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Suitable duration of grazing exclusion for restoration of a degraded alpine meadow on the eastern Qinghai-Tibetan Plateau

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ABSTRACT

Grazing exclusion (GE) is a key national ecological restoration project widely applied to rehabilitate degraded grasslands. To date, there have been many debates on the effectiveness of GE for grassland recovery, and it is still poorly understood how degraded alpine meadows in the semi-humid area with relative rich rainfall in the Qinghai-Tibetan Plateau respond to GE with different durations. We selected a chronosequence of grazing-excluded alpine meadows to examine the dynamics of grassland functions. The results showed that the dominant functional group shifted from forbs to graminoids after 8 to 10 years GE and then returned to forbs. The plant population density increased significantly with GE time ($P < 0.01$). The total biomass, species richness, Shannon diversity index, and relative importance value of graminoids first increased and then decreased with increasing plant population density, whereas the relative importance value of forbs presented the opposite trend. All turning points were between 1350 and 1650 plants per m^2 which occurred from 8 to 10 years of GE. As the duration of GE increased, the ecosystem multifunctionality first dramatically increased and then became steady after 8 to 10 years of GE. These findings imply that GE is of great practical significance to prevent degradation in semi-humid regions of the Qinghai-Tibetan Plateau, where we recommend that GE should cease after approximately 8 to 10 years to restore degraded alpine meadows from the perspective of plant productivity, diversity, community structure, and ecosystem multifunctionality.

1. Introduction

Approximately 25% of the global terrestrial surface is covered by grasslands, including 42% of China's total land area (Lu et al., 2012; Wang and Wesche, 2016); these grasslands play important roles in multiple ecological functions, economic development, and livestock husbandry (Harris, 2010). However, a considerable percentage of natural grasslands have been degraded to varying degrees due to climate change and overgrazing (Han et al., 2008; Sun et al., 2019); these threats to grasslands have recently become a global concern given that they not only jeopardise ecological security (Gao et al., 2009; Harris, 2010) but also constrain local economic development and the standard of living of herdsmen (Ravi et al., 2010). For this reason, the United Nations Convention to Combat Desertification (UNCCD) has proposed that humans should strive to halt and reverse land degradation, combat desertification, and enforce land degradation neutrality worldwide by 2030 (Toth et al., 2018). Grazing exclusion (GE) has become a primary management practice widely adopted by local and central governments to restore the degraded grasslands, such as with the programme 'Returning Grazing Land to Grassland' (RGLG) implemented since 2003 (Lu et al., 2015b; Zhao et al., 2019a).

The impacts of GE on grass community characteristics and soil properties have been extensively studied in recent years (Wu et al., 2010; Xiong et al., 2016; Zhao et al., 2019a), whereas there is continuing controversy about the effects of GE. Numerous studies have shown that GE has been an effective approach for accelerating plant growth and for improving species diversity (Bakker et al., 2006; Xiong et al., 2016), while others found that GE had no effect on species richness and

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Shannon diversity index (Guo et al., 2019; Lunt et al., 2010), or even negatively affected grassland primary productivity (Cheng et al., 2011) and biodiversity conservation (Zhao et al., 2019b). Previous studies observed that GE benefits the improvements of soil physical properties and fertility of degraded grasslands (Li et al., 2020; Niu et al., 2011; Wu et al., 2014; Zhang and Zhao, 2015). However, other studies emphasized that GE could have negligible (Lu et al., 2015a) or negative effects on soil properties (Reeder et al., 2004; Shi et al., 2013). Additionally, some scholars found that GE played a positive role in carbon sequestration (Deng et al., 2017; Xiong et al., 2016), while others reported GE decreased soil organic carbon storage (Shi et al., 2013). All these inconsistent effects of GE on grasslands are largely attributed to different land-use histories, grassland types, and climates, etc. (Cao et al., 2019; Wu et al., 2009).

Nevertheless, even under certain conditions, GE could show divergent impacts on grasslands depending on duration of enclosure. GE usually presents immediate effects on grassland restoration in the first few years after it is carried out, as shown by dramatic increases in plant coverage, density, biomass, plant structure and soil quality (Li et al., 2017; Xiong et al., 2014; Yan and Lu, 2015). However, previous studies showed that long-term (>8 years) GE would inhibit grassland renewal and had little sustainable benefit (Sun et al., 2020), may not increase the amount of desirable plant species (Firincioglu et al., 2007), or may even induce declines of above- and below-ground biomass (Jing et al., 2013), species richness and diversity (Nishizawa et al., 2016; Xiong et al., 2014), density of edible plants (Yao et al., 2019), soil water content (Cao et al., 2019), and soil enzyme activity (Du et al., 2020), and thereby causing grassland degradation again (Shang et al., 2008; Su et al., 2015). In summary, it is not necessarily a good thing to completely protect grasslands from grazing for a prolonged period of time; therefore caution should be exercise with long-term GE (Sacha, 2020; Sun et al., 2020).

It is apparent that determining the optimal length of GE is essential and has recently drawn extensive attention and heated debates. For example, previous studies documented that the suitable length of time for GE for grassland recovery is 6 years in semi-arid grasslands of Inner Mongolia (Wu et al., 2014), 20 years in the Loess Plateau region (Jing et al., 2013), 6 years on the north-eastern Qinghai-Tibetan Plateau (Li et al., 2018), 13 years in the eastern portion of the Qinghai-Tibetan Plateau (Cao et al., 2019), 4 years for degraded alpine meadows and 8 years for alpine steppe on the Qinghai-Tibetan Plateau (Sun et al., 2020), and 6–10 years in grasslands of China based on a meta analysis (Xiong et al., 2016). Obviously, how long GE should be applied to ensure optimal restoration effectiveness can vary considerably among study areas. An optimal GE time should consider the local habitat conditions including soil nutrients and hydrological status, etc. (Hu et al., 2016; Medinaroldan et al., 2012; Xiong et al., 2016). In particular, recent studies demonstrated that precipitation played an important role in the benefits of GE which were more effective in semi-humid regions than arid and semi-arid areas (Hu et al., 2016; Xiong et al., 2016).

However, knowledge about the effectiveness of GE for the widespread degraded alpine meadow restoration in the semi-humid area regions of the Qinghai-Tibetan Plateau is still rudimentary. To fill this existing gap, the purpose of this study was to explore (i) how the key plant and soil characteristics of degraded alpine meadows respond to the duration of GE; and (ii) the optimal duration of GE to restore the degraded alpine meadows to a relatively high quality in terms of plant productivity, diversity, community structure, and ecosystem multifunctionality. Specifically, optimally restored alpine meadow in this study is defined as alpine meadow with higher plant productivity, diversity, relative importance value (IV) of graminoids, and ecosystem multifunctional index (EMF) and lower IV of forbs than in other restored alpine meadows. By addressing these issues, we aimed to investigate the success rate of GE time for the restoration of degraded alpine meadows and further properly inform policy makers on how to develop useful management practices in the future to mitigate grassland deterioration.

