Biogeosciences Discuss., doi:10.5194/bg-2017-113, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 6 April 2017


## 1. Title page

# No long-term effect of land-use activities on soil carbon dynamics in tropical montane grasslands

Viktoria Oliver[1,2*], Imma Oliveras[3], Jose Kala[4], Rebecca Lever[5,2], Yit Arn Teh [1,2]

[1] Institute of Biological and Environmental Sciences, University of Aberdeen, Cruickshank Building, St. Machar Drive, AB24 3UU Aberdeen, UK.
[2] Formerly at the School of Geography and Geosciences, University of St Andrews, UK
[3] Environmental Change Institute, School of Geography and the Environment, University of Oxford. South Parks Road, OX13QY Oxford, UK.
[4] Universidad de Santo Antonio Abad del Cusco, Cusco, Peru.
[5] Department of Life & Environmental Sciences, University of California, Merced 5200 North Lake Rd. Merced, CA 95343, United States.

[*] Corresponding author: v.oliver@abdn.ac.uk

***Running title:*** Tropical montane grassland soil carbon dynamics

***Keywords:*** Andean montane grasslands, soil respiration, fire, grazing, puna, soil carbon, land-use activities, soil density fractionation.

Biogeosciences Discuss., doi:10.5194/bg-2017-113, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 6 April 2017


## 2. Abstract

Montane tropical soils are a large carbon (C) reservoir, acting as both a source and a sink of $CO_2$. Enhanced $CO_2$ emissions originate, in large part, from the decomposition and losses of soil organic matter (SOM) following anthropogenic disturbances. Therefore, quantitative knowledge of the stabilization and decomposition of SOM is necessary in order to understand, assess and predict the impact of land management in the tropics. In particular, labile SOM is an early and sensitive indicator of how SOM responds to changes in land use and management practices, which could have major implications for long term carbon storage and rising atmospheric $CO_2$ concentrations. The aim of this study was to investigate the impacts of grazing and fire history on soil C dynamics in the Peruvian montane grasslands; an understudied ecosystem, which covers approximately a quarter of the land area in Peru. A combination of density and particle-size fractionation was used to quantify the labile and stable organic matter pools, along with soil $CO_2$ flux and decomposition measurements. Grazing and burning together significantly increased soil $CO_2$ fluxes and decomposition rates and reduced temperature as a driver. Although there was no significant effect of land use on total soil C stocks, the combination of burning and grazing decreased the proportion of C in the free LF, especially at the lower depths (10-20 and 20-30 cm). The free LF in the control soils made 20 % of the bulk soil mass and 30 % of the soil C content compared to the burnt-grazed soils, which had the smallest recovery of free LF (10 %) and significantly lower C content (14 %). The burnt soils had a much higher proportion of C in the occluded LF (12%) compared to the non-burnt soils (7%) and there was no significant difference among the treatments in the heavy F (~70%).  The synergistic effect of burning and grazing caused changes to the soil C dynamics. $CO_2$ fluxes were increased and the dominant temperature driver was obscured by some other process, such as changes in plant C and N allocation promoting autotrophic respiration. In addition, the free LF was negatively affected when these two anthropogenic activities took place on the same site. Most likely a result of reduced detritus being incorporated into the soil. A positive finding from this study is that the total soil C stocks were not significantly affected and the long term C storage in the occluded LF and heavy F were not negatively impacted. Possibly this is because of low intensity fire, fire-resilient grasses and the grazing pressure is below the threshold to cause severe degradation.

Biogeosciences Discuss., doi:10.5194/bg-2017-113, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 6 April 2017


## 3. Introduction

High altitudinal montane grasslands (3200 - 4500 m a.s.l) account for a major proportion of land cover in the Andes, particularly in Peru, where they make-up approximately 25 % of land cover (Feeley and Silman 2010). Since the early 1500's, the main driving force for the expansion of montane grasslands has involved burning in order to maintain the highly productive forage grasses for cattle grazing (Luteyn 1992; Sarmiento and Frolich 2002; Balser and Wixon 2009; Johansson, Granström and Malmer 2012). To some extent, this natural system is tolerant of these management practices (Ramsay 1992). However, in recent years, it has become apparent that the combination of global warming and the considerable pressure from agricultural expansion have resulted in increased fire occurrence and subsequent destruction of tropical montane cloud forest (Cochrane and Ryan 2009).

Previous research in these Andean montane grasslands have measured large soil C stores, (Zimmermann *et al.* 2009; Oliveras *et al.* 2014). However, despite the concern on the effects of land management practices, there are very few studies on soil C balance in this tropical region of the Peruvian Andes. It is particularly unclear how land management affects the soil C dynamics and sequestration potential under the influence of grazing and burning. For example, (Oliveras *et al.* 2014), found that grazing and fire in montane grasslands resulted in decreased net primary productivity, but there were no differences between these two disturbances. Studies in other montane grasslands have found that an increase in the frequency of fire events can reduce the amount of soil organic matter (SOM) in the top soil (Knicker 2007), or it may increase the biomass growth period afterwards, causing more detritus to accumulate in the upper soil layers (Ojima *et al.* 1994).

Soil organic matter (SOM) is a complex and dynamic composite of organic compounds from progressively decayed plant, animal and microbial material in the soil matrix (Zimmermann *et al.* 2007). The turnover of SOM is a balance between the inputs of material into the soil (e.g., above and belowground litter, dissolved organic C) and the rate of SOM decomposition. This rate is partly a consequence of climate (Fierer 2007) the type of plant material and its susceptibility to degradation (i.e. biochemical recalcitrance), and the accessibility of SOM to decomposers (Six *et al.* 2002)- the latter including adsorption of SOM to reactive surfaces of mineral particles and the physical protection within aggregates. The rate of SOM decomposition is also influenced by functional composition and activity of the soil microbial community (Fierer 2007; Allison 2012), nutrient availability, dissolved organic carbon content, and other external environmental factors, such as soil moisture and soil temperature (Raich and Schlesinger 1992; Kirschbaum 1995).

Specifically, there are three biologically significant and measurable components (pools) that differ in their residence time, chemistry and origin (Trumbore 1993; Bol *et al.* 2009). These include: labile pools with a turnover time of 1 to 5 years, composed of easily available dead plant material as a C source for microorganisms; intermediate pools turning over on decadal time scales, which contain physically and chemically transformed material residing on and within the surface of clay and silt minerals; and more stable pools with a turnover time of centuries to millennia due to the nature of the biochemically recalcitrant and bio-actively unavailable material. Even when land use change does not appear to affect the bulk soil C, the distribution of these pools may change due to their differing sensitivities to environmental forcing or external perturbation (Zimmermann *et al.* 2007).

Uncertainties lie in how sensitive these pools are to land-use change. Labile pools are accepted as being the most sensitive to changes in vegetation management. Although they make up only a small part of the total C pool, they may dominate soil-atmospheric feedbacks because of large $CO_2$ fluxes into and out of this pool, coupled with high turnover rates (Bayer *et al.* 2001). However, while several studies have found the labile pool to be more sensitive to land management (Conant *et al.* 2011; Wang and Wang 2011), others have found no discernible effect on pool size (Leifeld and Kögel-Knabner 2005). For instance, labile pools can either increase (Poeplau and Don 2013) or decrease, depending on the magnitude of C inputs (e.g. roots, litter fall) or the level of grazing intensity (Figueiredo, Resck and Carneiro 2010). On the other hand, slower cycling pools may be a useful indicator of the long-term effects of land management on soil C storage, because of the stabilising effect of recalcitrant soil C fractions on total soil C storage (Six and Jastrow 2002; Marin-Spiotta *et al.* 2009).

