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Non-linear response of plant caloric value to N addition and mowing treatments in a meadow steppe

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Abstract

Background Caloric value is an important indicator of grassland ecosystem function, but the response of caloric value to nitrogen (N) addition and mowing is still unclear. We explored the adaptive changes of plant caloric value and energy standing crop along a N addition gradient after six-year NH_4NO_3 addition and mowing treatments in an Inner Mongolian temperate meadow steppe in northern China.

Results We found that the response of plant caloric value to N addition at different organizational levels was diverse. The caloric value of legumes increased linearly with N addition rates. The caloric value of grasses exhibited a non-linear response trend, initially increasing followed by saturation or decrease, with a N response threshold present. Due to the dominance of grass species, the caloric value at the community level followed a similar pattern to that of the grasses along the N addition gradient. Under mowing, the caloric value of plants at each organizational level increased and usually mowing enhanced the N response threshold. Amongst these, the N response threshold of *Leymus chinensis* increased from 3.302 to 5.443 $\text{g N m}^{-2} \text{yr}^{-1}$, grasses increased from 4.414 to 5.746 $\text{g N m}^{-2} \text{yr}^{-1}$, and community increased from 5.373 to 9.216 $\text{g N m}^{-2} \text{yr}^{-1}$. Under non-mowing treatment, the N response thresholds of the most dominant species, *Leymus chinensis*, and community energy standing crop were 10.001 and 15.119 $\text{g N m}^{-2} \text{yr}^{-1}$, respectively. Under mowing, the energy standing crops showed a linear increasing trend.

Conclusions N response thresholds of plant caloric value and energy standing crop vary at different organizational levels (community > functional group > species). The results reveal varying regulatory capabilities of plants on the ecological environment at different organizational levels. These findings enhance our understanding of plant-environment interactions in grassland ecosystems under N deposition from an energy perspective, which is of great significance to clarify the response mechanism of grassland ecosystem structure and function to N deposition.

Keywords N addition, Mowing, Caloric value, Energy standing crop, Meadow steppe

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Introduction

Caloric value refers to the heat released per unit weight of dry matter after complete combustion, serving as a metric for the energy quality of plants (Hnilička et al. 2020). It is a crucial plant trait that reflects, to a certain extent, plant's photosynthetic capacity, nutritional status, genetic composition, and life history (Golley 1961). Variations in caloric value can indicate differences in plant growth conditions and the influence of various environmental factors, providing a manifestation of plant overall growth status. Caloric value can also reflect the energy storage strategies of plants (Bao et al. 2006; Lin and Cao 2008). Although the caloric value of plants may change with environmental conditions and growth stages, it is relatively stable for a plant species, representing the net result formed during the long-term evolutionary process of adaptation between organisms and their environment, based on physiology and biochemistry. Additionally, the magnitude of caloric value reflects the functional position of a species within a community (Bao et al. 2007). There is a significant correlation between species' caloric values and their dominance within the community, with dominant species having higher caloric values than the secondary species (Bao et al. 2007). Therefore, the caloric value provides an accurate and objective evaluation of competition in the community and adaptation in the individual, two fundamentally important processes in plant life (Long 1934). The combination of caloric value and biomass, known as the energy standing crop, can make different types of ecosystems comparable, and is an important indicator for assessing the net primary productivity of ecosystems (Golley 1961). Grassland ecosystems are widely distributed globally and play a significant role in carbon storage and other ecosystem services (Lal et al. 2018; Richter et al. 2021). They are vital sources of human foods, medicines, and livestock forages, among others (Dubeux and Garcia 2022), and hold substantial ecological and economic values.

Grassland ecosystems are also N-limited terrestrial ecosystems (LeBauer and Treseder 2008). Numerous studies indicate that increased nitrogen (N) input alleviates species competition for N resources (Newman 1973), enhances photosynthesis (Shen et al. 2019; Wang et al. 2021a), boosts productivity (Thomas et al. 2010; Chen et al. 2015), intensifies light competition (Hautier et al. 2009), and simultaneously improves forage quality (Ding et al. 2021; Marcinkevičienė et al. 2021). However, long-term N addition leads to N accumulation in the soil, causing soil acidification (Stevens et al. 2004; Horswill et al. 2008; Tian and Niu 2015), reduced species diversity (Suding et al. 2005; Clark and Tilman 2008; Bobbink et al. 2010; Isbell et al. 2013), altered community composition (Dickson et al. 2014; Hu et al. 2021), and significant

damage to ecosystem structure and functions (Cardinale et al. 2012; Isbell et al. 2015), leading to grassland ecosystem degradation and impacting ecosystem stability (Bai et al. 2010; Hautier et al. 2014; Zhang et al. 2016). These studies have primarily focused on the impact mechanisms of N deposition on ecosystems from the perspectives of material production and ecological effects of environmental changes but overlooking the change of energy, an essential characteristic of ecosystem functions. Research has shown that with the increase of N addition rates, plants adapt to the N-enriched environment by altering a series of functional traits to adopt a faster nutrient cycling strategy (Wright et al. 2004; Yang et al. 2022). Previous studies have indicated that N fertilization can enhance the caloric values of rice, *Helianthus tuberosus* L., and grassland plant communities (Yang et al. 2001; Neitzke 2002; Gao et al. 2012). Further research is needed to explore whether such positive effect on plant caloric value strengthens with increasing N addition rates or whether there exists a N saturation threshold for plant caloric value.

Mowing is a common grassland utilization measure and the primary means of forage collection (Maron and Jefferies 2001; Tälle et al. 2016). In the context of N deposition, when combined with mowing treatments, it represents a prospective management practice for future grasslands (Lepš 2014). Mowing allows for the removal of a substantial amount of aboveground biomass and nutrients from the ecosystem, reducing N accumulation in the soil and mitigating the effects of eutrophication (Li et al. 2022). Mowing weakens the positive impact of N deposition on productivity, and this effect is stronger under enriched N conditions compared to conditions without N addition (Ferraro and Oesterheld 2002). Mowing also reduces light competition among plants (Borer et al. 2014), weakens the dominance of tall rhizomatous grasses like *Leymus chinensis* (Yang et al. 2019), and enhances the dominance of short-statured perennial grasses and forbs (Collins et al. 1998; Hautier et al. 2009), leading to shifts in community composition (Connell 1978; Zhang et al. 2017; Hou et al. 2019). Although the impacts of mowing on aboveground vegetation and soil physicochemical properties have been extensively reported, its influence on plant energy has received less attention. Existing research indicates that mowing treatments can affect plant caloric value. Bao et al. (2001; 2003) found that within a certain intensity range, grazing disturbance in alpine grasslands increased the caloric value and energy accumulation of *Trifolium repens* and *Dactylis glomerata*. Different species show varying responses in caloric value to mowing, with some species experiencing a reduction, others showing no significant change, and some benefiting from an increase

in plant caloric value (Bao et al. 2005). However, the effects of combined N addition and mowing treatments on plant energy have not been addressed.

Currently, there is a lack of global research quantifying the response patterns of plant caloric value to N addition rates in terrestrial ecosystems and investigating the existence of a N saturation threshold. Moreover, little is known about how this response pattern may alter with the imposition of additional mowing treatments. To address these knowledge gaps, we conducted a controlled experiment in a meadow grassland plant community of Inner Mongolia, China. Our study aimed to explore the impacts of N addition and mowing on plant energy parameters [caloric value (energy quality), energy standing crop (energy quantity), and fixation energy efficiency of N] in the temperate grasslands of northern China, focusing on three organizational levels: species, functional groups, and communities. Furthermore, we sought to quantitatively analyze the N saturation threshold of plant energy. The study aims to address the following key questions: (1) What is the linear or non-linear response of plant energy at different organizational levels to the N addition gradient? If a non-linear response is observed, what constitutes the non-linear N saturation threshold? (2) How does the mowing treatment impact the N response trajectory and N saturation threshold of energy at varying organizational levels, respectively and interactively? Our results provide insights into plant responses to N deposition environments from an energy perspective.

