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Alpine grassland soils contain large proportion of labile carbon but indicate long turnover times

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Abstract. Alpine soils are expected to contain large amounts of labile carbon (C) which may become a further source of atmospheric carbon dioxide (CO_2) as a result of global warming. However, there is little data available on these soils, and understanding of the influence of environmental factors on soil organic matter (SOM) turnover is limited. We extracted 30 cm deep cores from five grassland sites along a small elevation gradient from 2285 to 2653 m a.s.l. in the central Swiss Alps. Our aim was to determine the quantity, allocation, degree of stabilization and mean residence time (MRT) of SOM in relation to site factors such as soil pH, vegetation, and SOM composition. Soil fractions obtained by size and density fractionation revealed a high proportion of labile C in SOM, mostly in the uppermost soil layers. Labile C in the top 20 cm across the gradient ranged from 39.6–57.6 % in comparison to 7.2–29.6 % reported in previous studies for lower elevation soils (810–1960 m a.s.l.). At the highest elevation, MRTs measured by means of radiocarbon dating and turnover modelling, increased between fractions of growing stability from 90 years in free POM (fPOM) to 534 years in the mineral associated fraction (mOM). Depending on elevation and pH, plant community data suggested considerable variation in the quantity and quality of organic matter input, and these patterns could be reflected in the dynamics of soil C. ^{13}C NMR data confirmed a relationship of SOM composition to MRT. While low temperature in alpine environments is likely to be a major cause for the slow turnover rate observed, other factors such as residue quality and soil pH, as well as the combination of all factors, play an important role in causing small scale variability of SOM turnover. Failing to incorporate this interplay of controlling factors into models may impair the performance of models to project SOM responses to environmental change.

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1 Introduction

Globally, soils store more than twice as much carbon (C) as the atmosphere, with the soil-atmosphere annual C-exchange estimated at around 80–98 Pg (Raich et al, 2002; Bond-Lamberty and Thomson, 2010). Atmosphere-soil C interactions may be strongly influenced by global warming (Friedlingstein et al., 2006; Jones et al., 2005) through effects on both CO_2 assimilation by vegetation (primary production) and CO_2 release by ecosystem respiration. Yet, it remains uncertain whether, in response to rising temperatures, the net feedback effect of soil organic matter (SOM) will be positive or negative (Reth et al., 2009).

Soils in colder environments, such as arctic and alpine tundra that cover large areas in the northern hemisphere, may be of particular concern with respect to global warming as these regions are expected to be more strongly affected than temperate regions (Meehl et al., 2007; Rebetez and Reinhard, 2008). Alpine soils cover roughly 4×10^6 km^2 worldwide (Körner, 2003), but despite this large extent there is currently insufficient information available with respect to factors influencing SOM decomposition in these soils. Such information would be needed to improve predictions of the possible response of SOM to warming.

SOM, a heterogeneous mix of plant, animal and microbial residues existing in various states of microbial decomposition has been shown to contain fractions of varying stability and different turnover times ranging from a few years to centuries (Wang et al., 2005; Baisden et al., 2002). Fractions of different stability can be separated by size and density fractionation (Balesdent et al., 1998; Buyanovsky et al., 1994) into particulate organic matter (POM) fractions which have been shown to be particularly sensitive to changing environmental conditions (Cambarella and Elliott, 1992). A free POM (fPOM) fraction is made up of partially decomposed litter and is thus closely related to the amount and quality of incoming plant residues. The amount of residue

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input depends on vegetation productivity (Meentemeyer et al., 1982, Körner, 2003), whereas residue quality is largely determined by plant species and tissue type (Kögel-Knabner, 2002), particularly in ecosystems with slow transformation rates (Hobbie, 2000). More transformed material known as occluded POM (oPOM) is encapsulated in soil aggregates and is therefore expected to be less readily accessible to soil microbes. The remaining heavy fraction is the mineral associated (mOM) portion of SOM. The mOM fraction is the most transformed, and therefore the least accessible to further transformation due to its physically bound state; studies have indicated that mOM is older than POM fractions (Sollins et al., 1996; Leifeld et al., 2009).

The partitioning of C between the different fractions, which predetermines the sensitivity of SOM to environmental changes, is spatially highly variable as it varies depending on edaphic conditions, land use history and current management (John et al., 2005; Grandy et al., 2009). In temperate soils C in more transformed mineral associated fractions make up most of the total soil C (Zimmermann et al., 2007), whereas the limited data available from alpine tundra soils (Leifeld et al., 2009; Neff et al., 2002; Wang et al., 2008) suggest large soil organic carbon (SOC) contents and a comparatively high abundance of less decomposed, labile C material such as POM. A primary study of grassland soils in the Swiss Alps revealed increasing labile C content with elevation from 880 to 2200 m a.s.l. (Leifeld et al., 2009). The largest proportion of labile C, at the highest site above the timberline, was 86 % of total SOC in the top 0–5 cm, but only 24–61 % in soils at lower altitudes. Currently, it is unknown whether alpine POM has a similar or an even lower degree of transformation compared to temperate fractions, and how the chemical composition of SOM in alpine environments relates to its turnover rate.

Mean residence time (MRT) of labile C at high elevations exceeds that of temperate soils (ca. 90–170 years vs. 10 years, Leifeld et al., 2009). This decline in MRT with elevation and the associated accumulation of labile C in mountain soils has mainly been attributed to decreasing temperature (Trumbore et al., 1996; Wang et al., 1995). However, it has been suggested that temperature alone cannot explain the retarded decomposition and that other factors such as soil acidity may also play a crucial role (Leifeld et al., 2008). Moreover, residue quality from alpine plant species may differ greatly from that at lower sites and this may also affect the composition and degradability of SOM.

Our study started with the premise that the previously observed accumulation of labile C at high elevations needs to be confirmed by data from different sites. In addition, data for C distribution among SOM fractions, their turnover time and sensitivity to site conditions should help to improve predictions of the response of SOM in alpine soils to environmental changes. Using a collection of soil samples from across a small elevation gradient of an alpine grassland, the aim of the study was to determine the distribution, state of transformation and MRT of SOC with an emphasis on the quantity and quality of labile C, and to investigate how the distribution, degree of stabilisation and turnover of SOC relates to elevation and to different site factors.

2 Materials and methods

2.1 Site description and sampling details

As land management has been shown to affect the content of SOC and its distribution (Chan, 2001; Yamashita et al., 2006), sites with homogenous bedrock and management (sheep grazing) were selected to minimise variations due to management and geology. Samples were collected in October 2007 from sites on a westerly facing slope in an alpine pasture area with low-intensity grazing sheep near the Furka pass in the central Swiss Alps (Ellipsoidal WGS84, Lat 46.56°, Long 8.4°). Five sampling sites separated by altitude were selected: 2285, 2379, 2481, 2564 and 2653 m a.s.l. The aspect of all sites was the same and the average slope inclination was 35°. Six 30 cm soil cores (core diameter: 7.7 cm) were extracted at each site along a 20 m horizontal transect. ^{137}Caesium measurements (data not shown) and visual inspection of the soil profiles indicated no or negligible soil erosion. Weather data was taken from the Swiss hydrological atlas and extrapolated by means of a climate model to determine the mean annual air temperature (MAT) and mean annual precipitation (MAP) for the sampling location (Schwarb et al., 2001; Z'graggen, 2002). Calculated average MAT and MAP were 0 °C and 1890 mm respectively, with monthly mean temperature ranging from −7.3 °C in February to 6 °C in August. The soil type was identified as dystric cambisol (spodic) developed on mica schist (WRB, 2006).

