

*Original Research*

# Effects of Reseeding Duration and Mowing on the Soil Seed Bank of Alpine Meadows in the Sanjiangyuan Region

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## Abstract

The soil seed bank is fundamental to vegetation regeneration and the long-term stability of alpine meadow communities. Understanding its response to management practices is essential for improving ecological restoration outcomes. In the Sanjiangyuan region, we systematically evaluated the effects of different reseeded durations and mowing regimes on soil seed bank density, soil physicochemical properties, and plant community characteristics, and applied structural equation modeling to disentangle the pathways linking these factors. Our results show that reseeded consistently enhances soil seed bank density by increasing plant species richness and promoting the accumulation of seeds from dominant Poaceae and Cyperaceae species. Mowing exhibited stage-dependent effects: it limited seed bank development during later stages of recovery but facilitated seed input when vegetation was still establishing. Soil nutrients – particularly available nitrogen – were identified as primary drivers of seed bank variation, exerting stronger influences than plant community attributes. Structural equation modeling further revealed that reseeded indirectly strengthens the seed bank through its positive effect on species richness, whereas mowing may weaken this pathway by reducing plant diversity or altering nutrient availability. These findings highlight the tight coupling between aboveground vegetation recovery and belowground propagule reserves and provide a scientific basis for optimizing reseeded–mowing combinations to enhance the restoration efficiency of degraded alpine meadows.

**Keywords:** alpine meadow, soil seed bank, reseeded duration, mowing, soil physicochemical properties, structural equation model

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## Introduction

Alpine meadows are the most widespread and extensive grassland type on the Qinghai-Tibet Plateau, accounting for 49% of the total grassland area. This ecosystem plays a vital role in maintaining regional ecological security by providing multiple key services, including water conservation, soil and water retention, windbreak and sand fixation, biodiversity maintenance, and carbon balance regulation [1]. However, with accelerating climate change and increasing anthropogenic disturbances such as overgrazing, reclamation, and unsustainable land use, grassland degradation has intensified [2]. Degradation is manifested not only in reduced vegetation cover, shifts in dominant species, and deterioration of soil physicochemical properties, but also more profoundly in the decline of soil seed bank abundance and functional capacity, which critically undermines the natural regeneration and ecological restoration potential of grasslands [3, 4]. Within grassland ecosystems, the soil seed bank is often described as a “time capsule” for maintaining species diversity and a “potential reservoir” supporting community recovery [5]. The species composition, seed density, and diversity within the seed bank directly determine the trajectory of degraded grassland recovery and the resilience of ecosystems to disturbances [6]. Thus, restoring and enhancing the quantity, quality, and structural diversity of soil seed banks has become a central issue in the ecological restoration and sustainable management of grasslands.

Reseeding is a commonly used measure for restoring degraded grasslands and improving ecosystem functions [7]. By introducing well-adapted and high-quality grass species, reseeded can optimize plant community structure, enhance ecological stability, and increase productivity [8]. The duration of reseeded not only affects the establishment, growth, and reproduction of introduced species, but also determines their long-term impacts on aboveground communities, soil properties, and soil seed banks [9]. Previous studies have shown that long-term reseeded gradually alters plant composition, functional group structure, and reproductive strategies, thereby influencing the density, diversity, and spatial distribution of soil seed banks [10]. However, although the effects of reseeded on aboveground communities have been widely studied, its long-term impacts on belowground seed banks and the mechanisms linking aboveground vegetation recovery with seed bank dynamics remain unclear, particularly in the alpine ecosystems of the Qinghai-Tibet Plateau. Mowing is another commonly applied management practice in alpine meadows, playing an important role in regulating community structure, promoting species coexistence, and maintaining ecosystem functions [11]. Moderate mowing can suppress dominant species, create space for subordinate species, increase plant diversity, and enhance ecological stability [12, 13]. In contrast, excessive or improper mowing may disrupt plant growth

and reproductive cycles, reduce the number of seeds returning to the soil, and even accelerate degradation [14]. Mowing can also indirectly influence soil seed banks by altering litter accumulation, modifying soil microenvironmental conditions, and affecting plant resource allocation between growth and reproduction [15, 16]. Although mowing is ecologically significant, the combined effects and underlying mechanisms of reseeded and mowing on soil seed bank dynamics have not been systematically examined in alpine meadow ecosystems.

Although previous studies in the Three-River-Source region and other alpine ecosystems have examined the independent effects of reseeded or mowing on vegetation structure and ecological functions [17, 18], systematic research on how their combined effects influence the long-term dynamics of soil seed banks remains limited. Given the central role of soil seed banks in vegetation regeneration and grassland recovery, this study aims to: (1) quantitatively assess the effects of different reseeded durations and mowing treatments on seed bank density, species diversity, and community composition; and (2) use structural equation modeling to identify the pathways and underlying mechanisms through which reseeded and mowing affect soil seed banks.

We propose two hypotheses: (i) longer reseeded duration increases plant richness and consequently promotes seed bank accumulation; and (ii) mowing has stage-dependent effects that may alter the relationships among reseeded, plant richness, and seed bank attributes. The findings are expected to enhance understanding of the coupling mechanisms between aboveground vegetation changes and belowground propagule dynamics during alpine meadow restoration, and to provide scientific and practical guidance for optimizing reseeded–mowing management to improve the recovery efficiency of degraded grasslands.

## Materials and Methods

### Study Area

The field experiment was conducted from 2013 to 2019 in Gaqing Village, Saierlong Township, Henan County, Huangnan Prefecture, located in the Sanjiangyuan region. The experimental site is located on a flat terrain, characterized by medium soil fertility and abundant sunlight, at an average altitude of 3,562 m. The mean annual temperature ranges from  $-1.3^{\circ}\text{C}$  to  $1.6^{\circ}\text{C}$ , with 2,530–3,100 h of annual sunshine and a mean annual precipitation of 724.7 mm. The natural grassland type is alpine meadow dominated by *Elymus nutans* (Griseb.). Other major palatable species include *Carex capillifolia* (Decne.) S.R. Zhang and *Polygonum viviparum* L., while unpalatable or toxic species include *Ligularia virgaurea* (Maxim.) Mattf. and *Ranunculus japonicus* Thunb. [19]. The soil is classified

as mountain meadow soil, characterized by a loam texture, rich in organic matter, and high in potential fertility. However, its nutrient availability is limited due to the cold and oxygen-deficient conditions of the alpine environment.

