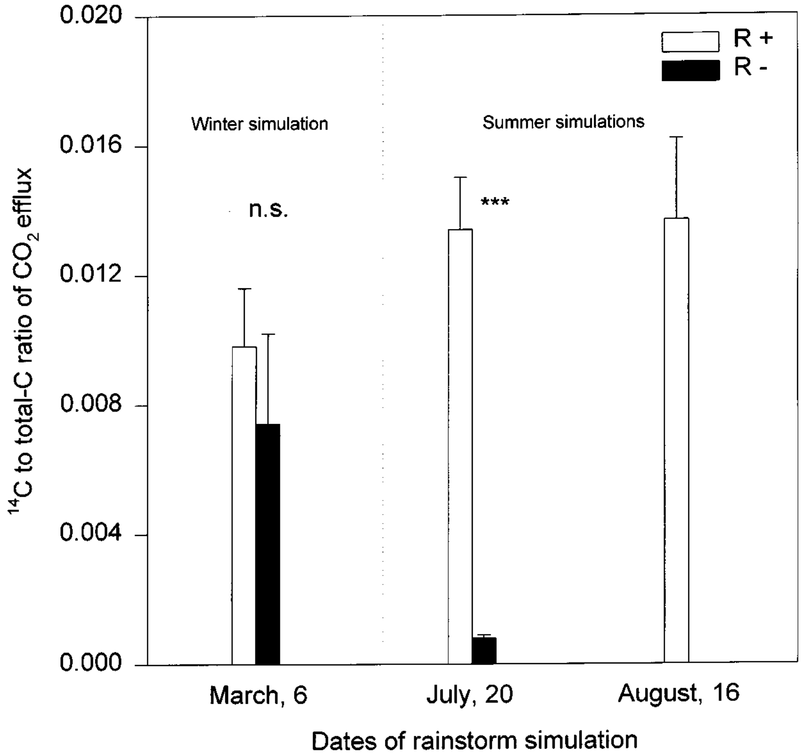

Figure 4. Ratio of ^{14}C to total-C efflux as measured after rainstorm simulations from irrigated (R+) and no irrigated (R−) cylinders. In August 16, all cylinders were irrigated so only R+ are shown. The standard error and significant differences between R+ and R− (*** $p < 0.001$, $n = 6$) are indicated.

This and the lack of response of soil CO_2 efflux to winter rainfall simulation indicates that winter soil respiration was temperature limited. Small increases in ^{14}C efflux that were also recorded after winter rainfall simulation suggest that, in winter, microbial activity in the H horizon had a low capacity of response to increased water availability.

High soil microbial respiration rates occur when Ψ is between −0.01 and −1 MPa (Glinski & Stepniewski 1985). However, the activity of soil bacteria and fungi can be detected down to a lower limit of −8 MPa for bacteria and −10 MPa for fungi (Smith & Paul 1990). In our semiarid site the uppermost soil horizons remained well below −6 MPa for long periods of time. In spring, after a period of frequent rainfall (72 mm), the increase in water content in the H and A1 horizons was followed by increases in total and labeled CO_2 release, especially in G+ cylinders. This onset of spring rainfall occurred when the mean temperature in the H horizon was about 10^0C. The response to spring rainfall suggests that despite the cool temperature, soil biological activity was limited by the availability of water. Indeed, the low labeled CO_2 efflux that occurred in late spring and during most of the summer coincided with periods of low soil Ψ (< -3 MPa) and high temperatures. Large increases in ^{14}C release after rewetting the soil in summer also indicate water limitation in the H horizon. Although soil Ψ also had a significant effect on total CO_2 efflux in the G− treatment, Ψ was especially relevant for predicting ^{14}C efflux. Because labeled material was incubated in the H horizon, changes in soil moisture that occur under semiarid conditions in the organic layers have a significant role in determining its biological activity.

It has been shown that the soil above a gravel layer retains more water than uniform soil when water is initially applied (Miller & Bunger 1963; Unger 1971). It has also been reported that a high content of rock fragments facilitates the penetration of the wetting front in the soil profile (Van Wesemael et al. 1995) and reduces evaporation losses as a result of its low unsaturated hydraulic conductivity (Poesen & Lavee 1994). In our experiment, despite the variability in data collected by the psychrometers in the H horizon, the day to day Ψ of the H horizon in G− treatment was lower than in G+. The mineral soil in the G+ treatments remained wetter for a longer time. The increased respiration rate in the G+ treatment affected both total CO_2 and ^{14}C efflux. Thus, it seems reasonable to suggest that the consistently lower soil efflux in G− was due to lower water availability in this treatment. Although the seasonal pattern of soil CO_2 efflux was mainly related to changes in soil temperature, increases in water availability promoted by the gravel resulted in an increase in the mean annual respiration rate of about 10%. This effect was even greater for ^{14}C (34%). Therefore, our results indicate that a stony topsoil enhances organic matter decomposition in the horizons adjacent to the gravel layer, and suggest that other processes may be responsible for this accumulation. For instance, the transfer of particulate soil organic matter could be reduced if rock fragments hampered litter comminution and transport meditated by soil fauna. High forest floor accumulation could also reflect and increase in litterfall input resulting from improved water availability in soils with a stone pavement.

