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Pedogenesis, permafrost, and soil moisture as controlling factors for soil nitrogen and carbon contents across the Tibetan Plateau

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Abstract

We investigated the main parameters [e.g. mean annual air temperature , mean annual soil temperature, mean annual precipitation, soil moisture (SM), soil chemistry, and physics] influencing soil organic carbon (C_{org}), soil total nitrogen (N_t) as well as plant available nitrogen (N_{min}) at 47 sites along a 1200 km transect across the high-altitude and low-latitude permafrost region of the central-eastern Tibetan Plateau. This large-scale survey allows testing the hypothesis that beside commonly used ecological variables, diversity of pedogenesis is another major component for assessing carbon (C) and nitrogen (N) cycling. The aim of the presented research was to evaluate consequences of permafrost degradation for C and N stocks and hence nutrient supply for plants, as the transect covers all types of permafrost including heavily degraded areas and regions without permafrost. Our results show that SM is the dominant parameter explaining 64% of C_{org} and 60% of N variation. The extent of the effect of SM is determined by permafrost, current aeolian sedimentation occurring mostly on degraded sites, and pedogenesis. Thus, the explanatory power for C and N concentrations is significantly improved by adding $CaCO_3$ content ($P = 0.012$ for C_{org}; $P = 0.006$ for N_t) and soil texture ($P = 0.077$ for C_{org}; $P = 0.015$ for N_t) to the model. For soil temperature, no correlations were detected indicating that in high-altitude grassland ecosystems influenced by permafrost, SM overrides soil temperature as the main driving parameter at landscape scale. It was concluded from the current study that degradation of permafrost and corresponding changes in soil hydrology combined with a shift from mature stages of pedogenesis to initial stages, have severe impact on soil C and plant available N. This may alter biodiversity patterns as well as the development and functioning of the ecosystems on the Tibetan Plateau.

Keywords: Alpine grassland, global warming, pedogenesis, permafrost degradation, plant available nitrogen, Qinghai-Tibetan Plateau, soil moisture, soil nitrogen, soil organic carbon, soil texture

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Introduction

The Tibetan Plateau is a key area concerning environmental evolution of the earth at regional as well as global scales and proves to be particularly sensitive to global warming (Yao *et al*., 1995; Liu & Zhang, 1998; Liu & Chen, 2000). It is the youngest, largest and highest plateau in the world, comprising an area of more than 2.4 million km^2 with an average altitude exceeding 4000 m a.s.l.

The Tibetan Plateau represents the largest high-altitude and low-latitude permafrost area on earth with 54.3% of its total surface affected by permafrost (Cheng, 2005). Mainly due to the low-latitudes, this permafrost subtype is characterized by strong diurnal patterns, high radiation on the surface as well as a distinct geothermal gradient (Wang & French, 1994). Permafrost degradation processes were found to have been even more enhanced over the past decades compared with

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high latitude–low altitude permafrost regions (Yang *et al*., 2004). The proposed decay of Tibetan permafrost (Wang *et al*., 2000; Böhner & Lehmkuhl, 2005) will have a strong impact on soil hydrology, leading to severe changes in soil moisture–temperature regimes (Zhang *et al*., 2003). Thus, there is a direct link to soils, which are the basic resources life in terrestrial ecosystems depends on and of particular importance for the global C cycle (Schimel, 1995; Sudgen *et al*., 2004). Global environmental change, largely caused by human activities, affects climate as well as soils, and consequently reassigns their role in ecosystem functioning (Vitousek *et al*., 1997; Chapin *et al*., 2000).

The key ecosystem attributes likely to impart feedback on climate change in this alpine grassland ecosystem are soil organic carbon (C_{org}) and soil nitrogen (N) stocks (Rodrigo *et al*., 1997; Wang *et al*., 2007). Many types of grasslands are highly productive, species-rich and consequently among the most responsive of terrestrial ecosystems to climate change, bearing on a global scale 10% of the terrestrial ecosystem's carbon (C) (Schimel *et al*., 1990; IPCC, 2001). Vegetation of the investigated region consists mainly of alpine meadow and alpine steppe grassland spreading over 60% of the plateau's total surface which corresponds to an area of 1.6×10^8 ha and equals 40% of the national Chinese grassland area (Wu, 1980). The alpine meadows of the Tibetan Plateau currently act as a C sink (Kato *et al*., 2004). Approximately 33.52 Pg C is stored in organic compounds, in which the alpine meadow and steppe ecosystem is responsible for 23.24 Pg (Wang *et al*., 2002) and hence retains the highest amount of C_{org} and total nitrogen (N_t) in Chinese soils (23.44%), which accounts for 2.5% of the global pool (Wang & Zhou, 1999; Ni, 2002). Therefore, periglacial environments of Central China play a major role in the global C and N cycle, especially due to the pronounced sensitivity of this region to climate change. Considerable losses in soil organic matter and N_t of heavily degraded ecosystems have been observed over the past 20–40 years on the Tibetan Plateau (Wang *et al*., 2001, 2007; Yang *et al*., 2009), indicating a significant modification of soil C and N cycles. This makes it essential to get a better understanding of the main parameters influencing C and N dynamics and consequently ecosystem functioning in the Tibetan grasslands.

On landscape scale, it is a common approach in ecology to use correlations between control variables, such as climate and topography, and dependent variables, such as vegetation composition and soil parameters (e.g. Wang *et al*., 2002; Yang *et al*., 2008). These correlations are also used as basis for modelling feedback interactions of ecosystems on climate change (Burke *et al*., 1997) as the results of laboratory incubations are not easy to evaluate because incubation conditions are difficult to reproduce and to compare in natural environments (Rodrigo *et al*., 1997). Most studies concerning stock dynamics in grassland ecosystems, particularly with respect to alpine steppe and meadows, have been carried out solely on a local scale. For example, Fisk *et al*. (1998) showed topographically related soil moisture (SM) patterns as the fundamental control on N cycling and production of biomass in alpine tundra ecosystems. Soil forming factors, as substrate composition and relief position, were considered only in few other studies on C and N dynamics of steppe ecosystems (e.g. Dodd *et al*., 2000; Hook & Burke, 2000; Dharmakeerthi *et al*., 2005).

Generally, soil temperature is considered as a key factor of many terrestrial biochemical processes like soil respiration, decomposition of organic matter, N mineralization, denitrification, plant productivity, and nutrient uptake by plants (e.g. Raich & Potter, 1995; Lindroth *et al*., 1998; Rustad *et al*., 2001; Shaw & Harte, 2001; Callesen *et al*., 2003; Shaver *et al*., 2006). However, as major parts of the research area in Tibet, particularly alpine steppes, are moisture-limited, SM has to be taken into account as another crucial parameter (Reichstein *et al*., 2003).

The main objective of our study was to investigate on a landscape scale the influence of pedogenesis on C and N stocks supplementary to the above-mentioned generally used ecological parameters like climate, temperature, moisture conditions, vegetation, topography, and hydrology. We hypothesize that diversity patterns of pedological features across a changing landscape are crucial to assess C and N dynamics more precisely.

Materials and methods

Environmental settings along the transect

During an expedition in summer 2006, launched in cooperation with Peking University, China and University of Tübingen, Germany, along a transect of about 1200 km length and 200 km width in the central-eastern part of the Tibetan Plateau from Xining to Lhasa, botanical, ecological and pedological settings have been investigated at 47 sites. The transect is situated between 91 and 101°E latitude and 30 to 36°N longitude with an eastern section from Xining to Yushu and a western part from Golmud to Lhasa (Fig. 1).

