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ORIGINAL PAPER

Soil organic carbon storage in mountain grasslands of the Pyrenees: effects of climate and topography

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Abstract The prediction of soil C stocks across the landscape has been increasingly studied in many areas of the world. Soil organic C storage in mountain areas is highly heterogeneous, mainly as a result of local-scale variability in the soil environment (topography, stoniness, parent material) and microclimate. The aims of the present study are to estimate soil organic C stocks (SOCS) in mineral soils of high-altitude grasslands of the Pyrenees and determine whether climatic and topographic variables can be used as predictors of SOCS and organic C content in the surface soil horizons of these ecosystems. For that purpose we sampled 35 soil profiles in subalpine and alpine grasslands including a range of altitudes, slopes and aspects. We analysed the soils for stoniness, bulk density, total C, texture, and C-to-N ratio and determined topographical variables. We used georeferenced climatic information for climatic descriptions of the sites. SOCS were highly correlated with soil depth. However, we were not able to predict soil depth by using environmental and topographic variables. In spite of this fact, altitude and aspect explained 41.2% of the SOCS variability while summer temperature and precipitation combined with aspect explained 56.9% of the variability of the organic C content of the surface layer (OC). The SOCS were low at high altitudes, probably as a result of an overall temperature limitation of net primary productivity. Under these conditions, the effect of aspect was small. The highest SOCS occurred at the lowest altitudes for ENE or WNW aspects, showing sharper decreases

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towards the south than to the north. The harsh climatic conditions and low-plant productivity that occur at the northern slopes reduced SOCS at the highest altitudes. In contrast, southern aspects showed similar organic C content along the altitudinal gradient. The OC variability in the surface soils not explained by climatic or topographic variables was partially related to the characteristics of soil organic matter, which may depend on the plant communities.

Keywords Climate · Mountain grasslands · Pyrenees · Soil organic carbon storage · Topography

Introduction

Soil C is a large component of the global carbon cycle. At a global scale, the amount of C in soil organic matter (SOM) is similar to the C stored in the atmosphere and the aboveground biomass together (Schimel 1995), making soil the largest terrestrial C sink. In most ecosystems, carbon stored in soils is higher than in the aboveground biomass (White et al. 2000). Assessments of soil organic carbon stocks (SOCS) at regional scale provide complementary information essential for calibration, verification and application of simulation models. Small variations in soil organic C stocks (SOCS) under different scenarios may affect predictions of global C assessments and storage change evaluations. Besides CO_2 sequestration, soil organic C is essential for the correct functioning of many other ecosystem functions and processes. This shows the importance of an accurate estimation of the soil C content of the ecosystems and the factors that regulate its accumulation.

Soil C content is the result of the net balance between C inputs and outputs. These biologically regulated fluxes mainly depend on primary production and organic matter decomposition. Both production and decomposition are strongly regulated by climate and soil variables such as texture, nutrients and water availability, which in turn determine the organic matter flux into the soil, its quality and its decomposition rates. Many authors have studied the relationship between climatic variables and C pools (Hontoria et al. 1999; Rodríguez-Murillo 2001; Ganuza and Almendros 2003; Miller et al. 2004; Leifeld et al. 2005) but few of them have investigated these relationships at high altitudes. Environmental and physical variables show steep gradients and the environmental constraints to ecosystems are stronger in alpine ecosystems than in middle or low altitudes. Furthermore, in mid and low latitudes, mountain areas hold the highest potential for C storage (Jones et al. 2003). Under these conditions, and as a result of the forecasted temperature increases for southern Europe, mountain ecosystems may behave as significant sources of CO_2, thus reducing their C content. In alpine ecosystems aboveground production and root turnover decrease with altitude as the climate conditions become harsher, therefore reducing C inputs into the soil (Hitz et al. 2001). But the harsh conditions typical of mountain environments also limit C fluxes from soil to the atmosphere (Rodeghiero and Cescatti 2005). Globally, the net balance may depend on the environmental conditions specific to each site.

Mountain ecosystems are spatially very heterogeneous as a result of local-scale variability in soil environment (aspect, slope, stoniness and depth) and microclimate. These changes may affect the timing of snowmelt, soil freezing and thawing and even their water retention capacity and soil nutrient cycling (C and N) as well as other ecosystem processes (O'Lear and Seastedt 1994; Neilsen et al. 2001). Furthermore, topographic-induced changes in the soil microenvironment often lead to changes in plant communities (Sebastià 2004), which can determine organic matter quality and C cycling. In Mediterranean montane meadows, the spatial variation of soil C and N at landscape scale seems to be exclusively and intensively related to plant community composition, but indirect effects of soil moisture and climate should be taken into account (Rey Benayas et al. 2004).

