Can composition and physical protection of soil organic matter explain soil respiration temperature sensitivity?

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Abstract The importance of soil organic matter (SOM) in the global carbon (C) cycle has been highlighted by many studies, but the way in which SOM stabilization processes and chemical composition affect decomposition rates under natural climatic conditions is not yet well understood. To relate the temperature sensitivity of heterotrophic soil respiration to the decomposition potential of SOM, we compared temperature sensitivities of respiration rates from a 2-year long soil translocation experiment from four elevations along a ∼3000 m tropical forest gradient. We determined SOM stabilization mechanisms and the molecular structure of soil C from different horizons collected before and after the translocation. Soil samples were analysed by physical fractionation procedures, ^{13}C nuclear magnetic resonance (NMR) spectroscopy, and differential scanning calorimetry (DSC). The temperature sensitivity (Q_{10}) of heterotrophic soil respiration at the four sites along the elevation transect did not correlate with either the available amount of SOM or its chemical structure. Only the relative distribution of C into physical soil fractions correlated with Q_{10} values. We therefore conclude that physical fractionation of soil samples is the most appropriate way to assess the temperature sensitivity of SOM.

Keywords Soil organic matter · Q_{10} · Fractionation · ^{13}C Nuclear magnetic resonance · Differential scanning calorimetry

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Introduction

Soil organic matter comprises a large range of carbon (C) compounds mixed with mineral particles. SOM originates from plant debris that is progressively broken down by a range of organisms and incorporated into the soil matrix; due to variable susceptibility to degradation some components are rapidly decomposed, whilst others decompose more slowly and accumulate in the soil over time. However, not only the chemical composition but also a variety of other stabilization mechanisms determines the fate of C as it is processed through the soil medium.

Mechanisms protecting SOM against decomposition can be divided into two main groups: mineral

protection and biochemical recalcitrance (Christensen 2001; Helfrich et al. 2007). Soil organic matter can be physically protected within aggregates (Golchin et al. 1994; Pulleman and Marinissen 2004) or adsorbed on the reactive surfaces of mineral particles (Schulten and Leinweber 2000; Kaiser and Guggenberger 2003) with both processes inhibiting microbial access to the organic substrate (Krull et al. 2003; von Lutzow et al. 2006). Biochemical recalcitrance is the 'inherent' chemical stability of the molecular components of SOM; recalcitrant molecules are less attractive than labile molecules as a C resource for microbes (Sollins et al. 1996; Six et al. 2002). Conceptual models of SOM decomposition separate the C substrate into several pools with different turnover rates (Smith et al. 1997; Davidson and Janssens 2006). Labile pools within these conceptual SOM compartments are defined by fast C exchange rates resulting from ready access to, and easy breakdown by microbes, whereas more stable pools comprise chemically recalcitrant or mineral protected SOM compounds.

Although these processes have been intensively studied, it is still a matter of debate whether labile or recalcitrant SOM pools have the higher temperature sensitivity. In view of the potential future global warming, there is a need to understand the response of SOM to rising temperatures. Liski et al. (1999) and Giardina and Ryan (2000) reported that the decomposition of recalcitrant SOM was insensitive to temperature, whereas Knorr et al. (2005) and Leifeld and Fuhrer (2005) found higher temperature sensitivities for recalcitrant SOM pools than for labile pools, consistent with kinetic theory (Fierer et al. 2005). Further studies have concluded that labile and recalcitrant SOM pools have similar temperature sensitivities (Fang et al. 2005; Conen et al. 2006). However, even slight differences in experimental approaches can lead to inconsistent results (Conen et al. 2008a).

Most approaches to quantify the temperature sensitivity of different soil C pools are based on fractionation of soil samples followed by incubation in controlled environmental conditions (Leifeld and Fuhrer 2005; Conen et al. 2006), or by fitting of mathematical functions to different C pools in order to match experimental data (Fang et al. 2005; Knorr et al. 2005). Here, we use a different approach by relating temperature sensitivities of SOM decomposition observed under field conditions to SOM

protection mechanisms determined from samples analyzed in the laboratory. The temperature sensitivity estimates derive from a translocation experiment of two years duration along a tropical forest elevation gradient spanning almost 3000 m in altitude (Zimmermann et al. 2010). This has the advantage over incubation experiments that SOM decomposes under more representative 'natural' climatic and edaphic conditions. Respiration rates of soil cores installed at sites with a mean annual temperature difference of 10°C were then compared, and temperature sensitivities calculated as Q_{10} values. The degree of mineral protection was quantified by soil fractionation and SOM composition determined by ^{13}C nuclear magnetic resonance spectroscopy and differential scanning calorimetry. We hypothesise that physical and chemical analysis of the soil substrates can be used to predict the temperature sensitivity of SOM in tropical forest soils, and that stabilization mechanisms affect the temperature sensitivity of SOM decomposition.

Methods

Study sites and experimental setup

To analyze the influence of warming on soil respiration rates, soil cores were translocated among four elevations along a continuous tropical forest gradient in Peru, ranging from upper montane cloud forest to lowland rainforest with a difference in mean annual temperature of 13.9°C (Table 1). Altitudinal gradients allow studying the impact of climate on the terrestrial C cycle under otherwise similar environmental conditions and are therefore ideal natural laboratories for translocation experiments (Malhi et al. 2010). The selected sites were at the border of permanent 1 ha study plots of the Andes Biodiversity and Ecosystem Research Group (ABERG, www.andesconservation.org). These sites were chosen to be representative for the corresponding elevations, and show unique vegetative features and climate with little seasonal variation (Salinas et al. 2010). Dominant tree families changed from Clusiaceae and Cunoniceae at 3030 m asl, to Clethraceae at 1500 m asl, to Elaeocarpaceae and Fabaceae at 1000 m asl, and Moraceae and Fabaceae at 200 m asl. The soils at the sampling sites were not different from the 1 ha permanent plots (Girardin et al. 2010), and were classified after FAO as:

Table 1 Site and soil description along the transect

	Property	3030 m	1700 m	1000 m	220 m
	MAT (°C)	12.5	18.3	21.3	26.4
	MAP (mm)	1700	2600	3100	2700
Soil layers					
Oh	Depth (cm)	17	7	3	1
	Density (g cm^{-3})	0.063	0.053	0.166	0.41
	pH (CaCl$_2$)	2.4	3.3	3.4	3.4
	% C	47.4	41.3	24.9	5.7
	δ^{13}C	−27.13	−29.08	−28.91	−29.39
	C/N	25	15	20	14
	C stock (kg m^{-2})	5.04	1.53	1.24	0.23
A	Depth (cm)	15	7		
	Density (g cm^{-3})	0.36 (± 0.09)	0.39 (± 0.03)		
	Texture	12/72/16	13/71/16		
	pH (CaCl$_2$)	3	3.5		
	% C	14.5	10.5		
	δ^{13}C	−25.79	−27.16		
	C/N	17	14		
	C stock (kg m^{-2})	7.76 (± 0.47)	2.85 (± 0.52)		
B1	Depth (cm)	15	15	25	25
	Density (g cm^{-3})	0.52 (± 0.3)	0.39 (± 0.5)	0.44 (± 0.11)	0.69 (± 0.02)
	Texture	7/79/14	69/27/4	13/68/19	44/41/10
	pH (CaCl$_2$)	3.9	4.0	4.1	3.7
	% C	7.9	4.8	4.9	1.3
	δ^{13}C	−24.91	−25.87	−27.28	−26.83
	C/N	14	18	13	9
	C stock (kg m^{-2})	6.22 (± 0.34)	3.92 (± 0.24)	5.42 (± 0.26)	2.29 (± 0.92)
B2	Depth (cm)	20	28	25	25
	Density (g cm^{-3})	0.60 (± 0.03)	0.45 (± 0.03)	0.62 (± 0.01)	0.76 (± 0.05)
	Texture	12/52/36	31/54/15	9/66/25	49/36/15
	pH (CaCl$_2$)	4	4.4	4.2	3.8
	% C	5.5	4.0	2.0	0.8
	δ^{13}C	−24.23	−24.97	−25.38	−24.96
	C/N	13	17	11	11
	C stock (kg m^{-2})	6.67 (± 0.47)	4.99 (± 0.35)	3.08 (± 0.03)	1.59 (± 0.07)
	Total C stock (kg m^{-2})	25.69 (± 1.28)	13.29 (± 1.11)	9.75 (± 0.29)	4.11 (± 0.99)

