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Soil organic matter changes under experimental pedoclimatic modifications in mountain grasslands of the French Alps

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ABSTRACT

Mountain grasslands contain large stocks of soil organic carbon (SOC), of which a good part is in labile particulate form. This labile SOC may be protected by cold climate that limits microbial activity. Strong climate change in mountain regions threatens to destabilize these SOC stocks. However, so far the climate response of SOC stocks in mountain grasslands remains highly uncertain, under either warming or cooling conditions. To overcome this knowledge gap, we studied the effect of pedoclimatic regime changes on topsoil (0–10 cm) SOC in two complementary experiments: 3 °C of warming or cooling by reciprocal transplanting to an alpine (2450 m a.s.l.) and a subalpine (1950 m a.s.l.) grassland and 1 °C of warming by open-top chambers in the same grasslands.

Topsoil SOC stocks were higher at the alpine site than at the subalpine site, and the biogeochemical signature of the soil organic matter (SOM) also differed between the two study sites. SOM was O-enriched, H-depleted, and more thermally stable at the warmer subalpine site. After three years, abrupt warming by transplanting tended to decrease topsoil SOC content. The remaining SOC was characterized by a more thermostable signature. This result suggests the preferential depletion of labile SOC upon experimental topsoil warming. Cooling did not modify overall SOC content but uphill transplanted topsoils showed a more thermolabile biogeochemical signature. In contrast, open-top chamber warming of alpine and subalpine topsoils caused limited changes to SOC stocks and SOM biogeochemical signature, possibly because the induced pedoclimatic change was more limited and more gradual compared to the warming by transplanting which reduced the annual snow cover period by around 60 days and increased cumulative degree days by a factor of ten as compared to the OTC-induced warming. Gradual temperature changes may take longer to become effective than a shock transplant treatment. We conclude that SOC in mountain grassland topsoils can be highly reactive to climate shocks.

1. Introduction

Mountain ecosystems cover about 27 % of the earth's continental surface and contribute benefits to more than half of humanity (Grêt-Regamey and Weibel, 2020; Palomo, 2017). Climate regulation through organic carbon sequestration in soils is one of these critical contributions (EEA, 2010; Jobbágy and Jackson, 2000; Schimel, 1995). Mountain soils in temperate regions are known to store large amounts of soil organic carbon (SOC; Doblas-Miranda et al., 2013; Martin et al., 2011;

Meersmans et al., 2012). The soils of grasslands in the European Alps can harbor between 53 and 260 Mg ha⁻¹ of SOC (Djukic et al., 2010; Leifeld et al., 2009), which is comparable with those of European forests (Beringer et al., 2015; Liski et al., 2002). The strong climatic constraints at high elevation (e.g. cold climate and frost) limit the decomposition activity of soil microbes and thus result in a high residence time of soil organic matter (Körner, 2003; Sjögersten et al., 2011). This is especially true in the upper soil horizons, where a large part of the SOC is often found in particulate form, that is not stabilized by mineral interactions,

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but can show a mean ^{14}C -age above one century (Budge et al., 2011; Hou et al., 2019; Leifeld et al., 2009; Martinsen et al., 2011; Saenger et al., 2015; Sjögersten, et al., 2011 but see Puissant et al., 2017). This particulate SOC is climatically stabilized (Trumbore, 2009) and therefore potentially highly vulnerable to climate changes predicted for the Alps, including rising temperatures and decreasing snow cover below 1500–2000 m above sea level (Gobiet et al., 2014; Jacob et al., 2014). In addition, soils of mountain grasslands are more exposed to climate variability compared to forest soils because the sparse vegetation cover has limited buffering capacity (Gavazov, 2013). The fate of the largely labile SOC stocks of mountain grasslands in response to climate change is therefore a real concern, but remains highly uncertain (Leifeld et al., 2009; Sjögersten et al., 2011).

Rising temperatures are expected to stimulate heterotrophic decomposition of organic matter and increase its mineralization (Bond-Lamberty et al., 2018; Bond-Lamberty & Thomson, 2010; Crowther et al., 2016). However, warming effects on the SOC budget are difficult to predict due to a multitude of interplaying processes: (i) the acclimation of vegetation to warming can result in quantitative and qualitative changes of organic matter inputs (Melillo et al., 2002), (ii) the acclimation of microbial community composition and/or functional strategies can affect decomposition (Conant et al., 2011), (iii) warming is often accompanied by increasing water deficits which limits decomposition (Davidson and Trumbore, 2000), and finally, (iv) the different SOC kinetic pools are prone to respond in different ways to these different dynamics (Davidson & Janssens, 2006). As a result of this multitude of processes acting in concert, experimental studies have shown very contrasting response of topsoil SOC stocks to warming. Some studies found a limited or neutral effect of warming on SOC content due to accompanying soil moisture limitation or acclimation of microbial communities (Marty et al., 2019; Reynolds et al., 2015), while others found very significant effects of warming on soil organic matter: Hicks Pries et al. (2017) observed an important increase of whole-soil profile respiration with warming. A 35-years monitoring study in the German Alps demonstrated a significant decrease in SOC stocks, especially at sites with high levels of particulate SOC and those with the greatest temperature changes (Prietz et al., 2016). In Western Himalaya alpine grasslands, Tiwari et al., (2021) found an increased net SOC uptake due to enhanced plant growth in open-top chamber (OTC with warming of 1.5–2 °C). These results highlight the variability of responses of SOC stocks and fluxes to both experimental and observational warming studies depending on initial conditions and studied timeframes and magnitude of temperature increase. The effect of cooling on SOC is even less studied and we thus do not know whether cooling just leads to opposite effects on decomposition processes to warming or to new responses. However, it would be interesting to understand the effect of cold on SOC, especially in mountain where climatic stabilization maintains the stocks of labile SOC. The few studies existing are based on reciprocal transplants along elevation gradients in forests and in semi-arid shrub-steppe. They have shown no or limited effects of cooling on SOC content (Link et al., 2003; Luan et al., 2014).