When considering the short and long term storage effects of SOC with land-use change, the importance of measuring the different C pools, as well as the bulk soil C content, have been highlighted in many tropical, temperate and boreal studies (Marin-Spiotta *et al.* 2009).

Biogeosciences Discuss., doi:10.5194/bg-2017-113, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 6 April 2017


Methods such as density fractionation have been routinely used as a way to physically separate SOM into fractions of varying reactivity and chemical recalcitrance, they have been very successful at assessing the short and long-term dynamics of soil C storage (Christensen 2001).

In this study, a combination of density and particle-size fractionation, along with soil $CO_2$ fluxes were quantified to gain further mechanistic insights into the impact of land-use management on soil C losses and different SOM fractions in Peruvian montane grasslands. In order to investigate the effects of burning and grazing on soil C stocks, we took advantage of an ongoing burning/grazing study that was established in July-August 2010 (Oliveras *et al.* 2014). The specific objectives of this study were to:

a. Quantify and compare total SOC stocks and estimate decomposition rates among grazing and burnt sites;
b. Evaluate the effect of different management systems on the labile and stable organic matter pools;
c. Quantify differences in soil respiration and evaluate the role of environmental drivers in regulating soil respiration fluxes, including factors such as: soil temperature and moisture.

## 4. Material and methods

### 4.1 Site descriptions

The undulating terrain in the montane grassland is commonly used by the local communities for extensive cattle grazing and although the study area is in the National Park, burning and grazing still occasionally takes place. This study included two sites that were identified as being burnt in 2003 (Wayqecha) and 2005 (Acjanaco) (refer to Fig 1). The site at Wayqecha is located at approximately 3085 m a.s.l. in Wayqecha Biological Station (13°18´S, 71°58´W), where the mean annual precipitation is 1560 mm and mean annual air temperature is 11.8 °C (Girardin *et al.* 2013). The site at Acjanaco (13°17'S, 71°63´W), is located on the Manu national park boarder at 3400 m a.s.l and has a mean annual precipitation of 760 mm and mean annual air temperature 6.8 °C. The wet season runs from October to March and there are more noticeable variations in diurnal temperatures than seasonal differences (Zimmermann *et al.* 2009). Grass species composition are similar on both sites (*Calamagrostis longearistata, Scirpus rigidus and Festuca dolichophylla)* (Oliveras *et al.,* 2014). The soils are classified as Umbrisols and are typically only 30 cm deep with a thick acidic organic rich A layer overlying a thin stony B/C horizons and no O horizon (Gibbon *et al.* 2010) (Table 1). The sites are predominantly on Palaeozoic (~450 Ma) meta-sedimentary mudstones (~80 %) (Carlotto *et al.* 1996).

**4.2 Experimental design**

The sites were set up in a factorial design in July-August 2010 to investigate the effects of fire (burnt, not burnt) and grazing (grazed, ungrazed) on soil C fractions and soil respiration. Both puna areas selected to include a burnt and an unburnt area (no more than 0.3 km apart), which were then split into two subplots (2 x 2 m); one with fencing constructed to stop cattle grazing and one left unfenced. Each site contained eight replicates of all four factorial combinations of the two treatments, i.e. burnt-not grazed; burnt-grazed; not burnt-grazed; and not burnt-ungrazed. Field sites are described in more detail in Oliveras *et al*., 2014.

On each land use, four permanent PVC chamber bases (diameter 20 cm, height 10 cm) were deployed randomly for the measurement of soil surface $CO_2$ fluxes, which took place morning and afternoon at two monthly intervals from July 2011 to July 2012.

**4.3 Soil respiration and environmental measurements**

Soil respiration measurements were quantified using a static flux chamber technique with a Vaisala CARBOCAP® carbon dioxide probe and temperature sensor fitted inside a PVC cylindrical chamber (diameter 20 cm, height 20 cm), covered with a gas tight lid. The rate of $CO_2$ accumulation was measured every 30 seconds for 3 minutes by placing the chamber on the fixed chamber base with a gas tight rubber seal. Simultaneously, air temperature and atmospheric pressure were measured, using a type K thermocouple (Omega Engineering Ltd., UK) and Garmin GPSmap 60CSx (Garmin Ltd., USA).

Flux rates were calculated in R 3.0.2 (R_Core_Team, 2012) using the *HMR* package (Pedersen, Petersen and Schelde 2010) by plotting the headspace concentration (ppm) against time

Biogeosciences Discuss., doi:10.5194/bg-2017-113, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 6 April 2017


(minutes) for each collar, which gave a linear or non-linear regression, depending on the best fit. Fluxes were then reported in μmol $m^{-2}$ $s^{-1}$ and annual emissions were estimated by extrapolating each bi-monthly measurement to a 60 day period and summing for a year.

In addition, soil temperature (at 5 cm and 10 cm depth) and soil moisture (at 10 cm depth) were simultaneously measured in three locations adjacent to the collars using a ML2x ThetaProbe equipped with 12 cm rods (Delta-T Ltd., UK) and type K thermocouples (Omega Engineering Ltd., Manchester, UK).

**4.4 Soil sampling and analysis**

*Soil sampling:* 50 g soil samples were taken in July 2012 with six replicates at 0-5, 5-10, 10-20 and 20-30 cm depths on each site. Soil samples were air-dried and sieved with a 2 mm mesh sieve before being shipped to the University of St Andrews for all further analysis (Brown and Lugo 1982).

*Bulk density:* soil bulk density was determined by the soil core method (Klute 1986). Undisturbed soil cores (30 $cm^3$) were taken from three of the soil pits at 0-10, 10-20 and 20-30 cm. The samples were dried at 105 °C for 48 hours and bulk density was estimated as the mass of oven-dry soil divided by the core volume.

*Soil fractionation:* Soils C fractions were separated using a method developed by (Marín-Spiotta *et al.* 2008) and (Mueller and Koegel-Knabner 2009), which combined both density and particle-size fractionation. This method is useful for separating SOM based on the location within the soil matrix and the degree of association with minerals. Prior to the experiment, a sub-sample of soil was taken for moisture correction. The air-dried soil material (15 g < 2 mm) was then saturated with 60 mL sodium polytungstate solution (NaPT, $Na_6[H_2W_{12}O_{40}]$, Sometu-Germany) at a density of 1.85g/mL and centrifuged for 45 minutes at 3600 rpm and allowed to settle overnight. The floating free light fraction (free LF) was aspirated via a pump and rinsed with 500 mL of deionised water through a 0.4 μm polycarbonate filter (Whatman Nuclepore Track Etch Membrane) to remove residual NaPT. The remaining slurry was further saturated with 60 mL sodium polytungstate solution (1.4 g $cm^{-3}$), mixed using a benchtop mixer (Mixer/Vortexer - BM1000) for 1 minute at 3200 rpm and dispersed ultrasonically (N10318 Sonix VCX500 sonicator Vibra-cell ultrasonic processor) for 3 min at 70 % pulse for a total input of 200 J/mL. Centrifugation (45 minutes at 3600 rpm) was used to separate the occluded light fraction (occluded LF) from the mineral residue and allowed to sit overnight to achieve further separation by flotation of organic debris and settling of clay particles in solution. The occluded LF was then aspirated via a pump and rinsed. In order to remove the NaPT from the heavy fraction (heavy F), deionised water was mixed with the material and centrifuged for 15 minutes at 4000 rpm 5 times. All fractions were oven dried at 100 °C overnight, weighed and physically ground to a fine powder before C analysis and isotope analysis.