Mean annual temperatures (MAT) and precipitation (MAP) were measured from 2007–2009. Bulk soil densities and C stocks are given with standard variations ($n = 3$), and values for texture represent proportions (%) of sand/silt/clay. Detailed sampling procedures and analytical methods are given in Zimmermann et al. (2009)

histic Lithosol at 3030 m asl, umbric Gleysol at 1500 m asl, fluvic Gleysol at 1000 m asl and haplic Ferralsol at 200 m asl.

At each site, twelve 50 cm long intact mineral soil cores with a diameter of 10 cm were excavated; three of these cores were then re-installed at the same site as controls (hereafter referred to as 'control'), and the other cores translocated to the three other elevations (hereafter referred to as 'warming', if translocated down the gradient) (Zimmermann et al. 2009). The length of 50 cm was chosen because this was the total depth of the mineral horizon at the highest, most

shallowest sampling site. The organic-rich topsoil layers (O) were collected separately prior to excavation, their density calculated and the same amount of organic material as was present at the sampling site refilled into the tubes after the installation of the cores at the new sites. To maintain the same rainfall amount per m^2 as at the site of origin, translocated tubes were capped with reduction collars or expansion funnels. Any new litter input was continuously removed, and root ingrowth stopped by installing a 63 μm nylon mesh at the bottom of the tubes.

Initial mineral soil samples with 3 replicates were collected in metal tubes of 35 mm diameter and stratified according to the soil horizons into humic layer (Ah) and mineral layers B1 and B2 to quantify bulk soil densities. Samples from the same site and horizons were then bulked for further chemical analysis and physical fractionation. The organic topsoils were collected by cutting a piece of 50 × 50 cm and measuring its volume and weight. At each elevation one subsample of the organic topsoil layer from each origin was taken 12 and 24 months after the start of the translocation to analyse its chemical composition by means of NMR. A detailed description of the experimental setup is given in Zimmermann et al. (2009).

Physical fractionation

The degree of SOM stabilization through chemical transformation and association with mineral particles can be expressed as the age of mineral-associated organic matter (MOM) relative to the age of particulate organic matter (POM) (Conen et al. 2008b). This concept is based on the assumption that unprotected SOM (POM) undergoes decomposition, during which some of the organic C is lost as CO_2, some organic N is mineralised, and part of the C and N is re-synthesized by micro-organisms. Re-synthesis reduces the initially high C:N ratio of mainly plant derived POM as it becomes increasingly similar to the lower C:N ratio of the soil microbial community (Kramer et al. 2003). Preferentially, ^{14}N is mineralised and lost from the POM, resulting in an increase of $\delta^{15}N$ values as it becomes MOM (Liao et al. 2006). The same applies to the stable isotope ratios of C. Knowledge of the relative proportions of POM and MOM, together with their $\delta^{15}N$ values and C:N ratios, enables the calculation of their relative turnover rates. This allows statements such as 'MOM has an *n*-times longer turnover rate than POM', or, '…is *n*-times more stable than POM', as the factor of relative increase in stability (*n*) has been shown to be related to the relative radiocarbon ages of these fractions (Conen et al. 2008b). Further, the same approach enables to estimate the fractions of C (*f*C) and N (*f*N) that were lost during the transformation of POM to MOM.

The POM fractions of the initial mineral soil layers (Ah, B1 and B2) were isolated by suspending 30 g of bulk soil material (< 2 mm) in 150 ml water and dispersing with an ultrasonic probe type with an energy application of 22 J/ml. The suspension was then sieved to 63 μm, and the fraction > 63 μm density-separated at 1.8 g/cm^3 with sodium polytungstate. Carbon in particles < 63 μm (silt and clay) and sand plus aggregates (> 63 μm, density > 1.8 g/cm^3) are assumed to be protected through mineral associations (Zimmermann et al. 2007; Leifeld et al. 2009). Total C and N values of bulk soils and fractions were measured together with $\delta^{13}C$ isotopes with a Finnigan Delta Plus XL mass spectrometer at the University of St Andrews, UK, and $\delta^{15}N$ isotopes with a Finnigan Delta Plus XP at the University of Basel, Switzerland. Isotopic signatures are given as per mill (‰) deviations from the international Vienna Pee Dee Belemnite standard.

Nuclear magnetic resonance

The C composition of the organic topsoils was analysed by means of solid-state cross polarization magic angle spinning (CP/MAS) ^{13}C NMR spectroscopy. The spectra of the original topsoils, the control soil cores that remained at the same sites for 24 months, and the cores that were translocated from their original site to the warmest site at 200 m asl (therefore with the potentially largest alterations in C composition) were recorded at the University of Durham, UK, using a Varian VNMRS spectrometer operating at 100.56 MHz with a 4 mm rotor MAS probe. The spectra were plotted in the chemical shift range from 0 to 200 ppm, and the integrated total signal intensity apportioned among different compound classes in the samples. The relative contributions of the different signal regions were corrected for spinning sidebands at 111 ppm. Chemical shift regions for C were identified as follows: alkyl (0–46 ppm),

O-alkyl (46–92 ppm), di-O-alkyl (92–110 ppm), aryl (110–140 ppm), O-aryl (140–165 ppm) and carbonyl (165–190 ppm) C (Knicker and Ludemann 1995; Baldock and Smernik 2002; Alarcon-Gutierrez et al. 2008). The degree of decomposition of SOM was quantified by the alkyl : O-alkyl ratio (Baldock and Smernik 2002; Alarcon-Gutierrez et al. 2008) and the aryl : O-alkyl ratio, which was suggested to be the better indicator for SOM decomposition in free POM (Kölbl and Kögel-Knabner 2004).

Differential scanning calorimetry

The thermal stability of all initial soil layers was determined using a differential scanning calorimeter DSC100 (TA Instruments) at ART Reckenholz Zürich, Switzerland. Finely ground and dried samples were diluted with Al_2O_3 and 0.5 mg C equivalent weighed into an open aluminium pan and then heated under a steady synthetic air flow of 50 ml/min from room temperature to 600°C at a heating rate of 20°C/min. An empty pan served as reference (Leifeld 2007). The exothermic heat flows were recorded, normalised to 150°C, and the 50% burn off values (i.e. the temperature at which 50% of the total energy was released) calculated. Grisi et al. (1998) separated DSC heat flows of tropical soils into a labile low temperature region and a high temperature region deriving from more strongly humified SOM. Lopez-Capel et al. (2005) attributed the exothermic heat flow between 300 and 350°C to relative labile SOM compounds comprising carboxylic and aliphatic C, and peaks between 400 and 450°C to SOM compounds rich in aromatic structures. Manning et al. (2005) assigned lower temperature peaks to relatively labile cellulose, and the peaks at higher temperatures to more refractory lignin and related materials such as polyphenolic and condensed structures (Rovira et al. 2008). Peaks above 500°C are considered to originate from thermal stable charcoal residues (Lopez-Capel et al. 2005; Leifeld 2007; Rovira et al. 2008). Note that aliphatic C is thermally labile but considered biochemically stable.

