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Patterns and determinants of the response of plant biomass to addition of nitrogen in semi-arid and alpine grasslands of China

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A R T I C L E I N F O

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A B S T R A C T

Although the effects of adding nitrogen (N) to grasslands have been studied worldwide, little is known about how those effects are, in turn, influenced by climate, soil, and vegetation. Data from such experiments conducted in two main types of grassland in China, alpine and semi-arid, which differed widely in terms of climate, soil, and vegetation, were compiled and analysed to examine the response of above-ground biomass to N. Adding N increased the above-ground biomass by 51% on average. Although the response of biomass showed no obvious trend with the dose of N in the alpine grasslands, the response in the semi-arid grassland peaked at 15–20 g m^{-2} of N applied annually. Nitrogen addition efficiency in the alpine grasslands was higher than that in the semi-arid grasslands. The difference was mainly due to the differences in total soil N and its interactions with the above-ground biomass, which were particularly influenced by the soil's capacity to provide available N. These results suggest that soil N and features of local vegetation should be taken into account in arriving at the appropriate dose of N for a given site.

1. Introduction

Nitrogen (N) is known to be a particularly important nutrient limiting plant growth, and the application of N to increase the productivity of grasslands has been widely studied for many years (Frink et al., 1999; Smith et al., 2000). The deposition of N is commonly regarded as a driver of ecosystem dynamics (Galloway et al., 2004; Phoenix et al., 2006). Thus the effects of adding N on grassland ecosystems have received considerable attention (Fu et al., 2015; Xia and Wan, 2008).

Although external application of N is known to increase biomass, the increase is known to stabilise or even decline as the dose of N increases beyond a threshold. This pattern is usually described as a nonlinear response or N saturation (Aber et al., 1989, 1998; Stevens et al., 2006; Tian et al., 2016) and was observed in several field experiments on grasslands (e.g. Bai et al., 2010; Song et al., 2012). In some cases, addition of excess N adversely affected the plant community (Emmett, 2007; Tian et al., 2016). Excess N may either be lost through volatilization and eluviation, or remain in the soil, leading to harmful effects on plants due to changes in soil properties such as acidification (Aber et al., 2003; Roem and Berendse, 2000). Saturation curves can be plotted along N gradient in grasslands, but the threshold values have not been studied adequately, with large variation in values suggesting that other factors such as differences in climate, soil type and vegetation, are also be at work (Chapin et al., 2002; Xia and Wan, 2008).

Grasslands in China occupy about 4 million km^2 (Ren, 1995), mostly in Inner Mongolia and the surrounding provinces, dominated by the semi-arid temperate steppe, and on the Qinghai–Tibet Plateau, dominated by the alpine steppe. The drought-sensitive semi-arid temperate steppe in northern China occupies 78% of the national grassland and constitutes 27% of the world's temperate grassland biome (Chen and Wang, 2000). The alpine high elevation steppe (~4000 m asl) with low temperature is mainly on the Qinghai–Tibet Plateau, and is sensitive to climate warming (Yang et al., 2009). Although China also has other types of grasslands, almost all experiments involving N have been conducted in these two grassland types, which we refer to hereafter as 'semi-arid' and 'alpine'.

In this paper we test the hypothesis that the semi-arid and alpine grasslands differ in their responses to external N because they differ from each other in terms of climate, soil, and vegetation. Specifically, we wanted to find out whether there were differences in the effect of N saturation on these two grassland types.

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2. Material and methods

2.1. Data collection

The database of papers dealing with the effects of adding N on above-ground biomass in the two grassland types in China comprised 59 research papers published before 2017. We searched the Web of Knowledge of the Institute of Scientific Information (ISI; now Clarivate Analytics) for papers written in English, and the China National Knowledge Infrastructure for papers written in Chinese with English abstracts. The following search terms were used: grassland, steppe, pasture, alpine meadow, rangeland, nitrogen addition, deposition, input, application, fertilization, enrichment, simulated, control manipulated experiments, above-ground biomass, ANPP, growth, forage yield, restoration, China, Inner Mongolia, and Qinghai-Tibet Plateau. The final selection of papers was based on the following criteria: (1) experiments conducted in China, with measurements of above-ground biomass or above-ground net primary production (ANPP), (2) treatments applied to natural ecosystems, with original or native vegetation, excluding artificial grasslands created by local governments, (3) methods and experimental durations clearly recorded, (4) means, standard errors, and sample sizes of above-ground biomass recorded or calculable, and (5) control treatments should be conducted for analysing the responses, and data on control treatments recorded. Mountain grasslands in Yunnan and Xinjiang, and salty meadows in north-eastern China were excluded because their samples were not large enough to yield valid patterns. More details of the database are given in Table S1, and the locations of these study sites are shown in Fig. 1a.

Data on the background factors included mean annual precipitation (MAP), mean annual temperature (MAT), and soil total nitrogen (STN), the values of which were either recorded in the papers or collected from the Internet, with data on STN collected from China soil scientific database (http://www.soil.csdb.cn/page/index.vpage) and those on MAP and MAT from the China meteorological data sharing service system (http://cdc.cma.gov.cn/home.do).

