Abstract

Vertical patterns of soil organic carbon (SOC), total nitrogen (TN) and C:N stoichiometry are crucial for understanding biogeochemical cycles in high-altitude ecosystems, but remain poorly understood. In this study, we investigated vertical distributions of SOC and TN as well as their stoichiometric relationships in alpine grasslands on the Tibetan Plateau using data of 405 profiles surveyed from 135 sites across the plateau during 2001–2004. Our results showed that, both SOC and TN in alpine grasslands decreased with soil depth, while C:N ratio did not exhibit significant change along soil profile. The associations of SOC and TN content (amount per area) with environmental factors diminished with soil depth. Soil carbon content was nearly proportional to nitrogen content with a slope of 1.04 across various various grassland types. The slope did not differ significantly between alpine steppe and alpine meadow or between alpine grasslands and global ecosystems, and also did not reveal significant differences among various soil depth intervals, suggesting that soil carbon-nitrogen coupling is irrespective of ecosystem types and soil depths.

1 Introduction

The soil organic carbon (SOC) stock in high-latitude ecosystems is an important component of global terrestrial carbon reservoir (Hobbie et al., 2000; Zimov et al., 2006; Ping et al., 2008; Schuur et al., 2008, 2009). Soils in high-altitude ecosystems, like those in high-latitude ecosystems, also play an important role in the global terrestrial carbon cycle because of their large carbon stock and potential sensitivity to climate warming (Davidson and Janssens, 2006; Yang et al., 2008; Post et al., 2009). SOC stock in high-latitude/altitude ecosystems may be determined by a number of unique factors, such as cold temperature, permafrost, and water-logging (Hobbie et al., 2000). However, these factors are mostly ignored by biogeochemical models used to examine the responses of these ecosystems to climate change (Hobbie et al., 2000). Therefore,
our understanding on patterns and controls of SOC stock in high-altitude ecosystems is critical for evaluating their roles in the global terrestrial carbon cycle and potential feedbacks to global environmental change (Yang et al., 2008; Baumann et al., 2009).

Vertical patterns of SOC can contribute as an input or as an independent validation for biogeochemical models and thus provide valuable information for examining the responses of terrestrial ecosystems to global change (Jobbágy and Jackson, 2000; Wang et al., 2004; Mi et al., 2008). However, a large number of biogeochemical models do not contain explicit algorithms of belowground ecosystem structure and function (Jackson et al., 2000). Moreover, previous studies primarily focused on the topsoil carbon stock, and carbon dynamics in deeper soil layers and driving factors behind vertical distributions of SOC remain poorly understood (Gill et al., 1999; Jobbágy and Jackson, 2000; Meersmans et al., 2009). Thus, improved knowledge of distributions and determinants of SOC across different soil depth is essential to determine whether carbon in deep soil layers will react to global change and accelerate the increase in atmospheric carbon dioxide (CO$_2$) concentration (Fontaine et al., 2007; Meersmans et al., 2009).

Globally, Jobbágy and Jackson (2000) described vertical distributions of SOC for different ecosystems and demonstrated that vegetation type determined vertical distributions of SOC through its root-shoot allocation and root distributions along soil profile. Compared with other ecosystems worldwide, high-altitude ecosystems own larger root: shoot ratios and shallower root distributions (Jackson et al., 1996; Yang et al., 2009a) and thus may have unique vertical distributions of SOC (Jobbágy and Jackson, 2000; Wang et al., 2004). However, little is known about vertical distributions of SOC in high-altitude ecosystems. Therefore, direct observations from high-altitude ecosystems are urgently needed to improve our understanding of biogeochemical cycles for cold regions and their potential feedbacks to global environmental change.

