Ecosystems (2010) 13: 62–74
DOI: 10.1007/s10021-009-9300-2

ECOSYSTEMS

No Differences in Soil Carbon Stocks Across the Tree Line in the Peruvian Andes

Michael Zimmermann,[1]* Patrick Meir,[1] Miles R. Silman,[2] Anna Fedders,[2] Adam Gibbon,[3] Yadvinder Malhi,[3] Dunia H. Urrego,[4] Mark B. Bush,[4] Kenneth J. Feeley,[2] Karina C. Garcia,[2,5] Greta C. Dargie,[1] Wiliam R. Farfan,[2,5] Bradley P. Goetz,[2] Wesley T. Johnson,[2] Krystle M. Kline,[2] Andrew T. Modi,[2] Natividad M. Q. Rurau,[5] Brian T. Staudt,[2] and Flor Zamora[5]

[1]School of Geosciences, University of Edinburgh, Edinburgh EH8 9XP, UK; [2]Department of Biology, Wake Forest University, 1834 Wake Forest Rd., Winston Salem, North Carolina 27106, USA; [3]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, UK; [4]Department of Biological Sciences, Florida Institute of Technology, 150 West University Boulevard, Melbourne, Florida 32901, USA; [5]Universidad San Antonio Abad, Cusco, Peru

Abstract

Reliable soil organic carbon (SOC) stock measurements of all major ecosystems are essential for predicting the influence of global warming on global soil carbon pools, but hardly any detailed soil survey data are available for tropical montane cloud forests (TMCF) and adjacent high elevation grasslands above (puna). TMCF are among the most threatened of ecosystems under current predicted global warming scenarios. We conducted an intensive soil sampling campaign extending 40 km along the tree line in the Peruvian Andes between 2994 and 3860 m asl to quantify SOC stocks of TMCF, puna grassland, and shrubland sites in the transition zone between the two habitats. SOC stocks from the soil surface down to the bedrock averaged (±standard error SE) 11.8 (±1.5, $N = 24$) kg C/m^2 in TMCF, 14.7 (±1.4, $N = 9$) kg C/m^2 in the shrublands and 11.9 (±0.8, $N = 35$) kg C/m^2 in the grasslands and were not significantly different ($P > 0.05$ for all comparisons). However, soil profile analysis revealed distinct differences, with TMCF profiles showing a uniform SOC distribution with depth, shrublands a linear decrease, and puna sites an exponential decrease in SOC densities with soil depth. Organic soil layer thickness reached a maximum (~70 cm) at the upper limit of the TMCF and declined with increasing altitude toward puna sites. Within TMCF, no significant increase in SOC stocks with increasing altitude was observed, probably because of the large variations among SOC stocks at different sites, which in turn were correlated with spatial variation in soil depth.

Key words: soil carbon stocks; tropical montane cloud forest; puna; tree line.

Introduction

Soils are recognized as large stores of carbon (C), and play a key role in the global C cycle (Houghton 2003; Janzen 2004). The size of the SOC stock is determined by the input of plant-derived C

Received 10 July 2009; accepted 20 October 2009;
published online 14 November 2009

Author Contributions: PM, MRS, AG, KJF, MBB, MZ designed the study; MRS, AF, AG, DHU, MBB, KJF, KCG, GCD, WRF, BPG, WTJ, KMK, ATM, NMQR, BTS, FZ, MZ performed the research; MZ, PM, MRS, AF, AG, YM, DHU analyzed the data; and MZ, PM wrote the paper.

**Corresponding author; e-mail:* michael.zimmermann@jcu.edu.au

entering the soil matrix, the potential to sequester C through physical and chemical stabilization processes, and the release of C through decomposition and leaching (Trumbore and others 2006). The most important environmental factors influencing the SOC stock are temperature and moisture, which also affect biomass production and respiration (Shaver and others 2000; Raich and others 2006). Because of this, SOC stocks in ecosystems within different climatic regions react differently to changes in climate (Walther and others 2002; Norby and Luo 2004).

Estimates of the nature and size of current SOC stocks are needed to parameterize models used to estimate net C changes in different biomes (Post and others 2001). However, extensive data sets of SOC stocks are not available for some ecosystems, and this is a source of uncertainty in model predictions of future global and regional SOC stocks. One such understudied ecosystem lacking detailed SOC stock estimates is Neotropical TMCF. These forests are typically found between 1000 and 3500 m above sea level (asl) with mean annual temperatures similar to regions in temperate zones but with very weak (or no) seasonality, and they tend to receive much larger amounts of precipitation in the form of rain and fog (Arteaga and others 2008). Here we focus on the Andean TMCFs, in which biodiversity and endemism is among the highest in the world and which are also among the most threatened of all ecosystems under predicted warming scenarios (Foster 2001).

At higher elevations in the tropical Andes (3000 m asl and above, depending on anthropogenic activity) there is a transition from TMCF first to open woody vegetation dominated by shrubs which we refer to here as 'shrubland', and then to grassland ('puna' or 'paramo'). With a predicted warming of 4°C for the tropical land surface over the twenty-first century (Cramer and others 2004), TMCF may migrate upwards, occupying land formerly dominated by shrubs and grasses (Bush and others 2004; Colwell and others 2008). Thus, to make a first-order estimate of the effects of a theoretical altitudinal shift in vegetation on SOC stocks, detailed SOC quantifications are needed.

Soil C-stocks were shown to change with altitude (Townsend and others 1995) and vegetation type (Sombroek and others 1993). Furthermore, climate and vegetation also influence soil C-distributions with depth (Jobbagy and Jackson 2000), which lead to the assumption that soil C-stocks might change significantly across altitudinal vegetation transects. In the present study, we collected soil samples from TMCF, shrubland, and grassland sites above the tree line in the Peruvian Andes, as these vegetation types around the tree line may experience the most marked alterations under global warming scenarios. The questions we addressed were: (1) What is the size of SOC stocks within these three vegetation types; and 2) Is the SOC stock distributed differently within the soil profiles in each of these zones. This information is needed to estimate how SOC stock might change if TMCF expanded to shrubland and grassland sites because of predicted warming and, or, land use. The aim of the present study was to provide SOC stock measurements across the tree line in Andean TMCF for prospective SOC simulations.