Soil properties in mountain areas are highly related to their parent material, profile depth and stone content, which are limiting factors for C storage (Leifeld et al. 2005). However, climate conditions often play a prime role in regulating SOC, as has been shown in the general models of SOM accumulation (Hontoria et al. 1999; Miller et al. 2004; Rey Benayas et al. 2004). The high-spatial variability that characterizes mountain areas suggests that regional studies must include a microclimatic component that may be defined by proxy variables such as altitude, slope and aspect. However, few studies include topographic variables when trying to find the relationships between environmental conditions and soil C storage.

Studying the relationships that climatic, site physical/topographic variables and parent material have with soil C accumulation in mountain areas may be useful to predict SOCS in these ecosystems, and can also help to predict how environmental changes could affect soil C content and its accumulation (Prichard et al. 2000).

The aims of this study were to estimate SOCS in mineral soils of high-altitude grasslands in the Pyrenees and determine to what extend climatic and topographic variables are sensitive to the spatial variability of SOCS in mountain areas. In addition, we aim to understand the C variability of the topsoil layer, as this layer has the highest potential of mobilising substantial amounts of C under climate or land use changes.

Material and methods

Study area

This study was carried out in subalpine and alpine grasslands along the Pyrenean chain (Fig. 1). The 35 locations selected included a wide range of altitudes (from 1,845 to 2,900 m a.s.l.), slopes and aspects. Climate conditions were typically alpine in all sites, with cold mean annual temperatures (MAT) that ranged between –0.7 and 5°C and high-mean annual precipitation values (between 1,416 and 1,904 mm) (Table 1) well distributed throughout the year.

Granites and slates are the most extended lithologies in the Pyrenees, but in the central and western areas granite peaks are flanked by layers of limestone, which are also very abundant. Soils are usually thin and, although the presence of carbonated bedrocks in some areas, at high altitudes they have always low pH due to the high-rainfall values.

The mean monthly temperatures and precipitation values were obtained by reconstructing 30-year climate data series following the Agustí-Panareda and Thompson (2002) method. Estimations were obtained by stepwise multiple regression that established linear functions between some existing upland records and many long lowland records. The mean annual and mean summer climatic data were derived from these estimations. To estimate the site water stress, we calculated the Rainfall Index of Lang (Lang 1915) for summer season (Slang) as the ratio between the mean monthly summer (June, July and August) precipitation and the mean monthly summer temperature.

Soil sampling and analysis

At each location, a soil profile was opened until the bedrock was reached and the main topographic variables (altitude, aspect and slope) and soil depth were recorded. Then, between one and four horizons were delimited according to a previous visual description. Surface horizons were defined in the field as the layer with the highest root density. For each profile, a soil sample from each horizon was taken with a 7 cm diameter PVC core, which was also used to determine soil bulk density. All the samples were sieved in the field with a 1 cm mesh to retrieve the stones, which were weighed with a dynamometer and discarded.

In the laboratory, the fresh soil samples were sieved to 2 mm to remove gravels and roots and the obtained fine earth was oven dried at 60°C until a constant weight was reached. The samples were then ground for chemical analyses. The total C and N concentration was analysed with a Carlo Erba elemental analyser. All the samples were free of carbonates.

The percentage of sand was determined by sieving the moist samples with a 250-μm (coarse sand) and 63-μm (fine sand) mesh. The proportion of silt (63–2 μm) and clay (<2 μm) fractions was determined by the size distribution measurement with a particle counter. The weight proportion of each of these fractions was determined by estimating the volume of particles, using their diameter and assuming the mean density to be approximately the same for all size fractions.

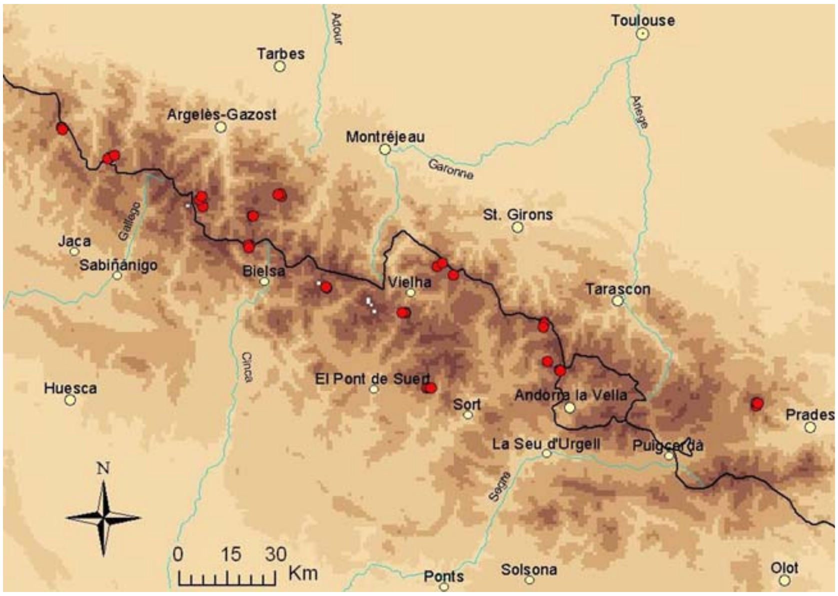

Fig. 1 Map of the study area with the sampled locations (*circles*)

