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How do short-term and long-term factors impact the aboveground biomass of grassland in Northern China?

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Abstract

The aboveground biomass (AGB) of grassland, a crucial indicator of productivity, is anticipated to widespread changes in key ecosystem attributes, functions and dynamics. Variations in grassland AGB have been extensively documented across various spatial and temporal scales. However, a precise method to disentangle long-term effects from short-term effects on grassland AGB and assess the attribution of explanatory factors for AGB change remains elusive. This study aimed to quantify the impact of key climatic factors, soil properties, and grazing intensity on grassland AGB changes, utilizing data spanning the 1980s and the 2000s in Northern China. The Co-regression model was explored to separate the long-term effects and short-term effects of grassland AGB, while the Generalized Linear Model (GLM) was utilized to analyze the contributions of key variables to AGB. This approach effectively avoids issues related to regression to the mean and mathematical coupling. The results revealed that the influence of climatic variables, soil texture and grazing intensity on grassland AGB changes could be decomposed into long-term, short-term and random effects. Long-term effects explained 73.6% of AGB variation, whereas short-term effect only accounted for 5.9% of AGB change. Additionally, the short-term effect was divided into direct and indirect effects, with the direct effect explaining 1.3% of AGB variation, and the indirect effect explained 4.6% of AGB dynamics. The relative importance of key variables in grassland AGB was assessed, identifying soil parameters and precipitation as the main driving factors in the study area. This study introduces a robust methodology to enhance model performance in distinguishing long-term and short-term effects on grassland AGB, contributing to the sustainable development of grassland ecology in similar regions.

Highlights

- Co-regression model was effective to separate long- and short- terms impact of AGB.
- The effect of long-term factors on AGB was higher than that of short-term factors.
- Soil parameter and precipitation were major driving factors to affect AGB change.

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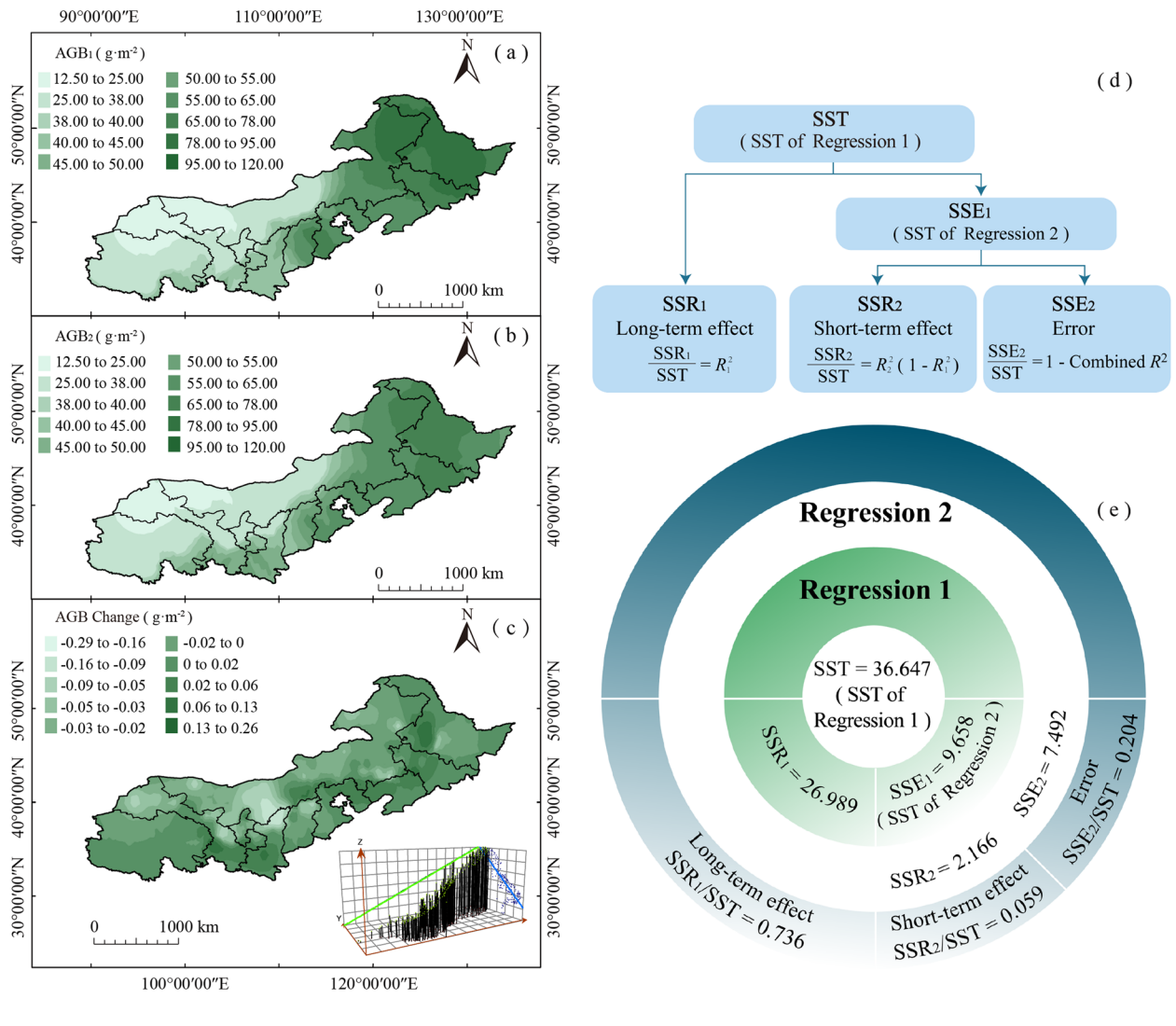
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Keywords Aboveground biomass (AGB), Co-regression, Variance partitioning, Spatiotemporal dynamics, Regression to the mean

Graphical Abstract



1 Introduction

Aboveground biomass (AGB) is a critical component of global carbon cycle and nutrient cycling (Costanza et al. 1997; Zhu et al. 2019). Amount in grassland AGB widely reflects the productivity and health status of grassland, contributing to monitoring grassland ecosystem functions and dynamics (Harris et al. 2020; Huang et al. 2018). Comprehensive dynamics of grassland AGB are influenced by key factors, and evaluating them is pivotal for assessing grassland productivity and conducting sustainable management for grassland

ecosystems (Pan et al. 2023). While it is common to separately discuss the influence of climate or human activities on grassland AGB (Zhang et al. 2023a, b), further studies are needed to comprehensively consider key factors over time (Lei et al. 2022; Li et al. 2023). Therefore, constructing an accurate estimation model for grassland AGB and analyzing long-term and short-term driving factors, such as temperature, precipitation, soil texture, and grazing intensity that influence AGB dynamics in vast regions remain a challenging endeavor. Accurately and quantitatively assessing the

driving factors of grassland AGB is of great significance for comprehending changes in grassland vegetation, establishing suitable livestock carrying capacity (He et al. 2022), evaluating the status of regional ecological environment (Huang et al. 2015), and promoting sustainable development of grassland resources (Campana et al. 2021; Adam et al. 2014; Delgado-Baquerizo et al. 2020; Godde et al. 2019).