Materials and methods

Study site

The field experiment was conducted in the Erguna Forest-Steppe Ecotone Research Station (50°10' N, 119°22' E, elevation 527 m), Inner Mongolia, northern China. The mean annual temperature (1957–2016) is -2.45 °C, ranging from -28.0 °C in January to 19.1 °C in July. The mean annual precipitation is 363 mm, with over 80% occurring in the growing season from May to September. The soil of the study site was classified as chernozem based on the US soil taxonomy classification. The pH and the organic matter concentration of topsoil (0–10 cm) under natural vegetation are 6.8–7.0 and 2%–4%, respectively. The dominant species in this ecosystem are *L. chinensis*, and *Stipa baicalensis*, which together account for more than 80% of the total aboveground biomass (Table S1). Previous studies from this region showed that this grassland is N-limited, as indicated by the great enhancement of aboveground biomass of *L. chinensis* following N enrichment (Bai et al. 2010; Zhang et al. 2015), and no fertilizers were applied before the experiment.

Experimental design

This N addition experiment started in 2014, following a completely randomized block design to study the effects of rates and types [NH_4NO_3 , $(\text{NH}_4)_2\text{SO}_4$, NH_4HCO_3 , $\text{CO}(\text{NH}_2)_2$, slow-release $\text{CO}(\text{NH}_2)_2$] of N addition on plants (Yang et al. 2019). For this study, we chose to add NH_4NO_3 as the N compounds. There were six N addition rates (0, 2, 5, 10, 20, and $50 \text{ g N m}^{-2} \text{ yr}^{-1}$), crossed with mowing treatments (unmown vs. mown) and resulting in twelve treatments. There were eight replicates for each treatment (96 plots in total). The size of each plot was $10 \text{ m} \times 10 \text{ m}$ and separated by 1 m walkways. N fertilizer was added annually at the beginning of the growing season (late May), for 7 continuous years (2014–2020). NH_4NO_3 was mixed with sand (0.5 kg in each plot) and then broadcast uniformly by hand to the N addition plots. To avoid the effects of sand addition, the same amount of sand was added to plots without N addition. Mowing was conducted annually in late August (that is after aboveground biomass sampling) at the height of 10 cm above the soil surface. The harvested biomass was removed from the plots to simulate hay harvest.

Sampling and caloric analysis

Plant aboveground biomass was sampled by a $1 \text{ m} \times 1 \text{ m}$ quadrat in mid-August across 2019–2020. To avoid edge effects, the quadrat was randomly placed at least 50 cm inside the border of each plot. All living vascular plants were sorted into species, weighed after oven-drying for 48 h at 65 °C, and then ground with a ball mill (Retsch MM 400, Retsch GmbH & Co KG, Haan, Germany). Species abundance and height were recorded in the same quadrat in which aboveground biomass was measured. The plant samples (powders) were thoroughly mixed after passing through a 20-mesh screen, and then compressed into pellets in preparation for caloric determination. Triplicate caloric determinations were performed for each sample using a Parr 6400 automatic isoperibol calorimeter (Parr Instrument Company, Moline, IL, USA). The relative variation between the three replicates of each sample was limited below 1%. Not all species collected enough biomass for each quadrat, so a total of 1309 samples of 49 species were pooled to determine caloric values (Table S1). In this article, the caloric values were expressed as the kJ g^{-1} oven-dry weight.

Calculation and statistical analysis

Data were analyzed at three levels: the species level, the functional groups level, and the community level. Four major species were selected for analysis: *L. chinensis* (dominant species), *S. baicalensis* (dominant species), *Thermopsis lanceolata* (common species, and unique

among legume plants), and *Potentilla bifurca* (common species). The functional groups were divided into three categories. The grassland is a meadow steppe dominated by *L. chinensis* and *S. baicalensis*. Grass plants have a high dominance, and due to the particularity of N fixation of their rhizobia of legume plants. Therefore, in this study, 49 species were divided into three functional groups: grasses (6 species in total), legumes (3 species in total), and forbs (non-grasses) (40 species in total) (Hector et al. 1999), the specific classification is shown in Table S1. The energy was analyzed from three perspectives: energy quality (caloric value), energy quantity (energy standing crop), and fixation energy efficiency of N. The study investigated the effects of N addition, mowing, and their interaction on the energy of different organizational levels.

Importance values of species served to indicate the function and dominant degree of species in the community, i.e. species dominance was expressed by relative biomass. That is:

$$\text{Relative biomass (\%)} = \frac{A_i}{B} \times 100$$

where A_i represents the aboveground biomass of species i , and B is the community biomass.

Energy standing crop refers to the total energy accumulated per unit area at a certain time, which is equal to the product of biomass and its caloric value, and is a measure of energy at the level of quantity.

$$\text{Energy standing crop of species} = B_i \times C_i$$

where B_i represents the biomass of species i , and C_i is the caloric value of the species.

Functional group (or community) caloric value is the overall mean of caloric value across all species (n) weighted by each species' relative aboveground biomass in each functional group (or plot):

$$\text{Functional group (or community) caloric value} = \sum_{i=1}^n D_i \times C_i$$

where D_i represents the relative biomass of species i in the functional group (or community), C_i is the caloric value of the species, and n is the number of species included in the functional group (or community).

$$\text{Energy standing crop of functional group (or community)} = \sum_{i=1}^n B_i \times C_i$$

where B_i represents the biomass of species i in the functional group (or community), C_i is the caloric value

of the species, and n is the number of species included in the functional group (or community).

The fixation energy efficiency of N refers to the energy added by plants per unit area for every 1 g of N addition.

$$\text{Fixation energy efficiency of N} = \frac{E_x - E_0}{x}$$

where x is the N addition rates (2, 5, 10, 20, and 50 g N m⁻² yr⁻¹) in the community, E_0 is the energy standing crop of the community (or species or functional group) in the N addition rates of 0, E_x is the energy standing crop of the community (or species or functional group) in the N addition rates of x .

Community production refers to the total biomass of all living species within a quadrat, which in this study consisted of 61 species. Community caloric value was estimated from data for all species' relative biomass and caloric values. Since not all species with each quadrat collected enough biomass to measure caloric values, missing data could potentially affect the analysis, community caloric values were computed only for quadrats having at least 80% of relative biomass. The biomass of the 49 species that we included in the caloric value study was more than 90% of the total biomass in the field N addition experiment.

Data were detected for normality by Kolmogorov–Smirnov test and for variance homogeneity by Levene's test. One-way analysis of variance (ANOVA) was used to analyze the differences in energy among species (or functional group) without N addition followed by Tukey's multiple comparison post hoc test. A repeated-measures mixed model ANOVA was performed using the "nlme" package in R to test the effects of N addition rate, mowing and their interaction on plant energy at different organizational levels. N addition rate and mowing were set as the fixed factors, year as a repeated-measures factor and plot as a random factor. All statistical analyses were performed in R 4.3.1 (R Core Team 2023).

Determination of the thresholds

A piecewise linear model (Origin 2021 built-in function) was used to identify the threshold for the responses of plant caloric value, energy standing crop, and fixation energy efficiency of N at different organizational levels to increasing N addition rates. The data were log₁₀

transformed to meet the assumption of normality, and two-stage linear fitting of non-mowing and mowing treatments

for their mean values of 2019–2020. A piecewise linear regression with one breakpoint (threshold) can be described as follows (Muggeo 2003; Toms and Lesperance 2003):

$$y = a_1 + k_1x \quad \text{if } (x < x_i)$$

$$y = a_1 + k_1x_i + k_2(x - x_i) \quad \text{if } (x \geq x_i)$$

where x is the variable, y is the response, a_1 is the intercept; k_1 is the slope for N addition rates (x) in the piecewise regression model to the left of the breakpoint (x_i); k_2 is the slope of the line segment to the right of the breakpoint (Table 4). Least-squares error technique is applied to fit the model to the observations to determine x_i and k_1, k_2 . The necessity of introducing turning points is tested statistically with the T -test under the null hypothesis that k_1 and k_2 are not different from zero. In addition to the T -test, diagnostic statistics are calculated for the regression analysis. These include the goodness-of-fit measure (R^2), the p -value for the overall model, and the p -values for the trends observed in each section. We consider $p < 0.05$ as significant.