On the other hand, terrestrial carbon and nitrogen coupling has increasingly received attention due to progressive nitrogen limitation on future carbon sequestration in terrestrial ecosystems (Hungate et al., 2003; Luo et al., 2004; Reich et al., 2006). A number of studies have been conducted to document C:N stoichiometry and its large-scale pattern for terrestrial plants (e.g. McGroddy et al., 2004; He et al., 2006). However, little information is available for soil C:N stoichiometry across broad geographic gradients (Tian et al., 2009). A recent analysis by Cleveland and Liptzin (2007) synthesized soil C$_{186}$:N$_{13}$:P$_1$ in different ecosystems worldwide, and found insignificant variations in soil C:N:P ratio among various ecosystems, and also observed an isometric relationship between carbon and nitrogen in surface soil (i.e. the slope of the log–log relationship between carbon and nitrogen is not statistically different from 1.0). Even though, our understanding of soil C:N stoichiometric pattern is much less well developed in comparison with plant parts. Particularly, it is unknown how C–N stoichiometric relationship changes along soil profile (i.e. different depth intervals), whether the isometric pattern observed in surface soil layer occurs in deep soil layer, and whether the isometric C–N relationship observed in other ecosystems exists in high-altitude ecosystems.

The Tibetan Plateau is the highest and largest plateau on Earth, with a mean elevation of ~4000 m and an area of ~2.0×10$^6$ km$^2$ (Li and Zhou, 1998). The alpine grasslands (alpine steppe and meadow) comprise over 60% of its area, with mean annual temperature of ~0.6 °C and mean annual precipitation of 591.1 mm. The unique climate, vegetation and minimal human disturbance make the plateau an ideal region for exploring large-scale patterns of soil carbon, nitrogen and their stoichiometry in high-altitude ecosystems. Up to now, spatial patterns and temporal dynamics of SOC stock in the Tibetan alpine grasslands had been investigated by Zhang et al. (2007), Yang et al. (2008, 2009b), and Baumann et al. (2009), respectively. However, vertical patterns of SOC and total nitrogen (TN) stock in alpine grasslands as well as their stoichiometric associations along soil profile remain unclear.

In this study, we investigated vertical distributions of SOC and TN in the Tibetan alpine grasslands, using data of 405 soil profiles obtained from a regional soil survey conducted on the plateau during 2001–2004. We then examined changes in associations of SOC and TN with environmental factors along soil profile. We further explored stoichiometric relationships between SOC and TN in alpine grasslands at different soil
depth intervals. Specifically, this study aimed to test the following hypotheses: (1) high-altitude ecosystems may have unique vertical distributions of SOC and TN compared with other ecosystems, (2) the isometric soil C-N relationship observed in other ecosystems exists in high-altitude ecosystems, and (3) the isometric pattern between SOC and TN observed in surface soil layer exists in deep soil layer.

2 Materials and methods

2.1 Regional soil carbon and nitrogen survey

During 2001–2004, we sampled 405 soil profiles from 135 sites (i.e., three soil profiles at each site) on the Tibetan Plateau (Yang et al., 2008, 2009b). At each profile, soil samples were taken at depth intervals of 0–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm. Soil samples were collected using a standard container with 100 cm$^3$ in volume, and then oven-dried at 105°C for determining bulk density. Soil samples for carbon and nitrogen analysis were air-dried, sieved through a 2-mm mesh, handpicked to remove plant detritus, and then ground on a ball mill. Soil organic carbon (SOC) concentration was measured using the wet oxidation method (Nelson and Sommers, 1982). Total nitrogen (TN) concentration was determined by dry combustion using an elemental analyzer (2400 II CHNS/O Elemental Analyzer, Perkin-Elmer, USA), with a combustion temperature of 950°C and a reduction temperature of 640°C (He et al., 2006). Soil texture was analyzed by a particle size analyzer (Mastersizer 2000, Malvern, UK) after removal of organic matter and calcium carbonates. For details about field investigation and laboratory analysis, see Yang et al. (2008).

2.2 Vertical distributions of SOC and TN

Vertical distribution of SOC was described in the top 1 m at five 20-cm intervals for each profile (Jobbágy and Jackson, 2000). Specifically, we calculated SOC density (amount per volume) at different sampling depths (Eq. 1), and then established the relationship between SOC density and soil depth (Eq. 2), and further integrated the relationship to depth intervals of 0–20, 20–40, 40–60, 60–80, and 80–100 cm (Eq. 3). In this study, the relative SOC content (amount per area) for each depth interval was calculated to eliminate the effect of total SOC content on the vertical distribution, and thus could make comparisons among different vegetation types and with the global-scale analysis by Jobbágy and Jackson (2000). The vertical distribution was represented by the proportion of SOC content in the surface layer (0–20 cm) relative to that in 1 m. A lower proportion of the 0–20 cm layer indicated a deeper SOC distribution, and vice versa. Vertical distributions of TN were described for alpine grasslands in a similar way. In such analyses, profiles with less than five horizons were excluded because they had insufficient information to characterize vertical distributions of SOC and TN (e.g. Jobbágy and Jackson, 2000).

