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Litter quality and pH are strong drivers of carbon turnover and distribution in alpine grassland soils

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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 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 above sea level (a.s.l.) in the central Swiss Alps. Our aim was to determine the quantity, degree of stabilization and mean residence time (MRT) of SOM in relation to site factors such as temperature, soil pH, vegetation, and organic matter (OM) structure. Soil fractions obtained by size and density fractionation revealed a high proportion of labile particulate organic matter C (POM C %) mostly in the uppermost soil layers. POM 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 indicated considerable variation in the quantity and quality of litter input, and these patterns could be reflected in the dynamics of soil C. ^{13}C NMR data confirmed the direct relationship of OM composition to MRT. While temperature is likely to be a major cause for the slow turnover rate observed, other factors such as litter quality and soil pH, as well as the combination of all factors, play an important role in causing small-scale variability of SOM turnover. Ignoring this interplay of controlling factors may impair the performance of models to project SOM responses to environmental change.

BGD

7, 6207–6242, 2010

1 Introduction

Globally, soils store more than twice as much carbon (C) as the atmosphere, with the atmosphere-soil annual C-exchange estimated at around 50–60 Pg (Schlesinger and Andrews, 2000). 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 raising 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 effected 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 litter. The amount of litter input depends on vegetation productivity (Meentemeyer et al., 1982; Körner, 2003), whereas litter quality is largely determined by plant species and tissue type (Kögel-Knabner,

BGD
7, 6207–6242, 2010

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 highly spatially 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 makes 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 SOC contents and a comparatively high abundance of less decomposed, labile POM material. A first 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.

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 other factors such as strong soil acidity may also play a crucial role (Leifeld et al., 2008). Moreover, litter quality from alpine plant species may differ greatly from that at lower sites and this may also affect the composition of SOM. As microbial decomposition proceeds, 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

BGD
7, 6207–6242, 2010

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). 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 OM in alpine environments relates to its turnover rate.

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 temperature 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°. ^{137}Caesium measurements (data not shown) and visual inspection of the soil profiles indicated

BGD
7, 6207–6242, 2010

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).

Six 30-cm soil cores (core diameter: 7.7 cm) were extracted at each site along a 20 m horizontal transect. Soil temperature loggers (Onset, Hoboware, USA) were inserted at 5 and 10 cm depths at the highest and lowest sites to determine variation in soil temperature across the gradient. Loggers were removed after 13 months (2008/2009) and mean soil temperature over one year was calculated.

2.2 Soil 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. Above-ground 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 total stone content (>2 mm) and fine earth (<2 mm). Fine earth was sieved further to separate very fine earth material of <63 µm from larger fine earth material of 63–200 µm, which still contained some fine roots (and litter material in upper sections). This additional fine root/litter material contained in the 63–200 µm fine earth section was separated by flotation in water to obtain a total root/litter fraction and a total fine earth section (0–200 µm) free of fine root/litter material.

After separation into 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.

BGD
7, 6207–6242, 2010

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 CN ratio and SOC content ($t\,ha^{-1}$).

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, calcium, magnesium and phosphorous) of fine earth were determined according to the Swiss reference methods after treatment with 1:10 NH_4-acetate solution (FAL, 1998).

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; CN 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 CN 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 soil C contained in POM (POM C%) and in mOM (MOM C%) were calculated from POC and MOC content relative to total SOC content.

BGD
7, 6207–6242, 2010

2.4 ^{14}C AMS measurements

POM fractions, fine soil and root/litter material were selected for ^{14}C measurement by accelerator mass spectrometry (AMS) at radiocarbon laboratory at the ETH, Zurich 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 was chosen for a detailed profile over four depths as this site had a particularly large proportion of labile material (root/litter/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 soil 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 ^{14}C dating. Radioactive C (^{14}C) from nuclear weapons tests in the 1960s released additional ^{14}C into the atmosphere, which, when taken up by vegetation, is incorporated into SOM through transformation of plant-derived litter. 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 is seems reasonable for alpine ecosystems as they occur naturally without a history of land use change. Combined with chemical analysis of OM, ^{14}C dating can indicate whether or not the chemical structure controls turnover of plant residues.

BGD
7, 6207–6242, 2010

AMS measurement of ^{14}C yielded percentage data of 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 from four depths taken at site 2564 m. A mean value of 14.5 years was derived from the calculation and used in the bomb model to recalculate soil MRT to account for the period of time that C remains in plants 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 bulk soil 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 bulk soil MRTs, later referred to as "fraction calculated bulk soil MRT", should provide a more accurate estimate of the bulk soil MRTs as the contribution from each soil fraction to the total soil turnover is integrated into the calculation.

