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Carbon and nitrogen dynamics in native *Leymus chinensis* grasslands along a 1000 km longitudinal transect in northeast China

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Received: 16 July 2014 – Accepted: 1 August 2014 – Published: 8 August 2014

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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The unprecedented variations in global precipitation regime could profoundly impact terrestrial ecosystem structure and function, with consequent feedback to climatic change. However, little is known about complexity in precipitation effects on grassland ecosystem carbon (C) and nitrogen (N) processes at regional scales. We investigated the patterns of shoot and root biomass, litter mass, soil C and N content, microbial community composition and C and N mineralization at 18 sites along a 1000 km precipitation gradient in native *Leymus chinensis* grasslands of northeastern China. The results show that, with increasing mean annual precipitation (MAP), the biomass of total plant, shoot and litter gradually increased while root biomass remained nearly constant along the gradient. Surprisingly, both soil C and N mineralization rates showed quadratic relationships with MAP, likely due to the relative changes in temperature, soil arbuscular mycorrhizal fungi biomass and N availability. Although soil total C and N content presented sustained increases with water availability, heavy fractions of C and N content reached stable and saturated phases in mesic sites. Overall, ecosystem C and N sequestration enhanced with water availability in terms of C and N storage in shoot, root, litter, and soil along the precipitation gradient. It was concluded from the current study that regional precipitation regime and the indirect effects of precipitation on changes in soil properties and microbial communities would strongly influence on ecosystem C and N dynamics. The temperate grasslands of northeastern China could be utilized as significant ecosystem C and N sinks in the context of mitigating climate change.

1 Introduction

It is well known that climatic factors, especially precipitation, have important influences on ecosystem C and N processes in grasslands which covering ca. 25% of the global terrestrial area and 40% of the land area in China (He et al., 2008; Kang et al.,

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properties and microbial communities will modulate the responses of C and N dynamics to variation in precipitation. In addition, we also expect the greater precipitation will contribute to the higher C and N sequestration at this region.

2 Materials and methods

2.1 Study sites

The field study was conducted with 18 sites on native *Leymus chinensis* grasslands, located in northeastern plain and Inner Mongolia plateau of China (114–124° E, about 1000 km-long transect from west to east) (Table 1, Fig. 1). Following an order of increasing MAP, vegetation shifts from desert steppes (dominate by perennial grass *L. chinensis* and with companion species *Agropyron cristatum*, *Stipa grandis*) in the west to typical steppes (dominate by *L. chinensis* accompanying with *A. cristatum*, *Artemisia frigida*, *Cleistogenes squarrosa*, *S. grandis*, *Setaira viridis*) and moist meadows (dominate by *L. chinensis* and *Lathyrus quinquenervius*, *Artemisia scoparia*, *Carex duriuscula*, *Phragmites australis* as companion species) in the east (Table 1). We selected sample sites have not been disturbed for at least 10 years (Wang et al., 2011).

2.2 Climate

This area has a continental monsoon climate, with large seasonal temperature and precipitation gradients. Long-term (1950–2000) mean annual temperature, mean annual precipitation and aridity index along the transect range from approximately 1.3–6.8 °C, 237–47 mm and 0.91–1.44, respectively. Because the transect runs parallel to a latitude line (43°30' N), it has approximately uniform theoretical radiation. The elevation gradients range from 140–1309 m (<http://www.worldclim.com>; Zhang et al. 1997; Table 1). A detailed description of vegetation types, climate factors and soil properties can be found in Table 1 (Ni and Zhang, 2000).

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2.3 Plant biomass and litter mass

Aboveground living shoot, standing litter and surface litter were harvested from 10–12 randomly located, 0.5 × 0.5 m plot of each plot, respectively. Root biomass was measured by soil coring method sampling to a depth of 30 cm using a cylindrical root sampler (8 cm inner diameter). All samples of aboveground living tissue, litter and root were oven-dried at 65 °C to constant weight. C and N content of shoot, root and litter were determined by elemental analyzer (Elementaranalyser vario Max CN, Germany).