2.2 Soil and plant analysis

Each soil core was cut into sections representing the following depths: 0–5, 5–10, 10–20 and 20–30 cm. Sections were oven dried at 40 °C before analysis. Aboveground plant material (phytomass) was cut from the topsoil sections of each core. Plant litter present in the upper core sections was removed by hand along with larger stones and roots. The remaining soil sample was sieved to obtain smaller stone content (>2000 µm), which was added to the larger stones to obtain total stone content, and the fine earth section (<2000 µm). As fine earth still contained some fine roots (and litter material in the upper sections) this section was sieved further to obtain very fine earth material of < 63 µm (which did not contain any root material) and the larger fine earth material of 63–2000 µm, which still contained some root and litter. This additional fine root and litter material was separated from the larger fine earth material by flotation in water to obtain a total root and litter fraction. The root and litter free 63–2000 µm larger fine earth section was then added to the very fine earth material of < 63 µm to achieve

a total fine earth section (0–2000 µm). Larger hand picked root material was added to flotation obtained root and litter material to obtain total root and litter material. We estimate a contribution of litter to that combined fraction of below ten percent in 0–5 cm and only negligible amounts in sections below 5 cm depth. Because complete physical separation of litter from living roots was not possible in the dense root mats of these alpine soils, we refer to that fraction as root + litter throughout the text.

After separation into aboveground phytomass, root + litter, fine earth and stones, each fraction was weighed. Root + litter weight was used together with the core surface area to determine root + litter content in $t\,ha^{-1}$. Stone % volume was calculated by applying a stone density of $2.65\,g\,cm^{-3}$ with the measured stone weights. Fine earth bulk densities ($g\,cm^{-3}$) were calculated by dividing fine soil weight by total core volume minus stone volume.

Root + litter and fine earth were milled with a ball-mill and analysed for C and nitrogen (N) concentrations after combustion using an elemental analyser (Hekatech Euro EA 3000, Wegberg, Germany). C and N concentrations were used to calculate C/N ratios and SOC contents ($t\,ha^{-1}$). Pooled aboveground phytomass samples and root + litter fractions per site were subjected to detergent fibre analysis after van Soest et al. (1967) do derive hemicelluloses, cellulose, and lignin.

To determine pH values of the fine earth, samples were mixed with 0.01 M $CaCl_2$ solution (2.5:1 dilution). Soil texture was determined by the pipette method after removal of organic matter with H_2O_2 (Gee and Bauder, 1986). Extractable soil nutrient concentrations (potassium (K), calcium (Ca), magnesium (Mg) and phosphorous (P)) of fine earth were determined according to the Swiss reference methods after treatment with 1:10 NH_4-acetate solution (FAL, 1998). Soil texture and nutrients were measured in composite samples per layer from each site.

2.3 Soil physical fractionation

Fine earth was separated by density fractionation into fPOM and oPOM. Samples were centrifuged with $1.8\,g\,cm^{-3}$ sodium polytungstate (SPT) solution until all heavy (pellet) material was separated from light (floating) material. All floating material ($\leq 1.8\,g\,cm^{-3}$) was collected as fPOM in a 20 µm sieve, washed thoroughly and oven dried overnight at 60 °C. The remaining pellet was re-suspended in SPT and treated with ultra sonification ($22\,J\,ml^{-1}$) to destroy aggregates before repeated centrifugation and collection of oPOM ($\leq 1.8\,g\,cm^{-3}$). This method was used to correspond with the fractionation method used by Zimmerman et al. (2007) and Leifeld et al. (2009) to allow direct comparison of the POM fraction values. Both fPOM and oPOM material were ball-milled and each fraction was measured for C and N concentrations with an elemental analyser; C/N ratios for each POM fraction and total (fPOM and oPOM) particulate organic C (POC) content were calculated as with fine earth. Mineral associated organic carbon (MOC) content and C/N ratio's for mOM, which in this case is the remaining heavy ($> 1.8\,g\,cm^{-3}$) mineral fraction, were calculated by difference. The proportion of labile C (i.e., fPOM-C plus oPOM-C) and mineral associated C were calculated (in %) from POC and MOC content relative to total SOC content.

2.4 ^{14}C AMS measurements

POM fractions, fine earth and root + litter material were selected for ^{14}C measurement by accelerator mass spectrometry (AMS) at the radiocarbon laboratory at the ETH Zurich University and for CPMAS ^{13}C NMR spectroscopy (Technical University Munich, Institute for Soil Science, see below). Fractions were selected, depending on quantity of sample material available, to cover variability of C allocation and composition in the soil. Three soil fractions (fPOM, oPOM, mOM by difference) from 5–10 cm were used from the two lowest and highest sites, and site 2564 m a.s.l. was chosen for a detailed profile over four depths as this site had a particularly large amount of root + litter and POM.

Site variability of MRT of fPOM was investigated with six horizontal sample replicates (5–10 cm) from two sites (2564 m and 2285 m). Replicates with similar SOC contents were selected, and 3 dual replicate combinations were pooled for each site. To obtain an overview of bulk soil turnover rates across the entire gradient, samples of fine earth using all six replicates from each soil depth were pooled.

2.5 Bomb model with time-lag and calculation of MRTs

MRT was estimated by means of radioactive C (^{14}C) dating. Nuclear weapon tests in the 1960's released additional ^{14}C into the atmosphere, which, when taken up by vegetation, is incorporated into SOM through decomposition and mineralisation of plant residues. The increase in isotopic signature of SOM provides an opportunity to measure the C residence time (Harkness et al., 1986). So called "bomb models" are used to relate the proportion of ^{14}C in SOM to the level of ^{14}C in the atmosphere during the last several decades, assuming a steady state system (i.e. the same amount of C enters the soil on an annual basis). The latter assumption is often questioned but it seems reasonable for alpine ecosystems as they occur naturally without a history of land use change. Combined with chemical analysis of SOM, ^{14}C dating can indicate whether or not the chemical structure controls turnover of plant residues.

AMS measurement of ^{14}C yielded data of percentage modern C (pMC) which were then inserted into the bomb model to obtain estimates of MRT for each SOM fraction. A detailed description of the model can be found in Harkness et al. (1986), and an application to soil fractions in Leifeld and Fuhrer (2009). MRTs were calculated for root + litter fractions in samples of the four depth sections within

the 0–30 cm core, taken at site 2564 m. Root + litter MRTs ranged from 12.5–15.5 years and did not indicate any trend with soil depth. A mean value of 14.5 years was derived from these values and used in the bomb model to recalculate soil MRT to account for the period of time that C remains in the roots before it enters the first fraction in the soil decomposition process. In this case, it is referred to as the time-lag period and the adjusted model is referred to as the bomb model with time-lag. All pMC values were inserted into the bomb model with time-lag to recalculate MRT of each SOM fraction. Corresponding fine earth MRTs for these fractions were calculated by using fraction specific MRTs in conjunction with SOC contents to provide a weighted average according to Leifeld and Fuhrer (2009). These fine earth MRTs, later referred to as "fraction calculated fine earth MRT", should provide a more accurate estimate of the fine earth MRTs as the contribution from each soil fraction to the total soil turnover is integrated into the calculation.

