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Belowground plant productivity responds similarly as soil microbial productivity rather than aboveground plant productivity to nitrogen deposition in the Eurasian steppe

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Abstract

Purpose It is a central goal in current ecology to investigate the effects of global changes on ecosystem productivity, which includes above- and below-ground plant productivity as well as soil microbial productivity, but most studies focus on aboveground plant productivity. As plant and microbial communities have different attributes, it is intuitive to hypothesize that belowground plant root productivity will respond to global changes more similarly as aboveground stem/leaf productivity than soil microbial productivity; however, this hypothesis remains largely unexplored.

Methods Here we conducted a long-term nitrogen deposition experiment in the Eurasian steppe, manipulating nine rates (0–50 g N m^{-2} yr^{-1}) at two frequencies under two management strategies (fencing or mowing).

Results Belowground plant productivity was found to respond similarly as soil microbial productivity rather than aboveground plant productivity, contrary to the hypothesis. And this pattern was more obvious under mowing than fencing, because mowing decreased soil water content and caused another pressure beyond the decreased pH induced by N addition.

Conclusions Overall, our results demonstrated the importance of microhabitat (below- or above-ground) relative to community attribute (plants or microorganisms) in determining productivity response to nitrogen deposition, emphasizing the necessity to integratively study the response of both above- and below-ground productivities to global changes.

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Keywords Belowground productivity, Microbial biomass, Nitrogen deposition

Multiple anthropogenic environmental changes such as climate warming and nitrogen (N) deposition have been affecting various types of terrestrial ecosystems, and investigating their influences on ecosystem functions is a central goal in current ecology (Gamfeldt and Roger 2017). Ecosystem productivity is the most studied function over the past two to three decades, although other functions, especially ecosystem multi-functionality, have also received increasing attention. Ecosystem productivity is composed of both aboveground and belowground parts; however, most previous studies quantified only aboveground plant productivity, while neglected belowground plant productivity (that is, the root productivity) and microbial productivity (Mittelbach et al. 2001). Although the roots and microorganisms are in the same belowground microhabitat, the roots and aboveground stems/leaves have the same biological attribute of plant; and thus, it is intuitive for us to hypothesize that belowground plant productivity will respond more similarly as aboveground plant productivity than soil microbial productivity to global changes. However, this hypothesis remains largely unexplored yet.

To test this hypothesis, we conducted a N deposition experiment with nine addition rates (0–50 g N m^{-2} yr^{-1}) at two addition frequencies (twice or 12 times every year) under two grassland management strategies (fencing (un-mowing) or mowing) in a typical steppe ecosystem of Inner Mongolia of China (see details in Method S1), which is representative of much of the Eurasian steppe region floristically and ecologically (Li et al. 1988). In each year from 2012 to 2014, we quantified aboveground plant productivity, belowground root productivity as well as soil microbial productivity (the amount of phospholipid fatty acids; PLFA) for each of 144 plots, and the average productivity of the three years was used to represent the productivity of each plot. Each plot was 8 m × 8 m in area. We adopted three-way ANOVA to evaluate the effects of grassland management strategy, N addition frequency, N addition rate, and their interactions on these productivities, and the effect of N addition frequency was found to be non-significant ($P > 0.05$). Thus, we neglected its influence in the following analyses.

Pearson correlation analysis showed that under fencing, as N addition rate increased (transformed by natural logarithm first, similarly hereinafter), aboveground plant productivity increased (Fig. 1a), while belowground plant and microbial productivity both decreased (Fig. 1b, c); accordingly, belowground plant productivity showed a significantly negative correlation with aboveground plant productivity ($P < 0.05$; Fig. 1d), but a marginally significant positive correlation with soil microbial productivity ($P < 0.10$; Fig. 1f).

The correlations among N addition rate, above- and below-ground plant productivity, and soil microbial productivity under mowing (Fig. 1g-l) were generally similar to those under fencing (Fig. 1a-f). However, the absolute values of these correlation coefficients were generally larger under mowing than under fencing (e.g., $r = 0.877$ in Fig. 1g versus $r = 0.817$ in Fig. 1a). Consistently, the correlation between soil microbial productivity and aboveground plant productivity changed from non-significant under fencing ($P > 0.10$; Fig. 1e) to significant under mowing ($P < 0.05$; Fig. 1k), and the correlation between soil microbial productivity and belowground plant productivity changed from marginally significant under fencing ($P < 0.10$; Fig. 1f) to significant under mowing ($P < 0.05$; Fig. 1l).

