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RESEARCH ARTICLE

Effects of snow absence on available N pools and enzyme activities within soil aggregates in a spruce forest on the eastern Tibetan Plateau

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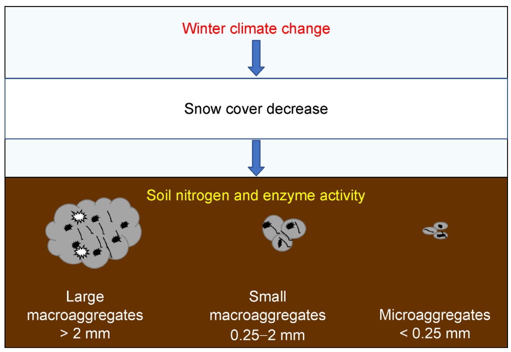
HIGHLIGHTS

• Snow absence increased soil N availabilities within soil aggregates.
• The effect the snow absence on soil enzymes depended on aggregate classes.
• The effect the snow absence soil N availabilities depended sampling year.

GRAPHICAL ABSTRACT



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ABSTRACT

Winter climate change has great potential to affect the functioning of terrestrial ecosystems. In particular, increased soil frost associated with reduced insulating snow cover may impact the soil nitrogen (N) dynamics in cold ecosystems, but little is known about the variability of these effects among the soil aggregates. A snow manipulation experiment was conducted to investigate the effects of snow absence on N cycling within soil aggregates in a spruce forest on the eastern Tibetan Plateau of China. The extractable soil available N (ammonium and nitrate), net N mineralization rate, and N cycling-related enzyme activities (urease, nitrate reductase, and nitrite reductase) were measured in large macroaggregate (>2 mm), small macroaggregate (0.25–2 mm), and microaggregate (<0.25 mm) during the early thawing period in the years of 2016 and 2017. Snow absence increased soil N availabilities and nitrite reductase activity in microaggregate, but did not affect net N mineralization rate, urease or nitrate reductase activities in any of the aggregate fractions. Regardless of snow manipulations, both soil inorganic N and nitrate reductase were higher in small macroaggregate than in the other two fractions. The effect of aggregate size and sampling year was significant on soil mineral N, net N mineralization rate, and nitrite reductase activity. Our results indicated that snow cover change exerts the largest impact on soil N cycling within microaggregate, and its effect is dependent on winter conditions (e.g., snow cover and temperature). Such findings have important implications for soil N cycling in snow-covered subalpine forests experiencing pronounced winter climate change.

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1 Introduction

Seasonal snow cover, as an effective insulator, decouples the influence of air temperature on soil biochemical processes (Stieglitz et al., 2003; Barnett et al., 2005;Li et al., 2017). However, currently winter snow is likely to be replaced by rainfall in boreal forests due to winter warming (Ballesteros-Cánovas et al., 2018). The increased soil frost as a result of the lack of snow cover may impact the structure and biological activity of soil aggregates in these ecosystems.

Soil generally consists of sand, clay and silt particles physically bonded into aggregates. Soil nutrient cycling in bulk soil is primarily controlled by microbial activity, and such processes might differ among aggregate scales (Mendes et al., 1999; Wilpiszeski et al., 2019). Soil enzymatic activities have been shown to be more profoundly concentrated within microaggregate than macroaggregate (Allison and Jastrow, 2006), but the opposite results have also been reported (Fansler et al., 2005; Dorodnikov et al., 2009). Few studies have demonstrated that global change drivers, including temperature, carbon dioxide and land-use change, can alter soil carbon (C) and nutrient cycles of aggregates (Dorodnikov et al., 2009; Fang et al., 2016). The effects of snow cover change on aggregate structure, however, remain poorly understood (Steinweg et al., 2008). Increased soil freezing due to snow removal inhibits root growth and biological activity (Repo et al., 2014; Yang et al., 2019). Increased soil frost associated with winter warming may potentially disrupt soil aggregation hence affect the biological factors (such as those involving roots, microbes and enzymes), which play a crucial role in forming and/or stabilizing macroaggregate. Studies have indicated that climate change differentially affects soil C and nitrogen (N) pools and biological activity among aggregates (Nie et al., 2014; Fang et al., 2016). However, the impact of a change in snow cover on soil N cycling across aggregate size classes has not been studied.