*Carbon analysis:* bulk soils were ground and homogenised using a grinding mill (Planetary Mono Mill PULVERISETTE) in preparation for C analysis at the University of St Andrews laboratories using a Finnegan Delta plus XP gas source mass spectrometer coupled to an elemental analyser (EA-IRMS).

*Decomposition estimates:* A decomposition experiment was set up as an additional estimate of soil organic matter mineralisation, using birch wood sticks as a common substrate. Five sticks were placed in a mesh bag with three 2 cm holes cut into each bag to allow accessibility for both microfauna and fauna. In July 2011, eighteen bags were buried at 10 cm depth, in close proximity, on each site and three bags collected every two months. The sticks were weighed before the experiment started and again after collection, once they were air dried, to determine mass loss. The rate of decomposition was then calculated from the slope of a linear regression with time against mass loss.

**4.5 Statistical analysis**

Statistical analyses were conducted in R version 3.0.2 (R_Core_Team, 2012). Outliers were observed by visual inspection of the boxplots where points outside of the hinges (third quartile) were removed and the data were checked for normal distributions. The $CO_2$ flux and volumetric water content (VWC) data were not normally distributed and therefore log transformed prior to parametric statistical analysis. Linear mixed effect models were conducted to identify any relationships between the environmental variables and soil characteristics with soil $CO_2$ fluxes for each site, individually. In this respect, mixed model

Biogeosciences Discuss., doi:10.5194/bg-2017-113, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 6 April 2017


restricted maximum likelihood analysis (REML) were computed using the *lme4* package (Bates *et al.* 2014) to include random intercepts for each collar and for the effect of grazing nested within the burnt sites. Analysis of variance (ANOVA) and Tukey's Honest Significant Different (HSD) post hoc test were used to examine statistically significant differences between means of the environmental data among the sites. Linear regression analysis was used on the decomposition data and tested to identify any relationships with the soil $CO_2$ fluxes. Differences in soil C between the areas were analysed using a one-way ANOVA and TukeyHSD post-hoc test, after testing for normality and homogeneity of variances.

## 5. Results

### 5.1 Soil respiration and environmental drivers

The overall annual $CO_2$ mean for the pooled data set, including all types of land management, was 1.39 ± 0.05 µmol $m^{-2}$ $s^{-1}$. The combination of grazing and burning significantly increased soil $CO_2$ fluxes. However, this was more noticeable at Wayqecha (2003) than at Acjanaco (2005) (Fig 2). Regardless of land use, the plots at Wayqecha (2003) had greater variability and overall higher mean annual soil temperature (15 °C) and $CO_2$ flux (1.34 ± 0.09 µmol $m^{-2}$ $s^{-1}$) compared to the sites in Acjanaco (2005) (12 °C and 0.79 ± 0.03 µmol $m^{-2}$ $s^{-1}$) (Table 2). The highest measured temperatures and $CO_2$ fluxes at Wayqecha were synchronously recorded during July-11, November-12 and March-12, whereas at Acjanaco the changes in $CO_2$ flux with season and temperature were less pronounced.

Season, soil and air temperature were the main drivers of soil respiration (*p*-values = 0.031, $9.3 \times 10^{-7}$ and 0.0001, respectively), with higher temperatures having a positive effect on soil $CO_2$ fluxes. However, when analyzing the grazed-burnt plots at both Wayqecha and Acjanaco, there was no relationship between $CO_2$ fluxes and temperature or any of the other environmental variables measured.

### 5.2 Decomposition rates

The decomposition of the birch wood sticks was slow, with an overall average weight loss of ~ 20 % in one year. Grazing alone appeared to slightly increase the rate of decomposition when all the data were pooled together (grazed: y = 104.53 + -4.23x, $R^2$ = 0.98, non grazed: y = 103.63 + -3.11, $R^2$ 0.94), but burning alone did not affect decomposition rate (burnt: y = 103.34 + -3.57, $R^2$ = 0.96, non burnt: y = 104.82 + -3.76x, $R^2$ = 0.97) (Fig 3). Site-specific differences were observed for decomposition rates; for example, decomposition was generally faster at Wayqecha compared to Acjanaco. In particular, the grazed - non burnt plot at Wayqecha showed the fastest overall rate of decomposition (y = 101.98 + -0.19x, $R^2$ = 0.77) and the non grazed - non burnt plots (controls) had the slowest decomposition rates (Fig 3) on both sites.

Decomposition was not a strong overall predictor for $CO_2$ fluxes for the pooled dataset, although there were some strong correlations between these two variables at specific study sites. For example, there was a strong relationship between decomposition and soil $CO_2$ fluxes at Acjanaco (y = 0.38 + -0.18x, $R^2$ = 0.99) (i.e. faster mass loss = higher soil respiration), whereas at Wayqecha, this relationship was weak (y = 1.56 + 0.06x, $R^2$ = 0.07). Land-use did not appear to influence the decomposition rate-soil $CO_2$ flux relationship.

### 5.3 Belowground C stocks

Grazing, burning and the combination of burning and grazing did not significantly alter total soil C at any depth down to 30 cm (Table 3). The overall sum of all the measured depths showed signs of a decrease in C stocks on the grazed soils, from 183 ± 62 Mg C $ha^{-1}$ on the undisturbed sites to 149 ± 35 Mg C $ha^{-1}$ on the grazed-burnt sites, but this was not statistically significant at the $P < 0.05$ level. On average, Acjanaco (2003) had significantly higher C stocks (170.89 ± 14.98 Mg C $ha^{-1}$) compared to Wayqecha (2005) (154.74 ± 14.88 Mg C $ha^{-1}$).

The pooled dataset demonstrated that these soils have a notably large free LF (~20 %). When looking at the different treatments and averaging the data across the soil profile (0-30 cm), burning and grazing had a significant negative effect on the proportion of C in the free LF

(Table 4). The free LF in the control soils made 20 % of the bulk soil mass and 30 % of the soil C content compared to the burnt-grazed soils, which had the smallest recovery of free LF (10 %) and had significantly lower C content (14 %). However, when analysing the depths individually, there was only a significant loss of C in the free LF at 10-20 and 20-30 cm depth, with a reduction of ~ 16 % (Fig 4). When analysing the two sites separately, the burnt- grazed soils at Wayqecha had a significantly smaller proportion of C in the free LF at 0-5 cm (*p*-value = 0.002), whereas at Acjanaco there were no significant differences among the land uses.