Grassland AGB presents a significant challenge for ecologists, due to its rapid variability and the influence of various factors (Li et al. 2020; Song et al. 2018). In addressing this challenge, researchers have focused on tackling statistical issues like regression to the mean (RtoM) in assessing AGB change (Muha et al. 2012; Wagg et al. 2014). Many studies have emphasized the unsuitability of directly regressing the change value of a variable between two periods on its control variables due to the high (negative) correlation propensity to its initial value (Stigler 1980; Tu et al. 2005). For instance, Stevens and Van Wesemael (2008) addressed this issue in the analysis of covariance (ANCOVA) for soil organic carbon (SOC) change by using the average of the initial and end SOC as the covariate, aiming to mitigate the impact of the initial SOC on the SOC change (Tang et al. 2019). Moreover, considering the relationship between change and the initial value, the impact of control variables on AGB change should be intertwined with the influence of the initial AGB, rather than directly regressing AGB change on its controls, given the existence of RtoM (Karambas et al. 2016; Muha et al. 2012). Another challenge is mathematical coupling (MC), where one variable directly or indirectly contains all or part of another, leading to their joint analysis through correlation or regression (Dirmeyer et al. 2013; Wu et al. 2022). Attempting to regress the change value on the initial value along with other control variables may render the *t* test of the coefficient in a regression model inappropriate (Calizza et al. 2018; Tu et al. 2005). However, problem of MC persists when regressing the change value on the mean AGB, as using mean AGB as a covariate involves first regressing it by AGB change. The initial value's influence significantly affects the change value, resulting in the RtoM problem. Successfully eliminating this influence from the change value enables a more effective exploration of the relationship between the adjusted change value and its relevant variables through regression.

To address this, the chosen approach and model validation strategies are crucial. Temporally, we classified the effects of driving factors into long-term and short-term categories, with a particular emphasis on separating short-term effects. This study was based on the mechanism of ecological disturbance and steady-state theory in time scale to distinguish the long-term and

short-term effects from the perspective of statistics, the Co-regression method was employed to mitigate RtoM and MC problems and enhance AGB estimation performance in grasslands. The primary questions were: (1) how can the Co-regression algorithm be utilized to assess long-term and short-term effects on grassland AGB change, improving model performance by identifying and addressing RtoM and MC problems? (2) What factors drive the variation of grassland AGB, and how can optimal variable combinations be determined for modeling grassland AGB? (3) How can the contributions of key variables to grassland AGB be quantitatively analyzed? This study broadens our understanding of how driving factors affect grassland AGB change, paving the way for better assessments of grassland AGB in the present and future.

2 Materials and methods

2.1 Study area

This investigation took place in Northern China, spanning latitudes 34.30° to 49.49°N and longitudes 94.34° to 126.99°E, covering Hebei Province, Shanxi Province, Inner Mongolia Autonomous Region, Ningxia Hui Autonomous Region, Liaoning Province, Jilin Province, Heilongjiang Province, Shaanxi Province, Gansu Province, and Qinghai Province (Fig. 1). The study area's elevation ranged from 500 m to 2,000 m. Climatic types in the region primarily included temperate continental, temperate monsoon, and cold temperate climates. Climatic conditions transitioned from semi-humid and semi-arid to arid areas from east to west, experiencing simultaneous rain and heat, along with substantial temperature variations between day and night. Mean annual temperature (MAT) varied between -0.36 °C and 12.23 °C, while mean annual precipitation (MAP) ranged from 43.82 mm to 627.06 mm (statistics are based on meteorological data from the 2000s), displaying a decrease from east to west (Peng et al. 2019). Soil types were divided into sandy soil, clay soil and loam soil according to the influencing factors of the parent material, among which sandy soil and clay soil were the main soil types in the study area.

2.2 Data sources

The grassland AGB data originated from routine sampling surveys conducted at 243 sample sites across Northern China during the peak grass growing period in the 1980s and 2000s (supported by the Grassland Branch Center of the National Agricultural Science Data Platform). For the investigation of grassland biomass, the most important grassland types and groups with the largest distribution area in the northern grassland were selected (at least relatively homogeneous within the surrounding 2 km×2 km), for which the geographical

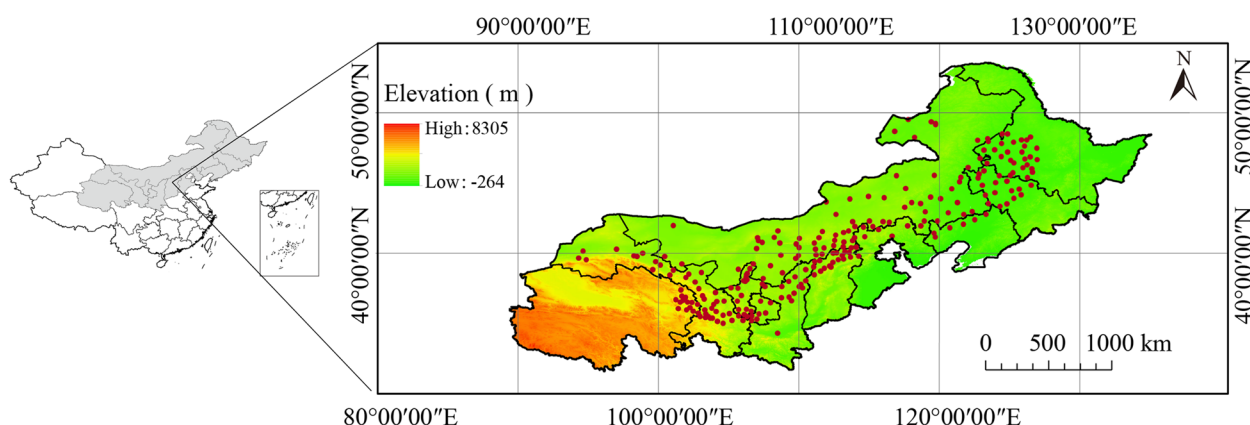


Fig. 1 Geographical location and distribution of sampling sites in Northern China

location of the center in each sample plot was precisely determined by GPS, and the species composition, distribution pattern, topography and soil conditions in the sample plot were determined. Mean AGB was computed for the peak season in both the 1980s and 2000s, and AGB was expressed as carbon density ($\text{g C}\cdot\text{m}^{-2}$) using the internationally commonly used conversion rate of 0.45 (Fang et al. 2007; Piao et al. 2004).

