Plant biomass of grasses in active restoration grasslands shows stronger association with its eco-physiological properties than native grasslands alongside degradation

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Abstract

Grassland degradation can affect plant eco-physiological properties and thus influence ecosystem productivity and ecosystem function. However, how land degradation affects the relationship between plant biomass and eco-physiological properties of active restoration grasslands and native grasslands in alpine meadow is less understood. A series of degraded grasslands (non-degraded, slightly degraded, moderately degraded, heavily degraded and extremely degraded grasslands) and a series of active restoration grasslands (active restored grasslands with different growth time, 5 years, 9 years, 11 years, 14 years and 17 years) were selected to investigate the relationship between eco-physiological properties and aboveground biomass (AGB) of grasses alongside degradation. Results showed that the AGB, net photosynthetic rate (Pn) and plant nitrogen (N) concentration decreased significantly with increased levels of degradation in native grasslands. Plant photosynthetic capacity, plant N and phosphorus (P) concentration significantly decreased at 9th year or longer than 9 years of replanting time in active restoration grasslands. Plant eco-physiological properties in active restoration grasslands shows stronger association with its AGB than native grasslands. In native grasslands, degradation affect AGB directly and through Pn indirectly. In active restoration grasslands, degradation affect AGB directly and through Pn, plant N and P indirectly. Our results indicated that through improving plant nutrients to restore degraded active grasslands may be more effective than to restore degraded native grasslands.

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Running title: different relationships between plant biomass and eco-physiological properties

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Grassland degradation can affect plant eco-physiological properties and thus influence ecosystem productivity and ecosystem function. However, how land degradation affects the relationship between plant biomass and eco-physiological properties of active restoration grasslands and native grasslands in alpine meadow is less understood. A series of degraded grasslands (non-degraded, slightly degraded, moderately degraded, heavily degraded and extremely degraded grasslands) and a series of active restoration grasslands (active restored grasslands with different growth time, 5 years, 9 years, 11 years, 14 years and 17 years) were selected to investigate the relationship between eco-physiological properties and aboveground biomass (AGB) of grasses alongside degradation. Results showed that the AGB, net photosynthetic rate (Pn) and plant nitrogen (N) concentration decreased significantly with increased levels of degradation in native grasslands. Plant photosynthetic capacity, plant N and phosphorus (P) concentration significantly decreased at 9th year or longer than 9 years of replanting time in active restoration grasslands. Plant eco-physiological properties in active restoration grasslands shows stronger association with its AGB than native grasslands. In native grasslands, degradation affect AGB directly and through Pn indirectly. In active restoration grasslands, degradation affect AGB directly and through Pn, plant N and P indirectly. Our results indicated that through improving plant nutrients to restore degraded active grasslands may be more effective than to restore degraded native grasslands.

Key words: Active restoration; Grassland degradation; Photosynthesis; Plant nitrogen concentration; SEM modeling

Introduction

Alpine grasslands cover more than 60% area of the Qinghai-Tibetan Plateau (QTP) (Li et al., 2014; Shen et al., 2015; Dong et al., 2020) and play an integral role as livestock production, biodiversity maintenance and water conservation in this region (Qiu et al., 2008; Wang et al., 2009; Miehe et al., 2019; Shen et al., 2021). However, due to climate change and human activity, these grasslands have been degraded in recent decades (Shang et al., 2008; Dong et al., 2020; Peng et al., 2020). This not only influenced local economic development but also altered the relationship between plant productivity and eco-physiological properties, leading to ecosystem instability (Andrade et al., 2015; Guo et al., 2019; Bai et al., 2020). To prevent grasslands degradation and to restore these degraded grasslands, the active restoration means has been applied widely in this region (Shang et al., 2008; Feng et al., 2010; Li et al., 2018; Bai et al., 2020). However, the active restoration grasslands degraded again and have led to a continuous undermine soil texture, plant productivity and plant eco-physiological properties (Shang et al., 2016; Li et al., 2018; Gao et al., 2019; Shen et al., 2019). Therefore, understanding the difference effect of land degradation on the relationship between plant biomass and eco-physiological properties alongside degradation is important for guiding the rebuilt of degraded grasslands.