2. Materials and methods

2.1. Study area

The Zoige region (32°20'-34°00'N, 101°30'-103°30'E) covering 6180 km^2 is located on the eastern edge of the Qinghai-Tibetan Plateau, and has a mean altitude of 3500 m (Liu et al., 2020c). The climate is characterized as cold and humid with an average annual temperature of approximately 1 °C, and a mean annual precipitation of approximately 700 mm which is concentrated mainly from May to August (Liu et al., 2020b). The common vegetation types consist of *Kobresia tibetica*, *Stipa capillata*, and *Carex lasiocarpa* (Liu et al., 2020a). Based on the WRB and USDA soil classification systems, the corresponding main soil types are Cambisols and Inceptisols, respectively (Liu et al., 2020a).

2.2. Data collection

Six adjacent restored alpine meadows with similar climatic and topographic conditions were selected in the Zoige region, according to the chronosequence of the plant succession process. They were all originally degraded alpine meadows resulting from a long history of over grazing with the main livestock of yaks and horses. The vegetation and soil baseline could refer to those of the most severely degraded alpine meadow in our previous paper (Liu et al., 2020c). All degraded alpine meadows were excluded from grazing for 2, 4, 6, 8, 10, and 12 years to prevent grazing and were denoted as GE_2, GE_4, GE_6, GE_8, GE_{10}, and GE_{12}, respectively. There were no treatment applied to the GE plots. Detailed information on these 6 restored alpine meadows is shown in Table 1. We arranged 3 representative sample plots (10 m × 10 m) as replicates in each alpine meadow. Three quadrats (1 m × 1 m) were randomly set within each plot for plant and soil sampling which was conducted after 5 no-rain days in August 2017. The degree of freedom and the number of statistical units in this study were 17 and 162, respectively.

Plant information including species, coverage, number, and height within each quadrat were recorded during the field survey. The aboveground parts of plants were clipped via scissors and oven dried at 65 °C to a constant weight for determining aboveground biomass (AGB). Within each quadrat, 6 soil cores with a 5 cm diameter were obtained at a 0–30 cm soil depth. Three core samples were washed via a 0.5 mm sieve to remove residual soil and to collect roots, which were oven-dried at 65 °C to a constant weight for belowground biomass (BGB) measurement. The other three soil cores were thoroughly mixed, air-dried, and sieved through a 2 mm mesh after removing visible plant residues. Then, the pre-treated soil samples were divided into three replicates to measure soil properties. In addition, at the same time (noon) of day, three replicate soil samples were obtained using cutting rings within each quadrat to determine the soil water content (SWC).

Soil compactness (SCOM) and pH were measured by a portable time domain reflectometer (TDR 100, Spectrum Technologies Inc., Chicago, IL, USA). According to the methods from Bao (2000), SWC was determined by ordinary gravimetric measurement; soil organic carbon (SOC) was measured via the $K_2Cr_2O_7$ volumetric method; a vario MACRO cube elemental analyser (Elementar Analysensysteme GmbH, Germany) was used to determine soil total nitrogen (STN); and soil total phosphorus (STP) was determined by using the $NaHCO_3$ alkali digestion method combined with molybdenum antimony colorimetry. Soil available nitrogen (SAN) and available phosphorus (SAP) were measured by using the continuous alkali-hydrolysed reduction-diffusion method and the Olsen method, respectively (Bao, 2000; Olsen et al., 1954).

2.3. Statistical analyses

The indices used to illustrate plant biodiversity information in the present study were calculated as follows:

Species richness index (R) (Margalef, 1951):

Table 1
General information of the sampling sites of natural restoration.

Restoration time (yr)	Location	Altitude (m)	Main species	Height (cm)	Coverage (%)
2	33°13′36.12″N 102°36′49.11″E	3705	*Herba Artimisiae, Deschampsia cespitosa, Pedicularis resupinata*, et al.	19.53 ± 1.34^a	34.27 ± 3.00^a
4	33°13′36.21″N 102°36′49.58″E	3715	*Koeleria cristata, Carex moorcroftii, Pedicularis resupinata*, et al.	16.89 ± 0.38^b	61.20 ± 3.78^b
6	33°13′36.47″N 102°36′49.77″E	3732	*Stipa capillata, Carex moorcroftii, Pedicularis resupinata*, et al.	15.91 ± 0.85^b	79.87 ± 2.21^c
8	33°13′36.85″N 102°36′49.96″E	3721	*Stipa capillata, Carex moorcroftii*, et al.	15.74 ± 0.50^b	85.67 ± 1.63^d
10	33°13′37.12″N 102°36′50.21″E	3745	*Stipa capillata, Carex moorcroftii, Pedicularis resupinata*, et al.	26.61 ± 0.75^c	92.67 ± 2.77^e
12	33°13′37.51″N 102°36′50.66″E	3726	*Stipa capillata, Carex moorcroftii, Anaphalis sinica*, et al.	27.03 ± 0.20^c	94.43 ± 3.21^e

Note: Different letters represent significant difference at the 0.05 confidence level.

$$R = (S-1)/lnN$$

Shannon diversity index (H) (Ma et al., 1995):

$$H = -\sum_{i=1}^{S}(PilnPi)$$

Pielou evenness index (E) (Ma et al., 1995):

$$E = H/lnS$$

where S and N represent the total number of plant species and individuals in the plot, respectively, P_i is the relative importance value of objective species i, which was calculated as follows (Wang et al., 2014):

$$P_i = (RH + RC + RB)/3$$

where RH, RC, and RB represent the relative height, relative cover, and relative biomass of species i, respectively.

We chose eighteen soil and plant variables to assess ecosystem functions: SWC, SCOM, pH, SOC, STN, STP, SAN, SAP, plant coverage, AGB, BGB, litter biomass (LB), total biomass (TB), species richness (SR), Shannon diversity index, Pielou evenness index, and IV of graminoids and sedges. An average method was used to calculate the EMF via the following formula (Maestre et al., 2012):

$$EMF = \frac{1}{N}\sum_{i=1}^{N}f(xi)$$

where N is the number of measured functions, x_i is the observation value of function i, and $f(x_i)$ represents the standardization of x_i as follows (Bradford et al., 2014):

$$f(x_i) = (x_i - x_{mean})/std$$

where x_i, x_{mean}, and std represent the measured value, mean value, and standard deviation of function i, respectively.