Temperature sensitivity of heterotrophic respiration

To calculate the temperature sensitivity of SOM decomposition, we analysed the heterotrophic respiration rates of the soil cores, which were measured fortnightly from April 2007 to March 2009 using a Li-Cor 8100 (Li-Cor, Nebraska, USA) portable infrared gas analyser equipped with a proprietary 10 cm survey chamber. The temperature sensitivity was determined following the approach of Conant et al. (2008), by which the temperature dependence of SOM decomposition is calculated through comparison of the time elapsed during the decomposition of a defined amount of C at different temperatures in order to avoid comparison of different SOM qualities. This method takes into account declining decomposition rates over time, which might occur following the removal of the SOM supply from plant growth (Kirschbaum 2004; Hartley and Ineson 2008). From the bi-weekly respiration measurements, we interpolated the number of days it took to respire any 0.1% fraction of SOC from the total C in the cores for the soils originating from the same site but installed at 3030 m asl (t_{3030}) and at 1000 m (t_{1000}), as these two sites have a difference in mean soil temperature (T_s) of ~ 10°C. The ratio of the time periods it took to respire this 0.1% portion of C is the temperature sensitivity of this particular C fraction:

$$Q_{10} = t_{3030}/t_{1000} \tag{1}$$

Details of the calculations for Q_{10} values are given in Zimmermann et al. (2010). Correlations among Q_{10} values and C distributions into physical fractions and chemical properties were calculated by means of Pearsons Product Moment Correlations.

Results and discussion

Soil carbon stocks and properties along the gradient

The amount of C in the top 50 cm of the original mineral soil plus the organic layers above increased steadily with altitude (decreasing mean annual temperatures). The C-stocks ranged from 4.11 kg C/m^2 at 200 m asl to 25.69 kg C/m^2 at 3030 m asl (Table 1) and were within the range of reported total soil C-stocks in other neotropical montane forests. Schrumpf et al. (2001) quantified C-stocks along an altitudinal gradient in Ecuador from lower montane rain forest to paramo grassland sites with forest soil C-stock increasing from 14.6 kg C/m^2 at 1100 m asl

to 29.5 kg C/m^2 at 2650 m asl, and Schawe et al. (2007) measured total soil C-stocks of 20.4 to 52.7 kg C/m^2 in tropical montane forests in Bolivia, ranging from 1700 to 3300 m in altitude.

The two higher sites along the gradient had thicker organic soil layers (O) than the two lower rainforest sites, which had only thin organic-rich topsoil layers followed by uniform mineral B layers. A change in the thickness of organic layers in tropical cloud forests was also observed for the altitudinal gradients reported by Schrumpf et al. (2001) and Schawe et al. (2007), whereby the amount of C in the organic layers increased with altitude from 10 kg C/m^2 at 1700 m asl to about 20 kg C/m^2 at 3300 m asl in Bolivia, and the thickness of the organic layers increased linearly by 4 cm/100 m from 1950 to 2450 m asl in Ecuador (Wilcke et al. 2008).

Various environmental parameters including temperature, moisture, radiation, vegetation and geology influence soil weathering and texture, litter stocks and composition, and C allocation to above- or below-ground components, all of which cause changes in soil C-stocks (Roderstein et al. 2005; Körner 2007; Gräfe et al. 2008). An important factor limiting decomposition along this study transect might be the observed low pH values (pH range of 2.4–4.4, with lower pH values at higher altitudinal sites). Low pH values can limit bacterial growth rates (Walse et al. 1998) and hinder microbial activities (Kok and Vandervelde 1991, Fierer and Jackson 2006), which reduces decomposition rates and can lead to soil C accumulation if plant growth is not suppressed. As the pH values increased down the elevation gradient, the pH constraint on decomposition may have been larger at higher altitudes.

Stabilization of soil organic matter

Soil organic matter can be physically and chemically protected against microbial decomposition within the soil matrix. Inclusion of SOM in aggregates separates the microbes and their enzymes physically from the substrate, limiting decomposition (Cambardella and Elliott 1992; Golchin et al. 1994; Six et al. 2002). Silt and clay particles bind SOM by adsorption on mineral surfaces, protecting SOM chemically against decomposition (Baldock and Skjemstad 2000; Kaiser and Guggenberger 2003; Krull et al. 2003). By fractionating mineral soil samples into POM (non-

aggregated particles lighter than 1.8 g/cm^3) and MOM (stable aggregates plus sand together with silt and clay sized particles), SOM can be divided into protected and unprotected portions (Conen et al. 2008b; Leifeld et al. 2009). The organic topsoils can be assumed to be unprotected, as there is minimal association with mineral particles.

The highest relative portion of unprotected C was obtained for the soil cores from 3030 m asl with 20% of total C stored in the organic layer and 13% in POM, followed by the soil originating from 200 m asl (6% topsoil, 18% POM) and then the soils from 1000 m asl (14% topsoil, 5% POM) and 1500 m asl (12% topsoil, 3% POM) (Fig. 1). The highest relative portion of POM was found at 200 m asl, where the sampling site was situated on an old river terrace. This site had a relative low clay content (10–15%), but a high sand content (44–49%), which probably limited the incorporation of POM into aggregates, as only 16% of total C was protected by aggregation. However, the absolute amounts of unprotected C decreased exponentially along the gradient from 8.48 kg C/m^2 at 3030 m asl to 1.99 kg C/m^2 at 1500 m asl and 1.72 kg C/m^2 at 1000 m asl to 0.986 kg C/m^2 at 200 m asl (unprotected C [kg/m^2] $= 0.627 \times e^{0.0009 \times \text{altitude [m]}}$, $r^2 = 0.99$, $P < 0.01$). Thus, the higher elevation sites had the larger absolute amounts of unprotected C.

The relative degree of physical and chemical SOM protection (n) can be further determined for mineral layers using the method introduced by Conen et al.
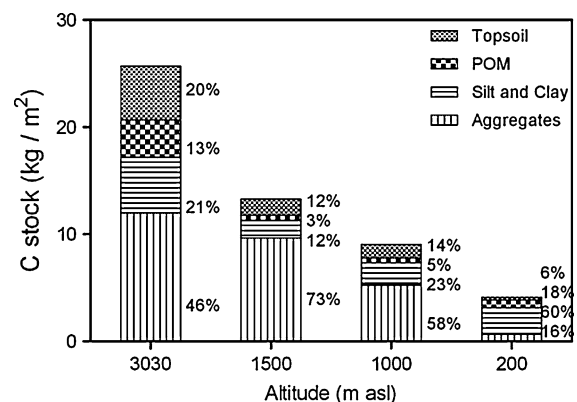
Fig. 1 Soil carbon stocks (organic layer plus 50 cm of mineral soil) along the gradient separated into organic topsoils, particulate organic matter (POM), stable aggregates, and silt and clay particles. Organic matter in stable aggregates, silt and clay particles is mineral associated (MOM)

(2008b), which compares the turnover rate of MOM relative to that of POM within a single soil layer. For all sites, where more than one layer was measured, *n* increased with depth, suggesting a more efficient SOM stabilization in deeper soil layers through transformation and association with mineral particles compared to that in shallower layers (Table 2). The efficiency of stabilization *n* declined with altitude. Furthermore, the proportions of C (*f*C) and N (*f*N) lost during transformation were larger at lower elevations, which means that a smaller proportion of POM remained as MOM after transformation at lower elevation sites, probably because of higher turnover rates at the warmer sites (Raich et al. 2006).