Calculations and statistical analysis

Total SOCS in kg m^{-2} were calculated as the sum of the content of each horizon and taking into account OC concentration and the measured soil bulk density and stoniness of each sample as follows:

$$SOCS = \sum_{n}^{i=1} OC_i \times (BD_i - CP_i) \times th_{i,}$$

where i represents each sampled horizon of the soil profile, OC is the organic carbon concentration (%) in the fine earth (≤2 mm), BD the soil bulk density (kg m^{-3}), CP the coarse-particle content (>2 mm) (kg m^{-3}) and th_i is the thickness (m) of each horizon.

Bedrock types were grouped into four categories: detrital (sandstones and lutites), metamorphic (shales and slates), plutonic (granodiorites and other granites) and carbonated (limestones).

The aspect values were cosine transformed to obtain a continuous variable with the same value for the E and W aspects. To avoid 0 values (E and W aspects), we added 2 to this variable, thus obtaining a continuous variable that ranged between 1 (south) and 3 (north).

The effect of bedrock type and texture on SOCS and C concentration of the surface horizon (OC) was analysed by comparing C contents at the different lithologies and texture classes using one-way ANOVA and a posteriori Duncan test.

Multiple regression analyses were carried out for the total SOCS and for organic C content of the surface horizon (OC) on a range of environmental predictor variables. The C content of this layer was studied in particular because this is the layer that is most affected by the local environmental conditions. The regression analyses were performed by the backward removal procedure with interaction with an F ratio probability of 0.1 to be included in the model. At each step the variable with higher F ratio was removed. Initial regression included some continuous climatic (mean summer temperature and precipitation and summer rainfall index of Lang) and topographic (altitude, aspect and slope) variables and lithology as categorical variables indicating for each observation the presence (1) or absence (0) of a given parent material. Interactions between climatic and topographic variables were also included.

The normality of all continuous variables was previously tested by the non-parametric Kolmogorov–Smirnov test. As all the continuous variables followed a normal distribution, they were not transformed prior to statistical analysis.

The normality of model residuals were also analysed by the non-parametric Kolmogorov–