Our research is mainly concentrated on plateau grassland areas largely excluding the high mountain regions. The east-west stretching mountain ranges have a major influence by marking important barriers for the relatively moist and warm tropical Indian monsoon coming from the south. The influence of the Asian monsoon

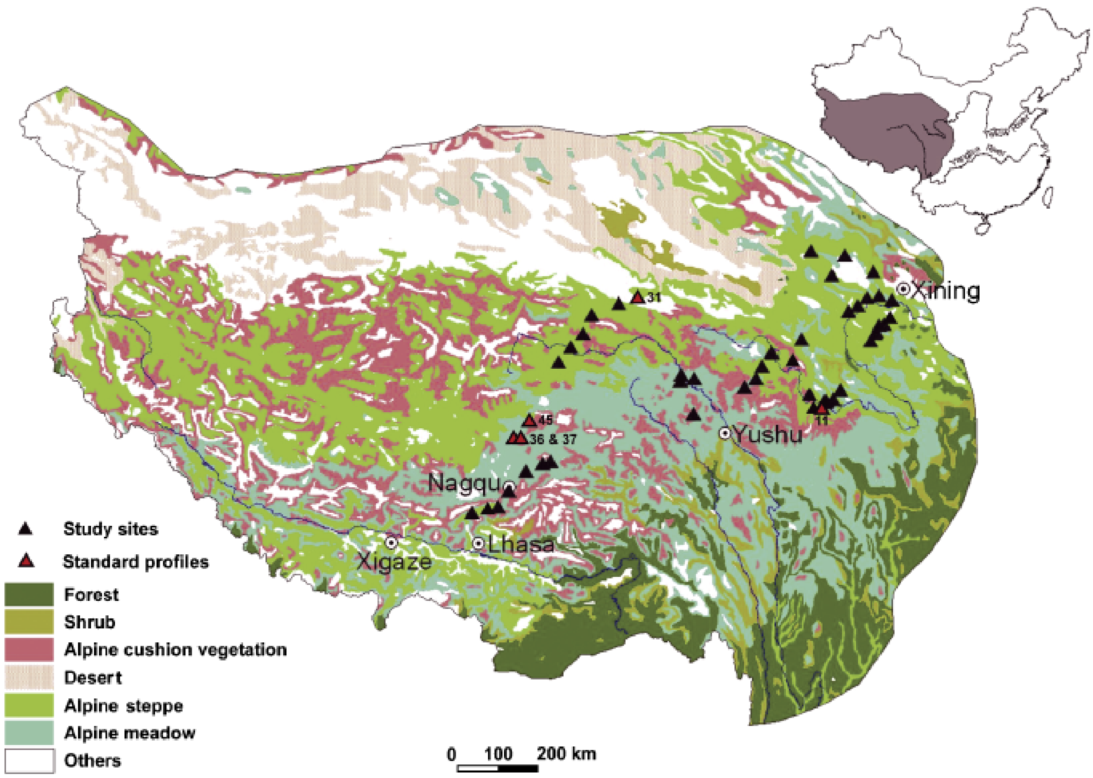


Fig. 1 Vegetation map of the Tibetan Plateau, adapted from the Vegetation Map of China (Hou, 1982), showing study sites and standard soil profiles representing the most important soil groups.

decreases westwards (Harris, 2006), leading to both higher temperature and precipitation in the south and east of the plateau. More than 80% of the annual precipitation is occurring during the summer months from July until September ranging from 218 to 600 mm mean annual precipitation (MAP). Mean annual air temperature (MAT) varies from −5.75 to 2.57 °C, mean annual evaporation from 1204 to 1327 mm (Yao *et al*., 2000; Wang *et al*., 2001; Zhang *et al*., 2003).

The permafrost characteristics closely follow the mean annual soil temperature (MAST) gradient (Wang & French, 1994; Ping *et al*., 2004). The depth of the active layer increases from north to south and overall with lower altitude, averaging around 1–2 m in continuous permafrost (Wang *et al*., 2000; Cheng & Wu, 2007). The diurnal fluctuation may reach 25–40 °C manifesting frequent daily freeze–thaw cycles and relating consequences for C and N stocks (Ping *et al*., 2004).

Soils in the study area can be characterized by young development, frequent polygenetic formation and strong degradation features affected by cryogenic or erosive processes. This leads to a high diversity and variety of substrates, geomorphological processes and soil forming factors. In many soil profiles, relict and mainly humic horizons can be observed. On steep upper slopes Leptic Cambisols and Leptosols are evident, whereas Gleysols are frequent next to rivers or lakes. Gelic Gleysols, Gelic Cambisols, and Permagelic/Gelic Histosols are predominantly developed on permafrost sites. In cold alpine meadow areas, felty turf-like topsoils mainly containing organic residuals are developed and described as Afe-horizons (Kaiser, 2004) having on average high soil organic C contents. This horizon is covering a wide range of different soil types.

Alpine *Kobresia* meadow ecosystems are the most widely distributed vegetation types on the plateau (Zhou, 2001) occurring at elevations ranging from 3200 to 5200 m asl (Kato *et al*., 2004). The main species are *Kobresia pygmaea*, *Kobresia humilis*, *Polygonum gentiana*, and *Saussurea* sp. In wetlands *Kobresia littledalei*, *Kabresia tibetica*, *Carex lanceolata*, and *Carex muliensis* occur. Alpine steppe vegetation consists mainly of *Stipa purpurea*, *Stip subsessiliflora* and *Carex moorcroffiana* (Chang, 1981).

Field methods

Detailed field investigations included soil profile description according to FAO (2006) and IUSS Working Group WRB (2006). Soil sampling was split into three parts: horizon-wise sampling for pedogenesis using soil pits; schematic sampling conducted by drilling at three depth-increments (0–5, 5–10, and 10–20 cm) for C and N analysis; volumetric samples at equal depths for bulk density and gravimetric water content determination.

This was accompanied by on-site extraction of mineralized N (N_{min}) consisting of NO_3-N (nitrate) and NH_4-N (ammonium). At each site four schematic samples of each depth-increment were mixed. The macroscopic root material and other organic compounds were removed. An aliquot of 10 g of homogenized soil was used for extraction with 50 mL 1 M KCl for 60 min immediately after sampling stirred with a glass stirrer every 10 min and then filtered through Whatman No. 42 cellulose filter paper into 100 mL PE-vials. Samples were conserved with 2 mL HCl (30%). For recalculating the contents in dry soil, the gravimetric water content was used.

SM was supplementary determined directly in the field by TDR-probes (Delta-T Devices Ltd., Cambridge, UK) for all pedogenetic horizons as well as for the depth increments. Above- and belowground biomass was investigated at a 1 m^2 sampling square at each site by clipping and digging out the roots. The same method was used to describe plant species composition.

Soil temperature was measured with buried temperature data loggers (Hobo U12, Onset Computer Corporation, Pocasset, MA, USA) at an interval of 1 h starting in July 2006 for 1 year.

Laboratory analysis

Grain size analysis was done by combined pipette and sieving method (seven fractions, Koehn, DIN 19683-1). Colour description was carried out with Munsell Soil Colour Charts. Electrical conductivity was determined in bidistilled H_2O while pH was measured in both 0.01 M $CaCl_2$ and bi-distilled H_2O potentiometrically. $CaCO_3$ was analyzed volumetrically. Soil-N_t and -C_{org} was measured with heat combustion (VARIO EL III, Elementar, Hanau, Germany). C bound in $CaCO_3$ was subtracted from the total amount of C (C_t) quantified with CN analysis to get the proportion of organic C (C_{org}). The KCl-extractions for N_{min} analysis were measured photometrically (CFA SAN Plus, Skalar, Breda, the Netherlands). Water content was determined gravimetrically by taking the skeleton content into account.

Data analysis and statistical applications

The investigated soil profiles were sorted into different groups based on field observations, soil description and laboratory analysis of the profile pits and horizon-wise samples. In this context, pedogenesis is described by acidity, carbonate content and grain size distribution. Five sites were chosen as representative soil profiles out of 47 sites, under which the other research areas could be subordinated. For statistical analyses the whole dataset of 47 sites was used.

Climate data for each site was calculated based on linear models using latitude, longitude, and altitude as variables from 50-year averaged temperature and precipitation records (1951–2000) at 680 well-distributed climate stations across China (He *et al*., 2006). For statistical approaches the results of the schematic sampling series was utilized with a sample size of $n = 141$. This dataset was split into the three sampling depths (0–5, 5–10, 10–20 cm). To examine dependencies, correlation, and regression analyses were conducted for SM, MAST, MAT, MAP, soil texture, carbonate content ($CaCO_3$), and soil acidity (pH). To address multicollinearity, out of these predictors only variables with $R^2 < 0.5$ were used for regression analysis in the same model.

The significant relationships were included into a least squares (OLS) regression analysis. A general linear model (GLM) was used to describe the effects of the dependent parameters (vide supra) on the independent variables (C_{org}, N_t, NH_4^+, and NO_3^-). This single condition models where used to investigate the impact of each dependent variable based on correlation analysis and multiple linear model explanation. The differences of the contribution of site parameters were compared by one-way analysis of variance (ANOVA). For all dependent parameters multicollinearity was tested. The analyses were performed with SPSS 10.0 J for Windows and R software package (R Development Core Team, 2009).