For many samples, only fine earth radiocarbon data were available. MRT calculated for fine earth samples may be biased as the calculation treats SOC erroneously as a homogenous pool (Trumbore et al., 1997). In order to improve the MRT estimates, a regression approach was applied using fraction calculated fine earth MRT. First, composite fine earth MRT estimates were determined from the pooled samples from all elevations and depths by inserting pMC values into the bomb model with time-lag, as previously with soil fractions. Measured composite fine earth MRTs were then plotted against their corresponding fraction calculated fine earth MRTs to determine the relationship between MRT estimated by these two different methods. This equation was then applied to the measured composite fine earth MRTs to adjust for the relative contribution of each fraction of varying stability and to obtain a more reliable MRT estimate of the fine earth for all elevations and depths. The following curved relationship was identified:

$$y = -1272 + 658 \times \mathrm{LOG10}(x);\ r = 0.96 \quad (1)$$

Where y = fraction calculated fine earth MRT and x = measured composite fine earth MRT[a].

Calibration encompassed composite fine earth MRTs of between > 70 and 2000 years and therefore was not applied to shorter MRTs. For measured composite fine earth MRT values of 70 years or shorter, the original composite fine earth MRT was kept. This was the case for 0–5 cm depth samples at all elevations and the 5–10 cm samples for site 2481 m. Therefore, for these fine earth samples of shorter MRT, the time-lag period is still accounted for. However, a recalculation according to Eq. (1) is not appropriate.

Annual C input into the soil at each depth for each site was calculated from SOC contents divided by MRTs. Total site productivity was indicated by the total annual C input into the 30 cm cores.

2.6 ^{13}C NMR Spectroscopy

During microbial decomposition organic compounds derived from plants are increasingly replaced by those derived from microbes (Berg and Meentemeyer, 2002). Initial breakdown of plant polysaccharides decreases O-alkyl-C and increases alkyl-C (Kölbl and Kögel-Knabner, 2004). Thus, the alkyl-C/O-alkyl-C ratio, which increases from light/coarse to fine/heavy soil fractions, can be used as an indicator of the degree of decomposition of SOM fractions (Golchin et al., 1994a; Helfrich et al., 2006). We studied SOM composition by means of NMR spectroscopy.

Milled fine earth, POM fraction and root + litter samples were selected for ^{13}C NMR spectroscopy analysis to correspond with those already measured for ^{14}C content for comparison, individual sample analysis was not replicated due to cost restrictions. The ^{13}C chemical shifts in ^{13}C CPMAS NMR spectra (Bruker DSX 200 NMR spectrometer, Bruker, Karlsruhe, Germany; resonance frequency 50.32 MHz, contact time 1.0 ms, pulse delay 150 ms, magic angle spinning speed 6.8 kHz) were measured relative to tetramethylsilane (0 ppm). Chemical groups from CPMAS ^{13}C NMR spectra were categorized by division of the spectra into 4 regions: Alkyl-C (−10–45 ppm), O-Alkyl-C (45–110 ppm), Aryl-C (110–160 ppm) and Carboxyl-C (160–220 ppm) (Knicker and Lüdemann, 1996). For studying the relationship between SOM composition and turnover time chemical group concentrations were compared with MRTs. The most significant relationship determined from this comparison was indicated from a narrowed O-alkyl region of 60–90 ppm, which excludes protonated C of lignin (resonance around 110 ppm) as well as methoxyl-C (resonance around 56 ppm). Integration peaks in each region were used to calculate the relative distribution (%) of each chemical group within the sample measured. Alkyl-C/O-Alkyl-C ratios were then calculated for each soil fraction as an indicator of microbial transformation (Baldock et al., 2007).

2.7 Phytomass

Aboveground phytomass was calculated (in g m^2) from the plant weights obtained from the soil cores. Median values were used as sampling area (0.00465 m^2) was relatively small and a single plant stem could significantly bias the mean of the six replicates per site.

2.8 Plant cover

At each site, plant species on top of and around the cores were identified and percentage area (25 cm × 25 cm) distribution was estimated by a modified Braun-Blanquet method at the location of each sampled core. This information was used to identify the plant functional group distribution by area.

2.9 Data analysis

Soil and root + litter characteristics were calculated as the mean of the 6 replicates at each site, with the exception of phytomass for which median values were used. Effects of the factors site and soil depth on amount and distribution of organic matter were tested by one-way ANOVA and, if significant at the 5 % error probability, a post-hoc Tukey's test was applied. Data were log-transformed where they did not pass tests of homogeneity of variances or normality of distribution. Correlation between selected variables is expressed as Pearsons' correlation coefficient and an indication of the error probability. These analyses, regression analysis, and the curved relationship between composite bulk soil MRTs and fraction calculated bulk soil MRTs in Eq. (1) were determined using Statistica 9.0.

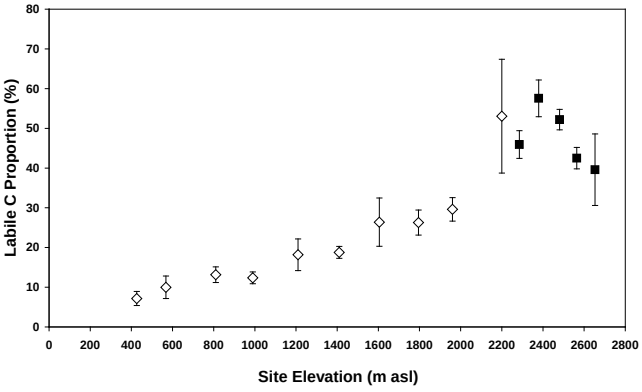

Fig. 1. POM (fPOM + oPOM) C proportion (%) in 20 cm deep soil cores. Squares indicate Furkapass data. Additional data (diamonds) taken from Zimmerman et al. (2007; symbols below 600 m a.s.l.) and Leifeld et al. (2009). Error bars indicate 1 SE of the mean.

3 Results

Soils were found to be strongly to moderately acidic with pH values ranging from 3.9 to 5.5, with the least acidic pH at the middle elevation (Table 1). Soil clay content varied from 1–24 % across all sites and depths, decreased with depth at all sites and averaged at 10 % in the 30 cm cores across all sites. Bulk densities and stone volumes increased, while root + litter densities decreased with soil depth. Total root + litter densities (0–30 cm) varied between 10.3 and 42.0 t ha^{-1} dry matter across sites, with higher densities at 2379 and 2564 m than at the other sites. SOC contents were also higher at these elevations (Table 2) and regression analysis revealed a significant linear relationship between site SOC content with both root + litter dry matter density ($r = 0.93$, $p = 0.02$, $n = 5$) and stone volume ($r = -0.98$, $p =< 0.01$, $n = 5$). Nutrient concentrations (K, Ca, Mg and P) were highest in the 0–5 cm layer where most roots occurred, and decreased steeply with soil depth. The highest elevation site contained the lowest concentration of soil nutrients.