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

$$y = -1272 + 658 * \log_{10}(x); \quad r = 0.96 \tag{1}$$

BGD
7, 6207–6242, 2010

Where y=fraction calculated bulk soil MRT and x=measured composite bulk soil MRT.

Calibration encompassed composite bulk soil MRTs of between 70 and 2000 years and was thus not applied to shorter MRTs. For measured composite bulk soil MRT values of 70 years or lower, the original composite bulk soil 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 a.s.l.

Annual C input into the soil at each depth for each site were 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

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 OM composition and turnover time, a narrowed O-alkyl region of 60–90 ppm was used, which excludes protonated C of lignins (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.

2.7 Phytomass

Above-ground phytomass was calculated (in g cm^3) from the plant weights obtained from the soil cores. Median values were used as sampling area (0.00465 m^2) was

BGD
7, 6207–6242, 2010

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 were identified and percentage area ($25 \times 25\,cm^2$) distribution was estimated by a modified Braun-Blanquet method at the location of each sampled core. This information was applied to the Ellenberg's indicator system (Ellenberg, 1988) to identify plant community characteristics. Ellenberg values indicate the ecological niche for environmental factors and can characterize ecological conditions based on plant species prevalence (Hawkes et al., 1997; Ersten et al., 1998). Ellenberg values were calculated for light, temperature, soil moisture, pH and soil nutrient status. At each site, total number of species was counted, and each species was categorized into one of the following functional groups: lichens, sedges, grasses, forbs, legumes and dwarf shrubs. Relative abundance (%) of each functional group was calculated.

2.9 Data analysis

Soil and root characteristics were calculated as the mean of the 6 replicates at each site, with the exception of phytomass for which median values were used. Regression analysis and the curved relationship between composite bulk soil MRTs and fraction calculated bulk soil MRTs were determined using Statistica 9.0. Correlation between selected variables is expressed as Pearsons' correlation coefficient and an indication of the error probability.

3 Results

Mean annual soil temperature at 5 and 10 cm depths varied little between the lowest and highest sites and was 2.8/2.6 °C at 2285 m and 2.7 /2.9 °C at 2653 m, respectively. Soil clay content of the 30-cm cores averaged 10% across sites. Table 1 lists data of

BGD
7, 6207–6242, 2010

the main soil characteristics for each site and depth. 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. 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 correlation analysis revealed a significant linear relationship between site SOC content with 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). POM C % also decreased with soil depth, in contrast to mOM C % which increased. Highest POM C (% of SOC) 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). POM C for 0–20 cm varied in the range of 45.9–57.6%. 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 POM 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 POM 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 across all sites, with 32 of these species only present at one 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 with a large proportion of dwarf shrubs and lichens, the predominant functional groups were forbs followed by grasses. The relative distribution of each functional group varied greatly between the sites (Fig. 2a). At the

BGD
7, 6207–6242, 2010

middle site (2481 m) the fraction of legumes was largest and a preference for higher pH was indicated by the Ellenberg value. Ellenberg values for soil moisture and nutrient availability did not indicate any trend with elevation. Temperature value decreased slightly from 1.7–1.8 at 2564 m and below to 1.5 at 2653 m (Fig. 2b), thus indicating a small shift in plant community towards a preference for colder temperatures.

Independent of site, the trend towards decreasing CN 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 CN ratios with soil depth, whereas mOM with the lowest CN ratio did not vary with depth.

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 3 show the related increase in Alkyl-C/O-Alkyl-C ratios, which reflected the progressive degree of microbial transformation. Additionally, in agreement with CN 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) correlated significantly to MRTs (r^2=0.95; p=<0.01, 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 with the corresponding bulk soil (fine earth) from the same soil layer indicating MRTs between those of mOM and oPOM (Fig. 5). 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). Bulk soil (fine earth) MRT was considerably lower at the middle site and did not increase with elevation across any soil depth (Fig. 6) while bulk soil MRTs did increase linearly with soil depth at all sites (2285 m: r=0.99, p=<0.01, n=4; 2379 m: r=0.99, p=<0.01, n=4; 2481 m: r=0.97, p=0.03, n=4; 2564 m: r=0.96, p=0.02, n=4; 2653 m: r=0.94, p=0.03, n=4). Site bulk soil MRTs were significantly correlated to site soil pH

BGD
7, 6207–6242, 2010

(r=−0.96, p=0.01, n=5) but within the soil profile bulk soil MRTs only showed a significant relationship with soil pH in the 0–5 cm depth sections (r=−0.96, p=<0.01, n=5) and 10–20 cm depth sections (r=−0.89, p=0.04, n=5).

