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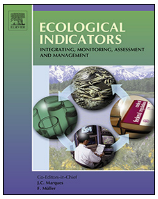

Original Articles

# Two contrasting seasonal patterns in microbial nitrogen immobilization from temperate ecosystems

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ABSTRACT

Ecosystems with seasonal snow cover and soil frost comprise more than half of the terrestrial ecosystems. Recent studies have reported peak microbial biomass carbon (MBC) and nitrogen (MBN) in late winter in alpine and arctic regions, followed by a rapid decline when soil temperatures rise to 0 °C. In these snow-covered ecosystems, the N incorporated into microbes from soil during winter is considered vital for plant nutrient uptake in the following growing seasons. However, evidence from temperate ecosystems has rarely been reported. We studied 24 ecosystems from two forest-steppe ecotones (Saihanba and Saihanwula) with similar climatic conditions, but different soil properties, to comprehensively analyze the seasonal dynamics of microbial biomass and its controlling factors. MBC consistently reached its annual peak in winter, and this seasonal trend was not influenced by different vegetation types or study areas. In contrast, the seasonal dynamics of MBN were strongly influenced by the study area. There were minimum values of winter MBN observed in the Saihanba area while maximum values of winter MBC observed in the Saihanwula area. Soil properties showed poor nutrient status in the Saihanba area compared with the Saihanwula area. Our results suggest winter microbes in the Saihanba area invest N to produce extracellular enzymes, rather than retaining in biomass. We argue that it is a possible strategy to cope with nutrient stress caused by plant competition in the following spring. However, the peak of MBN occurred in the winter in the Saihanwula area, suggesting a potential resource for spring plant N uptake in this area. We also found the magnitude of MBN was positively related to the soil water content under different vegetation types in the Saihanwula area. Our study demonstrates two contrasting seasonal patterns of soil MBN, suggesting that the general conceptual model of N cycle based on the studies from alpine and arctic areas may not be applicable to temperate ecosystems.

## 1. Introduction

Soil microbes serve as the main decomposers in ecosystems (Manzoni et al., 2012), mediating soil nitrogen (N) mineralization for plant nutrient uptake (Booth et al., 2005; Kujur and Patel, 2012). In addition, microbes are the active component of soil nutrient pool (Sun et al., 2010; Yadav, 2012), and determine the amount of organic matter stored in soils. Thus, microbes have a profound effect on nutrient immobilization, driving the belowground N cycling (Falkowski et al., 2008; Schimel and Schaeffer, 2012; Serna-Chavez et al., 2013; Ravindran and Yang, 2015).

Ecosystems with seasonal snow cover and soil frost comprise more than half of the terrestrial ecosystems, which have received increasing attention during the past decade (Zhang et al., 2014). It was often assumed that the belowground process was inactive during winter just as the aboveground, until later research findings showed that winter process was actively taking part in soils under snow pack which served as heat isolation materials and provided relatively warmer habitat for microbes (Groffman et al., 2006; Monson et al., 2006; Wang et al., 2010). Based on studies from alpine tundra and arctic ecosystems (Lipson et al., 2000; Groffman et al., 2001; Mikan et al., 2002; Edwards et al., 2006), a classical conceptual model for microbial seasonal succession concluded that maximum microbial biomass emerged in winter under snow cover, and a large amount of soil dissolved N was immobilized in the microbial biomass (Schmidt et al., 2007). In the following spring, the microbial biomass experienced an abrupt decline caused by snow melting and released dissolved N as an important nutrient resource for plant uptake (Schmidt et al., 2007). Thus the size of

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**Table 1**
Description of the forest ecosystems in the two study areas.

| Area | Site Name | Vegetation | Slope Direction | Forest Age (yr) | Soil Type | Height (m) | DBH (cm) |
|---|---|---|---|---|---|---|---|
| Saihanba National Forest Park | SNFP-P1 | *Pinus sylvestris* var. *mongolica* | north | 10 | sandy soils | 3 | 4 |
|  | SNFP-P2 | *P. sylvestris* var. *mongolica* | north | 23 | sandy soils | 8 | 12 |
| 42°10′–42°50′ N | SNFP-P3 | *P. sylvestris* var. *mongolica* | north | 37 | sandy soils | 15 | 21 |
| 117°12′–117°30′ E | SNFP-L1 | *Larix prinicipis-rupprechtii* | / | 10 | grey forest soils | 3 | 3 |
| 1400 m a.s.l | SNFP-L2 | *L. prinicipis-rupprechtii* | / | 20 | grey forest soils | 10 | 11 |
|  | SNFP-L3 | *L. prinicipis-rupprechtii* | / | 40 | grey forest soils | 16 | 21 |
|  | SNFP-BP | *Betula platyphylla* | north | 40 | grey forest soils | 14 | 13 |
| Saihanwula National Nature Reserve | SNNR-P | *P. sylvestris* var. *mongolica* | north | 10 | skeleton brown earths | 3 | 4 |
|  | SNNR-L1 | *L. prinicipis-rupprechtii* | north | ~40 | grey forest soils | 7 | 13 |
| 43°59′–44°27′ N | SNNR-L2 | *L. prinicipis-rupprechtii* | south | ~35 | grey forest soils | 9 | 12 |
| 118°18′–118°55′ E | SNNR-L3 | *L. prinicipis-rupprechtii* | / | / | mountain black earths | 8 | 11 |
| 1000 m a.s.l | SNNR-L4 | *L. prinicipis-rupprechtii* | / | / | grey forest soils | 10 | 12 |
|  | SNNR-BP | *Betula platyphylla* | north | 40 | typical brown earths | 16 | 19 |
|  | SNNR-BD | *B. dahurica* | north | 10 | typical brown earths | 9 | 13 |
|  | SNNR-QM | *Quercus mongolica* | south | 40 | skeleton brown earths | 16 | 21 |