Additionally, climate data, including mean annual temperature and mean annual precipitation for 243 sample sites across 56 counties in the study area, were obtained from the China Meteorological Administration (<http://cdc.cma.gov.cn/home.do>) through spatial analysis and statistics in the 1980s and 2000s. Livestock inventory data for the 1980s and 2000s were sourced from the Rural Socio-economic Survey Team database of the China Bureau of Statistics for each county in the study area. The number of livestock was used to characterize the influence of grazing intensity in the two reference periods, calculated in terms of DSE hm^{-2} (DSE representing the amount of feed required by a two-year-old, 50 kg Merino sheep to maintain its weight).

The two sets of AGBs, climate and soil factors, and grazing intensity were utilized to formulate the grassland AGB models. The denotation and description of dependent variables in this study are provided in Table 1. The key factors included temperature ($\text{MAT}_1, \text{MAT}_2, \Delta\text{MAT}$), precipitation ($\text{MAP}_1, \text{MAP}_2, \Delta\text{MAP}$), soil texture ($S_{\text{Clay}}, S_{\text{Silt}}$), and grazing intensity ($\text{LSK}_1, \text{LSK}_2, \Delta\text{LSK}$), which collectively referred to the explanatory variables of the model (Table 2).

2.3 Segregating long-term and short-term effects

The impacts of long-term and short-term factors on grassland AGB were quantitatively investigated using the Co-regression model, constructed with IBM SPSS 22.0. The Pearson correlation test was employed for correlation analysis, and the model's fitting degree was enhanced by eliminating relationships between observed variables. Apart from the long-term effects, the variation in AGB_{L2} was also influenced by the short-term effects of key factors, along with random fluctuations.

To separating long-term effects from short-term effects (Fig. 2):

Table 1 Denotation and description of dependent variables

| Variable | Description |
|------------------------------|---|
| AGB_1 | Average grassland AGB in 1980s |
| AGB_2 | Average grassland AGB in 2000s |
| AGB_{L1} | Logarithm of AGB_1 |
| AGB_{L2} | Logarithm of AGB_2 |
| $\text{PRED}_{\text{AGBL2}}$ | Predicted value of AGB_{L2} regressed to AGB_{L1} , also expressed as $\exp(\text{AGB}_{L2})$ |
| $\text{PRED}_{\text{AGB2}}$ | Predicted value of AGB_2 based on $\text{PRED}_{\text{AGBL2}}$ |
| CHG_T | Total change between AGB_{L2} and AGB_{L1} |
| CHG_L | Change incurred by long-term impacts of control variables |
| CHG_S | Change incurred by short-term impacts of control variables and random errors |

Table 2 Denotation and description of explanatory variables (controls)

| Category | Variable | Description |
|----------|-------------------|--|
| Climate | MAT ₁ | Mean annual temperature in 1980s |
| | MAT ₂ | Mean annual temperature in 2000s |
| | ΔMAT | The difference of mean annual temperature between 1980 and 2000s |
| | MAP ₁ | Mean annual precipitation in 1980s |
| | MAP ₂ | Mean annual precipitation in 2000s |
| | ΔMAP | The difference of mean annual precipitation between 1980 and 2000s |
| Soil | S _{clay} | The content of clay in the soil |
| | S _{silt} | The content of silt in the soil |
| Grazing | LSK ₁ | Number of livestock in 1980s |
| | LSK ₂ | Number of livestock in 2000s |
| | ΔLSK | The difference in livestock numbers between 1980 and 2000s |

$$CHG_T = AGB_{L2} - AGB_{L1} \tag{1}$$

$$CHG_S = AGB_{L2} - PRED_{AGBL2} \tag{2}$$

$$CHG_T = CHG_L + CHG_S \tag{3}$$

where CHG_T represents the total effect, which could be divided into change under long-term effect (CHG_L), and change under short-term effect and random error (CHG_S).

2.4 Co-regression model

The initial AGB served as the covariate, and AGB₂ was regressed on AGB₁ to predict the end AGB, thereby eliminating its impact from the end AGB. Consequently, an adjusted change in AGB was generated, as opposed to the (direct) change in AGB resulting from subtracting the (observed) initial value from the (observed) end value. Moreover, the adjusted change in AGB was statistically independent of the initial AGB. The Co-regression analysis method, akin to variance analysis in ANCOVA, is replaced by regression analysis after removing the impact of the covariate.

Two consecutive linear models, Regression 1 and Regression 2, were set up for the Co-regression model. Logarithmic values of the initial AGB (AGB_{L1}) and the end AGB

(AGB_{L2}) were employed in conformity with the normality assumption. The first regression (Regression 1) regressed AGB_{L2} on AGB_{L1}, and generated the predicted value of AGB_{L2} (PRED_{AGBL2}). Subsequently, the impact of AGB_{L1} (acting as the covariate) on AGB_{L2} was removed by subtracting the PRED_{AGBL2} from AGB_{L2}, and the difference (CHG_S) was taken as adjusted change between the two periods, in contrast to the direct difference between AGB_{L2} and AGB_{L1}.

CHG_S was totally independent of AGB_{L1}, and the second regression (Regression 2) could be set up by regressing the CHG_S on its relevant variables without problems about RtoM or MC.

The Co-regression model comprised following two linear regressions:

Regression 1: regress the AGB_{L2} on AGB_{L1}, subtract the predicted AGB_{L2} from the (observed).

AGB_{L2}, thus generated the CHG_S.

Regression 2: regress the CHG_S on variables such as temperature, precipitation, soil texture and grazing intensity.

$$Combined_R2 = R_1^2 + R_2^2(1 - R_1^2) \tag{4}$$

where R₁² is the R-square of Regression 1 and R₂² is the R-square of Regression 2.

Taking the effect of Regression 1 as the long-term effect, Regression 2 as the short-term effect of the model, the following equations were obtained.