Several studies have shown the interest of separating SOC into fractions with different mean turnover rates to better understand its vulnerability to climate change (e.g., Lugato et al., 2021). Thermal fractionation of SOC can be used to measure thermal and chemical properties that are specific to biogeochemically stable SOC: stable SOC is thermally stable and depleted in hydrogen (Barré et al., 2016; Gregorich et al., 2015; Plante et al., 2013). Due to the stabilization of mountain SOC by climate and the correlation between altitude and SOC lability (Sjögersten et al., 2011), warming is expected to result in the release of an important amount of labile SOC at high elevations. An experimental warming of a shrub-steppe ecosystem showed preferential loss of particulate SOC (Link et al., 2003) while Puissant et al. (2017) highlighted significant SOC losses in the mineral associated fraction, which is the most stable form, on an experimentally warmed subalpine grassland soil.

Here we studied the effects of soil warming and cooling on mountain grassland topsoil organic matter, focusing on changes in SOC contents and on the biogeochemical signature of organic matter. We compared two types of common warming experiments that simulate abrupt changes of topsoil temperature: a reciprocal transplant along an elevational gradient that warms an alpine grassland and cools a subalpine grassland and concurrently changes snow regimes, and an OTC warming experiment at the same subalpine and alpine grasslands. Our specific hypotheses are: (1) the SOC content of cooled topsoils increases and that of warmed topsoils decreases as the magnitude of warming increases, (2) topsoil warming will especially cause the release of labile SOC and cooling causes its enrichment and (3) SOC of the alpine topsoil is more sensitive to warming than that of the subalpine topsoil.

2. Materials and methods

2.1. Study area

The two study sites are located at the long-term Socio-Ecological Research platform Lautaret-Oisans (Zone Atelier Alpes), Grand Galibier Massif in the French South-Western Alps at 2450 m (alpine site, 45°03'19.65 "N 6°24'0.70 "E) on a South-East facing slope and at 1950 m (subalpine site, 45°02'24.04 "N 6°25'09.20 "E) on a South-West facing slope (Fig. 1). The meteorological data used to characterize these two sites were extracted from the S2M re-analyses developed by Météo France for the French Alps (Durand et al., 2009; Vernay et al., 2019; Vionnet et al., 2012). Over the period 1988–2017, the yearly accumulation of growing degree days (GDD; from snowmelt to end of July) at the subalpine site is 73 % higher than at the alpine site. This difference is largely due to contrasting snow melt dates. On average, snow melt occurs at the beginning of June at the alpine site and at the end of April at the subalpine site. The decadal trend of growing degree days (GDD) since 1959 is significantly positive for both sites. GDD have increased by 10 % between the period 1988–2017 and the period 1959–1988 for the subalpine site, and of 41 % for the alpine site.

The soil parent material of the two sites is composed of flysch sediments, called "Flysch des Aiguilles d'Arves" (Deharveng et al., 1987). The subalpine grassland is dominated by a tall fescue (*Patzkea paniculata*); other abundant species are *Carex sempervirens*, *Festuca nigrescens*, *Centaurea uniflora*, *Helianthemum nummularium* and *Meum athamanticum*. The alpine grassland is dominated by *Carex sempervirens*, *Festuca nigrescens*, *Poa alpina*, *Potentilla aurea*, *Trifolium alpinum*, and *Geum montanum*. Both sites were used for grazing before the experiment but are fenced off. The subalpine site was used for hay making before the 1960 s. Soils of both sites are silty and classified as Dystric Cambisols (FAO, 2014). They are composed of four soil horizons (see the photos and pedological description in the supplementary Figure S1). Soil bulk density to a depth of 10 cm is 0.77 g cm⁻³ at the subalpine site and 0.70 g cm⁻³ at the alpine site. Table 1 presents the physicochemical characteristics of the topsoil horizons found above 10 cm depth at the two sites (including two soil horizons for the alpine site and one soil horizon for the subalpine site). The topsoils of the two sites are quite similar regarding these physico-chemical characteristics. They are both acidic (pH in H₂O < 5.5), rich in clay (>30 %) with an exchangeable phosphorus (P) content corresponding to fairly high P soil availability in a context of natural grassland soils (>0.01 g/kg).

3. Experimental design and topsoil sampling

Two adjacent warming experiments were installed in 2016 at the two study sites.