Results

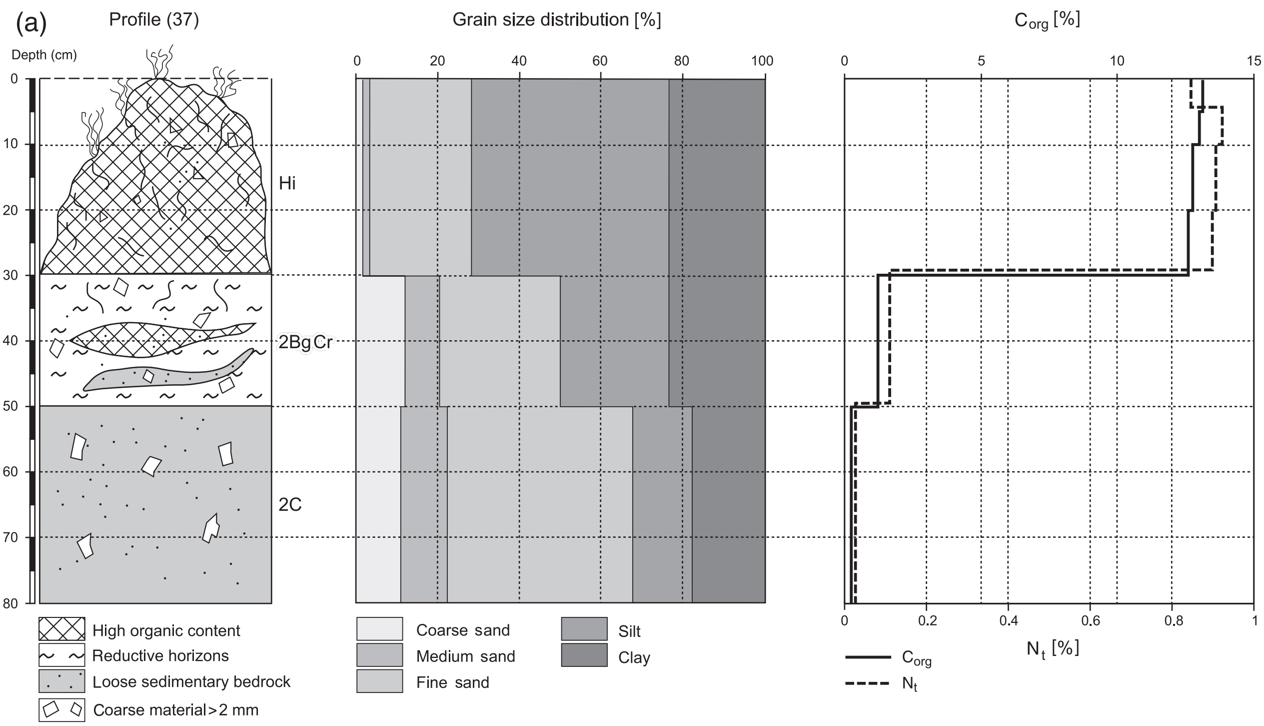
Pedogenesis

All investigated soil profiles were allocated to five different main soil groups, covering most soil types of the Tibetan Plateau (Table 1). These main soil groups represent different stages of maturity, from initial soil formation to long developed soils underlain by stable permafrost conditions. Soil development is often young and has been frequently disturbed or interrupted over time. Therefore, relict, mostly humic horizons can be observed in some profiles, representing phases of stability. The most important factor controlling these processes is recent active aeolian sedimentation, diluting the topsoil's chemical composition or burying the developed soils completely (cf. site 31). This explains the strong trend to accumulate carbonates and bases often also relocated to deeper horizons, recognizable by carbonate pseudo-mycelic structures. In the southern and eastern part, distinct weathering and enrichment of secondary Fe oxides in Bw horizons can be found disappearing to the north of the continuous permafrost zone. Strong gleyic or stagnic properties are evident towards the southern and eastern margin of the permafrost-affected area with increasing precipitation, although the permafrost table is deeper.

Table 1 Grouping of soil profiles

Pedological unit	Abbreviation	*n*
Initially formed soils	IS	13
Regosols	RG	7
Cambisols	CM	11
Groundwater influenced	GL	4
Permafrost influenced	PF	12

The main differences between sites are substantially related to the permafrost regime. For instance, sites 36 and 37 are situated only 150 m from each other in the discontinuous permafrost zone south of Amduo on a small mountain pass (4900 m asl) (Fig. 2). Position 36 is primarily vegetated by *Kobresia parva* and *K. humilis* forming very felty topsoils, whereas site 37 is domi-



Site 37: Calcaric Gelic Histosol; 4,902 m asl; 32.18°N, 91.72°E; MAT –4.2°C; MAP 472 mm/a; upper middle slope; *Kobresia schoenoides, Carex spp., Oxytropis spp., Aster spp.*

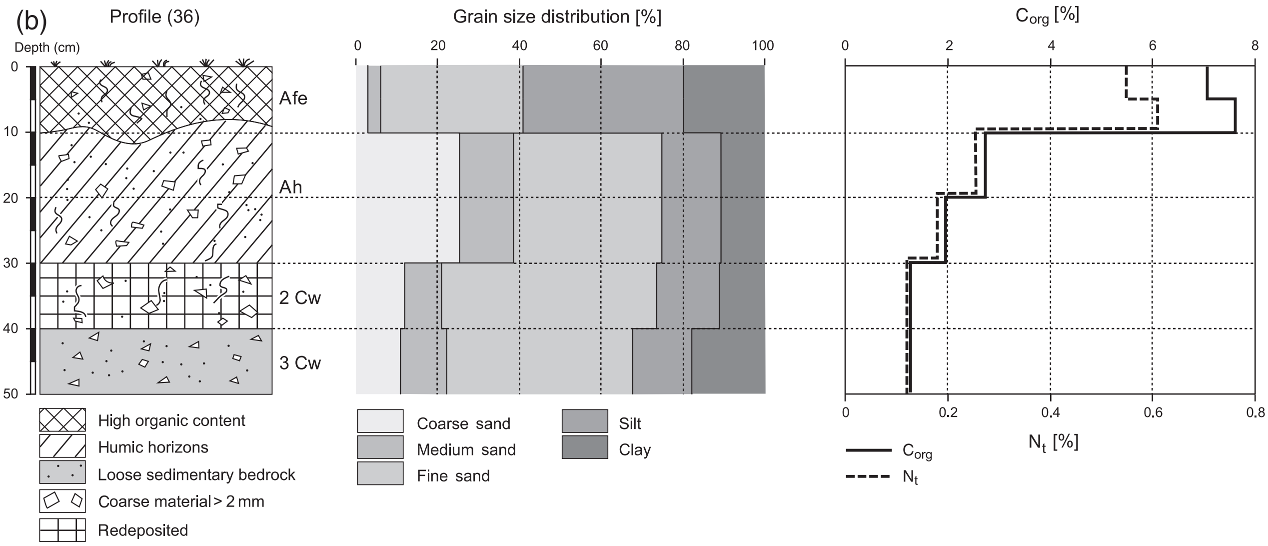
Pedogenetic samples

Horizon	Depth [cm]	Munsell Color moist	Particles > 2 mm [%]	$CaCO_3$ [%]	pH [$CaCl_2$]	EC [µS cm^{-1}]	C:N ratio
nHcw	0–30	10YR3/2	2.1	0.6	6.8	388	14.1
2BgCr	30–49	10YR4/4	8.8	8.8	7.1	145	11.1
2C	49–80+	7.5YR5/4	8.1	0.4	7.0	54	8.0

Schematic samples

Depth [cm]	SM [vol. %]	Bulk density [g cm^{-3}]	NH_4^+ [mg kg^{-1}]	NO_3^- [mg kg^{-1}]
0–5	4.4	0.48	7.49	0.23
5–10	11.1	0.40	8.31	0.22
10–20	11.6	0.45	6.21	0.21

Fig. 2 Comparison of sites 37 and 36 in discontinuous permafrost.



