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Effects of Mowing on Plant Stoichiometric Characteristics of Degraded Alpine Meadows in Northwestern Yunnan (Postprint)

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Abstract

To investigate the effects of environmental disturbance on plant stoichiometric characteristics of degraded alpine meadows, this study conducted a mowing experiment from 2018 to 2020 on alpine meadows with three degradation degrees (light degradation LD, moderate degradation MD, severe degradation SD) in Shangri-La City, and analyzed the differences in plant C, N, P contents, C:N:P ratios, and N-P power function relationships among different mowing years (0, 1, 2 years). The results showed: (1) Except for P content in Cyperaceae, the C, N, P contents of meadow plant community, grasses, and forbs showed no significant differences among degradation gradients ($P>0.05$). With increasing mowing years, the C, N, P contents of degraded meadow plants showed a trend of first increasing then decreasing ($P<0.05$). (2) The C:N and C:P ratios of meadow plants showed no differences among degradation gradients ($P>0.05$). From LD to SD, the N:P ratios of plant community, Cyperaceae, and forbs first decreased slightly then increased significantly ($P<0.05$), while the N:P ratio of grasses showed no significant change ($P>0.05$). (3) With increasing mowing years, the C:N and C:P ratios of meadow plants showed a trend of first decreasing then increasing, while N:P ratio showed a trend of first increasing then decreasing. At 0 mowing year, the C:P and N:P ratios of Cyperaceae were significantly higher than those of forbs ($P<0.05$), but showed no difference from the community and grasses ($P>0.05$); at 1 and 2 mowing years, the C:P and N:P ratios of Cyperaceae were higher than those of the community and other functional groups ($P<0.05$); at all mowing years, there were no differences in C:N ratio among the community and functional groups ($P>0.05$). (4) With increasing mowing years, the N-P power function relationship of degraded meadow plants changed from weak to strong, with the power exponent stabilizing. The N-P power exponent of Cyperaceae (less than 0.1) was distinctly different from those of plant community, grasses, and forbs (stabilized at 0.19~0.22). This

study found that under mowing disturbance, the differences in ecological stoichiometric characteristics of degraded alpine meadow plants among degradation gradients were not significant, but they changed significantly with increasing mowing years, indicating that alpine meadows with different degradation levels in northwestern Yunnan may have similar response processes to mowing disturbance.

Full Text

Effects of Mowing on Plant Stoichiometry in Degraded Alpine Meadows of Northwest Yunnan

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Abstract

To investigate the effects of environmental disturbance on the stoichiometric characteristics of plants in degraded alpine meadows, we conducted a mowing experiment from 2018 to 2020 on alpine meadows with three degradation levels (light degradation, LD; moderate degradation, MD; and severe degradation, SD) in Shangri-La City. We analyzed differences in plant carbon (C), nitrogen (N), and phosphorus (P) contents, C:N:P ratios, and N-P power function relationships across different mowing durations (0, 1, and 2 years). The results showed that: (1) Except for P content in Cyperaceae, the C, N, and P contents of the plant community, Gramineae, and forbs showed no significant differences across the degradation gradient ($P > 0.05$). With increasing mowing years, the C, N, and P contents of degraded meadow plants first increased and then decreased ($P < 0.05$). (2) Plant C:N and C:P ratios did not differ significantly across degradation levels ($P > 0.05$). From LD to SD, the N:P ratios of the plant community, Cyperaceae, and forbs first decreased slightly and then increased significantly ($P < 0.05$), while the N:P ratio of Gramineae showed no significant change ($P > 0.05$). (3) With increasing mowing years, plant C:N and C:P ratios first decreased and then increased, while N:P ratio

showed the opposite trend. At 0 years of mowing, the C:P and N:P ratios of Cyperaceae were significantly higher than those of forbs ($P < 0.05$) but did not differ from the community and Gramineae ($P > 0.05$). At 1 and 2 years of mowing, the C:P and N:P ratios of Cyperaceae were higher than those of the community and other functional groups ($P < 0.05$). At each mowing duration, no differences in C:N ratio were observed among communities and functional groups ($P > 0.05$). (4) With increasing mowing years, the N–P power function relationship in degraded meadow plants strengthened, and the power exponent stabilized. The N–P power exponent of Cyperaceae (<0.1) differed markedly from that of the plant community, Gramineae, and forbs (stable at 0.19–0.22). We conclude that under mowing disturbance, the ecological stoichiometric characteristics of degraded alpine meadow plants in northwest Yunnan showed little variation across the degradation gradient but changed significantly with mowing duration, suggesting that alpine meadows with different degradation levels may share similar response processes to mowing disturbance.