4. Reciprocal transplant

In autumn 2016, ten alpine grassland plots were transplanted from the alpine to the subalpine site (hereafter "alpine warmed transplant")

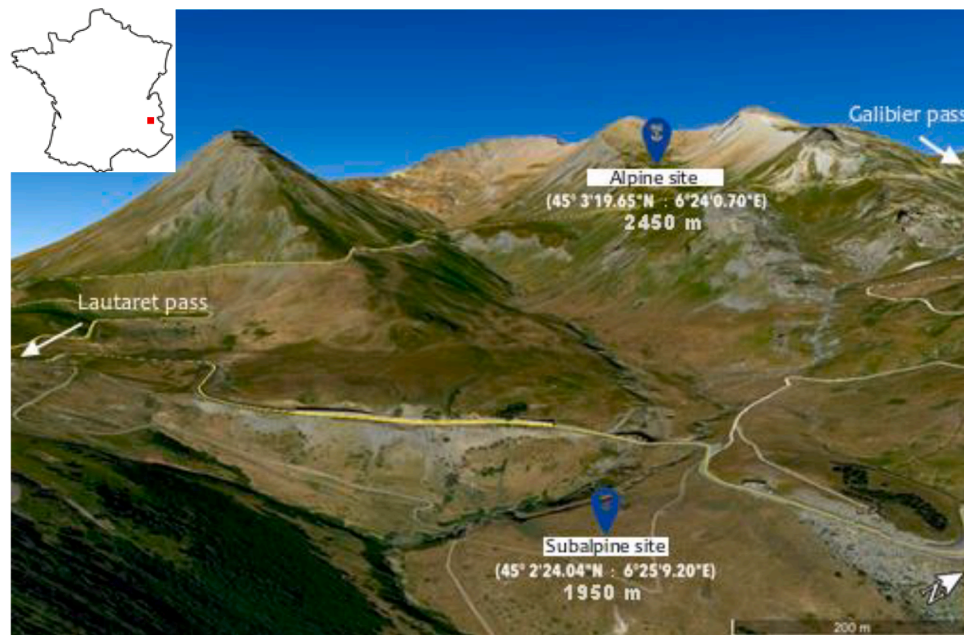


Fig. 1. Location of the two study sites in the French South-Western Alps (background picture modified from Google earth, 2018).

Table 1

Physicochemical characteristics of the topsoil horizons found above 10 cm depth at the subalpine and alpine study sites.

Site	Horizon WRB code	Depth (cm)	Clay (g/kg)	Silt (g/kg)	Sand (g/kg)	Corg (g/kg)	Ntot (g/kg)	P ₂ O ₅ (g/kg)	CaCO ₃ (g/kg)	pH H ₂ O soil	CEC (cmol+/kg)
Subalpine site	A	0–10	380	424	196	68.2	5.4	0.012	<1	5.4	13.3
Alpine site	A	0–3	442	433	125	171	12.6	0.059	<1	5.0	18.9
	A/Bw	3–20	324	459	217	38.7	3.4	0.011	<1	4.7	6.8

and ten subalpine grassland plots from the subalpine to the alpine site (“subalpine cooled transplant”) using a helicopter. Each 4 m² plot consisted of turfs with above- and below-ground parts of the plant communities and a layer of their associated soil of about 20 cm thickness. In order to account for the disturbing effect of the transplanting, ten 1 m² plots were also transplanted (i.e. simply switched) at the alpine (“alpine control transplant”) as well as the subalpine site (“subalpine control transplant”). Topsoil temperature was monitored at both study sites using a thermal sensor implanted in the soil at 5 cm depth at the beginning of the experiment. At the end of summer 2019, the topsoils of the twenty transplanted plots and the twenty control plots were sampled at 10 cm depth. The topsoil composites samples were dried at ambient temperature and sieved at 2 mm.

In addition to the warming, the reciprocal transplant decreased the period of snow cover and increased the GDD of the alpine warmed transplant. Conversely, it increased the period of snow cover and decreased the GDD of the subalpine cooled transplant.

5. Open top chambers

During the growing seasons of 2017, 2018 and 2019 (generally May until October), eight hexagonal open-top chambers were used to experimentally warm the alpine (hereafter “alpine warmed OTC”) and the subalpine (hereafter “subalpine warmed OTC”) soils and associated plant communities. The chambers are based on the design of the International Tundra Experiment (Molau and Mølgaard, 1996), with a 1.5 m diameter, 0.5 m height and covering an area of approximately 2 m² and are arranged in a randomized design to take into account micro-topographic and soil property variation. Paired control plots of 2 m² were

also established some 2–3 m away from each open topped chamber (“alpine control OTC” and “subalpine control OTC”). We monitored soil temperature of controls and warmed plots over the period of the growing season using thermal sensors (HOBO pendant UA1-64) implanted in soils at 10 cm depth. During July and August 2019, four soil cores (0–5 cm deep, 2.5 cm diameter) were randomly collected and mixed together to form a composite topsoil sample for each control and warmed plot. The topsoil samples were dried at ambient temperature and sieved at 2 mm.

6. Soil analyses and data treatment

All topsoil samples were finely ground in a disc mill. The soil organic matter bulk chemistry and the SOC thermal stability was characterized by Rock-Eval® thermal analysis (Rock-Eval® 6 Turbo, Vinci Technologies). A detailed description of this method can be found in Behar et al., (2001) and Disnar et al., (2003). It consists in carbon measurement as gaseous effluent during two phases. The first one is a pyrolysis stage (3 min isotherm at 200 °C followed by a 200 to 650 °C temperature ramp with a heating rate of 30 °C min⁻¹) in N₂ atmosphere during which CO and CO₂ were quantified with an infrared detector. Volatile hydrocarbon effluents (CH) were quantified with flame ionization detector. The second phase is an oxidation stage (1 min isotherm at 300 °C followed by a 300 to 850 °C temperature ramp with a heating rate of 20 °C min⁻¹ and a 5 min isotherm at 850 °C) in laboratory air atmosphere during which CO and CO₂ were quantified with an infrared detector. From each Rock-Eval® thermogram, we define three thermal SOC fractions: (i) a small and highly thermolabile pyrolysable SOC fraction (hereafter termed POC 1), corresponding to the carbon evacuated as CH, CO or CO₂ at 200