2.4 Soil property and microbial community analyses

Soil samples from 18 sites were collected along the systematically located transect lines in 12–18 July 2012. 8–16 soil core samples were collected randomly per site (100 × 100 m) for determination of soil properties. The samples were taken to a depth of 15 cm soil layer with a cylindrical soil sampler (5 cm inner diameter), and then immediately preserved at 4 °C in a cooler for transport to the laboratory within one week of collection. The fresh samples were processed using a 2 mm sieve and cleared of visible plant roots and organic debris.

Soil pH was measured with a pH electrode (PHS 29, China). Soil inorganic N content ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) was determined using a flow injection autoanalyzer (FIAs-tar 5000, Denmark). Soil total C and N content were measured by elemental analyzer (Elementaranalyser vario Max CN, Germany). Soil light and heavy fractions of C and N content were measured by density fractionation method (Sollins et al., 1984). Soil texture was determined by the optical size analyzer (Mastersizer 2000, England). Gravimetric soil water content was measured by oven-drying samples at 105 °C for 24 h.

Phospholipid fatty acids (PLFAs) analysis was used to quantify microbial community composition. PLFAs were extracted from soil samples following a procedure described by Bossio et al. (1998). The separation and identification of extracted PLFAs were carried out using a Microbial Identification System (Newark, DE, USA). Methyl nonadecanoate fatty acid (19 : 0) was used as internal standard. Thirty-one fatty acids

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were included in the analyses. (1) gram-positive bacteria: a13: 0, i14: 0, i15: 0, i16: 0, i17: 0 and a17: 0; (2) gram-negative bacteria: 16: 1@7c, 17: 1@8c, 18: 1@5c, 18: 1@9t, 17: 0cy and 19: 0cy (3) Fungi: 18: 2@6c, 18: 1@9c; (4) arbuscular mycorrhizal fungi (AMF): 16: 1@5c (Frostegård et al., 2011). The ratio of fungal to bacterial PLFAs (gram-positive plus gram-negative bacteria) has been used as the indicator of change in the soil microbial community composition (Fierer et al., 2002).

2.5 Statistical analyses

Regression analyses were conducted on relationships of total plant biomass, shoot and root biomass, shoot biomass C and N, root biomass C and N, ratio of root to shoot biomass, litter mass, litter biomass C and N, soil C and N mineralization rates, soil total C and N content, soil light and heavy fractions of C and N content, soil water content, inorganic N, pH, microbial biomass (PLFAs), ratio of fungal to bacterial PLFAs and AMF biomass with MAP. Redundancy analysis (RDA) was used to represent the relationships among environmental factors and ecosystem C and N processes along the gradient (Lepš and Smilauer, 2003) using the Canoco for Windows 4.5 package (Ithaca, NY, USA).

Stepwise linear regression analyses were used to determine the relationship between ecosystem C or N processes with environmental factors. If the several independent variables are existed higher correlations, which may contribute to overfitting correlation, stepwise regression can delete one or more correlated independent variables to lest including complexity such as interactions. Significant differences among the sites in measured variables were determined using One-way ANOVA. Data management and statistical analyses were performed using SPSS 17.0 software (SPSS, Chicago, IL, USA).

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3 Results

3.1 Plant and litter properties

Total plant biomass (shoot plus root biomass), shoot biomass and ratio of root to shoot biomass (R : S) varied significantly along the large-scale precipitation gradient. In general, average total plant biomass and shoot biomass increased from 131 to 440 g m⁻² ($R^2 = 0.43$, $P < 0.0001$; Fig. 2a) and 62 to 332 g m⁻² ($R^2 = 0.54$, $P < 0.0001$; Fig. 2b), but R : S dropped from 1.38 to 0.32 with increasing mean annual precipitation (MAP) ($R^2 = 0.46$, $P < 0.0001$; Fig. 2d). Surprisingly, root biomass showed no remarkable differences among all sites (Fig. 2c). Similarly, shoot biomass C and N changed significantly with variation in precipitation, whereas root biomass C and N varied slightly. Shoot biomass C and N, on average, increased from 33 to 150 g m⁻² ($R^2 = 0.50$, $P < 0.0001$; Fig. 2e) and 2.3 to 6.9 g m⁻² along the gradient ($R^2 = 0.29$, $P < 0.0001$; Fig. 2f). Consistent with plant biomass, the litter mass ($R^2 = 0.09$, $P = 0.007$; Fig. 2g) and litter biomass C and N ($R^2 = 0.12$, $P = 0.03$; $R^2 = 0.15$, $P = 0.0004$; Fig. 2h) also exhibited remarkable variations, and were all linearly increased with increasing MAP.

