

RESEARCH ARTICLE

Grassland management practices in Chinese steppes impact productivity, diversity and the relationship

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Abstract Grasslands are crucial parts of the terrestrial ecosystem, with an extremely high differentiation of productivity and diversity across spatial scales and land use patterns. The practices employed to manage grassland, such as grazing, haymaking, fertilization or reseeding, can improve the grassland condition. This study focuses on the changes in productivity and diversity and the relationship between them as affected by management practices. Productivity and diversity have unequivocally been altered in response to different management practices. When grazing intensity of a typical steppe increased from 1.5 to 9 sheep per hectare, both productivity and diversity declined. Higher grazing intensity (6 to 9 sheep per hectare) accelerated loss of diversity because of lower productivity. Productivity was significantly improved but diversity was lost by fertilizing. N fertilization also reduced the sensitivity of diversity to productivity. A similar response was found in mown grassland with increased productivity and diversity but their relationship was negatively affected. Mowing also slowed down the decline in diversity as productivity increased. Reseeding purple-flowered alfalfa led to an increased diversity, while yellow-flowered alfalfa increased productivity significantly. The negative productivity-diversity relationship was transformed to a positive one by reseeding alfalfa. These results enhance understanding of how productivity, diversity and their relationships change in response to altered grassland management practices, and support an integrated approach for improving both productivity and diversity.

Keywords diversity, fertilizing, grassland management practice, grazing, mowing, productivity, reseeding

1 Introduction

There is over 44.5×10^9 hm² of grassland, representing nearly 40% of the global land surface^[1–3]. Eurasian steppes are key component of the temperate grassland in China (3.92×10^9 hm²) and are suffering serious degradation^[4]. Production and diversity loss has occurred in nearly 90% of current grasslands^[5]. Grassland restoration is a long-term and complex ecological process, and restoring high productivity and diversity is a common goal of grassland management^[6]. Efforts have been made to explore management practices that result in a stable grassland status or cause a trade-off between plant productivity and diversity^[7,8].

Diversity is a major driver of ecological stability^[9]. Classic theories hold that higher diversity can enhance community stability through mechanisms of covariance andoveryielding^[10]. The relationship of productivity and diversity is a key issue in the study of biodiversity-ecosystem functioning. Hump-shaped curves, where diversity peaks at the intermediate level of productivity, have been used in established models, but this has been challenged^[11]. Data from global-scale grassland studies showed a positive linear relationship, with changes at regional or local scales^[12]. At a local scale, lack of competitiveness, limited persistence and seed dispersal were considered as the main obstacles to achieving highly productive and diverse grasslands^[13]. Korell concluded that diversity has a positive effect on productivity^[14–16]. This positive effect is explained by two processes: the complementary effect and the selection effect^[17].

Currently, global climate change and increasing population are anticipated to affect grassland management and livestock production^[18,19]. Integrated approaches are increasingly being implemented for the protection and restoration of grassland in China, including controlling grazing intensity, fertilization, haymaking and reseeding high-quality forages species^[2,20,21]. In some areas, this has resulted in systematic improvement in grassland. Productivity and diversity have been reestablished, and this has

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been recognized as a critical goal in restoration and an integral component of the ecological system. In a large scale study of the Eurasian steppes, a positive linear productivity-diversity relationship has been detected based on a large data set^[11]. However, the relationship is considered to be spatial scale-dependent^[12]. In this paper, we collected data on productivity and Shannon–Wiener diversity from experimental grazing, mowing, fertilization and reseeding. The aim was to evaluate responses of diversity, productivity and the relationship between them under these management practices.

2 Materials and methods

Data were collected from four different experiments at four research sites on the steppes of Inner Mongolia, China. Details of the study sites were as previously described^[22,23]. Standard sampling procedures were performed to measure the vegetation productivity and Shannon–Wiener diversity. The plant species community composition was assessed at the end of each growing season. All vascular plant species were identified and counted, and their aerial cover was visually estimated by quadrat for each plot. Shoots of each species were harvested at ground-level and oven-dried at 65°C for 72 h, then weighed to determine above-ground biomass. Diversity was estimated using Shannon’s diversity index, where $H = -\sum P_i \ln P_i$, and P_i represents the number of each individual in the total number of individuals.

SAS 8.2 (SAS Institute, Cary, NC, USA) was used to perform one-way or two-way ANOVA and correlation analysis. Tukey’s one-way ANOVA and Duncan’s multiple range tests were performed and significance was determined at $P < 0.05$.