Materials and Methods

Sampling Sites and Soil Description

Soil samples were collected along the western border of the Manu National Park in Peru at altitudes between 2994 and 3860 m asl (~13°00′ S/71°40′ W′). The study site comprised an area 40 km along the watershed separating the dry hilly Andean highlands and the wet and steep eastern flank of the Andes (Figure 1), in which the average

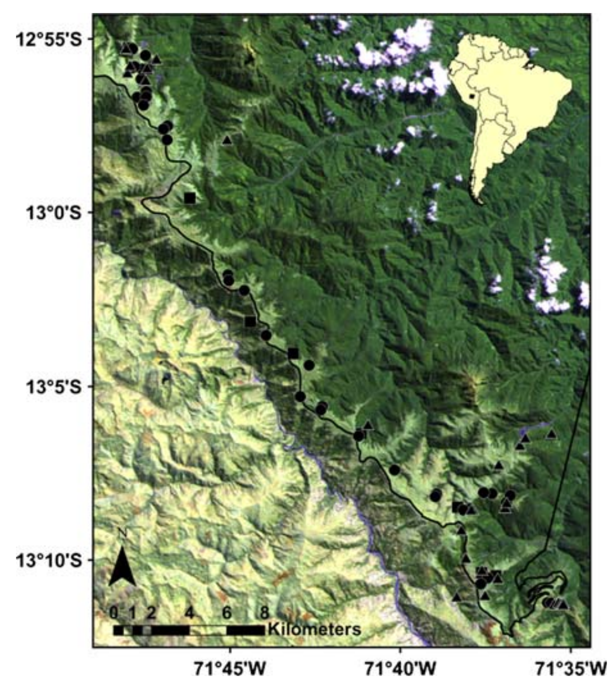

Figure 1. Sampling sites in the Peruvian Andes. *Triangles* are forest sites, *squares* are shrubland sites, and *circles* are grassland sites. The *black line* marks the Manu National Park border. *Dark colors* display forested areas, with the lowland tropical forests in the direction of the NE corner of the main map. The *inset* map of South America shows the location of the Manu National Park in Peru.

tree line was at about 3450 m asl. The mean annual temperature at this altitude is about 11°C and the annual rainfall 2500 mm. Diurnal variations in temperature are more pronounced than seasonal differences.

In general, the TMCF soils in the study region were characterized by an organic forest floor layer (Oh) of about 20 cm, but which could be as thick as 70 cm. This layer consisted mainly of a dense fine-root mesh and partly decomposed plant litter. The Oh layers typically overlaid organic-rich humic Ah layers of about 10 cm and purely mineral B layers of up to 70 cm thickness. Various forest sites contained mixed mineral layers with high stone contents as result of ancient landslides, which are common in this steep terrain. The full soil depth in the TMCF varied between 20 and 120 cm. Shrubland soils were slightly shallower and had only a thin Oh layer of about 2–5 cm, followed by a 10–20 cm thick A(h) layer. In this transition zone, soils were normally between 20 and 50 cm deep. Grassland soils in the puna had no Oh layers at all and consisted mainly of dark, organic-rich A layers of about 20 cm thickness and stony B/C layers. These soils were normally about 30 cm deep. Although very patchy, some peat-bog soils in the puna were deeper than 100 cm.

Soil Sampling Methods and Analysis

In total, 596 soil samples were taken along elevation transects traversing the TMCF, the shrubland vegetation in the transition zone and the grasslands in the puna above, and from various predefined sampling points. Coordinates of transect locations and sampling points were generated randomly but stratified to adequately represent regional variation in micro-meteorology and topography. Samples were collected from a total of 68 sites assigned to the three vegetation types (forest, shrubland, and grassland; Table 1). At each site, soil cores from five soil profiles were taken, with a central soil core being surrounded by four additional cores, positioned randomly 1–5 m away, in orthogonal directions. The slope at each site was measured with a clinometer and the coordinates and altitudes recorded with a GPS. All sites were inspected visually for any evidence of cattle (dung, grazing) and recent burns, whether natural or human-induced.

Soil cores from all profiles were taken between July and August 2008 using metal tubes of 50 mm diameter and 10 or 20 cm length. At all sites, the soil surfaces were cleared of leaf litter and plants, and the top soils collected with the 10 cm tubes, and all deeper soil layers down to the bedrock with the 20 cm tubes. Total soil depths were measured with an iron rod inserted to the bedrock, and the sampling depth adjusted accordingly. Additionally, the soil profiles were inspected visually for charcoal residues, and the thicknesses of the organic, humic and mineral layers were measured.

All soil samples were oven-dried at 60°C to constant mass, and the dry mass quantified. The samples were then crushed and sieved to 2 mm to remove all stones, and measured again. A subsample of every core was ground and C and nitrogen (N) concentrations determined after dry combustion with a Carlo Erba Elemental Analyzer (Milano, Italy) at the University of Edinburgh, UK. All soil samples were carbonate free.

Bulk soil densities (soil particles < 2 mm) were quantified using the stone-free dry weights and the sampling tube volumes corrected for the stone volumes. The density of a composite stone sample was quantified by displacement in a water bath and averaged 2.62 g/cm^3. Soil C and N stocks were then calculated according to the soil densities for each 10 or 20 cm soil layer, and SOC stocks of the single profiles summarized to average site values. Carbon densities as g C/cm^3 were calculated to compare soil layers of different thicknesses. Missing analytical values were interpolated according to correlations between bulk soil density and C concentration, distinguished among the three biome types as described in the ''Results'' section.

Table 1. Number of Samples and Sampling Site Descriptions

Dominant vegetation	Sites	Profiles	Samples	Lowest altitude	Highest altitude	Mean altitude	Typical vegetation
Forest	24	89	229	2994	3625	3370	Clusiaceae, Melastomataceae, Cunoniaceae, Symplocaceae
Shrubland	9	31	80	3283	3620	3454	Escalloniaceae, Myrsinaceae, Ericaceae, Loranthaceae, Clethraceae
Grassland	35	133	287	3348	3860	3547	Asteraceae, Poaceae, Pterydophyta
All	68	253	596	2994	3860	3470	

Statistical Analysis

The significance of the relationships among soil properties was tested using the Pearson's product moment correlation test (R) and regressions calculated with the function resulting in the highest coefficient of determination (r^2). A t-test was used to test for between-vegetation type differences if the data were normally distributed and had similar variances; otherwise a Mann–Whitney rank sum test was run (using a significance level of $P = 0.05$). More than two groups were compared with a one-way ANOVA if they were normally distributed and had similar variances; otherwise tests were performed with a Kruskal–Wallis one-way ANOVA of ranks. Mean values for sites or properties are always given with ±1 SE.

Results and Discussions

Soil Profile Data

Soil organic carbon densities (the amount of C per cm^3 soil) in forest soil profiles ($N = 89$) varied little with depth, but this pattern masked an exponential reduction in C concentrations and an increase in bulk density with depth (Figure 2). These patterns were caused by the typical organic forest floor layers in this biome containing large amounts of fine roots and plant debris. Surprisingly, the C:N ratio (an indicator of the degree of decomposition (Schrumpf and others 2001)) did not change significantly with depth in forest soil profiles. Shrubland soil profiles ($N = 31$) showed a linear decrease in SOC density with depth, with the SOC densities in the top 30 cm being significantly higher than in deeper layers. The C concentration decreased exponentially with soil depth, but the bulk soil densities showed no significant trend. The C:N ratio decreased exponentially from 16.2 in the top 10 cm to 11.8 at 50 cm to 70 cm, but these differences were not significant at $P = 0.05$. The grassland soil profiles ($N = 133$) showed a distinct exponential decrease in SOC density with depth, mainly caused by decreasing C concentration along the profiles coupled with scarcely significant differences in bulk soil densities.