Since summer rainstorms only reached the uppermost horizons in our semiarid site, sharp increases in soil respiration resulting from rainstorm simulations were especially large for ^{14}C. Under these conditions, the pulse of soil respiration after rewetting could be mainly attributable to changes in organic matter that take place in the uppermost horizons (H and A1) during dry periods in summer. During drying, organic matter from dead soil microorganisms and nonbiomass substrates is released and concentrated in the soil (Schaefer 1973; Bottner 1985; Kieft et al. 1987). Gallardo and Schlesinger

(1995) found that the maximum values for microbial biomass occurred 2 to 3 days after watering in desert soils. Thus, it appears that the flush of soil respiration recorded during the 24 h after rewetting the soil may be due to a persistent pool of enzymes capable of tolerating extended periods of desiccation (Gallardo & Schlesinger 1995; Moorhead et al. 1996). The large effects on ^{14}C release highlights the relevance of rewetting in Mediterranean soils which are frequently and severely dried. Despite low absolute values, the contribution of ^{14}C to total CO_2 during the winter rainstorm simulation was of the same order of magnitude as in the summer simulation. The lack of differences between R+ and R− cylinders in winter further suggests that the biological activity in the organic layers was limited by temperature in winter and by Ψ in summer.

The high soil CO_2 efflux that occurred from spring to mid summer coincided with a decrease in soil water potential. This high CO_2 efflux could result from an increase in soil biological activity associated with the temperature rise in spring. Other processes such as the release of CO_2 from the carbon-carbonate equilibrium in soil solution when the soil is dried or the increase in the CO_2 diffusion coefficient in dry soil could also contribute to summer soil CO_2 release. Given that the solubility of $CaCO_3$ at 20 °C is 0.014 g L^{-1} and the bulk density of soil is 1 Mg m^{-3}, with a gravimetric moisture content of 20% the amount of CO_2 added or removed by the mineral dissolution-precipitation processes that take place in the first 25 cm of soil cannot be greater than 1 g m^{-2}. The order of magnitude of this process is well below the measured values. Since CO_2 diffusion in the gas phase is dominant within almost the entire range of water contents (Simunek & Suarez 1993), changes in the gas diffusion coefficient could transiently double the transport of CO_2 through the soil profile. However, a few days after the D_s increases, CO_2 efflux stabilizes and is only dependent on CO_2 production (Piñol et al. 1995). Thus, it appears that the CO_2 efflux increase resulted mainly from biological CO_2 production.

Assuming that the ^{14}C remaining after 177 days of incubation was well incorporated in the H horizon, the ratio between ^{14}C and total CO_2 efflux can be considered an estimate of organic layer decomposition activity relative to total soil biological activity (Figure 5). In winter, when the temperature of the H layer was low and water availability was high, CO_2 release from this horizon made a significant contribution to total CO_2 efflux. However, this contribution to total annual release was low since total CO_2 efflux in winter was also low. When temperature increased, the contribution of the respiration of the H horizon to total CO_2 release showed two different patterns depending on its water potential. When the H horizon was dry (<-3 MPa) it did not significantly contribute to total CO_2 efflux, whereas when water availability