MRT of POM 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 (Table 4). C input varied by a factor of 3 at the lower and by a factor of 2 at the higher site.

MRT of C in 30-cm bulk soil samples was lowest at the middle site where annual C input and phytomass were highest (Table 5). Conversely, smaller phytomass and annual C input at the two highest sites were associated with higher MRT. Site pH revealed a significant positive linear relationship with phytomass (r=0.98, p=0.003, n=5) and a negative relationship with MRT (r=−0.96, p=0.011, n=5). However, calculated annual inputs were not related to soil pH. POM C % indicated a positive correlation with total C input (0–30 cm) across the all sites (r=0.96, p=0.012, n=5). This was also reflected in samples from 5–10 cm (r=0.89, p=0.042, n=5) and 20–30 cm (r=0.93, p=0.023, n=5).

4 Discussion

4.1 Soil organic matter and factors controlling turnover

Soil from the central Swiss Alps contains SOC contents comparable to those reported for lower elevations, but the percentage of root and litter material in the top 5 cm and POM contents 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 POM C % compared to values found at elevations below 2000 m confirms the high abundance of labile C in the top soil layer, whereas below 10 cm, POM C % is only slightly higher (10–20 cm) or very similar (20–30 cm) to that at lower elevations (Leifeld et al., 2009; Zimmermann et al., 2007). The high POM C % found here follows a general trend with elevation (Fig. 4) and is in line with data from the few studies carried

BGD
7, 6207–6242, 2010

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 higher elevations (Wang et al., 2005, 2008). However, the data found here reveal a maximum POM C of around 58% (0–20 cm) at 2379 m and a decline with a further increase in elevation due to declining contents mainly below 5 cm. The small variation in soil temperature observed between sites of this elevation gradient indicate that soil temperature cannot explain this trend. From repeated visual inspections of the site it seems that due to a longer lasting snow cover at lower sites in the study region soil temperature does not reflect the existing gradient in air temperature. A difference of 1.5–2 °C air temperature can be estimated from the difference in altitude between the highest and lowest sampling sites, and Ellenberg values confirm a shift in plant community towards preference for colder temperatures (Fig. 2b). Therefore, changes in C distribution attributed to temperature could occur through shifts in plant community rather than through direct effects on the soil.

MRT of bulk soil at the middle site (2481 m) is much shorter than expected from the trend across the elevation gradient (Table 5). The soil at this site is characterized by the highest soil pH, particularly in the upper soil layers, highest productivity and total annual C-input. Soil acidity could be a major driver for the plant-soil system. 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 the difference 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 stronger increase in MRT of 1.8 to 3.9 times was observed (Fig. 6). Across sites, the increase in mean MRT relative to the middle site was highest at the highest elevation, which also differed in vegetation community. This suggests that soil C turnover is not only directly influenced by soil acidity, but may also depend on plant species present and related indirect effects through litter quality.

BGD
7, 6207–6242, 2010

4.2 Plant community and litter quality

Litter quality is important in determining SOM formation (Scholes et al., 1997), and different plant tissues and their chemical composition influence SOM decomposition (Oades, 1988). The observed site-to-site variability in decomposition may thus be related to differences in plant communities. The most notable difference in vegetation species was observed between the top elevation site, which is dominated by dwarf shrubs and lichens, and at the middle site which has a larger proportion of legumes (Fig. 1a). This suggests that the quality of plant residue entering the soil may differ considerably. Dwarf shrub litter, particularly of *Ericaceae*, is considered to be of low decomposability (Springob and Kirchmann, 2002). The relatively high abundance of dwarf shrubs at the uppermost site, in combination with effects of low pH, may contribute to the long soil C residence time observed. At the middle site, the plant community reflects the higher pH observed, as indicated by the Ellenberg value (Fig. 1b). In addition to its effects on SOM turnover (see above), soil pH has important implications for plants trough 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. In addition, the high abundance of legumes at the middle site provides N through the activity of N_2-fixing bacteria. In turn, this may cause the high phytomass leading to the largest residue input of all sites (Table 5). Much shorter MRTs across all depths at this site indicate an accelerated SOM turnover. However, as the SOC content is similar to other sites with longer MRTs, the rapid turnover is compensated by larger litter input from the productive vegetation.