3.2 Soil properties

In general, soil water content, total C and N content, inorganic N, C : N, light and heavy fractions of C and N content differed significantly along the large-scale precipitation gradient (Fig. 3). Soil water content linearly increased with MAP ($R^2 = 0.72$, $P < 0.0001$; Fig. 3a), and varied 7.4-fold along the gradient. However, soil pH fluctuated only slightly, with very little significant variation (Fig. 3b). Soil total C and N content and C : N to a depth of 15 cm layer increased from 1316 to 4232 g m⁻² ($R^2 = 0.60$, $P < 0.0001$; Fig. 3d), 196 to 438 g m⁻² ($R^2 = 0.30$, $P < 0.0001$; Fig. 3e), and 5.8 to 12.8 ($R^2 = 0.37$, $P < 0.0001$; Fig. 3f) with MAP along the gradient, respectively. However, although soil light fractions of C and N content rapidly increased with MAP, heavy fractions of C and N followed by steady phases with MAP from 422–472 mm long the gradient (Fig. 3g–

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j). In contrast, soil inorganic N content had a quadratic relationship with precipitation ($R^2 = 0.40$, $P < 0.0001$; Fig. 3c), and varied 4-fold at this region.

3.3 Soil microbial community, C and N mineralization

The viable microbial biomass (i.e. total PLFAs) presented to an increase trend ($P < 0.0001$, $R^2 = 0.54$; Fig. 4a), but the ratio of fungal to bacterial biomass displayed a decrease style (data not shown) from the dry west end to the moist east end along the gradient. The meadows had the highest microbial biomass (ca. 33.8 nmol g^{-1}), having 1.8-fold greater than the desert steppes, which had the lowest value (ca. 19.2 nmol g^{-1}). Inconsistent with microbial biomass, the desert steppes and meadows had higher AMF biomass than the typical steppes, which varied 1.5-fold across all sites.

The patterns of soil C and N mineralization rates at the depth of 0–15 cm both followed quadratic relationships with MAP, which increase at first, reached the highest values, and then decreased along the transect ($R^2 = 0.35$, $P < 0.0001$; $R^2 = 0.37$, $P < 0.0001$; Fig. 4c, d). The highest C mineralization rate from the typical steppe (site No. 10) was 28 % and 13 % higher than the values from the driest and wettest sites, respectively ($P < 0.05$; One-way ANOVA). Similarly, the highest soil net N mineralization rate was 26 % and 9 % higher than that from the driest and the wettest sites ($P < 0.05$; One-way ANOVA). Overall, ecosystem C and N sequestration enhanced with increasing precipitation in terms of C and N storage in shoot, root, litter and soil along the gradient (Fig. 4e, f).

3.4 Relationship among ecosystem C and N dynamics and environmental factors

The ordination biplot diagram from redundancy analysis (RDA) exhibited the effects of environmental factors on C and N dynamics along the gradient (Fig. 5). Environmental factors and response variables with more similar locations had higher correlations than those with less similar locations. The first and second axes of RDA ordination explained

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gesting that primary production in this precipitation gradient is limited, at least in part, by water availability. Across the gradient, although shoot biomass showed positively dependence upon mean annual temperature (MAT) ($P < 0.05$; Table 2), stepwise multiple regression analyses demonstrated that MAT didn't contribute to the variation in shoot biomass (partial $R^2 = 0.02$; $P > 0.05$). These results are similar with that reported in grasslands (Barrett et al., 2002; Wang et al., 2003; Zhou et al., 2009), forests (Austin et al., 2002; Schuur and Matson, 2001), woodlands (Zerihun et al., 2006) along the large-scale precipitation gradients, and a former developed regional vegetation models in this area (Gao and Yu, 1998). Consistent with the variation in shoot biomass, we also found that litter mass (standing plus surface litter) was positively related to increasing MAP along the gradient (Fig. 2). These findings indicate that the increasing precipitation facilitates aboveground C and N accumulation in this water-limited region.