Table 1 Climate and soil characteristics of the 35 studied sites

Site	Longitude	Latitude	Altitude (m a.s.l.)	Depth (m)	MAT (°C)	ST (°C)	MAP (mm)	SP (mm)	pHw	OC (%)	SOCS (kg m^{-2})	C-to-N	Texture class (USDA)	Lithology
Acherito 1	0°42′26″W	42°53′09″N	1,980	0.26	4.2	11.6	1,544	297	4.3	8.7	15.72	10.82	Silt loam	Detrital
Acherito 2	0°42′20″W	42°53′00″N	1,900	0.25	4.6	12.0	1,544	297	4.4	8.0	12.34	10.58	Silt loam	Detrital
Acherito 3	0°42′09″W	42°52′52″N	1,910	0.24	4.6	12.0	1,544	297	4.3	11.1	19.10	10.45	Silt loam	Detrital
Bersau 1	0°29′31″W	42°50′25″N	2,090	0.36	3.7	11.3	1,597	316	4.6	3.8	15.46	10.64	Loam	Detrital
Bersau 2	0°29′52″W	42°50′14″N	2,200	0.33	3.1	10.8	1,597	316	4.7	4.4	15.19	11.26	Sandy loam	Detrital
Roumassot	0°28′39″W	42°51′04″N	1,845	0.32	5.0	12.7	1,485	294	5.2	16.5	19.48	13.25	Silt loam	Carbonated
Glacé	0°05′24″W	42°46′50″N	2,750	0.13	0.2	8.2	1,779	372	4.8	9.7	11.78	12.64	Silt loam	Metamorphic
Estom 1	0°06′34″W	42°47′46″N	2,200	0.26	3.3	12.7	1,416	297	4.8	9.1	-	12.63	Loam	Plutonic
Estom 2	0°06′12″W	42°48′26″N	1,900	0.34	4.8	11.2	1,416	297	5.0	12.1	19.69	12.88	Silt loam	Plutonic
Port Bielh 1	0°11′58″E	42°52′16″N	2,390	0.41	2.0	9.9	1,650	360	4.5	5.9	10.65	11.87	Loam	Plutonic
Port Bielh 2	0°11′37″E	42°52′33″N	2,340	0.28	2.2	10.2	1,650	360	4.6	7.5	13.76	11.92	Loam	Plutonic
Port Bielh 3	0°11′08″E	42°52′26″N	2,290	0.30	2.5	10.4	1,650	360	5.1	7.7	12.57	14.94	Loam	Plutonic
Gourg Cap de Long	0°06′37″E	42°57′34″N	2,900	0.20	–0.7	7.2	1,904	409	5.4	7.3	9.54	12.83	Sandy loam	Metamorphic
La Múnia superior 1	0°07′39″E	42°42′34″N	2,650	0.47	0.8	8.8	1,727	375	4.9	5.4	13.48	11.61	Loam	Metamorphic
La Múnia superior 2	0°07′22″E	42°42′28″N	2,560	0.78	1.2	9.3	1,727	375	5.5	2.1	14.34	8.90	Loam	Carbonated
La Múnia inferior	0°07′33″E	42°42′04″N	2,470	0.20	1.7	9.7	1,727	375	5.4	4.3	5.91	12.38	Loam	Carbonated
Eriste 1	0°27′47″E	42°39′48″N	2,450	0.35	1.7	9.9	1,638	389	4.9	8.7	15.20	12.88	Silt loam	Plutonic
Eriste 2	0°27′35″E	42°39′08″N	2,470	0.27	1.6	9.8	1,638	389	4.7	9.8	17.53	12.57	Loam	Plutonic
Pica Palomera	0°51′49″E	42°47′46″N	2,380	0.30	1.8	9.8	1,603	384	4.6	6.5	14.40	17.50	Silt loam	Metamorphic
Liat	0°52′48″E	42°48′30″N	2,163	0.23	3.0	10.9	1,523	367	4.6	7.6	8.21	13.79	Silt loam	Detrital
Montoliu	0°55′55″E	42°47′02″N	2,484	0.44	1.3	9.2	1,631	391	5.1	4.7	13.29	10.43	Silt loam	Carbonated
Filià 1	0°56′16″E	42°26′47″N	2,520	0.47	1.6	9.7	1,452	356	5.3	2.9	9.51	9.71	Silt loam	Carbonated
Filià 2	0°56′45″E	42°26′57″N	2,260	0.53	2.9	11.0	1,452	356	5.0	4.1	16.02	10.00	Loam	Carbonated
Filià 3	0°57′16″E	42°27′05″N	2,150	0.61	3.4	11.6	1,452	356	4.7	4.8	21.21	10.21	Silt loam	Carbonated
Redó 1	0°47′10″E	42°38′34″N	2,330	0.27	2.3	10.4	1,543	370	5.0	12.0	15.48	14.35	Silt loam	Plutonic
Redó 2	0°46′55″E	42°38′25″N	2,260	0.18	2.7	10.7	1,543	370	5.3	14.0	8.23	12.50	Silt loam	Plutonic
Redó 3	0°46′19″E	42°38′23″N	2,370	0.32	2.1	10.2	1,543	370	5.0	7.6	15.93	13.70	Sandy loam	Plutonic
Colatx	1°19′17″E	42°43′14″N	2,280	0.50	2.4	10.2	1,494	368	4.9	7.8	29.92	11.11	Loam	Plutonic
Senó	1°19′21″E	42°42′55″N	2,140	0.25	3.1	10.9	1,494	368	5.0	6.2	16.05	12.52	Sandy loam	Plutonic
Romedo de Dalt	1°19′33″E	42°42′16″N	2,120	0.67	3.3	11.1	1,483	368	4.6	10.6	23.58	12.94	Silt loam	Detrital
Baiau 1	1°25′29″E	42°35′45″N	2,585	0.25	0.9	8.6	1,648	404	4.6	9.8	11.41	10.76	Silt loam	Metamorphic
Baiau 2	1°25′48″E	42°35′46″N	2,490	0.76	1.3	9.1	1,648	404	4.6	6.8	18.10	10.84	Loam	Metamorphic
Aixeus	1°22′19″E	42°36′46″N	2,470	0.24	1.5	9.3	1,593	392	4.6	11.9	23.38	13.71	Silt loam	Metamorphic
Negre	2°12′29″E	42°38′19″N	2,140	0.20	3.1	10.7	1,565	357	5.3	6.2	9.77	13.48	Loam	Plutonic
Estelat	2°12′16″E	42°38′48″N	2,230	0.74	3.2	10.7	1,536	349	4.7	4.5	23.16	13.95	Sandy loam	Plutonic

MAT mean annual temperature, ST summer temperature, MAP mean annual precipitation, SP summer precipitation

Smirnov test and its independence were checked by the Durbin–Watson test.

All the statistical analyses were performed with the SPSS V.11.0 statistical package.

Results

Soil organic C stocks in mountain grasslands

The soil C content in mountain grasslands of the Pyrenees ranged between 5.9 and 29.9 kg C m^{-2} (mean ± SE: 15.3 ± 0.9 kg C m^{-2}). Due to the high variability in SOCS, there were no significant differences between the four bedrock types and texture classes (Table 2).