The occluded LF appeared to be more strongly affected by burning in comparison to grazing, with burnt soils displaying a significant increase in the occluded LF. For example, when pooling the data from across different soil depths (0-30 cm), for the two sites combined, the burnt soils had a much higher proportion of C in the occluded LF (12 %) compared to the non-burnt soils (7 %). There were no significant differences among the treatments in the heavy F, with an average of ~ 70 %.

## 6. Discussion

### 6.1 Soil respiration and decomposition rates

In this study, soil $CO_2$ fluxes ranged from 2.35 to 3.82 to Mg C ha$^{-1}$ yr$^{-1}$, which is in the lower range (0.7 – 14.8 Mg C ha$^{-1}$ yr$^{-1}$) of other high elevation montane grassland studies (Cao *et al.* 2004; Geng *et al.* 2012; Muñoz, Faz and Zornoza 2013; Fu *et al.* 2014) and corroborates prior work by Oliveras et al., 2014 (3.4 - 3.7 Mg C ha$^{-1}$ yr$^{-1}$). The absence of a seasonal trend in temperature and moisture has also been noted in other studies from the same region (Girardin *et al.* 2010; Teh *et al.* 2014).

Higher soil respiration and faster decomposition rates were consistently measured on the plots at Wayqecha (burnt in 2003) than at Acjanaco (2005), which is in keeping with Oliveras *et al.,* 2014. These site-specific differences may not be a reflection of the age of burning but rather Acjanaco being at a slightly higher elevation and on average 4 °C cooler. Despite the variance in mean annual temperature, the two sites both showed a positive correlation between temperature and soil respiration. Interestingly though, the decomposition rates at Acjanaco correlated with the $CO_2$ fluxes, suggesting that decay was a good predictor of $CO_2$

flux. This was in contrast to the lower elevation site in Wayqecha, where $CO_2$ fluxes did not correlate with decomposition rates, implying that autotrophic respiration or other environmental factors may have had a stronger influence on soil respiration.

Burning alone or grazing alone enhanced soil respiration and decomposition rates when these land management practices were considered separately, with soil temperature identified as the main environmental driver in each of these treatment types. However, when plots had been exposed to both burning and grazing together, soil temperature no longer correlated well with soil respiration. The combination of burning and grazing also produced higher soil respiration rates than the two treatments independently. While this pattern has been identified before in other studies (Ward *et al.* 2007), the drivers of this increase are less well understood, and the influence of grazing and burning have been known to have confounding effects (Michelsen *et al.* 2004). One potential explanation is that burning and grazing together act synergistically, and may obscure the influence of temperature due to the action of other complex processes or drivers, such as changes in plant C allocation and autotrophic respiration following the effects of the two combined disturbances. For example, studies have found that when foliage is cut, photosynthate and other resources are allocated to the growth of new shoots rather than to the roots (Schmitt, Pausch and Kuzyakov 2013), causing a decline in root respiration (García-Oliva, Sanford and Kelly 1999). The resulting root death enhances heterotrophic microbial activity, counteracting the effects of reduced root respiration.

Alternatively, burning can cause significant losses of N due to combustion, and grasses may compensate for increased N limitation by increasing their allocation to roots, thereby increasing root respiration and potentially promoting enhanced belowground C cycling (Johnson and Matchett 2001). Some evidence was found for this type of response in prior work; Oliveras *et al.,* 2014, found higher below and above-ground C stocks in undisturbed soils. While overall net primary productivity (NPP) was higher on undisturbed sites, NPP belowground was greater with grazing and fire, suggesting a shift in plant allocation patterns after these disturbances.

### 6.2 Belowground C stocks

Overall, large total SOC stocks were measured in these montane grasslands, which is in keeping with Páramo and other high elevation grassland studies (Hofstede 1995; Zimmermann *et al.* 2009; Li *et al.* 2013; Muñoz, Faz and Zornoza 2013; Oliveras *et al.* 2014) and are probably attributable to low temperatures and wet conditions causing slow mineralisation of SOM and turnover rates. Soil C stocks were significantly higher at Acjanaco than at Wayqecha. This is in agreement with Oliveras *et al.,* 2014, although the Acjanaco sites in this previous study were higher (253 compared to 152 Mg C $ha^{-1}$ reported here), perhaps reflecting within site spatial heterogeneity.

The negligible effect of burning on total soil C may be a consequence of low intensity fires, fire-resilient grasses, and potentially low fuel loads at the time of burning (Knicker 2007). Grassland fires on slopes can move very quickly, so even when intense, the transfer of heat to the soil is less damaging due to low residence times (Rollins, Cohen and Durig 1993). As a result, surface temperatures do not typically exceed 100 °C or 50 °C at 5 cm depth (Campbell *et al.* 1995), and organic matter can only be fully volatilized between 200 and 315 °C (Knicker 2007). Even if the soils were dry at the time of burning which is possible during the dry season, then belowground temperatures would rise very slowly because of the insulating properties of air-filled pores, which curtail heat transfer belowground (Neary *et al.* 1999).

Grazing on the other hand, had a more negative impact on total SOC content than burning but there was not a significant loss of total soil C. One explanation is that the grazing pressure in these sites may have been below the threshold required to cause severe degradation, supporting previous studies in the Peruvian Andes, where they also found no significant effect of grazing or burning on total SOC stocks (Gibbon *et al.* 2010; Oliveras *et al.* 2014).

Overall, the free LF was larger than in other tropical systems (30 % of total soil C). By comparison, studies in Puerto Rico found the free LF was only 10 % of total soil C (Marin-Spiotta *et al.* 2009). As a consequence, loss of the free LF due to disturbance may have a greater proportional impact on net ecosystem C loss in these systems. In addition, the larger free LF suggests that the decomposition of labile material may be slower in these montane grasslands than in other tropical environments. Grazing had a negative impact on the free LF.

As grazing is known for reducing aboveground biomass (Johnson and Matchett 2001; Gibbon *et al.* 2010), a lower incorporation of detritus into the soil is not surprising and has been observed in other grazing studies (Figueiredo, Resck and Carneiro 2010). The effects of grazing on the free LF were most pronounced when grazing and burning occurred together, in which case, the free LF showed the most pronounced declines.

The significant positive effect of burning on the occluded LF may be the result of charcoal particles (from burning) becoming incorporated into the occluded LF. Charcoal, because of its low density, tends to reside in the lighter fractions (Cadisch *et al.* 1996; Glaser *et al.* 2000; Sollins *et al.* 2006), despite its recalcitrance. Because the fires took place almost ten years ago, the charcoal may no longer be resident the free LF but may have become occluded into soil micro-aggregates due to its high sorptive capacity (Qayyum *et al.* 2014). Once incorporated into micro-aggregates, charcoal can be maintained for centuries after fire (Zackrisson, Nilsson and Wardle 1996).

## 7. Conclusions

This study highlights the complexities of how land management can affect soil C dynamics in montane tropical grasslands. The results suggest that montane grasslands are resilient to soil C losses under moderate intensity land use. Total C stocks appeared unaffected by burning and grazing, although a change was observed in the distribution of soil C across different soil C fractions, with burning leading to a significant reduction in the free LF pool and an enhancement of the occluded LF pool. Most specifically, our study shows that land management affected the magnitude and drivers of soil respiration and decomposition. Burning alone or grazing alone each increased soil $CO_2$ fluxes apparently driven by shifts in soil temperature. However, the combined effect of burning and grazing together interacted synergistically, leading to enhanced soil respiration rates, while simultaneously obscuring the role of temperature and other environmental drivers, potentially due to changes in patterns of plant C and N allocations.