### Experimental Design

This study employed a two-factor randomized block design, with reseeded year (2013 or 2017) and mowing treatment (mown or unmown) as the main factors. These yielded four treatment combinations: Y1C1 (2013 reseeded, unmown in 2018), Y1C2 (2013 reseeded, mown in 2018), Y2C1 (2017 reseeded, unmown in 2018), and Y2C2 (2017 reseeded, mown in 2018). Each treatment included five replicate plots, and each plot measured 5×5 m. A randomized block layout was applied to ensure comparability among treatments. Before reseeding, all plots received the same baseline improvement measures and were fenced to exclude grazing. Reseeding was conducted mechanically without tillage between early and mid-May of the respective years, using three high-quality forage species: *Elymus nutans*, *Poa pratensis* cv. Qinghai, and *Festuca sinensis* cv. Qinghai. No additional interventions were carried out after reseeding to allow natural succession to proceed. To provide baseline nutrient input, an organic compound fertilizer (“Tuokang Institute” brand; N+P<sub>2</sub>O<sub>5</sub>+K<sub>2</sub>O≥5%) was applied at 100 kg per mu. Mowing treatments followed the local traditional hay-harvesting period, with the stubble height standardized at 2 cm to maintain consistency among treatments, while unmown plots remained ungrazed and uncut throughout the growing season.

### Sample Collection

In August 2018, systematic surveys were conducted to evaluate plant community characteristics under different mowing treatments. Five quadrats (0.25 m<sup>2</sup>, 50×50 cm) were randomly established for each treatment. Within each quadrat, plant species were recorded, and total cover, species-specific cover, density, and mean plant height were measured. All aboveground biomass was clipped at ground level and classified into three functional groups: Gramineae, Cyperaceae, and forbs. Plant samples were initially oven-dried at 105°C for 0.5 h to inactivate enzymatic activity and subsequently dried at 70°C to a constant weight for biomass determination.

Soil samples were collected from the 0-30 cm soil layer, with five subsamples combined into a composite sample. Each composite sample was divided into two portions: one for soil physicochemical analysis and the other for seed bank germination testing. The measured soil properties included pH, total nitrogen (TN), available nitrogen (AN), available phosphorus (AP), and available potassium (AK). Soil pH was determined potentiometrically; TN and AN were measured using the micro-Kjeldahl digestion method; AP was

analyzed by the molybdenum–antimony colorimetric method following H<sub>2</sub>SO<sub>4</sub>–HClO<sub>4</sub> digestion; and AK was quantified by flame photometry after HF–HClO<sub>4</sub> digestion [20].

### Soil Seed Bank Germination Test

Soil samples were air-dried in a well-ventilated area to prevent mold growth. After drying, samples were sieved to remove gravel while avoiding seed damage, thereby ensuring sample homogeneity. The processed soils were then overwintered under dry, ventilated natural conditions. Seed bank composition was assessed using the seedling emergence method throughout the entire growing season (May–October 2019) [21]. For each sample, the soil was placed in plastic pots (25 cm in height, 3 cm in diameter) lined with sterile substrate and spread evenly in a thin layer, with five replicate pots per sample. The pots were maintained in a greenhouse with day/night temperatures of 20–25°C and 10–15°C, respectively, under a 12-hour light/12-hour dark photoperiod. Natural light was supplemented with fluorescent lamps to maintain a photosynthetically active radiation (PAR) of ≥300 μmol·m<sup>-2</sup>·s<sup>-1</sup>, and relative humidity was controlled at 55–65%. Soil moisture was maintained by periodic watering to keep the soil lightly moist. Seedling emergence was monitored every 2 days for 8 weeks, and newly emerged seedlings were removed after recording. Seedlings that could not be identified immediately were retained until sufficient morphological characteristics developed for accurate identification. All seedlings were identified to species or functional group based on morphological traits, with reference to the “Flora of Qinghai” and relevant seedling atlases. At the end of the experiment, all non-germinated seeds were tested for viability using a 1% tetrazolium chloride (TZ) staining method; seeds with red-stained embryos were considered viable. Each germination pot was treated as the statistical unit for data analysis. The experiment was terminated when no new seedlings emerged for three consecutive weeks [15].

### Statistical Analysis

Seed bank density was calculated as the number of germinated seeds per unit area (seeds/m<sup>2</sup>). Community diversity was assessed using  $\alpha$ -diversity indices: (1) species richness index (R), (2) Shannon-Wiener index (H), and (3) Pielou’s evenness index (J), calculated as follows [22]:

$$\text{Species richness: } R = S$$

$$\text{Shannon-Wiener index: } H = -\sum_{i=1}^S p_i^2$$

$$\text{Pielou’s evenness: } J = H/\ln S$$

where S is the number of species,  $p_i$  is the relative abundance of species i,  $N_i$  is the number of individuals

of species  $i$ , and  $N$  is the total number of individuals in the community.

Data organization was performed using Excel 2021. Normality and homogeneity of variance were tested using the Shapiro-Wilk and Levene's tests, respectively. Variables that did not meet these assumptions were log- or square-root transformed. Two-way ANOVA was used to assess the effects of reseeding year, mowing, and their interaction on soil seed bank density, community diversity, and soil properties. One-way ANOVA followed by Duncan's multiple range test was used for mean comparisons. All statistical analyses were conducted in SPSS 25.0 with a significance level of  $P = 0.05$ . Figures were generated using Origin 2024. Variance partitioning was conducted in Img to quantify the contribution of each predictor to the  $R^2$  of the optimal model. Structural equation modeling (SEM) was initially planned in Amos 24.0 (IBM SPSS) to evaluate the direct and indirect effects of treatments on the soil seed bank. Model fit would have been assessed using standard indices, including  $\chi^2/df$  ( $<3$ ),  $P$ -value ( $>0.05$ ),

comparative fit index ( $CFI > 0.90$ ), and root mean square error of approximation ( $RMSEA < 0.10$ ) [23]. Before SEM analysis, all variables were standardized using z-scores to meet statistical assumptions [24].

## Results

### Effects of Reseeding Duration and Mowing on Plant Community Species Diversity

The species diversity indices of plant communities did not show significant differences among different reseeding durations. However, mowing had a significant effect on species diversity ( $P < 0.05$ ). Specifically, compared with the unmown plots, mowing reduced the species richness index by 7.84% and significantly decreased the Shannon-Wiener diversity index by 2.11%. In addition, the interaction between reseeding duration and mowing significantly affected the Shannon-Wiener diversity index, with the lowest value observed