Plant photosynthetic capacity is very sensitive to varying environmental conditions and can reflect ecological strategies of plants to its survival habitat (Skelton et al., 2017; Wang et al., 2018; Trueba et al., 2019; Shen et al., 2021). Nitrogen (N) and phosphorus (P) are important component of photosynthesis pigments and photosynthetic enzyme that may be affected by grassland degradation, and thus to impact on plant photosynthetic capacity and biomass accumulation (Li et al., 2018; Guo et al., 2019; Shen et al., 2021). It has been suggested that plant photosynthetic capacity, plant N and P concentration could be used to identify the level of grassland degradation (Angassa, 2014; Giangiacomo et al., 2014). However, litter is known on how plant eco-physiological properties (including plant photosynthetic capacity, plant N and P concentration) can act as an indicator of degradation level, and how the differential relationship between plant biomass and the eco-physiological properties of native and active restoration grasslands of alpine grasslands.

Many studies have reported that grasses in native grasslands typically have higher belowground biomass and higher foliar N concentrations compared with active restoration grasslands (Shang et al., 2008, Li et al., 2014, 2018), this leading to plants with a competitive advantage in native grasslands. However, other research has also demonstrated that higher soil nutrient availability or higher degradation level could eliminate this advantage and negatively impact on photosynthetic activity, especially in N-richer ecosystems or in heavily degraded grasslands (Xu et al., 2015, 2018; Ye et al., 2018; Shen et al., 2021). Based on the above background, we hypothesized that: 1) plant eco-physiological properties of grasses would show differential responses between native grasslands and active restoration grasslands, and 2) aboveground biomass of grasses in active restoration grasslands shows stronger association with its eco-physiological properties than native grasslands alongside degradation, and 3) the different declining mechanisms of aboveground biomass exist between native grasslands and active restoration grasslands.

Materials and methods

Study site

The field experiment was carried out in an alpine meadow located the Dawu village, Maqu county of Qinghai Province, China. The geographic site is 100º 12´E, 34º 28´N and 4200 m ASL. The mean annual precipitation and mean annual temperature is 510 mm and -0.6, respectively. The soil is clay soil and the vegetation is alpine meadow.

We selected a series of degraded grasslands (non-degraded (ND), slightly-degraded (SLD), moderately degraded (MD), heavily degraded (HD) and extremely degraded (ED) grasslands) of native grasslands (Guo et al., 2019; Peng et al., 2020) and a series of active restoration grasslands (active restored grasslands with different growth time, five years (5Ys), nine years (9Ys), eleven years (11Ys), fourteen years (14Ys) and seventeen years (17Ys)). The 17Ys, 14Ys, 11Ys, 9Ys and 5Ys grasslands site were the severely degraded grasslands and were replanted with *E. mutans* in 2000, 2003, 2006, 2008 and 2012, respectively. Each site area were more than 10000 m^2.

Plant photosynthetic capacity measurements

Plant photosynthetic capacity (net photosynthetic rate (Pn), intercellular CO_2concentration (Ci), transpiration rate (Tr) and stomatal conductance (gs)) of all key plants of grasses were measured using a portable photosynthesis system (Li-6400, Lincoln, NE, USA) between 10:00 am-11:00 am in July, 2018. Six leaves of each grass species at each site were chosen for replication measurement. Instantaneous water use efficiency ($WUEi$) $=\mathrm{Pn}/Tr$.

Field sampling and laboratory analysis

In early August of 2018, a field survey was conducted and six sampling quadrats (0.5 mx0.5 m) were randomly selected at each site. In each quadrat, the coverage and species richness of community and grasses were recorded and plant aboveground biomass (AGB) of community and grasses were clipped and oven-dried at 70 to constant weight to get the AGB. Meanwhile, we collected the aboveground parts of grasses in each site for nutrient analysis. Plant nitrogen (N) and phosphorus (P) concentration were measured by a flow injection auto-analyzer (FIAstar 5000 Analyzer) (Bao, 2000; Guo et al., 2019).

Statistical analysis

One-way ANOVA was used to test the differences in plants eco-physiological properties and AGB in native grasslands and active restoration grasslands, respectively. A multi-comparisons of a least significant difference (LSD) test in analysis of ANOVA was used to test the effect of grasslands degradation of native grasslands and the effect of replanting time in active restoration grasslands of plant AGB, photosynthetic capacity and nutrient concentration. Principal component analysis (PCA) was used to assess the relationships between plant AGB and eco-physiological properties of grasses and two structural equation model (SEM) were used to identify the direct and indirect pathways that determined grasses' AGB in the two types of grasslands.

