Both biotic and abiotic management strategies facilitate biomass recovery and CO_2 absorption: evidence from three experiments in southern grasslands

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Abstract

Background

The southern grasslands of China sustain substantial livestock but face functional degradation due to overuse. The carbon flux responses to restoration strategies remain unclear.

Methods

In this study, we implemented a three-year restoration experiment in artificial grasslands using three approaches: reseeding (D: *Dactylis glomerata* monoculture, T: *Trifolium repens* monoculture, DT: their mixture), chemical fertilization ($NP_L/NP_M/NP_H$: nitrogen 2/4/8 g m^{-2} + phosphorus 0.7/1.4/2.8 g m^{-2}), and biofertilization with *Burkholderia* sp.($B_{30}/B_{60}/B_{120}$: 30/60/120 g m^{-2}).

Results

All treatments increased grassland biomass. Specifically, NP_H significantly enhanced above-ground biomass, while D, B_{30}, and NP_L notably boosted below-ground biomass. D, NP_L, NP_H, and B_{30} significantly increased total biomass. Restoration treatments usually had a negative effect on NEE, with DT (β = -0.383, P = 0.020), NP_L (β = -0.350, P = 0.027), NP_M (β = -0.422, P = 0.008), and B_{60} (β = -0.341, P = 0.029) showing significant effects. However, they exhibited positive effects on both ER and GPP. Specifically, NP_L, NP_M, NP_H, B_{30}, B_{60}, and B_{120} significantly enhanced ER (β = 0.290 to 0.525, P = 0.001 to 0.049), while all measures except T significantly increased GPP (β = 0.297 to 0.613, P < 0.001 to 0.048). Dissolved organic carbon, available phosphorus, and biomass contributed to the changes in carbon sequestration.

Conclusion

Our results demonstrate that both traditional fertilization and alternative strategies like reseeding and biofertilization can effectively restore grassland productivity and carbon sequestration capacity, providing multiple pathways for sustainable grassland management.

1. Introduction

Grasslands cover approximately 40% of terrestrial ecosystems and are critical for human life (Buisson et al., 2022). They also store one-third of the global terrestrial carbon reserves, playing an important role in mitigating climate change (Bai and Cotrufo, 2022). However, about half of the world's grasslands have begun to deteriorate to varying degrees (Bardgett et al., 2021). Moreover, grassland degradation greatly accelerates soil CO_2 emissions and thus diminishes the contribution of grasslands to the carbon sink (Li et al., 2015; Abdalla et al., 2018; Xu et al., 2022). Therefore, it is important to explore the dynamics of CO_2

flux under various grassland restoration strategies such as reseeding, chemical and biological fertilization, which help to understand the function of ecosystem carbon sink in grasslands.

Reseeding is one of simple and feasible grassland restoration techniques (Mi et al., 2024), which improves grassland community productivity by seeding forage seeds directly on degraded grasslands (Li et al., 2017). On the one hand, reseeding can increase vegetation coverage, biomass, and the proportion of high-quality forage in degraded grasslands (Yang et al., 2018). On the other hand, tillage-based reseeding can also enhance the nutritional content of degraded grasslands (e.g., soil carbon) (Ji et al., 2022; Zhang et al., 2022). Different seed selections have various effects on the grassland yield, with grass-legume mixtures often producing higher productivity compared to monocultures (Finn et al., 2013). Therefore, reseeding restoration of degraded grasslands may enhance their contribution to carbon sinks. However, research on the relationship between reseeding restoration and CO_2 fluxes in degraded grassland is still limited.

Fertilization is one of the effective methods to promote grassland restoration, which has an impact on severely degraded grasslands in the short term (Dong et al., 2020). Fertilization can significantly enhance biomass and soil nutrients in degraded grasslands (Li et al., 2023). Numerous studies have shown that nitrogen (N) addition can significantly enhance CO_2 absorption in grassland systems (Wu et al., 2021; Shi et al., 2022; Chen et al., 2023; Du et al., 2024; Wen et al., 2024). Phosphorus (P) is also a common limiting factor in soils (Elser et al., 2007; Fay et al., 2015), and combined nitrogen-phosphorus application typically had better restoration effects than added either nutrient alone (Wang et al., 2020). For example, NP addition experiments in temperate ecosystems suggested that NP addition increased biomass of rootlets and reduced heterotrophic respiration, thereby enhanced ecosystem carbon sequestration (Zeng and Wang, 2015). However, in grassland ecosystems, studies on fertilization and ecosystem carbon fluxes had mainly focused on nitrogen addition under the background of nitrogen deposition. Thus, it is important to explore the impact of combined nitrogen-phosphorus fertilization on carbon fluxes during grassland restoration.