°C over the first 200 s of the pyrolysis phase (Khedim et al., 2021); (ii) pyrolysable organic carbon pool (PC), corresponding to the carbon evacuated as CH, CO or CO₂ during the whole pyrolysis phase, (iii) pyrolysis-resistant organic carbon pool (RC), evacuated as CO or CO₂ during the oxidation stage. The sum of the PC pool and the RC pool inform on the total SOC content (Rock-Eval® parameter TOC). The organic carbon yield of Rock-Eval® SOC quantification was on average 85 % to 90 % of SOC content determined by elemental analysis, using respectively the Rock-Eval® parameter TOC or the sum of Rock-Eval® parameters TOC and MinC (see Behar et al., 2001 for a definition of these parameters) in these acidic topsoil samples free of carbonates (Table 1).

In the PC and RC thermal SOC fractions, we also determined the temperature corresponding to the release of 30 %, 50 %, 70 % and 90 % of the CH, CO and CO₂ during the pyrolysis phase and of the CO and CO₂ during the oxidation phase (T_{xx}CH_PYR, T_{xx}CO_PYR, T_{xx}CO₂_PYR, T_{xx}CO_OX and T_{xx}CO₂_OX in the following) in order to more accurately characterize the thermal stability of the SOC released (Cécillon et al., 2018). We also coupled the CH, CO, CO₂ pyrolysis signals to determine the temperature parameters T_{xx}_PYR of the full pyrolysis signal, and we couple the CO, CO₂ oxidation signals to determine the temperature parameters T_{xx}_OX of the full oxidation signal according to Khedim et al. (2021). The higher these indexes are, more thermally resistant the SOC is. Respectively, the CH, CO and CO₂ evacuated during the pyrolysis phase represented on average 24 %, 3 % and 10 % of the sum of TOC and MinC. The CO and CO₂ released during the oxidation phase respectively contribute to 4 % and 60 % of TOC + MinC. Then, the integrated signal of the full pyrolysis gases released represent 37 % and that of oxidation represent 63 % of TOC + MinC, on average.

The oxygen released as CO and CO₂ during the pyrolysis phase and the hydrogen released as hydrocarbons were quantified to respectively determine the oxygen index (OIRE6, mg O₂ g⁻¹C) and the hydrogen index (HI, mg CH g⁻¹C). The OIRE6 is correlated with the elemental O: C ratio of soil organic matter and the HI is correlated with the elemental H: C ratio of soil organic matter (Espitalié et al., 1977; Lafargue et al., 1998). Then according to Sebag et al. (2016), the I index was calculated, informing on the preservation of thermally labile SOC released as CH during the pyrolysis phase, as well as the R index, assessing the contribution of thermally stable SOC released as CH during the pyrolysis phase.

An elemental analysis (dry combustion; Flash EA1112, Thermo Scientific) was also performed to quantify the SOC content of the transplanted and the OTC warmed topsoil samples and to quantify the Ntot content of the transplanted topsoils. The C:N elemental ratio of soil organic matter was calculated as SOC/Ntot for the transplanted topsoils. SOC stocks were calculated to 10 cm depth (for the reciprocal transplant experiment) or 5 cm depth (for the OTC experiment) according to the equation (1) with t for soil thickness and BD for soil bulk density (initially measured at each site at 10 cm depth).

$$\text{SOC Stock}[\text{kg}/\text{m}^2] = (\text{soc}[\text{g}/\text{kg}] * t[\text{cm}] * \text{bd}[\text{kg}/\text{m}^3]) / 100 \quad (1).$$

6.1. Statistical analysis

We quantified the effects of the four climate manipulation treatments (warming alpine transplant, cooling subalpine transplant, OTC warming of subalpine grassland and OTC warming of alpine grassland) on all the above-mentioned soil organic matter parameters. We used a Mann-Whitney rank test to compare alpine plots with alpine controls and subalpine plots with subalpine controls, and to compare alpine and subalpine controls. In order to verify the absence of spatial variability between OTC-control pairs, an ANOVA with a mixed effect on the pairs was performed. The statistical tests and graphs were generated with R v.3.5 (R Core Team, 2018).

7. Results

7.1. Soil temperature

Both sites are seasonally snow covered. During winter, a deep snowpack insulated soil and the topsoil freezing was limited (Table 2). Soil freezing was slightly more pronounced at the subalpine site (lower Freezing Degree Day, FDD) and this was mainly due to early spring low temperature under snow free conditions. The first snow free date occurred two months earlier at the subalpine than at the alpine site (Table 2). Consequently, the yearly accumulation of GDD was 1.8 times higher at the subalpine site. By the time snow melted at the alpine site, the subalpine site had already accumulated 600 °C GDD on average and reached flowering of its dominant grass species, *Patzkea paniculata*. The mean daily temperature during summer was 3 °C warmer at the subalpine than the alpine site, and for both T_{min} and T_{max}.

Summer warming by the OTC was around 1 °C irrespective of the site (Table S1). Noticeably, we did not find a higher effect of OTC on daily minimum than maximum soil temperatures. Over the two months of treatment until the sampling date, this OTC-induced warming represented a gain of about 60 °C GDD, i.e. a 4 % increase of the annual GDD for the alpine soil and a 2 % increase for the subalpine site. By comparison, when the alpine grassland was transplanted in the subalpine site, the earlier snow melting date represented a GDD gain of 600 °C, i.e. 10 times more than the OTC-induced warming.