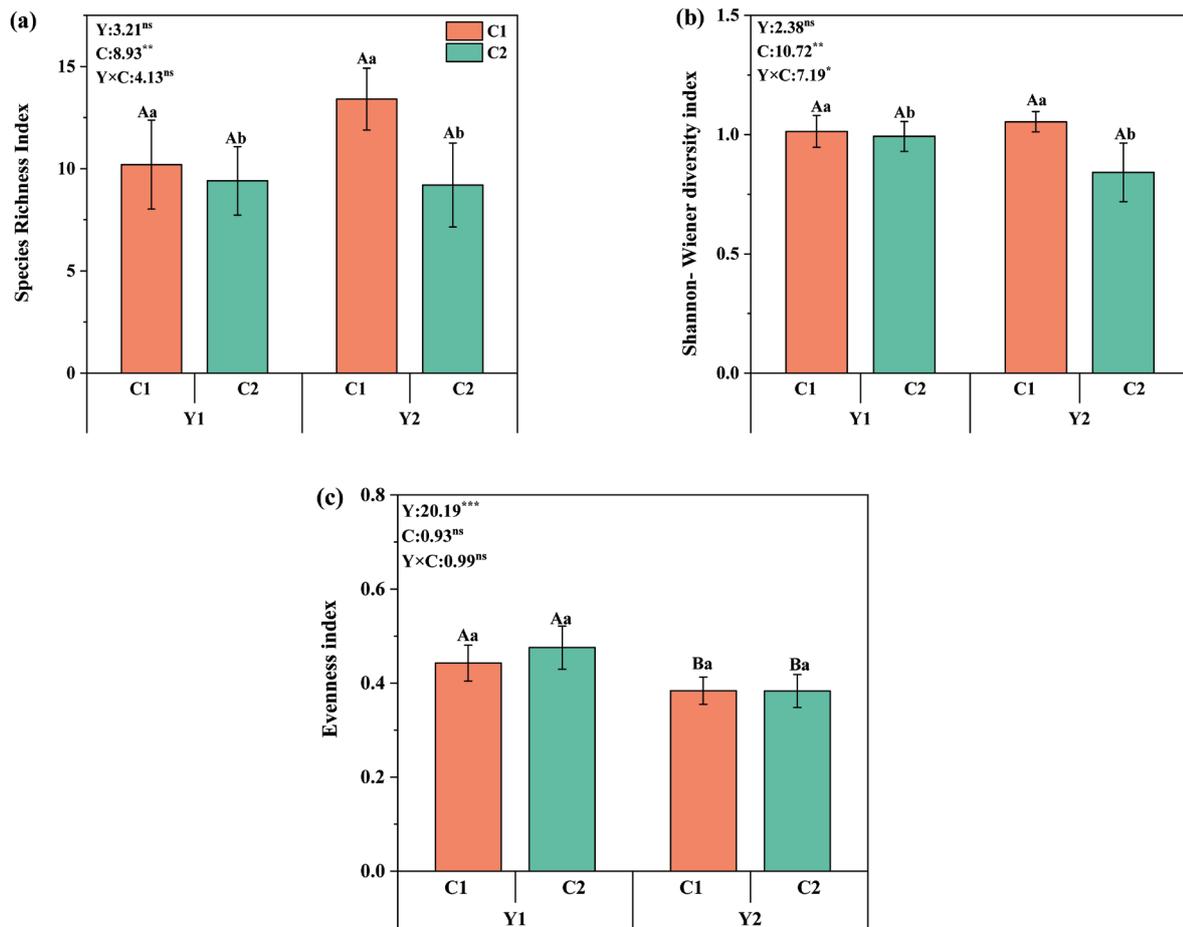


Fig. 1. Effects of reseeding duration and mowing on plant community species diversity. In the figure, Y1 denotes reseeding conducted in 2013, Y2 denotes reseeding in 2017, C1 denotes mowing, and C2 denotes no mowing.  $Y \times C$  represents the interaction between reseeding duration and mowing treatment. Different lowercase letters indicate significant differences among mowing treatments within the same reseeding year, whereas different uppercase letters indicate significant differences among reseeding years within the same mowing treatment.

under the treatment of reseeded in 2017 combined with mowing (Y2C2). These results suggest that the effect of mowing may vary with reseeded time, and their combined influence exerts a more complex regulatory role on community diversity (Fig. 1).

### Effects of Reseeding Duration and Mowing on Soil Physicochemical Properties

Different reseeded durations significantly affected soil pH, available phosphorus, and available potassium contents ( $P < 0.05$ ). Compared with reseeded in 2013, reseeded in 2017 significantly increased soil pH and available phosphorus by 7.23% and 44.52%, respectively,

while significantly decreasing available potassium by 19.31%. Mowing treatment also had significant effects on soil physicochemical properties. Specifically, compared with no mowing, mowing significantly increased total nitrogen (51.92%), available nitrogen (23.28%), available phosphorus (86.30%), and available potassium (14.13%). In addition, the effect of mowing on soil pH varied with reseeded duration: mowing after reseeded in 2013 increased soil pH by 1.84%, whereas mowing after reseeded in 2017 decreased soil pH by 7.85%. The interaction between reseeded duration and mowing treatment significantly influenced soil pH, total nitrogen, and available phosphorus, indicating that their combined effects induced complex