Total SOC content varied from 55.0 to 102.1 t ha^{-1} across sites, while bulk soil C concentrations ranged from 10.8–27.9 % in the 0–5 cm sections and decreased sharply with soil depth at all sites (Table 2). Labile C % also decreased with soil depth, in contrast to mineral associated C % which increased. Highest labile C in the range of 71.2–85.5 % was found in the uppermost layer (0–5 cm) and low values between 6.3–19.1 % in the lower depths (20–30 cm). Effect of soil depth was highly significant ($p < 0.01$) across all sites for soil C and N concentration, root + litter densities, proportions of labile C, and bulk densities. When separated by layer, significant site effects were visible for all of the soil attributes in Table 2 but did not change steadily with elevation. Cumulated over the upper 30 cm, the middle site had the highest relative abundance of labile C while sites 2379 and 2564 had both the highest C concentrations and largest stocks (Table 2).

Labile C for 0–20 cm varied in the range of 39.6–57.6 %. Compilation of these values with previous data obtained for lower elevation grassland soils (Leifeld et al., 2009; Zimmermann et al., 2007) showed an increase in labile C relative to elevation up to 57.6 % at 2379 m, followed by a trend towards decreasing values across the highest three sites sampled here (Fig. 1). From the soil profile, the decline in labile C % was not evident in the top 5 cm but occurred in the 5 and 20 cm depth sections.

A total of 56 plant species were identified at the location of the cores across all sites, with 32 of these species only present at single sites and 5 species (2 grass and 3 forbs: *Anthoxanthum odoratum, Geum montanum, Helictotrichon versicolor, Leontodon helveticus* and *Potentilla aurea*) present at all sites. Except for the top site, which contained a large proportion of dwarf shrubs and lichens, the predominant functional groups across the alpine grassland elevation were forbs followed by grasses. The relative distribution of each functional group varied greatly between the sites (Fig. 2). The proportion of legumes was largest at the middle site (2481 m).

Independent of site, the trend towards decreasing C/N ratios indicated an increase in the degree of microbial transformation from root + litter→fPOM→oPOM→mOM (Fig. 3). Root + litter material, fPOM and oPOM all displayed increasing C/N ratios with soil depth, whereas mOM with the lowest C/N ratio did not vary with depth. The depth effect on C/N ratios was highly significant ($p < 0.01$) for fine earth, root + litter, fPOM, and oPOM. Across sites and separated by depth, the difference in C/N ratios between root + litter; fPOM; oPOM, and mOM was highly significant ($p < 0.01$) for all fractions but fPOM and oPOM 0–5 cm. Between sites the C/N ratios, integrated over 0–30 cm, differed in the aboveground phytomass, fPOM and oPOM and were smallest at 2481 m; however this pattern was not indicated with the root + litter (Table 3). Neither aboveground nor belowground phytomass (root + litter) C/N ratios correlated with

Table 1. Mean soil properties at each sampling site. Different letters indicate significant differences for values 0–30 cm (Tukeys', $p < 0.05$).

Site elevation (m a.s.l.)	Soil depth (cm)	Bulk density ($g\,cm^{-3}$)	SE*	Fine earth pH_{CaCl2}	SE	Stone volume (%)	SE	root + litter dry matter ($t\,ha^{-1}$)§	SE	Fine earth clay (%)	Fine earth N ($g\,kg^{-1}$)	SE	Fine earth P ($mg\,kg^{-1}$)	Fine earth K ($mg\,kg^{-1}$)	Fine earth Mg ($mg\,kg^{-1}$)	Fine earth Ca ($mg\,kg^{-1}$)
2285	0–5	0.33	0.08	4.3	0.1	5.6	1.3	7.8	1.4	14	7.6	0.6	76	558	222	1155
	5–10	0.74	0.05	4.0	0.1	11.1	1.0	2.7	0.5	10	2.9	0.3	24	133	63	54
	10–20	0.73	0.04	4.2	< 0.1	17.0	1.2	4.0	2.7	9	1.4	0.1	5	42	12	82
	20–30	0.90	0.03	4.4	< 0.1	16.2	2.9	0.5	0.1	9	1.0	0.2	3	24	5	46
	0 – 30	0.72*B*	0.02	4.2*A*	0.1	13.8*B*	1.2	*15.0 AB*	4.3	-	1.9*A*	0.1	25	152	62	290
2379	0–5	0.23	0.03	4.6	0.1	0.4	0.1	18.1	4.0	N.A.†	15.5	0.8	111	946	726	3889
	5–10	0.45	0.06	4.1	0.1	3.3	1.0	6.0	2.1	17	7.5	0.9	39	258	228	934
	10–20	0.56	0.04	4.2	< 0.1	8.0	2.2	3.0	0.3	10	3.0	0.2	6	72	46	173
	20–30	0.72	0.02	4.4	< 0.1	13.4	4.4	1.0	0.2	6	1.6	0.1	2	21	8	48
	0 – 30	0.54*A*	0.02	4.3*A*	< 0.1	7.8*A*	1.3	*28.0 BC*	4.4	-	3.7*B*	0.3	24	173	135	554
2481	0–5	0.36	0.06	5.2	0.1	6.8	1.3	6.0	0.7	N.A.	8.6	0.4	59	596	424	3345
	5–10	0.64	0.05	4.6	0.1	11.9	2.2	1.7	0.3	6	2.7	0.4	13	117	135	851
	10–20	0.74	0.07	4.5	0.1	12.5	1.5	1.9	0.4	1	1.5	0.2	6	67	68	434
	20–30	0.85	0.03	4.4	0.1	14.0	1.6	0.8	0.1	6	1.1	0.1	3	40	28	195
	0 – 30	0.70*B*	0.04	4.7*B*	0.1	*11.9 AB*	0.8	10.3*A*	0.9	-	1.9*A*	0.2	17	160	163	1032
2564	0–5	0.25	0.02	4.0	0.1	1.2	0.4	29.0	1.9	N.A.	13.3	0.5	133	747	350	1269
	5–10	0.51	0.03	3.7	< 0.1	4.1	1.2	6.6	1.4	16	6.8	0.4	44	169	90	234
	10–20	0.62	0.01	4.0	< 0.1	6.9	0.7	3.2	0.7	8	2.8	0.2	7	40	17	55
	20–30	0.65	0.04	4.3	< 0.1	12.2	1.3	3.3	0.2	5	1.8	0.2	4	23	5	28
	0 – 30	0.55*A*	0.01	4.0*A*	0.1	7.3*A*	0.5	42.0*C*	2.9	-	3.5*B*	0.1	29	127	61	127
2653	0–5	0.51	0.07	4.0	0.1	4.1	0.7	14.1	3.1	24	5.8	0.8	45	261	150	609
	5–10	0.67	0.02	4.2	< 0.1	7.8	1.8	3.0	1.3	11	2.6	0.4	16	82	53	156
	10–20	0.76	0.03	3.9	< 0.1	12.4	1.9	0.7	0.2	6	1.4	0.2	4	26	12	59
	20–30	0.90	0.03	4.4	< 0.1	14.4	2.0	0.5	0.1	7	0.8	0.1	2	11	5	38
	0 – 30	0.75*B*	0.03	4.1*A*	< 0.1	*10.9 AB*	1.1	*18.3 AB*	3.6	-	1.8*A*	0.2	17	86	50	87

* Standard errors (SE) indicate 1 SE of the mean. No SE available for clay content, P, K, Mg and Ca content as composite samples were analysed. † N.A. = not analysed.
§ For definition see material and methods.