As unprotected SOM is assumed to be labile and a readily available C source for microbes (Olk and Gregorich 2006), the smaller amounts of unprotected SOM at lower sites indicate that SOM at lower sites is more rapidly transformed than at the higher elevation sites, due to environmental conditions that are more favourable for microbial activity.

Biochemical stability of organic topsoils

The complex chemical composition of SOM slows down decomposition and can be considered to be a form of 'biochemical protection'. This chemical complexity can be inherent to the original plant material, arise from newly formed microbial residues, or may result from condensation and complexation during the breakdown of plant litter (Six et al. 2002). The change in the chemical composition of SOM during decomposition has been graduated into several conceptual stages (Baldock et al. 1992; Quideau et al. 2000). In a first step (stage 1), microbes attack plant debris, dominated by *O*-alkyl components. The biochemically more labile components are preferentially decomposed, leading to an accumulation of (*O*-) aryl and alkyl structures. The remaining *O*-alkyl component of SOM therefore shifts from plant to microbial origin. In the second stage (stage 2), fungi decompose lignin, which reduces the quantity of aromatic structures and exposes additional labile *O*-alkyl groups to microbial attack. The biochemically most stable SOM compound is alkyl-C, which accumulates during the decomposition process (stage 3) and is also simultaneously formed by microorganisms (Baldock and Skjemstad 2000). A crucial assumption for this conceptual sequence of decomposition stages is the full access of soil organisms to C substrate.

One of the most comprehensive analytical tools to describe the complexity of SOM is ^{13}C NMR spectroscopy, by which the relative proportions of the different C compounds in SOM can be quantified (Knicker and Ludemann 1995; Mathers and Xu 2003; Leifeld 2006). Only NMR spectra of the organic topsoils were recorded, as these were not physically or chemically protected. We analyzed samples from before the translocation of the SOM monoliths

Table 2 Relative carbon stability in mineral horizons as revealed by fractionation into particulate organic matter (POM) and mineral-bound organic matter (MOM is silt and clay plus aggregate fraction) and shifts in δ^{15}N and C:N ratios.

Altitude (m)	Horizon	C distribution (%)		N distribution (%)		C:N			δ^{15}N (‰)			*f*N	*f*C	Age MOM/ Age POM
		POM	MOM	POM	MOM	Bulk	POM	MOM	Bulk	POM	MOM	Bulk	Bulk	Bulk
3030	Ah	39	61	27	73	17.2	24.1	14.6	3.5	2.1	4.0	0.6	0.77	6.9
3030	B1	6	94	4	96	14.3	21.9	14.1	7.1	4.8	7.2	0.8	0.81	91.8
3030	B2	2	98	1	99	13.3	35.7	13.2	7.6	4.7	7.6	0.9	0.91	696.7
1500	Ah	8	92	9	91	13.9	12.4	14.1	4.8	2.9	5.0	0.6	0.61	28.3
1500	B1	2	98	1	99	18.2	37.6	18.0	4.6	1.1	4.7	0.9	0.92	611.3
1500	B2	3	97	1	99	16.9	58.2	16.6	5.8	1.5	5.9	1.0	0.97	1061.2
1000	B1	8	92	4	96	13.4	24.3	12.9	5.5	1.4	5.7	0.9	0.94	198.0
1000	B2	3	97	1	99	10.5	37.3	10.2	6.5	2.0	6.5	1.0	0.97	985.3
200	B1	17	83	8	92	9.4	20.8	8.4	8.1	2.3	8.6	1.0	0.98	279.4
200	B2	22	78	7	93	10.5	32.3	n.d.	7.0	n.d.	n.d.	n.d.	n.d.	n.d.

Age MOM/Age POM is referred as degree of stability *n* in text, *n.d.* not defined

(originals) and following two years of depletion at the original sampling site (controls) and from monoliths that had been translocated to the warmest site 200 m asl (depletion and warming) (Fig. 2).

As quantified for the original organic topsoils along the transect, neither the alkyl : O-alkyl ratio ($r = -0.97$, $P = 0.33$) nor the aryl to O-alkyl ratio ($r = -0.44$, $P = 0.56$) correlated significantly with elevation. However, signal intensities of O-alkyl groups from carbohydrates and the methoxyl groups of lignin, polysaccharides and higher alcohols decreased steadily along the gradient from 59% at 3030 m asl to 31% at 200 m asl. At the same time, the contribution of aromatic-rich structures ((O-)aryl) such as lignin, tannin or charcoal (Chen and Chiu 2003; Skjemstad et al. 2008), increased from 12% at 3030 m asl to 44% at 200 m asl. Peaks of alkyl originating from methyl and methylene groups of lipids, fatty acids, aliphatic polymers and proteins (Knicker and Ludemann 1995) declined slightly in abundance with altitude, whereas carbonyl from aliphatic esters and amides did not show any major differences along the transect. The organic topsoils at 3030 m and 1500 m asl seemed therefore to be in stage 1 of the decomposition model of Baldock et al. (1992), whereas the corresponding SOM at 1000 m and 200 m asl were in transition to stage 2, as O-alkyl compounds were depleted, but recalcitrant aromatic structures were still not heavily decomposed. The topsoil layer from 200 m asl had a pronounced aryl component at around 130 ppm, indicative for condensed aromatic structures that may stem from vegetation fires (Knicker 2007).

The organic topsoils of the 'control' and 'warming' monoliths reacted to different extents to the field manipulations (Fig. 2). At 3030 m asl, the proportion of labile O-alkyl in the 'controls' decreased during depletion, whilst residual alkyl and carbonyl C components accumulated. The additional warming of 13.9°C induced by translocating the cores from 3030 m asl to 220 m asl further increased the relative proportion of aromatic structures. SOM in 'controls' and 'warming' cores both tended to convert from stage 1 to stage 2 of the decomposition model. The organic topsoil from 1500 m asl reacted similarly to depletion and the combination of depletion and warming (by 8.1°C). The relative C contributions from O-alkyl compounds decreased, leading to larger proportions of carbonyl and aromatic structures; thus
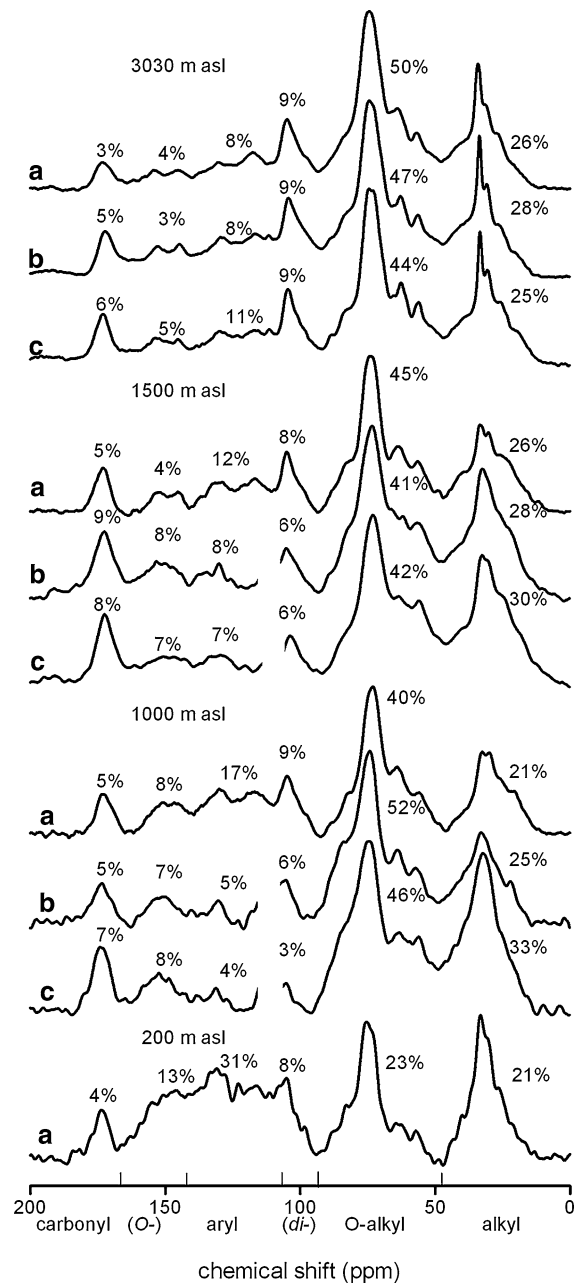
Fig. 2 CP ^{13}C nuclear magnetic resonance spectra of topsoil horizons at the start of the translocation experiment (**a**), and after 24 months of installation at the same site (**b**; depletion) or at 200 m asl (**c**; warming and depletion). Relative C contributions were assigned to carbonyl (165–190 ppm), phenolic (140–165 ppm), aryl (110–140 ppm), di-O-alkyl (92–110 ppm), O-alkyl (46–110 ppm) and alkyl (0–46 ppm)