Principal component analysis (PCA) was performed by *FactoMineR*, and *factoextra* packages in R software (R Core Team, 2016), based on data of soil properties and plant characteristics to explore their explanatory powers of variance among alpine meadows with different spontaneous recovery times. One-way analysis of variance was performed using SPSS 19.0 software (SPSS Inc., Chicago, IL, USA) to determine the significance level of the difference between soil and plant variables. A linear piece-wise quantile regression allows for the flexible and robust analysis of a database and analysis of the upper boundary of the distribution (95th and higher), which gives a better and ecologically more plausible estimation of responses to a given variable (Sun and Wang, 2016). Therefore, the 99th percentile was used to evaluate the response of TB, SR, Shannon diversity index, and IV of graminoids and forbs to plant population density as the potential constraint. Linear piece-wise quantile regression analysis was conducted via SigmaPlot for Windows version 10.0 (Systat Software, Inc., Chicago, IL, USA), to reveal the relationships between population density and other plant factors.

3. Results

3.1. Changes in plant and soil properties over the duration of grazing exclusion

The PCA results showed that the first two axes explained 65.6% of the total variance among the restoration grasslands (Fig. 1). Grasslands with different restoration times exhibited large differences, as indicated by the distribution patterns (Fig. 1). There was an increasing trend in AGB along the restoration chronosequence, with mean values of 186.46, 270.64, 339.87, 426.04, 450.15, and 535.68 g/m^2 for GE_2, GE_4, GE_6, GE_8, GE_{10}, and GE_{12}, respectively (Fig. 2A). The BGB in GE_{10} with a mean value of 2353.49 g/m^2, was noticeably higher than the BGB value of 755.03 g/m^2 in GE_2 ($P < 0.05$), while BGB presented no significant difference among the other grasslands ($P > 0.05$) (Fig. 2B). The mean TB (2803.64 g/m^2) in GE_{10} was distinctly larger than that in GE_2 (941.76 g/m^2), GE_4 (1493.80 g/m^2), and GE_8 (1576.42 g/m^2) ($P < 0.05$) (Fig. 2C). Additionally, LB tended to initially increase and then decrease with increasing restoration time (Fig. 2D); therefore, the LB in GE_{10} was significantly higher than those in GE_2, GE_4, GE_6, and GE_{12} ($P < 0.05$).

The SR in GE_2, with a mean value of 0.85, was significantly lower than the mean values of 1.92, 2.02, 2.22, 2.23, and 1.80 in GE_4, GE_6, GE_8, GE_{10}, and GE_{12}, respectively ($P < 0.05$) (Fig. 3A). The Shannon diversity index in GE_8 (2.02) was apparently higher than that (1.29) in GE_2 ($P < 0.05$) (Fig. 3B). The average value of the Pielou evenness index in GE_2 was 0.87, which was significantly higher than that in GE_4 (0.69), GE_6 (0.69), GE_{10} (0.68), and GE_{12} (0.67) ($P < 0.05$) (Fig. 3C). As shown in Fig. 4, SOC ($R^2 = 0.90$, $P < 0.01$), STN ($R^2 = 0.88$, $P < 0.01$), STP ($R^2 = 0.85$, $P < 0.01$), SAN ($R^2 = 0.87$, $P < 0.01$), and SWC ($R^2 = 0.71$, $P < 0.05$) in the 0–30 cm soil layer all apparently increased with increasing restoration time.

3.2. Changes in plant community structure over the duration of grazing exclusion

The mean IV of graminoids in GE_8 (0.41) and GE_{10} (0.38) was distinctly larger than that in GE_2 (0.29), GE_4 (0.26), GE_6 (0.26), and GE_{12} (0.27) ($P < 0.05$) (Fig. 3D). However, the IV of forbs was 0.48 in GE_{12}, which was significantly higher than the IV of 0.32 in GE_8 ($P < 0.05$) (Fig. 3E). The linear regression revealed significantly positive relationships between the population densities of the total plant community, graminoids, and forbs and the natural restoration time, with R^2 of 0.94, 0.88, and 0.93, respectively ($P < 0.01$) (Fig. 5A and B). Notably, the slope of the forbs had a larger value (83.43) than that of the graminoids (48.66).

The AGB of graminoids presented a unimodal pattern responding to the length of natural restoration time, with a peak value between 8- and 10-year restoration time ($R^2 = 0.72$, $P < 0.05$) (Fig. 5C). In contrast, the

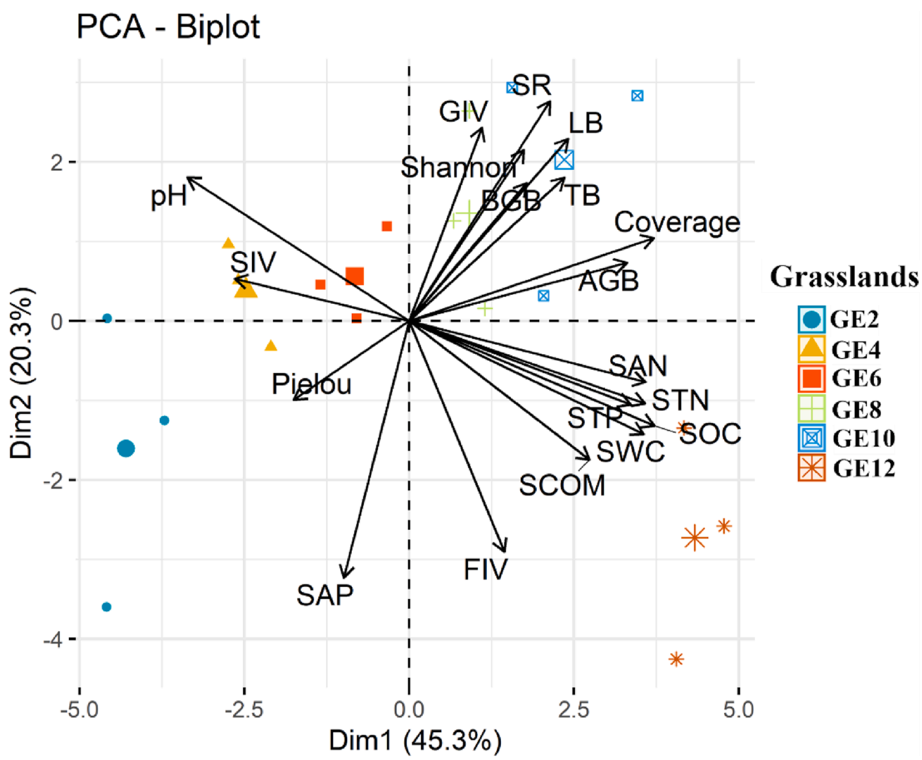

Fig. 1. Principal component analyses (PCA) based on the data of soil physicochemical properties and plant characteristics with different restoration times. SOC, STN, STP, SAN, SAP, SWC, SCOM, coverage, AGB, BGB, TB, LB, Shannon, Pielou, GIV, FIV, and SIV represent soil organic carbon, soil total nitrogen, soil total phosphorus, soil available nitrogen, soil available phosphorus, soil water content, soil compaction, soil temperature, plant coverage, aboveground biomass, belowground biomass, total biomass, litter biomass, Shannon diversity index, Pielou evenness index, importance value of graminoids, importance value of forbs, and importance value of sedges, respectively. GE2, GE4, GE6, GE8, GE10, and GE12 represent grasslands restored by grazing exclusion for 2, 4, 6, 8, 10, and 12 years, respectively.