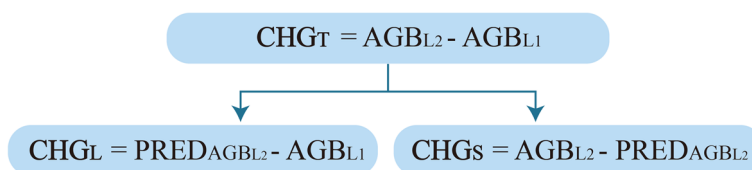


Fig. 2 Equations schematic diagram of CHG_T, CHG_L and CHG_S

$$\text{Long-term effect} = \frac{SSR_1}{SST} = R_1^2 \tag{5}$$

$$\text{Short-term effect} = \frac{SSR_2}{SSE_1} \times \frac{SSE_1}{SST} = R_2^2(1 - R_1^2) \tag{6}$$

$$\text{Error} = SSE_2/SST = 1 - \text{Combined_R2} \tag{7}$$

where SST is the total sum of square for AGB_{L2} ; SSR_1 is the regression sum of square for Regression 1; SSE_1 is the error (or residual) sum of square for Regression 1, and also the total sum of square for Regression 2; SSR_2 is the regression sum of square for Regression 2, and SSE_2 is the error sum of square for Regression 2. $\frac{SSR_2}{SSE_1}$ represents coefficient of determination of short-term effect, which is SSR_2 divided by SSE_1 (the total sum of squares of the short-term effect). $\frac{SSE_1}{SST}$ serves as adjustment factor, which equals to 1 minus $\frac{SSR_1}{SST}$, namely $(1 - R_1^2)$.

2.5 Generalized Linear Model (GLM) and sum of squares (type III)

The multiple regression models of target variables on key driving factors were established, and then GLM method and sum of squares (type III) were applied to assign relevant importance of each factor on target variables.

$$f(y_i; \theta_i, \Phi) = \exp\left\{ \frac{y_i \theta_i - b(\theta_i)}{a(\Phi)} + c(y_i, \Phi) \right\} \tag{8}$$

where parameter θ_i is a regular parameter, also known as identity link function, and variation with the exponent i ($i = 1, 2, \dots, n$), the disturbance factor Φ is a constant.

$$\eta_i = X_i^T \beta = \sum_{j=1}^P X_{ij} \beta_j, i = 1, 2, \dots, n \tag{9}$$

For the i^{th} observation Y_i , the linear predicted value of the system part was a linear combination of the variables under the study.

$$g(\mu_i) = \eta_i = X_i^T \beta, i = 1, 2, \dots, n \tag{10}$$

where $g()$ is the connection function, which connects the expectation of the random part to the system part, $\mu_i = E(Y_i)$ was the expectation of Y_i .

According to the correlation coefficient analysis results, different combinations of explanatory variables and CHG_5 were selected for regression analysis, and based on the selection criteria of explanatory variables (Table 2), the final model was determined. The explanatory variables under the short-term effect included the initial value, the end value, the difference between the end value and the initial value of all explanatory variables. According to the nature of target variables, MAP_2 , ΔMAP , MAT_2 , ΔMAT , LSK_2 , ΔLSK , S_{Clay} and S_{Silt} were selected as alternative explanatory variables. Finally, the Co-regression model's overall goodness of fit was assessed by applying variance decomposition.

3 Results

3.1 Decomposition of grassland AGB

Regression to the mean (RtoM) may arise from measurement error or natural causes, including the long-term impact of key driving factors on AGB change (Tu et al. 2005). In this study, the two AGB variables were positively correlated (Fig. 3a), suggesting either a genuine correlation or non-identical errors in initial and final measurements. Furthermore, the effect of RtoM was evident in the change of AGB_{L1} (CHG_T), which correlates negatively with AGB_{L1} (Fig. 3b).

Due to the presence of RtoM, it was inappropriate to directly regress the change of AGB_L to its controls before the impact of AGB_{L1} had been removed. It was even challenging to discern how much of the change was influenced by relevant controls versus RtoM. To focus on the influence of control variables on AGB_L change, AGB_{L2} was regressed to AGB_{L1} . Subsequently, the predicted AGB_{L2} was subtracted from the observed AGB_2 to eliminate the effect of RtoM by removing the impact of AGB_{L1}

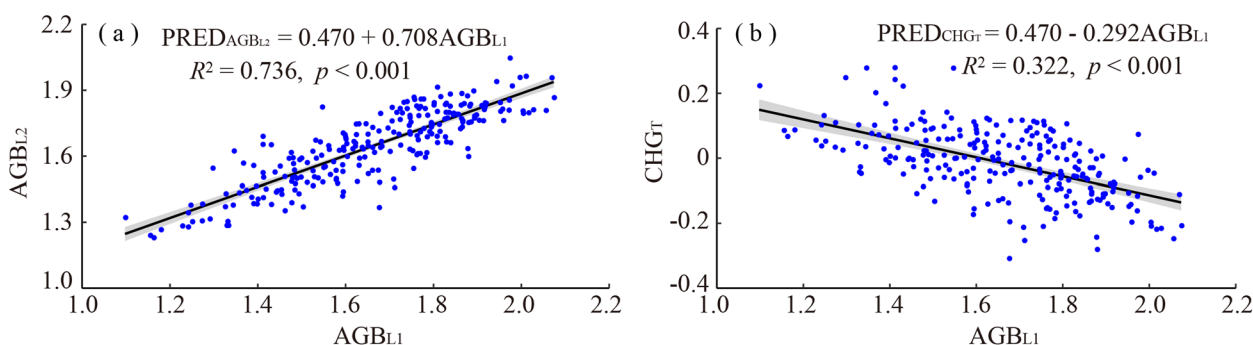


Fig. 3 The relation of AGB_{L1} and AGB_{L2} to CHG_T . (a) The relation between AGB_{L1} and AGB_{L2} ; (b) the relation between AGB_{L1} and CHG_T

from AGB_{L2} . As shown in Fig. 4d, the adjusted change (CHG_S) was almost entirely uncorrelated with AGB_{L1} , indicating successful removal of the effect of $RtoM$.

The average grassland AGB in Northern China was $50.59 \text{ g}\cdot\text{m}^{-2}$ in the 1980s and $47.33 \text{ g}\cdot\text{m}^{-2}$ in the 2000s. Spatial distribution patterns showed a consistent decline in grassland AGB from east to west during both periods (Fig. 4a, b). While the influence of initial AGB on AGB variation was mainly attributed to the long-term impact of key factors, the adjusted AGB change (Fig. 4c) was correspondingly interpreted as influenced by the short-term impact of control variables, including climate, soil texture and grazing intensity. In simpler terms, AGB change was affected by long-term controls, short-term controls, and random factors.

3.2 Separating long-term effect from short-term impact on grassland AGB

The adjusted AGB value can be regressed against various controls without the bias of initial values, as the adjusted AGB change shows minimal correlation with

the initial AGB value. In Regression 1, the adjusted AGB change, denoted as CHG_S , was derived after removing the impact of AGB_{L1} . The influence of AGB_1 on AGB_2 and subsequent AGB_L change could stem from measurement errors or natural causes, which were accounted for in CHG_S by considering the natural factors affecting AGB_{L1} 's impact on AGB_{L2} over time. CHG_S primarily reflects short-term control impacts.