a similar transformation process was experienced to that SOM observed from 3030 m asl. Different responses of the organic topsoils in the 'control'

and 'warming 'cores originating from 1000 m asl were observed. The proportions of *di-O*-alkyl and aryl compounds decreased, whilst *O*-alkyl and alkyl components accumulated in the 'controls'. This corresponds with decomposition stage 2, in which fungi decompose aromatically-rich structures and liberate labile *O*-alkyl groups, formerly protected within ligno-cellulose. Warming by 5.1°C (translocation of soil cores from 1000 m asl to 200 m asl) further enhanced the decomposition of released *O*-alkyl compounds and led to enhanced accumulation of alkyl components. No residual material of the organic topsoil from 200 m asl could be recovered after the two years, as all material was decomposed, illuviated down the soil cores or removed by soil fauna.

In conclusion, the chemical structures of the organic topsoil layers at higher altitudes were similar to that of plant litter in tropical forests (Zech et al. 1997, Skjemstad et al. 2008), whereas the organic layers at lower altitudes were stronger transformed and thus more stabilized. Both depletion and warming had the strongest impact on SOM composition at the lower elevation sites mainly caused by the substantial declines in the absolute amount of available substrate.

Thermal stability of carbon in soil layers

Thermally less stable C compounds are oxidised at lower temperatures, and more complex, polymerized and energy-rich components at higher combustion temperatures. Therefore, DSC can be used to describe the thermal stability of C in SOM. If we assign the definitions of SOC stability above to the results from soil samples along the altitudinal gradient, then the organic topsoils from 3030 and 1500 m asl are thermally the most stable, showing a double-peak signature typical of intact litter composed of cellulose and lignin (Fig. 3). With increasing soil depth, all thermograms shifted to lower temperatures, indicative for polymer breakdown and a smaller abundance of aromatic molecules (Leifeld 2008), peaking at around 380°C. The mineral layers at 1500 and 1000 m asl in particular contained some thermally very labile compounds, which were oxidized by 250°C. At the lowest site at 200 m asl, thermograms for all layers were similar, indicating a high degree of transformation throughout the soil profile. In addition, the small peak at around 530°C in the thermogram of this site and the shoulder at the similar temperature range in the spectra of the soil layer B2 from 3030 m asl indicate a high aromaticity of SOM,

Fig. 3 Thermal stability of soil organic matter as measured by differential scanning calorimetry (DSC) spectra for the different soil layers along the gradient (values for soil layer B2 from 1500 m asl were not available)
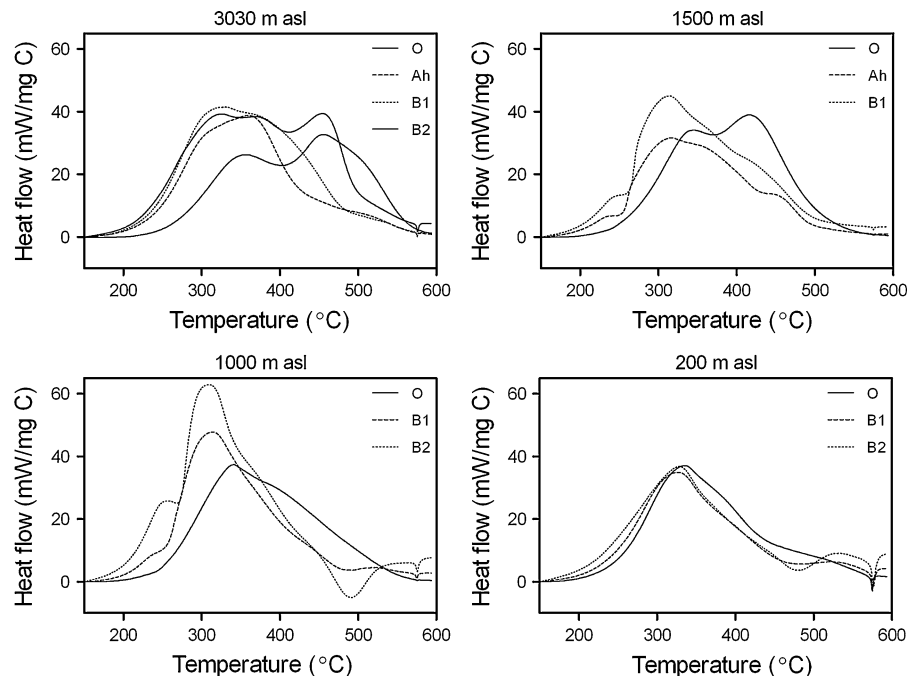
which can be attributed to the presence of charcoal (Leifeld 2007). These results in general are in accordance with the NMR results, showing a higher degree of decomposition down the altitudinal gradient.
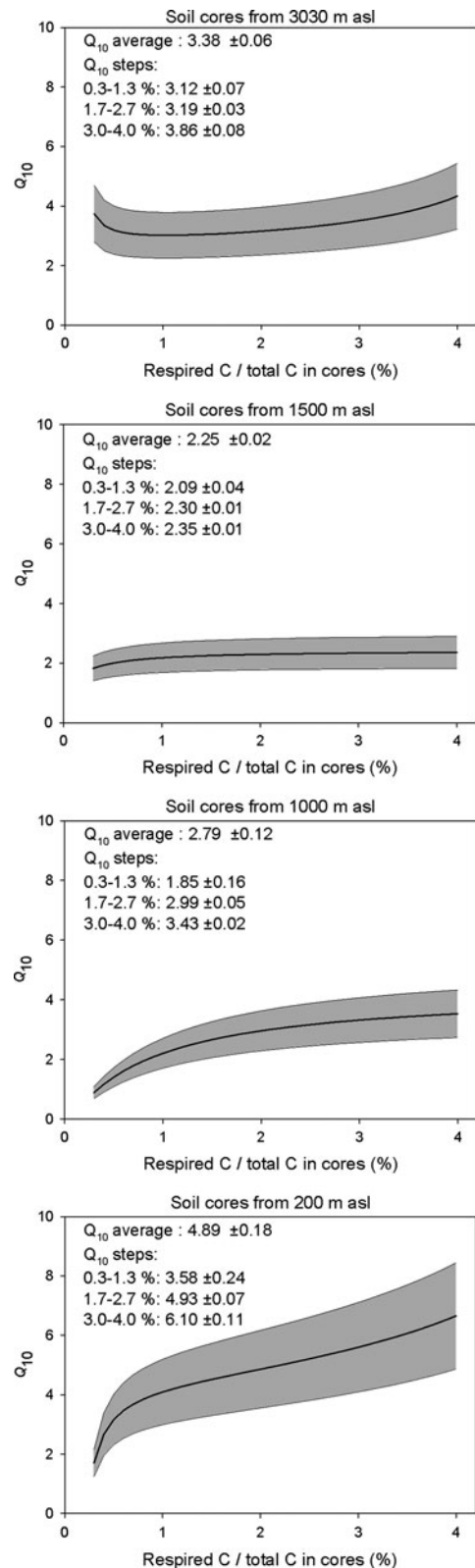
50% burn off temperatures as calculated from DSC analyzes have been shown to correlate positively with potential mineralization rates (Rovira et al. 2008; Kammer et al. 2009). This can be explained by the higher thermal stability of complex, polymeric molecules that constitute intact plant debris. The data in Fig. 4 reveals generally larger 50% burn off values throughout the profiles for higher altitudinal sites, indicating a larger share of largely undecomposed plant debris at higher elevations. An exception to this are the large 50% burn off values in the deeper soil layers at 200 m asl, which we attributed to the presence of charcoal. Furthermore, the proportion of undecomposed plant debris decreased with soil depth, except for soil layer B2 from 3030 m asl, which showed attributes of charred SOM.

