Soil carbon stocks along elevational gradients in Eastern Himalayan mountain forests

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\textbf{A B S T R A C T}

We quantified soil organic carbon (SOC) stocks and forest soil characteristics along elevational transects in the temperate conifer forests of Western and Central Bhutan, ranging from 2600 to 4000 m asl. Thereby 82 soil profiles were recorded and classified according to the World Reference Base for Soil Resources from 2014. Based on 19 representative profiles, genetic horizons were sampled and analysed. The results are presented with regard to ecological forest zones. The SOC stocks, up to 100 cm depth, ranged between 56.7 and 337.8 Mg ha\textsuperscript{-1}, with a mean of 168.1 ± 93.0 Mg ha\textsuperscript{-1}. The soils along the elevational gradient showed a unimodal curve for SOC stock with an increase in elevation, a peak at the cool conifer moist forest zone between 3200 and 3400 m asl and a subsequent decrease at the highest elevations. The soil chemical characteristics, CEC and pH-value showed a linear correlation with elevation in the topsoil, with higher values at lower elevations. In deeper soil horizons, elevation had no influence. The nitrogen stocks up to 100 cm depth ranged from 4.2 to 19.1 Mg ha\textsuperscript{-1}, with a mean of 11.4 ± 4.8 Mg ha\textsuperscript{-1}. The elevational distribution of the reference soil groups showed distinct distribution ranges for most of the soils. Cambisols were the most frequently recorded reference soil group at 58\%, followed by Podzol, restrained to high elevation, and Stagnosol, at intermediate elevation. Fluvisols occurred only at the lower end of the elevational transects and Phaeozems only at drier site conditions in the cool conifer dry forest zone. The soil characteristics and soil types along the elevational gradient showed a continuous and consistent change, instead of abrupt changes. We interpret these as manifestations of changes of temperature and precipitation with elevation which also drives forest zone distribution. Since forest zone distribution is easily recordable, it can also be used to infer to soil characteristics in these Himalayan forests.

\textbf{1. Introduction}

Soil formation is primarily driven by climate, parent materials and topography, vegetation and disturbances and the time available for soil formation (Jenny, 1941). The influence of climate along elevational and latitudinal gradients (Jenny, 1941) creates differences in both soil and vegetation distinct enough in many regions to be classified into soil and vegetation zones. This has spurred attempts to describe pedogenesis and soil chemical as well as soil physical properties along these gradients since the first half of the last century (e.g. Jenny, 1941; Jenny et al., 1949).

Such elevational gradients lend themselves not only to characterisations of vegetation patterns and nutrient pools in different elevations but also to studies of environmental controls on ecosystem functioning (Asner et al., 2014; Körner, 2007). Elevation can thus serve as a space-for-time substitute of climate change (e.g. Duboc et al., 2014). The recognition of the importance of soils as the largest terrestrial sink for organic carbon (Batjes, 1996) and the fact that reliable data on soil carbon (SOC) stocks is missing for many regions in the world (Pan et al., 2011; Scharlemann et al., 2014) has recently stimulated research on SOC in different regions, vegetation and land use types all over the world including mountain regions (Scharwe et al., 2007; Griffiths et al., 2009; Leifeld et al., 2009; Zimmermann et al., 2010; Bu et al., 2012; Dieleman et al., 2013; Prietzel and Christophel, 2014; Dori et al., 2014a, 2014b; Tashi et al., 2016).

Mountains and soils in mountains are particularly vulnerable to climate - and land-use changes for three reasons: (1) temperature sensitivity of organic matter decomposition decreases exponentially with increasing temperature (Kirschbaum, 1995, 2005), (2) mountain soils also show a high amount of C in labile fractions (Hagedorn et al., 2010)
and (3) many mountain regions exhibit stronger warming trends by elevation dependent warming (Liu et al., 2009; Oyler et al., 2015; Kotlarski et al., 2015). This corroborates the need for solid data on SOC contents and stocks in ecosystems of higher elevations and latitudes. We therefore aim at providing solid data on soil organic carbon stocks and fundamental information on forest soil characteristics along elevational transects for a study region for which only scarce information is available.

Along elevational gradients, the controls of SOC input of plant matter and decomposition vary with increasing elevation and decreasing temperature. While both production and decomposition rates decrease, the proportional decrease in decomposition is lower, leading to higher SOC contents at higher elevation (Raich et al., 2006; Dai and Huang, 2006; Grifiths et al., 2009; Dieleman et al., 2013; Prietzel and Christophel, 2014; Dorji et al., 2014a; Tashi et al., 2016). Soil moisture is a covarying factor in SOC contents with low and high soil water contents reducing decomposition, thus leading to higher SOC contents (Davidson et al., 2000; Wiesmeier et al., 2012; Prietzel and Christophel, 2014). In areas where SOC did not vary with elevation (Zimmermann et al., 2000) or showed a peaked distribution of SOC (Schawe et al., 2007), large variation within elevational zones masked potential elevational trends, or soil moisture variation in soil types influenced decomposition and production rates differently in different elevations.

The decomposability of plants varies strongly and the quality of litter is a strong control on litter decomposition. Plant species composition was shown to be a stronger driver on litter decomposition than climate (De Long et al., 2016; Cornwell et al., 2008) and can as well cause distinct peaks in SOC contents in vegetation zones with plants of poor litter quality (Djukic et al., 2010; Tashi et al., 2016).

The Himalayas, together with the Hindukush, are the source of freshwater for around 800 million people living downstream (Bolch et al., 2012) and are located in a region forming a tipping element in the Earth’s climate system (Lenton et al., 2008). Improving the understanding of environmental controls on carbon stocks and forest soil characteristics in a vulnerable mountain region will contribute to both, adaptation and mitigation strategies to climate change.

The high forest cover in Bhutan (70% (RGoB, 2009)) and the very low anthropogenic impacts in many of these forests predestines the country for studies on drivers of elevational soil and vegetation zonation. This has been corroborated by Wangda and Ohsawa (2006), who found tight linear relations between elevation and forest basal area and maximum tree heights as well as basic soil characteristics.