There was a positive relationship of SOCS with soil depth ($r = 0.474$, $p = 0.005$), which ranged between 0.13 and 0.78 m (mean ± SE: 0.36 ± 0.03). There was also a positive relationship of SOCS with the clay content of the whole profile (kg m^{-2}) ($r = 0.357$, $p = 0.045$) and with most climatic variables (Table 3) indicating lower SOCS as the climate became colder and wetter. There were no correlations between altitude, slope, aspect or climate variables and soil depth. The clay content (kg m^{-2}) showed a positive correlation with the MAT ($r = 0.373$, $p = 0.035$) and a negative correlation with altitude ($r = 0.382$, $p = 0.031$), showing the lowest clay content at the most elevated sites.

A multiple regression model using only the altitude and aspect variables explained about 41% of SOCS variability (Eq. 1, Table 4). The percentage of variability explained did not increase when the bedrock type was included in the multiple regression analyses. In spite of the relationships between soil depth and the clay content (not included in the model) with SOCS, those parameters did not correlate with the residual values of Eq. 1 model ($p > 0.05$).

The visualization of C predicted by Eq 1 (Table 4, Fig. 2) showed that the highest SOCS occurred at middle aspects slightly shifted towards the north (ENE, WNW) of the lowest altitudes (Fig. 2). On the other hand, the lowest

Table 2 Mean and standard error of SOCS and OC, N, C-to-N ratio, pH and clay content of the surface horizon by lithologies and textural classes

	Texture class				Lithology				
	Sandy loam	Loam	Silt loam	Sign.	Carbonated	Detrital	Metamorphic	Plutonic	Sign.
Number of cases	5	13	17		7	7	7	14	
SOCS (kg m^{-2})	16.0 ± 2.2 a	13.4 ± 1.0 a	15.4 ± 1.2 a	ns	14.3 ± 2.0 a	15.7 ± 1.8 a	14.6 ± 1.8 a	14.8 ± 1.2 a	ns
OC (%)	6.00 ± .7 a	6.2 ± 0.6 a	9.39 ± 0.9 b	**	5.6 ± 1.9 a	7.7 ± 1.1 a	8.2 ± 0.9 a	8.5 ± 0.7 a	ns
N (%)	0.47 ± 0.05 a	0.49 ± 0.06 a	0.76 ± 0.07 b	**	0.45 ± 0.14 a	0.68 ± 0.10 a	0.65 ± 0.08 a	0.65 ± 0.06 a	ns
C-to-N	12.9 ± 0.5 a	11.8 ± 0.4 a	12.3 ± 0.5 a	ns	10.7 ± 0.6 a	11.5 ± 0.5 ab	12.8 ± 0.9 b	13.0 ± 0.3 b	*
pH	4.87 ± 0.08 a	4.91 ± 0.09 a	4.78 ± 0.08 a	ns	5.15 ± 0.09 c	4.50 ± 0.06 a	4.70 ± 0.05 a	4.92 ± 0.07 b	***
Clay (%)	7.51 ± 1.5 a	10.62 ± 0.6 a	14.67 ± 1.0 b	***	11.95 ± 1.0 ab	15.70 ± 1.5 b	12.97 ± 1.8 ab	10.05 ± 1.1 a	*

ANOVA and a posteriori Duncan test results are also shown

ns no significant differences

Different letters indicate significant differences between textural classes or lithologies

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

Table 3 Pearson correlation coefficients and *p*-values between climatic and topographic variables and SOCS of whole profile and soil C, N, C-to-N ratio and clay content of the upper horizon

		MAT (°C)	MAP (mm)	ST (°C)	SP (mm)	Alt (m a.s.l)	Aspect (°)	Slope (%)	Clay[a] (%)
SOCS (kg m^{-2})	R	**0.382**	**–0.430**	**0.369**	–0.224	**–0.367**	–0.231	0.166	**0.381**
	p-value	**(0.028)**	**(0.012)**	**(0.035)**	(0.211)	**(0.036)**	(0.195)	(0.356)	**(0.034)**
OC (%)	R	0.287	–0.203	0.285	–0.194	–0.305	0.006	–0.132	**0.495**
	p-value	(0.095)	(0.241)	(0.097)	(0.263)	(0.074)	(0.971)	(0.448)	**(0.002)**
N (%)	R	0.314	–0.202	0.295	–0.257	–0.329	0.057	–0.168	**0.568**
	p-value	(0.066)	(0.245)	(0.085)	(0.137)	(0.053)	(0.747)	(0.335)	**(0.000)**
C-to-N	R	–0.034	0.029	–0.021	0.166	0.002	–0.034	–0.032	–0.140
	p-value	(0.845)	(0.868)	(0.903)	(0.342)	(0.992)	(0.846)	(0.855)	(0.422)

Significant correlations are in bold

[a] Correlation coefficient with SOCS refers to the clay content of whole profile (kg m^{-2})