Comparisons between the three different biomes showed that differences were more pronounced in the top 30 cm than in deeper soil layers. In general, forest soil profiles had higher C concentrations and lower bulk soil densities in the top 30 cm than the other two vegetation types. Grassland soil profiles showed the strongest decrease in SOC density with depth and the lowest C:N ratios, and the properties of most shrubland vegetation profiles were between the values of the two other systems.

The changes in SOC densities with depth for the shrubland and grassland soil profiles were very similar to global grassland and shrubland sites as presented in Jobbagy and Jackson (2000), who used 3 datasets with more than 2700 profiles to calculate SOC distributions with depth. However, none of the presented soil profiles in that study featured such a uniform SOC density distribution along the entire profile as measured here for the TMCF sites.

Correlations Between Soil Densities and C Concentrations

Correlations between C concentrations and bulk soil densities have been reported elsewhere (Heuscher and others 2005; Leifeld and others 2005) and C concentrations in combination with other soil parameters have been used to estimate bulk soil densities (Calhoun and others 2001). Here, we separated our dataset into the three vegetation types to calculate regression functions between C concentration and bulk soil density (Figure 3). For all three vegetation types, exponential functions returned the largest coefficients of determination between C concentration and bulk soil density (r^2 between 0.48 and 0.57). These functions were then used to calculate missing values for any samples that were lost during sample processing ($N = 47$).

The coefficients of determination observed here are in the same range as in Heuscher and others (2005), who calculated regression functions taking into account C concentration, soil moisture, particle size distribution, and soil depth for 47,000 soil samples from the USA ($r^2 = 0.45$). In other studies, sample sets were separated by soil depth to calculate regression functions between C and soil density (Bernoux and others 1998; Leifeld and others 2005), but as C concentration was correlated with soil depth in our data, we did not separate our dataset further to keep the sample number (N) large.

Differences Among Forest, Shrub Vegetation, and Grassland Sites

Summarized SOC stocks, C concentrations, bulk soil densities, C:N ratios, soil depths, and slopes for all sites distinguished among the three vegetation types are given as box plots in Figure 4 with the 10, 25, 75, 90 percentiles, medians and outliers (outside ± 95% confidence interval).

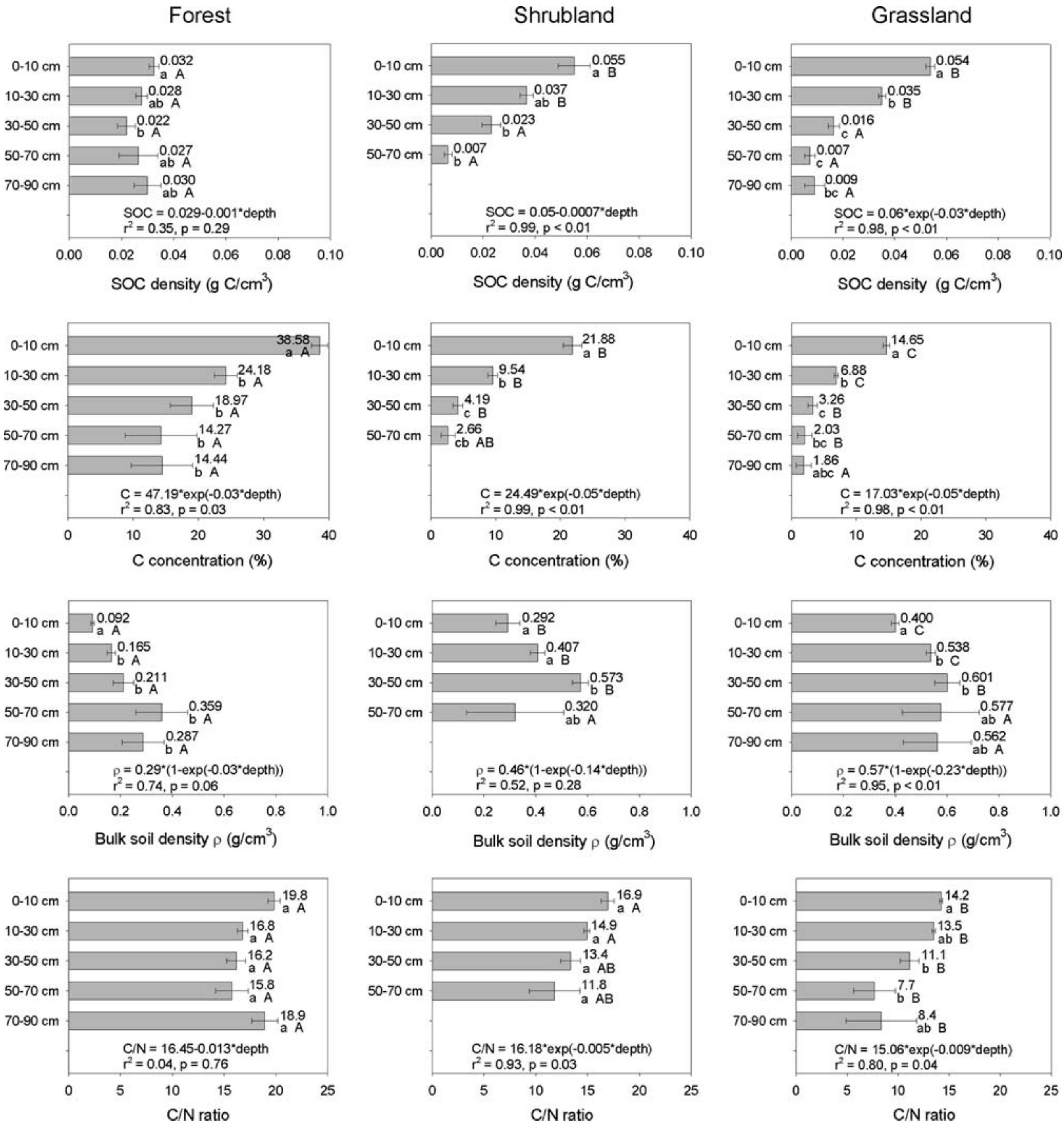

Figure 2. Soil property means with standard errors along profile depths for forest, shrubland, and grassland sites. *Numbers* represent mean values, *lower case* letters indicate significant differences with soil depth within each profile, and *capital letters* indicate significant differences of the same soil layers across the three different vegetation types ($P < 0.05$). The equations are the best fit regressions between soil properties and soil depth as calculated with the mean values.