We therefore hypothesise that (1) SOC contents and stocks increase with increasing altitude; (2) soil chemical characteristics and soil types show a clear elevational zonation and (3) differences in soils drive differences in vegetation types.

2. Methods

2.1. Study area

The study sites are located in the physiographic zone of the inner valleys and passes (Norbu et al., 2003) of west and central Bhutan. This zone with north-south valleys is characterised by a temperate to subalpine climate on slopes, with strong daily freeze-thaw alternation from late autumn to early spring, and drier conditions in the valley floors.

To investigate soil development and characteristics in this extensive zone, two study areas were selected, one in the west located in the administrative area of Thimphu and Paro and one representing the eastern part of the zone located in central Bhutan in the administrative area of Bumthang (Fig. 1).

The geological bedrock consists of siliceous metasediments varying between mica schists and paragneisses with quartz veins. These belong in the west to the Paro Formation and in the center to the Thimphu Formation (Gansser, 1983; Long et al., 2011). In the study area, the materials for soil development are characterised by softened preweathered bedrock material and aeolian sediments. Recent fluvial sediments were present only at lower slope positions. The influence of aeolian sediments for soil development was described by SSU (2000), Baillie et al. (2004), Caspari (2005) and Caspari et al. (2006, 2009) and could override elevational trends. In neighbouring regions of Eastern Nepal, however, Bäumler and Zech (1994) found that although sediment stratification was present in many of their eleven studied soil profiles, soil development could be inferred from clay content and clay
mineral analysis. In general, the parent materials did not show strong variation between and within the study areas which allows for quantitative examination of orographic effects on soil characteristics.

2.2. Sampling and analysis

At each of the two study areas, six elevational transects (Fig. 1) were investigated, ranging from 2600 to 4000 m asl. Along these transects, at steps of 100 m elevation, soil profiles were examined. Most transects in the side valleys were north exposed, mainly because these slopes had generally been continuously forested. Thus, differences of soil characteristics due to aspect were minimised.

In total, 82 soil profile descriptions were made according to FAO (2006). Therefore, we either dug soil pits at 31 sites or used soil corers (7 cm diameter) at 51 sites for soil diagnostic descriptions. At each sampling location, general site data such as GPS coordinates, elevation above sea level (asl), slope aspect, slope inclination and topography were recorded. Furthermore, outcrops of bedrock material, tree and shrub vegetation were surveyed. From each profile, all genetic horizons to a depth of at least 100 cm or until bedrock was reached, were described. The description included horizon thickness, boundaries, colour at moistened condition (according to Munsell, 2009), fine soil texture, coarse fraction content (> 2 mm), bulk density, root proportion and motting (oxidation/reduction attributes). The designation of soil profiles is according to the World Reference Base for Soil Resources (IUSS Working Group WRB, 2014).

From all described soil profiles, 19 profiles representative for the different soil types were selected and out of these, 66 samples were taken for chemical and physical analysis. At profile selection, care was taken to cover the entire elevation range and consider the proportion of studied forest zones. Therefore broadleaf-conifer was sampled with 4, cool conifer moist with 7, cool conifer dry with 1 and cold conifer with 7 profiles. The sampling was volumetric with 4 cores (47 cm³) from each of the master horizons (FAO, 2006). Transitional horizons (FAO, 2006) were described but not sampled. Furthermore, few horizons which only differed in one colour step according to Munsell (2009) but did not differ in other diagnostic characteristics, were not sampled.

Data on SOC stocks from SOC inventories have recently been questioned because they are often modelled using pedotransfer functions and not based on measured bulk densities and coarse fraction contents and do not include deeper soil horizons – factors which lead to systematic biases especially in forest soils (Wiesmeier et al., 2012).

Therefore, the bulk density was calculated on an oven-dry 105 °C basis, taking into consideration a volumetric reduction of the samples, for coarse fraction > 2 mm with 2.65 g cm⁻³ and living organic material (mainly roots) with 1.3 g cm⁻³ gross density, which were removed from the samples.

The following chemical parameters were measured for all samples. Soil pH-value was determined in 1:2.5 soil:H₂O and in soil:1 M KCl (ÖNORM L1083) rations respectively. The total N was analysed according to semi micro Kjeldahl-method (ÖNORM L1082). Organic C was traced through dry combustion with a LECO SC 444 element analyser (ÖNORM L1080), reducing it by inorganic C, applying the Schiebel method (ÖNORM L1084). Exchangeable cations were analysed with the ammonium acetate method (1 M NH₄OAc at pH 7.0) plus exchangeable Al (1 M KCl, unbuffered) (ÖNORM L1094, 1999). The CEC (Cation Exchange Capacity) was calculated as the sum of Ca²⁺, Mg²⁺, K⁺, Na⁺, Al³⁺, Fe³⁺ and Mn²⁺, and base saturation as percentage portion of base cations (Ca²⁺, Mg²⁺, K⁺, Na⁺) (Coops and De Vos, 2010).

To calculate the stocks to a depth of 100 cm, the data for the few horizons which were not sampled for above indicated reasons, were thoroughly estimated. The bulk densities were derived based on field estimations of bulk density (FAO, 2006), thereby the measured bulk density of the surrounding horizons was considered as reference values. For the interpolation of SOC and nitrogen an exponential function was fitted to the measured values for each profile, assuming a decrease with depth. The missing values were calculated with the mean depth of the respective soil horizon as input value for the fitted function.

In total, 23 out of 92 horizons up to 100 cm were interpolated. This represents 17.1% of the sampled soil horizons.

Stocks e.g. for SOC were calculated as:

\[
\text{SOC} = \sum_{i=1}^{n} \text{SOC} \times \text{BD} \times (100 - \text{CF}) / 100
\]

where SOC is the concentration of SOC in oven-dry basis, BD is bulk density, CF is coarse fraction (> 2 mm) and D is soil horizon depth.