Studies with durations longer than a year, studies containing more than one vegetation type (Bai et al., 2010), and those containing more than one N treatment (Qi et al., 1997) were treated separately while analysing the data. The amount of N added annually ranged from 0.36 g m^{-2} (e.g., Liu et al., 2007) to 50 g m^{-2} (e.g., Xu et al., 2015). The forms of N were urea ($CO(NH_2)_2$), ammonium nitrate (NH_4NO_3), ammonium sulfate $(NH_4)_2SO_4$, and monosodium orthophosphate ($NH_4H_2PO_4$).

2.2. Climate of study sites

Alpine and semi-arid grasslands differed greatly in terms of precipitation and temperature (Fig. 1b). Mean annual and monthly temperatures during 1981–2010 in Haibei, a representative of the alpine grasslands, were significantly lower than those in Xilinhot, a representative of the semi-arid grasslands, whereas the mean monthly and annual values of precipitation were higher in Haibei (Fig. 1c). Water was thus less of a limiting factor in Haibei, though the growing season in Haibei was shorter, with more months showing temperatures below 0 °C.

2.3. Statistical analysis

We followed the methods used in the earlier meta-analyses to evaluate the responses of grassland biomass to the addition of N (Fu et al., 2015; Lu et al., 2011; Luo et al., 2006) and used the log response ratio (lnRR) and nitrogen addition efficiency (NAE) to estimate the effect of N on biomass.

The aforementioned ratio is used as a measure of the magnitude of the effect of N, and the size of the effect was estimated by the natural logarithm of RR (the ratio of the mean value of the concerned variable in N treatment to that in the control), which is a suitable measure for meta-analyses with small bias and approximately normal distribution (Hedges et al., 1999; Luo et al., 2006). Therefore, log response ratio values (lnRR) were calculated as follows:

$$\mathrm{lnRR} = \ln(\overline{\mathrm{X}}_t) - \ln(\overline{\mathrm{X}}_c) \tag{1}$$

where $\overline{\mathrm{X}}_t$ is the mean above-ground biomass in the treatment and $\overline{\mathrm{X}}_c$, that in the control. If different treatments shared the same controls in a given paper, we treated them as independent observations and estimated their variance (v) as follows:

$$v = s_t^2/(n_t\overline{X}_t^2) + s_c^2/(n_c\overline{X}_c^2) \tag{2}$$

where n_t is the sample size for the treatment group and n_c, that for the control groups in the original papers; s_t is the standard deviation for the treatment group; and s_c, that for the control group. The weighted mean of lnRR (RR_{++}) were calculated from the lnRR of individual pair comparison between the treatment and the control, lnRR_{ij} (i = 1, 2,..., m; j = 1, 2,..., k_i). Here m is the number of groups (e.g. different grassland types, different doses of N) and k_i is the number of comparisons in the ith group (different observations). RR_{++} values were calculated as follows:

$$RR_{++} = \left(\sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij} lnRR_{ij}\right) \Big/ \left(\sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij}\right) \tag{3}$$

the standard error, as

$$s(RR_{++}) = 1\Big/\sqrt{\left(\sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij}\right)} \tag{4}$$

where w_{ij} is the weighting factor, estimated as

$$w_{ij} = 1/v \tag{5}$$

The 95% confidence interval (CI) for the log response ratio was

$$95\%\ \mathrm{CI} = RR_{++} \pm 1.96\, s(RR_{++}) \tag{6}$$

If the 95% CI of a response variable overlaps with zero, the RR_{++} of the treatment is not significantly different from that of the control. In this way, studies with greater precision (i.e., lower v) were given a higher weighing in computing RR_{++} so that the precision of the combined estimate and the power of the tests increased (Gurevitch and Hedges, 1999). We also used a Student t-test to examine whether the response ratio was significantly different between groups.

In addition to testing whether the treatment effects differed significantly, we also plotted frequency distributions of lnRR to reflect the variability of individual studies. The frequency distributions were assumed to follow normal distributions and fitted by a Gaussian function (i.e., normal distribution):

$$y = a\exp[(x-\mu)^2/(2\sigma^2)] \tag{7}$$

where x is lnRR, y is the frequency (i.e., number of lnRR values), a is a coefficient showing the expected number of lnRR values at $x = \mu$, μ is the mean of the frequency distributions of lnRR and σ is their variance, and e is the base of the exponent (Fu et al., 2015; Hedges et al., 1999; Lu et al., 2011; Luo et al., 2006).

Nitrogen addition efficiency was calculated as

$$\mathrm{NAE} = \mathrm{lnRR}/\mathrm{NAA} \tag{8}$$

where NAA is amount of N added (nitrogen addition amount). The calculation of NAE follows that of nitrogen use efficiency (NUE), which was originally defined as the dry mass produced per unit N taken up from soil (Hirose, 2011). Here, we use NAA instead of N taken up from the soil to evaluate the effect of adding N. To examine the effects of N on STN, we estimated the amount of STN in 1 m^2 to a depth of 0.4 m (the depth to which most of the grass roots penetrate), which was described as a 'soil block'. When converting mass percentages to mass unit volumes, we used a soil bulk density value of 1.35 g cm^{-3}, typical for