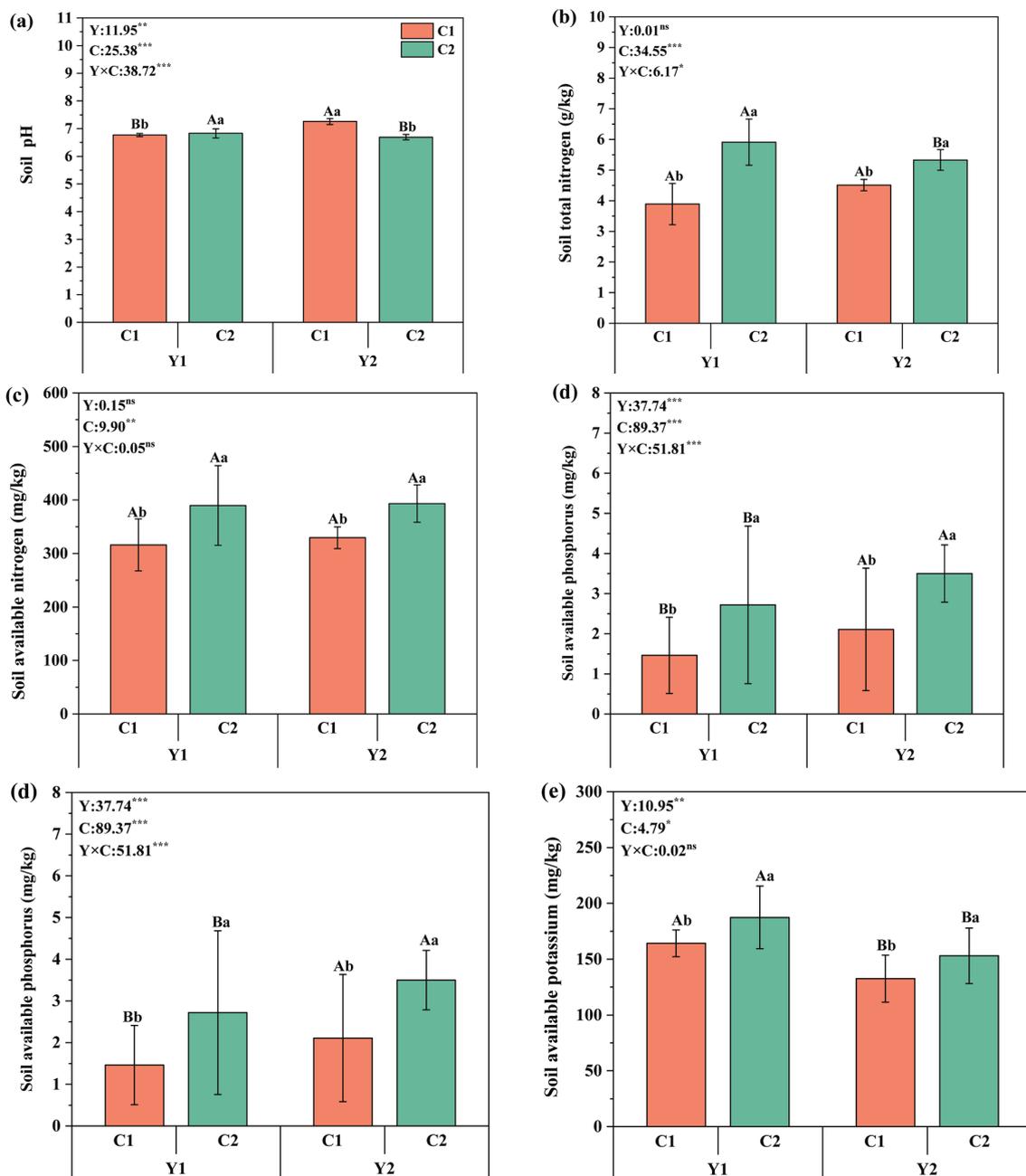


Fig. 2. Effects of reseeded duration and mowing on soil physicochemical properties.

changes in soil nutrient status and physicochemical properties (Fig. 2).

### Effects of Reseeding Duration and Mowing on Soil Seed Bank

As shown in Fig. 3, germinable seeds in the soil seed bank were primarily concentrated in the top 0-7 cm of soil. Seeds of Poaceae and Cyperaceae were markedly more abundant than those of other grasses, forming the main components of the seed bank. Two-way ANOVA results (Fig. 3d) indicated that reseeded duration had a significant effect on soil seed bank density ( $P < 0.05$ ). Compared with reseeded in 2013, reseeded in 2017 significantly increased soil seed bank density by 198.26%. Mowing also had a significant effect on seed bank density ( $P < 0.05$ ). Specifically, under the 2013 reseeded condition, mowing reduced soil seed bank density by 60.00%, whereas under the 2017 reseeded condition, mowing increased seed bank density by 27.11%. The interaction between reseeded duration and mowing treatment was also significant ( $P < 0.05$ ), with the highest seed bank density observed under the 2017 reseeded combined with mowing treatment (Y2C2), reaching 697.6 seeds  $m^{-2}$ .

### Regulatory Mechanisms of Reseeding Duration and Mowing on Soil Seed Bank Density

Fig. 4a) illustrates the relative contributions of plant and soil factors to soil seed bank density, showing that soil variables explained a substantially greater proportion of the variation than plant variables, with a total coefficient of determination ( $R^2$ ) of 0.81. Among these factors, soil available potassium (SAK), soil available nitrogen (SAN), the Shannon diversity index (H), and the species richness index (R) significantly influenced seed bank density. The structural equation model further clarified the pathways through which reseeded duration and mowing affected soil seed bank density (Fig. 4b)). The overall model demonstrated a good fit ( $\chi^2 = 1.12$ ,  $P = 0.08$ , CFI = 0.96, RMSEA = 0.00), and the standardized path coefficients clearly depicted the relationships among variables.

The structural equation model revealed that reseeded duration exerted a significant direct positive effect on soil seed bank density (path coefficient = 0.33,  $P < 0.05$ ), whereas mowing had a direct negative effect (path coefficient = -0.37,  $P < 0.05$ ). In addition, reseeded duration indirectly enhanced seed bank density by increasing plant species richness (path coefficient = 0.46,  $P < 0.01$ ), resulting in a significant positive

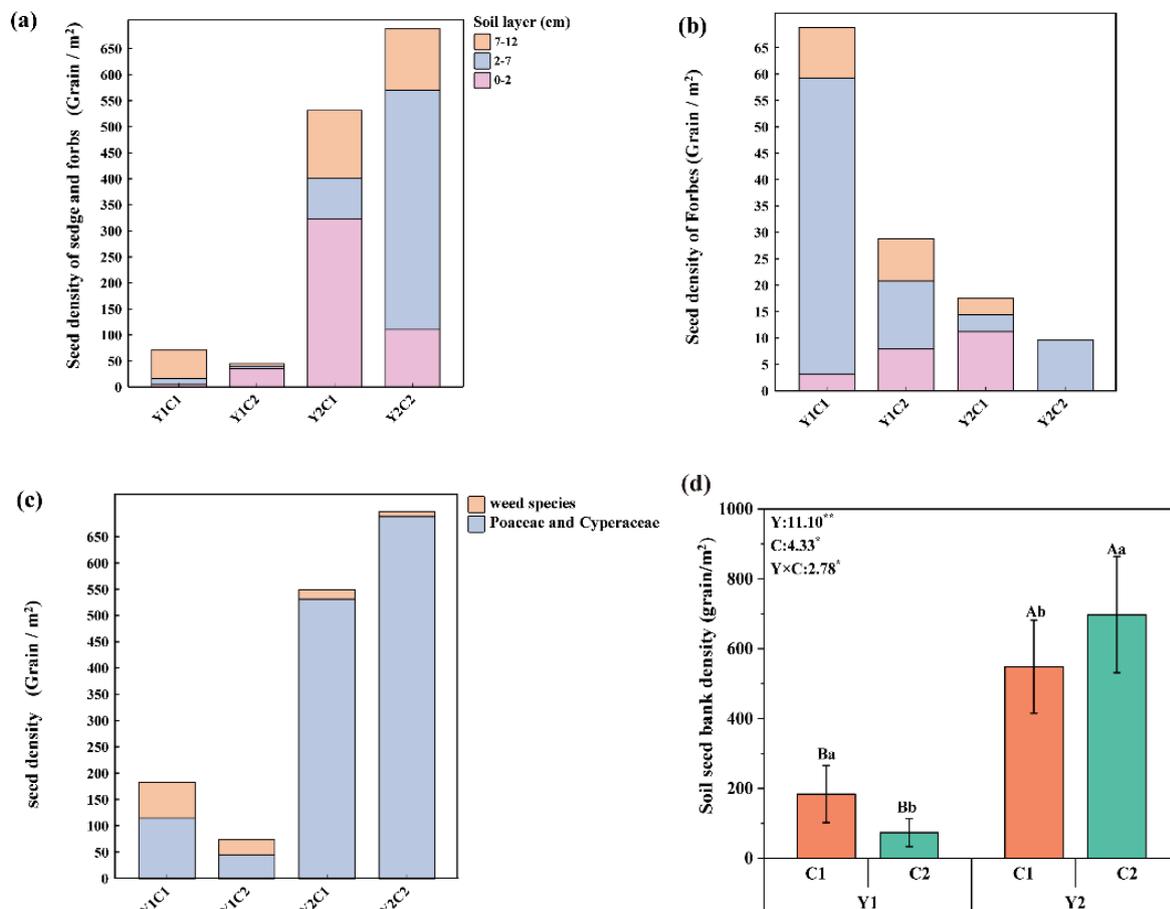


Fig. 3. Effects of reseeded duration and mowing on the soil seed bank.