Results

Effects of N addition and mowing on species energy

The results indicated that *T. lanceolata*, *L. chinensis*, and *S. baicalensis* exhibited significantly higher caloric values than *P. bifurca* (Fig. 1a). *L. chinensis* had the highest energy standing crop, significantly surpassing the other three species (Fig. 1c).

N addition treatments significantly influenced the caloric values of *L. chinensis*, *S. baicalensis*, *T. lanceolata*, and *P. bifurca* ($N: p < 0.05$; Table 1(a)). With increasing N addition rates, the caloric values of *L. chinensis* and *S. baicalensis* exhibited an initial increase followed by a decline (Fig. S1c, f; Fig. 2a, b). Piecewise linear regression analysis indicated a turning point in the relationship between caloric values and N for *L. chinensis* and *S. baicalensis* at $\ln(N+1) = 1.459$ and $1.792 \text{ g N m}^{-2} \text{ yr}^{-1}$, respectively (Fig. 2a, b; Table 4). The response thresholds to N were $3.302 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $5.001 \text{ g N m}^{-2} \text{ yr}^{-1}$ for *L. chinensis* and *S. baicalensis*, respectively. The caloric value of *T. lanceolata* exhibited a linear increase with N addition rates (Fig. S1i; Fig. 2c). Mowing significantly increased the caloric values of all species ($M: p < 0.001$; Table 1a; Fig. S1c, f, i, l; Fig. 2a, b, c, d). There was no significant interaction between N addition and mowing treatments on the caloric values of the species ($N \times M: p > 0.05$; Table 1a). Under mowing treatments, the trend

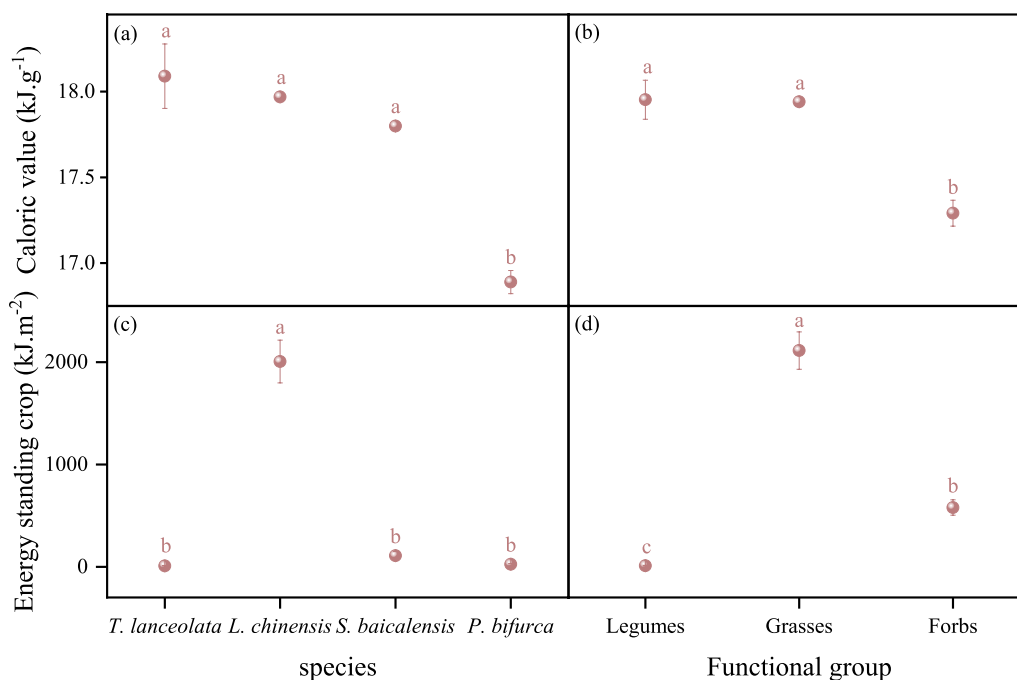


Fig. 1 The difference in caloric values and energy standing crop of four species and three functional groups without N addition (mean ± standard error). **a** and **b** represent the caloric values for species and functional groups, respectively, while **c** and **d** represent the energy standing crop for species and functional groups, respectively. The different lowercase letters indicate significant differences at $p < 0.05$ levels among species levels / functional group levels

Table 1 Results (*F* values) of the repeated-measures ANOVA for the effects of mowing (M), N addition rates (N), year (Y), and their interactions on species caloric value (a), energy standing crop (b), and fixation energy efficiency of N (c)

	<i>L. chinensis</i>			<i>S. baicalensis</i>			<i>T. lanceolala</i>			<i>P. bifurca</i>		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
(a)												
N	5,84	16.202	0.000	4,46	16.003	0.000	5,56	6.133	0.000	5,49	2.736	0.029
M	1,84	270.339	0.000	1,46	88.676	0.000	1,56	22.273	0.000	1,49	72.958	0.000
Y	1,81	26.759	0.000	1,14	0.284	0.602	1,14	19.499	0.001	1,22	4.702	0.041
N×M	5,84	2.005	0.086	4,46	1.323	0.276	5,56	1.467	0.215	5,49	1.484	0.212
N×Y	5,81	1.873	0.108	4,14	0.907	0.486	5,14	3.759	0.023	5,22	0.988	0.448
M×Y	1,81	88.133	0.000	1,14	4.791	0.046	1,14	83.334	0.000	1,22	71.773	0.000
N×M×Y	5,81	0.622	0.684	4,14	0.415	0.795	5,14	0.355	0.871	5,22	1.770	0.161
(b)												
N	5,84	33.613	0.000	4,46	3.801	0.009	5,56	0.579	0.716	5,49	1.873	0.116
M	1,84	83.890	0.000	1,46	9.761	0.003	1,56	2.464	0.122	1,49	1.233	0.272
Y	1,81	105.856	0.000	1,14	3.402	0.086	1,14	2.945	0.108	1,22	8.495	0.008
N×M	5,84	6.461	0.000	4,46	1.744	0.157	5,56	1.140	0.350	5,49	1.027	0.412
N×Y	5,81	4.696	0.001	4,14	0.537	0.711	5,14	2.168	0.117	5,22	1.108	0.384
M×Y	1,81	1.402	0.240	1,14	0.035	0.855	1,14	0.022	0.885	1,22	0.898	0.354
N×M×Y	5,81	2.704	0.026	4,14	0.148	0.961	5,14	0.522	0.756	5,22	1.895	0.136
(c)												
N	4,70	6.564	0.000	3,35	3.828	0.018	4,43	1.033	0.401	4,39	6.245	0.001
M	1,70	0.286	0.594	1,35	4.010	0.053	1,43	0.309	0.581	1,39	0.875	0.355
Y	1,66	2.631	0.110	1,12	2.079	0.175	1,9	3.453	0.096	1,16	10.721	0.005
N×M	4,70	0.278	0.892	3,35	2.141	0.113	4,43	1.262	0.300	4,39	0.814	0.524
N×Y	4,66	2.103	0.090	3,12	1.366	0.300	4,9	2.531	0.114	4,16	1.493	0.251
M×Y	1,66	0.133	0.717	1,12	0.934	0.353	1,9	0.080	0.783	1,16	1.043	0.322
N×M×Y	4,66	1.438	0.231	3,12	0.261	0.852	4,9	0.427	0.786	4,16	0.616	0.657

df denote the numerator and denominator degrees of freedom, respectively

in caloric values of each species along the N addition rates remained consistent with non-mowing (Fig. 2a, b, c, d). The N turning points for the caloric values of *L. chinensis* and *S. baicalensis* were $\ln(N+1)=1.863$ and 1.792 g N m⁻² yr⁻¹, respectively (Fig. 2a, b). The response thresholds to N were 5.443 g N m⁻² yr⁻¹ and 5.001 g N m⁻² yr⁻¹ for *L. chinensis* and *S. baicalensis*, respectively. Under mowing influence, the N response threshold for caloric value in *L. chinensis* increased, while the threshold remained unchanged for *S. baicalensis*.