3 Results

3.1 Grazing arc-shaped community productivity and diversity

Continuous grazing was conducted according to traditional grazing practices. Until 2013, 8-year of treatment resulted in large distinction in both vegetation productivity and plant composition (Table 1). Light grazing intensity (1.5 sheep per hectare) benefited both productivity and Shannon–Wiener diversity (H') of the community. With higher grazing intensity, these two indices rapidly declined. Above-ground biomass showed a sharp decline when grazing intensity increased from 4.5 to 6 sheep per hectare, and the Shannon–Wiener diversity (H') declined more sharply when grazing intensity was further increased (Fig. 1). Diversity was increased linearly with increasing productivity (y_1 , Fig. 1), and grazing altered the relation-

ship between productivity and diversity from linear to arc-shaped (y_2 , Fig. 1), indicating light grazing could maintain plant community diversity of Chinese steppes.

Table 1 Intensity of traditional grazing affects community productivity and diversity

Grazing intensity (sheep per hectare)	Productivity/(g·m ⁻²)	Diversity (H')
0.0	450.320±24.03	3.20±0.18
1.5	477.330±27.27	3.50±0.22
3.0	443.430±23.21	2.91±0.15
4.5	390.120±16.81	2.43±0.09
6.0	235.110±11.6	2.33±0.08
7.5	212.330±10.3	1.98±0.04
9.0	189.120±11.69	1.20±0.05

Notes: Data based on an investigation on a traditional grazing system, in which grazing intensity ranged from 0 to 9 sheep per hectare (mean±SD).

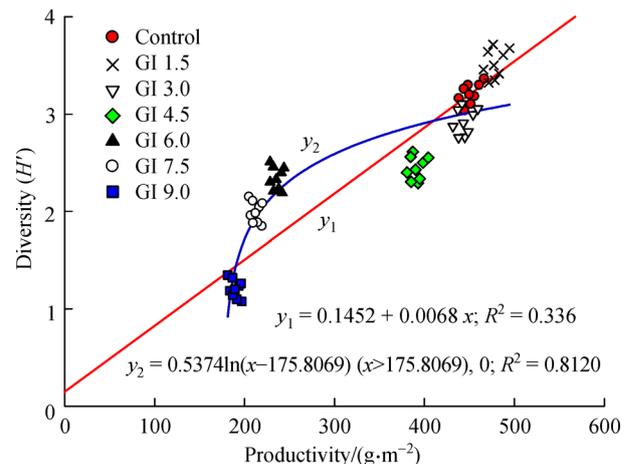


Fig. 1 Relationship between productivity and diversity in a grazing system

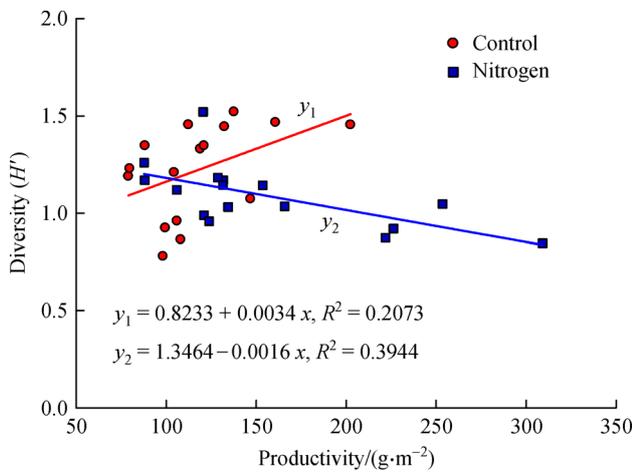
3.2 Fertilization reversed community productivity and diversity

N fertilization (10 g·hm⁻²·yr⁻¹) significantly increased above-ground biomass ($P < 0.05$), with the highest biomass (231±29.5 g·m⁻²) occurring in 2015 (Table 2). The Shannon–Wiener diversity (H') decreased in 2015 and 2016, which indicated N fertilization significantly accelerated diversity loss ($P < 0.05$). The entirely different relationships between productivity and diversity were evident in Fig. 2. The Shannon–Wiener diversity (H') was positively related to biomass in the control (y_1 , Fig. 2) but negatively related to the productivity of grassland with N fertilization (y_2 , Fig. 2). The shift in Shannon–Wiener diversity (H') was not significant as compared to the control based on the changes in the regression slope.