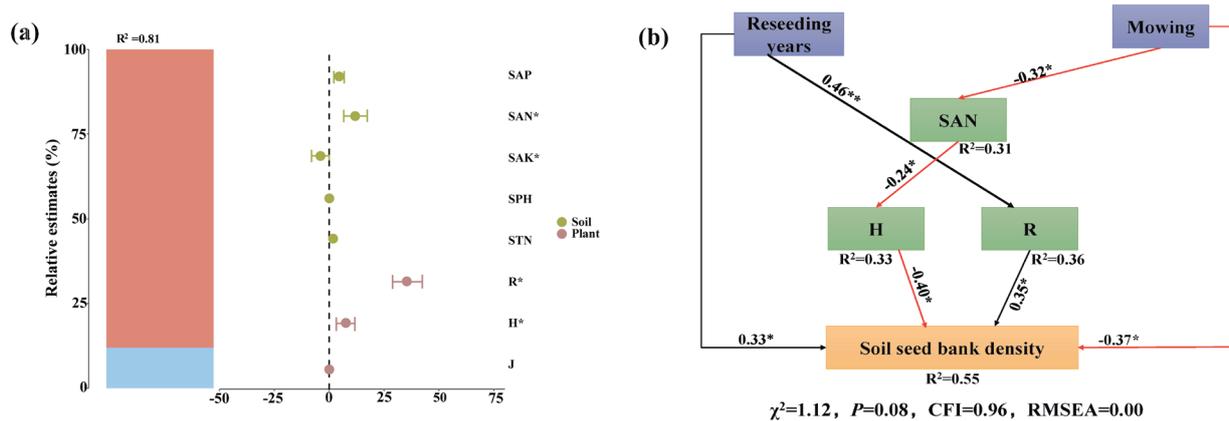


Fig. 4. Regulatory mechanisms of reseeding duration and mowing treatment on soil seed bank density. a) Relative contributions of plant factors to soil seed bank density. The average parameter estimates of the model predictors (standardized regression coefficients) are shown, along with their associated 95% confidence intervals. The relative importance of each predictor is expressed as the percentage of explained variance. \* $P<0.05$ ; \*\* $P<0.01$ ; \*\*\* $P<0.001$ . b) Structural equation model illustrating the effects of reseeding duration and mowing treatment on soil seed bank density. Black solid lines indicate significant positive relationships, whereas red solid lines indicate significant negative relationships. Line width is proportional to the strength of the correlation. Standardized regression coefficients along each path and the total variance explained ( $R^2$ ) for each variable (shown below the rectangles) reflect the contributions of all predictor variables. \* $P<0.05$ ; \*\* $P<0.01$ ; \*\*\* $P<0.001$  indicate statistically significant paths.

indirect effect (indirect path coefficient = 0.35,  $P<0.05$ ). In contrast, mowing reduced soil available nitrogen (path coefficient =  $-0.24$ ,  $P<0.05$ ), which indirectly suppressed plant community diversity and consequently exerted a negative indirect influence on soil seed bank density (indirect path coefficient =  $-0.40$ ,  $P<0.05$ ).

## Discussion

### Effects of Reseeding Duration and Mowing on Plant Community Diversity

The results of this study indicate that reseeding did not significantly alter the Shannon–Wiener diversity index of plant communities within the study period, suggesting that the short-term effects of reseeding on species diversity in alpine meadows are limited. In general, reseeding is expected to increase species numbers and thereby enhance community diversity [25]. However, studies on the Qinghai-Tibet Plateau have shown that reseeding exerts no significant effect on species richness in the early stages, while noticeable increases occur only after approximately ten years [26]. This may be because the introduced species have not yet exerted substantial influence on interspecific interactions during the initial years, whereas their positive effects on community diversity become evident only after they have successfully established and stabilized over time [27].

Many studies have shown that mowing plays an important role in maintaining grassland plant diversity [28]. Mowing can increase light availability, encourage the regeneration of rare species, and promote seedling emergence, thereby enhancing species diversity [29]. However, our results showed that mowing significantly

reduced both species richness and the Shannon–Wiener index, which is inconsistent with findings reported in some previous studies [30, 31]. Several factors may explain this discrepancy. First, mowing intensity, timing, and annual frequency are critical determinants of its ecological outcomes [32]. Low-intensity or intermittent mowing can stimulate tillering, flowering, and seed production, maintaining a dynamic balance between dominant and rare species. In contrast, frequent or high-intensity mowing may disrupt plant growth cycles, suppress regeneration, simplify community structure, and ultimately decrease diversity [33, 34]. Second, the background environmental conditions of different ecosystems can modify the magnitude and direction of mowing effects. For example, in nutrient-enriched grasslands, highly competitive species may recover rapidly after mowing and further homogenize the community. In contrast, in nutrient- and water-limited alpine meadows, mowing may exacerbate physiological stress on plants and reduce the recovery capacity of certain species, leading to decreased diversity [35, 36].

In addition, the interaction between reseeding and mowing significantly influenced the Shannon–Wiener diversity index, with the lowest values observed under mowing in the 2017 reseeded plots. This suggests that combining mowing with reseeding in the early stages may increase the risk of community degradation. Two mechanisms may explain this result: (1) newly introduced species are still in the adaptation phase and have not stabilized within the community, making them vulnerable to disturbance; and (2) mowing directly reduces aboveground biomass and disrupts community structure, and its combined effect with early-stage reseeding weakens community self-regulation, ultimately leading to decreased diversity.

Overall, plant community diversity in alpine meadows appears more sensitive to mowing than to reseeded and reseeded alone has limited short-term effects on diversity improvement. More importantly, improper integration of reseeded and mowing may result in negative ecological consequences. Therefore, in practical grassland management, frequent mowing should be avoided during the early reseeded period to ensure stable restoration and long-term enhancement of community diversity.

#### Effects of Reseeded Duration and Mowing on Soil Physicochemical Properties

The results of this study demonstrate that reseeded significantly affected soil pH and available nutrients (available phosphorus and potassium). Specifically, reseeded significantly increased soil pH. However, other studies have reported that reseeded may reduce the surface soil pH in degraded alpine meadows [37], suggesting that the response of soil pH may vary under different environmental or management conditions. In this study, the 2017 reseeded plots exhibited significantly higher available phosphorus content, which aligns with previous findings that reseeded significantly increases available phosphorus in the 0-30 cm soil layer of degraded alpine meadows [38]. This may be because plants in recently reseeded plots have relatively low phosphorus uptake capacity, coupled with potential phosphorus fertilizer application during reseeded, resulting in higher residual phosphorus in the soil [39]. In contrast, available potassium was significantly lower in the 2017 reseeded plots than in the 2013 plots. This may be related to the vigorous growth and strong potassium demand of newly established grasses, particularly fast-growing Poaceae species [40]. Moreover, soil structure in newly reseeded plots may not yet be fully restored, making potassium more susceptible to leaching losses [41].