N addition increased soil available N (NH_4^+-N and NO_3^--N) content but decreased soil pH (Fig. 2), with the former being beneficial to organisms and the latter being harmful (Zhang et al. 2014). Thus, the positive correlations between aboveground plant productivity and N addition rate under both fencing and mowing (Fig. 1a, g) are likely driven by the elevated soil available N content (Fig. 2a), the negative correlations between belowground plant productivity and N addition rate under both fencing and mowing (Fig. 1b, h) should be attributed to the decreased soil pH (Fig. 2b), and the negative correlations between soil microbial productivity and N addition rate (Fig. 1c, i) should also be due to the decreased soil pH (Fig. 2b). Taken together, it was the decreased soil pH that caused the positive correlations between belowground plant productivity and soil microbial productivity (Fig. 1f, l). In other words, the shared belowground microhabitat drove plant root productivity to respond similarly as soil microbial productivity to N deposition, which was in contrast with our hypothesis that the shared plant attribute would drive belowground root productivity to respond similarly as aboveground stem/leaf productivity to N deposition.

While these results demonstrated the critical role of microhabitat in determining the response of productivity of different biological groups to N deposition, they also revealed the other side of the complex organism-environment (microhabitat) relationship. In particular, the contrasting responses of above- and below-ground plant productivity to N deposition showed their effective adaptation strategy. The belowground roots could not escape the negative influence of decreased soil pH induced by N addition, and thus, their productivity decreased; the aboveground stems/leaves did not encounter the