It is well known that *Burkholderia* sp. has positive effects on plant growth and tolerance (Pal et al., 2022). For example, inoculation with *Burkholderia* promoted the secretion of indole-3acetic acid (IAA) and 1-aminocyclopropane-1-carboxylate (ACC) in soybeans (*Glycine max*) and thus enhanced plant growth (Ratnaningsih et al., 2023); *Burkholderia* could trigger plants defense mechanisms, protecting them from pathogens (Kong et al., 2022); *Burkholderia* could also enhance the solubility of potassium and phosphorus, improving phosphorus availability (Peix et al., 2001; Baghel et al., 2020). Additionally, *Burkholderia* is a nitrogen-fixing bacterium that improves nitrogen uptake and utilization by plants (Reis et al., 2004). Furthermore, *Burkholderia* can degrade various pollutants and promote plant ACC production to enhance stress resistance (Lu et al., 2012; Chen et al., 2017). Therefore, *Burkholderia* has potential for restoring degraded grasslands and influencing carbon fluxes in such ecosystems.

Although southern grasslands only account for 20% of the total grassland area in China (Fang et al., 2018), their adequate hydrothermal conditions and strong pasture regeneration ability (Teng et al., 2008), allowed these grasslands and related agricultural products to support nearly half of the China's livestock (Huangfu et al., 2012). However, over 70% of China's grasslands have already been experiencing degradation (Pan et al., 2023), which also severely affected the country's grassland carbon sink. In addition, previous research on grassland restoration focused primarily on typical grasslands in northern China, how about the restoration effect on southern grasslands is still less understood.

To fill the gap, we conducted the field experiments in the typical southern grasslands, Yunnan Province (Fang et al., 2018) and faces grassland degradation and soil erosion due to overgrazing (Deng, 2023). Therefore, we carried out a 3-year grassland restoration experiments by reseeding, inputting nitrogen-phosphorus chemical fertilization and adding biological organic fertilization with *Burkholderia* sp. We monitored grassland biomass, carbon effluxes, and their driving factors in order to answer the following hypotheses: (1) If management practices can promote plant growth, reseeding, fertilization, and addition *Burkholderia* sp. will enhance carbon sequestration. (2) Grassland degradation in southern regions is often driven by overgrazing, which leads to reduced community productivity and nutrient losses (Wang et al., 2015). Therefore, we hypothesize that soil nutrients after management practices, particularly soil phosphorus will be more important for improving grassland function.

2. Materials and methods

2.1. Site description and Experimental design

The experiments were established in September 2020 at the Field Grassland Experiment Platform in Maolin Town, Zhaotong City, Yunnan Province (27°66' N, 103°63' E). The area is characterized by a plateau monsoon climate, where warm temperate and subtropical conditions coexist. The annual average temperature is 12.6°C, and the average precipitation is 760 mm. The region experiences frequent rain, snow, and fog throughout the year. The dominant species are *Dactylis glomerata*, *Lolium perenne* and *Trifolium repens*.

The experiment was conducted from April 2021 to September 2023. Based on local vegetation surveys, *Trifolium repens* and *Dactylis glomerata* were selected as the reseeding species. The reseeding treatments included CK (no reseeding) and a seeding rate of 22.50 kg hm^{-2}, with three different species combinations: D (monoculture of *Dactylis glomerata*), T (monoculture of *Trifolium repens*), and DT (mixed *Trifolium repens* and *Dactylis glomerata* at 2:3). Five replicates were set for each treatment, resulting in 20 plots in total. The seeds are sown in April each year for a total of three times. To minimize soil disturbance, no tillage reseeding was used.

The fertilization treatments included CK (no fertilization) and three levels of nitrogen and phosphorus fertilization: NP_L (2 g m^{-2} $year^{-1}$ nitrogen + 0.7 g m^{-2} $year^{-1}$ phosphorus), NP_M (4 g m^{-2} $year^{-1}$ nitrogen + 1.4 g m^{-2} $year^{-1}$ phosphorus), and NP_H (8 g m^{-2} $year^{-1}$ nitrogen + 2.8 g m^{-2} $year^{-1}$ phosphorus). The nitrogen fertilizer used was [$CO(NH_2)_2$] and the phosphorus fertilizer was [$Ca(H_2PO_4)_2 \cdot H_2O$]. Five replicates were set for each treatment.