## 8. Acknowledgements

The authors wish to thank the Manu National Park forest rangers for allowing us to use their facilities and the field technicians for their assistance. We also thank the Amazon Basin Conservation Association for institutional support. This material is based upon work supported by the UK Natural Environment Council under grant joint grant references NE/H006583, NE/H007849 and NE/H006753). This publication is a contribution from the Scottish Alliance for Geoscience, Environment and Society (http://www.sages.ac.uk). I.Oliveras was supported with a NERC grant NE/G006385/1.

## 9. Authorship

V. Oliver designed the study, conducted the fieldwork, statistical data analysis and wrote the manuscript. I. Oliveras designed the study, provided supervision and contributed to writing the manuscript. J. Kala and R. Lever conducted fieldwork and laboratory analysis. Y. A. Teh obtained funding for the work, provided supervision for the whole study and contributed to writing the manuscript.

## 10. References

Allison S. A trait-based approach for modelling microbial litter decomposition. *Ecol Lett* 2012;**15**:1058–70.

Balser TC, Wixon DL. Investigating biological control over soil carbon temperature sensitivity. *Glob Change Biol* 2009;**15**:2935–49.

Bates D, Maechler M, Bolker B *et al.* lme4: Linear mixed-effects models using Eigen and S4. *R Package Version* 2014;**1**.

Bayer C, Martin-Neto L, Mielniczuk J *et al.* Changes in soil organic matter fractions under subtropical no-till cropping systems. *Soil Sci Soc Am J* 2001;**65**:1473–8.

Bol R, Poirier N, Balesdent J *et al.* Molecular turnover time of soil organic matter in particle-size fractions of an arable soil. *Rapid Commun Mass Spectrom* 2009;**23**:2551–8.

Brown S, Lugo AE. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 1982:161–87.

Biogeosciences Discuss., doi:10.5194/bg-2017-113, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 6 April 2017


Cadisch G, Imhof H, Urquiaga S *et al.* Carbon turnover (δ13C) and nitrogen mineralization potential of particulate light soil organic matter after rainforest clearing. *Soil Biol Biochem* 1996;**28**:1555–67.

Campbell GS, Jungbauer Jr J, Bristow KL *et al.* Soil temperature and water content beneath a surface fire. *Soil Sci* 1995;**159**:363–74.

Cao G, Tang Y, Mo W *et al.* Grazing intensity alters soil respiration in an alpine meadow on the Tibetan plateau. *Soil Biol Biochem* 2004;**36**:237–43.

Carlotto V, Gil W, Cardenas J *et al.* Mapa Geologico del Cuadrangula de Calca (27-s) Republica del Peru: Ministerio de engergia y minas Instituto geologico minero y metalurgico (INGEMMET); 1996.

Christensen BT. Physical fractionation of soil and structural and functional complexity in organic matter turnover. *Eur J Soil Sci* 2001;**52**:345–53.

Cochrane MA, Ryan KC. Fire and fire ecology: Concepts and principles. *Tropical Fire Ecology*. Springer, 2009, 25–62.

Conant RT, Ogle SM, Paul EA *et al.* Measuring and monitoring soil organic carbon stocks in agricultural lands for climate mitigation. *Front Ecol Environ* 2011;**9**:169–73.

Diem T, Morley NJ, Ccahuana AJ *et al.* Complex controls on nitrous oxide flux across a long elevation gradient in the tropical Peruvian Andes. *Biogeosciences Discuss* 2017;**2017**:1–44.

Feeley KJ, Silman MR. Land-use and climate change effects on population size and extinction risk of Andean plants. *Glob Change Biol* 2010;**16**:3215–22.

Fierer N. Microbial Diversity and Functional Group Characterization: Relationships to SOM Dynamics. 2007.

Figueiredo CC de, Resck DVS, Carneiro MAC. Labile and stable fractions of soil organic matter under management systems and native cerrado. *Rev Bras Ciênc Solo* 2010;**34**:907–16.

Fu G, Zhang X, Yu C *et al.* Response of soil respiration to grazing in an alpine meadow at three elevations in Tibet. *Sci World J* 2014;**2014**.

García-Oliva F, Sanford RL, Kelly E. Effects of slash-and-burn management on soil aggregate organic C and N in a tropical deciduous forest. *Geoderma* 1999;**88**:1–12.

Geng Y, Wang Y, Yang K *et al.* Soil respiration in Tibetan alpine grasslands: belowground biomass and soil moisture, but not soil temperature, best explain the large-scale patterns. *PloS One* 2012;**7**:e34968.

Biogeosciences Discuss., doi:10.5194/bg-2017-113, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 6 April 2017


Gibbon A, Silman MR, Malhi Y *et al.* Ecosystem Carbon Storage Across the Grassland–Forest Transition in the High Andes of Manu National Park, Peru. *Ecosystems* 2010;**13**:1097–111.

Girardin CAJ, Aragão LEOC, Malhi Y *et al.* Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Glob Biogeochem Cycles* 2013;**27**:252–64.

Girardin CAJ, Malhi Y, Aragao L *et al.* Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Glob Change Biol* 2010;**16**:3176–92.

Glaser B, Balashov E, Haumaier L *et al.* Black carbon in density fractions of anthropogenic soils of the Brazilian Amazon region. *Org Geochem* 2000;**31**:669–78.

Hofstede RG. The effects of grazing and burning on soil and plant nutrient concentrations in Colombian páramo grasslands. *Plant Soil* 1995;**173**:111–32.

Johansson MU, Granström A, Malmer A. Tending for cattle: traditional fire management in Ethiopian montane heathlands. 2012.

Johnson LC, Matchett JR. Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology* 2001;**82**:3377–89.

Kirschbaum MU. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biol Biochem* 1995;**27**:753–60.

Klute A ed. *Methods of Soil Analysis: Part 1—Physical and Mineralogical Methods*. Madison, WI: Soil Science Society of America, American Society of Agronomy, 1986.

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

Leifeld J, Kögel-Knabner I. Soil organic matter fractions as early indicators for carbon stock changes under different land-use? *Geoderma* 2005;**124**:143–55.

Li Y, Dong S, Wen L *et al.* The effects of fencing on carbon stocks in the degraded alpine grasslands of the Qinghai-Tibetan Plateau. *J Environ Manage* 2013;**128**:393–9.

Luteyn JL. *Páramo: An Andean Ecosystem under Human Influence*., 1992.

Marin-Spiotta E, Silver WL, Swanston CW *et al.* Soil organic matter dynamics during 80 years of reforestation of tropical pastures. *Glob Change Biol* 2009;**15**:1584–97.

Marín-Spiotta E, Swanston CW, Torn MS *et al.* Chemical and mineral control of soil carbon turnover in abandoned tropical pastures. *Geoderma* 2008;**143**:49–62.

Michelsen A, Andersson M, Jensen M *et al.* Carbon stocks, soil respiration and microbial biomass in fire-prone tropical grassland, woodland and forest ecosystems. *Soil Biol Biochem* 2004;**36**:1707–17.