Total SOC stocks were not significantly different among the three biomes. On average, shrubland sites had SOC stocks of 14.7 (±1.4) kg C/m^2 (1 kg C/m^2 = 10 Mg C/ha), grassland sites 11.9 (±0.8) kg C/m^2 and forest sites 11.8 (±1.5) kg C/m^2, whereas the forest sites revealed the widest variation (Table 2). One forest site had a much higher SOC stock of 37.0 kg/m^2. This particular site was characterized by a very thick Oh layer of about 50 cm, a total soil depth of more than 1 m, and an accumulation of coarse wood debris at the soil surface. The site with the largest SOC stock in the

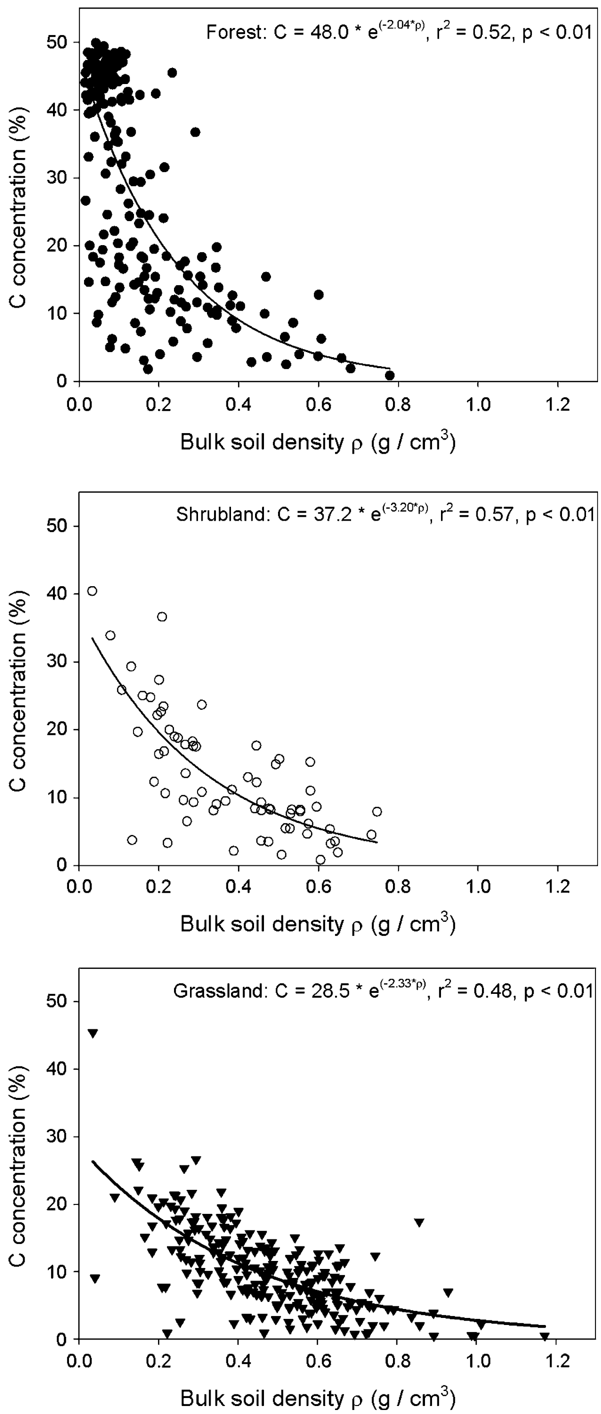

Figure 3. Correlations and regression functions between bulk soil densities and C concentrations calculated for all soil samples, separated into forest (*filled circle*), shrubland (*open circle*), and grassland (*inverted filled triangle*) sites.

grasslands (24.0 kg C/m^2) was within a peat-bog close to a small lake. Although sites like this might store large amounts of SOC, no other sampled puna site was within a peat-bog despite the intensity of the sampling protocol. Carbon concentrations decreased in order from forest to shrubland to grassland sites, and bulk soil densities showed the reverse trend (Figure 2). Forest sites had significantly higher C concentrations than grassland sites, whereas the C concentrations of shrubland sites were not significantly different from the two other biomes. Comparing soil bulk density for each vegetation type, shrubland and grassland soils had significantly larger bulk density values than the forest soils, but were not significantly different from each other.

Although total SOC stocks were not significantly different among vegetation types, the degree of decomposition among the three vegetation types—as reflected by the C:N ratio—showed that the organic matter in the grassland sites was more strongly altered (C:N = 13.9) from litter input (C:N = 25.3; Zimmermann and others 2009a) compared to forest and shrubland sites with C:N ratios of 17.2 and 15.9, respectively. Schawe and others (2007) reported C:N ratios between 20 and 28 for the top 1 m of Bolivian forest sites above 2700 m asl, and Schrumpf and others (2001) measured C:N ratios greater than 30 for high Andean root soil layers in Ecuador (>2800 m asl), concluding that decomposition rates at high elevations might not only be suppressed by low temperatures but also by low N supply. However, as the C:N ratios measured here are much smaller and the forests had on average smaller N stocks than the higher elevation shrub and grasslands (Figure 4), such processes appear to be much less significant in our study region.

Sombroek and others (1993) compared global SOC stocks of different ecosystems, and estimated SOC stocks of 14.5 kg C/m^2 for tropical forests and 12.4 kg C/m^2 for grasslands, which are in the range of the SOC stocks reported here. In contrast, Jobbagy and Jackson (2000) reported higher SOC stocks for lowland tropical forest sites (18.6 kg C/m^2) for the top 1 m, which could be caused by the different depth of soil sampling in their dataset and the general differences between lowland and montane rainforests, as tropical forests appear to allocate relatively more C belowground with increasing altitude (Soethe and others 2007). Schrumpf and others (2001) quantified SOC stocks of upper montane rain forests in Ecuador from 1850 to 2650 m asl and measured on average 21.5 kg C/m^2. Schawe and others (2007) even reported SOC stocks of 36.2 kg C/m^2, as averaged for 7 upper montane cloud forest sites between 2700 and 3300 m asl in Bolivia, which is 3 times as high as observed here. Jobbagy and Jackson (2000) also reviewed global SOC stocks in the top 1 m of