The *Burkholderia* sp. treatments included three application levels: B_{30} (30 g m^{-2} $year^{-1}$), B_{60} (60 g m^{-2} $year^{-1}$), and B_{120} (120 g m^{-2} $year^{-1}$). The same CK were used for fertilization treatment. Five replicates were set for each treatment, resulting in 35 plots both *Burkholderia* sp. treatments and fertilization treatments. Each plot was 3 m × 3 m, with a 1 m buffer zone among them. Fertilization and *Burkholderia* sp. application were carried out in April and October each year, with a total of five times.

2.2. Measurement of ecosystem CO_2 flux, soil temperature, and soil moisture

We measured soil carbon flux data during the growing season (April to September) from June 2021 to September 2023. Measurements were taken between 9:00 AM and 12:00 AM on clear days. Using a transparent assimilation tank (a cylinder with a base diameter of 20cm and a height of 25 cm made of plexiglass.) connected to the Li-8100a Automated Soil CO_2 Flux System monitored net ecosystem exchange of CO_2 (NEE) and ecosystem respiration (ER), and each measurement lasted 90 seconds (Due to COVID-19 restrictions in September 2022 and rainy weather during fertilization treatment in August 2023, data for these months were missed). After measuring NEE, the system was ventilated and purged for 30 seconds, and then blackout treatment was performed to measure ER (Niu et al., 2008). Gross primary productivity (GPP) was calculated using the formula GPP = ER - NEE (Ma et al., 2021). During CO_2 flux measurements, soil temperature (ST) and soil water content (SWC) were measured from 0–10 cm using the soil temperature and soil water content probes included with the Li8100a (SWC data for April 2022 and ST data for July 2023 were missing because the probes were damaged).

2.3. Sampling and measurement of grassland biomass and physicochemical properties

In October 2022, above-ground biomass (AGB) and below-ground biomass (BGB) were collected from each plot. Three 20 cm × 20 cm subplots were randomly selected from each plot. The above-ground parts of all plants were collected using scissors and dried to a constant weight to determine AGB. Below-ground parts were collected using a 6 cm diameter soil auger with five sampling points at a depth of 0–20 cm. Roots were separated from the soil. Then they were cleaned and dried to a constant weight to determine BGB. Total biomass (TB) was sum of AGB and BGB. After separating the roots and rocks, soil samples were divided into two portions. One portion was analyzed using Cleverchem380 (DeChem-Tech GmbH, Hamburg, Germany) to measure ammonium nitrogen (NH_4^+-N) by Sodium Salicylate Method, nitrate nitrogen (NO_3^--N) by Copper-zinc hydrazine reduction method, and available phosphorus (AP) by Olsen method, while another portion was analyzed with vario TOC cube (Elementar Analysensysteme GmbH, Langenselbold, Germany) to determine dissolved organic carbon (DOC) by high temperature catalytic combustion method, microbial biomass carbon (MBC) by fumigation method, and soil organic carbon (SOC) by dry combustion. All the above soil analysis methods were used from Liu (1996).

Data were organized and Z-score transformations were performed using Microsoft Office Excel 2010. Statistical analysis and graphical visualizations were conducted using R 4.3.3. The effects of treatments on CO_2 flux, grassland biomass, and soil physicochemical properties were analyzed using the lme4 package. Fixed effects included D, T, DT, B_{30}, B_{60}, B_{120}, NP_L, NP_M, and NP_H, while random effects were block and sampling time (for grassland biomass and soil physicochemical properties, only block was treated as a random effect). A linear regression analysis was used to examine the relationship between carbon flux and soil physicochemical properties and biomass.