Contrary to our expectation, root biomass changed only slightly along the gradient (Fig. 2c), resulting the decreases in R:S from the dry to the mesic sites (Fig. 2d). Our results are consistent with those of studies on effects of increased precipitation on root biomass at local and regional scales (Ma et al., 2012; Zhou et al., 2009), in which plants respond to increasing precipitation by decreasing the photosynthates allocation to root system relative to the aboveground parts (to enhance light capture). Such lack of response of the root biomass to changes in precipitation regime was likely because nutrients limit root growth along the gradient. Although we cannot prove this point, manipulating nutrient and water experiments demonstrated that nutrient addition increased plant growth, especially root growth, whereas water addition showed modest effect in this study region (Ma et al., 2012, 2013; Xiao et al., 2007).

Previous transect and manipulative studies have showed that soil C mineralization (CMR) and N mineralization rate (NMR) were positively related to increasing precipitation at local and regional scales (McCully et al., 2005; Xiao et al., 2007; Kim et al., 2012). However, surprisingly, both soil CMR and NMR followed quadratic relationships with MAP, which increase at first, reached the highest value, and then decreased along the gradient ($R^2 = 0.35$, $R^2 = 0.37$; Fig. 4c, d). The trends could have been attributed to

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findings indicate that soil heavy fractions of C and N storage in the temperate grasslands subjected to site No. 12 (MAP: 422 mm; Table 1) may reach stable or saturation and have some important implications to ecosystem C and N sequestration. A large number of shoot or litter biomass to soils only increased soil light rather than heavy organic matter in mesic sites suggesting that mineral soils in the *L. chinensis* grasslands have a limited capacity to accumulate mineral component (Chung et al., 2008; Stewart et al., 2007).

In generally, ecosystem C and N sequestration enhanced with water availability in terms of C and N storage in shoot, root, litter, and soil along the precipitation gradient (Fig. 4e, f). Although we did not detected belowground C and N allocation in deeper soil layer (30–100 m) due to sampling difficulties, about 80 % of the root and soil C and N were focused in the top 20 cm soil layer (Zhou et al., 2007; He et al., 2008). Therefore, these results may have not altered the overall patterns of C and N sequestration along the precipitation gradient.

Based on our results, changing in global precipitation regime would strongly influence on ecosystem C and N dynamics. These findings indicate regional precipitation regime and the changes in temperature, nutrient availability and microbial communities may play important roles in determining ecosystem C and N dynamics, and suggest that the *L. chinensis* grasslands of northeast China exhibit tremendous potential for enhancing C and N sequestration at the regional scale. The temperate grasslands of northeastern China could be utilized as significant ecosystem C and N sinks in the context of mitigating climate change.

Acknowledgements. We are grateful for the funding provided by the Natural Science Foundation of China (No. 31300440); and <http://www.worldclim.com> for providing meteorological data.

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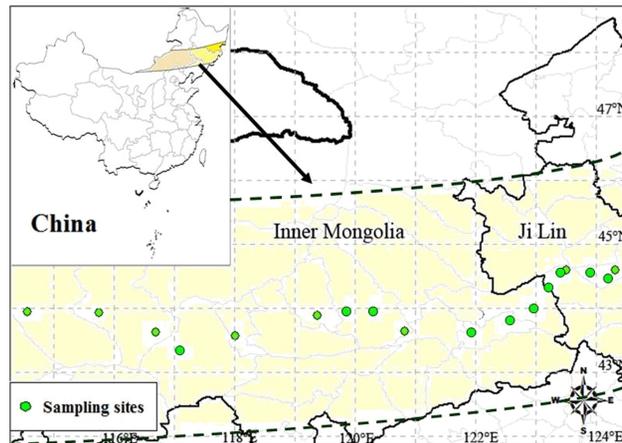


Figure 1. Study sites (1–18; see Table 1) along the 1000 km longitudinal transect in native *Leymus chinensis* grasslands of northeastern China.