Regression 2 explored the short-term effects of controls on CHG_S . Identifying these control factors posed a challenge, with temperature, precipitation, soil texture, and grazing intensity typically being primary influencers of grassland AGB. Short-term impacts on AGB_L change considered both long-term mean values and changes in relevant variables.

The combined R-square is the most effective measure to assess the Co-regression model's impact, revealing how much of AGB_{L2} 's variation (relative to its mean) is explained by the model. As the Co-regression model comprised two regressions, the combined R-square integrates two separate R-squares: the R-square of Regression

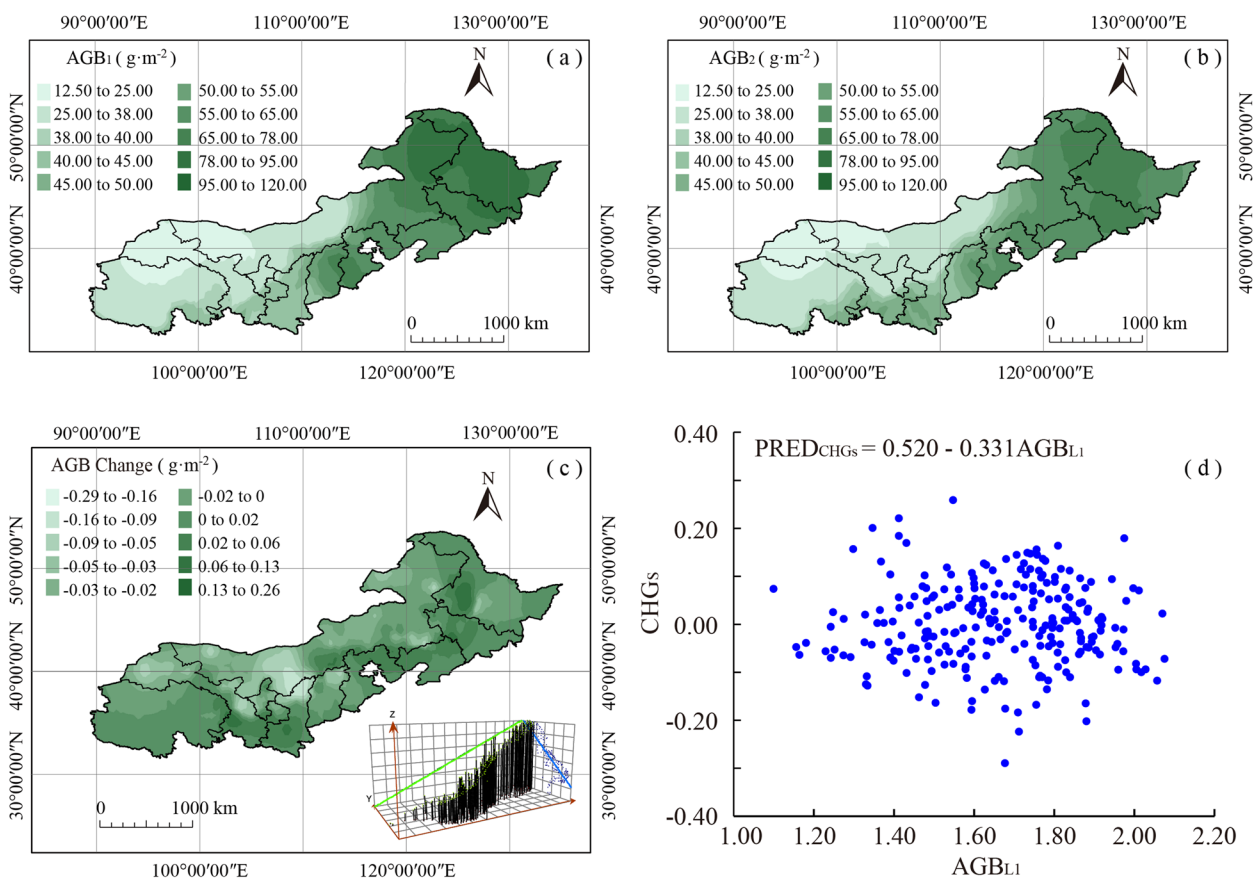


Fig. 4 Spatiotemporal trends in 1980s and 2000s, the change and relation of grassland AGB in the Northern China. **a** Trend of grassland AGB in 1980s; **b**) trend of grassland AGB in 2000s; **c**) changes of grassland AGB in the Northern China between 1980 and 2000s; **d**) the relation between AGB_{L1} and CHG_S

1 and product of the R -square of Regression 2 and $(1-R^2)$ of Regression 1. Figure 5 depicts the relationships between multiple sums of squares and R -squares. Therefore, the Co-regression model clarifies 79.5% of AGB_{L2} 's total variation. Additionally, it distinctly distinguishes between short-term and long-term control effects, with long-term impacts accounting for 73.6% of AGB_{L2} 's variation, and short-term impacts for only 5.9%.

3.3 Effects of key variables on grassland AGB

Figure 6a illustrates the relationship between grassland AGB change (CHG_S) and corresponding driving variables. During the study period, grassland AGB showed a positive correlation with mean annual temperature (Fig. 6d, e) and a negative correlation with mean annual precipitation (Fig. 6f, g). The maximum correlation coefficients were 0.17 ($p < 0.01$) and -0.29 ($p < 0.01$), respectively. The association between livestock carrying capacity (Fig. 6b, c) and grassland AGB varied over time, with correlation coefficients of -0.13 ($p < 0.05$) and -0.18 ($p < 0.01$) in the 1980s and 2000s, respectively, and an overall negative correlation (Coef. = -0.13, $p < 0.05$). Additionally, the correlation coefficient between soil clay content (Fig. 6h) and grassland AGB

was 0.01, while the correlation coefficient between soil sand content (Fig. 6i) and grassland AGB was -0.12.

The CHG_S was regressed under various combinations of these variables, and the best regression model was chosen based on three criteria: a higher R -squared value, significant t -values for each coefficient, and ecologically sensible explanations. Despite a strong correlation between MAP_1 and ΔMAP (Coef. = -0.462, $p < 0.001$), no serious issues of multicollinearity were found in the regression. Thus, both MAP_1 and ΔMAP were kept in the model due to their statistical significance. Moreover, the interactions between MAP_2 and MAT_2 were found to be insignificant. The results of the optimal regression, which aimed to reduce overfitting and improve transferability, are summarized in Table 3.