3. Results

3.1. Responses of plant biomass and soil physicochemical properties

Reseeding treatments had non-significant effect on AGB (Fig. 1a), but D had a significant positive effect on both BGB (β = 1.381, P = 0.033) and TB (β = 1.404, P = 0.027) (Fig. 1b and 1c). Except for NP_M, fertilization treatments had a positive effect on AGB, among which NP_H (β = 1.387, P = 0.023) showing significant positive effects (Fig. 1d). Additionally, NP_L (β = 1.398 P = 0.025) and NP_M (β = 1.305, P = 0.035) had a significant positive effect on BGB (Fig. 1e), while NP_L (β = 1.362 P = 0.029) and NP_H (β = 1.354 P = 0.030) significantly increased TB (Fig. 1f). *Burkholderia* sp. treatments showed no significant effect on AGB (Fig. 1g), but B_{60} had a significant positive impact on both BGB (β = 1.519 P = 0.018) and TB (β = 1.430 P = 0.027) (Fig. 1h and 1i).

Reseeding treatment showed a positive effect on DOC, with D (β = 1.665 P = 0.008) exhibiting a significant influence (Fig. 2a). In the fertilization treatment, NP_H (β = 1.445 P = 0.006) had a significant positive effect on NO_3^--N (Fig. 2b). All fertilization levels significantly increased AP (β = 1.440 to 1.692, P = 0.001 to P = 0.004) (Fig. 2c). However, grassland management strategies had no significant effect on other soil physical and chemical properties (Fig. S2, S3 and S4).

3.2. Responses of NEE, ER, and GPP to experimental treatments

Reseeding treatments had a negative effect on NEE, and the grass-legume mixture showed a significant negative effect (β = -0.383, P = 0.020) (Fig. 3a). Reseeding treatments had non-significant effect on ER (Fig. 3b). Reseeding treatments positively influenced GPP, where D (β = 0.345, P = 0.037) and DT (β = 0.414, P = 0.015) showed significant effects (Fig. 3c). Fertilization treatments had a negative effect on NEE, among which NP_L (β = -0.350, P = 0.027) and NP_M (β = -0.422, P = 0.008) showing significant negative effects (Fig. 3d). All levels of fertilization treatments significantly affected ER (β = 0.425 to 0.502, P = 0.005 to P = 0.015) and GPP (β = 0.418 to 0.613, P < 0.001 to P = 0.014) (Fig. 3e and Fig. 3f). *Burkholderia* sp. treatments had a positive effect on NEE under B_{120}, but B_{30} and B_{60} showed negative effects, of which B_{60} (β = -0.341, $P = 0.029$) being significant (Fig. 3g). *Burkholderia* sp. treatments had positive effects on ER (β = 0.290 to 0.525, $P = 0.001$ to $P = 0.049$) and GPP (β = 0.297 to 0.556, $P = 0.001$ to $P = 0.048$) (Fig. 3h and Fig. 3i).

3.3. Relationships between soil physicochemical properties, biomass and CO_2 fluxes

GPP was positively correlated with DOC under reseeding (Fig. 4a). Under fertilization, GPP was positively correlated with AP (Fig. 4b). No significant correlations were observed between other physicochemical properties and CO_2 fluxes (Fig. S9).

Under reseeding treatments, TB showed a negative relationship with NEE (Fig. 5a), but the relationships between AGB and BGB with NEE were not significant (Fig. S10). BGB and TB were positively correlated with GPP (Fig. 5b and 5c), and no significant relationships were observed between ER and AGB, BGB, or TB (Fig. S10). Under fertilization treatments, NEE was negatively related with TB (Fig. 5d), while its relationship with AGB and BGB was not significant (Fig. S11). ER was positively correlated with BGB (Fig. 5e), with no significant correlations observed between ER and BGB or TB (Fig. S11). BGB and TB were positively correlated with GPP (Fig. 5f and 5g). Under *Burkholderia* sp. additions, the effects of AGB, BGB, and TB on NEE and ER could not be determined (Fig. S12). However, BGB and TB were positively correlated with GPP (Fig. 5h and 5i).

4. Discussion

4.1 Effects of different managements on soil properties and grassland biomass

Our results showed that reseeding improved the AGB, BGB, and TB of degraded grasslands, and D improved the BGB and TB significantly (Fig. 1). This effect may be due to reseeding increasing the number of viable seeds in the soil seed bank, thereby enhancing grassland productivity (Li et al., 2017). Similar findings have been observed in northern grasslands, including the Loess Plateau (Liu et al., 2023c), Mongolian Plateau (Zhang et al., 2024), and Qinghai-Tibet Plateau (Li et al., 2024). However, unlike previous studies (Yan et al., 2022), our results indicated that the biomass-promoting effect of grass-legume mixtures (DT) is weaker than that of D. This may be because, in DT, *Dactylis glomerata* allocates part of its nutrients to counteract the allelopathic effects of *Trifolium repens* (Zhang et al., 2020), thereby reducing its biomass accumulation.