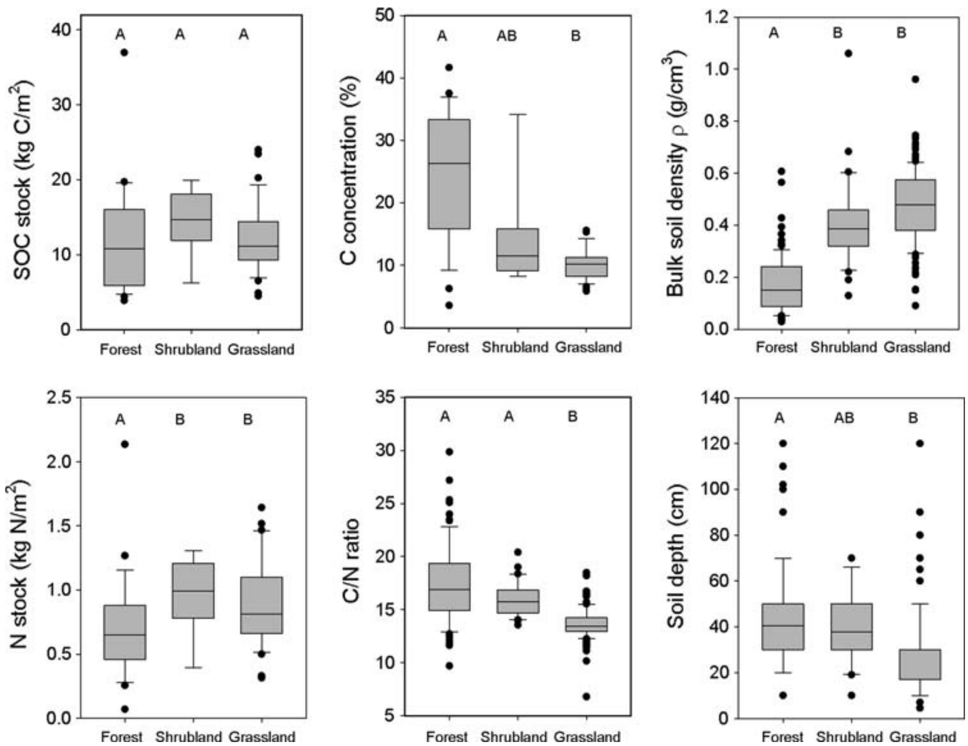

Figure 4. Box plots of soil properties over total soil depth of all sites showing 10, 25, 75, and 90 percentiles, medians and outliers for the different vegetation types. *Capital letters* indicate significant differences among groups (Kruskal–Wallis one-way ANOVA of ranks, $P < 0.05$).

Table 2. Comparison of Means, Standard Errors, and Variations Within Profiles of the Sampling Sites and Among All Sites as Calculated from Coefficients of Variation

Property	Biome	Mean	SE	CV among sites	CV within sites	95% Confidence interval within sites
SOC stock (kg/m^2)	Forest	11.83	1.49	0.33	0.41	0.30–0.51
	Shrubland	14.7	1.44	0.34	0.35	0.25–0.43
	Puna	11.91	0.79	0.36	0.37	0.30–0.42
C concentration (%)	Forest	24.47	2.06	0.37	0.41	0.24–0.51
	Shrubland	14.28	2.68	0.43	0.36	0.30–0.57
	Puna	10.19	0.43	0.38	0.37	0.32–0.44
Bulk soil density (g/cm^3)	Forest	0.186	0.023	0.51	0.52	0.40–0.61
	Shrubland	0.427	0.033	0.33	0.32	0.15–0.52
	Puna	0.480	0.021	0.24	0.25	0.19–0.29
N stock (kg/m^2)	Forest	0.699	0.085	0.41	0.45	0.30–0.53
	Shrubland	0.955	0.096	0.35	0.35	0.25–0.45
	Puna	0.879	0.057	0.42	0.41	0.29–0.54
C/N	Forest	17.2	0.7	0.13	0.13	0.10–0.17
	Shrubland	15.9	0.5	0.08	0.08	0.05–0.10
	Puna	13.9	0.2	0.08	0.08	0.05–0.11
Soil depth (cm)	Forest	43.5	4.3	0.30	0.39	0.20–0.40
	Shrubland	36.0	3.5	0.34	0.37	0.20–0.48
	Puna	32.5	2.8	0.41	0.43	0.34–0.48

If the CV among the sites was outside of the 95% confidence interval of the CV for the individual profile sites, then the variability among sites was considered significantly larger.

grassland sites (13.2 kg C/m^2), which were similar to grasslands in the puna as measured here. But as the puna soils here were on average only 32.5 cm deep, puna SOC densities were about threefold higher than the global average for grasslands. The puna SOC stocks were also more than twice as large as SOC stocks in pasture sites in montane Ecuador (5.7 kg C/m^2; Tian and others (1995)). In contrast, Schrumpf and others (2001) measured SOC stocks of 11.1 kg C/m^2 in Ecuadorian grassland sites from

2845 to 3050 m asl, which are more similar to our observations.

The large variance among SOC stocks suggest that regional variations are substantial in Andean TMCF, and in the absence of additional local spatial information, single point measurements will have limited use for large-scale interpolations of total SOC stocks. Importantly, the measurements presented here sample steep areas of the landscape which are often missed in other sampling protocols and are probably more reliable estimates for mean values in TMCF and puna grassland than the studies reported above, simply because we sampled a much larger area.

Variability of Soil Properties

To test whether the variability of soil profiles within single sampling sites was different from the variability among all sampled sites in one vegetation type, we analyzed the coefficients of variation (CV) within and among sites. If the CV among the sites was outside of the 95% confidence interval of the average CV within the single sites, then the variability among the sites was considered significantly different from the variability of the soil profiles within the sites. In all cases, CV values among and within sites were not significantly different, but forest soils tended to have a larger CV within the profiles of the single sites than among all averaged sites (Table 2).

The larger variation within forest profiles might be explained by micro-climatic and site-specific characteristics such as slope and exposure (Schulp and others 2008). We do not have climatic records for each sampling site, but we measured the topographical site characteristics soil depth and slope. Soil depth defines the maximal volume of SOC, and the slope affects mainly the water supply for vegetation and consequently biomass production. The average soil depths for the three vegetation types, forest, shrubland, and grassland were 43.5, 36, and 32.5 cm. Forest sites were steeper (average relative slope 58 ± 7%) than the shrubland (42 ± 6%) or grassland (33 ± 4%) sites, which is typical of the entire study region with its steep TMCF thinning out in the flatter puna. The SOC and N stocks of all three vegetation types were positively correlated with soil depth (r^2 from 0.33 to 0.67, $P < 0.05$), but showed no significant trends with slope (P values from 0.38 to 0.93) (Table 3); soil depths and slopes at the sampling sites were not correlated ($r^2 = 0.02$, $P = 0.28$). The correlations between soil depth and SOC stock showed that soil depth was probably responsible for the large variability in SOC stocks, and further soil sampling campaigns should take into account the greater depth of soils in forests to adapt the number of sampling sites accordingly.

Altitudinal Changes in Soil Properties

Altitudinal variations integrate various environmental parameters like temperature, moisture, atmospheric pressure, radiation, and soil weathering (Körner 2007), all of which influence the input and accumulation of C in soils. Several studies have demonstrated an increase in SOC stocks across altitudinal ranges of about 1000 m in tropical forests (Townsend and others 1995; Schrumpf and others 2001; Gräfe and others 2008). Larger SOC stocks at higher elevations were generally attributed to lower temperatures decelerating soil organic matter decomposition more than

Table 3. Correlations Between SOC Stocks and Site Characteristics Soil Depths and Slopes

	Soil depth (cm)				Slope (%)			
	Regression	SEE	r^2	P	Regression	SEE	r^2	P
SOC stock (kg/m^2)								
Forest	SOC = 1.39 + 0.24*depth	5.34	0.49	<0.01	SOC = 8.78 + 0.062*slope	9.21	0.06	0.42
Scrubland	SOC = 4.44 + 0.28*depth	3.34	0.47	0.04	SOC = 13.01 + 0.041*slope	4.55	0.03	0.68
Grassland	SOC = 5.15 + 0.21*depth	3.21	0.55	<0.01	SOC = 12.00 − 0.003*slope	4.75	<0.01	0.93
All	SOC = 4.55 + 0.21*depth	4.28	0.45	<0.01	SOC = 11.46 + 0.025*slope	5.97	0.01	0.38
N stock (kg/m^2)								
Forest	N = 0.208 + 0.011*depth	0.347	0.33	<0.01	N = 0.481 + 0.004*slope	0.512	0.07	0.38
Scrubland	N = 0.212 + 0.021*depth	0.203	0.56	0.02	N = 0.865 + 0.002*slope	0.305	0.02	0.74
Grassland	N = 0.336 + 0.017*depth	0.198	0.67	<0.01	N = 0.860 + 0.001*slope	0.344	<0.01	0.81
All	N = 0.391 + 0.012*depth	0.303	0.34	<0.01	N = 0.82 + 0.001*slope	0.386	<0.01	0.69

SEE standard errors of estimates.