Table 2. Mean soil carbon at each sampling site. Different lower case letters indicate significant differences for individual soil layers across sites and different capital letters indicate significant differences for values 0–30 cm (Tukeys', $p < 0.05$).

Site elevation (m a.s.l.)	Soil depth (cm)	Soil C (%)	SE	SOC ($t\,ha^{-1}$)	SE	Labile C proportion (%)	SE	Mineral associated C proportion (%)	SE
2285	0–5	11.8 a	1.1	17.8 a	2.6	71.2 a	3.5	28.8 a	3.5
	5–10	3.9 a	0.4	14.3 a	1.3	45.8 ab	4.6	54.2 ab	4.6
	10–20	1.7 a	0.1	12.5 a	0.7	20.7 a	2.9	79.3 a	2.9
	20–30	1.1 a	0.2	10.4 a	2.0	10.4 a	2.6	89.6 a	2.6
	0 – 30	2.5*A*	0.1	55.0*A*	2.2	*25.6 AB*	1.8	*74.4 AB*	1.8
2379	0–5	27.9 b	4.7	31.5 c	1.9	85.4 a	4.6	14.6 a	4.6
	5–10	11.4 b	2.2	24.1 b	1.7	66.6 b	9.0	33.4 b	9.0
	10–20	4.4 b	0.7	24.4 b	1.6	20.7 a	2.8	79.3 a	2.8
	20–30	2.5 b	0.4	18.2 b	1.1	11.9 ab	2.9	88.1 ab	2.9
	0 – 30	5.8*B*	0.4	97.9*B*	3.6	*25.1 AB*	2.4	*74.9 AB*	2.4
2481	0–5	12.9 a	2.9	20.7 ab	2.3	83.8 a	2.6	16.2 a	2.6
	5–10	3.8 a	0.8	11.5 a	0.7	49.4 ab	7.0	50.6 ab	7.0
	10–20	1.9 a	0.4	13.7 a	1.2	23.4 a	2.6	76.6 a	2.6
	20–30	1.2 a	0.3	10.2 a	1.2	14.3 ab	1.2	85.7 ab	1.2
	0 – 30	2.6*A*	0.3	56.0*A*	4.0	29.6*B*	1.6	70.4*B*	1.6
2564	0–5	24.2 b	1.4	29.6 bc	2.0	85.5 a	2.7	14.5 a	2.7
	5–10	9.8 b	0.8	24.6 b	1.0	26.1 a	3.7	73.9 ac	3.7
	10–20	4.3 b	0.2	26.4 b	1.0	16.0 a	1.4	84.0 a	1.4
	20–30	3.3 b	0.3	21.5 b	1.4	19.1 b	1.7	80.9 b	1.7
	0 – 30	5.7*B*	0.2	102.1*B*	2.3	20.5*A*	1.4	79.5*A*	1.4
2653	0–5	10.8 a	2.2	25.5abc	1.9	77.3 a	9.0	22.7 a	9.0
	5–10	4.3 a	1.0	14.3 a	2.5	26.9 a	3.8	73.1 a	3.8
	10–20	2.1 a	0.4	15.4 a	1.7	14.6 a	2.0	85.4 a	2.0
	20–30	1.3 a	0.2	11.5 a	1.2	6.3 a	0.3	93.7 a	0.3
	0 – 30	2.9*A*	0.3	67.8*A*	5.5	19.7*A*	1.6	79.3*A*	1.6

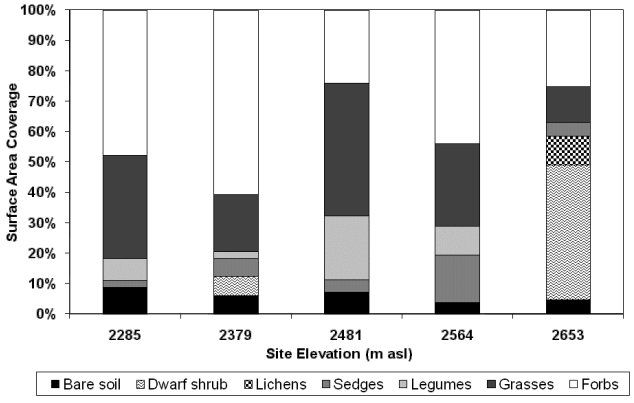

Fig. 2. Cover of plant functional groups at the sampled soil cores at each elevation.

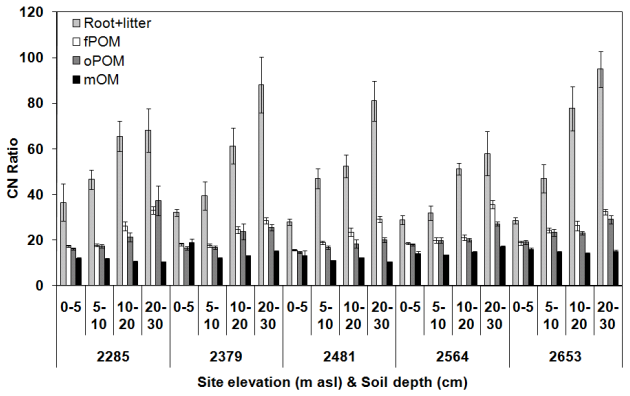

Fig. 3. C/N ratios of root + litter, fPOM, oPOM & mOM with depth. Error bars indicate 1 SE of the mean. For a definition of the root + litter fraction see material and methods.

Table 3. Overview of C/N ratios of plant material and labile organic matter fractions across sites (0–30 cm). Numbers in brackets are 1 SE. Different letters indicate significant differences across sites (Tukeys', $p < 0.05$).

Site elevation (m a.s.l.)	Aboveground phytomass	root + litter*	fPOM	oPOM
2285	26.2 (1.8) ab	54.2 (4.4) a	17.6 (3.4) ab	25.7 (3.3) b
2379	27.7 (2.0) ab	55.3 (5.9) a	15.9 (0.4) ab	20.6 (1.2) ab
2481	20.7 (1.4) a	50.9 (4.6) a	13.3 (0.3) a	17.7 (0.7) a
2564	23.3 (0.8) ab	42.6 (3.6) a	16.6 (0.4) b	21.3 (0.8) ab
2653	31.7 (4.2) b	62.0 (6.3) a	16.4 (0.4) b	26.6 (3.1) b

* For definition see material and methods.