In addition, our data showed that fertilization significantly increased grassland biomass (Fig. 1), similarly with results from the Mongolian Plateau's typical steppes and the alpine meadows of the Qinghai-Tibet Plateau (Xu et al., 2015; Xiao et al., 2020). Fertilization usually enhanced soil nutrient levels and promoted the recovery of grassland productivity (Zong and Shi, 2019). Furthermore, similar to pot experiment results (da Costa et al., 2020), our study found that adding B_{60} significantly increased BGB and TB (Fig. 1i). However, addition of *Burkholderia* sp. had a significant impact on AGB (Fig. 1g). On the one hand, *Burkholderia* sp. can promote plant growth by fixing nitrogen and resolving phosphorus. On the other hand, *Burkholderia* sp. can produce auxin to stimulate plant root growth (Zhang et al., 2021), so that grass biomass can be transferred to the ground.

Combining the three management methods, we found that all the methods had a positive effect on the TB of degraded southern grasslands, which supported our hypothesis 1. However, only the NP_H treatment significantly increased AGB (Fig. 1), while the other treatments increased TB primarily by enhancing BGB (Fig. 1). The intense grazing pressure in southern grasslands in China leads to the loss of viable grass seeds and the decline in soil nutrients. Plants general allocate more biomass to BGB, thus promoting plant access to soil nutrients (Hermans et al., 2006; Freschet et al., 2018).

The analysis of soil properties in our experiment showed that reseeding increased DOC (Fig. 2a), which was different from the findings from the Qinghai-Tibet Plateau (Wang et al., 2020), our results suggest that reseeding increased the active seed, which enhanced grass biomass and subsequently contributed to greater inputs of plant residues and rhizospheric carbon. Furthermore, consistent with previous studies (Xiao et al., 2021; Liu et al., 2023a), we found that fertilization had a significant positive effect on NO_3^--N and AP (Fig. 2c and 2d). However, AP levels were generally low across all treatments (5.82 mg kg^{-1} to 12.98 mg kg^{-1}) (Fig. S6, S7, and S8). This suggests that AP deficiency may be a key factor coursing the southern grassland degradation. For example, our reseeding treatments seem to cause AP depletion (Fig. S6)

4.2 Effects of different managements on carbon fluxes and potential drivers

We found that all treatments had a positive effect on GPP in the grassland, while all except B_{120} had a negative effect on NEE (Fig. 3). This result contradicted the hypothesis 1. Specifically, under reseeding treatment, our results showed that the grass-legume mixed reseeding had a significant positive effect on GPP (Fig. 3c) and a significant negative effect on NEE (Fig. 3a). The result was similar to the studies conducted in the eastern Pyrenees, because reseeding can restore biomass and promote carbon sequestration (Drewer et al., 2017; Ibañez et al., 2021). Additionally, studies on the Qinghai - Tibet Plateau have shown that NP fertilizer co-application significantly reduced NEE by 75.7% and increased GPP by 41.4% (Li et al., 2024). And the research on Inner Mongolia grasslands has revealed that fertilization significantly increases GPP and ER in the first two years, while significantly decreasing NEE (Niu et al., 2010). These findings are consistent with our results, indicating fertilization had a significant positive effect on both ER and GPP (Fig. 3e and 3f) and a significant negative effect on NEE (Fig. 3d). The reason should be that fertilization promoted the growth of grassland and microbial activity as shown in our results and other studies (Chu et al., 2007; Zhang et al., 2024). The addition of *Burkholderia* sp. had a significant positive effect on ER and GPP (Fig. 3h and 3i). B_{60} and B_{30} showed a negative effect on NEE, and B_{60} had a significant effect (Fig. 3g). This suggests that *Burkholderia* sp. promoted CO_2 uptake by plants but also promoted CO_2 emissions through its own respiration, leading to a positive effect on

ER. We proposed that at 30 g m^{-2} $year^{-1}$, the enhancement of CO_2 absorption by the ecosystem is limited, while at 60 g m^{-2} $year^{-1}$, it is most effective. However, at 120 g m^{-2} $year^{-1}$, the respiration of *Burkholderia* sp. covered the CO_2 absorption by plants, indicating that only lower application levels can improve degraded grasslands carbon sinks.