\[
\text{SOCD}_h = \frac{\text{BD}_h \times \text{SOC}_h \times (1 - C_h/100)}{1000} \tag{1}
\]

\[
\text{SOCD}(h) = a \times e^{b \times h} \tag{2}
\]

\[
\text{SOCC} = \int_{h_1}^{h_2} \text{SOCD}(h) d(h) \times 10 \tag{3}
\]

where $h$ is soil depth (cm), BD$_h$, SOC$_h$, and C$_h$ represent bulk density (g cm$^{-3}$), soil organic carbon (g kg$^{-1}$), and volume percentage of >2 mm fragments at $h$ (cm), respectively; $a$ and $b$ are coefficients; and SOCD is soil organic carbon density (g cm$^{-3}$), $h_1$ and $h_2$ are soil depths (cm), and SOCC is soil organic carbon content for each profile (kg m$^{-2}$).

2.3 Climate information and vegetation types

Dataset of mean annual temperature (MAT) and mean annual precipitation (MAP) used in this study were complied from the climatic database of the Tibetan Plateau during 2001–2004 (Piao et al., 2003). These data were spatially interpolated from the records...
of 43 meteorological stations located above 3000 m across the plateau.

In order to examine differences in vertical distributions of SOC, TN, and C:N stoichiometry among different vegetation types, we grouped all sampling sites into alpine steppe or meadow using a vegetation map at a scale of 1:1 000 000 (Chinese Academy of Sciences, 2001). The spatial distributions of alpine grasslands on the Tibetan Plateau are closely related to the corresponding precipitation gradient (Table 1). Alpine steppe occurs in arid regions, and is consisted of cold-xerophytic grasses such as Stipa purpurea and Carex moorcroftii, and is usually mixed with alpine forbs (e.g. Polygonum viviparum). In contrast, alpine meadow is distributed under relatively humid environments and dominated by perennial grasses such as Kobresia pygmaea, K. humilis, and K. tibetica (Zhang et al., 1988).

2.4 Statistical analysis

One-way ANOVA was conducted to evaluate whether vertical distributions of SOC and TN differed significantly between alpine steppe and meadow. Reduced major axis (RMA) regression was performed to examine stoichiometric relationships between soil carbon and nitrogen at different depth intervals (e.g. Cleveland and Liptzin, 2007). In addition, we compared the slope of soil C-N relationship between alpine steppe and meadow, and between alpine grasslands and global ecosystems. The slope and y-intercept of the stoichiometric function were determined using software package “Standardized Major Axis Tests and Routines” (Falster et al., 2003).

3 Results

Both SOC and TN in alpine grasslands decreased with soil depth (Figs. 1 and 2). The proportion of SOC in the top 20 cm averaged 55% for alpine meadow and 41% for alpine steppe ($P < 0.05$; Fig. 1d and e). Likewise, a higher proportion of TN in the upper layer was observed in alpine meadow than in alpine steppe ($46\%$ vs. $38\%; P < 0.05$).

The correlations of SOC and TN content with environmental factors were closest in the top 20 cm and decreased for deeper intervals (Fig. 4). Soil carbon and nitrogen in alpine grasslands exhibited an isometric relationship at different soil depth intervals (Fig. 5). The slope of the stoichiometric relationship across different grassland types was 1.04, with 95% confidence interval of 0.98–1.09 (Fig. 5f, Table 2). The comparison between alpine steppe and meadow did not show a significant difference ($P > 0.05$) (Table 2). Similarly, the slope did not differ significantly between alpine grasslands and global ecosystems ($P > 0.05$) (Fig. 5f).