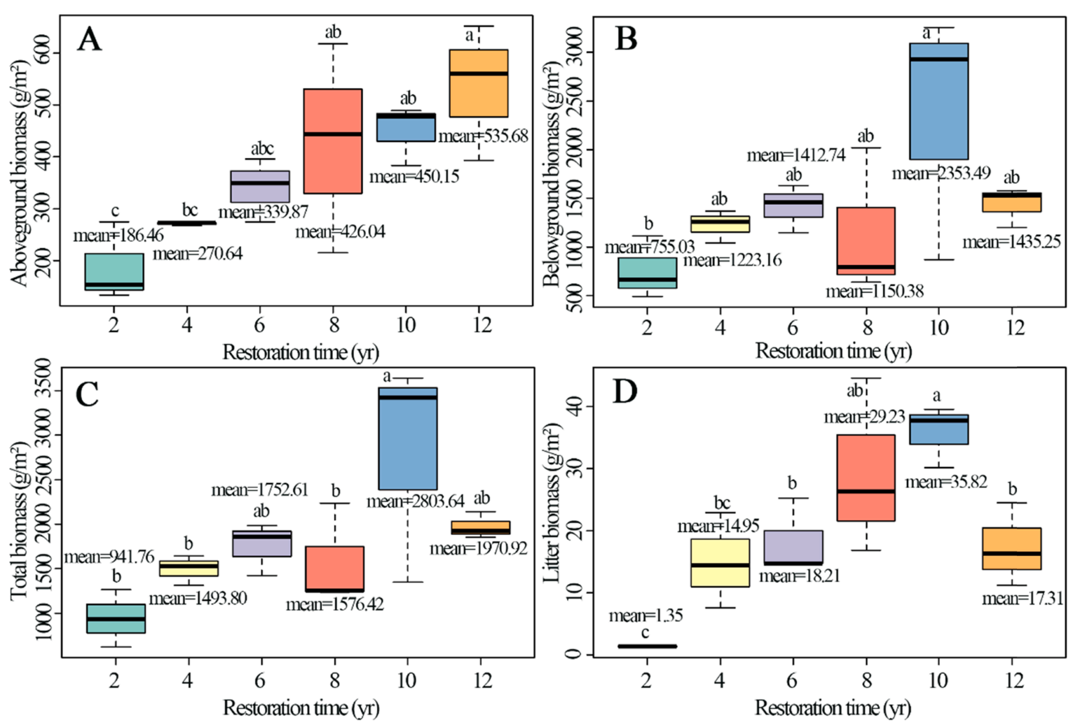

Fig. 2. Boxplot of plant biomass of alpine meadows with different restoration times. Different letters represent significant differences at the 0.05 confidence level.

AGB of forbs tended to slowly decrease first and then dramatically increase with increasing restoration time, and the turning point also appeared from 8 to 10 years of restoration time ($R^2 = 0.90$, $P < 0.05$) (Fig. 5). The mean AGB values of forbs (34.22, 25.18, 34.46, and 56.53 g/m^2, respectively) in GE_2, GE_4, GE_6, and GE_{12}, respectively, were higher than those of graminoids (19.33, 12.67, 20.14, and 42.95 g/m^2, respectively), while the former was lower than the latter in GE_8 and GE_{10} (Fig. 5C).

3.3. Changes in ecosystem multifunctionality over the duration of grazing exclusion

The variations in plant functions with total population density changes are shown in Fig. 6. The results of linear piece-wise quantile