Keywords: alpine meadow, plant community, degradation level, mowing duration, C:N:P, N–P power function relationship

Introduction

Plant ecological stoichiometry reveals core ecological issues such as biogeochemical cycling and habitat adaptation in ecosystems across organizational levels from ecosystems to communities and populations (Elser et al., 1996; Zhang et al., 2003; Du et al., 2020; Chen & Chen, 2021). Leaf C:N:P stoichiometric ratios of grassland plants in China' s Tibetan Plateau, Inner Mongolia Plateau, and Altun Mountains region exhibit general stability (He et al., 2006; Liu et al., 2015), a characteristic that facilitates plant community adaptation to environmental change (Liao et al., 2021; Wan et al., 2023). Alpine meadow degradation represents a typical ecological issue on the Tibetan Plateau, where community structure and functional indicators fluctuate with intensifying degradation (Wang et al., 2022). However, stoichiometric studies along degradation gradients have demonstrated strong homeostasis in leaf stoichiometry during alpine meadow degradation, with leaf C:N, C:P, and N:P ratios showing no significant changes with degradation level (Lin et al., 2013; Wang et al., 2020). Research on secondary succession in degraded alpine grasslands has also found stable C:N:P ratios in grassland plants (Zhang et al., 2023). Notably, beyond C:N:P ratios, the nonlinear coupling characteristics of plant N and P contents (i.e., the N-P power function) better reflect stoichiometric homeostasis (Reich et al., 2010; Tian et al., 2018). Globally, some studies suggest that the N–P power function for herbaceous plant leaves is conserved, with power exponents approaching 3/4 (Niklas & Cobb, 2005). However, recent research indicates that this conserved relationship may show significant regional variation and may differ among plant functional groups (Tian et al., 2018). As the "Third Pole" of the world, the Tibetan Plateau represents one of the global centers of alpine grassland distri-

bution. Investigating the N–P power function relationship of herbaceous plants in this region can help address these controversies.

Northwest Yunnan lies at the southern edge of the Tibetan Plateau, where alpine meadows cover approximately 1,400 km^2 in mountainous areas above 3,000 m elevation (Shen et al., 2016; Liu, 2017). More than 75% of these meadows are distributed in Shangri-La City, Diqing Tibetan Autonomous Prefecture. Since the 1990s, alpine meadows in Shangri-La have undergone obvious degradation, with area shrinking by nearly 40% (Cui, 2021). Previous studies have found that degraded alpine meadow plant communities in northwest Yunnan possess strong adaptive capacity to mowing disturbance: plant communities exhibit obvious compensatory growth (Zhao et al., 2020), and the sensitivity of community structure to mowing disturbance increases with degradation intensity (Ma et al., 2022). The stability of plant ecological stoichiometry represents an important aspect of plant community response to external disturbance (Yu et al., 2010; Liu et al., 2021). However, the effects of mowing on plant C, N, P stoichiometric ratios and N–P power function relationships in degraded alpine meadows of northwest Yunnan remain unclear.

To address these questions, based on a mowing control experiment conducted from 2018 to 2020 on typical degraded alpine meadows in Shangri-La, Yunnan Province, this study aims to explore: (1) whether meadow plant ecological stoichiometric characteristics differ significantly across degradation gradients under mowing disturbance; and (2) whether stoichiometric characteristics of degraded meadows change with mowing duration.