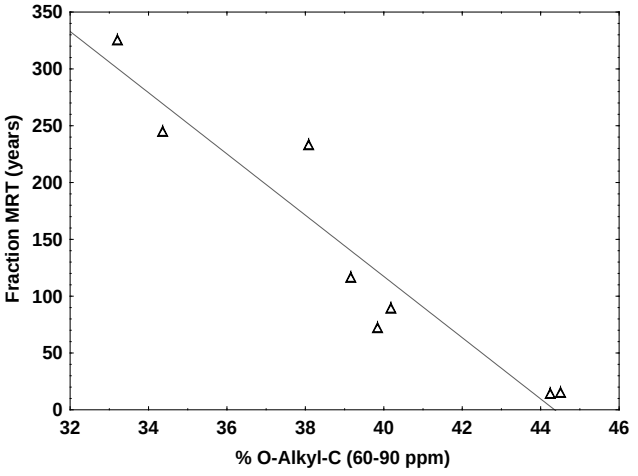

Fig. 4. Linear correlation between fraction MRTs and O-Alkyl-C % in fractions measured by NMR ($r = -0.95$; $p < 0.001$).

elevation. However, other root + litter quality parameters, as derived from fibre analysis, were more strongly graded along elevation than aboveground phytomass quality. Root + litter lignin content and the ratio hemicelluloses/lignin were significantly related to elevation (Table 4).

Chemical functional groups measured by NMR spectra in selected samples from the 5–10 cm layer confirmed the varying degree of transformation with a decrease in O-Alkyl-C and an increase in Alkyl-C from root + litter→fPOM→oPOM→bulk soil. The corresponding data summarized in Table 5 show the related increase in Alkyl-C/O-Alkyl-C ratios, which reflected the progressive degree of transformation. Additionally, in agreement with C/N ratios given in Fig. 3, Alkyl-C/O-Alkyl-C ratios from a single site (2564 m a.s.l.) revealed the decrease in the degree of transformation of fPOM with increasing soil depth. Sample values for the O-Alkyl-C % region (60–90 ppm) indicated a negative significant correlation to MRTs ($r = -0.95$; $p =< 0.001$, $n = 8$) (Fig. 4).

MRT of C in different fractions was determined in individual samples from the 5–10 cm layer. Comparison between fractions from four of the five sites showed that MRT increased from fPOM→oPOM→mOM (Fig. 5), with the corresponding fine earth of the fractions indicating MRTs between those of mOM and oPOM. While fPOM and oPOM MRTs showed no significant trend with elevation, MRT of mOM increased significantly with elevation across four sites ($r = 0.95$; $p = 0.046$; $n = 4$). Fine earth MRT was considerably lower at the middle site and did not increase with elevation across any soil depth (Fig. 6) while fine earth MRTs did increase linearly with soil depth at all sites (2285 m: $r = 0.99$; $p =< 0.01$; 2379 m: $r = 0.99$; $p =< 0.01$; 2481 m: $r = 0.97$; $p = 0.03$; 2564 m: $r = 0.96$; $p = 0.03$; 2653 m: $r = 0.94$; $p = 0.03$; all $n = 4$). Site fine earth MRTs (0–30 cm) were significantly negatively correlated to site soil pH ($r = -0.96$; $p = 0.01$; $n = 5$) and for single layers fine earth MRTs showed a significant relationship with soil pH in the 0–5 cm ($r = -0.96$; $p =< 0.01$; $n = 5$) and 10–20 cm depth sections ($r = -0.89$; $p = 0.04$; $n = 5$).

MRT of C in 30 cm fine earth samples was lowest at the middle elevation, least acidic site that also differed in terms

Table 4. Overview of plant quality parameters (g kg^{-1}dry weight) along the elevation gradient. Last row indicates correlation coefficient with elevation; asterisk shows significant relationships ($p < 0.05$).

Site elevation (m a.s.l.)	Hemicelluloses		Cellulose		Lignin		Hemicelluloses / Lignin	
	Aboveground	root + litter*	Aboveground	root + litter	Aboveground	root + litter	Aboveground	root + litter
2285	171.1	200.8	156.3	238.4	105.5	114.4	1.62	1.75
2379	95.2	275.3	244.5	206.0	177.8	134.2	0.54	2.05
2481	105.9	215.9	151.2	251.6	121.2	132.3	0.87	1.63
2564	190.5	179.5	243.2	147.2	121.8	165.0	1.56	1.09
2653	120.5	129.8	125.9	193.5	131.6	176.9	0.92	0.73
correlation	−0.03	−0.70	−0.17	−0.56	−0.03	0.95*	−0.14	−0.89*

* For definition see material and methods.

Table 5. Chemical group concentrations, Alkyl-C/O-Alkyl-C and mean residence time (MRT) for SOM fractions at two sites.

Site elevation (m a.s.l.)	Fraction	Soil depth (cm)	O-Alkyl-C (%)	Alkyl-C (%)	Alkyl-C/ O-Alkyl-C ratio	MRT with time-lag (years)
2653	fPOM	5–10	61.6	21.0	0.34	89.5
	oPOM	5–10	57.6	28.9	0.50	117.0
	Fine earth	5–10	54.0	31.3	0.58	325.5
2564	root + litter†	0–5	66.2	15.1	0.23	15.2
		5-10	66.6	14.7	0.22	14.6
		10–20	N.A.*	N.A.	N.A.	15.5
		20–30	N.A.	N.A.	N.A.	12.5
	fPOM	0–5	59.2	25.3	0.43	72.0
		5–10	N.A.	N.A.	N.A.	107.8
		10–20	60.7	19.5	0.32	233.0
		20–30	57.2	15.9	0.28	244.8

* N.A. = not analyzed. † For definition see material and methods.

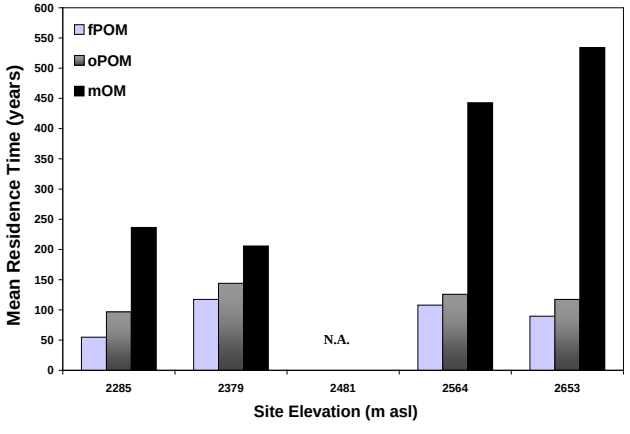

Fig. 5. MRTs (with time-lag) calculated for fractions at 5–10 cm depth at 4 sampling sites. Each value represents a single site replicate (composite of six cores) measured for ^{14}C content.

of high annual C input and aboveground phytomass (Table 6). Conversely, smaller aboveground phytomass and annual C input as well as wider aboveground phytomass C/N ratios at the uppermost sites (Table 3) were associated with longer MRT. Site pH revealed a significant positive linear relationship with aboveground phytomass ($r = 0.98$; $p = 0.003$; $n = 5$). However, calculated annual inputs were not significantly related to soil pH. Labile C % indicated a positive correlation with total C input (0–30 cm) across all the sites ($r = 0.96$; $p = 0.012$; $n = 5$).