Site 36: Colluvic Regosol; 4,903 m asl; 32.18°N, 91.72°E; MAT –4.2°C; MAP 473 mm/a; middle slope; *Kobresia parva, Kobresia humilis, Stipa regeliana*

Pedogenetic samples

Horizon	Depth [cm]	Munsell Color moist	Particles > 2 mm [%]	$CaCO_3$ [%]	pH [$CaCl_2$]	EC [µS cm^{-1}]	C:N ratio
Afe	0–12	10YR2/2	9.2	0.4	6.9	350	12.7
Ah	12–24	5YR3/2	38.3	0.3	7.0	168	10,9
2Cw	24–41	5YR3/2	15.2	0.2	7.3	89	10,7
3Cw	41–50+	7.5YR5/4	8.5	0.4	7.0	54	8.0

Schematic samples

Depth [cm]	SM [vol. %]	Bulk density [g cm^{-3}]	NH_4^+ [mg kg^{-1}]	NO_3^- [mg kg^{-1}]
0–5	2.3	0.71	7.08	0.00
5–10	5.5	0.83	4.18	0.03
10–20	5.5	1.19	2.27	0.00

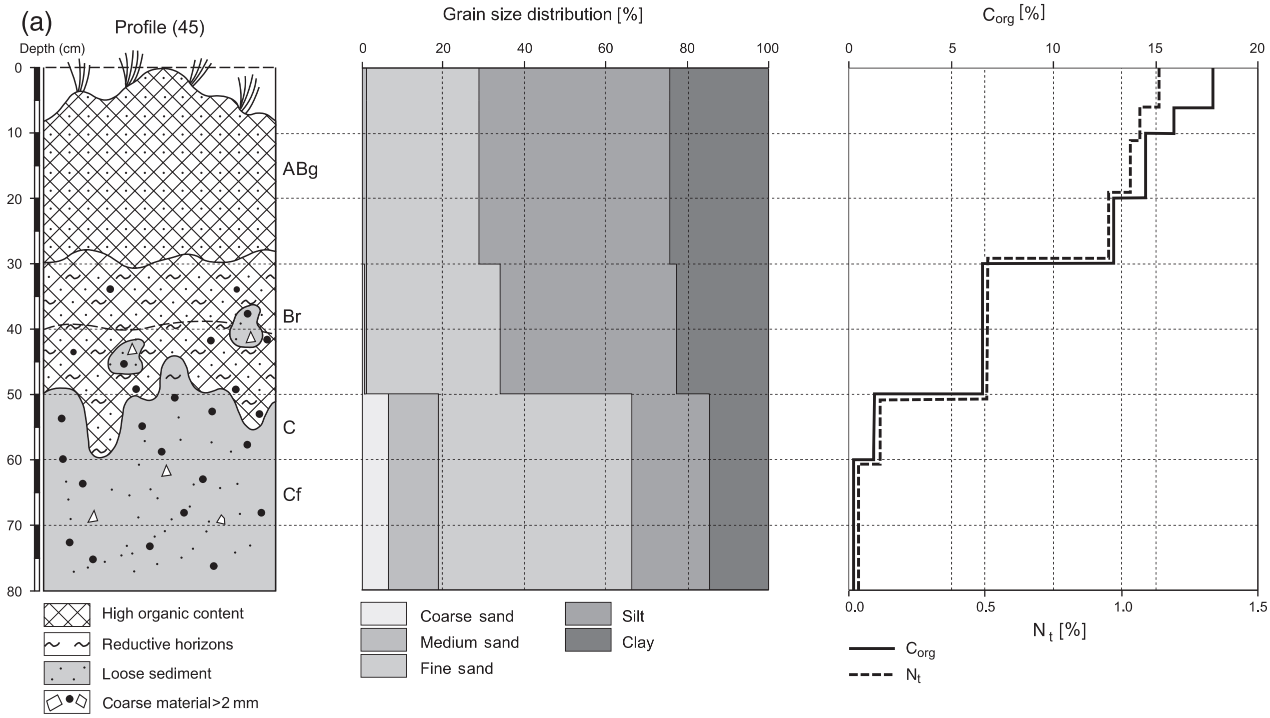
Fig. 2 (*Continued*)

nated by *K. tibetica* and *Carex* spp. community developing hummocks alternating with hollows (lower usually water-filled sectors). The distribution of the hummocks is inhomogeneous with an average diameter of 1.5 m and height of 40 cm. Permafrost could be detected at this site in 190 cm depth. No permafrost is evident in a depth of 240 cm at site 36.

Sites 45 and 31 (Fig. 3) show an example of the continuous permafrost area between Kunlun Shan and Tanggula Shan. Profile 45 (directly south of Tanggula Shan) is influenced by permafrost at a depth of 145 cm, whereas site 31 (close to Kunlun Shan) is exhibiting severe permafrost degradation features. This is typical for degraded permafrost areas with almost no C or N content due to recent aeolian sedimentation processes acting as a diluter ($C_{org} < 0.9\%$; $N_t < 0.06\%$). The microrelief at profile 45 is comparable to site 37, although SM is much higher at site 45 due to its relief position in a depression compared with site 37 situated on a mountain pass. Additionally, there is abundant perennial water supply by melting water of nearby snow fields in the mountain range. Strong redoximorphic features can be related to the high groundwater table due to present permafrost acting as an aquiclude. After heavier and longer rainfalls, the water table is reaching the ground level with only the vegetated bumps being outside the water.

Amount and distribution of C and N stocks

On a large scale, C and N stocks decrease from southeastern to northwestern regions corresponding to climate conditions and the influence of the southern tropical or eastern subtropical monsoon, respectively.



Site 45: Umbric Gleysol above Calcic Gelic Cryosol; 5,105 m asl; 32.58°N, 91.86°E; MAT - 5.8°C; MAP 488 mm/a; river floodplain; Kobresia schoenoides, Kobresia humilis, Poa annua

Pedogenetic samples

Horizon	Depth [cm]	Munsell Color moist	Particles > 2 mm [%]	$CaCO_3$ [%]	pH [$CaCl_2$]	EC [µS cm^{-1}]	C:N ratio
ABg	0-25	10YR3/1	1.2	0.8	6.7	444	14.1
Br	25-48	10YR3/1	0.8	0.5	6.7	223	11.1
C	48-68	10YR7/5	0.4	8.2	6.9	108	8.0
Cf	68-150+	10YR7/5	0.3	8.2	7.0	110	7.3

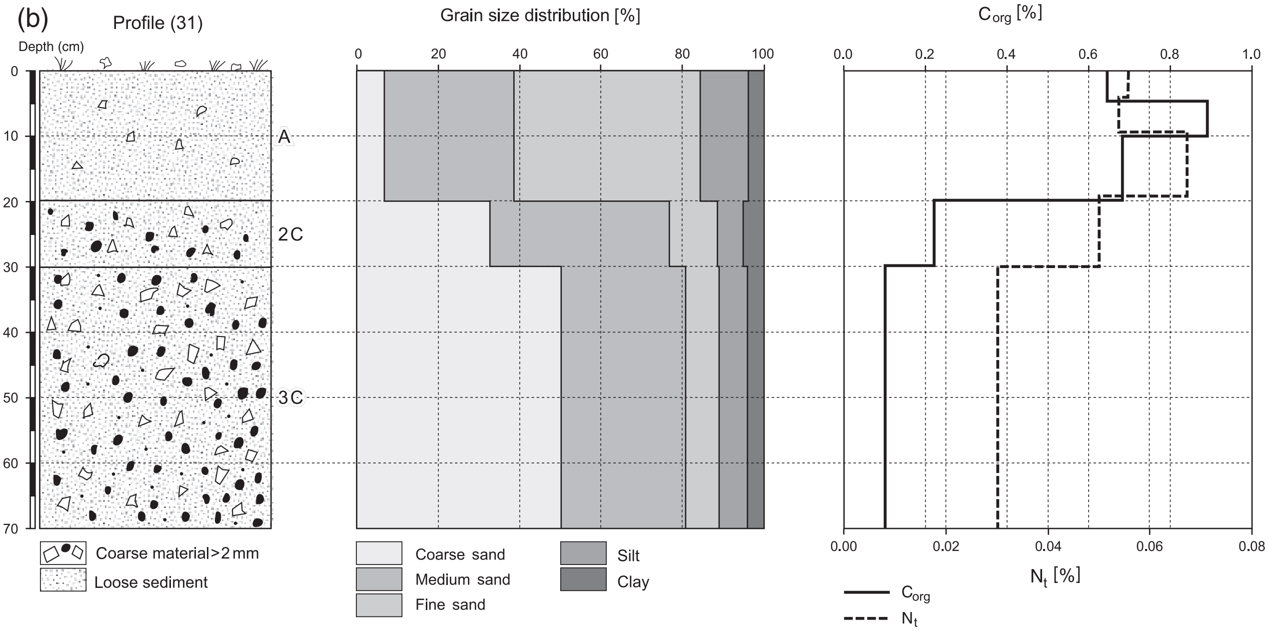
Schematic samples

Depth [cm]	SM [vol. %]	Bulk density [g cm^{-3}]	NH_4^+ [mg kg^{-1}]	NO_3^- [mg kg^{-1}]
0-5	55.35	0.44	18.05	0.51
5-10	54.91	0.39	13.37	0.89
10-20	55.91	0.45	11.41	0.54

Fig. 3 Comparison of site 45 (continuous permafrost) and site 31 (degraded). The latter as an example of aeolian sediment input due to permafrost degradation.