Temperature sensitivity of decomposition

The temperature sensitivity of heterotrophic respiration rates over two years has been analysed for each soil in a previous study (Zimmermann et al. 2010). From this work, we calculated that the relative
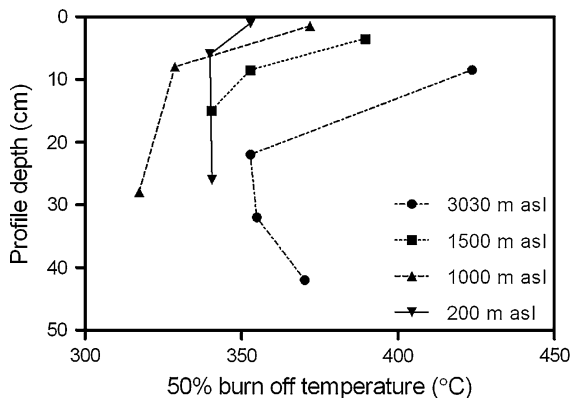
Fig. 4 50% burn-off temperatures as measured by DSC of all soil horizons plotted against their average soil depth (mineral and organic soil layers). These values describe the thermal stability of soil organic matter, i.e. at which temperature during combustion 50% of the C will be oxidised. (Values for soil layer B2 from 1500 m asl were not available)

amount of respired C per total C in the control core during two years increased down the study gradient from 4% at 3030 m asl to 25% at 200 m asl. Following translocation to 200 m asl, these losses increased to 16% for soil originating from 3030 m asl to 31.5% for the soil from 1000 m asl.

The average Q_{10} values ($\pm$ 1 standard error) were 3.38 ($\pm$ 0.06) for the soil from 3030 m asl, 2.25 ($\pm$ 0.02) for 1500 m asl, 2.79 ($\pm$ 0.12) for 1000 m asl and 4.89 ($\pm$ 0.18) for the soil from 200 m asl (Fig. 5), and were significantly different among each other (Kruskal–Wallis one way analysis of variance on ranks, $P < 0.01$ in all cases). For all four soils, Q_{10} values increased significantly as the proportion of respired C increased over time ($P < 0.01$ in all cases), but the average Q_{10} values were not correlated to mean annual temperatures at the site of origin ($r = 0.54$, $P = 0.46$) or the total amount of SOC ($r = -0.36$, $P = 0.64$).

Davidson and Janssens (2006) distinguished between two different types of temperature sensitivities. The 'intrinsic' temperature sensitivity of SOM decomposition is based on the kinetic properties of the various C compounds within SOM, whereas the 'apparent' temperature sensitivity is the observed response of SOM decomposition to changes in temperature, which can be suppressed by protection mechanisms of the substrate in the soil matrix and by other environmental conditions. The Q_{10} values given here represent the apparent temperature sensitivity, obscuring the intrinsic temperature sensitivities of the substrate. Intrinsic temperature sensitivity was shown to correlate positively with substrate complexity (Fierer et al. 2005). According to the NMR results for the unprotected organic topsoils, the intrinsic temperature sensitivity should therefore decrease with increasing elevation, as the degree of transformation of SOM declined with altitude in our study. But NMR spectra revealed no significant correlations

among average Q_{10} values and different C compounds, or aryl : O-alkyl ratios, or alkyl : O-alkyl ratios (Table 3). Also the change in Q_{10} values over time did not correlate with shifts in NMR spectra as quantified for the initial and depleted organic layers after 12 and 24 months (Table 3). Multiplying the relative contributions by the corresponding C-stocks reveals that the highest elevation site had 6.5 times more aromatic C structures than the lowest site, and 38 times more readily available *di-O*-alkyl compounds, complicating any simple interpretations of the intrinsic temperature sensitivity and SOM structure along the study gradient. Furthermore, the contribution of the organic topsoil layers to the CO_2 effluxes of the total soil columns, on which the Q_{10} calculations are based, are not distinguishable.

However, the largest parts of SOM at all sites were protected within the mineral layers, and the relative C distribution into the soil fractions POM, silt and clay, and sand plus aggregates correlated for all four sites with the average Q_{10} values (Table 3, $P < 0.04$ for all four sites), whilst the absolute C amounts within these fractions did not correlate with their temperature sensitivity (P values > 0.32, Table 3).

But whether intrinsic or apparent temperature sensitivity dominated the respiration rates initiated by the translocation is not distinguishable. The largest average temperature sensitivity was found for the soil from 200 m asl, which had the smallest C-stock, the largest proportion of complex substrates in the organic topsoil and the largest relative POM fraction. However, the second-highest average temperature sensitivity was found in the soil from 3030 m asl, which had the largest C-stock, the smallest proportion of complex substrates and the largest fraction of unprotected SOM (POM plus O layer). Finally, the mid elevation sites had the lowest temperature sensitivities and the lowest proportion of C stored in POM.