The short-term change within precipitation (ΔMAP) showed significant positive impacts on the short-term change of AGB_L , with ΔMAP (Beta = 0.232) being the most influential factors on CHG_S . Although MAT_1 is less significant ($p = 0.089$) than MAP_1 , it still contributed to the short-term variation of AGB_L . Despite its insignificance, MAT_2 was negatively correlated with CHG_S (B = -0.766), suggesting that increasing temperatures could lead to a decrease in AGB. Soil texture, specifically S_{Silt} , did not significantly influence CHG_S (Beta = -0.169). While LSK_2 was statistically insignificant in the model ($p = 0.136$), it showed a negative correlation with CHG_S (Beta = -0.143), aligning with the anticipated relationship between grazing intensity and CHG_S . Although the model's R -squared value may seem relatively low ($R^2 = 0.161$) for explaining the CHG_S variation, the Co-regression model provided a satisfactory overall explanation for the variation in AGB_{L2} .

In Regression 2, the main controls for CHG_S were ΔMAT , MAP_2 , ΔMAP , LSK_2 and S_{Clay} . The GLM was used to assign relevant importance of these controls. GLM analysis outcome is shown in Table 4.

Dependent variable was CHG_S ; $R^2 = 0.224$; Adjusted $R^2 = 0.208$; SS equaled to sum of squares (type III) / $SST \times 100\%$, which was proportion of variances explained by the variable.

The total sum of SS (0.178) for intersect and variables was less than the R -square or SSR/SST (0.224). This is because SS only reflects direct impacts of variables on the dependent variable. However, introduced into the model, they can indirectly affect the dependent variable by influencing other explanatory variables. The difference

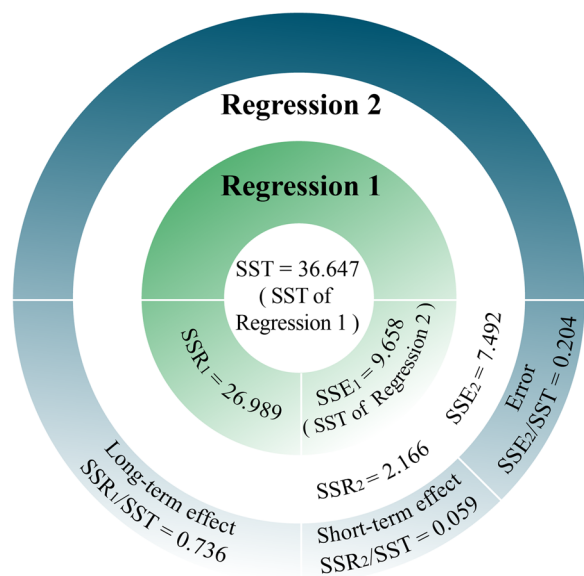


Fig. 5 The relation between multiple sums of squares and R squares. SST: sum of squares for total; SSR: sum of squares for regression; SSE: sum of squares for residual or error

(See figure on next page.)

Fig. 6 The relation between grassland AGB change and key variables. **a** Pearson correlations between grassland AGB change and the relevant variables; **(b, c)** relationship between AGB change and LSK; **(d, e)** relationship between AGB change and MAT; **(f, g)** relationship between AGB change and MAP; **(h, i)** relationship between AGB change and soil texture. The shade of the color and the size of the circle represent the strength of the correlation. * indicates the significant correlation at the 0.05 level; ** indicates the significant correlation at the 0.01 level; *** indicates the significant correlation at the 0.001 level. DSE represents Dry sheep equivalent

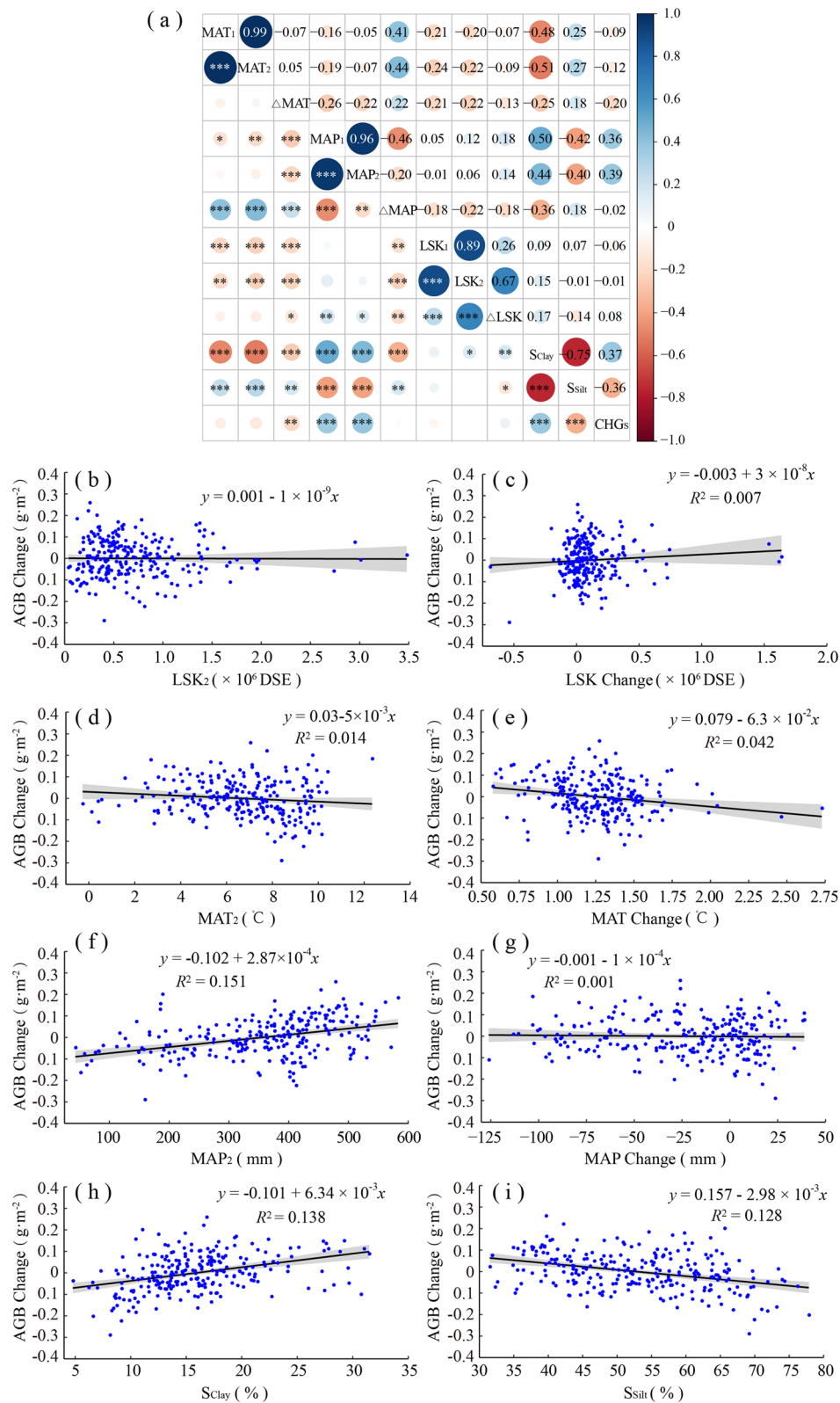


Fig. 6 (See legend on previous page.)