Mowing also significantly influenced soil nutrient status, particularly total nitrogen, available nitrogen, available phosphorus, and available potassium, all of which showed increasing trends. Studies in *Stipa grandis* grasslands have shown that appropriate mowing can enhance soil total nitrogen accumulation [42], and research in typical Inner Mongolian grasslands indicates that mowing significantly increases soil dissolved organic carbon and available nitrogen [43]. These effects may be due to mowing-induced stimulation of root turnover and microbial activity, which accelerates the return of plant residues and dead roots to soil and promotes nutrient cycling [44]. However, the effects of mowing on soil pH varied with reseeded duration: mowing increased pH in the 2013 plots but decreased pH in the 2017 plots, likely due to differences in how mowing-induced soil disturbance alters microenvironmental conditions [45].

More importantly, significant interactions were detected between reseeded duration and mowing,

jointly influencing soil pH, total nitrogen, and available phosphorus. This indicates that the impact of mowing on soil nutrients is not fixed but varies across different stages of grassland restoration. In summary, grassland management should consider the combined effects of reseeded duration and mowing to optimize soil nutrient conditions and promote sustainable ecosystem restoration.

#### Mechanisms Regulating Soil Seed Bank Density Under Different Reseeded Durations and Mowing Treatments

The results show that the soil seed bank was predominantly concentrated in the 0-5 cm surface layer, consistent with findings from natural grasslands in Hulunbuir, Inner Mongolia [46]. This vertical distribution pattern aligns with the general ecological understanding that seeds are usually concentrated near the soil surface where germination conditions are optimal. Several mechanisms contribute to this pattern. First, most seeds fall directly to the ground under gravity and are redistributed over short distances by wind, water, or animals before entering shallow soil layers [47]. Second, the surface soil layer offers better aeration, greater temperature fluctuation, and light penetration – conditions favorable for seed germination [46]. Regarding the taxonomic composition of the seed bank, seeds of Poaceae and Cyperaceae dominated, while forbs contributed relatively few seeds. This pattern likely reflects the strong reproductive capacity and rapid establishment of reseeded Poaceae species such as *Poa pratensis* and *Poa crymophila*, which produce abundant seeds that replenish the soil seed bank [48]. In contrast, many forbs have lower seed productivity or rely partly on clonal reproduction, placing them at a disadvantage in seed input and accumulation [49]. Differences among plant groups in seed dispersal traits, maturation timing, shedding height, and survival strategies further shape their representation in the seed bank [50].

Structural equation modeling revealed that reseeded duration had a significant direct positive effect on seed bank density, indicating that long-term reseeded enhances seed production of dominant grasses and promotes seed accumulation in the soil. This direct effect highlights the central role of reseeded in improving community structure and increasing seed input, consistent with previous findings on the strong colonization ability and prolific seed production of dominant Poaceae species [48]. Additionally, reseeded duration indirectly increased seed bank density by enhancing species richness. Reseeded increases the number of species, including well-adapted native plants, which improves vegetation cover and biomass [51]. Tillage before reseeded reshapes niche structure and spatial patterns, allowing new species to establish and increasing community richness [52-54]. These changes not only diversify aboveground communities but also strengthen seed return and seed bank renewal.

In contrast, mowing exerted both direct negative effects on seed bank density and indirect negative effects through reducing soil available nitrogen and subsequently decreasing plant diversity. Mowing often leads to community homogenization, with competitive species dominating and limiting opportunities for coexistence, thereby reducing both species richness and seed sources [55, 56]. Furthermore, mowing forces plants to allocate more energy to physiological compensation, leaving fewer resources for seed production, explaining the observed reduction in seed bank density under annual mowing [57].

Overall, this study demonstrates that reseeded and mowing influence soil seed banks through distinct but interconnected pathways: reseeded promotes seed accumulation by directly increasing seed input and indirectly enhancing species richness, while mowing reduces seed bank density by suppressing seed production and altering soil nutrients and community diversity. These findings highlight the importance of integrating reseeded and mowing strategies with soil nutrient management to maintain seed bank quantity and diversity and ensure long-term stability and ecological functioning of alpine meadow restoration.

### Conclusions

This study demonstrates that reseeded and mowing jointly influence the soil seed bank through both direct and indirect pathways, underscoring the critical role of management practices in the long-term restoration of alpine meadows. Reseeded not only directly increases seed input but also indirectly enhances seed bank accumulation by promoting species richness. Therefore, implementing periodic and phased reseeded is recommended to maintain a stable and continuous seed source. In contrast, mowing exerts potential negative effects on both the seed bank and plant diversity, particularly under nutrient-limited conditions. As such, mowing intensity should be carefully controlled, and mowing should be avoided during key reproductive periods of plants. Simultaneously, restoration management should place equal emphasis on maintaining soil nutrient status. Given the heightened sensitivity of alpine meadows to disturbance and nutrient fluctuations, developing an integrated strategy that combines “reseeded-moderate mowing-nutrient management” can effectively strengthen the long-term recovery capacity and ecological resilience of degraded grasslands.

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### Conflict of Interest

The authors declare no conflict of interest.

### References

- HE J.S., LIU Z.P., YAO T., SUN S.C., LU Z., HU X.W., CAO G.M., WU X.W., LI L., BU H.Y., ZHU J.X. Constraints and Restoration Techniques for Degraded Grassland on the Qinghai-Xizang Plateau. *Science & Technology Review*, **38** (17), 66, **2020**.
- LI Y., LI Y.X., QI W.W., LI S.Y., LI N., XU L., MA H.Y. Research Progress on the Causes, Restoration Techniques and Evaluation of Restoration Effects of Global Grassland Degradation. *Chinese Journal of Grassland*, **46** (11), 110, **2024**.
- AN H., BASKIN C.C., MA M.J. Nonlinear response of the soil seed bank and its role in plant community regeneration with increased grazing disturbance. *Journal of Applied Ecology*, **59** (10), 2593, **2022**.
- MA M.J., WALCK J.L., MA Z., WANG L.P., DU G.Z. Grazing disturbance increases transient but decreases persistent soil seed bank. *Ecological Applications*, **28** (4), 1020, **2018**.
- ESKELINEN A., JESSEN M.T., BAHAMONDE H.A., BAKKER J.D., BORER E.T., CALDEIRA M.C., HARPOLE W.S., JIA M.Y., LANNES L.S., NOGUEIRA C., VENTERINK H.O., PERI P.L., PORATH-KRAUSE A.J., SEABLOOM E.W., SCHROEDER K., TOGNETTI P.M., YASUI S.L.E., VIRTANEN R., SULLIVAN L.L. Herbivory and nutrients shape grassland soil seed banks. *Nature Communications*, **14** (1), **2023**.
- MA M.J., COLLINS S.L., RATAJCZAK Z., DU G.Z. Soil Seed Banks, Alternative Stable State Theory, and Ecosystem Resilience. *Bioscience*, **71** (7), 697, **2021**.
- ZHAO F.B., WU Y.P., YIN X.W., ALEXANDROV G., QIU L.J. Toward Sustainable Revegetation in the Loess Plateau Using Coupled Water and Carbon Management. *Engineering*, **15** 143, **2022**.
- ZHAO Y.H., WANG M.T., YANG Y.Y., SHANG P., ZHANG W.H. Tillage Promotes the Migration and Coexistence of Bacteria Communities from an Agro-Pastoral Ecotone of Tibet. *Microorganisms*, **10** (6), **2022**.
- JIANG H.X., ZHOU Y., LI W., LU Q., XU D.M., MA H.B., MA X.Z., TIAN X.W. Reseeded Native Species Promotes Community Stability by Improving Species Diversity, Niche, and Interspecific Relationships in the Desert Steppe of Northwest China. *Ecology and Evolution*, **15** (2), **2025**.
- WANG B., ZHU Y.H., CHEN X., CHEN D.M., WU Y., WU L.J., LIU S.G., YUE L.Y., WANG Y., BAI Y.F. Even short-term revegetation complicates soil food webs and strengths their links with ecosystem functions. *Journal of Applied Ecology*, **59** (7), 1721, **2022**.
- WANG X.Y., LI F.Y., TANG K.Y., WANG Y.N., SURI G., BAI Z., BAOYIN T. Land use alters relationships of grassland productivity with plant and arthropod diversity in Inner Mongolian grassland. *Ecological Applications*, **30** (3), **2020**.