The subalpine forest ecosystems on the eastern Tibetan Plateau are susceptible to climate change, with important consequences for the global C and N balance (Tan et al., 2014; Li et al., 2017). Winter soil temperature in this zone is close to physical melting point (Li et al., 2017). Thus snow cover change has great potential to alter winter soil temperature, and further affect soil physical and biological processes in boreal forest soils. Our previous studies have reported that snow exclusion inhibits soil respiration, but stimulates N availabilities in the bulk soil (Li et al., 2017; Yang et al., 2019). Exploring aggregate-based N availabilities and soil enzymes involved in N cycling may help us to understand the responses of N cycling to winter climate change in this system. Here, we carried out a snow manipulation experiment in a spruce forest to illustrate the influences of snow absence on N availabilities and soil enzymes involved in N cycling in soil aggregate fractions. We hypothesized that snow absence would increase soil N cycling, and that its effect would differ among aggregate size classes.

2 Materials and methods

2.1 Site description and experimental preparation

A snowpack manipulation experiment was carried out in a *Picea asperata* (Dragon spruce) stand at the Long-term Research Station of Alpine Forest Ecosystems, which is located at the eastern Tibetan Plateau, China (31°15′ N, 102° 53′ E; 3021 m a.s.l.). The mean annual temperature and precipitation are 3.0°C and 850 mm, respectively. Snow cover begins to accumulate in late November and melts in late March of the following year. The soil is classified as Cambic Umbrisols (IUSS Working Group WRB, 2007). Basic soil properties (0–15 cm) are as follows: soil organic C 88.5 g C kg^{-1}, total N 5.4 g N kg^{-1}, and pH 6.4 (Li et al. 2017).

To exclude winter snowfall, six wooden roofs with 2 m in height and 3 m × 3 m in ground area were installed in November 2015 to prevent snow accumulation on the ground. A control plot was established in the vicinity of each treatment (Li et al., 2017). Air temperature (2 m height) and soil temperature 5 cm below the soil surface in the snow-free and control plots were measured by the Thermochron iButton DS1923–F5 Recorders (Maxim Dallas Semiconductor Corp., USA). Soil moisture 5 cm below the soil surface was measured with a hand-held probe at about two-week intervals (Delta-T Devices, Cambridge, UK). Seasonal dynamics of soil temperature and moisture have been reported in our prior study (Yang et al., 2019). Snow absence induced more severe soil freezing but did not affect soil moisture content in the winters of 2015/2016 and 2016/2017. The mean air temperature during the months between November 2015 to April 2016 (−2.1°C) was lower than that in 2016/2017 (−0.9°C) (Yang et al., 2019).

Soil samples were collected in the early thawing periods (early April) of 2016 and 2017. Two soil cores were collected from each plot using an auger (15 cm in deep and 10 cm in diameter) and were mixed into one composite sample. Aggregates were isolated as described by Kristiansen et al. (2006). Large macroaggregate (>2 mm), small macroaggregate (0.25–2 mm) and microaggregate (<0.25 mm) were separated. See Yang et al. (2019) for further details. Our previous study showed that the snow-exclusion treatment did not affect the distribution of aggregate in the size classes in the transitional thawing periods of 2016 and 2017 (Yang et al., 2019).