Mueller CW, Koegel-Knabner I. Soil organic carbon stocks, distribution, and composition affected by historic land use changes on adjacent sites. *Biol Fertil Soils* 2009;**45**:347–59.

Muñoz M, Faz A, Zornoza R. Carbon stocks and dynamics in grazing highlands from the Andean Plateau. *Catena* 2013;**104**:136–43.

Neary DG, Klopatek CC, DeBano LF *et al.* Fire effects on belowground sustainability: a review and synthesis. *For Ecol Manag* 1999;**122**:51–71.

Ojima DS, Schimel DS, Parton WJ *et al.* Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* 1994;**24**:67–84.

Oliveras I, Girardin C, Doughty C *et al.* Andean grasslands are as productive as tropical cloud forests. *Environ Res Lett* 2014;**9**:115011.

Pedersen AR, Petersen SO, Schelde K. A comprehensive approach to soil-atmosphere trace-gas flux estimation with static chambers. *Eur J Soil Sci* 2010;**61**:888–902.

Poeplau C, Don A. Sensitivity of soil organic carbon stocks and fractions to different land-use changes across Europe. *Geoderma* 2013;**192**:189–201.

Qayyum M, Steffens D, Reisenauer H *et al.* Biochars influence differential distribution and chemical composition of soil organic matter. *Plant Soil Env* 2014;**60**:337–43.

Raich J, Schlesinger WH. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B* 1992;**44**:81–99.

Ramsay PM. The páramo vegetation of Ecuador: the community ecology, dynamics and productivity of tropical grasslands in the Andes. 1992.

Rollins MS, Cohen AD, Durig JR. Effects of fires on the chemical and petrographic composition of peat in the Snuggedy Swamp, South Carolina. *Int J Coal Geol* 1993;**22**:101–17.

Sarmiento FO, Frolich LM. Andean Cloud Forest Tree Lines. *Mt Res Dev* 2002;**22**:278–87.

Schmitt A, Pausch J, Kuzyakov Y. Effect of clipping and shading on C allocation and fluxes in soil under ryegrass and alfalfa estimated by 14 C labelling. *Appl Soil Ecol* 2013;**64**:228–36.

Six J, Conant R, Paul EA *et al.* Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant Soil* 2002;**241**:155–76.

Six, Jastrow. Organic matter turnover. *Encycl Soil Sci Marcel Dekker N Y* 2002:936–42.

Sollins P, Swanston C, Kleber M *et al.* Organic C and N stabilization in a forest soil: evidence from sequential density fractionation. *Soil Biol Biochem* 2006;**38**:3313–24.

Teh Y, Diem T, Jones S *et al.* Methane and nitrous oxide fluxes across an elevation gradient in the tropical Peruvian Andes. *Biogeosciences* 2014;**11**:2325.

Trumbore SE. Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements. *Glob Biogeochem Cycles* 1993;**7**:275–90.

Wang Q, Wang S. Response of labile soil organic matter to changes in forest vegetation in subtropical regions. *Appl Soil Ecol* 2011;**47**:210–6.

Ward SE, Bardgett RD, McNamara NP *et al.* Long-term consequences of grazing and burning on northern peatland carbon dynamics. *Ecosystems* 2007;**10**:1069–83.

Zackrisson O, Nilsson M-C, Wardle DA. Key ecological function of charcoal from wildfire in the Boreal forest. *Oikos* 1996:10–9.

Zimmermann M, Leifeld J, Schmidt M *et al.* Measured soil organic matter fractions can be related to pools in the RothC model. *Eur J Soil Sci* 2007;**58**:658–67.

Zimmermann M, Meir P, Bird M *et al.* Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest. *Soil Biol Biochem* 2009;**41**:1338–40.

**Table 1** Soil description (mineral soil particle size taken from (Diem *et al.* 2017 - *submitted to Biogeosciences*).

| Bulk density (g cm$^{-3}$) | pH | Soil C:N | Soil C (%) | Mineral Soil Particle Size | | |
|---|---|---|---|---|---|---|
| | | | | Clay | Silt | Sand |
| 0.36 ± 0.03 | 4.4 ± 0.1 | 12.9 ± 0.4 | 14.86 ± 1.5 | 2.6 ± 0.2 | 54.4 ± 3.0 | 43.0 ± 3.2 |

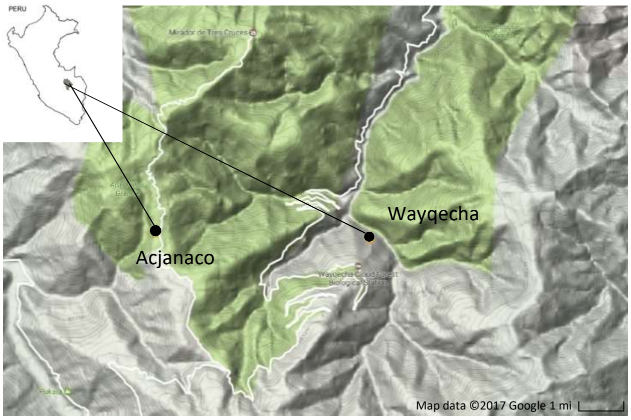


**Figure 1** Map illustrating the two sites in the high elevation montane grassland (circles).

The green area represents the Manu National Park.

Biogeosciences Discuss., doi:10.5194/bg-2017-113, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 6 April 2017


**Table 2** Annual and seasonal mean soil temperature, VWC and $CO_2$ flux for Wayqecha and Acjanaco in the montane grassland.