Regression analysis results showed that different experimental measures influence CO_2 flux through both biotic and abiotic factors. Under reseeding treatments, DOC was significantly positively correlated with GPP (Fig. 4a). The growth of reseeding plants resulted in an increase in root exudates and litter, which promoted the increase of DOC (Wu et al., 2013). These carbon inputs may change soil biotic and abiotic factors, leading to an increase in subsequent photosynthetic rates (van der Putten et al., 2013; Liu et al., 2023b), thereby enhancing GPP. Our results were similar to the previous studies (Shi et al., 2021), showing that AP was significantly positively correlated with GPP (Fig. 4b). Phosphorus deficiency can disrupt the balance between the carboxylation capacity of leaves and the electron transport capacity supporting ribulose-1, 5-bisphosphate regeneration, thereby reducing photosynthesis (Ellsworth et al., 2022).

Our results showed strong relationships between biomass and GPP, ER and NEE (Fig. 5), which were similar to previous studies (Wu et al., 2015; Oliver et al., 2019; Wang et al., 2021). Increased biomass is thought to improve GPP by increasing the leaf area index, which improves the plant's ability to capture light (Chu et al., 2019). However, unlike our results, GPP was significantly positively correlated with BGB and TB under all grassland restoration measures (Fig. 5), but not with AGB. This may be due to sampling at the end of the growing season, when plants transferred more biomass to the belowground (Garten et al., 2011). Additionally, our results showed that ER was significantly positively correlated with BGB only under fertilization treatments (Fig. 5e). This is because nitrogen application not only negatively affects microbial abundance and composition, thereby reducing soil microbial respiration (Zhang et al., 2018), but also promotes root growth, which enhances autotrophic respiration (Gough and Seiler, 2004). Consequently, this strengthens the correlation between BGB and ER. Therefore, plant factors contributed more to ER under fertilization, but *Burkholderia* sp. addition likely affected soil microorganisms, masking the plant's contribution to ER. Furthermore, NEE was significantly negatively correlated with TB under both reseeding and fertilization treatments (Fig. 5a and 5d), indicating that reseeding and fertilization increased the carbon sink of degraded grasslands by increasing plant biomass.

5. Conclusion

This study showed the effects of reseeding, fertilization, and the addition *Burkholderia sp.* on biomass production, soil nutrients, and carbon fluxes in southern grasslands. All management strategies increased total biomass and gross primary productivity, but they had different effects on biomass allocation, soil nutrients, and carbon sequestration. The addition of *Burkholderia sp.* had the strongest positive effect on below-ground biomass and total biomass, but excessive addition increased microbial respiration, thereby reducing carbon sequestration. Our study showed that phosphorus deficiency was the key factor of grassland degradation in southern China, so phosphorus fertilization had the strongest promotion effect on above-ground biomass and carbon sequestration. Reseeding increased biomass, dissolved organic carbon, and carbon sequestration, but it also exacerbated phosphorus limitation, which could lead to further grassland degradation with long-term use. Overall, future grassland managements should synthetically consider these strategies to enhance soil nutrients, increase biomass, and strengthen the carbon sink capacity in southern grasslands.

Declarations

Fundding

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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.

Authorship contribution

Xinghong Wang: Writing– review & editing. Meiyan Zhang: Writing– review & editing. Yun Liu: Writing– review & editing. Juan Zhou: Writing– review & editing. Meng Xia: Writing – review & editing. Sicheng Li: Writing – review & editing, Investigation. Haibian Xu: Writing – review & editing, Data curation. Yan Li: Writing – review & editing, Investigation, Data curation. Yi Xiong: Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation. Jinghang Xu: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. Janping Wu: Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization.

Data Availability

The datasets generated by the current study are available from the corresponding author on reasonable request.

Declaration of generative AI and AI-assisted technologies in the writing process.

Statement: During the preparation of this work the authors used ChaGPT 4 in order to improve the readability and language. After using this tool, the authors reviewed and edited the content as needed and takes full responsibility for the content of the published article.