For a subset of 10 profiles, the soil texture was analysed (ÖNORM L1061) and classified according to FAO (2006), mainly for verification of argi-horizons (IUSS Working Group WRB, 2014) and proper classification of the reference soil group.

For testing hypothesis two and three, the sampling sites were grouped into forest zones according to Wangda and Ohsawa (2006) and Ohsawa (1987) (Fig. 2). At the lowest elevations, several transects started in the broadleaf zone with dominant Quercus semecarpifolia Smith. In the broadleaf-conifer zone, Quercus glauca Thunb. and Pinus wallichiana A.B. Jackson (Wallich ex D. Don, McCeli., Loddi., Picea spinulosa (Griff.) Henry and Tsuga dumosa (D. Don) Eichler, were co-existing. The cool conifer zone is divided into moist and dry site conditions. In the cool conifer moist zone, Tsuga dumosa is dominant with single Abies densa Griff and Picea spinulosa. Furthermore, the bamboo species Borinda grossa (Yi.) Stapleton and Arundinaria racemosa Munro is becoming more important and can build thick understories. The cool conifer dry zone is dominated by Picea spinulosa with Pinus wallichiana and single Quercus semecarpifolia as indicators for warmer conditions and single Tsuga dumosa in transition to moist sites. The dominating tree species in the cold conifer zone is Abies densa Griff. with single Tsuga dumosa or Betula utilis D. Don with a thick understory of various Rhododendron species (Rhododendron hodgsonii Hook., R. barbatum Walllich ex G.Don, R. kesangiae D.G.Long and Rushforth, R. arborreum Smith).

As the broadleaf and the broadleaf-conifer zone do not differentiate clearly in elevation (Fig. 2), they are pooled for presentation of soil characteristics (Table 3, Fig. 6).

2.3. Statistical analysis

Statistical analysis and graphics generation were performed with R (vers. 3.1.2, R Development Core Team, 2015). For testing hypothesis one and two, SOC stocks and soil chemical characteristics were correlated with elevation using Pearson correlations and linear models. The data was tested for normal distribution using Kolmogorov-Smirnov-Test.
and considering normal qqplots both from the R package: stats. In order to test if SOC and other soil chemical characteristics vary with soil type rather than altitude, we tested these characteristics for differences between soil types. Since in almost all cases the data was non-normally distributed (Kolmogorov-Smirnov-Test, normal qqplots), Kruskal-Wallis-Tests with posthoc Nemenyi-Tests (method = Tukey) from the R package: PMCMR were used (Pohlert, 2014). We also characterised the distribution of soil types along the elevational gradients.

For testing hypothesis three (differences in soils drive differences in vegetation types), we compared soil chemical characteristics and the distribution of soil types in different forest zones. Again, Kruskal-Wallis-Tests with posthoc Nemenyi-Tests were used since data was non-normally distributed.

For testing if the probabilities for occurrence of genetic soil horizons vary with forest zones (Fig. 7), the package aqp was used (Beaudette et al., 2013). The types of genetic horizons up to 100 cm depth were computed. The probabilities for slices to belong to a certain soil-genetic horizon were calculated as the frequency of the horizon type in relation to all slices (all profiles) at the same depth.

All values in the text are given as mean ± standard deviation, unless mentioned otherwise. Graphical output was done utilizing the package: lattice (Sarkar, 2008) and cartography with ArcMap 10.2.2 (ESRI, 2011).

3. Results

3.1. SOC along elevational gradients

3.1.1. SOC and elevation

The SOC stocks down to 100 cm ranged between 56.7 and 337.8 Mg ha\(^{-1}\), with a mean of 168.1 ± 93.0 Mg ha\(^{-1}\) (standard deviation) and showed no linear correlation with elevation. The maximum SOC accumulation in the soil was between 3200 and 3400 m asl corresponding with the cool conifer moist forest zone. With further increases in elevation, it declined (Fig. 3).

3.1.2. SOC and soil types

The reference soil groups showed the following SOC stocks: Cambisol_Dystric (238.0 Mg ha\(^{-1}\) ± 50.4), Stagnosol (211.8 Mg ha\(^{-1}\) ± 178.1), Podzol (176.7 Mg ha\(^{-1}\) ± 91.7), Phaeozem (141.4 Mg ha\(^{-1}\) ± 56.5), Cambisol_Eutric (74.1 Mg ha\(^{-1}\) ± 18.2), Fluvisol (73.6 Mg ha\(^{-1}\) ± 0.3) and Gleysol (56.7 Mg ha\(^{-1}\) ), without significant differences between all reference soil groups (Kruskal-Wallis-Test, \(\chi^2 = 11.66, p = 0.06\)).

The Phaeozems are the shallowest profiles recorded. With Ah-horizons > 25 cm, a dark-colour (value = 3, chroma = 1–2) (Munsell, 2009), high SOC content and a base saturation between 60 and 80%, the features of the required mollic horizons (IUSS Working Group WRB, 2014) are fulfilled. The podzol profiles display clearly visible leaching of organic matter in the topsoil (albic-horizon) at 5–15 cm depth. This goes along with the development of the E-horizon in the cold conifer forest zone (Fig. 7D). The organic matter accumulates in deeper horizons (Bh, spodic horizon) and leads to a second peak in the SOC content (Fig. 4, Podzol).

3.2. Soil characteristics along elevational gradients and soil types

3.2.1. Chemical soil characteristics along elevational gradients

From the chemical characteristics shown in Table 3, CEC at the topsoil shows a linear correlation with elevation (depth: 0–20 cm, \(r^2 = 0.28, p = 0.01\)). It had higher values at lower elevation. In deeper soil horizons, elevation had no more influence. The pH-value showed the same trend, with a significant correlation with elevation only at the topsoil (depth: 0–20 cm, \(r^2 = 0.32, p = 0.01\)). For base saturation, significantly negative correlations with elevation were only found in deeper soil horizons, depth: 20–60 cm (\(r^2 = 0.27, p = 0.02\)) and depth: 60–100 cm (\(r^2 = 0.3, p = 0.01\)). Furthermore, only a weak linear correlation of the total stocks of exchangeable elements with elevation could be detected. This was negative for Ca (\(p = 0.07\), Mg (\(r^2 = 0.18\), p = 0.03) and K (\(p = 0.09\)) and positive for Al (\(p = 0.3\)) and Fe (\(r^2 = 0.14, p = 0.05\)).