4 Discussion

4.1 The unique vertical distributions of SOC, TN, and C:N ratio

To our knowledge, this study firstly reported vertical distributions of SOC and TN for the Tibetan alpine grasslands. Our results showed that, the proportion of SOC in the top 20 cm in alpine grasslands (49%) was larger than that in global ecosystems (42%) (Jobbágy and Jackson, 2000), indicating shallower distributions of SOC in the Tibetan alpine grasslands than in other vegetation types worldwide. Likewise, the proportion of TN in the top 20 cm in alpine grasslands (43%) was higher than that in global ecosystems (38%) (Jobbágy and Jackson, 2001). The shallower distributions of SOC and TN in alpine grasslands could be induced by their shallower root distributions (Jobbágy and Jackson, 2000; Wang et al., 2004). Specifically, a recent analysis by Yang et al. (2009a) reported that 90% of roots in alpine grasslands were concentrated in the top 30 cm compared with 65% in global ecosystems (Jackson et al., 1996).

Theoretically, vertical patterns of SOC and TN are determined by a dynamic balance between carbon inputs from plant production and outputs through microbial decompo-
siton (Gill et al., 1999). As a major source of carbon inputs in soil, vertical distributions of roots should play an important role in shaping vertical distributions of SOC (Jobbágy and Jackson, 2000). In addition, depth-dependent decomposition rates have been proposed as another potential mechanism for explaining vertical patterns of SOC because a higher proportion of total root biomass occurred in surface soil than that of SOC (Weaver et al., 1935; Gill et al., 1999). Similar to that reported in temperate grasslands in the United States of America (Gill et al., 1999), soil in the upper 20 cm in the Tibetan alpine grasslands contained 64% of total roots (Yang et al., 2009a) but only accounted 49% of SOC, suggesting that the decrease of decomposition rates with soil depth may also affect vertical distributions of SOC in alpine grasslands (Weaver et al., 1935; Gill et al., 1999; Gill and Burke, 2002). Anyway, to test the above-mentioned hypothesis, future studies are required to carefully examine changes in decomposition rates along soil profile in the Tibetan alpine grasslands.

In contrast to soil carbon and nitrogen, soil C:N ratio in alpine grasslands remained relatively stable at different soil depth intervals (Fig. 3). Likewise, a recent analysis by Cleveland and Liptzin (2007) observed that soil C:N ratio was relatively consistent across various ecosystem types although soil was characterized by high biological diversity, structural complexity and spatial heterogeneity. The well constrained C:N ratio along soil profile accorded well with stoichiometric principles that the formation of organic matter requires a certain amount of nitrogen and other nutrients in a relatively fixed ratio with carbon (Sterner and Elser, 2002). Interestingly, although insignificant, soil C:N ratio in alpine grasslands tended to decrease with soil depth (Fig. 2), possibly reflecting a greater degree of breakdown and older age of the humus stored in the deeper soil layer (Batjes, 1996; Callesen et al., 2007). As decomposition proceeds, easily decomposed material disappears and nitrogen is immobilized in microbial biomass and decay products, leaving behind more recalcitrant material with slower decomposition rates and lower C:N ratio (Post et al., 1985). The organic matter in subsoil layers is older and more humified than that in topsoil layers, and thus it is frequently observed a decreasing soil C:N ratio with soil depth (Callesen et al., 2007).

4.2 The diminishing relationships of SOC and TN with environmental factors along soil profiles

The correlations of SOC and TN content with environmental factors diminished with the increase in soil depth (Fig. 4). The decreasing associations between SOC content and climatic variables were consistent with those observed by Jobbágy and Jackson (2000). However, our results did not support that the associations between SOC content and soil texture increased with soil depth (Jobbágy and Jackson, 2000). In contrast, we found that the correlation of SOC content with soil texture was lowest in deeper intervals. This discrepancy may be associated with different soil depth involved in these two studies. In the analysis of Jobbágy and Jackson (2000), the associations between SOC content and clay content became closer for deeper intervals in the upper 3 m, but showed slight changes within the top 1 m.