4.3 Chemical composition of OM in relation to turnover rates of SOM fractions

Root/litter and POM fraction CN ratios (Fig. 3) and bulk fine earth soil MRTs (Fig. 6) generally increased with soil depth. In contrast, CN ratios of mOM, which are generally lower than in other fractions, revealed no consistent trend with soil depth. This increase

BGD
7, 6207–6242, 2010

in CN ratio of root/litter fraction is reflected in the increase of CN ratio of both POM fractions with soil depth and i) suggests an important role of roots as precursors for POM formation and ii) indicates a decreasing degree of transformation in labile material with soil depth. This finding is corroborated by NMR results whose alkyl-C/O-alkyl-C ratios suggest a pronounced difference in the degree of microbial transformation of fPOM between increments in soil depth (Table 3). Restriction of decomposition may be a result of litter quality in combination with low macronutrient content; particularly at lower depths where 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 CN ratio, nutrient limitations, and possibly restricted physical access due to higher bulk densities and missing bioturbation, may cause the longer MRT of soil C in deeper soil layers.

Our data support the 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 CN 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), and is 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 bulk soil (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 much higher degree of transformation. In addition, oPOM was more transformed than those from temperate soils. Together this suggests that long

BGD
7, 6207–6242, 2010

residence times of POM goes along with a higher degree of transformation, as compared to temperate soils. Put into perspective, compared to temperate soils a relatively large proportion of the overall microbial transformation in alpine soils takes place in the POM-state, and therefore the transformation of POM to mOM must be retarded. This supports the notion that, in alpine soils, accumulation of both POM fractions is due to their long MRT, with variability in POM C% at the field scale being related to variability in residue inputs.

MRT 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). Strong soil profile gradients in litter quality and nutrient availability additionally shape the distribution and turnover of POM with depth. Most strikingly, across a variety of fractions and sites 90% of the variability in MRTs could be explained by the content of O-alkyl-C (mainly polysaccharides) (Fig. 4), showing the strong role of litter or POM quality on C turnover in alpine soils.

4.4 Causes for small-scale spatial variability in C contents

Examination of replicate samples at two sites reveals considerable spatial variability in SOC storage and MRT of fPOM in 5–10 cm sections (Table 4). 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 greater than variation in MRT (Table 4). This suggests that litter input may be a more important factor than turnover rates in determining the spatial variation in C stocks at each elevation.

BGD
7, 6207–6242, 2010

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

The bomb model assumes a steady state environment, but in any 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 extensively 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 often contain a larger pMC than slower fractions. For some post-bomb samples, the model can indicate two rather 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). In our case, the inclusion of the time-lag period (i.e., the mean age of roots) into the bomb model indicates which values should be disregarded and therefore the only likely possible MRT time was allocated to the pMC value. The application of the time-lag period, which accounts for the period of C residence within the living plant tissue, may be particularly important in these soils with a large input from long-lived roots.

The measurement of individual soil fractions revealed increasing age between POM fractions and mineral-associated fractions. This characteristic is an important feature of the soil when considering MRT of bulk soil C, particularly at the higher elevation sites where MRT of mOM is over 4 times that of fPOM fractions. The method used for final MRT estimates, referred to as fraction calculated MRTs, allowed for the overall contribution of the soil fractions to the bulk soil. The combination of the addition of the time-lag period derived from root dating into the bomb model, and equation recalculation to the bulk soil MRTs with respect to fraction contribution, enables a more realistic estimation of the actual bulk soil MRTs. This is an improvement over single

BGD
7, 6207–6242, 2010

measurements which would require a homogenous system and not take this characteristic into account.

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.
- Less acidic soil corresponds to higher plant productivity and, in turn, to larger inputs of litter with lower MRT; higher productivity is compensated for by faster turnover leading to similar SOC contents as in alpine soils of lower productivity and longer turnover times.
- Small-scale variations in plant productivity, unfavorable conditions for litter 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 suggests that these soils may be sensitive to soil warming, the importance of factors other than temperature, such as pH, litter 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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BGD
7, 6207–6242, 2010

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BGD
7, 6207–6242, 2010

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BGD
7, 6207–6242, 2010

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BGD
7, 6207–6242, 2010

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BGD
7, 6207–6242, 2010

Table 1. Mean soil properties at each sampling site and soil depth.