2.2 Soil chemical analysis

Nitrate (NO_3^-) and ammonium (NH_4^+) were extracted with 2 M KCl (1:5 soil:solution), and then determined using indophenolblue and phenol-disulphonic acid colorimetry, respectively (Xu et al., 2010). Soil net N mineralization rate was quantified following the method of Xu et al. (2014): 10 g fresh soil was incubated for one week at 20°C and 50% moisture. Net N mineralization rate on a dry-mass basis was calculated as the difference in inorganic N between the initial and incubated samples. Soil urease activity was assayed with a buffered urea solution, extraction of NH_4^+ with 1 N KCl and 0.01 N HCl, and colorimetric NH_4^+ determination by a modified indophenol reaction (Kandeler and Gerber, 1988). The soil nitrate and nitrite reductase activities were measured by α-naphthylamine and sulfanilic acid colorimetry, respectively (Xiong et al., 2014).

2.3 Statistical analysis

Repeated measures ANOVA was performed to test the effects of snow manipulation, sampling date, aggregate size, and their interactions on measured parameters. One-way ANOVA was used to analyze the snow condition, aggregate size and sampling date for significant differences. All statistical analyses were considered as a significant level at $P < 0.05$. All statistical analyses were performed using SPSS 23.0 (IBM Deutschland GmbH, Ehningen, Germany) software package for Windows.

3 Results

3.1 Soil N availabilities and net N mineralization rate

The snow absence did not affect either NH_4^+-N or NO_3^--N content, but did increase inorganic N content (Fig. 1; Table 1). Snow absence also increased NH_4^+-N, NO_3^--N and inorganic N content in microaggregate in 2016 (Fig. 1). Snow absence, however, did not affect any of the N variables in 2017 (Fig. 1). The contents of NH_4^+-N were often lower in the second treatment year (Fig. 1; Table 1). Both NH_4^+-N and inorganic N contents were higher in the small macroaggregates than microaggregates and large macroaggregates in 2016 (Fig. 1). Snow absence, aggregate size and sampling year alone did not affect net N mineralization rate (Fig. 2; Table 1), but the interaction of soil aggregates and sampling date had significant effect on this rate (Table 1). Soil net N mineralization rate was higher in the macroaggregate than microaggregate and large-macroaggregate in the snow absence plots in 2016 (Fig. 2).

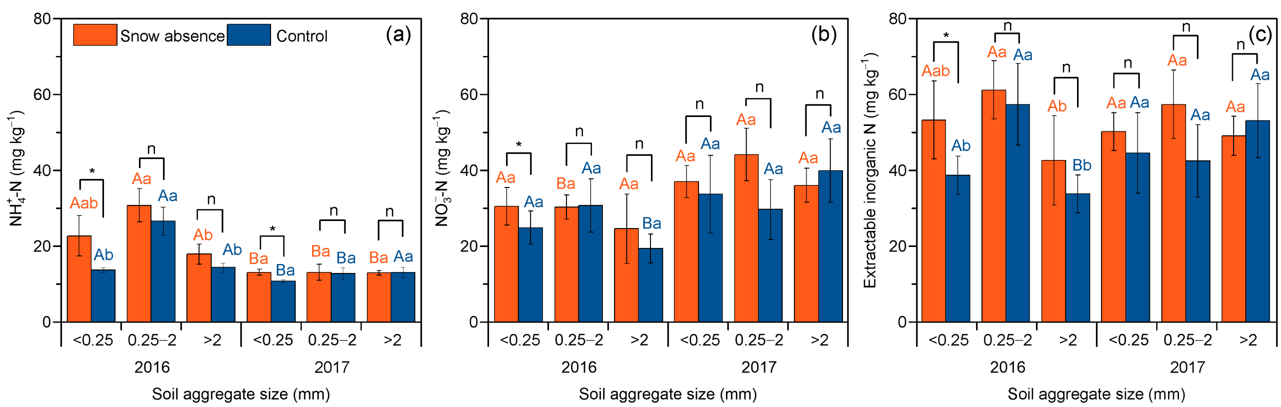

Fig. 1 Soil NH_4^+-N (a), NO_3^--N (b), and extractable inorganic N (c) concentrations in snow absence and control plots. The significant difference between snow absence and control in the same soil aggregate and sampling date is indicated by asterisks ($P < 0.05$) or n ($P > 0.05$). Different lowercase letters denote significant difference between soil aggregate sizes within the same treatment (control or snow absence) in the same sampling date ($P < 0.05$). Different uppercase letters denote significant difference between 2016 and 2017 in the same aggregate sizes and treatment ($P < 0.05$).