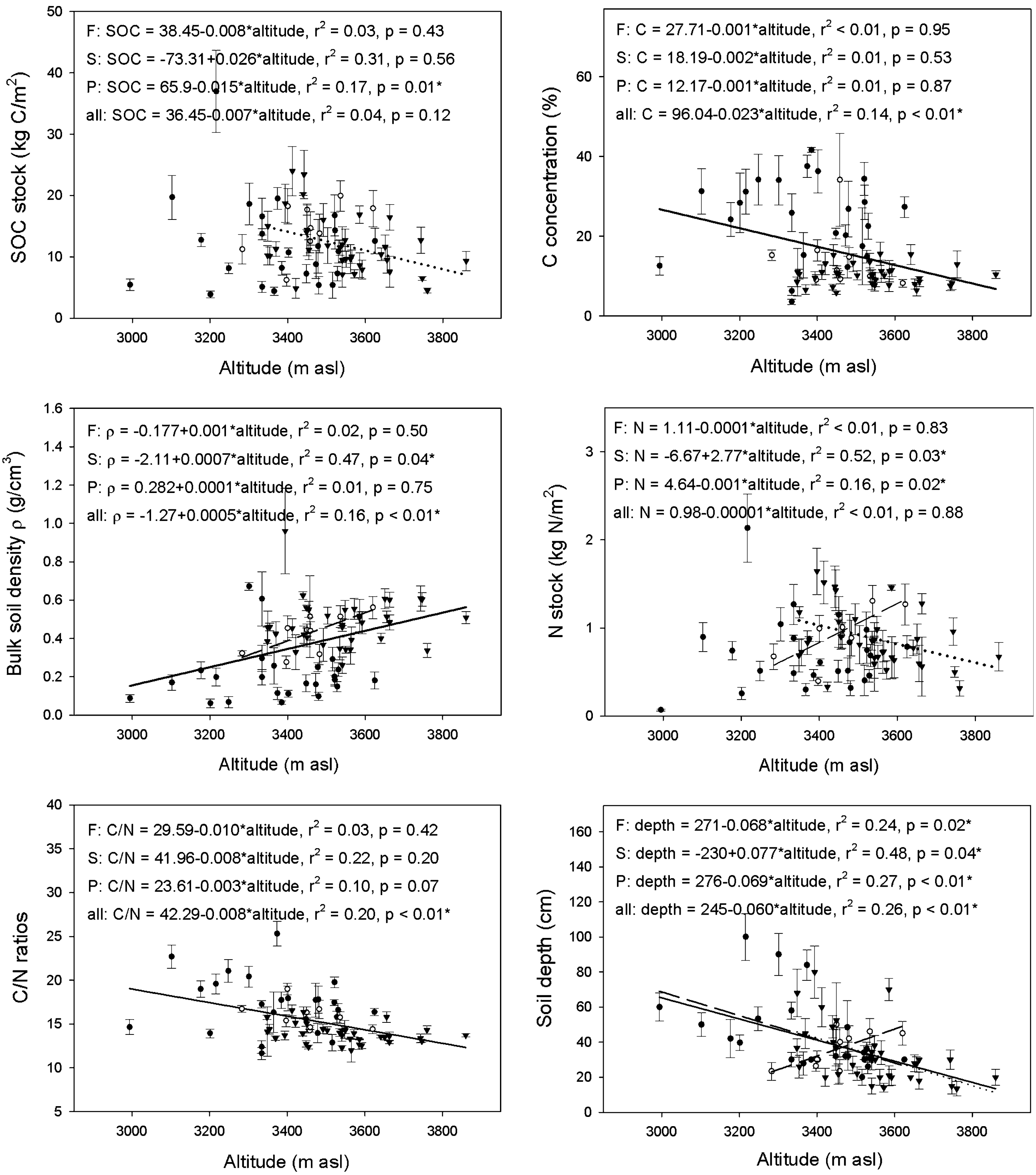

Figure 5. Average site properties with standard errors in relation to altitude. The regression functions are also supplied, and, where significant ($P < 0.05$*), the regression lines (*long dashed lines* for forests, *mid-dashed lines* for shrub, *dotted lines* for grasslands, and *solid lines* for all data points).

biomass production (Raich and others 2006; Zimmermann and others 2009b). In contrast, the forest SOC stocks reported here did not show any significant change in altitude (Figure 5). This is consistent with Schawe and others (2007) who also did not detect any trend in SOC stocks with elevation in TMCF in Bolivia between 2700 and 3300 m asl. The reason for this observation might be that the large variation in SOC stocks among different micro-sites discussed above was larger than any trend in SOC stocks with altitude. Furthermore, the TMCF sampled here traversed only 650 m in elevation, probably not enough to reveal any trend with altitude.

The only vegetation type showing a significant change in SOC stocks with elevation was the grassland. This trend could be explained by the decrease in soil depth with elevation, limiting plant growth, rooting depth, and the potential to accumulate SOC. Although soil depth in the forest also correlated with altitude, SOC stocks were not correlated with elevation and thus soil depth is probably a correlating but not limiting factor in TMCF. Surprisingly, soil depth in the shrubland vegetation showed a significant inverse trend with altitude. Carbon concentration, bulk soil density, and C:N ratios were not correlated with altitude for forest or grassland sites. The only significant increase with altitude in bulk soil density was found in the shrubland. Overall C concentration, bulk soil density, and C:N ratios were significantly correlated with altitude, but these shifts with altitude were because of changes in the dominant vegetation rather than because of changes in elevation per se, as the average values for each vegetation type were significantly different (Figure 4).