Table 2 N fertilization affects community productivity and diversity

Year	Productivity/(g·m ⁻²)		Diversity (<i>H'</i>)	
	Control	N fertilization	Control	N fertilization
2013	92.343±7.46 a	103.380±10.40 a	1.15±0.06 A	1.18±0.03 A
2014	98.577±4.08 b	123.53±1.86 a	0.98±0.13 A	1.16±0.12 A
2015	161.970±14.3 b	230.795±29.50 a	1.38±0.10 A	1.03±0.09 B
2016	121.214±4.16 a	168.300±28.90 a	1.39±0.03 A	1.12±0.02 B

Notes: Data are mean±SE, $n = 4$. Lowercase letters represent productivity differences between control and treatments; capital letters represent diversity (H') differences between control and treatments ($P < 0.05$).

**Fig. 2** Nitrogen fertilization in grassland affects the relationship of productivity and diversity

3.3 Mowing improved community productivity and diversity

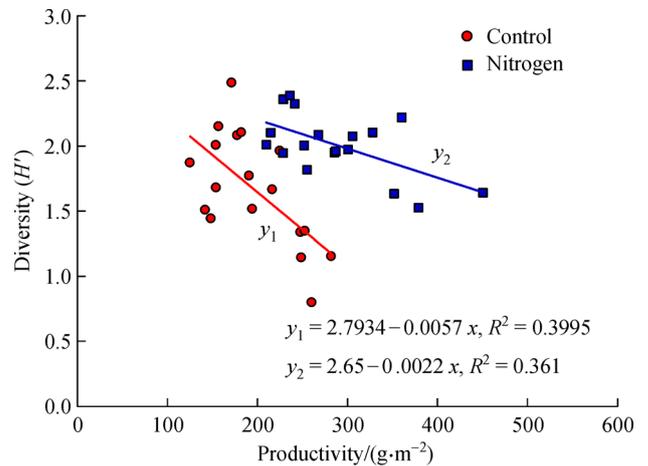
Based on three years of data, results of two-way ANOVA showed positive effects of mowing on both productivity and diversity (Table 3). In the first year, productivity showed no difference, but Shannon–Wiener diversity (H') significantly increased in the mown plots ($P < 0.05$). In the second year, productivity reached the highest level in the mown plots ($P < 0.05$), but the diversity remained consistent between the control and mowing treatment. However, both the productivity and community Shannon–Wiener diversity (H') showed no significant response to mowing in the third year. Significant linear regressions were observed (Fig. 3), but the regression lines differed.

Table 3 Mowing for hay influences community productivity and diversity

Year	Productivity/(g·m ⁻²)		Diversity (H')	
	Control	Mowing	Control	Mowing
2014	228.820±17.15 a	267.817±16.66 a	1.49±0.23 B	2.22±0.06 A
2015	170.187±14.43 b	354.593±24.18 a	1.85±0.09 A	1.82±0.10 A
2016	189.496±20.11 a	241.113±11.92 a	1.65±0.16 A	1.97±0.03 A

Notes: Data are mean±SE, $n = 6$. Lowercase letters represent productivity differences between control and treatments; capital letters represent diversity (H') differences between control and treatments ($P < 0.05$).

The slope of the negative regression line under mowing (y_2 , Fig. 3) was not as sharp as for the control (y_1 , Fig. 3), indicating that loss of diversity slowed down with the increasing productivity resulting from mowing.

**Fig. 3** Relationship between productivity and diversity in a mowing system

3.4 Effect of reseeding with high quality forages

Reseeding high quality forage of purple alfalfa and yellow-flowered alfalfa increased productivity ($P < 0.05$), with the highest productivity observed in yellow-flowered alfalfa reseeded plots in 2014 (Table 4). Across 3 years, reseeding of purple-flowered alfalfa significantly increased plant community diversity ($P < 0.05$), but yellow-flowered alfalfa had no significant effect compared to the control. There was a negative relationship between productivity

Table 4 Reseeding affects community productivity and diversity

Year	Productivity/(g·m ⁻²)			Diversity (<i>H'</i>)		
	Control	WL168	YFA	Control	WL168	YFA
2014	228.82±17.1 b	250.223±9.63 b	313.9±21.2 a	1.49±0.23 B	2.10±0.06 A	1.81±0.11 AB
2015	170.187±14.4 b	197.809±8.63 b	300.582±14.38 a	1.85±0.09 B	2.10±0.06 A	1.92±0.03 AB
2016	189.496±20.1 b	184.764±4.15 b	197.786±9.11 a	1.65±0.16 A	1.55±0.07 A	1.68±0.05 A

Notes: Data are mean±SE, *n* = 6. Lowercase letters represent productivity differences between control and treatments; Capital letters represent diversity (*H'*) differences between control and treatments (*P* < 0.05).

and Shannon–Wiener diversity (y_1 , Fig. 4) in the control. However, Shannon–Wiener diversity (H') positively increased with enhanced above-ground biomass with reseeded both types of alfalfa (y_1 and y_2 , Fig. 4). The slope of the regression line for the yellow-flowered alfalfa (y_2 , Fig. 4) was not so sharp as that for purple-flowered alfalfa (y_3 , Fig. 4), which indicated that diversity was enhanced slightly more by purple-flowered alfalfa than by yellow-flowered alfalfa.