Table 1 Summered results regarding the effects of snow absence, aggregate size, sampling date and their interaction of soil N pools, mineralization, and enzyme activities under the repeated measure ANOVA.

	NH_4^+-N	NO_3^--N	EIN	Mineralization	URA	NARA	NIRA
Snow absence (SA)	0.277	0.579	**0.006**	0.525	0.263	0.245	0.197
Aggregate size (AS)	**0.017**	0.751	**0.007**	0.105	**0.035**	0.113	**0.001**
Sampling year (SY)	**0.014**	0.116	0.506	0.070	**0.002**	0.737	**0.001**
SA × AS	0.278	0.891	0.379	0.802	0.952	0.781	**0.050**
SA × SY	0.236	0.730	0.472	0.440	0.357	**0.050**	**0.006**
AS × SY	**0.002**	**0.049**	**0.004**	**0.008**	0.100	0.105	**0.010**
SA × AS × SY	0.466	0.575	0.124	0.991	0.919	0.927	0.592

EIN: extractable inorganic nitrogen. URA: urease activity. NARA: nitrate reductase activity. NIRA: nitrite reductase activity.

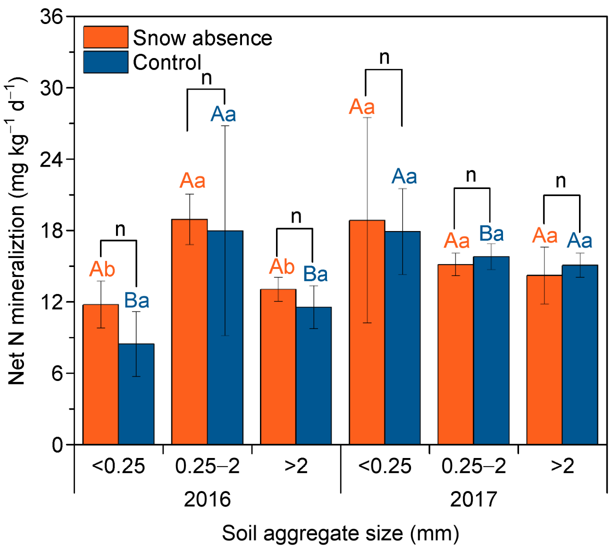

Fig. 2 Net N mineralization rate in snow absence and control plots. The significant difference between snow absence and control in the same soil aggregate and sampling date is indicated by asterisks ($P < 0.05$) or n ($P > 0.05$). Different lowercase letters denote significant difference between soil aggregate sizes within the same treatment (control or snow absence) in the same sampling date ($P < 0.05$). Different uppercase letters denote significant difference between 2016 and 2017 in the same aggregate sizes and treatment ($P < 0.05$).

3.2 Soil enzyme activities

Snow absence alone did not affect any enzyme activities involved in soil N cycling in either year (Table 1). However, both the activities of urease and nitrite reductase were significantly affected by both aggregate size and sampling year (Table 1). The activities of urease and nitrite reductase was presented in an order of microaggregate, small macro-aggregate, and large macroaggregate in 2016 (Fig. 3a, c), but had no differences in 2017 (Fig. 3c). In general, the activities of urease and nitrite reductase were lower in 2017 than in 2016 (Fig. 3a, c). The interaction of snow absence and aggregate size was significant on the activity of nitrite reductase (Table 1). Snow absence stimulated the activity of nitrite reductase in microaggregate in 2016 (Fig. 3c). The ANOVA indicated that the effect of snow absence on nitrate and nitrite reductase was dependent on aggregate size (Table 1).