| Site / land use / season | Soil temp. (°C) at 5 cm | VWC (%) at 5 cm | $CO_2$ flux ($\mu mol\ m^{-2}\ s^{-1}$) | Annual $CO_2$ emission ($Kg\ C\ m^{-2}\ yr^{-1}$) | pH 0-5 cm | Soil C 0-5 cm ($Mg\ C\ ha^{-1}$) |
|---|---|---|---|---|---|---|
| **Wayqecha (2003)** | 14.7 ± 0.1 | 62.3 ± 0.4 | 1.31 ± 0.09 | 0.49 | | |
| Grazed – burnt | 15.3 ± 0.3$^{a}$ | 63.4 ± 0.3$^{ab}$ | 1.88 ± 0.23$^{a}$ | 0.40 | 4.3 ± 0.1$^{a}$ | 40.0 ± 1.3$^{a}$ |
| Grazed - non burnt | 14.5 ± 0.2$^{ab}$ | 63.8 ± 0.2$^{ab}$ | 1.07 ± 0.07$^{b}$ | 0.38 | 4.3 ± 0.1$^{a}$ | 41.3 ± 8.9$^{a}$ |
| Non grazed - burnt | 14.6 ± 0.3$^{ab}$ | 60.9 ± 1.0$^{c}$ | 0.99 ± 0.08$^{bc}$ | 0.41 | 4.1 ± 0.0$^{a}$ | 40.3 ± 2.6$^{a}$ |
| Non grazed - non burnt | 14.1 ± 0.2$^{b}$ | 62.5 ± 0.8$^{bc}$ | 1.10 ± 0.07$^{ab}$ | 0.31 | 4.6 ± 0.0$^{a}$ | 38.7 ± 4.1$^{a}$ |
| Dry season | 14.1 ± 0.2 | 61.4 ± 0.8 | 1.35 ± 0.16 | | | |
| Wet season | 15.1 ± 0.20 | 63.8 ± 0.3 | 1.31 ± 0.10 | | | |
| Minimum | 11.6 | 29.9 | 0.22 | | | |
| Maximum | 18.0 | 65.8 | 8.33 | | | |
| **Acjanaco (2005)** | 11.6 ± 0.1 | 64. 5 ± 0.1 | 0.91 ± 0.03 | 0.29 | | |
| Grazed - burnt | 12.0 ± 0.2$^{c}$ | 64.0 ± 0.2$^{ab}$ | 0.82 ± 0.05$^{bc}$ | 0.31 | 4.7 ± 0.1$^{a}$ | 40.2 ± 5.0$^{a}$ |
| Grazed – non burnt | 11.5 ± 0.2$^{cd}$ | 64.5 ± 0.2$^{ab}$ | 0.84 ± 0.07$^{bc}$ | 0.31 | 4.2 ± 0.0$^{a}$ | 41.4 ± 2.4$^{a}$ |
| Non grazed - burnt | 11.9 ± 0.1$^{cd}$ | 64.2 ± 0.2$^{ab}$ | 0.77 ± 0.05$^{c}$ | 0.29 | 4.6 ± 0.1$^{a}$ | 53.5 ± 3.5$^{a}$ |
| Non grazed - non burnt | 10.8 ± 0.1$^{d}$ | 65.1 ± 0.2$^{a}$ | 0.72 ± 0.05$^{c}$ | 0.27 | 5.1 ± 0.1$^{a}$ | 48.0 ± 1.3$^{a}$ |
| Dry season | 11.6 ± 0.1 | 63.8 ± 0.2 | 0.81 ± 0.04 | | | |
| Wet season | 11.7 ± 0.1 | 65.1 ± 0.1 | 0.74 ± 0.03 | | | |
| Minimum | 9.5 | 57.1 | 0.09 | | | |
| Maximum | 13.7 | 67.7 | 2.69 | | | |
| GRAZED – BURNT | 13.8 ± 0.2$^{a}$ | 63.7 ± 0.2$^{a}$ | 1.35 ± 0.13$^{a}$ | 0.51 | | |
| GRAZED – NON BURNT | 13.2 ± 0.2$^{a}$ | 64.1 ± 0.1$^{a}$ | 0.95 ± 0.05$^{b}$ | 0.36 | | |
| NON GRAZED – BURNT | 13.3 ± 0.2$^{a}$ | 62.6 ± 0.5$^{a}$ | 0.88 ± 0.05$^{b}$ | 0.33 | | |
| NON GRAZED – NON BURNT | 12.6 ± 0.2$^{a}$ | 63.8 ± 0.4$^{a}$ | 0.91 ± 0.05$^{b}$ | 0.35 | | |

Different letters down the columns represent significant differences between sites. Soil C and pH values are given with 1 standard deviation of the mean ($n$ = 3).

Biogeosciences Discuss., doi:10.5194/bg-2017-113, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 6 April 2017


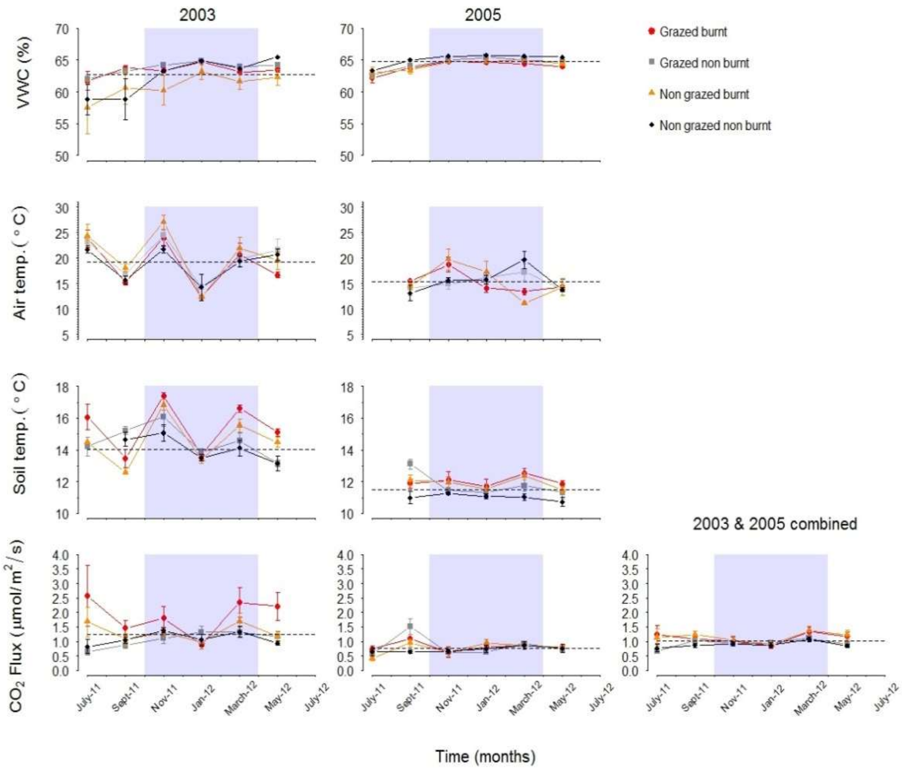


**Figure 2** Monthly soil temperature (5 cm), air temperature, soil VWC (0-10 cm) and soil $CO_2$ flux from grazed and non-grazed subplots on sites burned in 2003 (Wayqecha) and 2005 (Acjanaco) and adjacent non burnt sites in the montane grassland. The graph on the right represents the mean $CO_2$ flux of both burnt sites combined. For $CO_2$ fluxes, each symbol is a mean of 4 chambers with morning and afternoon measurements combined and standard errors ($n$ = 8) are plotted as error bars. The dotted line represents the mean for that site and the blue band represents the wet season (Oct-March).

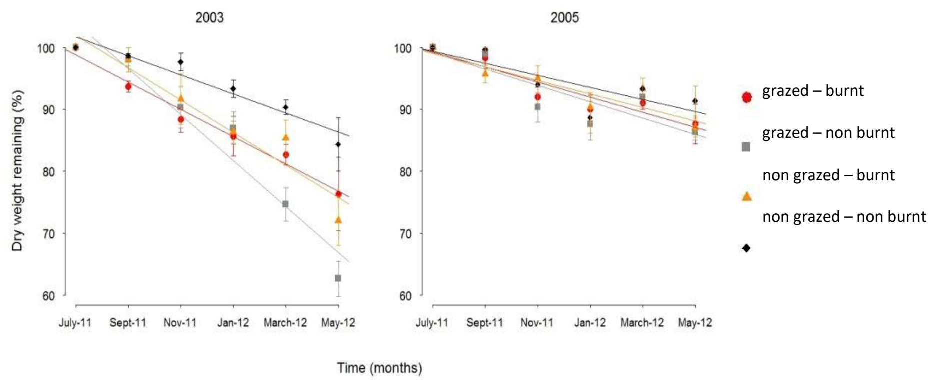


**Figure 3** Mass losses (%) of sticks from the decomposition experiment on two burnt sites (2003 = Wayqecha and 2005 = Acjanaco) with grazed subplots and control plots.