The bulk density of the sampled profiles ranges from 0.26 to 1.27 g cm\(^{-2}\), with a majority (25–75%-quantiles) of the soils with very low bulk density (< 0.6 g cm\(^{-2}\)) in an elevation range between 3000 m to 3400 m asl. Furthermore, the bulk density showed a strong correlation with SOC content (linear regression function: bulk density = 0.963739–0.049126 * C[%], \(r^2 = 0.61, p < 0.0001\), non-linear regression function: bulk density = 0.01588 + 0.89258 * C[%]–0.26207, \(r^2 = 0.72, p < 0.0001\); model range: 0–16% C).

3.2.2. Soil types along elevational gradients

The elevational distribution of the reference soil groups is given in Fig. 5, with distinct distribution ranges for most of the groups. In order to identify a potential elevational zonation of Cambisols (the most frequently recorded at 58%), they are differentiated based on secondary soil horizons. These horizons were subordinated to the diagnostic cambic horizon (Bw). Cambisols with temporary waterlogging and a weak stagnic horizon are categorised as StagnicCambisol. Profiles with minor illuvial processes, but still insufficient for designation of Spodic Horizons are categorised as Spodic_Cambisol. All others are summarised as Cambisol (Fig. 5). The grouping follows the principal qualifier system (IUSS Working Group WRB, 2014), except for spodic characteristics which are not intended for the combination with Cambisols.

3.2.3. Chemical soil characteristics of soil types

Eutric and dystric Cambisols (Table 4) were segregated considering the base saturation of > 90% for two of the analysed

![Fig. 3. SOC stocks at elevation classes. Point = median, numbers indicate count of profiles.](image)
Cambisol profiles. The other Cambisols showed base saturations between 20 and 40% in the major part of the profile (20–100 cm) and therefore fulfill the requirements for suffix-qualifier: dystric (IUSS Working Group WRB, 2014). Furthermore, these two groups have considerable differences in SOC content (Fig. 4) and stocks (Kruskal-Wallis-Test, $\chi^2 = 9.05$, $p = 0.002$) (Kruskal-Wallis-Test), with lower content in deeper soil horizons. The linear correlation with the mean horizon depth ($r^2 = 0.26$, $p = 0.01$), confirm that result and contradict a frequent occurrence of clay mitigation. For the individual Cambisol profiles, the quotient of the clay content between subsoil and topsoil (Table 2) ranges between 0.27 and 0.90 with a mean of 0.55. This is below the threshold of 1.2 increase of clay content for argic-horizons (IUSS Working Group WRB, 2014). With this, the classification as Cambisols could be confirmed.

The amount of exchangeable elements (Table 1) showed significant difference for Ca ($\chi^2 = 14.2$, $p = 0.02$), Mg ($\chi^2 = 12.4$, $p = 0.02$), K ($\chi^2 = 14.1$, $p = 0.02$) and Fe ($\chi^2 = 12.6$, $p = 0.04$) between the reference soil groups (Kruskal-Wallis-Test), but the differences could only be verified for K between Cambisol_Eutric and Podzol ($p = 0.04$) using a posthoc test (Nemenyi-Test).

The nitrogen stocks up to 100 cm ranged between 4.2 and 19.1 Mg ha$^{-1}$, with a mean of 11.4 ± 4.8 Mg ha$^{-1}$. The reference soil groups showed for Cambisol_Dystric (15.7 Mg ha$^{-1} ± 3.1$), Stagnosol (13.1 Mg ha$^{-1} ± 6.1$), Podzol (10.4 Mg ha$^{-1} ± 4.7$), Phaeozem (9.4 Mg ha$^{-1} ± 5.1$), Cambisol_Eutric (7.9 Mg ha$^{-1} ± 0.9$), Fluvisol (7.7 Mg ha$^{-1} ± 2.3$) and Gleysol (4.2 Mg ha$^{-1}$) and thereby the same order as the SOC stocks, also without a linear correlation with elevation.

The values for the soil texture are displayed in Table 2. Only Cambisols had enough samples to be tested for significant texture changes with soils depths. The differences were only significant for clay content ($\chi^2 = 9.05$, $p = 0.002$) (Kruskal-Wallis-Test), with lower content in deeper soil horizons. The linear correlation with the mean horizon depth ($r^2 = 0.26$, $p = 0.01$), confirm that result and contradict a frequent occurrence of clay mitigation. For the individual Cambisol profiles, the quotient of the clay content between subsoil and topsoil (Table 2) ranges between 0.27 and 0.90 with a mean of 0.55. This is below the threshold of 1.2 increase of clay content for argic-horizons (IUSS Working Group WRB, 2014). With this, the classification as Cambisols could be confirmed.
1.4 cm ± 1.1 is not significant different between warm, dry (broadleaf-conifer, cool conifer dry) and cold conifer forests (p > 0.3). Probabilities for Bw-horizons at depths of 100 cm decrease slightly from the broadleaf and mixed broadleaf forests (p > 0.85) to the dry cool conifer forests (p < 0.8) and stronger to the wet cool conifer forests (p < 0.55) and particularly the cold conifer forests (p < 0.25).

Eluvial horizons show very low probabilities (p < 0.1) in the dry aspect of the cool conifer zone but close of 0.2 in the moist aspect of this forest zone. In the cool conifer dry zone (Fig. 7B), the probability for a Cw-horizon is higher which reflects shallow soil development of Phaeozems (see also Fig. 4) which only occur in this forest zone.