The N addition treatments significantly influenced the energy standing crop of *L. chinensis* (N: $p<0.001$; Table 1b). The energy standing crop exhibited an initial increase followed by saturation with changing N addition rates (Fig. 2e; Table 4). The N turning point in the relationship between energy standing crop and N for *L. chinensis* was $\ln(N+1)=2.398$ g N m⁻² yr⁻¹ (Fig. 2e; Table 4), with a N response threshold at 10.001 g N m⁻² yr⁻¹. However, mowing treatments reduced the energy standing crop of *L. chinensis* (M: $p<0.001$; Table 1b), and there was a significant interaction between N addition

and mowing (N×M: $p<0.001$; Table 1b). Under mowing treatments, the energy standing crop of *L. chinensis* exhibited a linearly increasing trend with N addition rates. N addition and mowing treatments significantly influenced the energy standing crop of *S. baicalensis* (N: $p<0.01$; M: $p<0.01$; Table 1b), and the energy standing crop of *S. baicalensis* increased first and then decreased with the increase of N addition rates under mowing treatments (Fig. 2f). The N turning point in the relationship between energy standing crop and N for *S. baicalensis* was $\ln(N+1)=2.132$ g N m⁻² yr⁻¹ (Fig. 2f; Table 4), with a N response threshold at 7.432 g N m⁻² yr⁻¹.

The N addition treatments significantly influenced the fixation energy efficiency of N in *L. chinensis*, *S. baicalensis*, and *P. bifurca* (N: $p<0.05$; Table 1). Specifically, *L. chinensis* exhibited a distinct linear decrease trend (Fig. 2i), while *P. bifurca* demonstrated a linear increase trend in response to N addition (Fig. 2l). The impact of mowing on the fixation energy efficiency of N of all species was not significant (M: $p>0.05$; Table 1c; Fig. 2i–l).

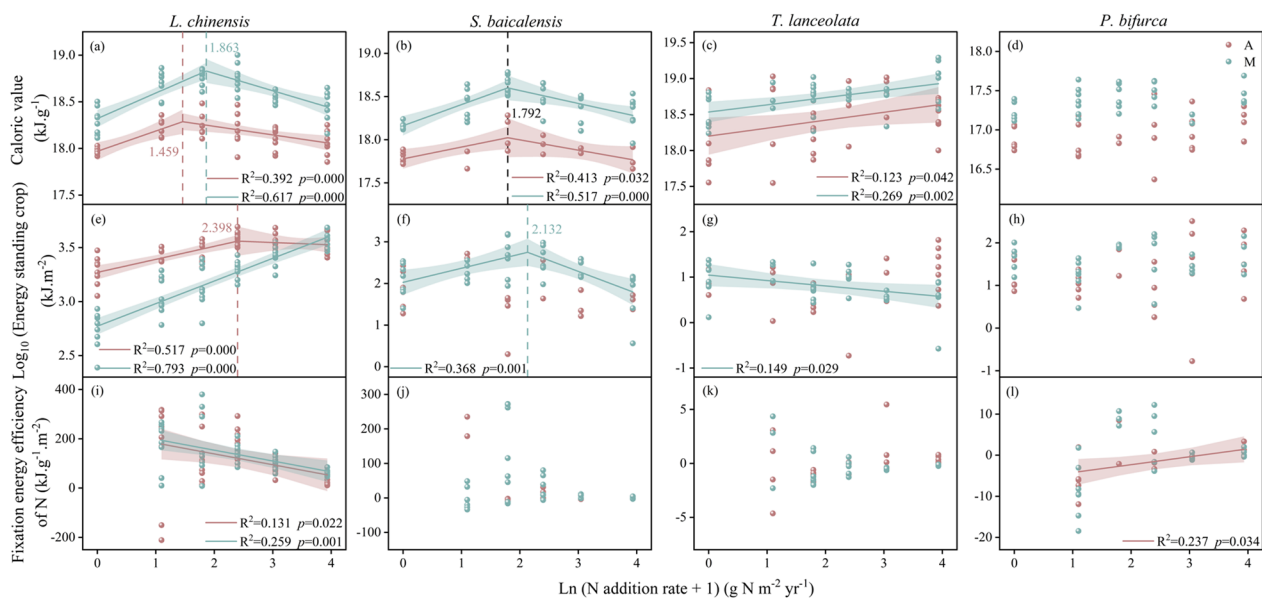


Fig. 2 The relationship between N addition rates and caloric value (a–d), energy standing crop (e–h) and fixation energy efficiency of N (i–l) of species on average from 2019 to 2020. Nonlinear fit is piecewise linear regression model with breakpoints estimation, \ln indicates natural logarithm, A indicate non-mowing treatment, M indicate mowing treatment, shaded indicate 95% confidence interval

Effects of N addition and mowing on functional group energy

As for different functional groups, legumes and grasses exhibited significantly higher caloric values than forbs (Fig. 1b). In terms of energy standing crops, the pattern was grasses > forbs > legumes (Fig. 1d).

The analysis of variance indicated that N addition significantly affected the caloric values of the three functional groups (N: $p < 0.01$; Table 2a). With increasing N addition rates, legumes showed a linear increase in caloric value (Fig. S2c; Fig. 3a). Caloric values of grasses exhibited an initial increase followed by a decrease (Fig. S2f; Fig. 3b), with a N turning point at $\ln(N+1) = 1.689$ $\text{g N m}^{-2} \text{yr}^{-1}$ (Fig. 3b; Table 4), and a N response threshold of 4.414 $\text{g N m}^{-2} \text{yr}^{-1}$. Forbs showed irregular changes in caloric value in response to the N addition gradient (Fig. S2i; Fig. 3c). Mowing significantly increased the caloric values of legumes and grasses (M: $p < 0.001$; Table 2a; Fig. S2c, f), but had no significant effect on the caloric value of forbs (M: $p = 0.816$; Table 2a; Fig. S2i). Under mowing treatments, the trend of caloric values for legumes and grasses along the N addition gradient remained consistent with the non-mowing condition. The N turning point for grasses was $\ln(N+1) = 1.909$ $\text{g N m}^{-2} \text{yr}^{-1}$ (Fig. 3b; Table 4), with a N response threshold of 5.746 $\text{g N m}^{-2} \text{yr}^{-1}$, slightly higher than that of the non-mowing condition. Forbs showed an initial increase followed by a decrease in caloric value (Fig. S2i; Fig. 3c), with a N turning point at $\ln(N+1) = 2.405$ $\text{g N m}^{-2} \text{yr}^{-1}$ (Fig. 3c; Table 4), and a N response threshold of 10.078 g N

$\text{m}^{-2} \text{yr}^{-1}$. The interaction between N addition and mowing significantly affected the caloric values of grasses and forbs (N \times M: $p < 0.01$; Table 2a; Fig. S2f, i).

N addition significantly affected the energy standing crop of grasses and forbs (N: $p < 0.01$; Table 2b), but had no significant impact on legumes (N: $p > 0.05$; Table 2b). Along the N addition gradient, grasses exhibited a linear increase in energy standing crop (Fig. 3e), while forbs showed a linear decrease (Fig. 3f). Mowing significantly impacted the energy standing crop of grasses and forbs (M: $p < 0.001$; Table 2b), and did not alter the trend of energy standing crop for grasses and forbs in response to N addition (Fig. 3e, f). Under mowing treatments, the mean energy standing crop of legumes demonstrated a linear decrease (Fig. 3d). The interaction between N addition and mowing significantly affected the energy standing crop of grasses and forbs (N \times M: $p < 0.01$; Table 2b).