Table 4 Multiple regression models between total SOCS (kg m^{-2}) (Eq. 1) or OC concentration (%) of the surface layer (Eq. 2) and the abiotic variables

Equations	adj R^2	*p*-value	Equation number
log(SOCS) (kg m^{-2}) = –9.519 – 0.118 Asp^2 + 36.996 log(Asp + 1) + 2.945 log(Alt) – 10.176 log(Alt) log(Asp + 1)	0.412	0.001	1
OC (%) = CT + 348.451 log(ST) – 405.106 log(SP) + 5.303 SLang – 12.912 Asp + 0.127 SP × Asp – 0.931 SLang × Asp	0.569	0.000	2

CT detritic, Metamorphic and carbonates: 501.199; Plutonic: 503.786. Aspect values in degrees were previously cosine transformed to achieve a continuous variable that does not distinguish between east and west aspects. To avoid 0 values (E and W aspects) we added 2 to this variable

Alt altitude (m a.s.l.), ST summer temperature (June–August) (°C), SP summer precipitation (mm), SLang summer rainfall index of Lang (mm °C^{-1}), Asp aspect

values occurred at the highest altitudes for both N and S aspects. The SOCS at the highest altitudes showed a slight increase at the middle aspects, in this case shifted towards the south (ESE, WSW). Thus, the differences in the SOCS between aspects decreased with altitude. While on northern aspects SOCS largely decreased with altitude, on southern aspects the model predicted similar SOCS along the elevation gradient (Fig. 2).

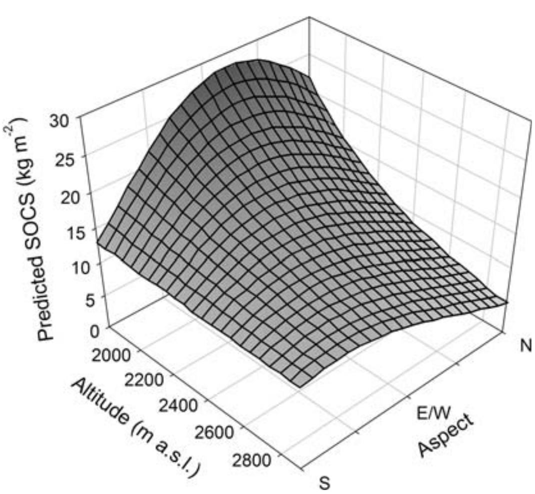

Fig. 2 Predicted soil organic C stocks (kg m^{-2}) along altitude (m a.s.l.) and aspect according to Eq. 1 (Table 4)

Effects of climate and topography on OC concentration

The surface horizon contained 64.4 ± 4.3% of the total SOCS ranging from 20.3 to 100%. The OC concentration of this layer ranged between 2.1 and 16.5%, with a mean value of 7.7% (Table 1) and was negatively correlated to its thickness (r = –0.414, p = 0.013). The clay content of the surface horizon decreased significantly with altitude (adj R^2 = 0.250, p = 0.002) and showed a positive correlation with the OC concentration

(Table 3). Silt loam soils showed higher OC contents than loam or sandy loam soils (p = 0.008). Although there were some significant differences in the clay content between bedrock types (p = 0.014, Table 2), there were no significant effects of bedrock types on the OC.

Climatic and topographic variables did not show any significant correlation with the OC (Table 3). But multiple regression analyses combining climatic and topographic variables explained about 57% of variability of the OC concentration of the surface horizon (adj $R^2 = 0.569$, $p < 0.001$) (Eq. 2, Table 4). Changes in lithology did not interact with climatic and topographic variables. These changes shifted the equation upwards or downwards by modifying the constant (CT; Eq. 2, Table 4) and indicated higher OC on plutonic lithologies than in other bedrock types.

Significant interactions between climatic variables [summer precipitation (SP) and SLang] and aspect indicated different trends of the OC along the climatic gradient depending on aspect. While at the coldest sites (highest altitudes) the OC was higher at southern aspects, at the warmest locations (lowest altitudes) the OC content was higher at the northern aspects. At middle temperatures, the effect of aspect on the OC is much less perceptible (Fig. 3a).

Our model also predicted a decrease of OC as SP becomes lower, except for the sites with the warmest temperatures, where there was a slight increase of OC (Fig. 3). In fact, the effect of SP decreased as temperatures increased until this effect was reversed. The effect of SP was lowest at the northern aspects.

C-to-N ratios of the surface horizon correlated to OC (r = 0.367, p = 0.030). And the residual values of the OC model (Eq. 2, Table 4) showed a positive relationship with soil C-to-N ratio (r = 0.456, p = 0.007), indicating that the model overestimated OC when the C-to-N ratio is low and underestimated it at high C-to-N ratios. Samples from all lithologies follow this trend, except for those obtained in sites with plutonic bedrocks (Fig. 4). No other available variables correlated with residuals.