Site elevation (m a.s.l.)	Soil depth (cm)	Bulk density (g cm^{-3})	SE*	Fine soil pH_{CaCl_2}	Stone volume (%)	SE	Root/litter dry matter (t ha^{-1})	SE	Phosphorous (mg kg^{-1})	Potassium (mg kg^{-1})	Magnesium (mg kg^{-1})	Calcium (mg kg^{-1})
2285	0–5	0.33	0.08	4.3	5.6	1.3	7.8	1.4	76	558	222	1155
	5–10	0.74	0.05	4.0	11.1	1.0	2.7	0.5	24	133	63	54
	10–20	0.73	0.04	4.2	17.0	1.2	4.0	2.7	5	42	12	82
	20–30	0.90	0.03	4.4	16.2	2.9	0.5	0.1	3	24	5	46
	0–30	**0.72**	**0.02**	**4.3**	**12.5**	**1.2**	**15.0**	**4.3**	**25**	**152**	**62**	**290**
2379	0–5	0.23	0.03	4.6	0.4	0.1	18.1	4.0	111	946	726	3889
	5–10	0.45	0.06	4.1	3.3	1.0	6.0	2.1	39	258	228	934
	10–20	0.56	0.04	4.2	8.0	2.2	3.0	0.3	6	72	46	173
	20–30	0.72	0.02	4.4	13.4	4.4	1.0	0.2	2	21	8	48
	0–30	**0.54**	**0.02**	**4.3**	**6.3**	**1.3**	**28.0**	**4.4**	**24**	**173**	**135**	**554**
2481	0–5	0.36	0.06	5.2	6.8	1.3	6.0	0.7	59	596	424	3345
	5–10	0.64	0.05	4.6	11.9	2.2	1.7	0.3	13	117	135	851
	10–20	0.74	0.07	4.5	12.5	1.5	1.9	0.4	6	67	68	434
	20–30	0.85	0.03	4.4	14.0	1.6	0.8	0.1	3	40	28	195
	0–30	**0.70**	**0.04**	**4.6**	**11.3**	**0.8**	**10.3**	**0.9**	**17**	**160**	**163**	**1032**
2564	0–5	0.25	0.02	4.0	1.2	0.4	29.0	1.9	133	747	350	1269
	5–10	0.51	0.03	3.7	4.1	1.2	6.6	1.4	44	169	90	234
	10–20	0.62	0.01	4.0	6.9	0.7	3.2	0.7	7	40	17	55
	20–30	0.65	0.04	4.3	12.2	1.3	3.3	0.2	4	23	5	28
	0–30	**0.55**	**0.01**	**4.1**	**6.1**	**0.5**	**42.0**	**2.9**	**29**	**127**	**61**	**127**
2653	0–5	0.51	0.07	4.0	4.1	0.7	14.1	3.1	45	261	150	609
	5–10	0.67	0.02	4.2	7.8	1.8	3.0	1.3	16	82	53	156
	10–20	0.76	0.03	3.9	12.4	1.9	0.7	0.2	4	26	12	59
	20–30	0.90	0.03	4.4	14.4	2.0	0.5	0.1	2	11	5	38
	0–30	**0.75**	**0.03**	**4.2**	**9.7**	**1.1**	**18.3**	**3.6**	**17**	**86**	**50**	**87**

* Standard errors (SE) indicate 1 SE of the mean.

BGD
7, 6207–6242, 2010

Table 2. Mean soil carbon at each sampling site and soil depth.

Site elevation (m a.s.l.)	Soil depth (cm)	Soil C (%)	SE	SOC (t ha^{-1})	SE	POM C proportion (%)	mOM C proportion (%)	SE
2285	0–5	11.8	1.1	17.8	2.6	71.2	28.8	3.5
	5–10	3.9	0.4	14.3	1.3	45.8	54.2	4.6
	10–20	1.7	0.1	12.5	0.7	20.7	79.3	2.9
	20–30	1.1	0.2	10.4	2.0	10.4	89.6	2.6
	0–30	**7.2**	**0.3**	**55.0**	**2.2**	**41.4**	**58.6**	**2.0**
2379	0–5	27.9	4.7	31.5	1.9	85.4	14.6	4.6
	5–10	11.4	2.2	24.1	1.7	66.6	33.4	9.0
	10–20	4.4	0.7	24.4	1.6	20.7	79.3	2.8
	20–30	2.5	0.4	18.2	1.1	11.9	88.1	2.9
	0–30	**10.8**	**0.6**	**97.9**	**3.6**	**49.8**	**40.2**	**3.7**
2481	0–5	12.9	2.9	20.7	2.3	83.8	16.2	2.6
	5–10	3.8	0.8	11.5	0.7	49.4	50.6	7.0
	10–20	1.9	0.4	13.7	1.2	23.4	76.6	2.6
	20–30	1.2	0.3	10.2	1.2	14.3	85.7	1.2
	0–30	**6.8**	**0.6**	**56.0**	**4.0**	**49.6**	**50.4**	**2.8**
2564	0–5	24.2	1.4	29.6	2.0	85.5	14.5	2.7
	5–10	9.8	0.8	24.6	1.0	26.1	73.9	3.7
	10–20	4.3	0.2	26.4	1.0	16.0	84.0	1.4
	20–30	3.3	0.3	21.5	1.4	19.1	80.9	1.7
	0–30	**11.3**	**0.4**	**102.1**	**2.3**	**39.3**	**60.7**	**1.3**
2653	0–5	10.8	2.2	25.5	1.9	77.3	22.7	9.0
	5–10	4.3	1.0	14.3	2.5	26.9	73.1	3.8
	10–20	2.1	0.4	15.4	1.7	14.6	85.4	2.0
	20–30	1.3	0.2	11.5	1.2	6.3	93.7	0.3
	0–30	**7.7**	**0.5**	**67.8**	**5.5**	**36.8**	**63.2**	**3.5**