12. DIAZ S., LAVOREL S., DE BELLO F., QUETIER F., GRIGULIS K., ROBSON M. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America*, **104** (52), 20684, **2007**.
13. YANG H.J., JIANG L., LI L.H., LI A., WU M.Y., WAN S.Q. Diversity-dependent stability under mowing and nutrient addition: evidence from a 7-year grassland experiment. *Ecology Letters*, **15** (6), 619, **2012**.
14. GUO N., SANG C., HUANG M., ZHANG R., DEGEN A.A., MA L.N., BAI Y.F., ZHANG T., WANG W.Y., NIU J.H., LI S.S., LONG R.J., SHANG Z.H. Long-term active restoration of degraded grasslands enhances vegetation resilience by altering the soil seed bank. *Agronomy for Sustainable Development*, **43** (1), **2023**.
15. ZHANG R., HU X.W., BASKIN J.M., BASKIN C.C., WANG Y.R. Effects of Litter on Seedling Emergence and Seed Persistence of Three Common Species on the Loess Plateau in Northwestern China. *Frontiers in Plant Science*, **8**, **2017**.
16. LIU J.S., CHEN Y., DU C., LIU X.X., MA Q.H., ZHANG X., WANG D.L. Interactive effects of nitrogen addition and litter on soil nematodes in grassland. *European Journal of Soil Science*, **70** (3), 697, **2019**.
17. ESKELINEN A., ELWOOD E., HARRISON S., BEYEN E., GREMER J.R. Vulnerability of grassland seed banks to resource-enhancing global changes. *Ecology*, **102** (12), **2021**.
18. OMIDVAR N., XU Z.H., NGUYEN T.T.N., SALEHIN B., OGBOURNE S., FORD R., BAI S.H. A global meta-analysis shows soil nitrogen pool increases after revegetation of riparian zones. *Journal of Soils and Sediments*, **21** (2), 665, **2021**.
19. WANG W., DE K.J. The influence of different replanting years on the diversity and biomass of alpine meadow communities in Henan County. *Qinghai Journal of Animal Husbandry and Veterinary Medicine*, **46** (4), 15, **2016**.
20. SUN L., YU Z.C., TIAN X.F., ZHANG Y., SHI J.Y., FU R., LIANG Y.J., ZHANG W. Leguminosae plants play a key role in affecting soil physical-chemical and biological properties during grassland succession after farmland abandonment in the Loess Plateau, China. *Journal of Arid Land*, **15** (9), 1107, **2023**.
21. MA M.J., COLLINS S.L., DU G.Z. Direct and indirect effects of temperature and precipitation on alpine seed banks in the Tibetan Plateau. *Ecological Applications*, **30** (5), **2020**.
22. ZHANG Z.C., LIU Y.F., CUI Z., HUANG Z., LIU Y., LEITE P.A.M., ZHAO J.X., WU G.L. Shrub encroachment impaired the structure and functioning of alpine meadow communities on the Qinghai-Tibetan Plateau. *Land Degradation & Development*, **33** (14), 2454, **2022**.
23. YANG S.Q., ZHAO W.W., PEREIRA P. Determinations of environmental factors on interactive soil properties across different land-use types on the Loess Plateau, China. *Science of the Total Environment*, **738**, **2020**.
24. ZUO X.A., SUN S.S., WANG S.K., YUE P., HU Y., ZHAO S.N., GUO X.X., LI X.Y., CHEN M., MA X.J., QU H., HU W.G., ZHAO X.Y., ALLINGTON G.R.H. Contrasting relationships between plant-soil microbial diversity are driven by geographic and experimental precipitation changes. *Science of the Total Environment*, **861**, **2023**.
25. WOOSAREE J., OTFINOWSKI R. Importance of species diversity in the revegetation of Alberta's northern fescue prairies. *Biodiversity and Conservation*, **27** (3), 665, **2018**.
26. GAO X.X., DONG S.K., XU Y.D., FRY E.L., LI Y., LI S., SHEN H., XIAO J.N., WU S.N., YANG M.Y., ZHANG J., ZHI Y.L., LIU S.L., SHANG Z.H., YEOMANS J.C. Plant biomass allocation and driving factors of grassland revegetation in a Qinghai-Tibetan Plateau chronosequence. *Land Degradation & Development*, **32** (4), 1732, **2021**.
27. GANJURJAV H., LI M.J., HAN L., SHA Y.B., LI Z., HAN X.Y., JI G.X., WU R.H., MA Y.D., HU G.Z., GORNISH E., GAO Q.Z. Reseeding increased plant biomass production and soil fertility, but not plant species diversity in degraded grasslands in China. *Journal of Environmental Management*, **370**, **2024**.
28. SMITH A.L., BARRETT R.L., MILNER R.N.C. Annual mowing maintains plant diversity in threatened temperate grasslands. *Applied Vegetation Science*, **21** (2), 207, **2018**.
29. WILSEY B.J., MARTIN L.M. Top-down control of rare species abundances by native ungulates in a grassland restoration. *Restoration Ecology*, **23** (4), 465, **2015**.
30. HASSAN N., WANG Z.W. Paralleled grazing and mowing differentially affected plant community diversity and productivity in a semi-arid grassland. *Ecological Processes*, **13** (1), **2024**.
31. HASSAN N., ZHONG Z.W., WANG D.L., ZHU Y., NAEEN I., AHUNGU A.B., WAN H.Y., LI X.F. Effects of long-term mowing on species diversity, biomass and composition of plant community in a semi-arid grassland in northeastern China. *Applied Vegetation Science*, **26** (3), **2023**.
32. ZHANG H.Y., LIU C.X., TAN J.L., BI W.H., CHEN X.F., BAI B., NAMUHAN, WUYUNNA, LI G.D., SONG Y.T. Effect of nutrient addition and mowing on plant diversity and soil carbon content of meadow steppe in Inner Mongolia. *Journal of Environmental Management*, **393**, **2025**.
33. WANG W., XU C.T., ZENG P. The influence of reseeding on the biomass and nutrients of alpine meadows. *Qinghai Journal of Animal Husbandry and Veterinary Medicine*, **47** (6), 9, **2017**.
34. HEJCMAN M., SCHELLBERG J., PAVLU V. Long-term effects of cutting frequency and liming on soil chemical properties, biomass production and plant species composition of *Lolio-Cynosuretum* grassland after the cessation of fertilizer application. *Applied Vegetation Science*, **13** (3), 257, **2010**.
35. PRUCHNIEWICZ D. Abandonment of traditionally managed mesic mountain meadows affects plant species composition and diversity. *Basic and Applied Ecology*, **20**, 10, **2017**.
36. ZHAO T.Q., ZHANG F., SUO R.Z., ZHEN J.H., QIAO J.R., ZHAO M.L., BAI K.Y., ZHANG B. The importance of functional diversity in regulating forage biomass and nutrition: evidence from mowing in semiarid grasslands. *Restoration Ecology*, **31** (2), **2023**.
37. JI W.Z., WANG Q.H. Effects of Reseeding on Vegetation and Physical and Chemical Properties of Soil in High-altitude Degraded Grassland in Tianzhu. *Grassland Science*, **33** (5), 886, **2016**.
38. ZHANG R., YANG W., WANG W., REN J., TIAN J.F., LIU L., MA X.L. The influence of reseeding on the nutrients of forage and the physical and chemical properties of soil in degraded alpine meadows. *Grassland Science*, **39** (6), 1059, **2022**.
39. CHOMEL M., GUITTONNY-LARCHEVÊQUE M., FERNANDEZ C., GALLET C., DESROCHERS A., PARÉ D., JACKSON B.G., BALDY V. Plant secondary