Biogeosciences Discuss., doi:10.5194/bg-2017-113, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 6 April 2017


**Table 3** Bulk soil mean C concentrations (%), C content (Mg C ha$^{-1}$) for each depth and total C stocks (0-30 cm)

| **Land use** | **Depth (cm)** | **Bulk C concentration (%)** | **Bulk C (Mg C ha$^{-1}$)** |
|---|---|---|---|
| G - B (Grazed – burnt) | 0-5 | 20.2 ± 1.5$^{a}$ | 40.5 ± 3.0$^{a}$ |
| G - NB (Grazed - non burnt) | | 20.8 ± 2.7$^{a}$ | 41.3 ± 5.3$^{a}$ |
| NG - B (Non grazed - burnt) | | 23.5 ± 1.9$^{a}$ | 46.9 ± 3.9$^{a}$ |
| NG - NB (Non grazed - non burnt) | | 19.8 ± 2.2$^{a}$ | 43.4 ± 3.2$^{a}$ |
| G - B | 5-10 | 14.9 ± 1.2$^{a}$ | 29.7 ± 2.5$^{a}$ |
| G - NB | | 17.9 ± 2.6$^{a}$ | 35.9 ± 5.1$^{a}$ |
| NG - B | | 16.4 ± 2.2$^{a}$ | 34.0 ± 4.5$^{a}$ |
| NG - NB | | 18.9 ± 2.1$^{a}$ | 37.7 ± 4.3$^{a}$ |
| G - B | 10-20 | 7.7 ± 1.1$^{a}$ | 41.6 ± 6.1$^{a}$ |
| G - NB | | 8.9 ± 1.5$^{a}$ | 47.9 ± 7.9$^{a}$ |
| NG - B | | 13.6 ± 2.2$^{a}$ | 69.7 ± 10.0$^{a}$ |
| NG - NB | | 12.7 ± 2.7$^{a}$ | 59.0 ± 8.4$^{a}$ |
| G - B | 20-30 | 4.1 ± 1.6$^{a}$ | 26.4 ± 8.7$^{a}$ |
| G - NB | | 4.4 ± 2.2$^{a}$ | 23.6 ± 10.6$^{a}$ |
| NG - B | | 7.8 ± 3.2$^{a}$ | 19.0 ± 4.6$^{a}$ |
| NG - NB | | 8.0 ± 2.7$^{a}$ | 43.2 ± 14.2$^{a}$ |
| G - B | 0-30 | 12.6 ± 6.8$^{a}$ | 149 ± 35$^{a}$ |
| G - NB | | 14.7 ± 7.9$^{a}$ | 149 ± 38$^{a}$ |
| NG - B | | 15.2 ± 8.1$^{a}$ | 175 ± 41$^{a}$ |
| NG - NB | | 14.9 ± 7.3$^{a}$ | 183 ± 62$^{a}$ |

Different letters down the columns within each depth represent significant differences among sites. All values are given with 1 standard error of the mean (n = 3).

**Table 4** Mean mass recovery of density fractions and proportion of total C residing in the three density fractions (%) from the total soil profile (0-30 cm). Different letters down the columns represent significant differences.

| | **Free LF** | | **Occluded LF** | | **Heavy F** | |
|---|---|---|---|---|---|---|
| | **Fraction of total C (%)** | **Mass of soil recovered (%)** | **Fraction of total C (%)** | **Mass of soil recovered (%)** | **Fraction of total C (%)** | **Mass of soil recovered (%)** |
| **GB** | 14.0 ± 5.3$^{b}$ | 9.9 ± 3.6$^{a}$ | 10.8 ± 2.6$^{ab}$ | 9.8 ± 3.4$^{ab}$ | 76.0 ± 8.0$^{a}$ | 78.4 ± 7.2$^{a}$ |
| **GNB** | 22.7 ± 13.3$^{ab}$ | 16.2 ± 8.5$^{a}$ | 8.9 ± 2.1$^{bc}$ | 5.3 ± 1.6$^{bc}$ | 68.3 ± 14.0$^{a}$ | 76.7 ± 8.1$^{a}$ |
| **NGB** | 19.7 ± 8.3$^{ab}$ | 15.1 ± 8.5$^{a}$ | 14.2 ± 2.5$^{a}$ | 11.3 ± 4.7$^{a}$ | 66.1 ± 10.5$^{a}$ | 76.6 ± 8.3$^{a}$ |
| **NGNB** | 30.0 ± 5.7$^{a}$ | 19.5 ± 5.5$^{a}$ | 5.2 ± 0.8$^{c}$ | 4.3 ± 0.7$^{c}$ | 64.7 ± 6.1$^{a}$ | 69.7 ± 5.8$^{a}$ |

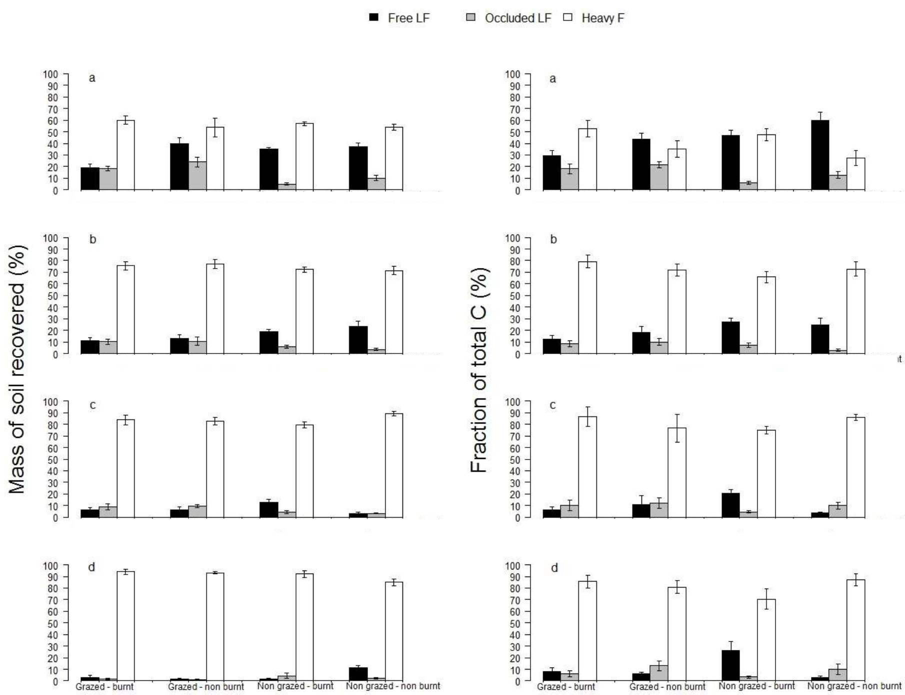


**Figure 4** Mass of soil recovered in the three density fractions (%) on the four left bar plots and the proportion of total C residing in the three density fractions (%) on the four right bar plots for the different land uses (a = 0-5 cm, b = 5-10 cm, c = 10-20 cm, d = 20-30 cm). Error bars indicate 1 standard error of the mean (*n* = 6).