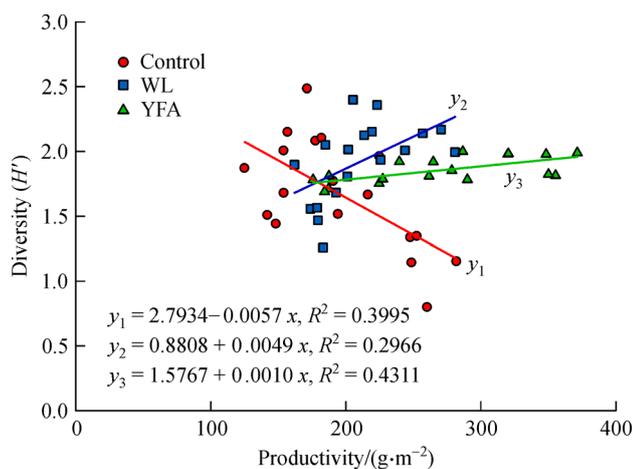


Fig. 4 Reseeding in grassland affects the relationship of productivity and diversity (WL, purple-flowered alfalfa WL168; YFA, yellow-flowered alfalfa)

4 Discussion

4.1 Grazing

Grazing by domestic ungulates has long been a grassland management practice, and a majority of grasslands are currently experiencing overgrazing^[24], which not only threatens the productivity and diversity of grasslands, but also deteriorates grassland ecosystem services^[2,25]. Experiments have shown that greater species diversity promotes greater temporal stability of above-ground net primary production (ANPP)^[26]. One major underlying mechanism is that species respond asynchronously to environmental fluctuations by compensating for increasing the biomass of some species but decreasing others^[27].

Grazing intensity is an important component of grazing management strategy, which strongly affects plant community structure^[2]. Grazing intensity can either positively or negatively affect species diversity of plant communities^[28,29]. Most grazing experiments, either fixed grazing intensity or technical rest grazing, are designed based on controlling grazing intensity versus herbage allowance during the grazing season, thus the herbage-to-animal relationship determines the grazing intensity^[4]. In response to grazing intensification, the data showed that productivity declined and the diversity-productivity regressed in a logistic curve. Compared with the undisturbed treatment, the resilient diversity-productivity relationship implied an asynchronous response of productivity and diversity along the grazing gradient. Diversity in high grazing intensity with lower productivity was more vulnerable to disturbance. Negative effects on ecological services (e.g., carbon sequestration) have been attributed to the increasing grazing intensity, which is directly dependent on loss of productivity and diversity^[2,25,30].

4.2 Fertilization

Most of the natural grasslands are unfertilized systems in which nutrient transformation and allocation sustain the fertility, depending on the decomposition by microbes and enzymes^[31]. Plant communities govern this process by taking up nutrients and releasing various substances for microorganisms. The ability of self-fertilization declines with succession in a plant community^[2].

In the grasslands of northern China, N is one of the major limiting factors for vegetation development^[32]. In recent years, N fertilization has become a common practice in the managed grasslands and provides important benefits for production. Such N enrichment has been reported to exert positive impacts on ecosystem ANPP and negative effects on species richness, species asynchrony and ecosystem stability, consistent with our predictions^[33]. In steppe grasslands, most studies have found that N enrichment can increase the dominance of grasses and inhibit forbs, thus leading to a diversity loss^[34]. Our experiment was established in seriously degraded grassland. Maximum natural N deposition (10 g·hm⁻²·yr⁻¹ N) in northern China, led to a significant increase in above-ground productivity and a declining trend in diversity. The

response of productivity and diversity encountered in our data are consistent with the results of other studies^[20,32]. Compared to the control, the Shannon–Wiener diversity slightly changed as the productivity increased in fertilized plots, in which productivity was relatively high (Fig. 2). These asynchronous dynamics can explain the diversity response seen in the third year (Table 2). The phenomenon further indicates that productivity is more sensitive to N-fertilization management, and it drives diversity.