BGD
7, 6207–6242, 2010

Table 3. Alkyl-C/O-Alkyl-C, CN ratio's 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
	Bulk Soil	5–10	54.0	31.3	0.58	325.5
2564	Root and 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
		10–20	60.7	19.5	0.32	233.0
		20–30	57.2	15.9	0.28	244.8

N.A.=not analyzed

BGD
7, 6207–6242, 2010

Table 4. Site variability of fPOM (5–10 cm depth) at two elevations.

Site elevation (m a.s.l.)	Replicate	% Modern carbon	MRT with time-lag (years)	SOC ($t\,ha^{-1}$)	Annual input ($t\,C\,ha^{-1}$)
2285	1	110.9	76	3.2	0.04
	2	114.0	50	5.0	0.10
	3	114.0	50	7.6	0.15
2564	1	107.0	126	4.8	0.04
	2	108.6	102	7.8	0.08
	3	108.9	98	3.0	0.03

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7, 6207–6242, 2010

Table 5. Mean bulk soil MRT, annual C input, and above ground phytomass at each site.

Site elevation (m a.s.l.)	MRT with time-lag (years)	Annual C-input ($t\,C\,ha^{-1}$)	Above ground phytomass ($g\,cm^{-2}$)
2285	105.5	0.52	8.31×10^{-2}
2379	115.2	0.85	8.19×10^{-2}
2481	55.7	1.01	11.69×10^{-2}
2564	185.6	0.55	6.27×10^{-2}
2653	168.3	0.40	6.39×10^{-2}

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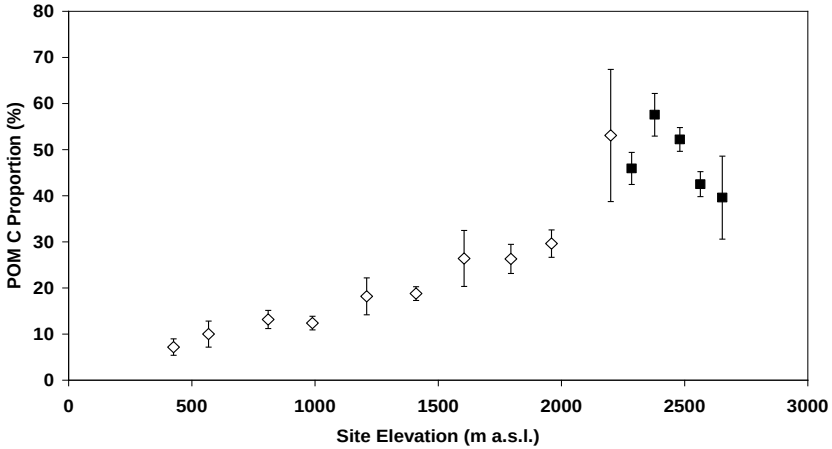

Fig. 1. POM C proportion (%) in 20 cm deep soil cores. Squares indicate Furkapass data. Additional data (diamonds) taken from Zimmerman et al. (2007) and Leifeld et al. (2009). Error bars indicate 1 SE of the mean.