Table 3 The coefficients of Regression 2

| Variable | Unstandardized coefficient | Standardized coefficient | | t | P value |
|-------------------|----------------------------|--------------------------|--------|--------|---------|
| | Beta | Standard error | Beta | | |
| MAT ₁ | 0.043 | 0.025 | 0.871 | 1.709 | 0.089 |
| MAT ₂ | -0.038 | 0.026 | -0.766 | -1.453 | 0.147 |
| MAP ₁ | -0.000 | 0.000 | -0.166 | -2.195 | 0.029 |
| ΔMAP | 0.001 | 0.000 | 0.232 | 3.123 | 0.002 |
| LSK ₂ | -0.000 | 0.000 | -0.143 | -1.498 | 0.136 |
| ΔLSK | 0.000 | 0.000 | 0.020 | 0.213 | 0.831 |
| S _{Clay} | 0.002 | 0.002 | 0.090 | 0.812 | 0.418 |
| S _{Silt} | -0.002 | 0.001 | -0.169 | -1.801 | 0.073 |
| Intercept | 0.143 | 0.104 | | 1.378 | 0.170 |

Dependent variable was CHG_S; R² = 0.161

(R² - ΣSS=0.046) represents total indirect impacts of all controls on CHG_S. Notably, S_{Clay}, ΔMAP and MAP₂ were the most crucial factors, explaining 6.5%, 5.2%, and 2.6% of CHG_S variation. Short-term precipitation changes like ΔMAP directly affect grassland AGB (Welti et al. 2020), while long-term changes in precipitation patterns, including alterations in annual precipitation averages or shifts in the timing and intensity of precipitation events, also influence aboveground biomass (Dullinger et al. 2020; Feng et al. 2021). Conversely, LSK₂ had the smallest impact (0.6%). Precipitation and soil properties were identified as primary drivers of AGB dynamics, with long-term factors outweighing short-term ones and mutually reinforcing impacts.

4 Discussion

4.1 The validation and effect of Co-regression model

Oldham’s (1962) method is utilized to examine the presence and characteristics of RtoM. It asserts that if the

actual end AGB value (observed value minus measurement error) is unrelated to the true initial AGB value, and if the variances of the initial or end measured values are identical, then the change in AGB is independent of the mean of the initial and end values. The accuracy verification of the model demonstrated a strong alignment between the estimated grassland biomass data and the measured data (Fig. 7a). The target AGB variable, influenced by the long-term joint action of all explanatory variables, exhibited a stable trend of development and change. This stability resulted in a clear correlation between the observed AGB values in the 1980s and 2000s (Fig. 7b). Subsequently, a linear correlation between AGB_{L1} and AGB_{L2} was established in Regression 1, generating an exponential relationship between AGB₁ and AGB₂. The effect of RtoM was shown in Fig. 7b. Let P represent an AGB₁ value at which PRED_{AGB2} equaled AGB₁ (P=40.33). If AGB₁ < P, then PRED_{AGB2} > AGB₁, indicating a positive change in AGB; if AGB₁ > P, then PRED_{AGB2} < AGB₁, indicating a negative change in AGB.

In the Co-regression model, the temporal variation of AGB between two periods was investigated. While it wasn’t possible to generate a growth curve for each site due to the limited two-sample data for each site, spatially distributed data served as the foundation for analyzing the relationship between AGB and its controls for each specific site. Spatial differences were observed in the influence of climate drivers on the spatiotemporal dynamics of grassland AGB in the study area. For instance, AGB_{L2} on AGB_{L1} was regressed based on the data from 243 sample sites, and the resulting regression line illustrated the relationship between AGB_{L2} and AGB_{L1} for each sample site. It’s important to note that although this method adhered to statistical rules and assumptions, there was a notable issue of spatial autocorrelation specific to this study. Fortunately, this challenge could potentially be addressed by employing a multilevel model that conducts regressions based on different data

Table 4 The result of GLM analysis

| Variable | Sum of squares (type III) | Mean square | F | P value | VIF | SS (%) |
|-------------------|---------------------------|-------------|--------|---------|-------|--------|
| ΔMAT | 0.105 | 0.105 | 3.316 | 0.070 | 1.157 | 1.1 |
| MAP ₂ | 0.252 | 0.252 | 7.973 | 0.005 | 1.286 | 2.6 |
| ΔMAP | 0.500 | 0.500 | 15.823 | 0.000 | 1.216 | 5.2 |
| LSK ₂ | 0.055 | 0.055 | 1.750 | 0.187 | 1.102 | 0.6 |
| S _{Clay} | 0.630 | 0.630 | 19.914 | 0.000 | 1.392 | 6.5 |
| Intercept | 0.178 | 0.178 | 5.619 | 0.019 | | 1.8 |
| SSR | 2.166 | 0.433 | 13.704 | 0.000 | | 22.4 |
| SST | 9.658 | | | | | |
| SSE | 7.492 | 0.032 | | | | |

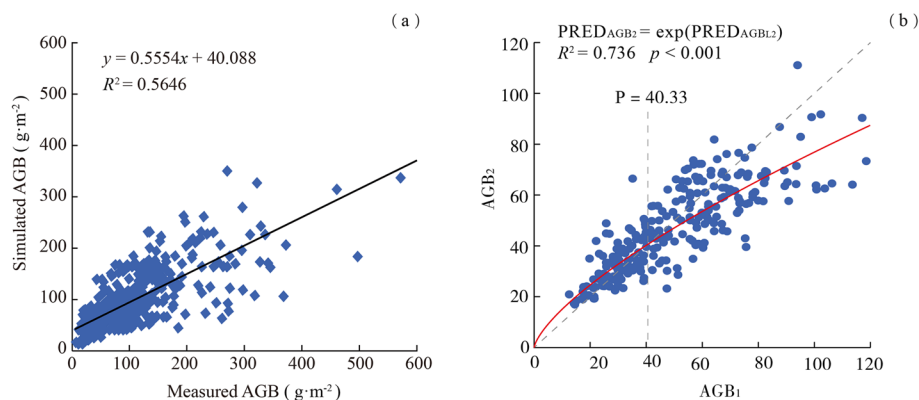


Fig. 7 The validation and relation of grassland AGB. (a) Validation of AGB estimation; (b) the relation between AGB₁ and AGB₂

groups (e.g., forming groups for sample sites with correlated data) (Ishikawa et al. 2021).