4. Discussion

4.1. SOC along elevational gradients

The mean SOC stocks up to 100 cm soil depth in the studied forest types (168.1 ± 93.0 Mg ha⁻¹) were slightly higher than those reported from montane temperate forests in India (161.9 ± 19.2, Chhabra et al., 2003), and in the range of SOC values of forest soils in the Alps (Ojukic et al., 2010). The soil SOC stocks are also comparable to those in tropical forest soils at around 2000 m altitude (Dieleman et al., 2013) but below those reported for tropical forests in altitudes beyond 3000 m (see e.g. the overview in Dieleman et al., 2013). Giri (2011) reported 127–149 Mg ha⁻¹ and 135 Mg ha⁻¹ from mixed broadleaf forests and pine forests at lower elevations in Nepal.

The recorded SOC stocks at elevation ranges between 2450 and 3000 m asl with 126.2 ± 82 Mg ha⁻¹ and 3000–3300 m asl with 164.1 ± 102 Mg ha⁻¹ are considerably lower than values presented in Tashi et al. (2016) for these elevation ranges (408.2 Mg ha⁻¹, 403.5 Mg ha⁻¹ respectively). The same holds for the SOC values presented by Dorji et al. (2014a) which were 248.4 Mg ha⁻¹ for forests in Bhutan in general.

Our SOC stock calculation differs from others in the region (Tashi et al., 2016; Dorji et al., 2014a, 2014b) by considering smaller coarse fraction of the extracted soil samples and greater coarse fraction in the

### Table 1

<table>
<thead>
<tr>
<th>Soil Type</th>
<th>Ca [kg ha⁻¹]</th>
<th>Mg [kg ha⁻¹]</th>
<th>K [kg ha⁻¹]</th>
<th>Al [kg ha⁻¹]</th>
<th>Fe [kg ha⁻¹]</th>
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<tr>
<td>Cambisol_Dystic (6)</td>
<td>106.6 ± 10.3</td>
<td>49.8 ± 6.8</td>
<td>148.1 ± 19.4</td>
<td>268.3 ± 263.0</td>
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<td>(42.4)</td>
<td>(29.8)</td>
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<td>(175.1)</td>
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<td>Cambisol_Eutric (2)</td>
<td>3027.5 ± 325.7</td>
<td>469.1 ± 27.4</td>
<td>1192.7 ± 175</td>
<td>236.4 ± 223.8</td>
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<td>(34.5)</td>
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<td>Podzol (4)</td>
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<td>43.0 ± 10.4</td>
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<td>(7.8)</td>
<td>(34.5)</td>
<td>(133.0)</td>
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<td>Stagnosol (2)</td>
<td>400.1 ± 212.1</td>
<td>62.2 ± 19.8</td>
<td>289.3 ± 182.6</td>
<td>246.0 ± 91.2</td>
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<td>(212.1)</td>
<td>(19.8)</td>
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<td>(226.0)</td>
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<td>Phaeozem (2)</td>
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<td>52.2 ± 19.8</td>
<td>119.5 ± 45.4</td>
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<td>(77.6)</td>
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<td>Fluvisol (2)</td>
<td>716.7 ± 343.4</td>
<td>137.1 ± 42.0</td>
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<td>(42.0)</td>
<td>(42.0)</td>
<td>(2.9)</td>
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<td>Gleysol (1)</td>
<td>784.6 ± 592</td>
<td>176.4 ± 95.1</td>
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### Table 2

<table>
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<th>Depths [cm]</th>
<th>Cambisol (6 profiles)</th>
<th>Podzol (2 profiles)</th>
<th>Stagnosol (1 profile)</th>
<th>Phaeozem (1 profile)</th>
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<td>Clay [%]</td>
<td>45.0 ± 40.4 (12.1)</td>
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<td>(1)</td>
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<td>60–100</td>
<td>21.9 ± 22.4 (8.1)</td>
<td>22.3 ± (3.9)</td>
<td>22.3 ± (11.3)</td>
<td>9.9 ± (0.9)</td>
</tr>
<tr>
<td>Silt [%]</td>
<td>37.2 ± 36.7 (9.5)</td>
<td>46.2 ± 37.0 (12.3)</td>
<td>37.8 ± (9.1)</td>
<td>27.5 ± (9.1)</td>
</tr>
<tr>
<td>0–30</td>
<td>(8.1) [8]</td>
<td>(2.5) [4]</td>
<td>(2)</td>
<td>(1)</td>
</tr>
<tr>
<td>30–100</td>
<td>40.7 ± 46.7 (16.6)</td>
<td>49.2 ± (3.9)</td>
<td>41.7 ± (3.4)</td>
<td>24.5 ± (3.3)</td>
</tr>
<tr>
<td>Sand [%]</td>
<td>20.7 ± 22.8 (18.3)</td>
<td>21.4 ± 31.6 (14.1)</td>
<td>40.6 ± (13.1)</td>
<td>43.9 ± (13.1)</td>
</tr>
<tr>
<td>0–30</td>
<td>(8.1) [8]</td>
<td>(2.5) [4]</td>
<td>(2)</td>
<td>(1)</td>
</tr>
<tr>
<td>30–100</td>
<td>37.3 ± 30.9 (21.2)</td>
<td>28.5 ± (3.9)</td>
<td>36.1 ± (7.8)</td>
<td>65.6 ± (4.2)</td>
</tr>
</tbody>
</table>

### 3.3. Soil characteristics along forest zones

#### 3.3.1. Chemical soil characteristics along forest zones

The pH-value in the topsoil (depth: 0–20 cm) was the only soil chemical characteristic that was significantly different between the broadleaf-conifer and cold conifer forest zone (Table 3). For all other analysed chemical soil characteristics, no significant differences could be determined at the given sample size. Nevertheless, a decreasing trend for the CEC in the topsoil (depth: 0–20 cm) and for the base saturation in the subsoil (depth: 20–60 cm and depth: 60–100 cm) can be observed between warm, dry (broadleaf-conifer, cool conifer dry) and cold, moist (cool conifer, cool conifer moist) forest zones. For the base saturation the difference is significant (χ² = 6.82, p = 0.008; χ² = 5.37, p = 0.020 (Kruskal-Wallis-Test), respectively), for CEC in the topsoil (depth: 0-20 cm) the difference is not significant.