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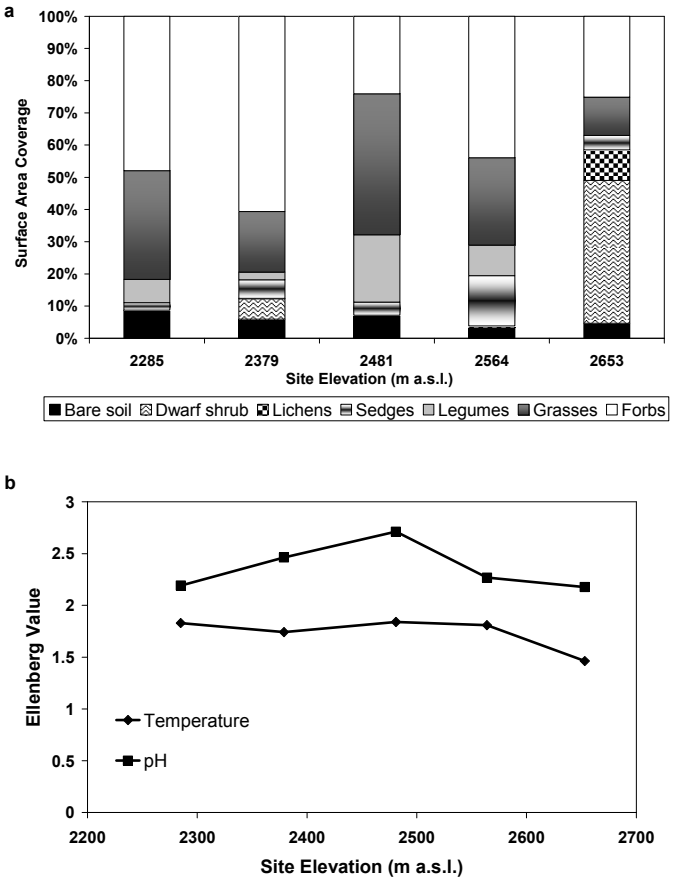

Fig. 2. **(a)** Functional group surface area distribution (%) of vegetation at each elevation site. **(b)** Ecological preference of vegetation indicated by vegetation species across Furka elevation gradient.

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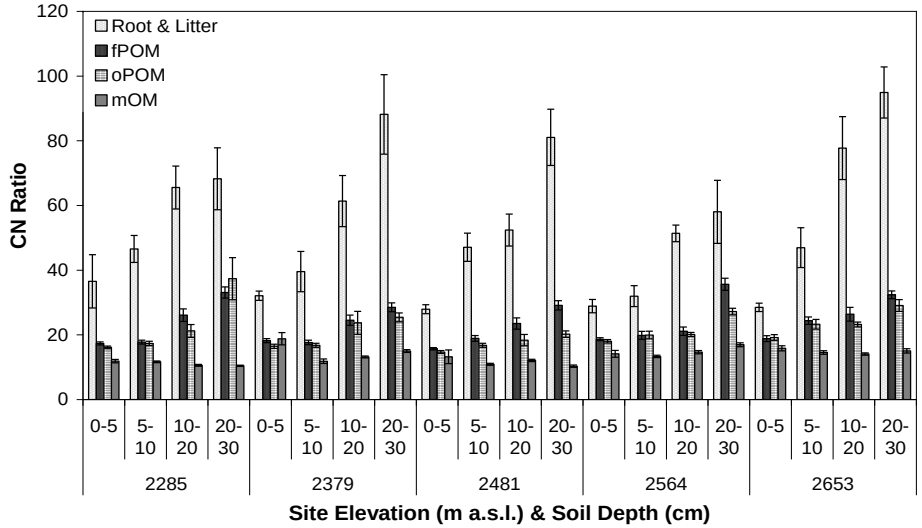

Fig. 3. CN ratio's of root and litter, fPOM, oPOM and mOM with depth. Error bars indicate 1 SE of the mean.