We therefore conclude that neither the absolute amount of C in different soil fractions nor the chemical composition of the soil layers act as simple indicators of the temperature sensitivity of SOM along this transect. However, the relative portion of C stored in the physical soil fractions correlated with the Q_{10} values of the respired C of the first two years. As smaller the relative proportion of C stored in the fractions sand plus aggregates was, as higher was the temperature sensitivity of the soil

Table 3 Pearson Product Moment Correlation parameters among temperature sensitivity values (Q_{10}) and chemical and physical soil properties

Average Q_{10} versus relative C distribution (%) into fractions:

$n = 4$	Organic topsoil	POM	Silt and clay	Sand plus aggregates		
r	−0.51	0.96	0.96	−0.99		
P	0.49	0.04	0.04	<0.01		

Average Q_{10} versus absolute C distribution (kg C/m^2) into fractions:

$n = 4$	Organic topsoil	POM	Silt and clay	Sand plus aggregates		
r	−0.24	0.14	0.22	−0.69		
P	0.76	0.86	0.78	0.32		

Average Q_{10} versus relative C distribution (organic topsoils only) into chemical shift regions as revealed by NMR:

$n = 4$	Carbonyl	Aryl	O-alkyl	Alkyl	aryl : O-alkyl	Alkyl : O-alkyl
r	−0.51	0.79	−0.77	−0.52	0.86	0.82
P	0.49	0.21	0.23	0.48	0.14	0.18

Change in Q_{10} over time versus relative C distribution (depletion of organic topsoils only) into chemical shift regions as revealed by NMR spectra of initial samples, and after 12 and 24 months:

Soil from 3030 m asl

$n = 3$	Carbonyl	Aryl	O-alkyl	Alkyl	Aryl : O-alkyl	Alkyl : O-alkyl
r	0.55	−0.31	−0.79	0.61	−0.03	0.69
P	0.63	0.8	0.42	0.58	0.98	0.52

Soil from 1500 m asl

$n = 3$	Carbonyl	Aryl	O-alkyl	Alkyl	Aryl : O-alkyl	Alkyl : O-alkyl
r	0.48	−0.37	−0.07	0.83	−0.25	0.65
P	0.67	0.95	0.95	0.37	0.84	0.55

Soil from 1000 m asl

$n = 3$	Carbonyl	Aryl	O-alkyl	Alkyl	Aryl : O-alkyl	Alkyl : O-alkyl
r	0.72	−0.96	0.25	0.92	−0.93	0.72
P	0.49	0.17	0.84	0.26	0.25	0.49

($r = -0.99$, $P < 0.01$), independent of the absolute C amounts. Therefore, physical fractionation of soil samples seems a suitable way to assess the temperature sensitivity of SOM decomposition. Furthermore, we showed that the method by Conen et al. (2008b) is useful in describing mineral protection mechanisms of SOM at different sites and soil depths, and that NMR can track conceptual decomposition stages for a diverse set of organic soil layers. The decisive component obscuring temperature sensitivities of SOM substrate analysis could be microbial communities, which might (Bradford et al. 2008) or not (Hartley et al. 2008) acclimate to elevated temperature. According to our findings, any microbial respiratory adaptation to higher temperatures could depend on access to substrate in combination with its quality rather than climatic constraints alone.

References

Alarcon-Gutierrez E, Floch C, Ziarelli F, Albrecht R, Le Petit J, Augur C, Criquet S (2008) Characterization of a

mediterranean litter by 13C CPMAS NMR: relationships between litter depth, enzyme activities and temperature. Eur J Soil Sci 59:486–495

Baldock JA, Skjemstad JO (2000) Role of the soil matrix and minerals in protecting natural organic materials against biological attack. Org Geochem 31:697–710

Baldock JA, Smernik RJ (2002) Chemical composition and bioavailability of thermally, altered Pinus resinosa (Red Pine) wood. Org Geochem 33:1093–1109

Baldock JA, Oades JM, Waters AG, Peng X, Vassallo AM, Wilson MA (1992) Aspects of the chemical structure of soil organic materials as revealed by solid-state C-13 NMR-spectroscopy. Biogeochemistry 16:1–42

Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, Mohan JE, Reynolds JF, Treseder KK, Wallenstein MD (2008) Thermal adaptation of soil microbial respiration to elevated temperature. Ecol Lett 11:1316–1327

Cambardella CA, Elliott ET (1992) Particulate soil organic-matter changes across a Grassland cultivation sequence. Soil Sci Soc Am J 56:777–783

Chen JS, Chiu CY (2003) Characterization of soil organic matter in different particle-size fractions in humid subalpine soils by CP/MAS C-13 NMR. Geoderma 117:129–141

Christensen BT (2001) Physical fractionation of soil and structural and functional complexity in organic matter turnover. Eur J Soil Sci 52:345–353

Conant RT, Drijber RA, Haddix ML, Parton WJ, Paul EA, Plante AF, Six J, Steinweg JM (2008) Sensitivity of organic matter decomposition to warming varies with its quality. Glob Change Biol 14:868–877

Conen F, Leifeld J, Seth B, Alewell C (2006) Warming mineralises young and old soil carbon equally. Biogeosciences 3:515–519

Conen F, Karhu K, Leifeld J, Seth B, Vanhala P, Liski J, Alewell C (2008a) Temperature sensitivity of young and old soil carbon—same soil, slight differences in 13C natural abundance method, inconsistent results. Soil Biol Biochem 40:2703–2705

Conen F, Zimmermann M, Leifeld J, Seth B, Alewell C (2008b) Relative stability of soil carbon revealed by shifts in delta N-15 and C:N ratio. Biogeosciences 5:123–128

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173

Fang C, Smith P, Moncrieff JB, Smith JU (2005) Similar response of labile and resistant soil organic matter pools to changes in temperature. Nature 433:57–59

Fierer N, Jackson RB (2006) The diversity and biogeography of soil bacterial communities. Proc Natl Acad Sci USA 103:626–631

Fierer N, Craine JM, McLauchlan K, Schimel JP (2005) Litter quality and the temperature sensitivity of decomposition. Ecology 86:320–326

Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature 404:858–861

Girardin CAJ, Malhi Y, Aragao LEOC, Mamani M, Huasco WH, Durnad L, Feeley KJ, Rapp J, Silva-Espejo JE, Silman M, Salinas N, Whittaker RJ (2010) Net primary productivity allocation and cycling of carbon along a tropical forest elevational gradient in the Peruvian Andes. Glob Change Biol 16:3176–3192

Golchin A, Oades JM, Skjemstad JO, Clarke P (1994) Study of free and occluded particulate organic-matter in soils by solid-state C-13 Cp/MAS NMR-spectroscopy and scanning electron-microscopy. Aust J Soil Res 32:285–309

Gräfe S, Hertel D, Leuschner C (2008) Estimating fine root turnover in tropical forests along an elevational transect using minirhizotrons. Biotropica 40:536–542

Grisi B, Grace C, Brookes PC, Benedetti A, Dell'Abate MT (1998) Temperature effects on organic matter and microbial biomass dynamics in temperate and tropical soils. Soil Biol Biochem 30:1309–1315

Hartley IP, Ineson P (2008) Substrate quality and the temperature sensitivity of soil organic matter decomposition. Soil Biol Biochem 40:1567–1574

Hartley IP, Hopkins DW, Garnett MH, Sommerkorn M, Wookey PA (2008) Soil microbial respiration in arctic soil does not acclimate to temperature. Ecol Lett 11:1092–1100

Helfrich M, Flessa H, Mikutta R, Dreves A, Ludwig B (2007) Comparison of chemical fractionation methods for isolating stable soil organic carbon pools. Eur J Soil Sci 58:1316–1329

Kaiser K, Guggenberger G (2003) Mineral surfaces and soil organic matter. Eur J Soil Sci 54:219–236

Kammer A, Hagedorn F, Shevchenko I, Leifeld J, Guggenberger G, Goryacheva T, Rigling A, Moiseev P (2009) Treeline shifts in the Ural mountains affect soil organic matter dynamics. Glob Change Biol 15:1570–1583

Kirschbaum MUF (2004) Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? Glob Change Biol 10:1870–1877

Knicker H (2007) How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. Biogeochemistry 85:91–118