The diminishing relationships between SOC content and environmental factors may result from the following several aspects. First, the increased proportion of slower cycling organic matter in deep soil layer may be responsible for such pattern (Jobbágy and Jackson, 2000). With the increase in soil depth, the proportion of labile carbon decreases while that of recalcitrant carbon increases (Fang et al., 2005). The labile and recalcitrant carbon may exhibit divergent dynamics along environmental gradients, and thus could result in the diminishing relationships between SOC content and environmental factors along soil profile. Second, soil buffering capacity may reduce the effects of environmental variables on SOC content in deep soil layers (personal communication with Prof. Pete Smith). Compared with surface soil, the effects of external environmental are becoming less important in deep soil due to soil buffering capacity. Temperature and moisture content in deep soils vary much less than those in surface soils (e.g. Luo et al., 2009). As a consequence, the relationships between SOC content and environmental factors tend to be weaker along soil profile. Since environmental factors have less influence at depth, SOC content in deep soil layer may be more strongly determined by carbon inputs from the surface layer. A recent analysis
by Fontaine et al. (2007) supported this deduction and demonstrated that stability of organic carbon in deep soil layers was largely controlled by fresh carbon supply from surface layer. Third, the broader range of SOC content in surface soil layer than that in deep soil layer (0–20 vs. 20–80 cm: 0.39–11.20 vs. 0.02–4.52 kg m$^{-2}$) may also lead to the diminishing relationships between SOC content and environmental factors.

4.3 Isometric carbon-nitrogen relationships at different soil depths

Soil carbon and nitrogen in alpine grasslands exhibited an isometric pattern (Fig. 5), consistent with that observed in a recent global-scale analysis by Cleveland and Liptzin (2007). Specifically, Cleveland and Liptzin (2007) examined the stoichiometric relationship between soil carbon and nitrogen across various ecosystems by synthesizing 186 observations from 48 published literatures, and found that the relationship between soil carbon and nitrogen was isometric with a slope not significantly different from 1.0. As a result, the comparison of C-N stoichiometric relationship between alpine grasslands and global ecosystems did not reveal significant differences (Fig. 5), suggesting the generality of the isometric relationship between soil carbon and nitrogen across various ecosystems.

The isometric relationship between soil carbon and nitrogen may stem from the isometric C-N stoichiometry occurs in plants since plants are the major source of soil carbon and nitrogen (Cleveland and Liptzin, 2007). Plant carbon and nitrogen has been observed to exhibit an isometric relationship in different organ-types. For instance, McGroddy et al. (2004) observed statistically strong log–log relationships between carbon and nitrogen in foliage, and scaling slopes between carbon and nitrogen in foliage did not differ from 1.0 across global forest ecosystems. Similarly, Niklas and Cobb (2005) demonstrated that carbon scaled isometrically with respect to nitrogen for leaves, aerial stems, reproductive organs, roots, and tubes of 17 actively growing *Eranthis hyemalis* plants differing in body size. In addition, He et al. (2006) reported that leaf C:N stoichiometry was surprisingly stable in three grassland distribution regions under different environmental conditions: Inner Mongolia, Tibetan Plateau, and Xinjiang in China.

Consequently, the close coupling between carbon and nitrogen in plant may lead to the isometric relationship between carbon and nitrogen in soil.

The isometric pattern between soil carbon and nitrogen indicates carbon is closely coupled with nitrogen in soil (Cleveland and Liptzin, 2007). In general, deep soils have older age and larger proportion of recalcitrant organic matter than surface soils (Fontaine et al., 2007). The isometric relationship between soil carbon and nitrogen at different soil depths implies that soil C-N coupling may be irrespective of soil age. This deduction is supported by results obtained from the successional gradient. For example, Vitousek (2004) reported that soil carbon and nitrogen exhibited similar temporal dynamics along the Hawaiian age gradient. The close C-N coupling in soil may reflect an intrinsic nature of ecosystem development, and should be considered when projecting carbon sequestration in terrestrial ecosystems under future global change scenarios (Schimel et al., 1997; Luo et al., 2006).

5 Concluding remarks

Vertical patterns of SOC, TN and their stoichiometric relationships in the Tibetan alpine grasslands were examined using data of 405 soil profiles surveyed from 135 sites across the plateau. Our results indicated that vertical distributions of SOC and TN in the Tibetan grasslands were distinctly different from those in other ecosystems worldwide, with a higher proportion of SOC and TN occurring in the surface soil. Considering that SOC stored in surface layer is more vulnerable and less stable than that in deeper layer (Fontaine et al., 2007), the upper layer of Tibetan soils should be strictly protected to minimize the risk of a potentially large carbon release (Zimov et al., 2006). Moreover, our results showed that the associations of SOC content with environmental factors exhibited an ecologically meaningful decrease with soil depth. Furthermore, our results demonstrated that soil carbon content was nearly proportional to nitrogen content with a slope not significantly different from 1.0, suggesting that carbon and nitrogen are closely coupled across various ecosystem types and different soil depths.
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References


Table 1. Environmental and vegetational differences between alpine steppe and meadow on the Tibetan Plateau. The numbers denote the range of environmental variables across the plateau. MAT: mean annual temperature, MAP: mean annual precipitation.