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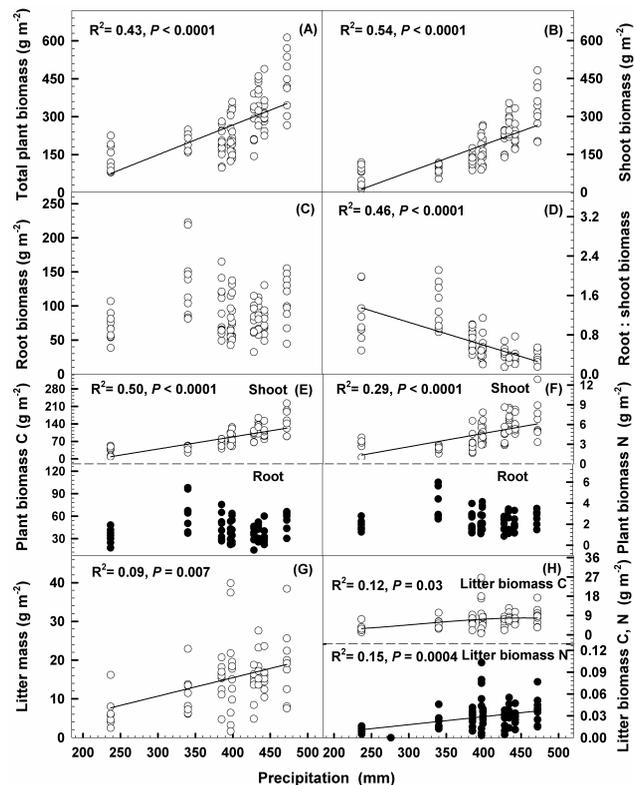


Figure 2. Patterns of total plant biomass (a), shoot and root biomass (b, c), the ratio of root to shoot biomass (d), shoot and root biomass C (e), shoot and root biomass N (f), litter mass (g) and litter biomass C and N (h) along the precipitation gradient in native *Leymus chinensis* grasslands of northeastern China.

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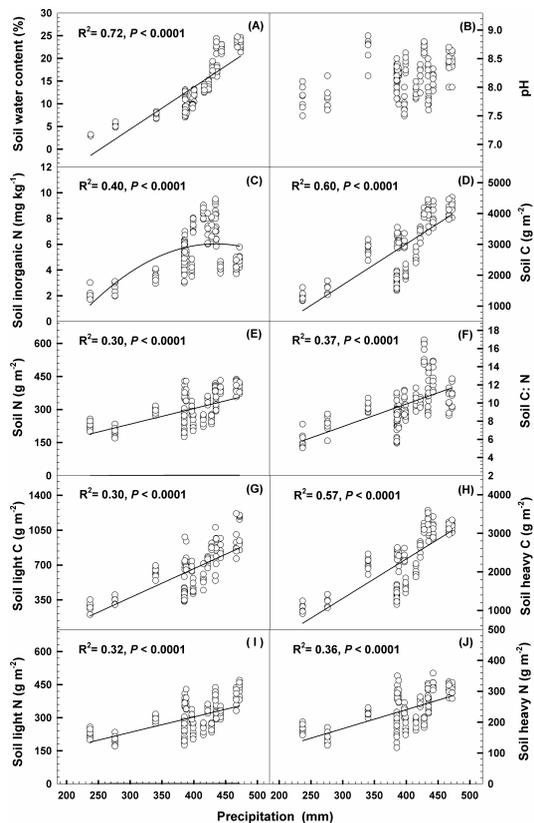


Figure 3. Soil properties along the large-scale precipitation gradient in *Leymus chinensis* grasslands of northeastern China. Soil water content (a), pH (b), soil inorganic N (c), soil total C and N (d, e), ratio of soil total C to N (f), soil light and heavy fractions of C and N (g–j).