Results

3.1 AGB of grasses and plant community

AGB of grasses and community decreased significantly with land degeneration intensifying. Compared to ND grassland, AGB of grasses and community decreased by 21.3% and 9.6%, 66.2% and 32.6%, 75.9% and 54.8%, and 95.0% and 69.2% in the SLD, MD, HD and ED grasslands, respectively (Fig.1a, 1c). Meanwhile, The AGB of grasses decreased significantly with the increase of the replanting time in active restoration grasslands. Compared to 5Ys, AGB of grasses decreased by 8.3%, 32.9%, 65.5% and 81.3% in the 9Ys, 11Ys, 14Ys and 17Ys grasslands, respectively (Fig.1b). Compared to 5Ys, AGB of community kept stable in 9Ys grasslands and then decreased with the increase of replanting time (Fig. 1d).

Insert Figure 1

3.2. Photosyntheticcapacity and its relationship with AGB of grasses

In native grasslands, Pn decreased with land degradation intensifying (Fig. 2a). Compared to control (ND grassland), Pn significantly decreased by 4%, 18.7%, 35.8% and 39.6% in the SLD, MD, HD and ED grasslands, respectively. In addition,*gs* and *WUEi* initially kept stable and later decreased with land degradation intensifying (Fig. 2c, 2e). Intercellular CO_2 concentration initially increased and later decreased with land degeneration (Fig. 2g). In active restoration grasslands, Pn (Fig. b), *WUEi* (Fig. 2f) and *Ci*(Fig. 2h) significantly decreased with the increase of replanting time. Compared to 5Ys grassland, Pn, *WUEi* and *Ci* significantly decreased by 0.6%, 4.0%, and 4.7%, 15.1%, 23.0% and 9.1%, 24.3%, 23.0% and 12.2%, 31.4%, 35.3% and 13.6% in the 9Ys, 11Ys, 14Ys and 17Ys grasslands, respectively. Stomatal conductance increased first and then decreased with the increase of replanting time.

Insert Figure 2

Net photosynthetic rate (R^2 =0.938, P <0.001) (Fig. 3a) and *WUEi* (R^2 =0.302, P =0.007) (Fig. 3c) were positive correlated with AGB in native grasslands. Net photosynthetic rate (R^2 =0.881,P <0.001), *WUEi*(R^2 =0.839, P<0.001), *gs*(R^2 =0.803, P <0.001) and *Ci* (R^2 =0.665, P <0.001) were highly positive correlated with AGB in active restoration grasslands (Fig. 3). Plant photosynthetic capacity in active restoration grasslands shows stronger association with its AGB than native grasslands.

Insert Figure 3

3.3. Plant N and P concentration and its relationship with AGB of grasses

In native grasslands, SLD, MD, HD and ED grasslands decreased plant N concentration by average of 2.0%, 16.0%, 28.7% and 34.1%, respectively, as compared to the ND grassland (Fig. 4a). However, land degradation did not impact on P concentration (Fig. 4b). Compared to 5Ys grassland, plant N and P significantly decreased by 22.0% and 6.72%, 30.7% and 21.5%, 41.6% and 32.7%, and 47.5% and 45.7% in the 9Ys, 11Ys, 14Ys and 17Ys grasslands, respectively (Fig. 4).

Insert Figure 4

There were significantly positive relationships between plant N and AGB (R^2 =0.829, P <0.001), plant P and AGB (R^2 =0.869, P <0.001) of grasses in active restoration grasslands, and between plant N and AGB (R^2 =0.809,P <0.001) in native grasslands (Fig. 5a). However, there were insignificant correlations between AGB and plant P in native grasslands (R^2 =0.105, P =0.224) (Fig. 5b). Plant N and P of grasses in active restoration grasslands shows stronger association with its AGB than native grasslands.

Insert Figure 5

3.4. Influencing way of land degradation on AGB of grasses

A principal component analysis of photosynthetic capacity, nutrient content and AGB showed that PC1 and PC2 explained % of the variance of 69.2% and 86.5% in native and active restoration grasslands, respectively. In native grasslands, AGB was mainly positively related with Pn and plant N (Fig. 6a). In active restoration grasslands (Fig. 6b), AGB was mainly positively related with Pn, plant N and P, *gs* and *WUEi* .

Insert Figure 6

Two structural equation models (SEM) were used to explore the effects of degradation on the AGB of grasses in the two types of grasslands (Fig. 7). In native grasslands, degradation affect AGB directly and through Pn indirectly (R^2 =0.90,P <0.001) (Fig. 7a). In active restoration grasslands, degradation affect AGB directly and through plant N (R^2 =0.91, P <0.001), plant P (R^2 =0.93, P <0.001) and Pn (R^2 =0.85,P <0.001) indirectly (Fig. 7b).