1.1 Study Site and Mowing Experiment

The mowing experiment was conducted on an alpine meadow at the foot of Shika Snow Mountain in Shangri-La City, Diqing Tibetan Autonomous Prefecture, Yunnan Province (99°38 49.7 E, 27°48 03 N, elevation 3,310 m). This region has a mean annual temperature of 6.9 °C and annual precipitation of approximately 620 mm, with subalpine meadow soil (Liu et al., 2017). Based on survey data of road disturbance intensity, soil moisture content, and vegetation coverage (Zhao et al., 2020), and referring to the National Standard of the People' s Republic of China "Indicators for Classification of Natural Grassland Degradation, Sandification, and Salinization" (GB19377-2003), we identified three meadow degradation gradients (light degradation, LD; moderate degradation, MD; and severe degradation, SD) in the study area (Ma et al., 2022). Dominant plants in LD plots were *Potentilla reptans* var. *sericophylla* and *Habenaria glaucifolia*; in MD plots were *Gentiana parvula* and *Habenaria glaucifolia*; and in SD plots were *Aster alpinus* and *Salvia przewalskii*. Three 1 m × 10 m replicate plots were established at each degradation gradient, with three 1 m × 1 m quadrats randomly selected in each plot. Mowing experiments were conducted during the growing season (late July) from 2018 to 2020, with

a stubble height of 1 cm. Plant samples were collected by functional group: Gramineae, Cyperaceae, and forbs. During the experiment, each mowing plot experienced three mowing durations: 0, 1, and 2 years. The land management history of the mowing control area was: yak grazing summer pasture before 2018, followed by fencing enclosure starting in 2018 (Ma et al., 2022).

1.2 Plant Carbon, Nitrogen, and Phosphorus Content Measurement and Calculation

We first measured the C, N, and P contents of Gramineae, Cyperaceae, and forbs. Total organic carbon was determined as follows: (1) 3–5 mg of ground plant sample was packaged; (2) total organic carbon was measured using a total organic carbon analyzer (Vario TOC, Germany). Plant N and P contents were determined using the H_2SO_4-H_2O_2 method: (1) 0.1 g of plant sample was weighed, moistened with 1 mL distilled water, then soaked in 5 mL concentrated sulfuric acid and left to stand; (2) samples were digested at gradually increasing temperatures from 80 °C to 350 °C, with H_2O_2 added every 20–30 min for catalysis until the digestion solution became colorless, then cooled; (3) samples were diluted, filtered, transferred to centrifuge tubes, and plant N and P were measured using an AA3 continuous flow analyzer (SEAL Analytical GmbH, AA3, Germany).

Plant community C, N, and P contents were calculated using the dominance of each functional group in the community as weights. Functional group dominance was calculated as:

Formula (1):

$$DF_i = \sum_{j=1}^{n} (C_{ij} \times R_{ij})$$

where DF_i is the dominance of functional group i; C_{ij} and R_{ij} are the relative coverage (ratio of species j coverage to total community coverage) and relative height (ratio of species j height to total community height) of species j in functional group F_i, respectively. The sum of dominance values for the three functional groups equals 1.

Plant community nutrient content (i.e., C, N, P) was calculated as:

Formula (2):

$$Con_{com} = \sum_{i=1}^{3} (Con_{Fi} \times DF_i)$$

where Con_{com} is plant community nutrient content; Con_{Fi} is plant nutrient content of functional group i (i.e., the mean of species within the same functional group); and DF_i is the dominance of functional group i in the community.

1.3 Statistical Analysis

Two-way ANOVA was used to analyze the effects of degradation level (LD, MD, and SD) and mowing duration (0, 1, and 2 years) on meadow plant community and functional group (Gramineae, Cyperaceae, and forbs) C, N, P contents and their stoichiometric characteristics, with LSD post-hoc tests at a significance level of $\alpha = 0.05$. Specifically, when analyzing differences in plant stoichiometric characteristics across degradation gradients, data from the three mowing years were pooled for each degradation gradient. When analyzing effects of mowing duration on degraded meadow plant stoichiometric characteristics, data from the three degradation gradients were pooled for each mowing year. After log-transformation of N and P contents, power functions were fitted to the N-P regression relationship (i.e., $N_c = \beta P_c^{\alpha}$) to explore the effects of mowing on N-P power function conservation in degraded meadow plant communities and functional groups. In the regression analysis, models for each mowing duration were constructed using pooled data from the three degradation gradients. All analyses were performed in SPSS Statistics 17.0.