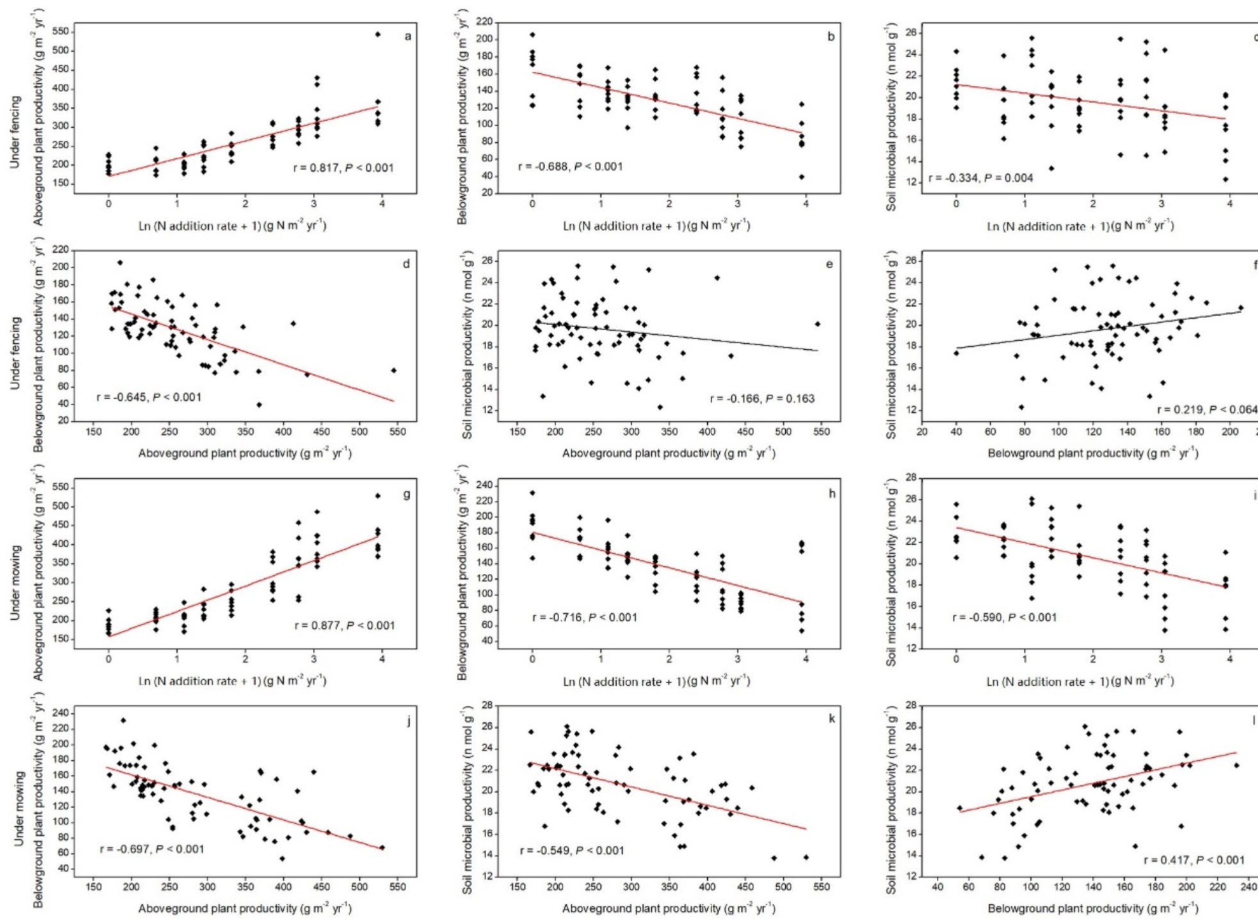

Fig. 1 Results of Pearson correlations among N addition rate (transformed by natural logarithm first), aboveground plant productivity, belowground plant productivity, and soil microbial productivity under fencing (**a**-**f**) or mowing (**g**-**l**)

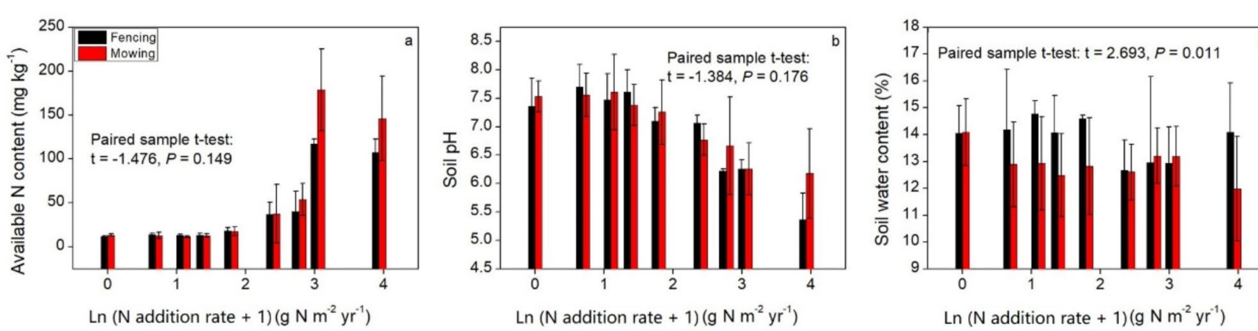

Fig. 2 Effect of grassland management strategies on soil physicochemical indices along the N addition gradient. The N addition rate was transformed by natural logarithm

acidified soil directly, and thus, they selectively enjoyed only the beneficial effect of elevated available N content, leading to the increased aboveground productivity.

The larger absolute values of these correlation coefficients under mowing than under fencing (e.g., Fig. 1a versus Fig. 1g) and the more significant correlations (the smaller *P* values) under mowing than under fencing (Fig. 1e versus Fig. 1k, and Fig. 1f versus Fig. 1l) meant that mowing caused these relationships to be much closer than fencing, which should be due to that mowing decreased soil water content relative to fencing (Fig. 2c), causing another selective pressure to both plants and microorganisms, beyond the selective pressure of the decreased pH. In other words, the double selective pressures strengthened the correlations among N addition rate, above- and below-ground plant productivity, and soil microbial productivity.

Overall, this study revealed that belowground plant productivity responded similarly as soil microbial productivity rather than aboveground plant productivity, contrary to the hypothesis. And thus, these results demonstrated the importance of microhabitat (below- or above-ground) relative to community attribute (plants or microorganisms) in determining productivity response to nitrogen deposition, emphasizing the necessity to integratively study the responses of both above- and below-ground productivities to various global changes under different ecosystem management strategies (Wang et al. 2019).

Supplementary Information

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Supplementary Material 1

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Not applicable.

Author contributions
ZZ, HL and XZ designed the research, BH, JY, ZH, YZ and HG carried out the experiment and drafted the manuscript. XZ improved the writing of the manuscript. All authors have read and approved the final manuscript.

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Data availability
All data analyzed during this study are included in this published article and its supplementary information files.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that there is no competing interest.

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