Insert Figure 7

Discussion

4.1 Plant AGB in response to grassland degradation

Generally, AGB is a one of most important index and can be used to assess the growth status of plants and stability of plant community to their surrounding environment (Liu et al., 2018; Xu et al., 2018; Shen et al., 2019). In our study, there were negative changes in AGB of community and grasses with increased levels of degradation, this result is consistent with previous studies (Shang et al., 2008; Benaya et al., 2009; Wang et al., 2010; Li et al., 2014, 2018; Zhou et al., 2021). Livestock selective palatable grasses, soil nutrients and soil water loss were mainly responsible for the decreasing of AGB of community and grasses alongside degradation (Shang et al., 2008, 2016; Guo et al., 2019).

The establishment of active restoration grasslands increased AGB both of grasses and community, it was reasonable to conclude that the artificial replanting in ED grassland is the most effective approach to restore degraded grasslands (Wu et al., 2010; Li et al., 2018; Guo et al., 2019; Bai et al., 2020). However, the AGB of grasses and community in those grasslands have decreased at 9th year or longer than 9 years of replanting time. Therefore, in order to prevent grassland degeneration of the active restoration, management intervention such as weeding and fertilization should be taken into consideration at 9th restoration year (Shang et al., 2008; Li et al., 2014, 2018; Gao et al., 2019).

4.2 Plant photosynthetic capacity in response to grassland degradation

In this study, grasses showed higher Pn in ND and SLD relative to MD, HD and ED in native grasslands, and showed higher Pn in 5Ys and 9Ys relative to 11Ys, 14Ys and 17Ys in active restoration grasslands, respectively. Degradation of both the native grasslands and active restoration grasslands can decrease soil total carbon (C), soil total N content and soil water content (Li et al., 2014; Xu et al., 2015; Liu et al., 2020), and which could limit plant photosynthesis activity by reducing the supplements of C, N and water to photosynthetic tissues (Chaves et al., 2009; Jilling et al., 2018; Quan et al., 2019 Shen et al., 2019). Our results also indicated that the different responses of grass' photosynthetic capacity to land degradation were exist between the two types of grasslands, which means different mechanisms may be responsible for these differential responses (Skogen et al., 2011, Shen et al., 2021). In native grasslands, land degradation significantly decreased Pn, but Ci (Fig.2g) andgs (Fig. 2c) kept relatively stable, we can confirm that the decline of Pn mainly caused by non-stoma limitation. However, in active restoration grasslands, with the decrease of Pn, Ci(Fig.2h) and gs (Fig.2d) were significant decreased, which indicated that the decline of Pn mainly caused by stoma limitation (Xu et al., 2010; Carriqui et al., 2015; Bartlett et al., 2017; Brodribb et al., 2020).

Our study also indicated that plant photosynthetic capacity of grasses in active restoration grasslands shows stronger association with its AGB than native grasslands, this would suggest that plant photosynthetic capacity were very sensitive to soil degradation and should be considered as an indicator of degradation level. In native grasslands, the relationship between plant photosynthetic capacity and its AGB of grasses is less stronger, this may attribute to its higher belowground biomass (Li et al., 2014; Crouzeilles et al., 2017; Guo et al., 2019), higher soil water content and higher nutrient content (Shang et al., 2008; Jensen et al., 2020) as compared to the active restoration grasslands, which maybe can modulate the relationship. So, the relationships among plant photosynthetic capacity, soil water content and nutrient content of native and active restoration grasslands need to be further investigation.

4.3 Plant N and P concentration in response to grassland degradation

Consistent with other studies (Li et al., 2014; Guo et al., 2019; Zhou et al., 2021), plant N concentration of grasses decreased with degradation intensify both in native grasslands and active restoration grasslands. In alpine grassland, soil N concentration is relatively low and the ecosystems are usually N-limited (Guo et al., 2017; Xu et al., 2018; Shen et al., 2019). Continuous grassland degeneration altered soil carbon and N availability and decreased soil carbon and N storage (Chen et al., 2016; Wang et al., 2018; Peng et al., 2020), which not only had negative feedbacks on plant N concentration, but also would decrease plant carbon gain and biomass accumulation (BassiriRad, 2015; Carriqui et al., 2015; Bartlett et al., 2017; Shen et al., 2019).