3.3 Pearson correlation coefficient

There were significant correlations between NH_4^+-N and the activities of urease, nitrate and nitrite reductase in the snow absence plots (Fig. 4a). Soil urease activity showed a negative relationship with net N mineralization rate in the control plots (Fig. 4b). Significant relationships were found between nitrate reductase activity and NH_4^+-N, NO_3^--N, extractable inorganic nitrogen and net N mineralization rate in the control plots (Fig. 4b). Moreover, soil urease was positively correlated with nitrite reductase in each treatment (Fig. 4).

4 Discussion

Soil N availability is a crucial limiting factor for below-ground biological activities, especially in cold biomes (Lavoie et al., 2011). Thus snow cover alteration-induced changes in soil available N pools may play a vital role in soil N cycling through physic-chemical routes (Freppaz et al., 2008; Li et al., 2017). Numerous studies have shown that snow removal increased soil mineral N content (Steinweg et al., 2008, Shibata et al., 2013, Li et al., 2017). Similarly, the higher NH_4^+-N, NO_3^--N, and extractable inorganic N content were found within microaggregate in 2016, which may be caused by the degradation of vegetal root and microbial mortality (Durán et al., 2013; Li et al., 2017).

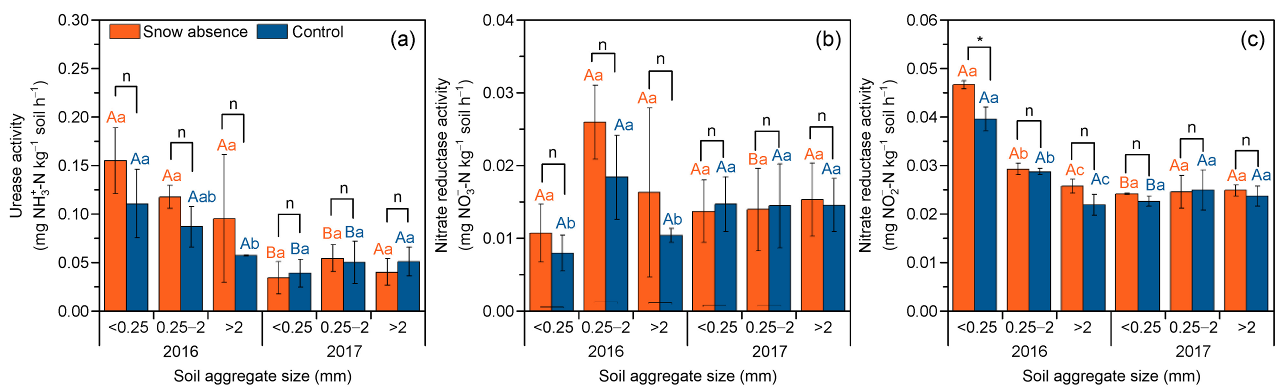

Fig. 3 Soil urease (a), nitrate reductase (b) and nitrite reductase (c) activities in snow absence and control plots. The significant difference between snow absence and control in the same soil aggregate and sampling date is indicated by asterisks ($P < 0.05$) or n ($P > 0.05$). Different lowercase letters denote significant difference between soil aggregate sizes within the same treatment (control or snow absence) in the same sampling date ($P < 0.05$). Different uppercase letters denote significant difference between 2016 and 2017 in the same aggregate sizes and treatment ($P < 0.05$).