8. Soil organic carbon content and stocks

Alpine grassland topsoils had higher SOC contents than subalpine grassland topsoils, especially in the transplant experiment (Table S2; p-value < 0.001). The 0–10 cm SOC stocks were also higher at the alpine site (7.8 kg/m²) compared to the subalpine site (5.6 kg/m²). This difference did not apply for SOC stocks of the 0–5 cm layer (OTC control plots), which for both sites were estimated at about 3.1 kg C/m².

In the transplant experiment, SOC content tended to decrease with warming and did not respond to cooling (Fig. 2a; Table 3). In the OTC experiment, warming slightly decreased SOC content at the subalpine but not at the alpine site. Overall, no significant changes of SOC stocks were observed (Table S2).

9. Soil organic matter biogeochemical signature

The soil organic matter biogeochemical signature of control plots in both experiments (transplants (0–10 cm) and OTC (0–5 cm)) were very similar (comparable values for most Rock-Eval® parameters, Table S2). Conversely, topsoil soil organic matter characteristics of the alpine and the subalpine sites differed strongly, with a higher C:N ratio and a higher proportion of thermolabile SOC in the alpine site compared to the subalpine site, as shown by the different Rock-Eval® parameters (i.e. a

Table 2

Topsoil temperature parameters at the two study sites. Data are averages over the three years of the experiment. Time series of soil temperatures are presented in Figure S2. GDD_{xxx} date: date at which the accumulated GDD over the year reaches the xxx °C threshold.

	Alpine control transplant	Subalpine control transplant
Snowmelting date (sd)	31/05 (±7)	31/03 (±22)
GDD600 date (sd)	21/07 (±5)	11/06 (±9)
GDD1200 date (sd)	10/09 (±9)	18/07 (±9)
cumulated GDD (sd)	1490 °C (±121)	2654 °C (±34)
cumulated FDD (sd)	-18 °C (±30)	-32 °C (±36)
Tmax July (sd)	15.3 °C (±0.9)	18.8 °C (±2.0)
Tmin July (sd)	9.8 °C (±1.6)	12.8 °C (±9)
Tmean July (sd)	13.2 °C (±1.6)	16.3 °C (±1.5)
Tmax July (sd)	15.4 °C (±0.7)	18.8 °C (±0.5)