As the reductions in soil depth with altitude were similar for forests and grasslands, there was no strong evidence for a strong impact of the presence of vegetation on the development of soil depth. By contrast, however, the vegetation played a major role in affecting the character of the soil profile below it, because the loss of woody vegetation coincided with the disappearance of the Oh layer. With the exception of peat bogs, Oh layers were only found in forest and shrub-dominated sites. The thickness of the Oh layer peaked with about 42 cm at about 3300 m asl, with C concentrations of 35–50% and bulk soil densities of 0.015–0.03 g/cm^3 (Figure 6). A very similar increase in Oh layer thickness for TMCF was also observed in southern Ecuador (Wilcke and others 2008). However, Schawe and others (2007) showed that organic layer thickness in a tropical forest in Bolivia did not reveal any trend over 600 m altitudinal difference. Soethe and others (2007) measured an increase in root biomass as a major component of the trend with elevation in TMCF in the thickness of the Oh layer, probably the result of a shift in the allocation of C from above- to below-ground associated with lower temperatures (Raich and others 2006). The

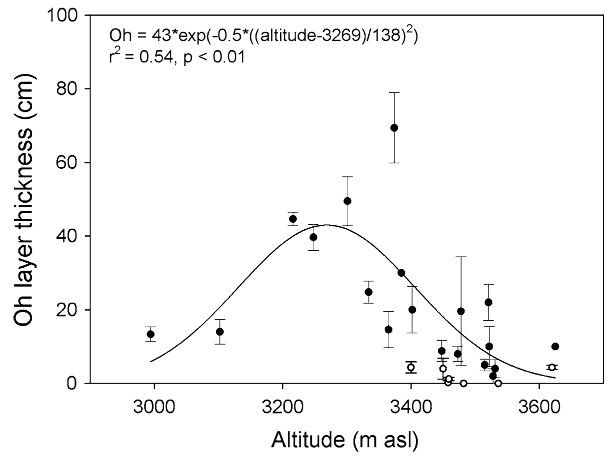

Figure 6. Measured Oh layer thickness for the forest (*filled circle*) and shrubland sites (*open circle*) with standard errors in relation to altitude.

decline in the thickness of the Oh layer above 3300 m asl in the present study could have been caused by the reduction in the density of woody vegetation, resulting in lower root biomass and litter inputs.

Disturbance Effects

High Andean grasslands have been used for hundreds of years as pastures (Sarmiento and Frolich 2002) by farmers who manage them by burning the vegetation to increase and/or maintain the grazing area, and to establish new plant communities in grasslands which are better suited as feed for livestock like cattle, horses, sheep, and llamas (Ramsay and Oxley 1996). New pastures are also created by clearing shrubs and forests, thereby lowering the natural tree line (Kok and others 1995). These practices can also affect soil processes, as summarized by Hofstede (1995): fire leads to an enhanced cycling of nutrients in soils, and trampling by livestock compacts the soil. As result, reduced vegetation cover and higher soil density leads to relative increases in soil temperature, which can then accelerate soil organic matter decomposition. We compared the grassland sites in the puna with evidence for recent fire or cattle presence with sites considered to be undisturbed to examine the possible effects of fire or livestock disturbance on SOC and N stocks (Table 4).

Puna sites with signs of recent burnings had slightly lower SOC and N stocks, but only the N stocks were significantly different from apparently undisturbed sites. The concentrations of C and N tended to be higher in fire-disturbed sites, but the bulk soil densities were similar. Lower N stocks

Table 4. Puna Sites Grouped According to Fire or Cattle Evidence, and Comparisons Between Means and Standard Errors as Calculated with *t*-Tests

Property	Effect	Mean	SE	N	*P*
SOC stock (kg/m^2)	Fire	9.58	1.10	9	0.13
	No fire	12.34	1.05	21	
N stock (kg/m^2)	Fire	0.717	0.077	9	0.02*
	No fire	0.920	0.082	21	
C concentration (%)	Fire	11.32	0.80	9	0.05
	No fire	9.46	0.50	21	
N concentration (%)	Fire	0.84	0.06	9	0.15
	No fire	0.68	0.04	21	
C/N ratio	Fire	13.5	0.3	9	0.29
	No fire	13.9	0.3	21	
Bulk soil density (g/cm^3)	Fire	0.474	0.035	9	0.93
	No fire	0.496	0.030	21	
SOC stock (kg/m^2)	No cattle	12.39	1.36	10	0.46
	Cattle	11.09	1.00	21	
N stock (kg/m^2)	No cattle	0.93	0.12	10	0.45
	Cattle	0.83	0.07	21	
C concentration (%)	No cattle	9.60	0.80	10	0.42
	Cattle	10.39	0.54	21	
N concentration (%)	No cattle	0.750	0.074	10	0.48
	Cattle	0.756	0.040	21	
Bulk soil density (g/cm^3)	No cattle	0.486	0.032	10	0.69
	Cattle	0.485	0.031	21	

**Significant differences ($P < 0.05$).*

were thus significantly related to the presence of fire, but not to grazing by cattle (Table 4); the N and SOC stocks and the bulk soil densities were similarly unaffected by the presence of cattle. These observations are consistent with those of Harris and others (2007) who showed in Argentinean grasslands that fire and grazing altered the N stocks, but not the SOC stocks. They explained this effect by fire- and grazing-induced changes in plant tissue chemistry, which were then incorporated in the plant–soil biomass cycle. However, other studies have shown that grazing can decrease SOC stocks in grasslands through shifts in soil temperature, bulk soil density, and moisture content (Hofstede 1995), with faster annual shoot turnover leading to a redistribution of SOC within the plant–soil cycle (Reeder and Schuman 2002), or alterations in soil aggregate stabilities through cattle trampling (Li and others 2007). It is thus likely that grazing intensity is a determining factor, suggesting further that the puna sites in our study region might not be overgrazed in terms of SOC accumulation. Furthermore, the presence of cattle was not correlated with burning, although this may be because of small sample size or also because of the detection method used (visual observation without known historical grazing intensity).

Charcoal residues within soil profiles were only found at 3 sampling sites in the forest. The average SOC stock at the sites with charcoal was large, at 23.1 kg C/m^2, significantly higher (Mann–Whitney rank sum test, $P = 0.04$) than the average SOC stocks in charcoal-free forest sites (10.2 kg C/m^2). However, SOC stocks in charcoal-free forest sites were still not significantly different from SOC stocks in shrubland or grassland sites ($P > 0.05$). Two of the 3 sites where charcoal was found were above 3300 m asl, which could mean that they were burnt in the past to lower the tree line. Most of the upper TMCF tree lines in the Andes are thought to have been influenced in the medium-term past (centuries) by human-induced fires (Sarmiento and Frolich 2002). A reason for the relative lack of large charcoal pieces in the sampled soil profiles may be that hardly any wood was charred during the fires. Ramsay and Oxley (1996) showed that soil temperatures during fires in Andean grasslands were below 65°C, which does not lead to charring of wood. Furthermore, wood from forests might have been harvested as a fuel source before fires were induced, reducing the overall charcoal output from the burning process (Kok and others 1995). In any case, a higher density of charred residues from the roots of trees or shrubs might have been expected, suggesting that the collection of charcoal samples solely by visual inspection of soil profiles may not be a reliable predictor for determining the extent of fires and its effect on lowering the tree lines. Further scrutiny of the soil samples for microscopic charcoal might reveal more detailed information about the fire history in the study area.