2.1 Effects of Mowing on Plant C, N, and P Contents in Degraded Alpine Meadows

Across the degradation gradient, C, N, and P contents of alpine meadow plant communities and functional groups remained relatively stable—most indicators showed no significant differences among degradation levels (n = 108, P > 0.05). Mowing duration had significant effects on C, N, and P contents of meadow plant communities and functional groups—all indicators differed significantly among mowing years. Additionally, the interactive effects of degradation and mowing duration on meadow plant C, N, and P contents were weak (Table 1).

Across degradation gradients, C, N, and P contents of plant communities, Gramineae, and forbs showed no significant differences (n = 108, P > 0.05). Cyperaceae showed no significant differences in C and N contents (P > 0.05), but P content increased significantly (n = 108, P = 0.003) (Figure 1 [Figure 1: see original paper], Table 1).

At each degradation gradient, plant C and N contents showed no significant differences among communities and functional groups (n = 108, P > 0.05) (Figure 1). Differences in plant P content among communities and functional groups varied by degradation gradient: in the SD gradient, Cyperaceae P content was significantly lower than the community and other functional groups; in the MD gradient, community and forb P contents were (2.59 ± 0.08) $mg \cdot g^{-1}$ and (2.81 ± 0.10) $mg \cdot g^{-1}$, respectively, significantly higher than Gramineae [(2.29 ± 0.08) $mg \cdot g^{-1}$] and Cyperaceae [(2.22 ± 0.08) $mg \cdot g^{-1}$] (n = 108, P < 0.0001); in the LD gradient, Cyperaceae P content was (2.14 ± 0.09) $mg \cdot g^{-1}$, not significantly different from Gramineae [(2.38 ± 0.10) $mg \cdot g^{-1}$] (n = 108, P > 0.05) but significantly lower than the community [(2.54 ± 0.11) $mg \cdot g^{-1}$] and forbs [(2.67 ±

0.15) mg · g^{-1}] (n = 108, P = 0.011) (Figure 1).

As mowing duration increased from 0 to 2 years, C, N, and P contents of degraded alpine meadow plant communities and functional groups showed consistent patterns: an initial increase followed by a decrease (Figure 2 [Figure 2: see original paper]).

Differences in plant C, N, and P contents among plant communities and functional groups varied with mowing year. At 0 years of mowing, plant C and N contents were (382.98 ± 3.49) mg · g^{-1} and (14.45 ± 0.14) mg · g^{-1}, respectively, with no significant differences among communities and functional groups (n = 108, P_C = 0.55, P_N = 0.14). Forb P content was (2.47 ± 0.10) mg · g^{-1}, significantly higher than the community and other functional groups (n = 108, P = 0.003) (Figure 2).

At 1 year of mowing, C contents of forbs and Gramineae were (414.73 ± 9.45) mg · g^{-1} and (406.50 ± 5.34) mg · g^{-1}, respectively, significantly higher than Cyperaceae [(383.02 ± 5.78) mg · g^{-1}] (n = 108, P = 0.008) (Figure 2). Plant N content was (20.19 ± 0.26) mg · g^{-1}, with no differences among communities and functional groups (n = 108, P = 0.85). Plant P content ranked as: forbs [(3.12 ± 0.13) mg · g^{-1}] > Gramineae community > Cyperaceae [(2.25 ± 0.10) mg · g^{-1}] (n = 108, P < 0.0001) (Figure 2).

At 2 years of mowing, plant C and N contents were (363.17 ± 3.29) mg · g^{-1} and (14.99 ± 0.26) mg · g^{-1}, respectively, with no differences among communities and functional groups (n = 108, P_C = 0.19, P_N = 0.44). Plant P content ranked as: forbs [(2.43 ± 0.09) mg · g^{-1}] community [(2.24 ± 0.07) mg · g^{-1}] > Gramineae [(2.05 ± 0.07) mg · g^{-1}] Cyperaceae [(1.85 ± 0.08) mg · g^{-1}] (n = 108, P < 0.0001) (Figure 2).

2.2 Effects of Mowing on Plant C:N:P Ratios in Degraded Alpine Meadows

Compared with differences across degradation gradients, mowing duration had greater effects on meadow plant C:N:P stoichiometric ratios, with weak interactive effects between degradation level and mowing duration (Table 1).