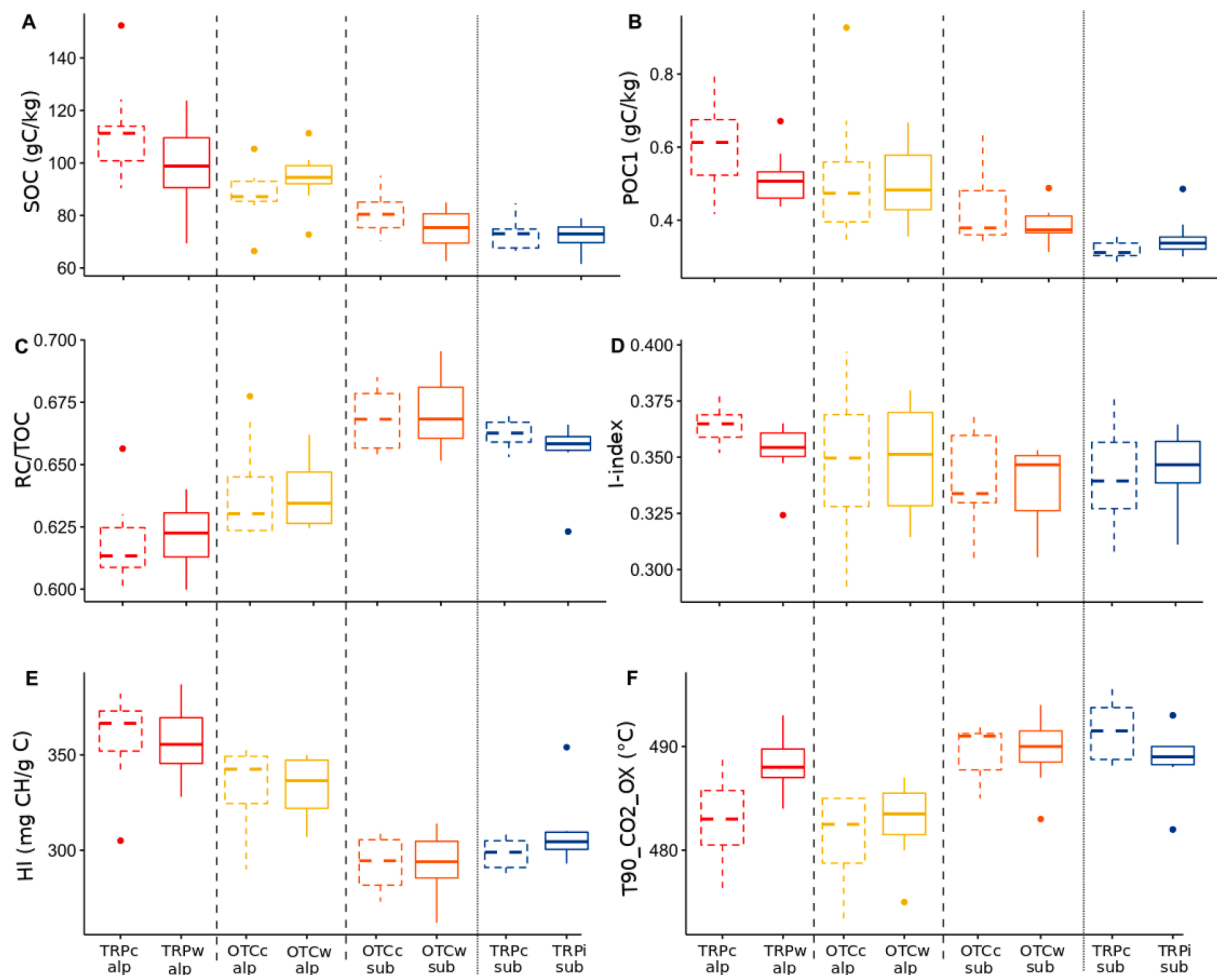


Fig. 2. Treatments effect comparisons between control soils (dashed lines) and treated soils (full lines) on (a) SOC content, (b) POC1 content, (c) RC/TOC ratio, (d) I-Index, (e) HI, (f) $T_{90_CO_2_OX}$ parameter. With TRP: transplant, OTC: open-top chamber, c/w/i: control/warmed/cooled, alp: alpine site, sub: sub-alpine site.

higher POC1 proportion (POC1/TOC), a higher PC proportion (PC/TOC), a reduced thermal stability (lower values for Rock-Eval® temperature parameters and R index, and a higher I index), higher HI and a lower OIRE6 at the alpine site than at the subalpine site).

The values of Rock-Eval® parameters measured in the transplanted soils layed between the values measured on the soils of the alpine and subalpine control plots. Thus, most of the changes in the Rock-Eval® parameters induced by the pedoclimatic modifications were in the expected direction even though not all responses were strong enough to significantly deviate from the controls (Table 3).

As expected, POC1 content significantly decreased for the alpine warmed transplants and the proportion of pyrolysis resistant carbone (RC/TOC) slightly increased (Fig. 2b, c). The I index decreased significantly, such as the C:N ratio which decreased very significantly for the alpine warmed transplants (Fig. 2d, Table 3). The Rock-Eval® temperature parameters that represent the majority of the SOC analyzed ($T_{xx_CO_2_OX}$, T_{xx_PYR} , T_{xx_OX}) showed a significant SOC thermostability increase with warming (Fig. 2f, Tables 3, S2). With cooling, we observed an increase in POC1, PC and RC contents associated with a RC/TOC ratio decrease (Table 3, Fig. 2b, c). The HI and the I indexes showed an increasing trend contrary to the R index, which decreased (Fig. 2d, e). The C:N ratio increased significantly. Moreover, the Rock-Eval® temperature parameters showed a decreasing global trend (Fig. 2f, Table 3).

No significant changes in the Rock-Eval® parameters were observed for the OTC warmed soils. Overall, alpine and subalpine topsoils warmed by OTC showed weaker and more complex warming responses

of their soil organic matter biogeochemical signature compared with warmed transplants (Table S2). The Rock-Eval® temperature parameters showed an increasing SOC thermostability trend for the alpine OTC soils which did not appear for the subalpine OTC soils (Fig. 2f, Tables 3, S2).

10. Discussion

SOC stocks in mountain grasslands are important but may be vulnerable under predicted climate changes for the end of this century. So far studies in different regions, with different warming treatments, and over different time scales do not concur on the risk climate warming is imposing on these carbon stocks. Here, we compared two different types of warming experiments in the French Alps. Over the short period of three years, the two pedoclimatic regime changes experiments showed contrasted alpine and subalpine grassland topsoils responses according to the experimental pedoclimatic modifications. The abrupt warming by transplanting caused a thermolabile SOC release and the cooling an overall modification of the SOC biogeochemical signature, with enhanced SOC thermolability. Alpine and subalpine topsoils warmed by OTC reacted differently to the same treatment, and also much less strongly than the transplanted warmed soils. Our study underlines the importance of analyzing SOC stock responses with complementary techniques and for different scenarios of climate change anticipated for the next decades or until the end of this century.

We found higher amounts of SOC in the alpine grassland topsoils

Table 3

Effect of the experimental treatment on soil parameters. The significance was estimated using a non-parametric Mann-Whitney rank test. An ANOVA with mixed effect on pairs confirms the absence of spatial variability for OTC plots (Table S4). The orange color highlights the results that contradict our expectations (↑ increase, ↓ decrease, = no change). A complementary part of the results is presented in Table S3. Symbols for p-values: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; † $p < 0.1$; NS $p > 0.1$.