4.2 Driving factors influencing grassland AGB

Climatic changes exert a significant influence on AGB, with grassland ecosystems typically maintaining a dynamic equilibrium where vegetation growth, death, and decomposition balance to sustain a relatively stable AGB level (Shabbir et al. 2019). Ongoing climate change is a long-term trend that affects the entire productivity level of a region, with a stable baseline over a long time scale. Empirical studies highlight precipitation as the primary climatic factor affecting grassland AGB, influencing various functional and structural aspects (Ghani et al. 2022; Ghimire et al. 2019). Temperature is also crucial, shaping AGB responses and driving environmental changes like desertification (Ghimire et al. 2019). Short-term climate fluctuations disrupt ecosystem balance, notably impacting grassland AGB (Hossain et al. 2023). Disturbances such as extreme weather events (e.g., rainstorms, droughts, high temperatures) can damage grassland vegetation, reducing ecosystem productivity and lowering AGB (Hoover et al. 2014).

Strong correlations between soil parameters and grassland AGB have been consistently observed in various studies (Graham et al. 2021). This study underscores the significant impact of clay content on grassland AGB, attributed to clay's unique properties. Clay particles possess a large specific surface area and adsorption capacity, enabling them to absorb and retain water. Additionally, their negatively charged surface facilitates the absorption and retention of vital nutrients like nitrogen, phosphorus, and potassium, essential for plant growth (Munira et al. 2018). The microporous structure between clay particles enhances water retention, mitigating water loss, improving soil resilience to drought, and ensuring a steady water supply. Moreover, the adsorption and release of mineral

elements in clay are integral to soil nutrient cycling, while its microporous structure fosters an optimal habitat for microbial communities, enhancing soil biodiversity and microbial activity (Zia et al. 2021).

The concept of grazing intensity has emerged as a scientific approach for understanding grassland AGB dynamics, with increased livestock density often linked to grassland degradation (Rinot et al. 2019; Zhao et al. 2023), which is not consistent with our result. Sustained grazing pressure is a long-term effect, while year-to-year grazing fluctuations are a short-term effect. Grazing by herbivores is a significant form of land use, impacting plant diversity and ecosystem function through livestock trampling, selective foraging, and excrement deposition (Estes et al. 2011). The effects of grazing on grassland AGB can vary across different succession stages (Zhang et al. 2023a, b). Grazing typically alters plant resources availability, fostering a more diverse environment and influencing soil nutrient cycling, consequently affecting plant productivity (Eskelinen et al. 2022).

4.3 Implications and limitations

The Co-regression model offers distinct advantages in accurately capturing complex nonlinear relationships between biophysical parameters and intricate environmental factors (Scheller et al. 2005; Zeng et al. 2019). Compared to traditional statistical methods, this model proves to be an effective and robust algorithm, showcasing superior abilities in distinguishing long-term variables from short-term factors influencing grassland AGB while establishing intricate interactions with fewer parameters (Kibret et al. 2016; Lehnert et al. 2015). While the Co-regression model tended to underestimate high AGB values and overestimate low AGB values, a phenomenon likely arising from the algorithmic properties and the averaging of single-tree predictions in the Co-regression model (Zwicke et al. 2013).

Approximately 2% of extreme values in the dataset contribute to this bias towards average values. While the model simplifies complex ecosystem processes and separates interactions between main factors affecting AGB change, this may affect the accuracy of assessing real ecological status and the reliability of research results.

Grassland AGB, a vital indicator of complex ecological systems, is influenced by a blend of long-term and short-term factors, including climate change, soil parameters, and grazing intensity (Epstein et al. 1997; Peng et al. 2020). The long-term effect is a trend and the instinct, and the short-term effect reflects random fluctuations in the environment, interannual fluctuations, pulses, or extreme events, disasters, and changes in human activity caused by disasters. This study delves into effects of key driving factors on grassland AGB, distinguishing between long-term and short-term impacts, and further categorizing short-term effects into direct effects and indirect effects to understand the mechanism driving AGB changes. However, the study has certain limitations. It primarily considers temperature, precipitation and their variations, while other climatic factors, including wind direction, relative humidity, sunshine duration and other environmental conditions, are crucial for quantitative and in-depth study of grassland AGB (Gui et al. 2021; Jiang et al. 2021). The impacts of climate change on vegetation or AGB vary in different regions and time periods. Gui et al. (2023a, b) studied the effects of drought and climate change on vegetation dynamics, highlighting the time-delay and time-cumulative effects on vegetation coverage, which pose challenges for data collection and analysis.

This study further highlights that the contribution of climate to grassland AGB outweighs that of grazing in Northern China, challenging previous assumptions regarding the predominant role of human activities driving grassland AGB changes (Zhang et al. 2023a, b). Non-climatic factors may include microbial activity, soil pH, soil texture, topographic relief, and various human activities (Hu et al. 2020). Gui et al. (2023a, b) revealed that the climatic changes caused by anthropogenic emissions through aerosols and clouds affected vegetation photosynthesis and carbon flux. They advocate further consideration for impacts of climate change on atmospheric circulation and water cycle to better understand the impacts of anthropogenic emissions on terrestrial ecosystems.

5 Conclusion

This study effectively differentiated long-term and short-term impacts on grassland AGB, quantifying contributions from climatic factors, soil texture, and grazing intensity. Trends in AGB were analyzed using Co-regression and

Generalized Linear Model methods, highlighting long-term factors' predominant influence. Divergent impacts from key variables on AGB trends emerged. Soil parameters, notably clay content, explained 6.5% of AGB variation, while mean annual precipitation played a substantial role, accounting for 5.2% and 2.6% of AGB variation, respectively. Determining grazing intensity's influence on AGB change proved challenging, with only marginal contribution detected. The pivotal role of soil properties and climate change in driving grassland AGB dynamics in Northern China became evident. Co-regression significantly enhanced model performance, mitigating issues like regression to the mean. This research expands understanding of AGB dynamics, informing grassland ecosystem management and conservation efforts.

Abbreviations

| | |
|------|---------------------------|
| AGB | Aboveground biomass |
| GLM | Generalized Linear Model |
| RtoM | Regression to the mean |
| SOC | Soil organic carbon |
| MC | Mathematical coupling |
| MAT | Mean annual temperature |
| MAP | Mean annual precipitation |
| LSK | Livestock |
| SS | Sum of squares |

Authors' contributions

All authors contributed to the study conception and design. Resources and supervision were performed by Wenneng Zhou & Xiaoping Xin. Material preparation, data collection and analysis were performed by Xiaoyu Zhu, Yifei Qin, Yutong Li, Changling Shao & Ruirui Yan. Software and validation were performed by Yi An & Dawei Xu. The first draft of the manuscript was written by Xiaoyu Zhu and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

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

Declarations

Competing interests

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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