- metabolites: a key driver of litter decomposition and soil nutrient cycling. *Journal of Ecology*, **104** (6), 1527, **2016**.
40. MI W.T., ZHENG H., CHI Y., REN W.B., ZHANG H.X., ZHANG W.Y., YUAN F., LIU Y.L. Reseeding restoration significantly improves the physical and chemical properties of degraded grassland soil in China—a meta-analysis. *CATENA*. **252**, **2025**.
  41. QU Q., DENG L., SHANGGUAN Z.P., SUN J., HE J.S., WANG K.B., ZHOU Z.C., LI J.W., PEÑUELAS J. Belowground C sequestrations response to grazing exclusion in global grasslands: Dynamics and mechanisms. *Agriculture Ecosystems & Environment*. **360**, **2024**.
  42. WANG Q., ZHENG J.H., ZHAO M.L., ZHANG J. The influence of mowing intensity on the original plant community characteristics and soil physicochemical properties of *Sedum lineare*. *Journal of Grassland Science*, **32** (2), 26, **2023**.
  43. CUI Q., YANG H.J., WANG G.M., MA J.Z., FENG L., LIU J.T. Response of soil carbon fractions and enzyme activities to mowing management on in a coastal wetland of the yellow river delta. *Frontiers in Marine Science*, **9**, **2022**.
  44. LIU J.Y., LI L., JI L., LI Y.L., LIU J.J., LI F.Y. Divergent effects of grazing versus mowing on plant nutrients in typical steppe grasslands of Inner Mongolia. *Journal of Plant Ecology*, **16** (1), **2023**.
  45. LUO W.J., PETTICORD D.F., ZHU S.W., ZHU S.W., WU Y.L., YI X., WANG X.Y., GUO Y.L., SONG X.X. Biochar Application and Mowing Independently and Interactively Influence Soil Enzyme Activity and Carbon Sequestration in Karst and Red Soils in Southern China. *Agronomy-Basel*, **15** (1), **2025**.
  46. ZHANG Z.T., YU T.Q., XIN X.P., LIU H.M., LV S.J., WEI Z.J., HAN G.D., YAN R.R. Response of the germinable soil seed bank of temperate *Leymus chinensis* meadows to mowing regimes. *Frontiers in Plant Science*, **15**, **2025**.
  47. TÓTH A., DEÁK B., TÓTH K., KISS R., LUKÁCS K., RÁDAI Z., GODÓ L., BORZA S., KELEMEN A., MIGLÉCZ T., BÁTORI Z., NOVÁK T.J., VALKÓ O. Vertical distribution of soil seed bank and the ecological importance of deeply buried seeds in alkaline grasslands. *PEERJ*. **10**, **2022**.
  48. YAN R.R., YU T.Q., LIU H.M., LV S.J., CHEN B.R., WU Y.L., QUE G.P., WEI Z.J., XU L.J., ZHU X.Y., YANG G.X., XIN X.P. Effects of different grassland utilization methods on the germinable soil seed bank of the Hulunbuir meadow steppe. *Frontiers in Plant Science*, **14**, **2023**.
  49. LI Y.Y., DONG S.K., WEN L., WANG X.X., WU Y. Soil seed banks in degraded and revegetated grasslands in the alpine region of the Qinghai-Tibetan Plateau. *Ecological Engineering*, **49**, 77, **2012**.
  50. SHI Y.F., SHI S.H., JIANG Y.S., LIU J. A global synthesis of fire effects on soil seed banks. *Global Ecology and Conservation*, **36**, **2022**.
  51. YANG Z.Z., ZHANG C.P., DONG Q.M., YANG X.X., CHU H., LI X.A., WEI L.N., ZHANG Y.F. The Impact of Reseeding on the Community Characteristics and Diversity of Moderately Degraded Alpine Grassland. *Journal of Grassland Science*, **26** (5), 1071, **2018**.
  52. TILMAN D. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, **101** (30), 10854, **2004**.
  53. ROHDE K. Vacant niches and the possible operation of natural laws in ecosystems. *Rivista di Biologia-Biology Forum*, **101** (1), 13, **2008**.
  54. WU W.P., MA H.B., LU Q., ZHOU Y., SU T.T., ZHU L. The influence of reseeded on plant communities and physical and chemical properties of Soil in Ningxia Desert Steppe. *Grassland Science*, **37** (10), 1959, **2020**.
  55. MIAO R.H., GUO M.X., MA J., GAO B.W., ALAMUSA, MIAO Y., YANG Z.L., LIU Y.Z. Shifts in soil seed bank and plant community under nitrogen addition and mowing in an Inner Mongolian steppe. *Ecological Engineering*, **153**, **2020**.
  56. MIAO R.H., MA J., LIU Y.Z., LIU Y.C., YANG Z.L., GUO M.X. Variability of Aboveground Litter Inputs Alters Soil Carbon and Nitrogen in a Coniferous-Broadleaf Mixed Forest of Central China. *Forests*. **10** (2), **2019**.
  57. PISEDDE F., BELLOCCHI G., PICON-COCHARD C. Mowing and warming effects on grassland species richness and harvested biomass: meta-analyses. *Agronomy for Sustainable Development*, **41** (6), **2021**.