Our result indicated that there were no significant difference in P concentration in grasses alongside degradation in native grasslands. This not only suggested that plant P was not or less sensitive to degradation than N, but also confirmed that alpine soil were less P-limited than N-limited (Xu et al., 2015; Liu et al., 2018; Zhou et al., 2021). The main reasons are the different relationships of plant N and P content with soil water content, difference cycle processes of N and P and difference nutrients resorption mechanism of N and P by plants (Pastor et al., 1984; Reich and Oleksyn, 2004; Rui et al., 2012; Yan et al., 2018; Zhou et al., 2021). In this study, in active restoration grasslands, plant P concentration of grasses decreased with the increase of replanting time, and positively related with its AGB. This means that a possible change in the balance of P nutrient alongside degradation, which had negative feedbacks on plant photosynthetic activity and plant productivity (Dijkstra et al., 2012; Pistocchi et al., 2018; Zhou et al., 2020). The above results indicated that through improving plant N and P concentration to restore degraded active grasslands may be more effective than to restore degraded native grasslands.

4.4 Way of degradation influence AGB of grasses

Degradation significantly decreased AGB of grasses both through direct way and indirect way in those two types of grasslands. Degradation declined AGB of grasses directly and through decreased Pn indirectly in native grasslands, and declined AGB of grasses directly and through decreased Pn, plant N and P indirectly in active restoration grasslands. So, plant Pn plays important role in determining AGB of grasses both in native grasslands and active restoration grasslands (Xu et al., 2018; Shen et al., 2019, 2021). For the direct way, land degeneration decreased biomass accumulation through restricting plant abundance, declining plant individual height and plant richness (Xu et al., 2015, 2018; Li et al., 2018; Guo et al., 2019). For the indirect way, in native grasslands, land degeneration first decreased plant N concentration (Elser et al., 2007; Gusewell and Gessner, 2009; Dlamini et al., 2014; Peńuelas et al., 2015) and thus to decrease photosynthetic activity (Wright et al., 2004, 2010; Güsewell, 2010; Sundqvist et al., 2014; Castellano et al., 2016). In active restoration grasslands, the main reason for the indirect way was that land degradation declined soil nutrient content such as C, N and P and the *gs* and *Ci* of grasses, the former declined plant N and P content and the later inhibited plant photosynthetic rate (Sundqvist et al., 2014; Zhou et al., 2021; Shen et al., 2019).

Conclusions

In conclusion, land degeneration both the native and active restoration grasslands significantly influenced AGB, photosynthetic capacity and nutrient concentration of grasses. In native grasslands, the decline of Pn mainly caused by non-stoma limitation, and in active restoration grasslands, the decline of Pn mainly caused by stoma limitation. Plant photosynthetic properties and N and P concentration in active restoration grasslands shows stronger association with its AGB than native grasslands. Land degradation decreased AGB of grasses through both direct way and indirect way in those two types of grassland. Plant N and P are the two key nodes that matter in the way of declining AGB of grasses and can indicate the of degradation level of active restoration grasslands.

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Conflict of 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.

Data availability statement:

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Authors' Contributions

D.H.X. and X.W.F. conceived the study and designed the methodology; W.B.M., X.J.W. and R.Y.Z collected and analyzed the data; D.H.X., J.L.Y. and G.Q.Y. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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List of Figures

Fig. 1. Aboveground biomass of grasses (a, b) and community (c, d) in native grasslands and active restoration grasslands. Various alphabetical characters depict significant difference at $P < 0.05$.

Fig. 2. Pn (net photosynthetic rate) (a, b), *gs* (stomatal conductance) (c, d), *WUEi* (instantaneous water use efficiency) (e, f) and *Ci* (intercellular CO_2 concentration) (g, h) of grasses in native grasslands and active restoration grasslands. Various alphabetical characters depict significant difference at $P < 0.05$.