	WARMING						COOLING			
	Expectation	Alpine transplant		Alpine OTC		Subalpine OTC		Expectation	Subalpine transplant	
		observed	pvalue	observed	pvalue	observed	pvalue		observed	pvalue
SOC (gC/kg)	↓	↓	NS	↑	NS	↓	NS	↑	=	NS
Stock SOC (kg/m ²)	↓	↓	NS	↑	NS	↓	NS	↑	=	NS
POC1 (gC/kg)	↓	↓	†	↑	NS	↓	NS	↑	↑	†
POC1/TOC	↓	↓	NS	↑	NS	↓	NS	↑	↓	NS
PC (gC/kg)	↓	↓	NS	↓	NS	↑	NS	↑	↑	†
RC (gC/kg)	=	↓	NS	↓	NS	↑	NS	=	↑	†
PC/TOC	↓	↓	NS	↓	NS	=	NS	↑	↑	†
RC/TOC	↑	↑	NS	↑	NS	=	NS	↓	↓	†
HI (mg CH g/C)	↓	↓	NS	↓	NS	↓	NS	↑	↑	NS
OIRE6 (mg O ₂ g/C)	↑	↑	NS	↑	NS	↓	NS	↓	↓	NS
C:N	↓	↓	***	↓	NS	↓	NS	↑	↑	**
I index	↓	↓	*	↑	NS	↑	NS	↑	↑	NS
R index	↑	↑	NS	↓	NS	=	NS	↓	↓	NS
T30_CO2_OX (°C)	↑	↑	**	↑	NS	↑	NS	↓	=	NS
T50_CO2_OX (°C)	↑	↑	*	↑	NS	=	NS	↓	=	NS
T70_CO2_OX (°C)	↑	↑	*	↑	NS	↓	NS	↓	↓	NS
T90_CO2_OX (°C)	↑	↑	**	↑	NS	↓	NS	↓	↓	†
T50_PYR (°C)	↑	=	NS	=	NS	↓	NS	↓	↓	NS
T90_PYR (°C)	↑	↑	NS	↑	NS	↓	NS	↓	↓	NS
T50_OX (°C)	↑	↑	*	↑	†	=	NS	↓	↓	NS
T90_OX (°C)	↑	↑	**	↑	NS	↓	NS	↓	↓	†
Consistent results		27/38		16/37		13/37			23/38	

compared to the warmer subalpine grassland topsoils. Following [Lugato et al. \(2021\)](#) and using a space-for-time approach while such an approach on SOC dynamics may be controversial, this result could be interpreted as a potential strong long-term warming-induced loss of SOC stocks (-30 % under a *ca.* + 3 °C climate change scenario; [Abramoff et al., 2019](#); [Cécillon, 2021](#); [Varney et al., 2020](#)). Beyond the effect of lower soil temperature, the climatic stabilization of topsoil soil organic matter at the alpine site is probably also related to its lower topsoil pH, which limits soil organic matter degradation ([Leifeld et al., 2009](#); [Smith et al., 2002a, 2002b](#); [Trumbore et al., 1996](#)), and its higher C/N ratio, commonly negatively correlated with nitrogen soil mineralization and nitrification rates ([Sahrawat, 2008](#) and references therein; [Zhang et al., 2012](#)). The SOC stocks estimated around 78 t C/ha for the alpine site and 56 t C/ha for the subalpine site over the first 10 cm are nevertheless higher than other estimations on grassland soils at comparable altitudes and depths (50 t C/ha for a subalpine grassland according to [Leifeld et al., 2009](#); 53 t C/ha mean in grasslands between 1900 and 2100 m a.s.l for [Saenger et al., 2013](#); 32 t C/ha for an alpine grassland in [Budge et al., 2011](#)).

11. Experimental warming and cooling effects on soil organic carbon contents and stocks

Our hypothesis that SOC content of mountain topsoil will decrease when exposed experimentally to warmer conditions and will increase in colder conditions was only partly supported by the results, after three years of treatment. On the one hand, we found a non-significant decrease of *ca.* 11 % in SOC content of the alpine warmed transplants. This result is consistent with other findings in a subalpine warming transplantation experiment which showed after 5 years a non-significant decreasing trend in topsoil SOC content warmed up by 2 or 4 °C ([Puisant, 2015](#)). In another transplant experiment in a shrub-steppe ecosystem, [Link et al. \(2003\)](#) showed a 32 % SOC content loss after 5 years of 5 °C warming in the first 5 cm of soil. Our results are also consistent with the decrease of about 8 % on topsoil SOC content (0–10 cm) observed by [Marañón-Jiménez et al. \(2018\)](#) on subarctic silt-loam andosols after seven years of 1.8 °C warming. For the two OTC-warmed topsoils, the SOC content responses were weak. Since the

OTCs were only installed during the growing season, this treatment had a different effect than a more drastic change in thermal regime with soil transplanting. [Tiwari et al. \(2021\)](#) also noted a limited effect of OTC warming (+1.5 °C) on alpine grassland soil respiration in contrast to the increased total respiration, suggesting an increase in carbon sequestration by plants. This highlights the effect of the intensity, the time and the type of warming experiment, supporting our hypothesis that the magnitude and time of soil organic matter response to warming is positively related to the magnitude of warming. Our results of SOC content maintaining with cooling is inconsistent with the results of [Wu et al. \(2017\)](#) who observed a significant decrease in SOC content on a soil cooling transplant experiment.

In temperate mountains, the duration of the snow cover plays an important role in ecosystem functioning ([Choler, 2015](#)). It is likely that the combined effect of the increasing soil temperature and the extension of the growing season affected the microbial activity of the alpine warmed transplants, which explains a slight decrease in SOC content. Microbial decomposition activity is largely temperature-dependent and SOC is generally greater in cold and wet climates compared to hot, dry climates because carbon loss is more limited than carbon input ([Jobbágy & Jackson, 2000](#); [Streit et al., 2014](#); [Trumbore, 2000](#); [von Lütow and Kögel-Knabner, 2009](#); [Wiesmeier et al., 2019](#)). In addition to its effect on microbial activity, warming affects the physical protection of organic matter within organo-mineral complexes and may increase its vulnerability ([Conant et al., 2011](#)). Some authors who have observed the decline in SOC content with warming suggest that SOC losses only occur early in warming processes and that carbon mineralization decreases over time due to substrate limitation or a decline in microbial biomass ([Allison et al., 2010](#); [Li et al., 2019](#); [Walker et al., 2018](#)). Here, the weaker topsoil soil organic matter stock in the warmer subalpine site does not support this, suggesting a long-term sustained warming-induced SOC loss (see above). Contrary to previous reports by [Melillo et al. \(2002\)](#) and [Sistla et al. \(2013\)](#) in other ecosystems, the warming-induced increase in plant production observed on our alpine warmed transplants soils by [Bektaş et al. \(2021\)](#) did not fully compensate SOC losses. There have been conflicting results about SOC balance with ecosystem warming in a number of studies ([Poeplau et al., 2020](#); [Qin et al., 2015](#); [Tiwari et al., 2021](#); [Zhou et al., 2016](#)). Longer time-period of experimentation is

needed, to verify whether the trend of incomplete SOC output compensation by increased SOC inputs by plants.