The C-to-N ratio did not correlate with the climatic and topographic variables and was only sensitive to the bedrock type (Table 2), showing the lowest values for carbonated lithology.

Discussion

The soil C content in the Pyrenean grasslands (5.9–29.9 kg C m^{-2}) was of the same order of magnitude as those found by Jobbágy and Jackson (2000) to 1 m depth in temperate grasslands (11.7 kg C m^{-2}) or in tundra soils (14.2 kg C m^{-2}), by Tate et al. (2000) in pastures of New Zealand (20 kg C m^{-2}) or by Townsend et al. (1995) in tropical pastures of Hawaii (14 kg C m^{-2}). However, the values found by Leifeld et al. (2005) in Swiss alpine grasslands (6–9 kg C m^{-2} down to 100 cm depth) or by Rodriguez-Murillo (2001) in pastures of Spain

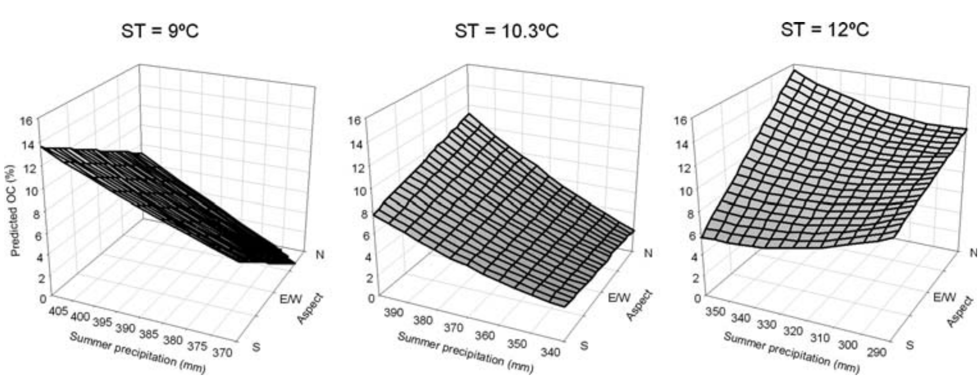

Fig. 3 Predicted organic C content (%) of the upper layer distribution along summer precipitation (*SP*) and aspect gradients by three representative temperatures according to Eq. 2 (Table 4). In all cases predicted values for detritic, metamorphic or carbonate bedrocks are presented

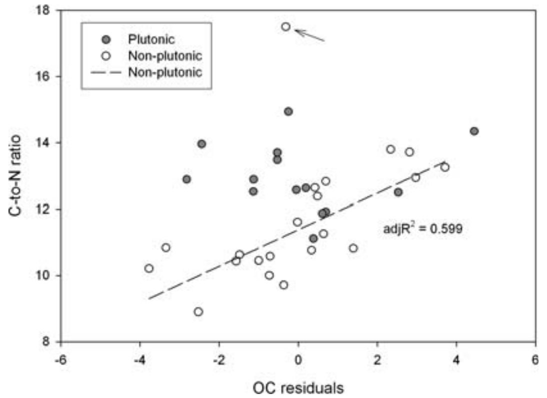

Fig. 4 Relationship between C-to-N ratios and the residuals of OC model (Table 4, Eq. 2). The point with an *arrow* has been excluded of the fitting

(7.3 kg C m^{-2}) are similar to the low values found in this study.

In grassland soils, the proportion of C stored in depth is usually higher than in other ecosystems because their root-to-shoot ratio is normally high (Jobbágy and Jackson 2000). In fact, Mokany et al. (2006) found that tundra and cool temperate grasslands were the biomes with the highest root-to-shoot ratios. This fact makes it difficult accurately to estimate soil organic C content excluding plant dynamics. Our data showed great variability in the soil C content, which can be partially accounted for by soil depth, climate and topographic variables. In our study, soil depth appears as an important variable to explain the SOCS. However, soil depth is a parameter that is difficult to measure extensively and, although it may be inferred from topographic variables, we have not found any relationship between soil depth and climatic or topographic variables using our database. Given the difficulty of measuring soil depth extensively, SOCS predictions-based only on climatic and topographic variables, excluding it, may be useful to describe C storage across the mountain landscapes using the generally available georeferenced information that often does not include soil depth. On the other hand, predictions of the OC concentration of the surface horizon (high-root density layer) are indicative of the soil functioning (soil fertility and erosion risk).