<table>
<thead>
<tr>
<th>Grassland type</th>
<th>MAT (°C)</th>
<th>MAP (mm)</th>
<th>Clay (%)</th>
<th>Sand (%)</th>
<th>Dominant species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alpine steppe</td>
<td>−3~3</td>
<td>230~520</td>
<td>0.5~4.6</td>
<td>49~51</td>
<td>Stipa purpurea, Carex moorcroftii</td>
</tr>
<tr>
<td>Alpine meadow</td>
<td>−3~4.5</td>
<td>280~700</td>
<td>0.9~5.5</td>
<td>41~93</td>
<td>Kobresia pygmaea, K. humilis, K. tibetica</td>
</tr>
</tbody>
</table>
Table 2. Reduced major axis (RMA) analysis of log-transformed soil C-N stoichiometric relationships at different soil depth intervals. The numbers in parentheses are 95% confidence intervals of the slope of C-N stoichiometric relationship.

| Soil depth (cm) | Alpine steppe | | | Alpine meadow | | | Alpine grasslands | | |
|----------------|---------------|---------------|---------------|-----------------|---------------|---------------|-----------------|---------------|
|                | Stage | Intercept | $\alpha$ | $\beta$ | $\rho$ | Intercept | $\alpha$ | $\beta$ | $\rho$ | Intercept | $\alpha$ | $\beta$ | $\rho$ |
| 0–20           | [0.96, 1.21] | 0.86 | 36 | 0.83 | <0.001 | 0.84 | 48 | 0.83 | <0.001 | 0.85 | 84 | 0.67 | <0.001 |
| 20–40          | [0.95, 1.21] | 0.91 | 36 | 0.38 | <0.001 | 0.76 | 48 | 0.66 | <0.001 | 0.77 | 84 | 0.68 | <0.001 |
| 40–60          | [0.94, 1.17] | 0.70 | 36 | 0.31 | <0.001 | 0.69 | 48 | 0.68 | <0.001 | 0.71 | 84 | 0.68 | <0.001 |
| 60–80          | [0.86, 1.16] | 0.66 | 36 | 0.07 | <0.001 | 0.67 | 48 | 0.63 | <0.001 | 0.66 | 84 | 0.44 | <0.001 |
| Total          | [0.94, 1.16] | 0.87 | 36 | 0.02 | <0.001 | 0.90 | 48 | 0.77 | <0.001 | 0.89 | 84 | 0.70 | <0.001 |

Fig. 1. Vertical distributions of absolute SOC (a–c) and relative SOC (d–f) in alpine grasslands. Black bars indicated the proportional distribution of SOC in the first meter at 20 cm intervals. Different letters denote significant difference between alpine steppe and alpine meadow (Tukey test, $P<0.05$). Error bars express standard deviation of the mean.
Fig. 2. Vertical distributions of absolute TN (a–c) and relative TN (d–f) in alpine grasslands. Black bars indicated the proportional distribution of TN in the first meter at 20 cm intervals. Different letters denote significant difference between alpine steppe and alpine meadow (Tukey test, $P < 0.05$). Error bars express standard deviation of the mean.

Fig. 3. Box- and Whisker plots showing changes in C:N ratio in alpine steppe (a), alpine meadow (b), and overall alpine grasslands (c) along soil profile. Different letters denote significant difference between alpine steppe and alpine meadow (Tukey test, $P < 0.05$).
Fig. 4. Correlations of SOC (a–d) and TN (e–h) with environmental factors at different soil depth intervals. (a, e): mean annual temperature, (b, f): mean annual precipitation, (c, g): clay content, (d, h): sand content. ***: \( P < 0.001 \), **: \( P < 0.01 \), *: \( P < 0.05 \).

Fig. 5. C-N stoichiometric relationship at different soil depths (a–e), and comparison of C-N relationship between Tibetan and global datasets (f). (a) 0–20, (b) 20–40, (c) 40–60, (d) 60–80, and (e) 80–100 cm. Dataset of soil carbon and nitrogen in global ecosystems are obtained from Cleveland and Liptzin (2007).