12. Biogeochemical soil organic matter signature response to experimental climate change

Consistent with other studies, our results indicate that the alpine site topsoil contains more thermally labile soil organic matter than the warmer subalpine site (Budge et al., 2011; Hou et al., 2019; Leifeld et al., 2009). Generally, our findings on the biogeochemical signature of SOM were consistent with our hypotheses, especially for transplanted soils (Tables 3). The warming-induced SOC loss upon transplanting increased the thermal stability of remaining SOC. Conversely, transplanting soils from the subalpine site to the alpine site (i.e., cooling) decreased the overall SOC thermal stability. Our findings therefore indicate a preferential degradation of thermally labile SOC when the alpine topsoil is abruptly exposed to warmer subalpine conditions, which is consistent with the monitoring by Priezel et al. (2016) in German Alps forest soils, and also with our own observations of a more thermally stable topsoil SOC at the subalpine site than at the alpine site. The fact that the proportion of pyrolysable carbon (POC1/TOC, PC/TOC) did not decrease significantly in alpine warmed transplants does not mean that the labile SOC pool remained unchanged. Indeed, no currently available SOC fractionation method can reliably isolate non-composite SOC fractions in terms of soil carbon turnover time (Smith et al., 2002a, 2002b; von Lützow et al., 2007), including Rock-Eval® thermal analysis (Cécillon et al., 2021). On the other hand, our results showed increased values of Rock-Eval® temperature parameters (accounting for the majority of the SOC analyzed, i.e. $T_{xx_CO_2_OX}$ and T_{xx_OX}) with soil warming, indicating that the SOC remaining after experimental warming is more thermally stable.

It is likely that more significant changes in the SOC biogeochemical signature will take longer to establish. Poeplau et al. (2019) reported significant changes in the bulk chemistry and thermal stability of the SOC after a six-and-a-half years intense warming of a high latitude grassland soil. They showed that the warming-resistant SOC was thermally stable, and also depleted in hydrocarbons and enriched in oxygen, a trend that is found in our experimental warming treatment, although not significant. It is worth noting that our results showed that topsoil soil organic matter was significantly H-depleted and O-enriched at the warmer subalpine site compared with the alpine site. Our results are also consistent with the observations of several authors, who had observed an initial preferential depletion of the labile SOC pool during soil warming experiments (Eliasson et al., 2005; Link et al., 2003; Marañón-Jiménez et al., 2019). The labile SOC fraction (thermally labile, H-enriched) is an easily available substrate providing more energy to microorganisms than the biogeochemically stable SOC fraction (Barré et al., 2016; Li et al., 2019). Thus, SOC resistant to warming is characterized by higher biological stability, which would require higher energy budgets to be degraded (Barré et al. 2016, Marañón-Jiménez et al., 2018). With cooling, we observed the opposite effect compared to warming (decrease in soil organic matter thermal stability), indicating that the newly accumulated SOC is thermally more labile. This result also points towards topsoil soil organic matter preservation from decomposition by climatic conditions unfavorable to the mineralization activity of microorganisms at the colder alpine site (Budge et al., 2011; Hou et al., 2019; Leifeld et al., 2009; Martinsen et al., 2011; Saenger et al., 2015; Sjögersten et al., 2011).

Contrary to our hypothesis, we did not detect clear differences in the responses of alpine and subalpine soil organic matter signature to OTC-warming. A possible explanation is that the warming was not pronounced enough or implemented over a too short experimental period to show significant changes. Poeplau et al. (2019) showed that a warming of 9.9 °C was necessary to detect significant changes in the Rock-Eval® signature of soil organic matter. Nevertheless, there was a consistent, though not significant, trend towards an increased SOC thermal stability

for the alpine warmed OTC soil, a trend that was not observed for the subalpine warmed OTC. This suggests a greater sensitivity of alpine topsoil soil organic matter biogeochemical signature to warming than the subalpine topsoil, but the lack of statistical significance prevents us from going further in our conclusions.

13. Conclusions

Our results showed that the transplantation of high elevation alpine grassland soils to a warmer-subalpine site led to the loss of thermally labile topsoil SOC after three years of experiment. These warming-induced SOC losses modified the biogeochemical signature of the remaining SOC, which was characterized by a more thermally resistant signature. This confirms the presence of an easily mineralizable SOC fraction in alpine grassland topsoils that is sensitive to a three-years climate change of + 3 °C. Such warming intensity would, on long-term, decrease significantly SOC stocks in this alpine grassland ecosystem, as reflected by the observed differences of SOC stocks between the alpine and the subalpine sites. On the other hand, weak-intensity warming, represented by OTC experiments, is not expected to have a short-term measurable impact on SOC stocks. The continued monitoring of SOC stock and plant productivity in the study site will provide further evidence on the dynamics of long-term carbon inputs and outputs.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Norine Khedim reports financial support was provided by French National Research Agency.

Data availability

Data available in supp materials

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2022.116238>.

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