#### 3.3.2. Characteristics of the humus layer along forest zones

While the O-layer (humified organic layer) thickness of the humus differed between forest zones (Kruskal-Wallis-Test, χ² = 13.71, p = 0.008), the F-layer (fragmented organic layer) thickness with a mean of 2.3 cm ± 1.3 and the L-Layer (litter) thickness with a mean of 1.4 cm ± 1.1 is not significantly different between forest zones and elevation (Fig. 6).

#### 3.3.3. Occurrence of soil horizons along forest zones

The depth function for occurrence probabilities of different genetic horizon types were calculated for the forest zones (Fig. 7) (Beaudette et al., 2013). The probabilities show strong differences in the occurrence of diagnostic soil horizons along forest zones (and thus altitude) and between moist and dry aspects of mid altitudes: probabilities for Ah horizons increase from the broadleaf and broadleaf conifer forests and decrease again strongly in the cold conifer forest, thus mirroring the elevational distribution of SOC stocks. The probabilities for eluvial (Eh, Ah) and illuvial horizons strongly increase from the lower altitude broadleaf and mixed broadleaf forests (p < 0.1) to the high altitude cold conifer forests (p > 0.3). Probabilities for Bw-horizons at depths of 100 cm decrease slightly from the broadleaf and mixed broadleaf forests (p > 0.85) to the dry cool conifer forests (p < 0.8) and stronger to the wet cool conifer forests (p < 0.55) and particularly the cold conifer forests (p < 0.25).

Eluvial horizons show very low probabilities (p < 0.1) in the dry aspect of the cool conifer zone but close of 0.2 in the moist aspect of this forest zone. In the cool conifer dry zone (Fig. 7B), the probability for a Cw-horizon is higher which reflects shallow soil development of Phaeozems (see also Fig. 4) which only occur in this forest zone.
Considering aboveground biomass data presented in Wangdi et al. (2017), these forests would fall into the highest above ground biomass category of > 400 Mg ha$^{-1}$ used by Saatchi et al. (2011) in an assessment and mapping of live biomass in the tropics and thus represent a global carbon storage hotspot.

Bhutanese forest soils have mineral SOC stocks at the upper range, especially in the cool conifer zone, compared to soil in other mountain forest ecosystems. SOC stocks in soil profiles aggregated to forest zones, values are medians and means (unless the same) over the depth with standard deviation in parentheses, numbers in brackets display the quantity of samples, letters indicate significant differences (A, B) between forest zones tested with Kruskal-Wallis, posthoc Nemenyi-Test $p = 0.05$ (AB are not different from A or B).

### Table 3

General chemical characteristics of soil profiles aggregated to forest zones, values are medians and means (unless the same) over the depth with standard deviation in parentheses, numbers in brackets display the quantity of samples, letters indicate significant differences (A, B) between forest zones tested with Kruskal-Wallis, posthoc Nemenyi-Test $p = 0.05$ (AB are not different from A or B).

<table>
<thead>
<tr>
<th>Depths [cm]</th>
<th>Broadleaf-conifer (4 profiles)</th>
<th>Cool conifer moist (7 profiles)</th>
<th>Cool conifer dry (1 profiles)</th>
<th>Cold conifer (6 profiles)</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH (KCl)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–20</td>
<td>4.63; 4.01 (0.19)$^A$</td>
<td>3.66; 3.60 (0.28)$^{AB}$</td>
<td>3.73 (–)$^{AB}$</td>
<td>3.36; 3.36 (0.30)$^A$</td>
</tr>
<tr>
<td>20–60</td>
<td>4.40; 4.39 (0.20)$^A$</td>
<td>4.29; 4.29 (0.20)$^A$</td>
<td>3.96 (–)$^A$</td>
<td>4.54; 4.33 (0.08)$^A$</td>
</tr>
<tr>
<td>60–100</td>
<td>4.63; 4.61 (0.36)$^A$</td>
<td>4.46; 4.42 (0.21)$^A$</td>
<td>3.97 (–)$^A$</td>
<td>4.52; 4.78 (0.47)$^A$</td>
</tr>
</tbody>
</table>

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Fig. 6. Thickness of the humus layer at the forest zones, L = litter-layer, F = fragmented humus-layer, O = humified humus-layer, point = median, numbers indicate count of profiles.

soil profile. Up to 100 cm depth, the 82 described profiles had a mean coarse fraction of 17.7% ranging from 0% up to 60%. This proportion reduces SOC stocks significantly and its inclusion in this study could explain at least a part of the variation between the studies.

The high SOC stocks in general (Fig. 3) and their vertical distribution (Fig. 4), with high contents in deeper soil horizons, indicate a long continuity in soil development and forest cover. Compared to other land cover (e.g. agricultural land, grassland, shrubland) the SOC stocks under forests are the highest in the region (Dorji et al., 2014a).

Dorji et al. (2014a) and Tashi et al. (2016), reported a continuous increase of SOC stocks with altitude up to 4000 m asl and up to 3300 m asl respectively. While we did find a continuous increase of SOC up to the altitudinal range of Tashi et al. (2016) (3300 m asl), SOC decreased again in higher altitudes in our study, resulting in a unimodal curve of SOC stocks, with the peak between 3200 and 3400 m asl. We thus reject hypotheses one. This is in line with Sheik et al. (2009), who reported lower SOC contents in higher elevations in forest soils and attributed this to lower tree density and lower litter inputs into soils. Djukic et al. (2010) interpreted a similar SOC distribution along altitude to be a result of reduced NPP with elevation and reduced input into soils while Becker et al. (2007) explained this with shallower soils at higher elevations. The cool conifer moist forests of Bhutan had the highest SOC with a max. of 337.8 Mg ha$^{-1}$ (mean: 206.1 ± 105 Mg ha$^{-1}$) and also had remarkably high aboveground carbon storage (Wangda and Ohsawa, 2006; Wangdi et al., 2017).