The effects of N addition on the fixation energy efficiency of N of grasses and forbs were significant (N: $p < 0.001$; Table 2c), while there was no significant impact on legumes (N: $p > 0.05$; Table 2b). With increases in N addition rates, the fixation energy efficiency of N in grasses demonstrated a linear decrease (Fig. 3h), while legumes and forbs exhibited a linear increase (Fig. 3g, i). Mowing treatment did not alter the N response trend of fixation energy efficiency of N in grasses (M: $p > 0.05$; Table 2c), whereas fixation energy efficiency of N in

Table 2 Results (*F* values) of the repeated-measures ANOVA for the effects of mowing (M), N addition rates (N), year (Y) and their interactions on caloric value (a), energy standing crop (b), and fixation energy efficiency of N (c) of functional group

	Legumes			Grasses			Forbs		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
(a)									
N	5,55	7.935	0.000	5,84	22.676	0.000	5,82	3.537	0.006
M	1,55	24.069	0.000	1,84	143.794	0.000	1,82	0.054	0.816
Y	1,16	23.852	0.000	1,81	28.295	0.000	1,69	3.535	0.064
N×M	5,55	1.846	0.119	5,84	4.958	0.001	5,82	3.627	0.005
N×Y	5,16	3.901	0.017	5,81	2.111	0.072	5,69	1.273	0.286
M×Y	1,16	87.094	0.000	1,81	67.056	0.000	1,69	10.505	0.002
N×M×Y	5,16	0.620	0.687	5,81	0.526	0.756	5,69	3.285	0.010
(b)									
N	5,54	0.865	0.511	5,84	34.521	0.000	5,81	4.697	0.001
M	1,54	2.403	0.127	1,84	32.521	0.000	1,81	38.157	0.000
Y	1,11	2.785	0.123	1,81	95.688	0.000	1,68	4.909	0.030
N×M	5,54	1.427	0.229	5,84	4.941	0.001	5,81	5.056	0.000
N×Y	5,11	1.040	0.442	5,81	4.601	0.001	5,68	1.274	0.286
M×Y	1,11	0.001	0.983	1,81	2.973	0.089	1,68	0.415	0.521
N×M×Y	5,11	0.574	0.719	5,81	3.073	0.014	5,68	0.771	0.574
(c)									
N	4,43	1.447	0.235	4,70	12.768	0.000	4,67	11.024	0.000
M	1,43	1.088	0.303	1,70	3.249	0.076	1,67	36.763	0.000
Y	1,10	0.171	0.688	1,67	1.009	0.319	1,55	3.574	0.064
N×M	4,43	2.692	0.043	4,70	1.406	0.241	4,67	6.478	0.000
N×Y	4,10	0.418	0.792	4,67	0.604	0.661	4,55	0.382	0.821
M×Y	1,10	7.514	0.021	1,67	4.999	0.029	1,55	3.218	0.078
N×M×Y	4,10	1.300	0.334	4,67	2.422	0.057	4,55	0.788	0.538

df denote the numerator and denominator degrees of freedom, respectively

legumes and forbs showed irregular changes under the influence of mowing (N×M: $p < 0.05$; Table 2c; Fig. 3g, i).

Effects of N addition and mowing on community energy

N addition and mowing significantly affected the community's caloric value, energy standing crop, and fixation energy efficiency of N (N: $p < 0.001$; M: $p < 0.001$; Table 3), with a significant interaction between the two (N×M: $p < 0.01$; Table 3).

With an increase in the N addition rates, the caloric value of the community showed an initial increase followed by a saturation trend (Fig. S3c; Fig. 4a; Table 4). The turning point for the relationship between the caloric value of community and N was $\ln(N+1) = 1.852 \text{ g N m}^{-2} \text{ yr}^{-1}$, with a N response threshold of $5.373 \text{ g N m}^{-2} \text{ yr}^{-1}$. Under mowing treatments, the turning point shifted to $\ln(N+1) = 2.324 \text{ g N m}^{-2} \text{ yr}^{-1}$, with a N response threshold of $9.216 \text{ g N m}^{-2} \text{ yr}^{-1}$. Mowing treatment increased the N response threshold for the community's caloric value.

The energy standing crop of the community showed an initial increase followed by a saturation trend with changes in N addition rates (Fig. S3f; Fig. 4b; Table 4). The turning point for the relationship between the energy standing crop of the community and N was $\ln(N+1) = 2.780 \text{ g N m}^{-2} \text{ yr}^{-1}$, with a N response threshold of $15.119 \text{ g N m}^{-2} \text{ yr}^{-1}$. Under mowing treatments, the energy standing crop of the community showed a linear increase trend along the N addition gradient.

With an increase in the N addition rates, the fixation energy efficiency of N in the community showed a linear decrease (Fig. S3i; Fig. 4c). The addition of mowing treatments did not change this decreasing trend. However, in the low N treatment, the fixation energy efficiency of N in the mowing community was significantly higher than that of the non-mowing community. As the N addition rates increased, this difference gradually narrowed, and by $50 \text{ g N m}^{-2} \text{ yr}^{-1}$, the two were roughly equal (Fig. S3i).

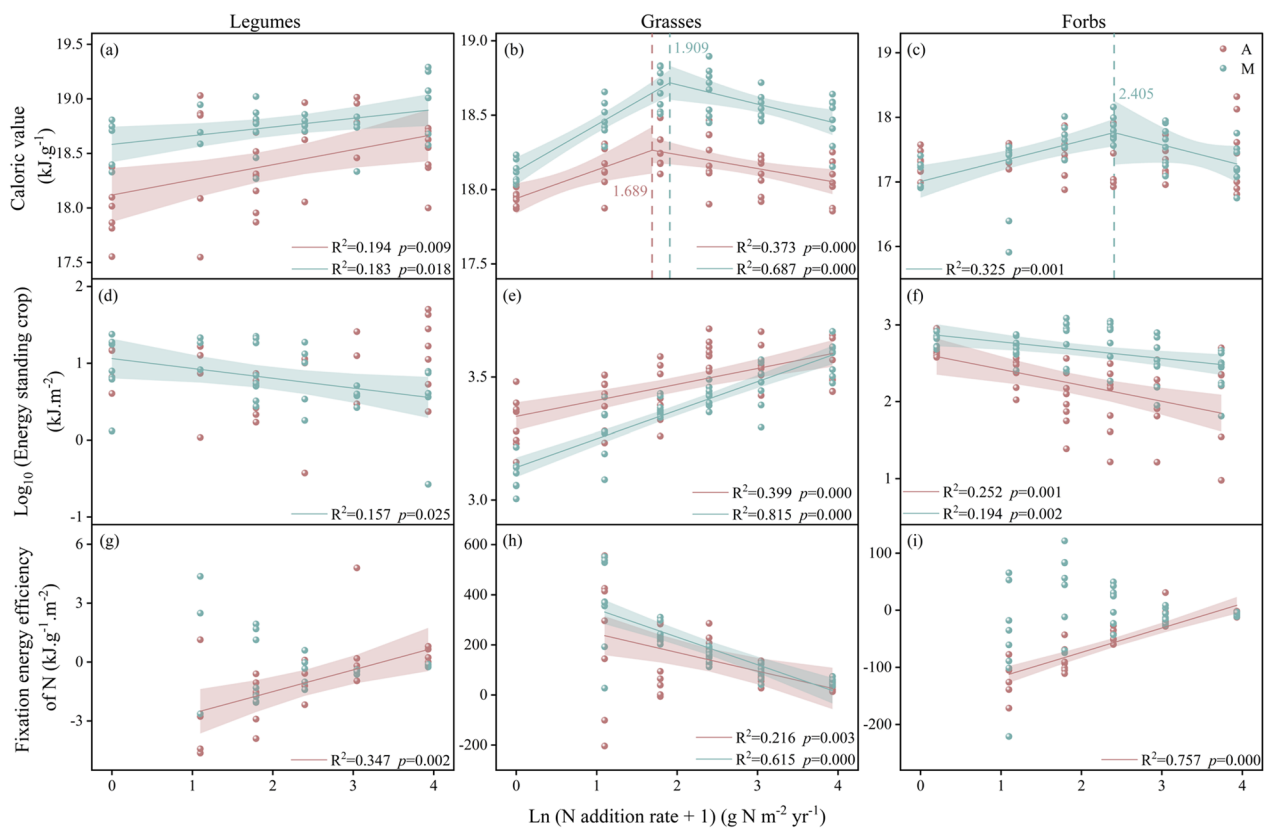


Fig. 3 The relationship between N addition rates and caloric value (a–c), energy standing crop (d–f) and fixation energy efficiency of N (g–i) of functional groups on average from 2019 to 2020. Nonlinear fit is piecewise linear regression model with breakpoints estimation, ln indicates natural logarithm, A indicate non-mowing treatment, M indicate mowing treatment, shaded indicate 95% confidence interval