A number of studies indicate an increase of soil SOCS with altitude (Ganuza and Almendros 2003; Miller et al. 2004; Rey Benayas et al. 2004; Leifeld et al. 2005). However, Bardgett (2005, p 8) indicates that this trend may reverse beyond the tree line and that SOM content may reach almost zero at the unvegetated substrates of the upper alpine areas. Our results indicate that in high-altitude grasslands of the Pyrenees total SOCS decreased with altitude in the northern aspects and remained quite constant in the south facing slopes. Summer climate may influence specific processes and patterns in alpine and subalpine plant communities as more favourable warm temperatures and less abiotic stress may increase biomass accumulation (Kikvidze et al. 2005). In alpine grasslands, both above and belowground C inputs into the soil decrease with altitude (Hitz et al. 2001) and decomposition rates also decrease as the climate becomes colder (Hobbie et al. 2000; Rodeghiero and Cescatti 2005). On northern aspects, despite the increase of water availability with altitude, the reduction of temperatures and the increase of freezing episodes or the snow cover may lead to a reduction of plant productivity. Grieve (2000), studying soils of the Scottish mountains, found a reduction of total SOM content due to the length of freezing episodes. Although the increase of the severity of soil frost could reduce heterotrophic activity and, consequently, could limit decomposition rates, the increase of the duration of snow cover also limits primary production (Brooks and Williams 1999). The low SOCS that occurs at the most elevated sites, even with the limited decomposition rates, suggests that soil C input [related to net primary productivity (NPP)] is the main driver for organic matter accumulation under these conditions.

At southern aspects the effect of altitude was almost negligible, likely as a result of its milder climate, with shorter periods of snow cover and higher insulation, which may allow substantial plant productivity even at the highest altitudes. In consequence, in the southern aspects, the general reduction of plant productivity with altitude occurring in mountain areas (Hitz et al. 2001) may be counteracted by the increasing climatic limitation of organic matter decomposition and result in similar C content along the altitudinal gradient. At the most elevated sites, although the effect of aspect we observed was mild, the highest values of SOCS occurred at the southern faces.

The low-clay content found at the most elevated sites and the relationship of this parameter with OC and SOCS suggest that the climatic effects on SOCS are not only related to plant productivity and litter decomposition, but also its effects on soil development. Increases in fine particles that occur in most developed soils can be important for soil C stabilization (Hassink 1997; Müller and Höper 2004).

At low altitudes, where conditions are more favourable for biological activity (longer growing season, lower frequency of freezing episodes), the highest SOCS occurred at the northern aspect in sites with high-plant productivity. Indeed, at the southern aspects our model predicted high-OC content in grasslands with the lowest temperatures. In contrast, other authors working in high latitudes found that south-facing grasslands showed longer growing seasons and pointed out that this fact may lead to higher plant productivity (O'Lear and Seastedt 1994). In our case, under warmer conditions at lower altitudes, within the Mediterranean area, the occasional water deficits of the southern aspect grasslands receiving high radiation may have counteracted this effect. Under these conditions, the shaded sites (northern faces) or the colder southern sites often maintain high-moisture levels for longer periods of time and thus become more productive and show higher stocks of soil C.

We did not find any correlation between the C-to-N ratio and climatic or topographic variables. Vinton and Burke (1997) found significant effects of plant species on soil C-to-N ratios and concluded that plant species may play an important role in soil organic C dynamics. Our study did not find any significant relationship with the C-to-N ratio of the surface horizon to explain the regional variation of soil C. However, the residuals of the OC regression model for the non-plutonic parent materials (Eq. 2, Table 4, Fig. 4), which represent the non-explained variability by climatic and topographic variables, showed a significant relationship with the C-to-N ratio, suggesting that the effects of organic matter quality on soil C accumulation in non-plutonic areas were not fully accounted for in our model with climatic and topographic variables. In the sites with a high C-to-N ratio, organic matter may be more stabilized biochemically (as is defined by Six et al. 2002) and consequently soil OC accumulation can be highly underestimated if predicted only with climatic and topographic variables. However, C-to-N ratio did not show any relationship with the residuals of the sites with plutonic substrates. Low C to N ratio in carbonated bedrock soils can result form high-biological activity associated to high pH occurring in these soils (Table 2). The residuals of our OC model showed an overestimation for soils with low C to N ratio that could be related to an increase in biological activity associated to soil chemical properties occurring mainly in areas with carbonated bedrocks. Indeed, these areas showed low OC accumulation.

Conclusions

Climatic and topographic variables were able to predict a significant part of the C storage variability in the grasslands of the mountain landscapes of the Pyrenees, but soil depth is an important variable to improve SOCS estimations.

The harsh climatic conditions and low-plant productivity that occur on northern slopes reduced SOCS storage at high altitudes. In contrast, on the southern aspects, under more favourable conditions for plant productivity, C accumulation along the altitudinal gradient did not change very much.

Low SOCS at the highest altitudes resulted from the reduced NPP of the high-elevation grasslands. Altitudinal changes in C content depended on the aspect and slope. Microclimate conditions related to topographic position (aspect and slope) are important factors for predicting C storage in soils of the high-altitude grasslands of the Pyrenees and must be taken into account to achieve accurate estimations of C stocks in mountain ecosystems.

In non-plutonic substrates, the variability of the OC content that was not explained by climatic or topographic variables was partially related to soil C-to-N ratios, which may in turn be related to plant communities.

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