Because no longitudinal trend can be observed, it is assumed that latitudinal climate effects are stronger. Related to vegetation patterns, stocks of alpine meadows are larger than of alpine steppes (Fig. 4).

Highly fluctuating C and N contents of topsoils can be observed on small spatial scales, mainly controlled by relief position and in particular by related permafrost distribution in discontinuous permafrost areas (Fig. 2). The mineralized fraction of N at the investigated sites can be found almost exclusively as ammonia (NH_4^+), with the highest contents occurring at water saturated sites underlain by permafrost (Fig. 5). Highest C and N contents occur in permafrost and groundwater influenced soils, whereas the lowest amounts appear in initially formed soils with little soil genesis (Fig. 6). There is a clear trend to higher C and N stocks with an advanced degree of maturity of soil development observable, with increasing soil acidity, decreasing carbonate content (Fig. 5) and grain size distribution showing more fine-rich textures (Figs 2 and 3).



Site 31: Calcaric Regosol; 4,222 m asl; 35.74°N, 94.25°E; MAT –3.1°C; MAP 218 mm/a; plain valley bottom; Stipa purpurea, Kengylia thoroldiana, Carex spp.

Pedogenetic samples

Horizon	Depth [cm]	Munsell Color moist	Particles > 2 mm [%]	$CaCO_3$ [%]	pH [$CaCl_2$]	EC [μS cm^{-1}]	C:N ratio
A	0–17	10YR4/3	7.3	4.3	7.6	134	8.2
2C	17–30	10YR5/2	38.2	3.5	7.6	136	4.4
3C	30–70+	10YR5/2	45.2	4.8	7.6	126	3.3

Schematic samples

Depth [cm]	SM [vol. %]	Bulk density [g cm^{-3}]	NH_4^+ [mg kg^{-1}]	NO_3^- [mg kg^{-1}]
0–5	1.8	1.17	2.75	0.23
5–10	2.6	1.47	2.02	0.00
10–20	3.2	1.39	1.69	0.00

Fig. 3 (*Continued*).

C and N dynamics

Analyses of schematic soil samples show high significant correlations for SM and C contents as well as for SM and N contents (Table 2). Furthermore, significant, but relatively weakened relationships are evident for MAP, whereas no high significant correlations ($P<0.01$) were found concerning MAT and MAST. The only exception marks the significant temperature dependency of NO_3^- stocks shown by the correlation coefficient after *Spearman*. For all three main fractions of soil texture (sand, silt, and clay) also high significant relationships ($P<0.01$) with C and N contents are evident, whereas only the sand fraction is negatively correlated. Both pH and carbonate content ($CaCO_3$) have negative relationships to the dependent variables.

Variables used as predictors for pedogenesis show strong relationships within the independent parameter set. Most importantly, this is true for MAP and SM ($R^2=0.42$, $P<0.001$) as well as for pH and $CaCO_3$ ($R^2=0.50$, $P<0.001$). But also other parameters correlate, for example soil texture and soil moisture. Interestingly, SM and MAST show a comparably weak negative correlation (Table 2).

The GLM suggests SM as the most important parameter explaining 64% of C_{org} variation. Slightly lower values can be identified for N_t (Fig. 7). Both C_{org} and N_t predictions can be significantly improved by adding

$CaCO_3$ and sand contents to the model, explaining 65% and 64% of the variation, respectively (Table 3, Fig. 7). MAT as well as MAST has no influence on the model. Looking at the control parameters, SM explains 64%, MAP 20%, pH 38%, $CaCO_3$ 23%, and sand 29% for C_{org}. Concerning N_t, SM accounts for 60%, MAP 27%, pH 24%, $CaCO_3$ 26% and sand for 35% of the variation. The best-fit model of the GLM regression can be expressed as follows:

$$C_{org}(\%) = 0.398 + 0.009\text{SM} - 0.004\text{Sand} - 0.018\text{CaCO}_3 \quad (1)$$

$$\text{Nt}(\%) = 4.929 + 0.146\text{SM} - 0.248\text{CaCO}_3 - 0.040\text{Sand} \quad (2)$$

$$\text{NH}_4^+(\text{mg kg}^{-1}) = 4.321 + 0.135\text{SM} - 0.201\text{CaCO}_3 \quad (3)$$

Discussion

Impact of pedogenesis and spatial heterogeneity of C_{org}, N_t, and N_{min}

The landscape along the investigated transect is a patchwork of geochemically very diverse microecosystems that show variations in organic matter, nutrient stocks, plant communities and productivity. These differences are closely related to topographic position and permafrost distribution, particularly in areas affected by discontinuous permafrost (Fig. 2). The main controlling mechanism of this heterogeneity on the Tibetan Plateau is related to soil hydrological regimes, reflecting different soil drainage classes.

The stage of soil development is an important covariable to explain nutrient stocks in grassland ecosystems on the Tibetan Plateau (cf. Fig. 6). The lower amount of C and N in soils not influenced by permafrost, can be explained by shorter duration of pedogenesis, predominantly linked to different moisture regimes. Particularly at sites with initial soil formation, frequently affected by aeolian sedimentation, extremely low contents of C and N combined with a high spatial variability were observed. The airborne layers are composed of sandy and coarse-silty, mostly proximal generated material, often linked to direct (e.g. overgrazing, construction) (Zhang *et al*., 2006) and indirect (climate change) human impact. These processes may be inferred from the status of pH and $CaCO_3$ contents: initially formed soils have highest pH values and carbonate contents with an opposite trend in more mature stages of pedogenesis (Fig. 5).

Grain size distribution has a large influence on C and N stocks. Many studies found strong evidence for relationships between different soil textures and C_{org} (e.g. Parton *et al*., 1994; Schimel *et al*., 1994) often describing positive correlations between clay and C_{org} or N_t. The relationships between texture and dependent variables of our data show that sand and silt have the strongest impact, whereas clay is correlated to a much lower extent (Table 2). Thus, the ecosystem is dominated by sandy and silty grain size compositions. Sand and silt have an extremely high negative relationship ($R = -0.947$**). Consequently, processes controlling the formation of these particular grain size distributions have to be different and thus, recent aeolian sedimentation contributes mainly fine sand rather than silty material to the surface layers. Contrarily, mature soils, which are silt-dominated, show clear positive correlations between the stage of pedogenesis and C stocks, i.e. these soils have higher N and C contents. Highly fluctuating C and N contents of topsoils can therefore be found on a small spatial scale.

NH_4^+ is an essential parameter when N mineralization and microbial activity is studied near saturation (Rodrigo *et al*., 1997) that is the case at many permafrost influenced sites in our research area. Nitrate-N contents are mostly very low (e.g. Iwatsubo *et al*., 1989). Aerobic nitrification is restricted at water contents near saturation and denitrification increases as soil water content increases. Ammonification works well even near saturation (Chapin *et al*., 2002). The high microbial demands for these nutrients in comparable ecosystems may limit plant N availability in arctic and obviously in permafrost influenced soils (Nadelhoffer *et al*., 1991). Furthermore, nitrate-N can be leached or denitrified especially from wet soils more easily than ammonium-N (Schlesinger, 1997). Although nitrate contents at our sites are low, the dataset shows a significant relationship of nitrate-N with temperature (Table 2), which can be explained by the strong temperature dependency of nitrification processes (Chapin *et al*., 2002; Robinson, 2002). Overall, NH_4^+-N dominated N availability was highest on wet permafrost-influenced sites supporting the assumption that specific organic matter and moisture characteristics, not microclimatic factors, are responsible for the high N availability (Nadelhoffer *et al*., 1991).

Main independent variables and their interactions

Except SM, $CaCO_3$, and sand no other variables were included in the GLM as they show no significant contribution to enhance the explanatory power of the model, despite high correlations of these parameters with the dependent variables (Table 3).