Discussion

Diverse responses of caloric value at different organizational levels to N addition

Owing to the influence of their inherent genetic characteristics, different species exhibit varying assimilation capacities towards the environment, resulting in differences in caloric values among species (Table S1). It is widely accepted that the caloric values of legumes and grasses are higher than those of forbs (Smith 1967; Chen and Zhang 1993; Bao et al. 2007). Under natural conditions, we studied the caloric values at the species level (four dominant or common species) and the functional group level. The results showed that legumes and grasses had significantly higher caloric values than forbs (Fig. 1a, b). The caloric value differences among different life forms of plants may be due to differences in the chemical components within the plant body (Bao et al. 2006; Gao et al. 2012). The carbon content of plants affects the size of their caloric values (Song et al. 2016), as carbon constitutes the framework of high-energy organic substances such as lignin and fats. Our study also revealed a highly significant positive correlation between

plant caloric value and carbon content (Fig. 5, $R^2=0.591$, $P<0.001$). The higher caloric value of legumes is mainly related to their higher protein and fats content and lower cellulose content (Chen and Zhang 1993; Buxton and Redfearn 1997; Wen et al. 2022). The differences in plant caloric values also reflect disparities in competitiveness and energy storage strategies among vegetation in different ecological niches (Mendes et al. 2001; Lin and Cao 2008; Bao et al. 2007). Among them, the grasses *L. chinensis* and *S. baicalensis* are the dominant species in the community, while the forb *P. bifurca* is considered a companion species. Our study found that under the conditions of human disturbance (N addition and mowing), plants with high caloric value have a high dominance in the meadow steppe community (Fig. S4).

Our findings revealed that the addition of N can enhance the caloric values of species (*L. chinensis*, *S. baicalensis*, and *T. lanceolata*), functional groups (legumes and grasses), and communities. Previous studies on the effects of N addition on caloric value have also found that the addition of N can significantly enhance it, but these studies have only been conducted on a single species or

Table 3 Results (F values) of the repeated-measures ANOVA for the effects of mowing (M), N addition rates (N), year (Y) and their interactions on caloric value, energy standing crop, and fixation energy efficiency of N of community

	Caloric value			Energy standing crop			Fixation energy efficiency of N		
	df	F	p	df	F	p	df	F	p
N	5,84	25.622	0.000	5,84	24.521	0.000	4,68	37.555	0.000
M	1,84	22.415	0.000	1,84	13.625	0.000	1,68	24.241	0.000
Y	1,73	9.432	0.003	1,73	63.522	0.000	1,60	0.002	0.967
N×M	5,84	7.158	0.000	5,84	4.364	0.001	4,68	6.103	0.000
N×Y	5,73	1.553	0.184	5,73	3.720	0.005	4,60	2.197	0.080
M×Y	1,73	45.799	0.000	1,73	0.750	0.390	1,60	8.469	0.005
N×M×Y	5,73	1.197	0.319	5,73	2.811	0.022	4,60	3.855	0.008

df denote the numerator and denominator degrees of freedom, respectively

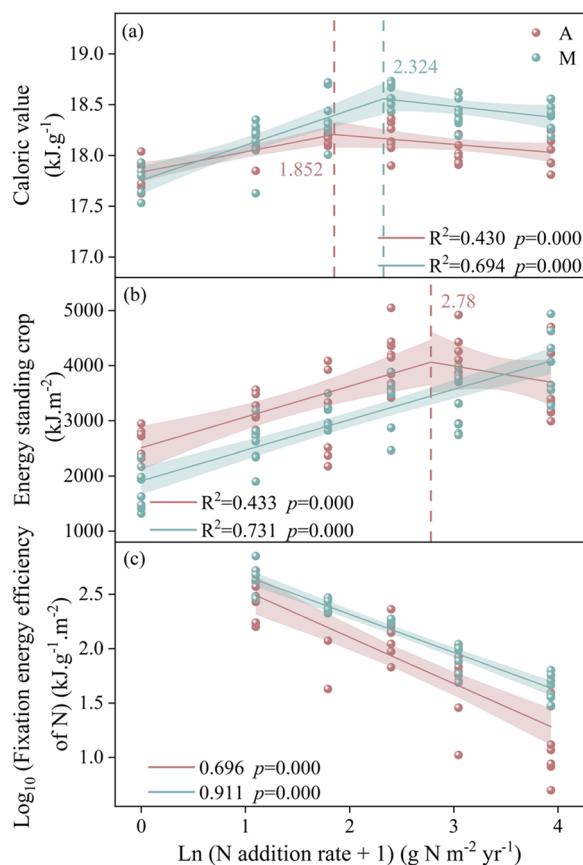


Fig. 4 The relationship between N addition rates and caloric value (a), energy standing crop (b) and fixation energy efficiency of N (c) of community on average from 2019 to 2020. Nonlinear fit is piecewise linear regression model with breakpoints estimation, ln indicates natural logarithm, A indicate non-mowing treatment, M indicate mowing treatment, shaded indicate 95% confidence interval

community. Since grassland plants are primarily limited by N, N addition alleviates the N limitation of plants (Bai et al. 2010; Peng et al. 2022), thereby increasing the

availability of N resources. Plants gradually shift from a conservative resource utilization strategy to an acquisitive one (Wright et al. 2004; Yang et al. 2022). The key competition shifts from underground (nutrient competition) to aboveground (light competition) (Newman 1973; Hautier et al. 2009). Plants increase their height or specific leaf area to enhance their light capture ability (Freschet et al. 2015), which leads to an increased photosynthesis rate, and they adopt a faster nutrient cycling strategy to adapt to the N-enriched environment (Wright et al. 2004; Yang et al. 2022), resulting in the accumulation of more energy-rich substances. Existing research has found that the application of N can significantly increase the content of crude fat, crude protein, and crude fiber in forage grasses (Ding et al. 2021), while also reducing the content of crude ash (Marcinkevičienė et al. 2021).

One of our most important findings is that N addition enhances the community's caloric value, but the response trends of different species and functional groups' plant caloric values to N addition rates are different, with species and functional groups showing diverse responses such as 'initial increase followed by a decrease, linear increase, or no significant change' along the N addition gradient. Different species adopt different resource utilization strategies to adapt to the N-enriched environment. Our results reveal that the relationship between the caloric value of grasses (*L. chinensis* and *S. baicalensis*) and N addition rates exhibits a 'low N promotion, high N inhibition' unimodal trend, peaking at N addition rates of 3–5 g N m⁻² yr⁻¹ (*L. chinensis*, 3.302 g N m⁻² yr⁻¹; *S. baicalensis*, 5.001 g N m⁻² yr⁻¹; grasses, 4.414 g N m⁻² yr⁻¹), indicating that the nutrient balance state of plants may be achieved near this rate, and N becomes saturated. Subsequently, when N is in excess, N:P imbalance occurs, and the nutrient demand of plants shifts to other nutrients (e.g., P, K), limiting

Table 4 Results of the piecewise linear regression for caloric value (energy standing crop) and N addition rates at species, functional group, and community levels