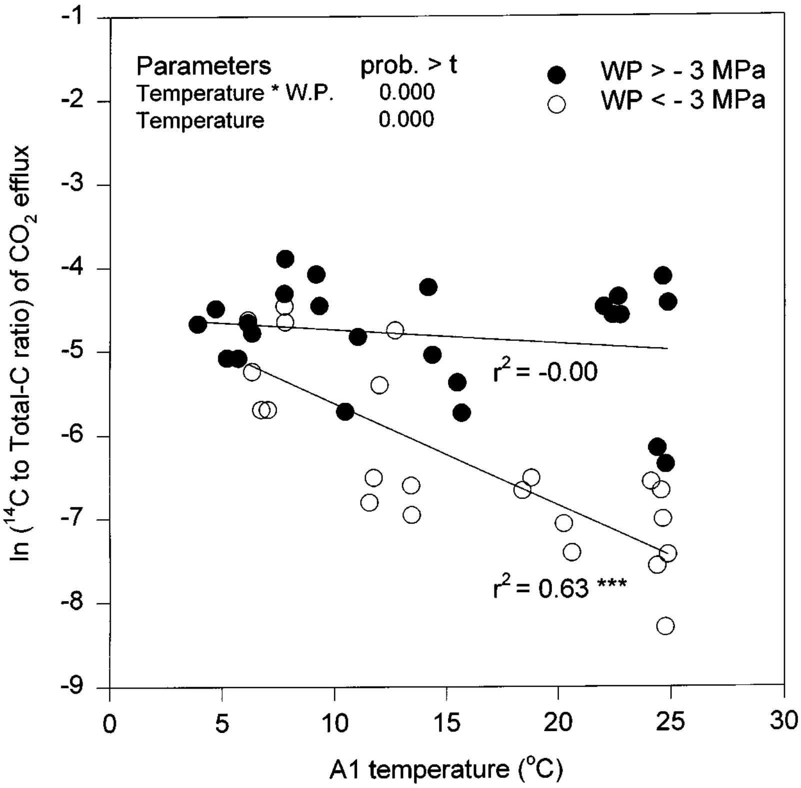

Figure 5. Regression between log natural ^{14}C to total CO_2 efflux ratio versus mineral soil temperature grouped by two ranges of H-horizon water potential (Ψ). Model adjustment and the level of significance (** $p < 0.01$) of regression parameter estimates are indicated.

was high, ^{14}C release made a significant contribution to total CO_2 efflux. Therefore, decomposition in organic layers and upper mineral soil mainly takes place during wet episodes. Furthermore, the gravel layer improved the Ψ conditions of the organic layer for decomposition mainly in hot periods.

As discussed above, high total CO_2 efflux under dry conditions may partly be due to increased soil biological activity. Because respiration in surface soil is depressed in dry conditions, increased soil CO_2 efflux in summer may arise from decomposition in deep horizons and from root respiration. Roots are better able to maintain turgor than shoots under dry conditions and therefore gradually become the preferred sink for soluble carbohydrates of plants (Huck & Hillel 1983). As the canopy begins to experience water stress at lower soil water contents, the fraction of soluble carbohydrates allocated to root growth increases, resulting in higher root respiration. In a Mediterranean evergreen forest, Piñol et al. (1995) found that during late spring-early summer, and in late summer soil pCO_2 was highest at the maximum measured depth (80 cm). A model simulation based on the gas diffusion theory explained this fact by assuming homogeneous CO_2 production throughout the soil profile. This vertical distribution of CO_2 production is explained by a possible displacement of root activity to deeper horizons during dry periods (Piñol et al. 1995). The small differences found between our cylinders, where living roots were excluded, and site-reference data suggest that root respiration in the first 25cm of soil had a less significant contribution to total CO_2 efflux. In addition, these differences were highly variable and depended on the time of the year. Therefore it is suggested that the contribution of root respiration in the first 25 cm of soil to total CO_2 efflux was also very variable throughout the year.

The CO_2 efflux increased continuously from spring to mid summer, where the maxima values were obtained. Despite the continued high temperatures, this was followed a strong decrease in total CO2 efflux from the reference site in late summer. This pattern has been observed by other authors in Mediterranean and arid soils (Lossaint 1973; Fouseki & Margaris 1981; Fließbach et al. 1994; Piñol et al. 1995). In spite of low late summer values of soil CO_2 efflux, the response to rewetting the uppermost horizons was as large as the response to rewetting the soil in mid summer when the soil CO_2 efflux was high. Given that increases in soil respiration associated with rewetting originate form the uppermost soil horizons, the late summer reduction in total CO_2 efflux may be attributed to depressed soil biological activity in deep horizons. In dry periods, high respiration before a steep depression could be an early indicator of stress. Under these conditions energy would divert from growth to maintenance (Odum 1985).

Conclusions

Seasonal variations in soil CO_2 efflux in a semiarid Mediterranean forest were mainly related to changes in soil temperature. In spite of drought, high respiration rates were observed in mid summer. Most of the CO_2 apparently originates from deep soil horizons, and thus, a decrease in CO_2 efflux resulting from drought may only be evident under extreme conditions. In contrast, the forest floor is subjected to rapid microclimatic changes which result in temperature limitations in CO_2 efflux in winter, and moisture limitations in summer. Rewetting a dry soil resulted in large increases in soil CO_2 efflux only at high temperatures. The amount of organic matter decomposed in the uppermost horizons may be highly dependent on the occurrence of a few summer rainstorms.

The high forest floor accumulation observed in stony soils could not be explained by our experiments. We have demonstrated that microclimatic conditions both above and below a layer of gravel may enhance organic matter decomposition. Thus, other fluxes of forest floor carbon may be negatively affected by gravel.

Acknowledgements

The authors are indebted to the European Community (VAMOS, Environment and Climate Research Program; Global Changes, DG XII, project number EV5CVT92-0141) and to the Spanish government (CICYT, AMB-1504/94-CO2-CE) for funding this project. Furthermore, the authors are grateful to P. Rovira and M.C. Roca for their assistance in the field work, and to J. Piñol, J. Fons and two anonymous reviewers for constructive comments on the manuscript.

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