Nevertheless, it is comprehensible why MAP and pH were not included into the model. Generally, one would

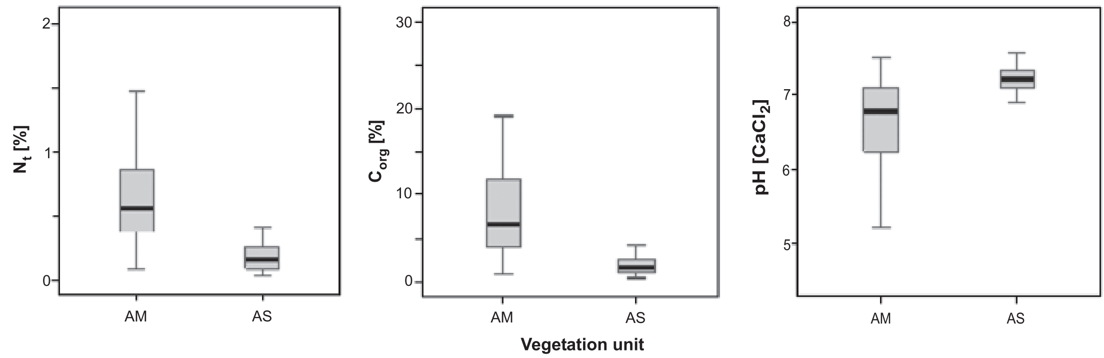


Fig. 4 Distribution for N_t, C_{org}, and soil acidity (pH) for main vegetation units: alpine meadow (AM) and alpine steppe (AS). Higher amounts of N_t and C_{org} and more acid conditions are noticeable in alpine meadow soils indicating a relationship between immature soil development and AS vegetation. The boxplots show median, 25% and 75% quartiles with the error bar indicating 5–95% range of the observation.

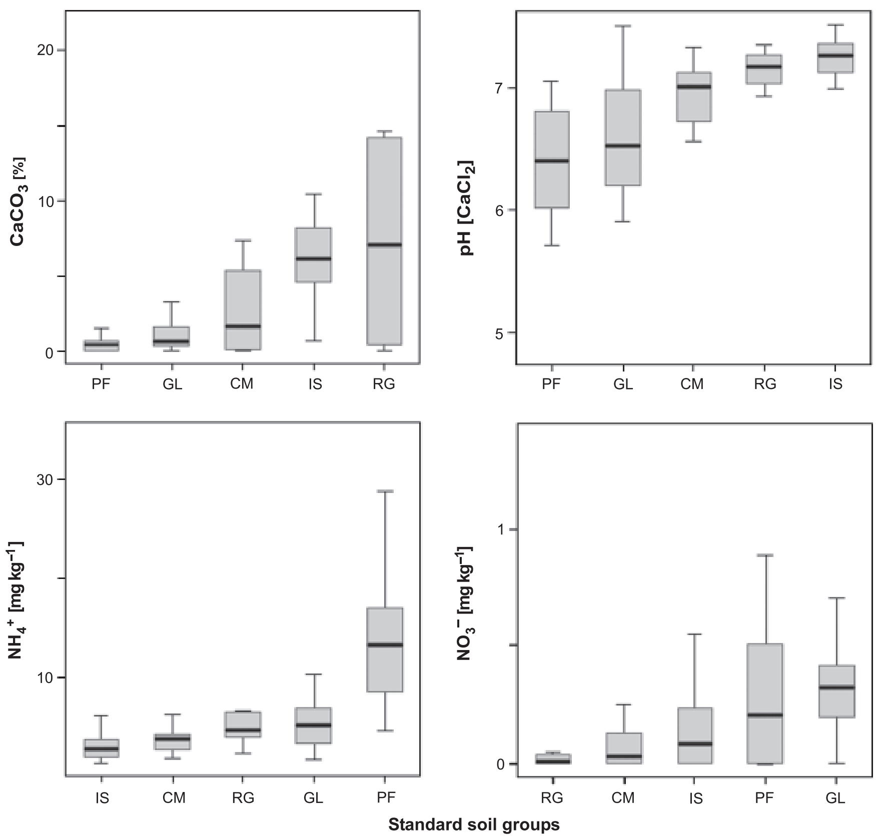


Fig. 5 $CaCO_3$, pH, NH_4^+, and NO_3^- related to standard soil groups. $CaCO_3$ and pH show an overall trend to higher soil acidity and respectively lower $CaCO_3$ content with increasing maturity of soil development. Order of soil groups according to increasing contents (abbreviations for standard soil groups see Fig. 6). The boxplots show median, 25% and 75% quartiles with the error bar indicating 5–95% range of the observation.

expect a strong relationship between SM and MAP. The relatively moderate correlation coefficient ($R^2 = 0.45^{**}$) shows, however, that other important environmental controls must be involved. In the study area, permafrost is the second, even more effective mechanism, determining SM content of soils emphasizing the role of permafrost for the ecosystem. Contrarily, MAT and MAST are highly correlated ($R^2 = 0.91^{**}$), where MAST is modified only weakly by SM ($R^2 = -0.29^{**}$). This means a more or less direct tracing of air into soil temperatures and explains the major difference of temperature and moisture regime features in high-altitude

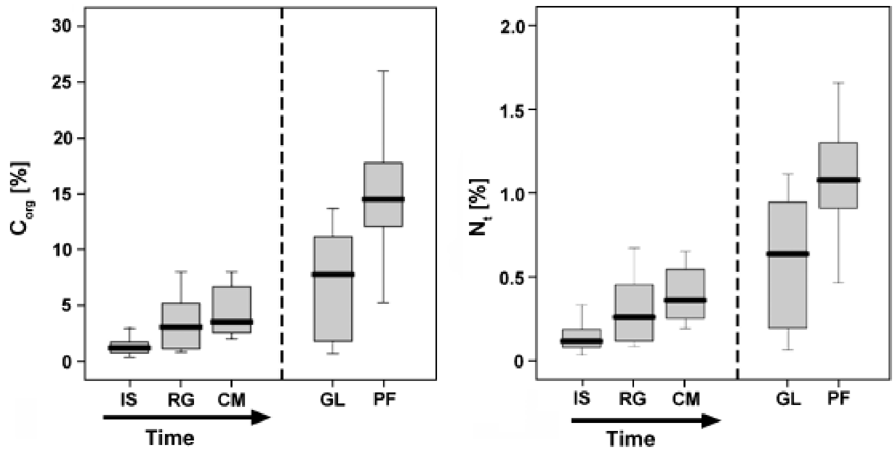


Fig. 6 C_{org} and N_t stocks related to the stage of pedogenesis. IS, initially formed soils; RG, Regosols; CM, Cambisols; GL, groundwater influenced; PF, permafrost influenced. The boxplots show median, 25% and 75% quartiles with the error bar indicating 5–95% range of the observation.

grassland ecosystems as well as why SM is such a powerful predictor for C and N stocks compared with temperature. $CaCO_3$ proves to be a more stable predictor compared with pH and was therefore confirmed by ANOVA as a significant contributor to an improved model quality. As the two parameters are soil chemically closely linked, including one is sufficient for an appropriate prediction. Soil acidity as a selective single measurement in the laboratory is in contrast very labile and dependent on many general conditions, such as actual temperature and moisture contents in the field.

For estimating the average moisture regime, deeper layers prove to give a better estimation. The highest R^2 for SM occurs in the deeper increments between 5 and 20 cm (Fig. 7). Because of isolation effects of covering material, the average moisture content in lower layers is more stable than closer to the surface. The uppermost part is more susceptible for strong radiation, diurnal temperature differences and accentuated precipitation events characterizing the special climate conditions on the Tibetan Plateau. Therefore, the average of all depth increments is the most appropriate predictor for moisture regimes for calculating the GLM. This is mainly the case because the dataset consists of single measurements instead of continuous monitoring which makes it likely to pick extreme events for the measurements. Moreover, it has to be mentioned that 2006 was a comparably dry year which implies a general underestimation of SM content especially at wet sites leading to an overall undervaluation of the impact of SM on the model. Dry sites do not show as high variation in dry years as wet sites which are generally groundwater level dependent. Topsoils are drying out rather quickly due to commonly found coarse grain size compositions, especially at sites with fresh airborne sediment. At sites, where water is retained for example by permafrost, moisture supply is proportionally linked to the groundwater level which is in turn related to the amount of precipitation. Consequently, for the variable sand the opposite is true indicating the top layers as the strongest predictors. This reflects clearly the process of aeolian sedimentation being mainly responsible for the sand input.