Saihanba National Forest Park of China = SNFP, Saihanwula National Nature Reserve of China = SNNR, DBH = diameter at breast height.

winter microbial biomass N can be taken as an indicator of available nutrient source for above-ground plants. However, this extrapolated inference has rarely been reported from temperate ecosystems. Not only reports of winter microbial biomass from temperate ecosystems are very limited, but also results are inconclusive (Wu et al., 2012; Zhang et al., 2014). Whether the seasonal pattern of microbial biomass in temperate regions is in line with that in the high latitude regions is still unclear. By studying the seasonal pattern of microbial biomass, especially the situation of winter microbial biomass N, this work is expected to shed light on whether winter microbial biomass N can be a persistent indicator for maintaining plant nutrient demand in spring.

Based on studies from the perspective of spatial dynamics, it is commonly accepted that the size of microbial biomass is strongly influenced by soil nutrient status, with more biomass produced when there are more nutrient available (Cleveland and Liptzin, 2007; Fierer et al., 2009). Soil temperature was considered as another major factor for determining microbial biomass, with increased microbial biomass built by higher temperature. As temperature governed the activity of living microorganism, it was generally believed that microbial biomass was positively correlated with temperature. While in fact, soil temperature was less connected with microbial biomass compared with soil water content (Serna-Chavez et al., 2013). The significant positive effect of soil water content on microbial biomass is related to nutrient diffusion (Bachar et al., 2010; Blankinship et al., 2011). Other studies have also pointed out that the accumulation of microbial biomass can vary due to the input of root exudates and litter with different quantity and quality originating from different vegetation types (Kara et al., 2008; Ravindran and Yang, 2015). However, much attention has been drawn to spatial dynamics, and most of these studies fail to take into account temporal dynamics. Characterized by fast generation time and quick turnover rate, microbes can respond to environmental changes in a very short time-scale (Björk et al., 2008). But it is still unclear if the factors responsible for spatial dynamics of microbial biomass also influence its temporal dynamics. More than that, another important factor we think of is extracellular enzyme, which represents a tradeoff between N held within microbes and release into environment. Microbes produce extracellular enzyme to access restricted resources from the environment (Sinsabaugh et al., 2008; Bell et al., 2014). But the production of extracellular enzyme requires the investment of N from microbial biomass. If N is retained in microbe itself, it turns microbial biomass a sink as observations from the winter of alpine and arctic ecosystems. Yet, releasing N to extracellular enzyme may influence the N retention by microbes, and potentially accelerates degradation and nutrient release from surrounding soil. Whether the production of extracellular enzyme will influence seasonal pattern of microbial N immobilization has not been fully understood.

This study was conducted at two typical temperate forest-steppe ecotones in northern China, with collection of large soil samples covering a broad range of vegetation types (i.e., evergreen conifer, deciduous conifer, broadleaved forest, shrub land and grassland), and enabled us to carry out a comprehensive investigation of microbial biomass C (MBC) and N (MBN) to answer the following questions. Is there a consistent seasonal pattern of MBC- and MBN-dynamics across different study areas and vegetation types in temperate ecosystems? What are the key seasonal changes in soil environmental conditions that result in this seasonal pattern of MBC- and MBN-dynamics?

## 2. Material and methods

### 2.1. Site description and experimental design

The two forest-steppe ecotones are located in the Saihanba National Forest Park (SNFP) of Hebei Province (42°10′–42°50′ N, 117°12′–117°30′ E, 1400 m a.s.l) and the Saihanwula National Nature Reserve (SNNR) of the Inner Mongolia Autonomous Region (43°59′–44°27′ N, 118°18′–118°55′ E, 1000 m a.s.l). The climate for both areas is semi-arid and -humid, with a long and cold freezing period (November–March) and a relatively short growing season. The annual mean temperature (MAT) is −1.4 °C and 2.0 °C for Saihanba and Saihanwula, respectively. The annual precipitation (MAP) is 400 mm for Saihanba and 450 mm for Saihanwula. Details on the two areas are provided in Tables 1 and 2.

*Saihanba area in Hebei Province:* Five dominant vegetation types were chosen: ever-green coniferous forest dominated by *Pinus sylvestris* var. *mongolica*; deciduous coniferous forest dominated by *Larix principis-rupprechtii*; deciduous broadleaved forest dominated by *Betula platyphylla*; shrubland dominated by *Malus baccata*; and grassland dominated by *Leymus chinensis*. Both coniferous plantations contained three forest ages (~10, 20, and 40 years old). In total, nine plots were established (Tables 1 and 2), which were less than 10 km from one another (Appendix: Fig. A.1).

*Saihanwula area in the Inner Mongolia Autonomous Region:* Six dominant vegetation types were chosen: ever-green coniferous forest dominated by *P. sylvestris* var. *mongolica*; deciduous coniferous forest dominated by *L. prinicipis-rupprechtii*; deciduous broadleaved forest dominated by *B. platyphylla*, *B. dahurica*, and *Quercus mongolica*; shrubland dominated by *Ostryopsis davidiana* and *Rhododendron dahuricum*; grassland, and meadow. One site of grassland was dominated by *L. chinensis*, the other grassland and meadow sites had no clear dominant species. Four different microsites were chosen for *L. prinicipis-rupprechtii* (northern slope, southern slope, 1050 m a.s.l, and 200 m a.s.l). In total, 15 plots were designed (Tables 1 and 2) with no more