4.3 Mowing

Mowing by harvesting above-ground biomass for hay is essential for grassland-based husbandry, and is especially crucial for forage security during cold winters^[35]. In China, 11% to 17% of grasslands in semi-arid area are mown hay, and the area used for hay production continues to increase^[33]. Earlier reports show that community diversity can be restored because mowing increases both availability of light for small subdominant plant species and also their seed germination rates^[36]. However, frequent or intensive mowing can decrease seed production, seed bank diversity and germination, thereby decreasing diversity^[37].

Defoliation by clipping has been used to explore appropriate mowing systems, with the finding that biennial mowing was better than continuous mowing in quantitative characteristics of community and biomass^[6]. Our data were collected from an annual mowing experiment in meadow grassland. Biomass removal by mowing at the end of the growing season would lead to the removal of substantial amounts of nutrients sequestered in plant tissues^[4,38]. Increasingly, mowing practices are performed together with N fertilization in order to secure sustainable production. Both mowing and N addition resulted (Fig. 2; Fig. 3) in a higher productivity, but the Shannon–Wiener diversity declined, which was opposite to the effect of N enrichment. The results of our study support the contention that mowing can buffer diversity decline, but it may also endanger stability of the ecosystem^[33]. Based on seven years of grassland mowing and N enrichment in a typical steppe, Yang et al. suggested that grassland communities with higher species diversity tend to exhibit greater temporal stability^[20]. It is species asynchronous population dynamics in such communities with higher diversity that contributes compensative growth^[20]. In our research, mowing induced a significant increase in diversity one year after treatment. Then two years later, the mown plots showed an extremely high forage production ($355 \pm 24.2 \text{ g} \cdot \text{m}^{-2}$), double that of the control plots (Table 3). The amplitude of the alteration in diversity (or k , coefficient of x in regressed equations) declined in response to change in productivity (Fig. 3), which might also result from asynchronous dynamics in productivity and diversity interruption of the competitive relationship of

the original community and reducing species diversity by mowing^[36,39]. The productivity of the assembled community can benefit from the increased diversity^[14].

4.4 Reseeding

Reseeding appropriate species into degraded grasslands can increase the overall production and benefit grassland ecosystem services. This approach to ecological restoration has been widely applied. Reseeding legumes into native grassland can decrease the use of N fertilizers by providing a sustainable source of soil nitrogen through biological N-fixation^[21,40]. Increased soil N from legumes can also lead to greater niche complementarity in grasslands, benefiting species coexistence and enhancing plant diversity^[41].

Yellow-flowered alfalfa is a winter-hardy, drought- and grazing-tolerant species, due to a deep-set crown and fibrous root system. Reseeding with yellow-flowered alfalfa in rangelands can facilitate long-term grassland productivity^[42] and successfully improve total yield (Table 4). In contrast, the common cultivated purple-flowered alfalfa (WL168) is more sensitive to drought and extreme cold. Reseeding WL168 led to a higher diversity but low productivity because of weak competition with native species. In grassland reseeded with alfalfa, species diversity increased as total productivity increased. This management reversed the negative relationship between productivity and diversity to a positive one. Also, community diversity increased as the proportional biomass of legumes increased (data not shown), but declined when legume proportional biomass exceeded 30%. Plant community composition is crucial to mediating productivity and diversity relationships as described by Fukami^[43].

4.5 Productivity-diversity relationship

Presently the relationship between productivity and diversity remains controversial. The influence of disturbance, consumers, niche specialization, spatial scale and the history of community assembly influence this relationship^[12,43,44]. A positive linear relationship was found based on data from 854 field sites distributed widely across the Eurasian steppes^[11]. Our data support the view that the productivity-diversity relationship is spatial scale-dependent. A grazing and N-fertilization experiment conducted in the Xilin River catchment, the center of the typical Chinese steppes, found a positive linear relationship between productivity and diversity in the control plots, but the relationship was negative in Hulunbeier, over 600 km north-east of the Xilin steppe. Management practices can lead to asynchronous responses in productivity and diversity, which further determine the productivity-diversity relationships^[43,45].

5 Conclusions

In this study, we examined the effects of grazing N fertilization, mowing and reseeding on productivity, diversity and their relationship in grassland. Productivity and Shannon–Wiener diversity were unequivocally altered in response to different management practices. The relationship between productivity and diversity differed with scale and was altered by management practices at a local scale. Individual management practices might not reconstruct plant communities sufficiently to benefit both productivity and diversity. Community composition and environmental conditions should be considered for restoring high productive and diverse grasslands.

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This article does not contain any studies with human or animal subjects performed by any of the authors.

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