Ecosystem ecology has usually focused on temperature and modelled soils mostly as an ecosystem feature whose attributes vary strongly by thermodynamic principles (Craine *et al*., 1999). C and N stocks are assumed to decrease with increasing temperature due to enhanced decomposition processes because temperature sensitivity of decomposition is thought to be greater than of net primary productivity (Shaver *et al*., 1992; Kirschbaum, 1995). By performing a spatially small scale study at Haibei Alpine Meadow Research Station located at the northeastern margin of the Tibetan Plateau, Kato *et al*. (2006) found no significant relation of seasonal averages of CO_2 exchange to moisture conditions. Therefore, warming climate conditions have positive effects on plant growth in alpine meadows or tundra and wet meadow ecosystems (cf. Kato *et al*., 2006). The results of our transect study suggest, however, that particularly nutrient supply is the crucial point limiting plant growth even when having higher temperatures. A major result of our transect study is the main control of nutrient supply by moisture conditions. Especially at sites where permafrost has been degraded or fresh airborne material was deposited, the proportion of plant available N dropped rapidly. Therefore, rising temperatures have even an indirect negative effect by accelerating permafrost decay, thus lowering SM and therewith plant available nutrient contents. The

Table 2 Correlation matrix for the most important site variables

	Altitude (m asl)	MAT (°C)	MAST (°C)	MAP (mm a^{-1})	SM (%)	pH (CaCl2)	$CaCO_3$ (%)	N_t (%)	C_{org} (%)	NH_4^+ (mg kg^{-1})	NO_3^- (mg kg^{-1})	Sand (%)	Silt (%)	Clay (%)
Altitude (m asl)		−0.75**	−0.72**	0.10	0.21*	−0.26**	−0.03	0.15	0.23**	0.15	−0.24*	0.30	−0.34**	−0.08
MAT (°C)	−0.74**		0.91**	0.04	−0.29**	0.11	−0.17*	−0.14	−0.17*	−0.15	0.14	−0.13	0.12	0.12
MAST (°C)	−0.72**	0.89**		0.09	−0.29**	0.05	−0.14	−0.18*	−0.20*	−0.17	0.13	−0.07	0.08	0.04
MAP (mm a^{-1})	0.08	−0.04	0.01		0.42**	−0.56**	−0.51**	0.49**	0.43**	0.29**	−0.13	−0.38**	0.39**	0.21*
SM (%)	0.12	−0.27**	−0.12*	0.43**		−0.49**	−0.33**	0.75**	0.73**	0.60**	0.05	−0.48**	0.55**	0.15
pH ($CaCl_2$)	−0.21*	0.15	0.06	−0.61**	−0.46**		0.50**	−0.53**	−0.53**	−0.43**	0.17	0.26*	−0.28**	−0.09
$CaCO_3$ (%)	−0.05	−0.07	0.01	−0.56**	−0.35**	0.64**		−0.50**	−0.47**	−0.37**	−0.05	0.15	−0.11	−0.17
N_t (%)	−0.01	−0.02	−0.03	0.54**	0.60**	−0.61**	−0.61**		0.95**	0.72**	−0.00	−0.59**	0.60**	0.33**
C_{org} (%)	0.05	−0.04	−0.05	0.53**	0.59**	−0.63**	−0.61**	0.99**		0.82**	−0.02	−0.52**	0.53**	0.31**
NH_4^+ (mg kg^{-1})	0.08	−0.15	−0.12	0.38**	0.55**	−0.53**	−0.47**	0.84**	0.85**		0.01	−0.33**	0.35**	0.15
NO_3^- (mg kg^{-1})	−0.25**	0.27**	0.34**	0.02	0.03	0.09	−0.11	0.24*	0.23*	0.23*		−0.19	0.19	0.11
Sand (%)	0.35**	−0.22*	−0.15	−0.17	−0.47**	0.25*	0.27**	−0.66**	−0.63**	−0.45**	−0.15		−0.95**	−0.71**
Silt (%)	−0.39**	0.16	0.12	0.21	0.56**	−0.28**	−0.24*	0.65**	0.61**	0.48**	0.12	−0.91**		0.45**
Clay (%)	−0.10	0.16	0.09	0.12	0.23*	−0.14	−0.24*	0.47**	0.46**	0.27**	0.13	−0.76**	0.45**	

Product–moment correlation coefficients (Pearson) are shown in the upper triangle; rank correlation coefficients (Spearman) in the lower part. The level of significance is marked.
**$P<0.01$; *$P<0.05$; others $P>0.05$).
MAP, mean annual precipitation; MAT, mean annual temperature; MAST, mean annual soil temperature; SM, soil moisture.

resulting drainage increases soil aeration and soil respiration rates by improving the oxygen supply to microorganisms. Similar results for soil respiration are evident for northern peatlands showing close linkages to the water table (Moore & Knowles, 1989). Furthermore, parameters affecting photosynthesis and whole-plant C gain (e.g. SM and nutrient availability), are correlated strongly to C_{org} contents in soils (Craine *et al*., 1999). Therefore, understanding the N cycle is crucial to get an appropriate understanding of the complete ecosystem's feedback mechanisms.

Recent research has also shown that changes in moisture and drainage conditions will have serious impact on N and C cycling of soils in particular ecosystems (Johnson *et al*., 1996; Rodrigo *et al*., 1997; Hook & Burke, 2000; Janssens *et al*., 2001; Robinson, 2002; Kato *et al*., 2004; Shaver *et al*., 2006). In our research area the impact of moisture has to be seen even more severe due to permafrost control of soil hydrological conditions in vast areas of the Tibetan Plateau. Higher SM together with improved C_{org} quality may lead to enhanced plant productivity and substrate availability in ecosystems and consequently to higher C and N contents in soils (Schimel *et al*., 1994; Reichstein *et al*., 2003; Reichstein & Beer, 2008) overshadowing the effect of temperature as shown also in a study about European forest ecosystems (Janssens *et al*., 2001). Therefore, decomposition may be controlled by substrate quality and quantity as well as moisture rather than by low temperatures. Giardina & Ryan (2000) postulate relatively constant decomposition rates of organic C contained in forest mineral soils across a global-scale gradient in MAT. Their data show no direct influence of temperature limitations on microbial activity and no stimulation of decomposition by increased temperature alone. However, it is questionable if large scale studies across various climates (cf. Giardina & Ryan, 2000) are feasible due to potential (co-) variations of parameters by large magnitude. Therefore, it was proposed to interpret the data under the aspect that other factors rather override the temperature effect, than negating the fundamental relationship of temperature to C and N cycling (Reichstein & Beer, 2008). The difficulty of multicollinearity within the independent parameter set presented was mentioned above. Nevertheless, our study was performed in a clearly defined ecosystem compared with global datasets. For the GLM, parameters were selected appropriately and the correlation between MAT and SM was comparably weak. Yang *et al*. (2008) found similar patterns and controls of C_{org} in Tibetan grasslands. C_{org} density increased with SM, clay, and silt content, but only on a low level with MAT. Although, it seems possible that taking annual average temperature data are rather difficult as the climate shows strong diurnal