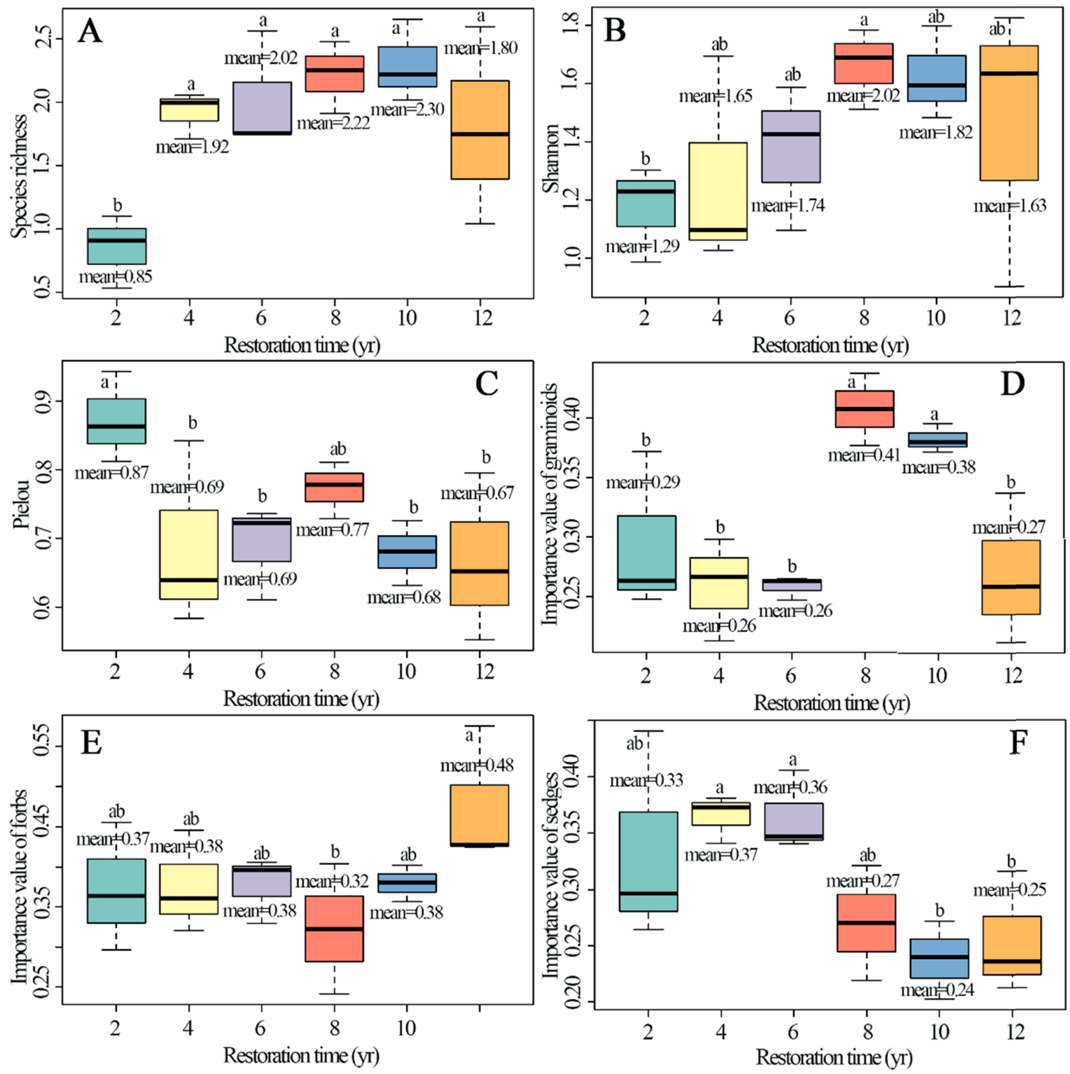

Fig. 3. Boxplot of plant species richness (A), Shannon diversity index (B), Pielou evenness (C), and importance values of graminoids, forbs, and sedges (D-F) in alpine meadows with different restoration times. Different letters represent significant differences at the 0.05 confidence level.

regression analysis revealed that the TB, SR, Shannon diversity index, and IV of graminoids initially increased and then decreased with increasing population density, while the IV of forbs exhibited the opposite trend ($P < 0.01$). Interestingly, almost all change points were observed between a total plant population density of 1350 and 1650 plants per m^2 which was reached after 8 and 10 years of GE, respectively (Fig. 6). The best-fit model based on adjusted R^2 values showed that the EMF dramatically increased along the restoration chronosequence and became be stable after 8 to 10 years of restoration (Fig. 7).

4. Discussion

4.1. Changes in plant and soil characteristics over the duration of grazing exclusion

Plant species richness, diversity, and community structure serve as important metrics of ecosystem functioning for restoring grasslands (Jing et al., 2013; Sarmiento et al., 2003; Wang et al., 2012), and are key attributes of the success of ecological restoration (Ruizjaen and Aide, 2005; Wortley et al., 2013). Plant diversity and richness can reflect the suitability of the land as a habitat, and are commonly considered primary goals for grassland restoration (Wortley et al., 2013). In the present study, we found increases in SR and diversity during the early stages of GE (Fig. 3 A and B), in line with previous studies (Guo et al., 2019; Tang et al., 2016). This is because GE facilitates the appearance of suppressed species that, because of poor adaptability, are lost in the original degraded grassland after suffering from excessive grazing disturbance that disadvantages plant growth and reproduction (Zhao et al., 2019a). However, long-term GE had a negative impact on SR and diversity in the current study (Fig. 3 A and B), which is consistent with other studies (Oba et al., 2001; Wu et al., 2009). Explanations for these results are as follows: long-term GE promotes litter accumulation (Fig. 2 D), which induces a lower temperature, thereby restraining the decomposition of soil organic matter and thus nutrient cycling (He et al., 2011). The thicker litter layer suppresses the photoperiod and reproductive success of low-growing species which are more sensitive to light resources (Zhu et al., 2016; Zou et al., 2016). Moreover, interspecific competition intensifies in high-productivity grasslands with a longer period of recovery, which is not conducive for less competitive species and leads to their decrease or even disappearance (Kelemen et al., 2013; Wu et al., 2009).

Plant community composition largely affects nutrient cycling at the ecosystem level (Olofsson et al., 2001), and is described as the most rapid and efficient method for site-condition assessment (Gibbons and Freudenberger, 2006). Previous studies observed that the process of grassland restoration was always accompanied by plant community

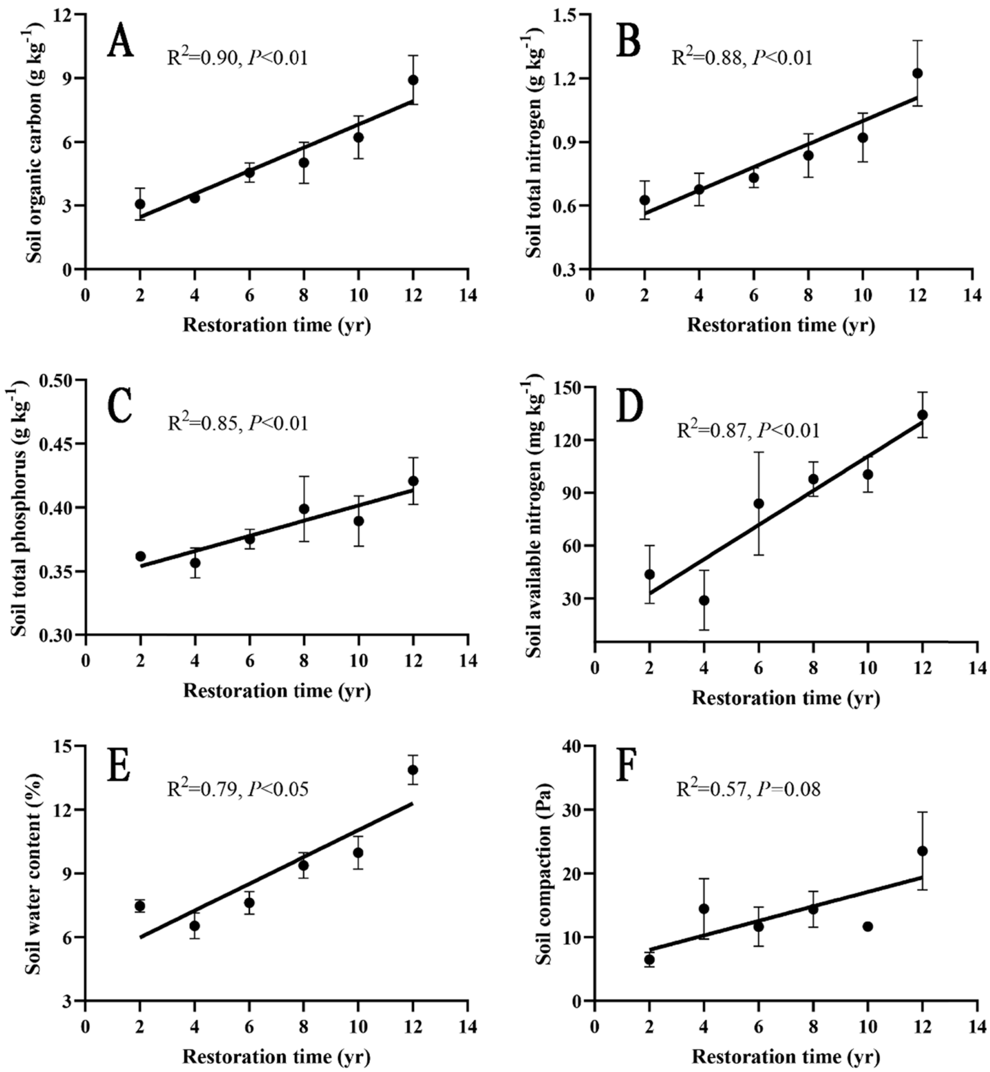

Fig. 4. The changes in soil properties at 0–30 cm soil depth over the duration of grazing exclusion.