Considering aboveground biomass data presented in Wangdi et al. (2017), these forests would fall into the highest above ground biomass category of > 400 Mg ha$^{-1}$ used by Saatchi et al. (2011) in an assessment and mapping of live biomass in the tropics and thus represent a global carbon storage hotspot.

Bhutanese forest soils have mineral SOC stocks at the upper range, especially in the cool conifer zone, compared to soil in other mountain forest ecosystems. SOC stocks in soil profiles on silicate bedrock in the Austrian Alps were 115.8 Mg ha$^{-1}$ for Dystric Cambisols and 127.7 and 160.8 Mg ha$^{-1}$ for Cambisols with illuvial processes (in the article at hand termed Spodic Cambisol) (Leitgeb et al., 2013). Podzols near the treeline in the Swiss Alps show 109.6 and 262.7 Mg ha$^{-1}$ for Cambisols with illuvial processes (in the article at hand termed Spodic Cambisol) (Leitgeb et al., 2013). While in the German Alps, 50–100 Mg ha$^{-1}$ SOC on easily weatherable parent material (Pflysch, Tertiary molasse) are described (Prietzel and Christophel, 2014). Subalpine pine and spruce forest in the Rocky Mountains (Colorado and Wyoming) showed 51–73 Mg ha$^{-1}$ mineral SOC stocks (Bradford et al., 2008). SOC stocks of the common soil types, Cambisol_Dystric (238.0 Mg ha$^{-1}$ ± 50.4), Stagnosol (211.8 Mg ha$^{-1}$ ± 178.1) and Podzol (176.7 Mg ha$^{-1}$ ± 91.7) are all higher than those references. However, the discussed results are predominantly from north facing slopes and our findings cannot be up-scaled to all aspects. The drier, south exposed slopes are dominated by the dry variant of the cool conifer forest zones in mid elevations and the broadleaf-conifer zone in lower elevations. This sides, with mainly Phaeozems, had generally shallower soil development (Fig. 7), which supports lower SOC stocks.

In our study, the azonal soils (Gleysol, Fluvisol) showed the lowest...
SOC stocks. The Fluvisols are young soils, developed on fluvial terraces. The low age is confirmed by weak intermixing of SOC only to a depth of 20 cm (Fig. 4). Nevertheless, relict fluvial terraces in other parts of Bhutan show considerable soil development (Baillie et al., 2004). The unusually low SOC stocks of the Gleysol can be ascribed to a shallow landslide and therefore disturbed soil development.

4.2. Soil characteristics along elevational gradients and soil types

Though the correlations between elevation and soil characteristics are not significant in each case, there is a distinct trend of less favourable soil chemistry for plant growth with increasing elevation. The decreasing pH-value of the topsoil with increasing elevation reflects soil acidification at colder temperatures and higher precipitation (Rosset, 1998; Wangda and Ohsawa, 2006). The decreasing CEC with increasing elevation is a product of slower weathering (lower clay content) and shallow soil development (Fig. 7). This is in line with lower clay \( (r^2 = 0.15, p = 0.08) \), lower silt \( (r^2 = 0.11, p = 0.12) \) and higher sand \( (r^2 = 0.26, p = 0.03) \) contents at higher elevation in the topsoil (0–30 cm, Table 2). The results are confirmed by Bäumler and Zech (1994), who showed a decrease in clay content with elevation in high mountain region of Eastern Nepal. In addition, they determined a clear differentiation of soils due to elevation.

Fig. 7. Probability of soil horizon development. A: broadleaf and broadleaf-conifer forest, B: cool conifer dry, C: cool conifer moist, D: cold conifer; soil horizons labels according to FAO (2006) except Ah,E = transition horizon, Bfs = characteristics of suffixes: h and s, Bg = pooled waterlogged horizons (suffixes: g, l, r).

The missing or low statistical significance of soil texture changes with altitude is most probably caused by the small sample number (Table 2). Furthermore, the base saturation of the topsoil is often influenced by anthropogenic nutrient exports like grazing or leave litter collection, which are both common in Bhutanese forests (Roder et al., 2002; Darabant et al., 2007). Therefore, it is likely that topsoil base saturation is influenced by different land use intensities and does not show a correlation with elevation. In deeper soil horizons, the negative correlation between base saturation and elevation is a result of shallow soil development.

Bulk density was very low, with a strong correlation to the SOC content. A low bulk density has already been reported from Bhutan (Caspari, 2005) and is ascribed to Al-humus complexes (Bäumler et al., 2005). The Fe, Al and Si compounds extracted by acid ammonium oxalate solution (Blakemore et al., 1987), necessary for the clear distinction between Cambisols and Andosols (IUSS Working Group WRB, 2014) were not analysed. Due to this remaining gap, the soils with potential Aluandic properties developed from non-volcanic material, were classified as Cambisols and not as Aluandic Andosols.

The Podzol and Cambisol_Dystric showed very low stocks of Ca, Mg and K available in short- and medium-term, which is typical for acidified soils (Table 1). Phaeozem, Fluvisol and Stagnosol showed average stocks and Gleysol and Cambisol_Eutric had high stocks. Thereby,
variability was highest for Cambisol_Eutric (Table 1). The two recorded profiles occurred close to each other at one transect in the western study area (Fig. 1). The pH-values of app. 4.0 and a CEC (0.45 cmol kg$^{-1}$) at the deepest horizons are comparable with other Cambisols and corroborate that there were no differences in parent material. For both profiles, the K stocks (1363 ± 135 kg ha$^{-1}$) were high. Moreover, one profile showed unusually high stocks for Ca (5847 kg ha$^{-1}$) and Mg (716 kg ha$^{-1}$). At that site, the forest was a young secondary successional Pinus wallichiana stand which most likely developed after a recent disturbance. Although no charcoal remains were detected, the significantly lower SOC content (Fig. 4) and nitrogen stocks are an indicator for forest fire, which is a common disturbance in lower elevation Bhutanese forests (RGoB, 2005).