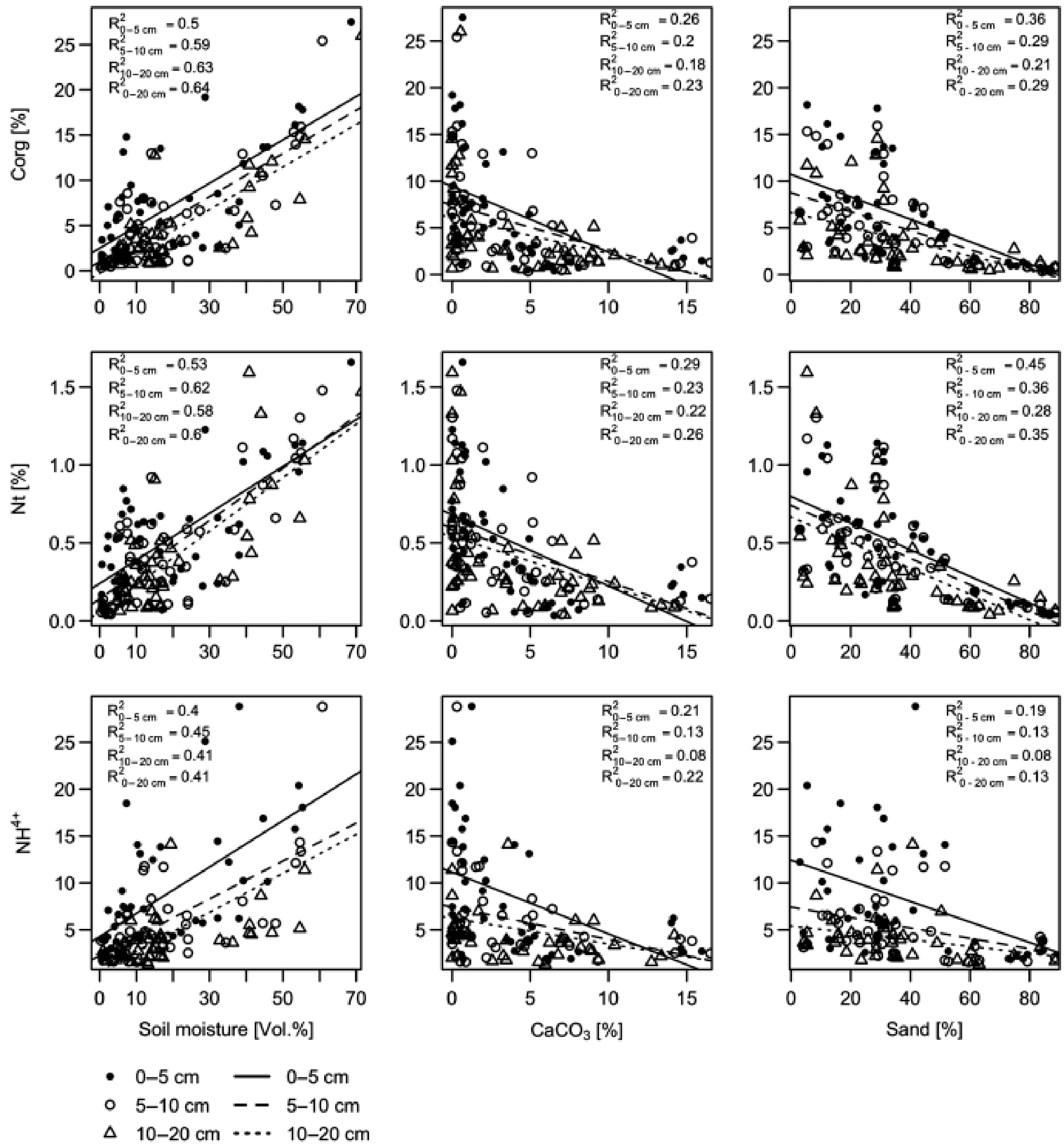


Fig. 7 Relationships between dependent and independent variables with the highest impact on the regression model. The three different depth increments are shown on the graphs.

patterns. Moreover, studies from northern Alaska showed insensitivity to temperature between 3° and 9 °C but a doubled effect in arrange between 9 and 15 °C (Nadelhoffer *et al*., 1991). Thus, temperature insensitivity of investigated sites on the Tibetan Plateau can be partly caused by the low range of MAT between −5.8 and 2.6 °C and range of average July temperatures from 4.9° to 13.8 °C. Recent studies in plant physiology also highlight the importance of plant adaptation to the low temperature resulting in a moderate modification of leaf chemical traits and photosynthesis by temperature and precipitation (He *et al*., 2006).

Our study shows that other factors than temperature are more important between sites at regional and continental scales (cf. Janssens *et al*., 2001). Summarizing, soil temperature is more likely to account for seasonal and diurnal variations (Kato *et al*., 2006), not so much when comparing intersite relationships as in the presented study. Temperature dependency may rather be relevant for ecosystems when SM or other factors are not limiting or altering the relationship between temperature and soil processes (Craine *et al*., 1999; Reichstein *et al*., 2003).

Table 3 Summary of the general linear model (GLM) and ANOVA indicating the integrative effects of soil moisture (SM), $CaCO_3$, and texture for the depth of 0–20 cm

Source	Estimate	SE	*t*-value	Significance Pr (> |*t*|)	MS	*F*-value	Significance Pr (>*F*)
Dependent variable: C_{org} *(0–20 cm); multiple* $R^2 = 0.65$*; residual SE = 0.198 on 35 df*							
SM	0.009	0.003	3.546	0.00113	374.75	52.423	0.000000019
Sand	−0.004	0.002	−2.497	0.01737	23.76	3.324	0.07685
$CaCO_3$	−0.018	0.008	−2.425	0.02059	49.63	6.943	0.01245
Dependent variable: N_t *(0–20 cm); multiple* $R^2 = 0.64$*; residual SE = 2.638 on 36 df*							
SM	0.146	0.033	4.447	0.00008	1.93	49.360	0.000000035
$CaCO_3$	−0.248	0.091	−2.728	0.00979	0.34	8.673	0.005708
Sand	−0.040	0.022	−1.847	0.07292	0.25	6.514	0.015227
Dependent variable: NH_4^+ *(0–20 cm); multiple* $R^2 = 0.48$*; residual SE = 2.731 on 35 df*							
SM	0.135	0.032	4.209	0.00017	205.19	27.515	0.0000076
$CaCO_3$	−0.201	0.097	−2.083	0.04461	32.36	4.340	0.04461

SE, standard errors; MS, mean square; df, degree of freedom.

Permafrost degradation and its impact on ecosystem functioning

Under present climate conditions, two processes refer to permafrost degradation and corresponding low C and N contents in soils of the Tibetan plateau: (i) a higher mineralization rate under warmer and drier conditions, (ii) the deposition of aeolian sediments. Hence, under increasing temperatures and decreasing annual precipitation, sequestration of large amounts of C can be expected in areas with permafrost (cf. Figs 3 and 6; Shaver *et al.*, 2006; Zimov *et al.*, 2006). In case of amplified permafrost degradation during warmer climate conditions in the future (Liu & Chen, 2000; Wang *et al.*, 2000), a strong increase in areas with recent aeolian sedimentation of blown out material can be expected. Additionally, the mineralization of bound organic matter can be assumed over the period of only some decades for the light fraction of organic C fractions (Hirota *et al.*, 2006; Wang *et al.*, 2008).

Semi-natural systems like alpine grasslands on the Tibetan Plateau are generally limited in available plant nutrients. Thus, the productivity of alpine grassland ecosystems is determined by the available nitrogen pool, the amount of nitrogen input as well as by nitrogen fixation (Körner, 1999), modified by water availability to plants over the year (Gründling & Scholten, 2006). Hence, plants' nutrients availability is closely linked to the degradation processes. This is a major issue to address in terms of climate change when discussing about how higher vegetation could potentially sequestrate C lost by enhanced decomposition (Hungate *et al.*, 2003) and how the system will behave under elevated CO_2 conditions (Morgan, 2002). Our results indicate a rapid decrease of plant available N leading to the assumption, that the general nutrient situation may limit plant growth even more severely than the changing direct environmental parameters in the first place (cf. Fig. 5).

Conclusions

Three basic features characterize soil genesis on the Tibetan Plateau: young stage of development, frequent polygenetic formation, and strong degradation phenomena triggered by diverse erosive and cryogenic processes. The soil development stage is an important predictor for C and N contents in these soils. This is emphasized by significant contributions of $CaCO_3$ and sand to the GLM, which are used to describe pedogenesis.

However, the results imply that SM is the major controlling parameter of C and N stocks in high altitude grassland ecosystems influenced by permafrost, explaining 65% of C_{org} and 64% of N_t variations, respectively. As MAP and SM show only a moderate correlation compared with the very high relationship between MAT and MAST, it can be concluded that SM is closely linked to permafrost. Consequently, C and N stocks and ecosystem functioning are predominantly affected by permafrost, aeolian sedimentation and the stage of soil development. Permafrost and aeolian sedimentation are also a function of relief position, parent material, human impact, and seasonal climatic fluctuations. Given a shift to drier and warmer climatic conditions, the Tibetan Plateau could change from a net C sink to a net source, implying that C loss by respiration is higher than C fixation connected to enhanced photosynthesis activity.

Including SM as a major factor will be crucial for developing large scale models evaluating C and N dynamics on the Tibetan Plateau. Nevertheless, we infer from our results, that SM tends to explain intersite variations on landscape scale, whereas ST rather accounts for seasonal or diurnal fluctuations in these particular ecosystems.

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