succession (Deng et al., 2014; Shang et al., 2008; Wu et al., 2009). In our study, alpine meadows with different GE times presented noticeable environmental heterogeneity (Fig. 1), providing corresponding favourable conditions for divergent grass community structures (He et al., 2011; Zuo et al., 2008). The dominant plant functional group was forbs, which exhibited stronger suitability to drought and infertile abiotic conditions (Fig. 4), and thereby higher colonization capacity (Kelemen et al., 2013; Klein et al., 2008) during the first 6 years of GE (Fig. 5C). By this time facilitation and other plant interspecific interactions may play an important role in species colonization (Bonet, 2004). With increasing grazing exclusion time, there was a shift in plant community composition due to the changes in dominant functional groups (He et al., 2011). Specifically, graminoids apparently increased while forbs gradually decreased before 8 to 10 years of GE (Fig. 5C), in accordance that reported that GE stimulated the growth and development of graminoids (Gao et al., 2007). This is largely attributed to the removal of selective plant intake by livestock after GE (Guo et al., 2019). Graminoids with higher availability of microsites for establishment quickly respond to GE-induced soil nutrient and water increases (Fig. 4) (Wang et al., 2010), and consequently dominated the plant community via excluding other species after 8 to 10 years of grazing exclusion (Fig. 5C).

Nevertheless, interspecific competition intensifies due to relatively limited resource availability as GE time increases (Der Wal et al., 2004; Liu et al., 2019). Many annual plants and short-lived perennials are generally displaced over time by slow-growing, long-lived, and highly resilient clonal perennial forbs, which are superior competitors for limited resources compared with graminoids and sedges, and gradually exhibit competitive advantages, for example, increasing light limitation to shorter species via relatively higher height (Borer et al., 2014). With the sharp increases in plant density and biomass along the restoration chronosequence (Fig. 5), the relative availabilities of soil water and nutrients such as carbon and nitrogen decrease (Bonet, 2004). Forbs can capture water and nutrients from deeper soil layers via their long and deeply distributed roots (Zhang et al., 2020). Moreover, nitrogen and light deficiencies limit the success of seedling establishment after a longer period of recovery (Zhu et al., 2016; Zou et al., 2016). The high susceptibility of newly emerged seedlings of annual graminoids and sedges to environmental stresses is a serious bottleneck that prevents them from establishing; in contrast, the relatively higher survival rates of older seedlings of perennial forbs help their encroachment (Su et al., 2015). As a result, the forbs become the dominant functional group again creating high cover and low richness values after 12 years of GE (Fig. 3A and Fig. 5C). This finding is consistent with similar studies in other areas in which the graminoid-dominated community was altered to a forb-dominated community during long-term grassland succession (Angassa and Oba, 2010; Deng et al., 2014; Su et al., 2015), indicating that long-term GE may lead to a degradation in plant community structure. The grass community structure dynamics in this study support

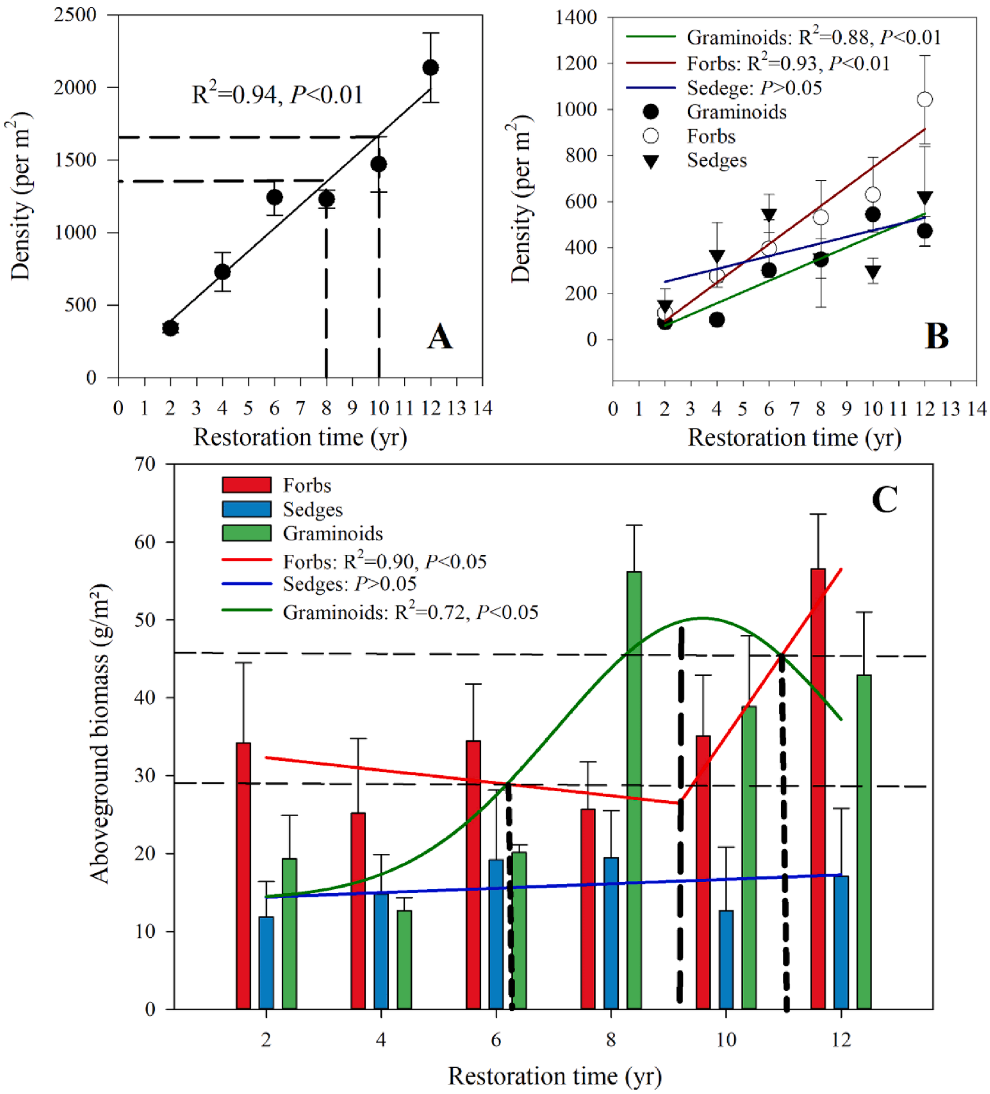

Fig. 5. Changes in density and aboveground biomass of 3 plant functional groups along the restoration chronosequence.

the resource ratio hypothesis that the resource-supply trajectory controls interspecific competition and thus species replacement during grassland recovery succession (Thompson, 1987). The resource ratio gradient undergoes a change from resource-poor soil but high light availability to resource-rich soil but low light availability through the length of time without grazing. The shift in the composition of grass community results from this gradient and the evolution of plant life histories responding to it (Tilman, 1985).