Across degradation gradients, C:N and C:P ratios of alpine meadow plant communities and the three functional groups remained stable, with no significant changes (n = 108, P > 0.05). Gramineae N:P ratio ranged from (6.84 ± 0.13) to (7.25 ± 0.14), showing no change with meadow degradation level (n = 108, P > 0.05). With increasing degradation level, N:P ratios of plant communities, Cyperaceae, and forbs first decreased slightly and then increased significantly (n = 108, P < 0.05) (Table 1, Table 2).

At each degradation gradient, plant C:N ratio showed no significant differences among communities and functional groups (n = 108, P > 0.05) (Table 2). In SD and MD gradients, C:P ratios of Cyperaceae and Gramineae tended to be higher than those of the community and forbs; in the LD gradient, C:P ratio showed

no significant differences among plant communities and functional groups (n = 108, P > 0.05). At each degradation gradient, Cyperaceae N:P ratio was significantly higher than the community and other functional groups (n = 108, P < 0.05) (Table 2).

As mowing duration increased from 0 to 2 years, C:N ratios of meadow plant communities, Gramineae, Cyperaceae, and forbs, as well as C:P ratios of communities and Gramineae, all showed a decreasing then increasing pattern: values at 0 and 2 years of mowing were significantly higher than at 1 year (n = 108, P < 0.05) (Table 3). C:P ratios of Cyperaceae and forbs, and N:P ratio of forbs, did not change with mowing duration (n = 108, P > 0.05). N:P ratios of plant communities and Gramineae showed an increasing trend (n = 108, P < 0.05), while Cyperaceae N:P ratio first increased and then decreased (n = 108, P < 0.05) (Table 3).

At each mowing duration, plant C:N ratio showed no differences among plant communities and functional groups (n = 108, P > 0.05). At 0 years of mowing, C:P ratios of Gramineae and Cyperaceae were significantly higher than those of forbs (n = 108, P < 0.05). After 1 year of mowing, Cyperaceae C:P ratio was significantly higher than the community and other functional groups (n = 108, P < 0.05). After 2 years of mowing, Cyperaceae C:P ratio was significantly higher than the community and forbs (n = 108, P < 0.05) but did not differ from Gramineae (n = 108, P > 0.05). At 0 years of mowing, Cyperaceae N:P ratio was significantly higher than forbs (n = 108, P < 0.05) but did not differ from the community and Gramineae (n = 108, P > 0.05). At 1 and 2 years of mowing, Cyperaceae N:P ratio was significantly higher than the community, Gramineae, and forbs (n = 108, P < 0.05) (Table 3).

2.3 Effects of Mowing on N-P Power Function Relationships in Degraded Alpine Meadows

Overall analysis of mowing experiment data revealed that N-P power function relationships of degraded meadow plant communities, Gramineae, and forbs were similar, with power exponents ranging from 0.19 to 0.22. However, Cyperaceae had a power exponent of 0.07, much smaller than the other three groups (Figure 3 [Figure 3: see original paper]).

Mowing duration caused significant changes in N-P power function relationships of degraded meadow plants. At 0 years of mowing, N-P power function relationships for Gramineae and Cyperaceae were not statistically significant (n = 27, P > 0.05), while those for the plant community and forbs were significant (n = 27, P_{community} = 0.008, P_{forbs} = 0.001), but their power exponents were all less than 0.1 (Figure 3). After 1 and 2 years of mowing, N-P power function models for plant communities and all three functional groups were statistically significant (n = 27, P < 0.01). Except for Cyperaceae with a power exponent less than 0.1, power exponents for the community, Gramineae, and forbs remained stable between 0.17 and 0.20 (Figure 3).

3 Discussion and Conclusion

A global study by Tian et al. (2021) reported that herbaceous leaf N, P contents, and N:P ratio were approximately 20.56 $mg \cdot g^{-1}$, 1.56 $mg \cdot g^{-1}$, and 13.17, respectively. He et al. (2008) found that Chinese grassland plants had leaf N, P contents, and N:P ratio of 29.07 $mg \cdot g^{-1}$, 1.9 $mg \cdot g^{-1}$, and 15.3, respectively. Compared with these results, our study found that N content (16.4–16.6 $mg \cdot g^{-1}$) and N:P ratio (6.7–7.6) of degraded meadow plants were far below global and Chinese averages, while P content (~2 $mg \cdot g^{-1}$) was comparable to the Chinese average and higher than the global average. This indicates strong regional specificity in N, P contents, and N:P ratio of degraded alpine meadow plants in northwest Yunnan, and future research should explore the causes of this regional specificity.