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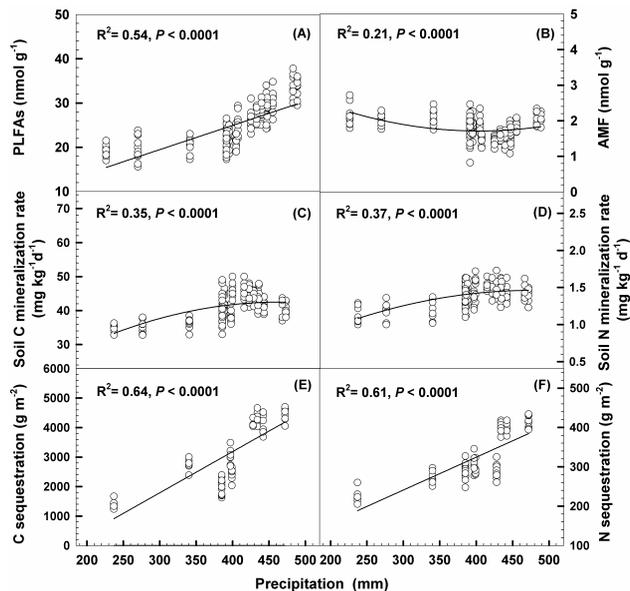


Figure 4. Patterns of soil microbial biomass (PLFAs) **(a)**, arbuscular mycorrhizal fungi biomass (AMF) **(b)**, soil C mineralization rate **(c)**, soil net N mineralization rate **(d)**, ecosystem C and N sequestration **(e, f)** across the precipitation gradient in *Leymus chinensis* grasslands of north-eastern China.

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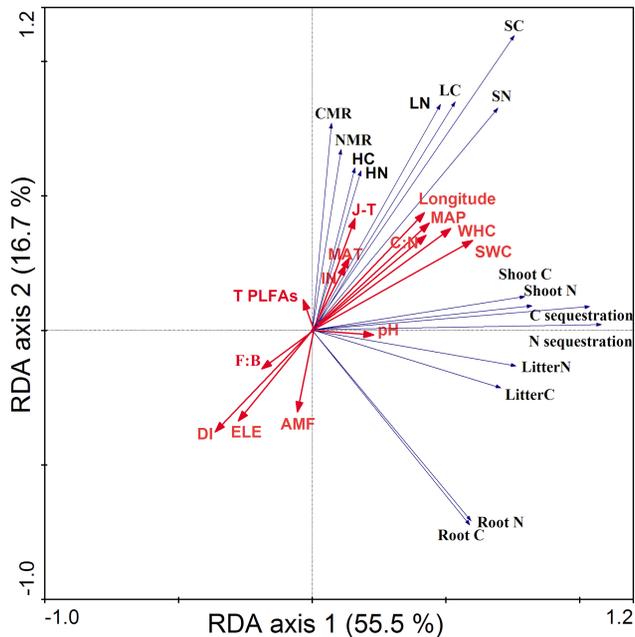


Figure 5. Ordination biplot diagram from redundancy analysis (RDA) displaying the effects of environmental factors on C and N dynamics along the large-scale precipitation gradient in native *Leymus chinensis* grasslands of northeastern China. Mean annual precipitation (MAP), mean annual temperature (MAT), mean July temperature (J-T), aridity index (DI), elevation (ELE), longitude, soil water content (SWC), soil inorganic N (IN), soil C:N, total (T) PLFAs, ratio of fungal to bacterial biomass (F:B), arbuscular mycorrhizal fungi biomass (AMF), water holding capacity (WHC) and soil pH were environmental variables (red arrows). Shoot and root biomass C and N, litter biomass C and N, soil C and N mineralization rates (CMR, NMR), soil total C and N content (SC, SN), light and heavy fractions of C and N content (HC, HN, LC, LN) were response variables (blue arrows).