4.2. Suitable enclosure duration for restoring degraded alpine meadows

GE is well proven to successfully restore degraded alpine grasslands by removing disturbances due to livestock, as indicated by the noticeable improvement in the status of soil and grass community (Sun et al., 2018; Xiong et al., 2016; Zhao et al., 2019a). Specifically, recent studies have demonstrated that the high rainfall at Zoige greatly improved the efficiency of GE in grassland restoration (Liu et al., 2020a; Liu et al., 2020b). We thus hypothesized that GE may be an effective way to halt and reverse widespread land degradation in this region. Although degradation occurred due to overgrazing in the original grassland, there was a high density of buried seeds that played an important role in plant regeneration once GE occurred (Ma et al., 2013). The absence of livestock trampling not only benefits soil aggregate structure and thereby modifies microclimates (Wiesmeier et al., 2012), but also enhances plant root growth (Fig. 2B) facilitating nutrient uptake (Sun and Wang, 2016), which encourages plant growth. GE directly excludes grazer from consuming AGB, and thereby contributes to the increases in AGB and LB, which are deposited from AGB (Du et al., 2020) (Fig. 2A and D). In turn, the increased plant biomass and litter materials can improve organic matter input into the soil (Zeng et al., 2017), reduce water loss by soil evaporation (Miao et al., 2009), and can decrease soil erosion from water and wind by improving soil surface roughness (Hoffmann et al., 2008), which led to increases in soil water and fertility in our study (Fig. 4), consistent with previous studies (Gao et al., 2011; Liu et al., 2020a; Liu et al., 2020b).

Our results showed that the plant population density increased linearly along the GE chronosequence (Fig. 5A and B). However, population density is known to reach equilibrium regulated by density-dependent competition in crowded stands under a specific environmental carrying capacity (Chesson, 2018; Kenkel, 1988). The fact that the period of GE time was not long enough may account for the linear increase in population density during grassland recovery succession. Notably, long-term GE led to significant increases in the population densities of both forbs and graminoids, and the former slope was steeper than the latter (Fig. 5B). Density-dependent interspecific competition occurs when the community densities of the two functional groups reach a critical level. As a result, the IV of graminoids first increased and then showed a downward trend as the total plant population density

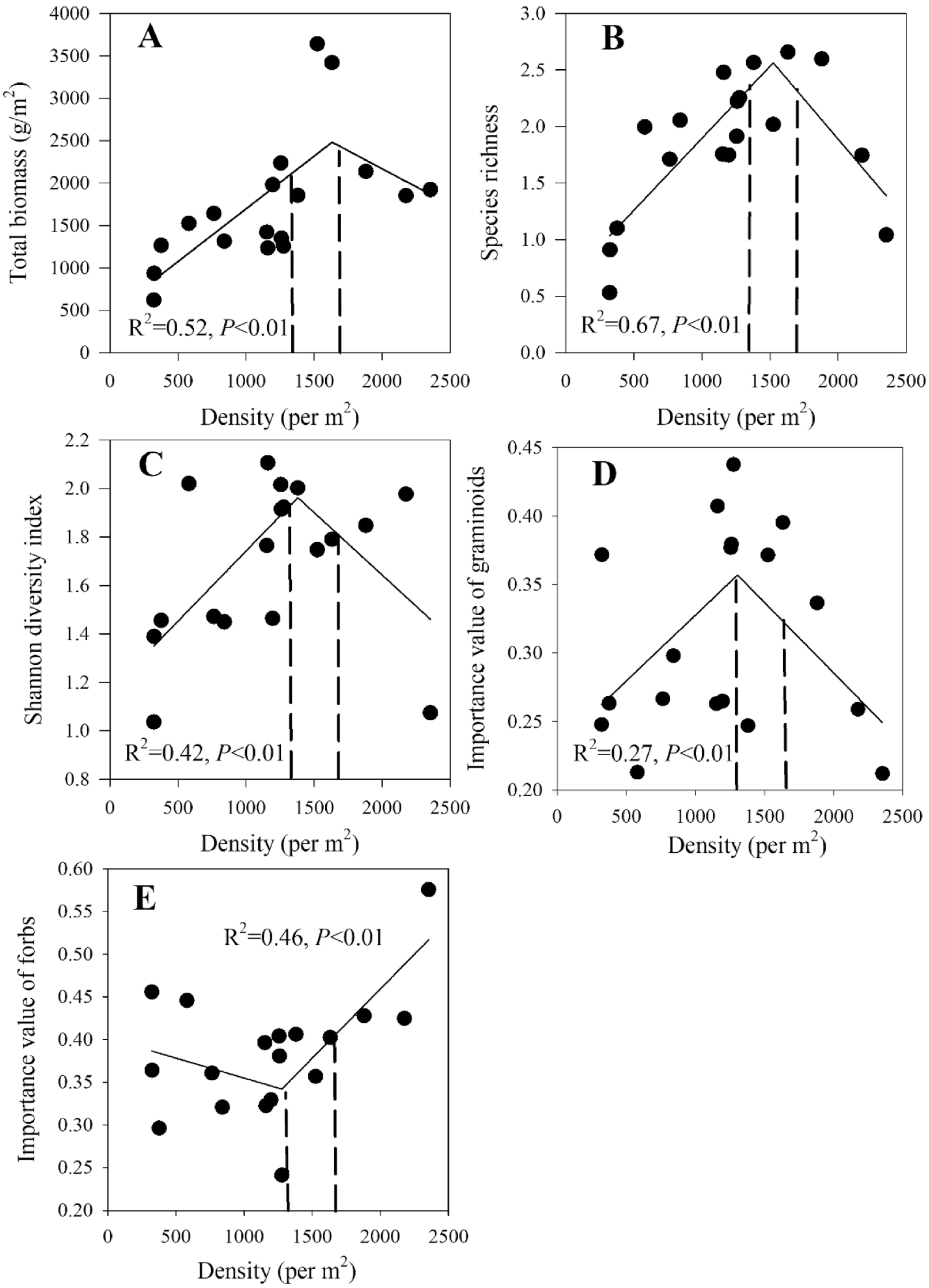

Fig. 6. Relationships between population density and total biomass (A), species richness (B), Shannon diversity index (C), and importance values of graminoids and forbs (D and E) during the restoration period.

increased, while the IV of forbs presented the a reverse trend (Fig. 6D and E). We hypothesized that there may be an optimal population density for grassland restoration and found that plant functions (productivity, richness, and diversity) were strongly influenced by population density. Specifically, the TB, SR, and Shannon diversity index first increased and then gradually decreased as the total plant population density increased, and the inflection points were all between 1350 and 1650 plants/m^2 (Fig. 6A, B and C) which occurred from approximately 8 to 10 years with GE (Fig. 5A). That is, the plant productivity, species richness and diversity of degraded grassland reached peak values after approximately 8 to 10 years of natural restoration.