Piecewise Regression	Caloric value			Energy standing crop			
	Breakpoint (mean ± 1 SE)	Slope	p	Breakpoint (mean ± 1 SE)	Slope	p	
Species	<i>L. Chinensis</i> (A)	3.302 ± 0.289	0.217	0.000	10.001 ± 0.677	0.121	0.000
			-0.092	0.003			-0.021
	<i>L. Chinensis</i> (M)	5.443 ± 0.183	0.274	0.000			
			-0.186	0.000			
	<i>S. Baicalensis</i> (A)	5.001 ± 0.618	0.137	0.011			
			-0.119	0.113			
<i>S. Baicalensis</i> (M)	5.001 ± 0.239	0.245	0.000	7.432 ± 0.301	0.339	0.007	
		-0.149	0.004			-0.529	0.001
Functional group	Grasses (A)	4.414 ± 0.362	0.192	0.004			
			-0.094	0.004			
	Grasses (M)	5.746 ± 0.175	0.311	0.000			
Community	(A)	10.078 ± 0.523	0.315	0.000			
			-0.318	0.146			
	(M)	5.373 ± 0.323	0.199	0.000	15.119 ± 0.481	559.442	0.000
Community	(M)	9.216 ± 0.234	-0.084	0.069		-316.297	0.346
			0.345	0.000			
			-0.112	0.054			

A indicate non-mowing treatment, M indicate mowing treatment

plant growth (Han et al. 2005; Vitousek et al. 2010; Crowley et al. 2012; Zhong et al. 2023). Plants need to expend a large amount of energy to absorb excess N and carry out various biosynthetic functions, which reduces the caloric value. The 50 g N m⁻² yr⁻¹ treatment causes ion (Al³⁺, NH₄⁺) toxicity due to excess N (Horswill et al. 2008; Zhang et al. 2014; Tian et al. 2016, 2022) and other nutrient limitations (C) (Ning et al. 2021), forcing plants to use their energy reserves to maintain nutrient balance, hence the caloric value shows a decreasing trend.

The responses of legumes and grasses to N addition differ; the caloric value of the legumes functional group and its representative species *T. lanceolata* shows a linear increase trend with the N addition rates. Compared with grasses without N fixation ability, the growth of legumes is less affected by N limitation (Elgersma and Søgaard 2016; Zhong et al. 2023). On the other hand, biological N fixation is beneficial for mycorrhizal growth and reproduction, as well as soil microbial activity (Nasto et al. 2014). It contributes to the mineralization of organic phosphorus, alleviates phosphorus limitation in ecosystems (Peng et al. 2022), and releases nutrients from minerals in rhizosphere soil into more soluble forms for plant absorption and utilization (Phillips et al. 2013; Xu et al. 2019). Legume plants form a mutualistic community with mycorrhizae, changing their N

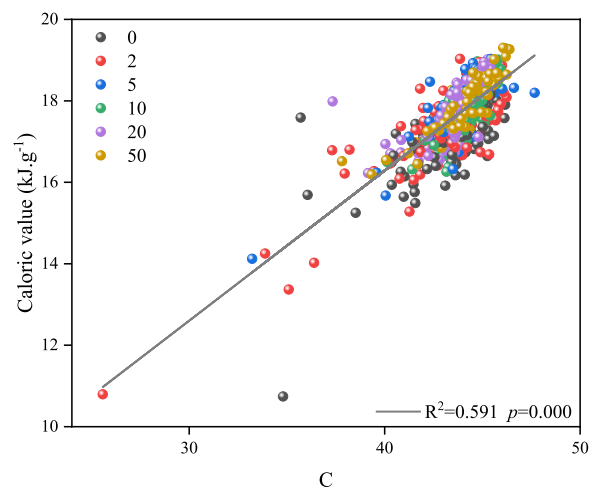


Fig. 5 The relationship between caloric value and carbon (C) concentration of plants during 2019–2020. Six N addition rates at 0, 2, 5, 10, 20 and 50 g m⁻² yr⁻¹ were included in our experiment

absorption strategy. The maximum experimental N addition rate of 50 g N m⁻² yr⁻¹ has not yet reached the N excess state of *T. lanceolata*. However, the caloric value of forbs and their representative species *P. bifurca* did not change significantly with increasing N addition rates. Existing research indicates that N addition is generally

unfavorable to forbs' growth (Bobbink et al. 2010; Wang et al. 2021b). On the other hand, since forbs are generally located in the middle and lower layers of communities with limited competition for various resources such as light (light asymmetry) and nutrients (Hautier et al. 2009; Borer et al. 2014; DeMalach et al. 2017; Xiao et al. 2021), their caloric value did not show significant changes.

The caloric value at the community level follows a similar pattern to that of grasses along the N addition gradient. Grasses, as the dominant functional group in this ecosystem, drive the response of community-level caloric values to N addition, with *L. chinensis* and *S. baicalensis* together accounting for 81.58% of the community biomass (Table S1). This supports the mass ratio hypothesis, which posits that the effects of species on ecosystem properties are proportionally related to their abundance (Grime 1998). The non-linear response of plant caloric value at different organizational levels in the meadow steppe to the N addition rates indicates that the threshold at the community level is higher than that at the functional group and species levels, and different species (*L. chinensis* and *S. baicalensis*) and functional groups (grasses) have different response ranges to N addition. The diverse response of various species caloric values in the community (the non-linear increase of grasses and the linear increase of legumes) and their dominance collectively result in an increase in the community-level threshold. Therefore, in future grassland management and utilization, to enhance the caloric value of the steppe community, the optimal annual N addition rate for the meadow steppe is 5.373 g m^{-2} .

Effects of mowing on plant caloric value and its N response

The effects of mowing on grassland caloric value are not well studied. It was found that moderate grazing can enhance the caloric value of *Trifolium repens* in alpine grasslands (Bao et al. 2001). Our study found that mowing significantly enhances the caloric values of four representative species, the functional groups of grasses and legumes, and the community in meadow steppe. This effect may be linked to the growth and development rhythm (phenological period) of plants and environmental changes. Typically, in non-mowing grasslands, the reproductive growth of forage grass entering July and August will inhibit vegetative growth, while mowing slows down the reproductive growth, keeping most forage grass in a vegetative growth state, tenderizing plants, reducing nutrient recovery, and increasing high caloric value nutrient content. Mowing can increase plant tillering, curb apical dominance (Shao et al. 2012), and release nutrients like N, P, and K from roots to supply the aboveground parts, fostering

compensatory growth (Connell 1978). Consequently, the crude protein content in forage grasses increases and the crude fiber content decreases, improving forage quality (Gilhaus and Hölzel 2016), which in turn enhances the caloric value of dominant plants in grasslands. However, mowing had no significant effect on the caloric value of forbs. The varying responses in caloric value to mowing among different plant functional groups likely relate to their competitive status and their capacity to tolerate and adapt to mowing (Bao et al. 2005).

Mowing treatment does not change the response trends of species (*L. chinensis*, *S. baicalensis*, *T. lanceolata*, and *P. bifurca*), functional groups (legumes, grasses), or community caloric value to N addition, but changes the response trend of the caloric value of the forbs functional group, causing their caloric value to initially increase followed by saturation trend in response to N addition. This is primarily due to mowing treatments altering community composition (Hu et al. 2021), weakening the competitive interference of tall rhizomatous grasses like *L. chinensis*, reducing the dominance of dominant species, and improving the light availability of forbs to promote their growth (Collins et al. 1998; Hautier et al. 2009). Compared with non-mowing, mowing has a trend to increase the N response threshold of plant caloric value (*L. chinensis*: from $3.302 \text{ g N m}^{-2} \text{ yr}^{-1}$ to $5.443 \text{ g N m}^{-2} \text{ yr}^{-1}$, grasses: from $4.414 \text{ g N m}^{-2} \text{ yr}^{-1}$ to $5.746 \text{ g N m}^{-2} \text{ yr}^{-1}$, community: from $5.373 \text{ g N m}^{-2} \text{ yr}^{-1}$ to $9.216 \text{ g N m}^{-2} \text{ yr}^{-1}$). This increase may be related to mowing reducing soil N accumulation, changing phenological period, and increasing effective P content in the soil.