Another reference soil group that was exclusively found in a specific forest zone, are Phaeozems, in the cool conifer dry zone. The azonal soils (Gleysol, Fluvisol, Histosol) are more driven by the slope morphology than by elevation or forest zone. Cambisols occurred in different forms (Haplic, Stagnic, Endoleptic, Pisoplinthic; IUSS Working Group WRB, 2014) in all forest zones, except for the highest elevation. The further classification displays a distinct distribution range (Fig. 5) of the different forms of Cambisol and emphasizes the importance of the principal-qualifiers. The Spodic_Cambisol had a focus in cool conifer moist (55%) and cool conifer forests (45%). It is characterised by weak leaching and illuvial transport processes, mainly of organic matter and Fe (Ah.E-horizons; Fig. 7C, D). Hence, it differed clearly from other forms of Cambisols. Based on this, the principal-qualifier: spodic is suggested for transitions between Cambisol and Podzol. Similarly, the Stagnic_Cambisol is a transition between Cambisol and Stagnosol and its elevational distribution (Fig. 5) is below Stagnosols. This is in line with the occurrence of waterlogged horizons (Bg) in higher elevations (Fig. 7C, D). Since no clear stratification of the parent material within the considered soil depth (100 cm) were discovered, the horizon sequences were interpreted as a result of change in temperature (along elevation) and vegetation along elevational gradients.

4.3. Soil characteristics along forest zones

Vegetation-soil interactions are important for soil development, hence, a classification in forest zones along elevation is also a means for zonation of soils. The chosen forest zones segregate well along elevation (Fig. 2) and dominant tree species, except for the broadleaf and broadleaf-conifer. This is because the main distribution of the broadleaf tree species is below the studied elevational range (Grierson and Long, 1983; Sargent et al., 1985; Wangda and Ohsawa, 2006). Although the cool conifer dry and cool conifer moist overlap in elevation (Fig. 2), they differentiate clearly at slope aspects and moisture classes, which is also reflected in different species composition. A similar differentiation of soil characteristics, albeit on steeper environmental gradients, was found by Fritzche et al. (2007) in a transect from the Ethiopian Rift Valley into high elevation Ericaceous forests. Bockheim et al. (2000) highlighted an important role of plant-soil feedback particularly in highest elevations of an elevational transect study in the Rocky Mountains where a sedge community appeared to strongly contribute to high base-cation amounts in the soils at the highest elevations. We did not detect such a strong role of plant soil feedback but a rather continuous and consistent change of soil types and soil characteristics along the elevational gradient.

Tree species composition and litter properties usually influence L-layer and F-layer thickness. Distinctions in forest floor SOC stocks between conifer and broadleaf forests (Schulp et al., 2008) most likely reflect different decomposition rates of litter of different quality. In the studied forest zones, the O-layer thickness increased with elevation (Fig. 6) However, the L-layer and F-layer thickness was not related to elevation and forest zone. It is unlikely that decomposition rates are not restrained by temperature and litter quality. More likely, the reduced biomass productivity and subsequently lower litter input compensates for the slower decomposition rates of conifer litter. The increasing O-layer thickness is an indicator of restrained intermixing of organic and mineral components by soil organisms at higher elevation. Thereby, seepage of SOC becomes a more important process. Litter of Rhododendron species, which are common in the cold conifer zone, support slow decomposition rates (Gratzer et al., 1997) and formation of hemic acids. Thus pH-value in topsoil decreases (Table 3) and development of albic horizons (Ah.E to E-horizon) is fostered (Fig. 7D). This is in line with the humusform mor or transitional forms between moder and mor for all recorded Podzols which were restricted to the cold conifer zone, above 3250 m (asl) (Fig. 5), and is in accordance with Zanella et al. (2011) in the reference base of European humus forms.

The reduced net primary productivity (NPP) of vegetation with elevation and therefore reduced SOC stocks seem to be the strongest vegetation soil feedback. We interpret these as manifestations of changes of temperature and precipitation with elevation and could not detect an indication for differences in soils driving differences in vegetation types or abrupt changes in soil characteristics as e.g. found by Dahlgren et al. (1997) at the snow line of the Sierra Nevada in California. Since forest zone distribution is mainly driven by climate and is easily recordable, it would thus also reflect soil characteristics. The elevational transects would thus also serve as elevation for time substitution for estimation of consequences of climate change to soil development and soil characteristics.

5. Conclusion

The high SOC stocks in general (Fig. 3) and their vertical distribution (Fig. 4), with high contents in deeper soil horizons, indicate a long continuity in soil development and forest cover. Along the elevational gradient, soils showed a unimodal curve for SOC stock with an increase in elevation followed by a decrease at the highest elevations. We explain this by shallow soils and a reduction of NPP at the highest elevations. We also observed a shift towards organic carbon accumulation in humus with elevation. The cool conifer forests, particularly in their moist aspects, where the SOC peaks also show very high above ground biomass and thus represent a global carbon storage hotspot. These forests are also among those which were logged over first in Bhutan and which still have high extraction rates.

The soil types and soil characteristics along the elevational gradient showed continuous and consistent rather than abrupt changes. We interpret these as manifestations of changes of temperature and precipitation with elevation which also drives forest zone distribution. Since forest zone distribution is easily recordable, it can also be used to infer to soil characteristics in these Himalayan forests. It may also serve as an elevation-for-time substitution for estimation of consequences of climate change to soil development and soil characteristics.

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We sincerely thank Dr. Kinley Tenzin, Dr. Andras Darabant, Mr. Tshewang Dorji and the involved staff of the RNR-RDC Yusipang and RNR-RDC Bumthang for their cooperation and Dr. Cindy Prescott for prereview. Furthermore, we thank two anonymous reviewers for a detailed review which improved our work considerable. The fieldwork was part of the FORED project, funded by the Austrian Government through the Austrian Development Agency (Project number: 1111-00/2009).

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at https://doi.org/10.1016/j.geoder.2017.11.004. These data include the Google map of the most important areas described in this article.