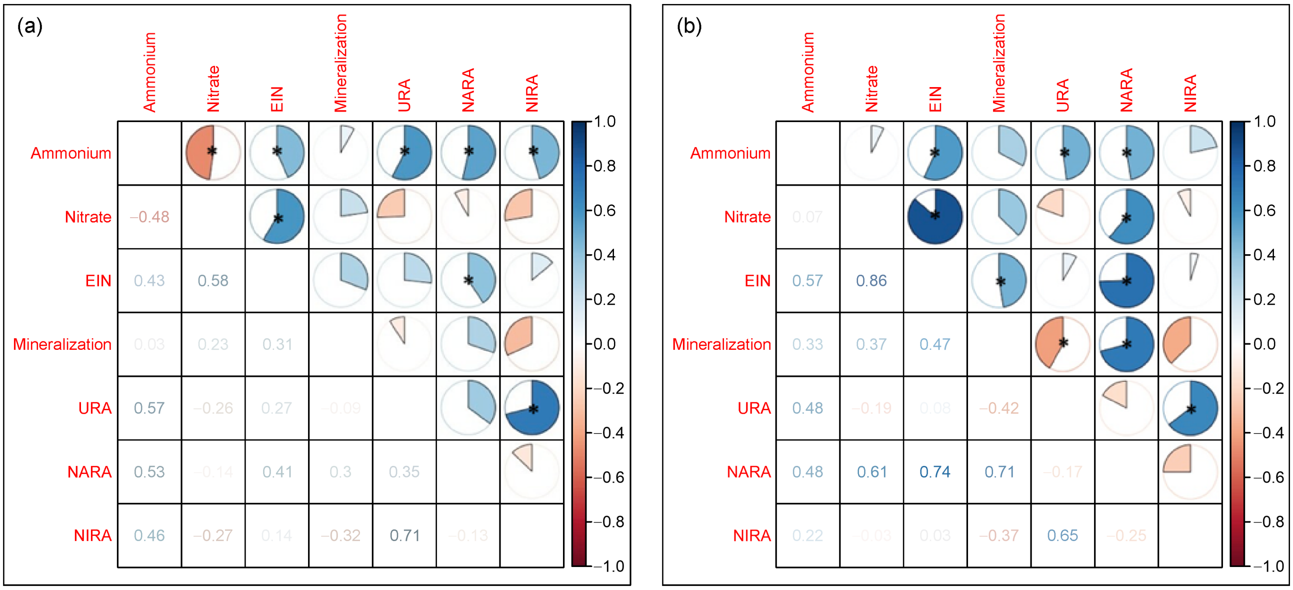

Fig. 4 The Pearson correlation coefficient between soil N pools, net N mineralization rate, and enzyme activities in snow absence (a), and control (b) plots. Abbreviations: EIN: extractable inorganic nitrogen; URA: urease activity; NARA: nitrate reductase activity; NIRA: nitrite reductase activity.

Macroaggregates are more susceptible to the disruptive forces of frost than microaggregate (Six et al., 2004). In this study, snow absence increased soil mineral N in microaggregate but not in macroaggregates. This is because that macroaggregate presents a higher restricted microbial C:N ratio than microaggregate (An et al., 2010). With the input of available C, microbes are forced to assimilate N to maintain the physiologic C:N balance which simultaneously mitigated the effect of snow absence on N dynamic in macroaggregate (Reichel et al., 2018). Macroaggregate contained comparably higher microbial biomass, and the microbial mucilage or hypha improved aggregate structural stability (Six et al., 2004; Jiao et al., 2020). However, due to susceptibility to the disruptive forces of frost, snow absence inevitably disturbed the structural stability to a higher degree in macroaggregate, and, to some extent, increased the microaggregate fraction (Gupta and Germida, 1988; Edwards 1991 and 2013; Steinweg et al., 2008). Thus, a portion of nutrition, microbial biomass, and mineral N was transferred from broken macroaggregate to microaggregate and made a significant difference to mineral N content in different snow condition in microaggregate.

The degradation of SOM (soil organic matter) was controlled by both biotic and abiotic factors, including temperature, moisture, and microorganisms (Freppaz et al., 2008). Freeze–thaw cycles resulted in intensely frozen soil pore water and slower oxygen (O_2) diffusion, which may limit the activity and biomass of soil microorganisms, and the mortality of plant root (Durán et al., 2013; Li et al., 2017). Soil temperature is a vital factor controlling the N dynamics. The observed higher NH_4^+-N content and more intense freezing in 2016 than 2017 implied soil frost is an important driver of winter soil N cycling in spruce forest on the eastern Tibetan Plateau. In addition, studies have showed that soil moisture is also a key factor regulating soil N cycling in cold ecosystems (Xiong et al., 2014; Li et al., 2017). However, no significant differences in soil moisture were found in either winter or growing season between snow manipulations, indicating soil moisture may be less important in affecting N cycling in winter at this site (Yang et al., 2019).