Knicker H, Ludemann HD (1995) N-15 and C-13 CPMAS and solution NMR-studies of N-15 enriched plant material during 600 days of microbial degradation. Org Geochem 23:329–341

Knorr W, Prentice IC, House JI, Holland EA (2005) Long-term sensitivity of soil carbon turnover to warming. Nature 433:298–301

Kok CJ, Vandervelde G (1991) The influence of selected water-quality parameters on the decay-rate and exoenzymatic activity of detritus of Nymphaea-Alba L floating leaf blades in laboratory experiments. Oecologia 88:311–316

Kölbl A, Kögel-Knabner I (2004) Content and composition of free and occluded particulate organic matter in differently textured arable Cambisol as revealed by solid-state ^{13}C NMR spectroscopy. J Plant Nutr Soil Sci 167:45–53

Körner C (2007) The use of 'altitude' in ecological research. Trends Ecol Evol 22:569–574

Kramer MG, Sollins P, Sletten RS, Swart PK (2003) N isotope fractionation and measures of organic matter alteration during decomposition. Ecology 84:2021–2025

Krull ES, Baldock JA, Skjemstad JO (2003) Importance of mechanisms and processes of the stabilisation of soil organic matter for modelling carbon turnover. Funct Plant Biol 30:207–222

Leifeld J (2006) Application of diffuse reflectance FT-IR spectroscopy and partial least-squares regression to

predict NMR properties of soil organic matter. Eur J Soil Sci 57:846–857

Leifeld J (2007) Thermal stability of black carbon characterised by oxidative differential scanning calorimetry. Org Geochem 38:112–127

Leifeld J (2008) Calometric charcaterization of grass during its decomposition. J Therm Anal Calorim 93:651–655

Leifeld J, Fuhrer J (2005) The temperature response of CO_2 production from bulk soils and soil fractions is related to soil organic matter quality. Biogeochemistry 75:433–453

Leifeld J, Zimmermann M, Fuhrer J, Conen F (2009) Storage and turnover of carbon in grassland soils along an elevation gradient in the Swiss Alps. Glob Change Biol 15:668–679

Liao JD, Boutton TW, Jastrow JD (2006) Organic matter turnover in soil physical fractions following woody plant invasion of grassland: evidence from natural C-13 and N-15. Soil Biol Biochem 38:3197–3210

Liski J, Ilvesniemi H, Makela A, Westman CJ (1999) CO_2 emissions from soil in response to climatic warming are overestimated - The decomposition of old soil organic matter is tolerant of temperature. Ambio 28:171–174

Lopez-Capel E, Sohi SP, Gaunt JL, Manning DAC (2005) Use of thermogravimetry-differential scanning calorimetry to characterize modelable soil organic matter fractions. Soil Sci Soc Am J 69:136–140

Malhi Y, Silman M, Bush P, Meir P, Saatchi S (2010) Introduction: elevational gradients in the tropics: laboratories for ecosystem ecology and global change research. Glob Change Biol 16:3171–3175

Manning DAC, Lopez-Capel E, Barker S (2005) Seeing soil carbon: use of thermal analysis in the characterization of soil C reservoirs of differing stability. Mineral Mag 69:425–435

Mathers NJ, Xu Z (2003) Solid-state 13C NMR spectroscopy: characterization of soil organic matter under two contrasting residue management regimes in a 2-year-old pine plantation of subtropical Australia. Geoderma 114:19–31

Olk DC, Gregorich EG (2006) Overview of the symposium proceedings, "Meaningful pools in determining soil carbon and nitrogen dynamics". Soil Sci Soc Am J 70:967–974

Pulleman MM, Marinissen JCY (2004) Physical protection of mineralizable C in aggregates from long-term pasture and arable soil. Geoderma 120:273–282

Quideau SA, Anderson MA, Graham RC, Chadwick OA, Trumbore SE (2000) Soil organic matter processes: characterization by 13C NMR and 14C measurements. For Ecol Manag 138:19–27

Raich JW, Russell AE, Kitayama K, Parton WJ, Vitousek PM (2006) Temperature influences carbon accumulation in moist tropical forests. Ecology 87:76–87

Roderstein M, Hertel D, Leuschner C (2005) Above- and below-ground litter production in three tropical montane forests in southern Ecuador. J Trop Ecol 21:483–492

Rovira P, Kurz-Besson C, Couteaux MM, Vallejo VR (2008) Changes in litter properties during decomposition: a study by differential thermogravimetry and scanning calorimetry. Soil Biol Biochem 40:172–185

Salinas N, Malhi Y, Meir P, Silman M, Roman-Cuesta R, Huaman J, Salinas D, Huaman V, Gibaja A, Mamani M, Farfan F (2010) The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. New Phytologist, doi:10.1111/j.1469-8137.2010.03521.x, (in press)

Schawe M, Glatzel S, Gerold G (2007) Soil development along an altitudinal transect in a Bolivian tropical montane rainforest: podzolization versus hydromorphy. Catena 69:83–90

Schrumpf M, Guggenberger G, Valrezo C, Zech W (2001) Development and nutrient status along an altitudinal gradient in the south Ecuadorian Andes. Die Erde 132:43–59

Schulten HR, Leinweber P (2000) New insights into organic-mineral particles: composition, properties and models of molecular structure. Biol Fertil Soils 30:399–432

Six J, Conant RT, Paul EA, Paustian K (2002) Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant Soil 241:155–176

Skjemstad JO, Krull ES, Swift RS, Szarvas S (2008) Mechanisms of protection of soil organic matter under pasture following clearing of rainforest on an Oxisol. Geoderma 143:231–242

Smith P, Smith JU, Powlson DS, McGill WB, Arah JRM, Chertov OG, Coleman K, Franko U, Frolking S, Jenkinson DS, Jensen LS, Kelly RH, Klein-Gunnewiek H, Komarov AS, Li C, Molina JAE, Mueller T, Parton WJ, Thornley JHM, Whitmore AP (1997) A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. Geoderma 81:153–225

Sollins P, Homann P, Caldwell BA (1996) Stabilization and destabilization of soil organic matter: mechanisms and controls. Geoderma 74:65–105

von Lutzow M, Kogel-Knabner I, Ekschmitt K, Matzner E, Guggenberger G, Marschner B, Flessa H (2006) Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions - a review. Eur J Soil Sci 57:426–445

Walse C, Berg B, Sverdrup H (1998) Review and synthesis of experimental data on organic matter decomposition with respect to the effect of temperature, moisture, and acidity. Environ Rev 6:25–40

Wilcke W, Oelmann Y, Schmitt A, Valarezo C, Zech W, Homeier J (2008) Soil properties and tree growth along an altitudinal transect in Ecuadorian tropical montane forest. J Plant Nutr Soil Sci 171:220–230

Zech W, Senesi N, Guggenberger G, Kaiser K, Lehmann J, Miano TM, Miltner A, Schroth G (1997) Factors controlling humification and mineralization of soil organic matter in the tropics. Geoderma 79:117–161

Zimmermann M, Leifeld J, Schmidt MWI, Smith P, Fuhrer J (2007) Measured soil organic matter fractions can be related to pools in the RothC model. Eur J Soil Sci 58:658–667

Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana AJQ (2009) Climate dependence of heterotrophic soil respiration from a soil-translocation experiment along a 3000 m tropical forest gradient. Eur J Soil Sci 60:895–906

Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana AJQ (2010) Temporal variation and climate dependence of soil respiration and its components along a 3000 m tropical forest gradient. Global Biogeochemical Cycles, 24, GB4012, doi:10.1029/2010GB003787