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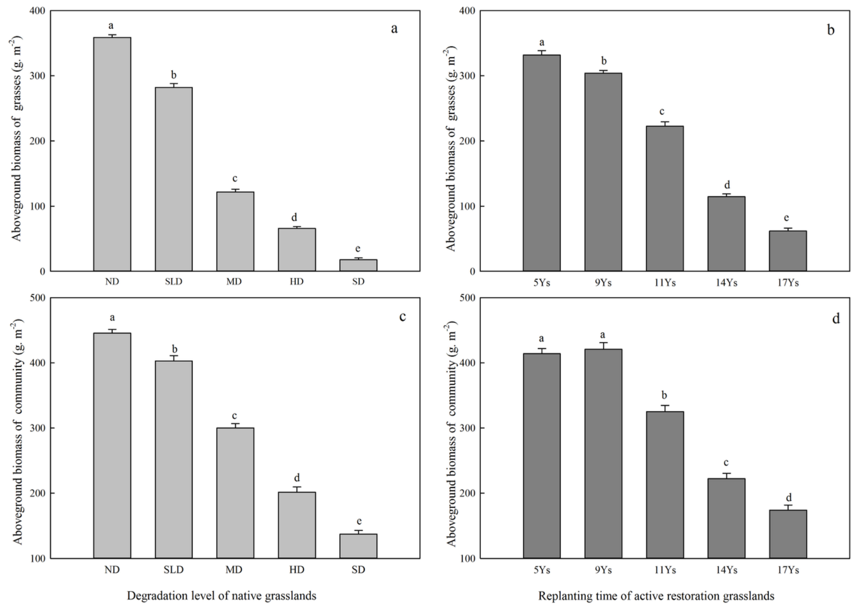
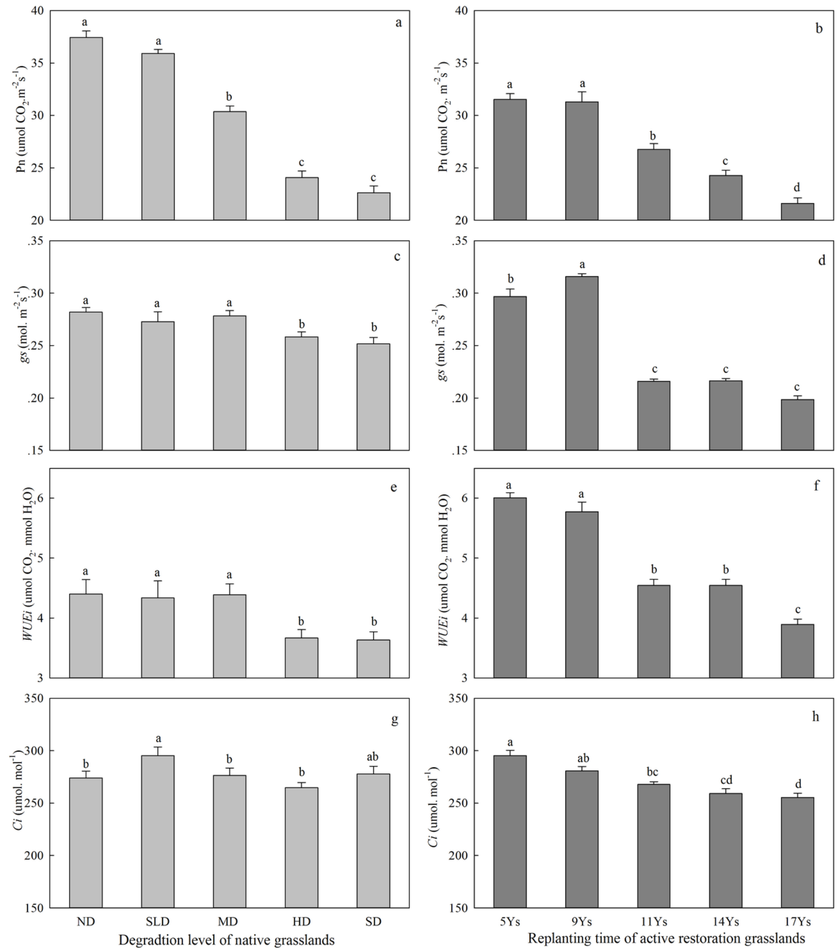
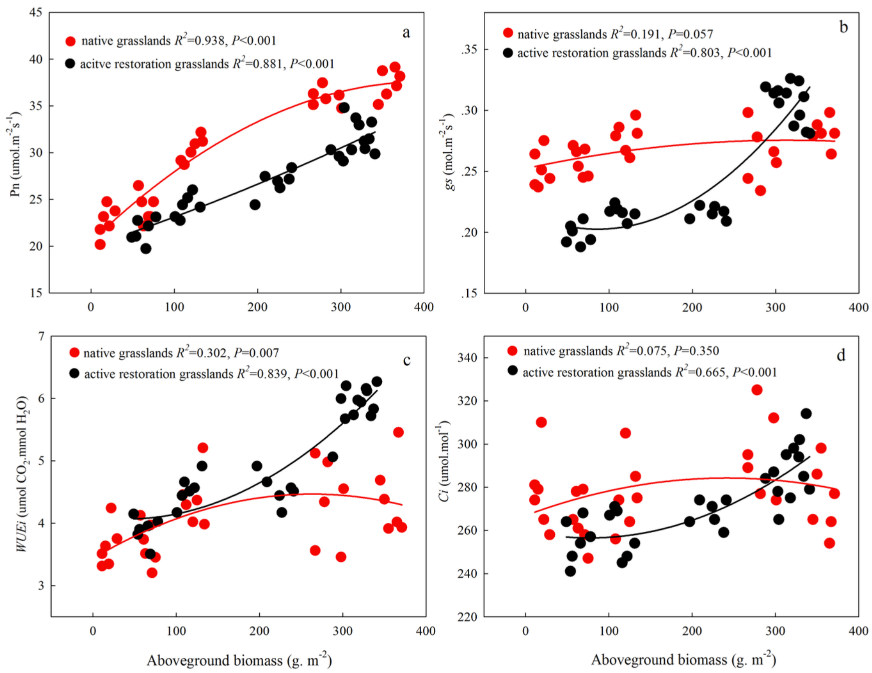
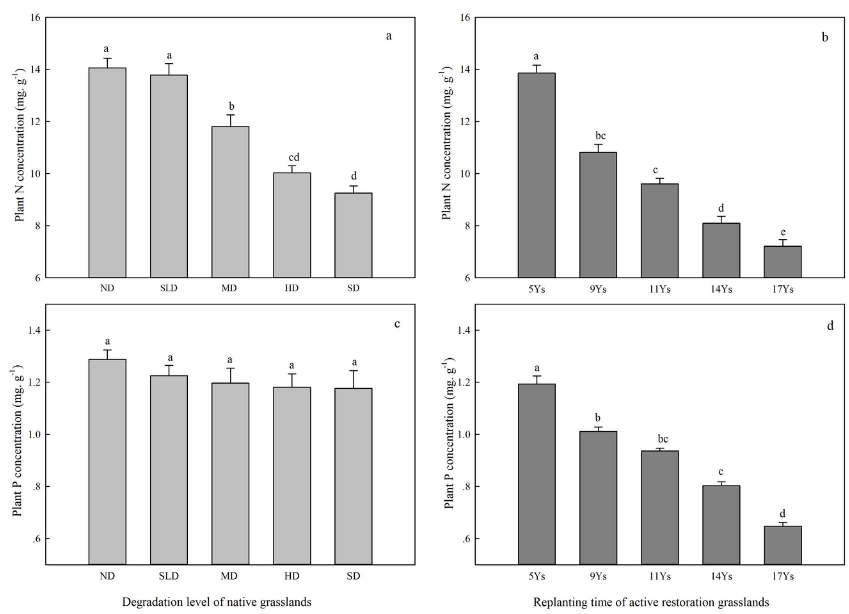
Fig. 7. Structural equation models (SEM) based on the effects of degradation level of native grasslands and replanting time of active restoration grasslands on eco-physiological properties and AGB. Black and red arrows indicate negative and positive relationships, respectively. The width of arrows is proportional to the strength of path coefficients. As in other liner models, R^2 indicates the proportion of variance explained and appears above every response variable in the model. Significance levels are as follows: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. (a) native grasslands ($\chi 2$/DF=0.843, $P = 0.537$, CFI=1.000, RMSEA=0.000; NFI=0.976; RFI=0.917) (b) active restoration grasslands ($\chi 2$/DF=0.881, $P = 0.508$, CFI=1.000 RMSEA=0.000; NFI=0.985; RFI=0.947).