Net N mineralization rate is an important indicator to characterize the soil N supply capacity and evaluate the N cycling process (Zaman and Chang, 2004; Li et al., 2019). Studies have indicated that net N mineralization rate varied with aggregate size fractions (Steinweg et al., 2008). In our experiment, compared to microaggregate and large macroaggregate, the comparably higher net N mineralization rate was found in small macroaggregate in 2016. Several underlying mechanisms can explain this observation. First, macroaggregate coupled with high SOM may stimulate the release of available substrates by the metabolism of soil microorganisms. Second, the relatively rich microbial biomass (e.g., bacteria and fungi) in macroaggregate could be beneficial for SOM mineralization (Guggenberger et al., 1999; Yang et al., 2019). Furthermore, snow absence did not affect soil N mineralization rate but increased soil extractable N content within microaggregate, implying that the increased soil extractable N could be primarily derived from microbial and root mortality rather than from microbial degradation.

Soil enzymes are highly catalytic proteins released from the decomposition of soil animals (e.g., earthworm), microorganisms, and fine root residues (Yi et al., 2018) and their activities are essential sensors for cycling of terrestrial elements (Aon and Colaneri, 2001). Both nitrate and nitrite reductase are key soil enzymes controlling denitrification process (Yi et al., 2018). In this study, snow absence increased soil nitrite activities only within soil microaggregates in 2016, implying that soil denitrification process is not susceptible to snow cover change. The frost-induced increase in soil extractable N may alter soil biological community composition and diversity, which could in turn affect soil enzyme activities. However, further evidence is needed for confirmation.

Furthermore, enzyme activities are also largely regulated by the class size of soil aggregate (Six et al., 2004). However, the aggregate-based pattern in enzyme activities is still inconsistent (Fansler et al., 2005; Bach and Hofmockel, 2014; Fang et al., 2016). For example, extracellular enzyme activity has been found to be higher in small macroaggregate than in microaggregate and large macroaggregate in a corn agroecosystem (Bach and Hofmockel, 2014), but studies in native prairie and agricultural ecosystems observed that enzymes for nutrition cycling presented much higher activities in microaggregate (Fansler et al. 2005). In this case, enzyme activities involved N cycling had distinct distribution patterns within aggregate sizes. Nitrite reductase activity followed a trend of microaggregate > small macroaggregate > large macroaggregate in 2016. This may be due to the fact that microaggregate with small particle size and low O_2 diffusion may provide a suitable environment for anaerobic bacteria (Gupta and Germida, 1988). Moreover, aggregates create a spatially heterogeneous habitat for the synthesis of enzymes due to divergent microorganisms (Jiang et al., 2013). As a result, the aggregate-based patterns of enzyme activities could depend on soil texture-associated microbial composition.

5 Conclusion

This study examined the influence of snow absence on soil N cycling within aggregate in a subalpine spruce forest on the Tibetan Plateau of China. The snow absence generally did not affect the measured parameters related to soil N cycling, indicating that aggregates-based soil N cycling is not vulnerable to winter climate change. Soil N availabilities and enzymatic activity generally differed among the aggregate classes, further highlighting the importance of aggregates as vital units in soil. The effect of snow absence and aggregate size was different between two contrasting years (cold winter and thick snow cover in 2015/2016 and mild winter and thin snow cover in 2016/2017), indicating the importance of winter conditions (e.g., snowfall), and the complexity and uncertainty of winter warming in this specific area. Such findings can further account for the increased N cycling in bulk soil in snow absence plots reported by our previous study (Li et al., 2017). This study can help us to understand below-ground responses to winter climate change in snowy ecosystems.

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