This study found that during the entire mowing experiment, meadow plant C, N, P contents and C:N, C:P ratios showed little variation across degradation gradients, partially confirming the stability of ecological stoichiometric ratios in degraded alpine meadows on the Tibetan Plateau. However, C, N, P contents and stoichiometric ratios of degraded meadow plants changed significantly with mowing duration. Our previous research indicated that mowing caused obvious changes in community species composition (Ma et al., 2022), which may explain the altered plant C, N, P stoichiometric characteristics. Since plant N and P contents are determined by the relative abundance of proteins and nucleic acids in plant tissues (Tian et al., 2021), plant community C, N, P stoichiometric characteristics are primarily influenced by species composition differences (Zhang et al., 2021; Wu et al., 2023) and show certain zonal characteristics with species distribution (Martiny et al., 2013). Local climate conditions and environmental factors such as flooding have limited effects on plant community C, N, P stoichiometric characteristics (He et al., 2006, 2008; Xie et al., 2016; Mi et al., 2016). These results suggest that if external disturbances (including mowing) do not alter plant community species composition, community C, N, P stoichiometric characteristics can remain stable. In other words, ecological stoichiometric characteristics can be used to assess the sensitivity of plant community responses to environmental disturbance.

Numerous studies have shown that compared with plant C:N or C:P ratios, plant N:P ratio responds more significantly to environmental changes such as warming and nutrient addition (He et al., 2008; Xu et al., 2014; Wan et al., 2023). Our study also found that during the mowing experiment, meadow plant N:P ratio was not only affected by mowing duration but also showed a "slight decrease followed by significant increase" trend with degradation level. This suggests that plant N:P ratio has potential as an indicator of environmental change (e.g., disturbance, degradation). At the community level, this indicator function may be relatively weak (Lin et al., 2013), but at the functional group or species level, its indicator function may be more robust. Specifically, Cyperaceae

plants are constructive species in alpine meadows, and their N:P ratio deserves in-depth study as an indicator of environmental disturbance. We found that with increasing mowing duration, changes in Cyperaceae N:P ratio were more pronounced than in the community. Furthermore, He et al. (2008) also showed that leaf N:P ratio of *Kobresia* species (Cyperaceae) responded markedly to precipitation. Therefore, research on grassland environmental change in alpine regions should focus on N:P ratio changes in certain Cyperaceae genera (or species).

Additionally, our study of N–P power function relationships showed that N–P power exponents of plant communities and functional groups in degraded alpine meadows of northwest Yunnan were all less than 1/4, far below the 3/4 proposed by Niklas and Cobb (2005). Moreover, the N–P power function relationship of Cyperaceae differed markedly from that of the community, Gramineae, and forbs. These results support the view that leaf N–P stoichiometric characteristics vary significantly with geographic location and plant functional group (Tian et al., 2018). Notably, we found that compared with pre-mowing (0 years), the N–P power function relationship in degraded meadows strengthened significantly after 1 and 2 years of mowing—indicating that the coupling relationship between plant N and P contents intensified following mowing disturbance. This enhanced coupling may play an important role in maintaining stable short-term compensatory growth capacity in degraded alpine meadows (Zhao et al., 2020). However, long-term plant compensatory growth in alpine regions can lead to decreased soil nutrient supply capacity (Zhang et al., 2020). Future research should explore issues related to the maintenance of compensatory growth capacity and community degradation in alpine meadows after soil nutrient supply declines, from the perspective of changes in plant N–P coupling relationships.

In summary, this study found that under mowing disturbance, plant C, N, P contents and C:N:P ratios of degraded alpine meadows in northwest Yunnan showed little variation across degradation gradients but changed significantly with increasing mowing duration. Furthermore, the interactive effects of mowing duration and degradation level on most plant stoichiometric characteristics were not significant, suggesting that alpine meadows with different degradation levels in northwest Yunnan may share similar response processes to mowing disturbance.

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