A common primary goal of ecological restoration is to return functions and services to degraded ecosystems. In addition to plant characteristics, soil which is a fundamental actor in providing ecosystem processes and services and supports diverse communities of organisms cannot be ignored in restoration. Therefore, we integrated our observations with the concept of the EMF which involves 18 plant and soil properties to assess overall grassland quality (Hector and Bagchi, 2007). Our results showed that the EMF gradually increased with increasing GE time and reached a steady state after 8 to 10 years of GE (Fig. 7), suggesting that the rational time of GE was a crucial factor in ecological restoration. Considering a synthesis of the effect of GE on grassland processes and functions, the optimal restoration time required for GE is 8 to 10 years for degraded alpine meadows on the Zoige Plateau. These result are consistent with another *meta*-analytical study of China's grasslands (Xiong et al., 2016); the suitable 8- to 10-year GE duration is

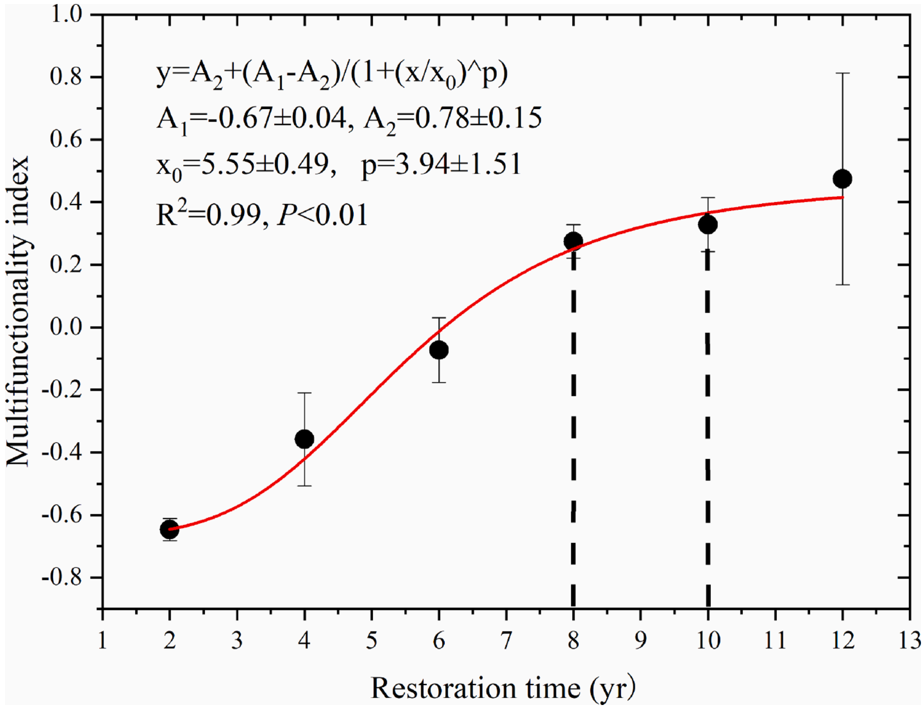

Fig. 7. Changes in the ecosystem multifunctionality index of alpine meadows along the restoration chronosequence.

between the 6 (Li et al., 2018) and 13 years (Cao et al., 2019) found in previous studies that were conducted in alpine grasslands on the eastern Qinghai-Tibetan Plateau, whereas it is much shorter than the 20 years found on the Loess Plateau (Jing et al., 2013).

As grazing-excluded grasslands are commonly assumed to 'look after themselves' (Wu et al., 2010), the effectiveness of GE has been shown to be largely affected by precipitation (Hu et al., 2016; Xiong et al., 2016), which is the main factor controlling plant growth (Sun and Qin, 2016). There should be different optimal GE durations in divergent grassland ecosystems (Sun et al., 2020), and GE is more effective for plant recovery in humid than arid regions (Xiong et al., 2016). Liu et al. (2020b) demonstrated that a short-term GE had a strong positive effect on grassland rehabilitation on the Zoige Plateau because the mean annual precipitation is approximately 700 mm which mostly occurs during the plant-growing season and can provide abundant water for plant growth. In the current study, we observed that plant productivity, diversity, and proportion of graminoids first increased and then decreased along with GE time with the turning point between the 8th and 10th years; moreover, the EMF gradually increased and became relatively steady after 8 to 10 years of GE. Based on these findings, we suggest that GE should cease after approximately 8 to 10 years in this humid region, because grazing exclusion can be useful tools but only when they are transitional and impermanent (Sacha, 2020).

In the present study, there was one plot for each of the treatments (grasslands with different years of GE) restricted by experimental conditions. We placed three representative sample plots (subplots) as replicates in each treatment, but the chance of pseudo-replication is high. Moreover, the effects of inter annual variation in climate between the years of GE were not considered, which may play important roles in plant growth and community structure, although a recent study in a Tibetan alpine grassland reported that climate change had not changed annual biomass production over the past 35 years (Wang et al., 2020). These potential problems may limit the assessment of the effects of GE in different years on restoring grasslands. Therefore, long-term continued monitoring data on the efficiency of GE time for restoring degraded grasslands on large spatial scales that take into account other factors including climate change on large temporal scales are needed in the future.

5. Conclusions

In the current study, we identified the effectiveness of grazing exclusion for degraded alpine meadow restoration involving the effects of grazing exclusion time on plant productivity, diversity, community structure, and the EMF. The grazing exclusion of 8–10 years was proven to yield a higher benefit of functional recovery of degraded alpine meadows in the semi-humid region since, at this stage, the plant biomass, species diversity, IV of graminoids, and EMF were greater, while the IV of forbs was smaller than that from other time-scales. Our results demonstrate that grazing exclusion is a suitable grassland management regime in the semi-humid Zoige region where rich rainfall can provide abundant soil water for plant growth and grassland restoration. As the effectiveness of GE for restoring degraded grassland is higher in the semi-humid area areas than in the arid and semi-arid regions, the optimal grazing exclusiontime should be various in different grassland ecosystems. These findings could offer a better guidance for the long-term adaptable management practices of degraded alpine grasslands in the semi-humid areas of the Qinghai-Tibetan Plateau. Our experiment was conducted within a particular site, while environmental conditions such as soil type and climate could have affected the results. Further studies are needed to examine how habitat conditions influence the effects of grazing exclusion time on grassland restoration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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