Effects of N addition and mowing on energy standing crop and fixation energy efficiency of N

As the process progresses from N limitation to N saturation and then to N excess, the community's energy standing crop also exhibits a non-linear increasing trend of initial increase followed by saturation, and the N saturation threshold was $15.119 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Fig. 4b). The N saturation threshold of community biomass was $16.082 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Fig. S5), which was $0.963 \text{ g N m}^{-2} \text{ yr}^{-1}$ higher than that for energy standing crops. Based on data from this experiment from 2016 to 2020, it was found that the N saturation threshold for aboveground net primary productivity (ANPP) in this steppe was $13.11 \text{ g m}^{-2} \text{ yr}^{-1}$ (Yang et al. 2023), with differences in community biomass thresholds possibly due to differences in N addition and sampling years. Other research on productivity N response thresholds also found a global average N saturation threshold for grassland ANPP's non-linear response to N addition rates at $15 \text{ g m}^{-2} \text{ yr}^{-1}$ (Peng et al. 2020). These studies are based on the effect of N addition on biomass. Due to

differences in plant species and various environmental conditions, the energy stored in biomass of the same dry weight is different. We further rise to the energy standing crop index on the basis of biomass, which can more accurately quantify its impact.

Our study showed that different species and functional groups exhibit varying responses to N addition in terms of energy standing crops. The energy standing crops of *L. chinensis* show a non-linear increasing trend, initially increasing and then reaching saturation, while grasses exhibit a linear increasing trend, whereas forbs show a linear decreasing trend. Similarly, community energy standing crops also exhibit a 'low N promotion, high N saturation' non-linear relationship with the increase in N addition rates, indicating that an appropriate amount of N addition can enhance the amount of solar energy fixed and transformed by meadow grassland communities. This impact is reflected both in energy quality and energy quantity. The change trend of caloric value of plants was consistent with the change of plant energy standing crop, but the N response thresholds for energy standing crop of *L. chinensis* and communities are higher than those for their caloric values, respectively 10.001 and 15.119 g N m⁻² yr⁻¹, possibly due to a higher N response threshold for biomass (16.082 g N m⁻² yr⁻¹) (Fig. S6). This suggests that the responses of aboveground biomass and energy to N addition were different, with responses in energy being more sensitive than those in aboveground biomass. The different sensitivities of aboveground biomass and energy in the community that occurred to N deposition highlight the importance of caloric value in mediating ecosystem functioning in the face of N deposition.

Mowing reduces the energy standing crops of *L. chinensis*, grasses, and communities, primarily because it directly reduces their biomass. The negative impact of mowing on biomass exceeds the compensatory growth ability of plants themselves. Moreover, due to consecutive years of mowing that take away a large amount of aboveground plant parts, litter cannot be returned, leading to the loss of C and nutrient resources (Jones et al. 2017), which affects plant photosynthesis and decreases the amount of energy accumulated by the plants. Concurrently, mowing treatment changes the trend of species (*L. chinensis*, *S. baicalensis*, and *T. lanceolata*), legume functional group, and community energy standing crop. Among them, *L. chinensis* and community energy standing crop exhibit a linear increasing trend; *S. baicalensis* shows an initial increase followed by a decreasing trend; and *T. lanceolata* and legumes exhibit a linear decreasing trend. This may be due to the impact of mowing on soil N enrichment and resource competition, causing the response trends of different species' biomass to change. Under mowing treatments, community biomass

response to N addition is a linear increase (Fig. S5), consistent with the negative correlation observed between N-induced biomass increase and litter accumulation in 47 grasslands worldwide (Seabloom et al. 2021).

The study of energy fixation efficiency of plants under different N conditions showed that different species and functional groups exhibit varying responses to the N addition gradient in terms of fixation energy efficiency of *N. L. chinensis* and grasses functional groups display a linear decreasing trend, i.e., with the increase in N addition rates, the energy fixed by each additional 1 g N per square meter of plant decreased. However, *P. bifurca*, legumes, and forb functional groups show a linearly increasing trend. The different trends are related to their dominance in the community, leading to different abilities to compete for N. The fixation energy efficiency of N in the community is mainly influenced by dominant plants, such as grasses, and follows a similar pattern to that of the grasses along the N addition gradient (Fig. 4c). This indicates that the beneficial impact of N addition on the fixation energy efficiency of plant communities will weaken with the continuous increase in N. The mowing treatment increased the fixation energy efficiency of N for grasses and community, but it did not change the N response trend. In future restoration processes of degraded grasslands through artificial reseeded or in the fertilization and quality improvement management of artificial grasslands, the N response threshold and fixation energy efficiency of N indicators of plant energy can be considered comprehensively. The optimal amount of N fertilizer application can be determined by calculating the ratio of economic input from N fertilizer application to energy output, in order to make more effective use of resources.

This study found that there were interannual differences in the caloric value at various organizational levels and their response amplitude to N addition (Tables 1–3; Fig. S1–3), characterized by higher caloric value and smaller amplitude in 2019, and lower caloric value and larger amplitude in 2020. Despite intraspecific variability, caloric value is still a relatively stable parameter for the same species; the range of intraspecific variation is not enough to reveal the differences among species (Bao et al. 2007). In this study, the amplitude of interannual variation in community caloric values (0.736%–3.025%) is less than the amplitude of variation between N addition treatments (0.227%–5.064%). Although climatic factors can affect the magnitude of caloric values, the N response trends of caloric values are similar over the two years. In this study, we focus more on the similarity of N response trends. This may be due to interannual climatic differences, as the effectiveness of water and N may jointly limit plant growth in semi-arid regions (Niu et al. 2010). Compared

with 2019, precipitation was less in 2020 (Fig. S6), and drought has a significant negative impact on leaf N concentration and net photosynthetic rate (Yu et al. 2019), resulting in lower caloric value. Drought inhibits plant N absorption, therefore, changes in precipitation regimes and the global increase in N will act interdependently (Shen et al. 2020). Both the direct and indirect impacts of precipitation on caloric value are deserved more attention under the scenarios of increasing N deposition and altering precipitation regime. So, in studies, broadly based temporal or spatial averages are most appropriate.

Conclusions

To the best of our knowledge, this study is the first to analyze the effects of N addition and mowing treatment on the plant community of meadow steppe from the perspective of plant energy fixation. The results indicate that in the 6th–7th year of continuous N addition in the Inner Mongolia meadow steppe ecosystem, N addition and mowing had a positive effect on plant caloric value at each organizational level. Mowing treatments usually do not change the N response trend of the caloric value of plants at each organizational level and will enhance the N response threshold. N response thresholds of energy vary at different organizational levels, indicating varying regulatory capabilities of plants in the ecological environment at different biological levels. The N response pattern of community energy represents the overall response of steppe ecosystem energy. N addition positively affected the quantity and quality of community energy by stimulating the dominance of grasses, and consequently mediated the positive effects of N enrichment. Moreover, the N response threshold for the quantity of energy was higher than that for the quality, indicating that the caloric value was more sensitive to the response of N addition. However, the fixation energy efficiency of N in the community showed a linearly decreasing trend with N addition rates. Identifying the thresholds for the positive responses of community energy to N enrichment is an essential prerequisite for predicting the benefits of N deposition on ecosystem energy fixation. Our findings provide an empirical basis for improving the energy utilization efficiency of grassland communities under N deposition and mowing.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00544-2>.

Additional file 1.

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Author contributions

Jiaqi Ye conducted field collections, analyzed and interpreted the data, and wrote the manuscript. Xingguo Han, Yajing Bao, Zhenghai Li and Cunzhu Liang contributed to the study conception and design. Material preparation, data collection and fieldwork were assisted by Siqi Yang, Yu Zhao, Jing Zhang, Xiaotao Lü and Guojiao Yang. Data analysis assisted by Shuai Wu and Yu Mo. Yajing Bao and Zhenghai Li provided supervision and reviewed the final draft of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no relevant financial or non-financial interests to disclose.

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