SUMMARY

Total SOC stock as determined from 596 soil cores from 68 sites ranging from 2994 to 3860 m asl across the tree line in the Peruvian Andes were not significantly different among forest, shrubland, and grassland sites. The forest soils showed a uniform distribution of SOC within the soil profile, whereas the density of SOC in the grassland decreased exponentially with depth. Variations in SOC stocks among sampling sites could be partly attributed to differences in soil depth, which may also have masked any biophysical effects of elevation. The stocks of SOC in TMCF and shrubland vegetation were not correlated with altitude. Organic layers reached a maximum thickness at 3300 m asl, where TMCF began to thin in terms of stem density, and grade toward shrub-dominated vegetation. Therefore, the expansion of TMCF into former shrubland and grassland sites might change the SOC distribution through altered vegetation rooting and plant litter inputs within soil profiles, but probably not the total amount of SOC sequestered in these systems. The presence of cattle and occurrence of fire appeared to have no significant impact on the stocks of SOC in the puna, and this may reflect low-intensity agricultural land use in the region. However, warming might lead to higher decomposition rates of SOC and effect soils under all three vegetation types.

ACKNOWLEDGMENTS

This study is a product of the ABERG consortium (http://www.andesconservation.org). We thank the Blue Moon Fund and the Gordon and Betty Moore Foundation 'Andes to Amazon' Programme for support. We especially thank Manu National Park and the Peruvian Instituto Nacional de Recursos National (INRENA) and the Amazon Conservation Association (ACCA) for allowing access to their sites. Luis Imunda Gonzales and students from Wake Forest University and the Universidad San Antonio de Abad, Cusco were essential for the completion of this project.

REFERENCES

Arteaga A, Calderón GNE, Krasilnikov PV, Sedov SN, Targulian VO, Velázquez RN. 2008. Soil altitudinal sequence on base-poor parent material in a montane cloud forest in Sierra Juárez, southern Mexico. Geoderma 144:593–612.

Bernoux M, Cerri C, Arrouays D, Jolivet C, Volkoff B. 1998. Bulk densities of Brazilian Amazon soils related to other soil properties. Soil Sci Soc Am J 62:743–9.

Bush MB, Silman MR, Urrego DH. 2004. 48,000 years of climate and forest change in a biodiversity hotspot. Science 303: 827–9.

Calhoun FG, Smeck NE, Slater BL, Bigham JM, Hall GF. 2001. Predicting bulk density of Ohio soils from morphology, genetic principles, and laboratory characterization data. Soil Sci Soc Am J 65:811–19.

Colwell RK, Brehm G, Cardelus CL, Gilman AC, Longino JT. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258–61.

Cramer W, Bondeau A, Schaphoff S, Lucht W, Smith B, Sitch S. 2004. Tropical forests and the global carbon cycle: impacts of atmospheric carbon dioxide, climate change and rate of deforestation. Tellus B 359:331–43.

Foster P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. Earth Sci Rev 55:73–106.

Gräfe S, Hertel D, Leuschner C. 2008. Estimating fine root turnover in tropical forests along an elevational Transect using minirhizotrons. Biotropica 40:536–42.

Harris WN, Moretto AS, Distel RA, Boutton TW, Bóo RM. 2007. Fire and grazing in grasslands of the Argentine Caldenal: effects on plant and soil carbon and nitrogen. Acta Oecol 32:207–14.

Heuscher SA, Brandt CC, Jardine PM. 2005. Using soil physical and chemical properties to estimate bulk density. Soil Sci Soc Am J 69:51–6.

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

Houghton RA. 2003. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. Tellus B 55:378–90.

Janzen HH. 2004. Carbon cycling in earth systems—a soil science perspective. Agric Ecosyst Environ 104:399–417.

Jobbagy EG, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol Appl 10:423–36.

Kok K, Verweij PA, Beukema H. 1995. Effects of cutting and grazing in Andean treeline vegetation. In: Churchill S, Balslev H, Forero E, Luteyn JL, Eds. Biodiversity and conservation of neotropical Monatne forests. New York: New York Botanical Garden. p 527–39.

Körner C. 2007. The use of altitude in ecological research. Trends Ecol Evol 22:569–74.

Leifeld J, Bassin S, Fuhrer J. 2005. Carbon stocks in Swiss agricultural soils predicted by land-use, soil characteristics, and altitude. Agric Ecosyst Environ 105:255–66.

Li XG, Wang ZF, Ma QF, Li FM. 2007. Crop cultivation and intensive grazing affect organic C pools and aggregate stability in arid grassland soil. Soil Tillage Res 95:172–81.

Norby RJ, Luo Y. 2004. Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world. New Phytol 162:281–93.

Post WM, Izaurralde RC, Mann LK, Bliss N. 2001. Monitoring and verifying changes of organic carbon in soil. Clim Change 51:73–99.

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

Ramsay PM, Oxley ERB. 1996. Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. Plant Ecol 124:129–44.

Reeder JD, Schuman GE. 2002. Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. Environ Pollut 116:457–63.

Sarmiento FO, Frolich LM. 2002. Andean cloud forest tree lines: naturalness, agriculture and the human dimension. Mt Res Dev 22:278–87.

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

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

Schulp CJE, Nabuurs GJ, Verburg PH, de Waal RW. 2008. Effect of tree species on carbon stocks in forest floor and mineral soil and implications for soil carbon inventories. For Ecol Manag 256:482–90.

Shaver GR, Canadell J, Chapin FS, Gurevitch J, Harte J, Henry G, Ineson P, Jonasson S, Melillo J, Pitelka L, Rustad L. 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. Bioscience 50:871–82.

Soethe N, Lehmann J, Engels C. 2007. Carbon and nutrient stocks in roots of forests at different altitudes in the Ecuadorian Andes. J Trop Ecol 23:319–28.

Sombroek WG, Nachtergaele FO, Hebel A. 1993. Amounts, dynamics and sequestering of carbon in tropical and subtropical soils. Ambio 22:417–26.

Tian G, Brussaard L, Kang BT. 1995. Breakdown of plant residues with contrasting chemical compositions under humid tropical conditions: effects of earthworms and millipedes. Soil Biol Biochem 27:277–80.

Townsend AR, Vitousek PM, Trumbore SE. 1995. Soil organic matter dynamics along gradients in temperature and land-use on the island of Hawaii. Ecology 76:721–33.

Trumbore S, da Costa ES, Nepstad DC, de Camargo PB, Martinelli L, Ray D, Restom T, Silver W. 2006. Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration. Glob Change Biol 12:217–29.

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. Nature 416:389–95.

Wilcke W, Oelmann Y, Schmitt A, Valarezo C, Zech W, Homeier J. 2008. Soil properties and tree growth along an altitudinal transect in Ecuadorian tropical montane forest. J Plant Nutr Soil Sci 171:220–30.

Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana A. 2009a. Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest. Soil Biol Biochem 41:1338–40.

Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana A. 2009b. Climate dependence of heterotrophic soil respiration from a soil translocation experiment along a 3000 m altitudinal tropical forest gradient. Eur J Soil Sci. doi:10.1111/j.1365-2389.2009.01175.x.