Finally, we examined small-scale variability of fPOM contents and their MRTs within single sites. MRT of fPOM for individual site replicates (5–10 cm) varied from 50–76 years along the lower elevation site to 98–126 years along the higher site (Fig. 7). C input varied by a factor of 3 at the lower and by a factor of 2 at the higher site, i.e., input rates were more variable than turnover rates.

Table 6. Mean fine earth MRT, annual C input, and aboveground phytomass at each site. Site values are calculated from 0–30 cm cores. Numbers in brackets are 1 SE.

Site elevation (m a.s.l.)	MRT with time-lag (years)	Annual C input ($t\,C\,ha^{-1}$)	Aboveground phytomass ($g\,m^{-2}$)
2285	105.5	0.52	826 (134)
2379	115.2	0.85	877 (91)
2481	55.7	1.01	1301 (484)
2564	185.6	0.55	643 (57)
2653	168.3	0.40	616 (98)

4 Discussion

4.1 Improved turnover estimates through fraction-based and time-lag measurements

The bomb model assumes a steady state environment but in the soil studied this assumption may not be the case. However, we consider that no long term trend in input and turnover exists at the selected sites given that they are only very moderately grazed. The model is based on a number of calculated atmospheric and fraction curves which indicate an increasing pMC with time until reaching a peak concentration. The curves thus mimic the atmospheric concentration, but are smoothed depending on the fraction's MRT. The overall pMC observed in each fraction curve depends on the rate of atmospheric absorption; hence faster fractions contain a larger pMC than slower fractions. The model can thus indicate more than one possible MRT, particularly in the fast moving fractions where many fraction curves overlap. Knowing the signature of C entering the system may help to solve this issue (Trumbore et al., 1997).

The method used for final MRT estimates, referred to as fraction calculated MRTs, allowed for the overall contribution of the soil fractions to the fine earth. The combination of the addition of the time-lag period derived from root + litter dating into the bomb model, and equation recalculation to the fine earth MRTs with respect to fraction contribution, enables a more realistic estimation of the actual fine earth MRTs. This is an improvement over single measurements which would require a homogenous system and not take this characteristic into account. The application of the time-lag period, which accounts for the period of C residence within the plant tissue, may be particularly important in these soils with a large input from roots. In our case, the inclusion of the time-lag period (i.e., the mean age of the root + litter fraction) into the bomb model indicates which MRT values should be disregarded and therefore the only possible MRT time was allocated to the pMC value.

4.2 Soil organic matter content, composition, and turnover – general findings

Soil from the central Swiss Alps contains SOC contents comparable to those reported for lower elevations (Zimmermann et al., 2007), but the percentage of roots and labile material in the top 10 cm are considerably higher than those reported for temperate and subalpine grasslands (Ammann et al., 2009; Leifeld et al., 2009). A higher labile C percentage compared to values found at elevations below 2000 m confirms the high abundance of labile C in the top soil layers, whereas below 10 cm, labile C is only slightly higher (10–20 cm) or very similar (20–30 cm) to that at lower sites (Leifeld et al., 2009; Zimmermann et al., 2007). The high labile C percentage found here follows a general trend with elevation when compiled with data obtained from lower elevation soils (Fig. 1) and is in line with data from the few studies carried out on drier alpine tundra soils, e.g. in the Tibet mountains where similar total C contents were found at high and low elevations, but where the labile C content in the top soil layers was considerably higher at the higher sites (Wang et al., 2005; Wang et al., 2008). However, the data found here also reveal maximum labile C of around 58 % (0–20 cm) at 2379 m and a decline with a further increase in elevation, indicating an upper limit of POM accumulation in mineral soil of cold environments.

Labile C allocation in our alpine soils supports the previously reported view of soil as a hierarchical system of aggregates, where intra-aggregate material is protected but already more transformed (Tisdal and Oades, 1982; Six et al., 2004). The trend towards increasing degree of transformation from root + litter → fPOM → oPOM → mOM both in C/N ratios and in alkyl-C/O-alkyl-C ratios is consistent with findings from temperate soils (Golchin et al., 1994a,b; Baisden et al., 2002). The results are also in line with systematic differences in composition between fPOM and oPOM reported for soils in climatically different regions (Golchin, 1994a; Kölbl and Kögel-Knabner, 2004). In subtropical soils, Golchin et al. (1994b) reported mean alkyl-C/O-alkyl-C ratios of 0.43 (fPOM) and 0.92 (oPOM). Ratios reported for POM in temperate soils indicated POM to be less decomposed and to range from 0.20–0.32 in fPOM, 0.28–0.36 in oPOM (Kölbl and Kögel-Knabner, 2004), 0.37 in mineral associated SOM and 0.44–0.50 in fine earth (Helfrich et al., 2006). In our alpine soils, alkyl-C/O-alkyl-C ratios of the root + litter fraction were similar to those reported previously for agricultural crops including grass-clover roots (Leifeld and Kögel-Knabner, 2005). Alkyl-C/O-alkyl-C ratios of fPOM in layers below 10 cm depth were also similar to those reported in temperate soils but ratios in the 0–10 cm layers pointed to a higher degree of transformation. In addition, oPOM was more transformed than those from temperate soils.

Root + litter and POM fraction C/N ratios (Fig. 3) and fine earth soil MRTs (Fig. 6) generally increased with soil depth. In contrast, C/N ratios of mOM, which are generally lower

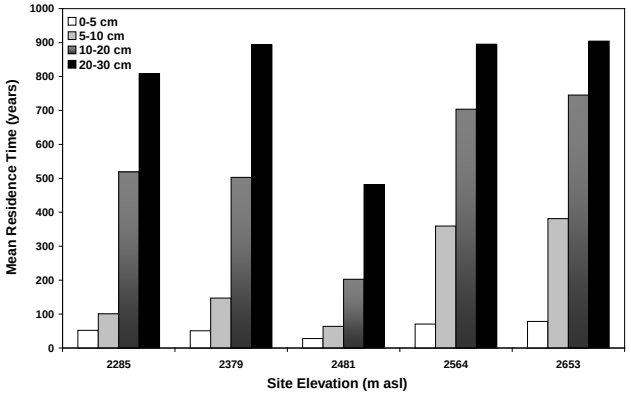

Fig. 6. Fine earth carbon MRT with time-lag and recalculation with Eq. (1), where appropriate, for all depths and sites. pMC values used for calculation were obtained from composite samples measured for ^{14}C content.