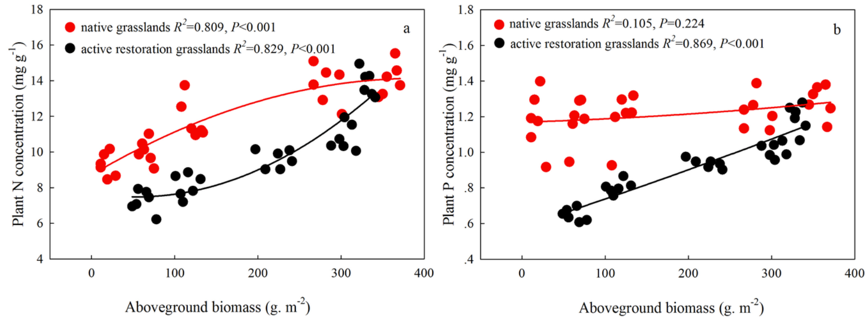


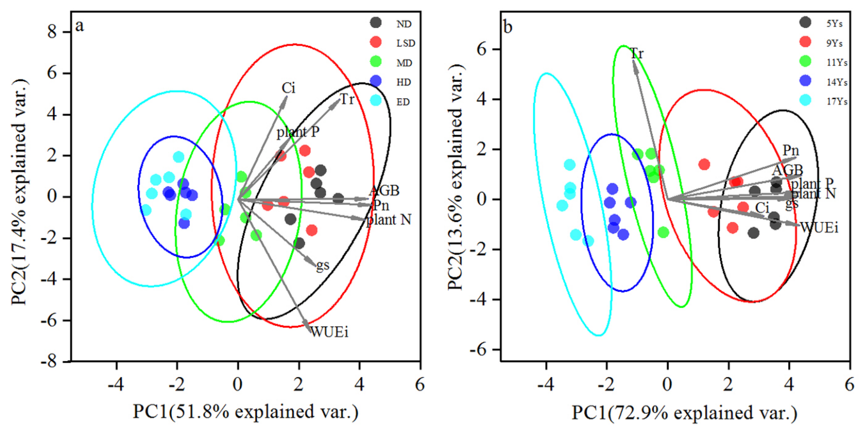
a
b
c
d
Aboveground biomass of grasses (g. m-2)
Aboveground biomass of community (g. m-2)
ND
SLD
MD
HD
SD
5Ys
9Ys
11Ys
14Ys
17Ys
Degradation level of native grasslands
Replanting time of active restoration grasslands

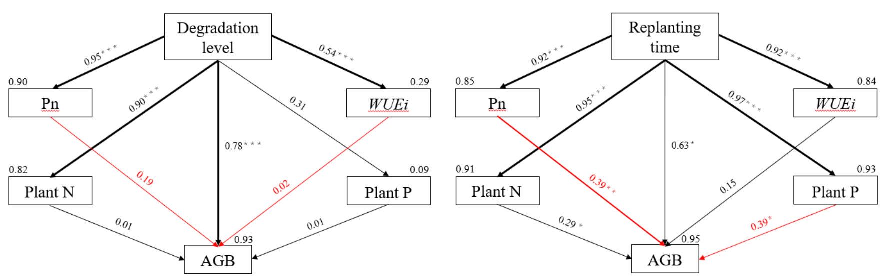

Pn (umol CO2. m-2s-1)
gs (mol. m-2s-1)
WUEi (umol CO2. mmol H2O)
Ci (umol. mol-1)
ND
SLD
MD
HD
SD
Degradtion level of native grasslands
5Ys
9Ys
11Ys
14Ys
17Ys
Replanting time of active restoration grasslands


a
native grasslands R2=0.938, P<0.001
acitve restoration grasslands R2=0.881, P<0.001
Pn (umol.m-2.s-1)
b
native grasslands R2=0.191, P=0.057
active restoration grasslands R2=0.803, P<0.001
gs (mol.m-2.s-1)
c
native grasslands R2=0.302, P=0.007
active restoration grasslands R2=0.839, P<0.001
WUEi (umol CO2.mmol H2O)
d
native grasslands R2=0.075, P=0.350
active restoration grasslands R2=0.665, P<0.001
Ci (umol.mol-1)
Aboveground biomass (g. m-2)
Aboveground biomass (g. m-2)


a
b
c
d
Plant N concentration (mg. g-1)
Plant P concentration (mg. g-1)
ND
SLD
MD
HD
SD
5Ys
9Ys
11Ys
14Ys
17Ys
Degradation level of native grasslands
Replanting time of active restoration grasslands


a
native grasslands R^2=0.809, P<0.001
active restoration grasslands R^2=0.829, P<0.001
Plant N concentration (mg g^{-1})
Aboveground biomass (g. m^{-2})
b
native grasslands R^2=0.105, P=0.224
active restoration grasslands R^2=0.869, P<0.001
Plant P concentration (mg g^{-1})
Aboveground biomass (g. m^{-2})


a
ND
LSD
MD
HD
ED
Ci
Tr
plant P
AGB
Pn
plant N
gs
WUEi
PC2(17.4% explained var.)
PC1(51.8% explained var.)
b
5Ys
9Ys
11Ys
14Ys
17Ys
Tr
Pn
AGB
plant P
plant N
gs
Ci
WUEi
PC2(13.6% explained var.)
PC1(72.9% explained var.)


Degradation level
Pn
WUEi
Plant N
Plant P
AGB
Replanting time
Pn
WUEi
Plant N
Plant P
AGB