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7, 6207–6242, 2010

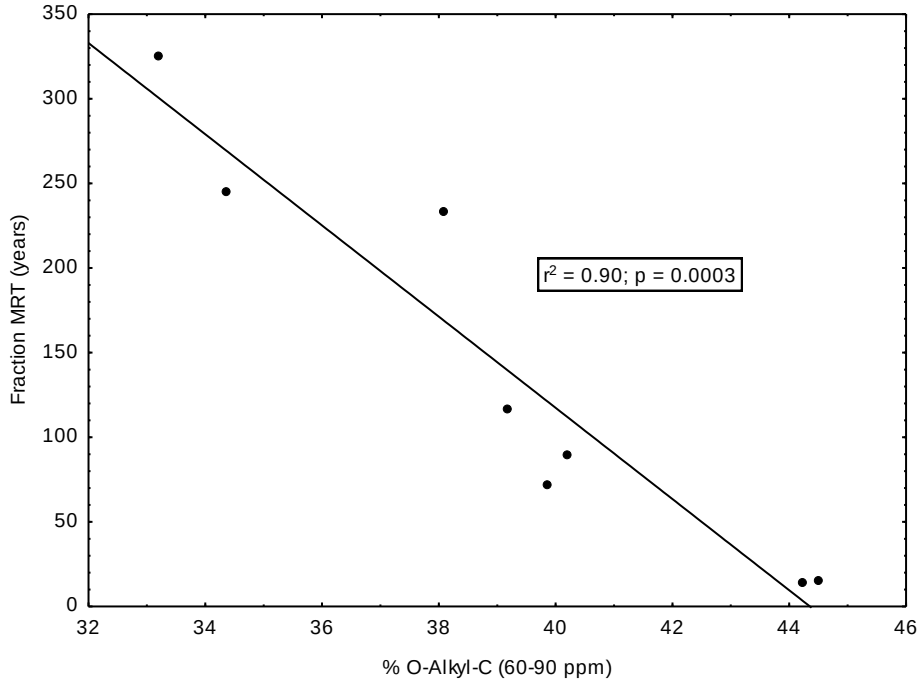

Fig. 4. Linear correlation between fraction MRTs and O-Alkyl-C % in fractions measured by NMR.

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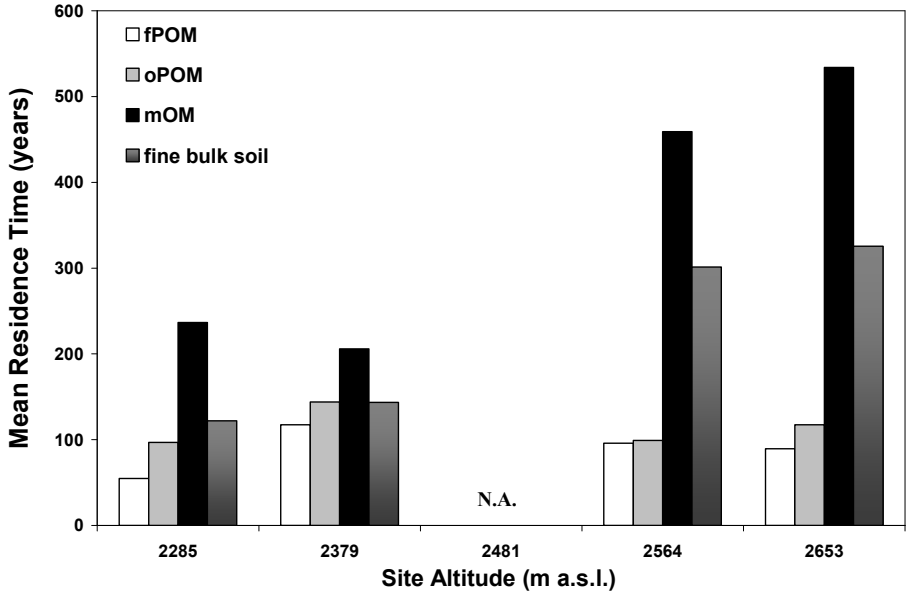

Fig. 5. MRT's of individual fractions at 5–10 cm depth at 4 sampling sites.

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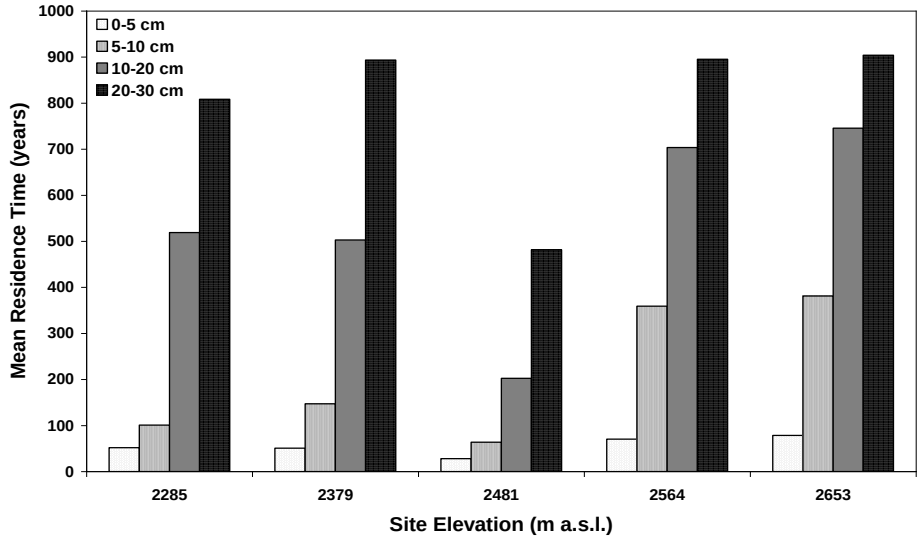

Fig. 6. Bulk soil carbon MRT (with time lag) according to Eq. (1) for all depths and sites.

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