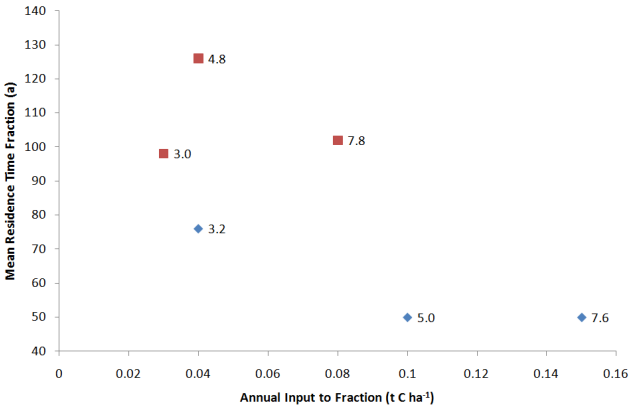

Fig. 7. Site variability of mean residence times and calculated input rates for fPOC (5–10 cm depth) at two elevations. Diamonds are for site 2285, squares for site 2564. Numbers next to symbols are carbon stocks for the same fraction ($t\,C\,ha^{-1}$).

than in other fractions, revealed no consistent trend with soil depth. This increase in C/N ratio of root + litter fraction is reflected in the increase of C/N ratio of both POM fractions with soil depth, thus indicating a decreasing degree of transformation in labile material with soil depth. This finding is corroborated by NMR results which suggest a pronounced difference in the degree of microbial transformation of fPOM between increments in soil depth (Table 5). Together this indicates that the long residence times of POM in topsoil goes along with a higher degree of transformation, as compared to temperate soils. On the other hand, POM in deeper layers is only slightly transformed which, together with long MRTs, indicate alpine subsoils to be biologically quite inactive.

Slow decomposition of plant residues at lower depths may not only be due to the corresponding wide C/N ratios of deep roots, the latter being considered the main precursors of POM (Leifeld et al., 2009) but may be enforced by low macronutrient content. Across the five sites, nutrient concentrations in the 10–20 and 20–30 cm layers were only ∼10 % of that in the top 5 cm. In combination, high C/N ratio, nutrient limitations, and possibly restricted physical access due to higher bulk densities, may cause the longer MRT of labile soil C in deeper soil layers. Therefore, potentially labile and little transformed C sources, such as fPOM, may age at deeper layers without being further transformed due to environmental constraints in these alpine soils.

4.3 Spatial patterns in SOM contents and dynamics as related to site factors and vegetation

We observed pronounced and sometimes significant spatial variability in SOM across and within our sites (Tables 1, 2). Examination of fine-scale patterns using replicate samples at two sites reveals considerable within-site spatial variability in SOC storage and MRT of fPOM in 5–10 cm sections (Fig. 7), the latter chosen to exemplify the situation. At the lower of the two sites, MRT varied by as much as 34 % between replicates, while at the upper site the coefficient of variation was 22 %. This difference in MRTs between replicates at a single sampling site is important for the estimation of MRT by the bomb model as, due to the high costs of radiocarbon measurement, often only very few representative samples are measured and site variability is not considered. However, variation in C input between replicates was even greater than variation in MRT (Fig. 7). This suggests that residue input may be a more important factor than turnover rates in determining the spatial variation in C stocks at each elevation, however, as a small number of replicates were used, further replicate measurement is necessary to establish if this is a consistent pattern.

No significant pattern in the amount or distribution of the various SOM fractions was found along the gradient. At this larger scale only mOM MRTs' increased significantly with elevation, probably related to the small climate gradient associated with elevation whereas POM MRTs' were not related to elevation but showed site-specific turnover rates. MRTs' of POM fractions were in the range of 55 to 144 years and thus higher than those estimated for temperate or tropical soils (Hsieh, 2009), but similar to values found for other cold and acidic soils (Schulze et al., 2009). Across a variety of fractions and sites 90 % of the variability in MRTs of C could be explained by the content of O-alkyl-C (mainly polysaccharides) (Fig. 4), showing the important role of OM quality on C turnover in alpine soils. The close correlation between root + litter and POM C/N ratios as well as the significant effect of O-alkyl-C on labile C MRTs' indicate that OM quality superimpose possible albeit small climate effects in the case of POM turnover.

Across sites the most important environmental driver for the turnover of bulk soil OM is soil pH, which was significantly positively related to turnover rate for 0–30, 0–5, and

10–20 cm sections. In particular, the MRT of fine earth carbon at the middle site (2481 m) is much shorter than expected from the trend across the elevation gradient (Table 6). The soil at this site is characterized by the highest soil pH, particularly in the upper soil layers. Soil acidity could be a major driver for the plant-soil system because of its various implications e.g. through nutrient availability and exoenzyme activity (Kalburtji et al., 1997; Kok and Vandervelde, 1991; Griffith et al., 1995). Acidic soils are often depleted in major cations while on less acidic soils plants benefit from higher availability of macronutrients, which in our study was the case for calcium. Based on a previous study on pH effects on C turnover in higher elevation grasslands (Leifeld et al., 2008), we estimate that in the range of pH 4–5, a decrease of ca. 0.5–1 units between the higher and lower sites relative to the less acidic middle site, should induce an increase in MRT by a factor of 1.6 to 2.3. However, averaged over the four soil depths, an even greater increase in MRT of 1.8 to 3.9 times was observed (Fig. 6), indicating that direct pH effects on turnover rates may explain some but not all of the difference found at the middle site.

Sites differed distinctly in vegetation (Fig. 2) therefore some of the observed site to site variability in SOM turnover time may be related to differences in plant communities and residue qualities as for example indicated by gradients towards declining root + litter quality with elevation (Table 4). The most notable difference in vegetation species was observed between the top elevation site, which is dominated by dwarf shrubs and a comparatively large proportion of lichens, and at the middle site which has a larger proportion of legumes compared to the other sites. The middle site also revealed highest aboveground phytomass, highest input rates and thus productivity, highest labile C content with smallest C/N ratios, all of which are indicative of a more biologically active system. These observations combined with the significant influence of soil pH with MRT discussed previously, suggest that the faster turnover observed at this site may depend not only on the direct pH effects on soil processes, but may also be a result of the indirect effects on turnover through vegetation composition and probably residue quality. While at the uppermost site, the relatively high abundance of dwarf shrubs in combination with effects of low pH, may contribute to the long soil C residence time observed because dwarf shrub litter, particularly of *Ericaceae*, is considered to be of low decomposability (Springob and Kirchmann, 2002). It is important to note that despite the much faster SOC turnover indicated at all depths of the middle site, the SOC content is similar to those of the other sites with slower turnover. This suggests that the rapid turnover at this site is compensated by larger residue input from the productive vegetation.

5 Conclusions

– The analysis of samples from across a small elevation gradient in the central Swiss Alps confirmed the high proportion of labile C present in the uppermost layers of alpine soils, and long MRTs of all SOM fractions compared to soils from lower elevations.

– In our alpine soils, slightly less acidic soil corresponded to higher plant productivity and, in turn, to larger inputs of organic matter with lower MRT; higher productivity was compensated for by faster turnover leading to similar SOC contents as in alpine soils of lower productivity and longer turnover times.

– Variations in plant productivity, unfavourable conditions for residue decomposition due to poor quality, and nutrient limitations due to low pH, may be of particular importance in determining the small scale spatial variability, long MRT, and preferential accumulation of POM.

– Although the high proportion of labile C found suggests that these soils may be sensitive to soil warming, the importance of factors other than temperature, such as pH, residue quality and plant productivity, and their interplay, need to be considered; models that do not take into account soil pH and changes in vegetation may be biased in predicting future SOC storage in alpine grasslands.

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