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Figures

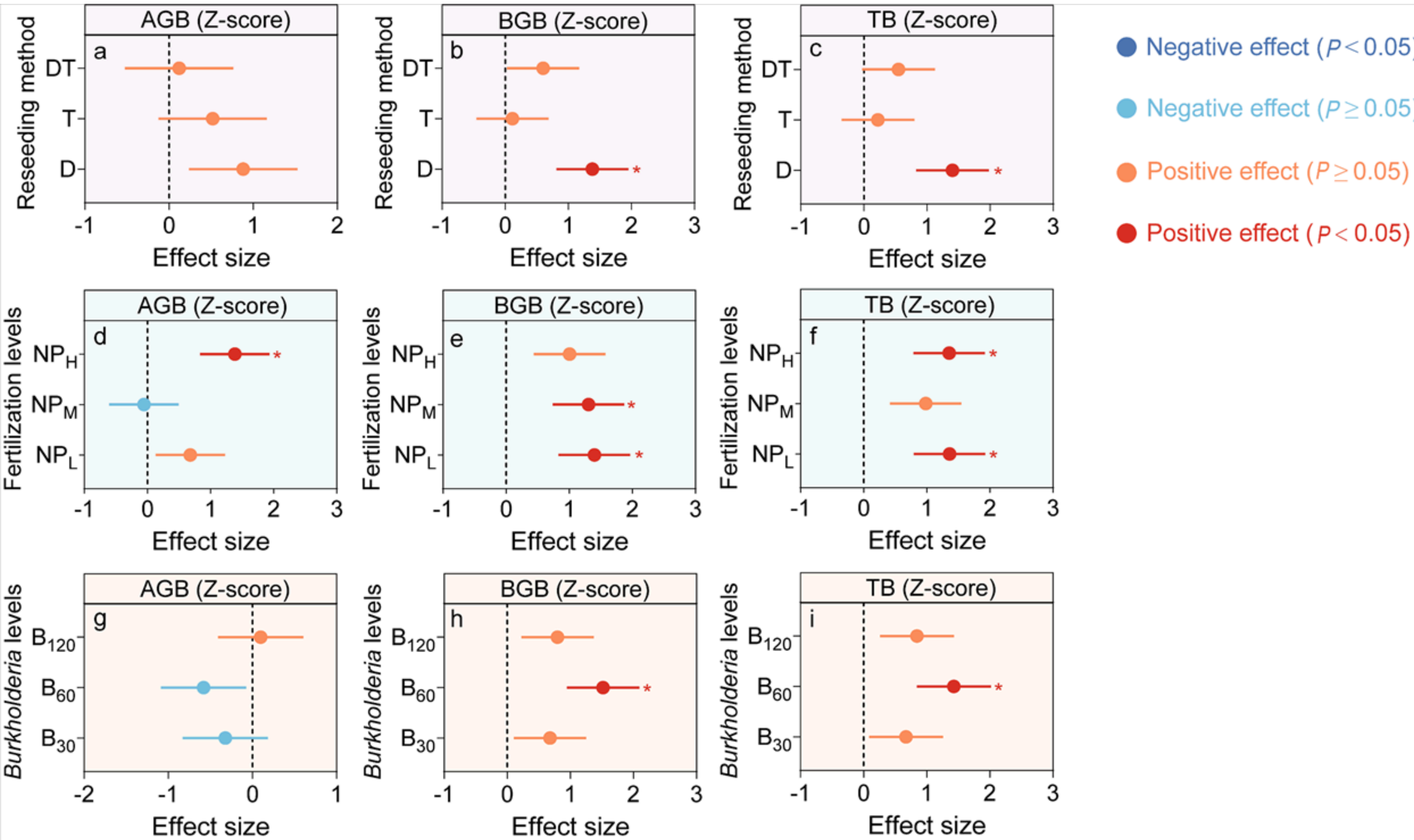

Figure 1

Effects of experimental treatments on Z-Score transformed AGB, BGB, and TB. a, AGB under reseeding; b, BGB under reseeding; c, TB under reseeding; d, AGB under fertilization; e, BGB under fertilization; f, TB under fertilization; g, AGB under *Burkholderia* sp. addition; h, BGB under *Burkholderia* sp. addition; i, TB under *Burkholderia* sp. addition. Linear mixed-effects models were applied to calculate the estimated effect size. Wald type II χ2 tests are applied to determine statistical significance. The estimated effect sizes are represented as mean values ± standard errors. Significant effects are denoted by asterisks: * $P < 0.05$.

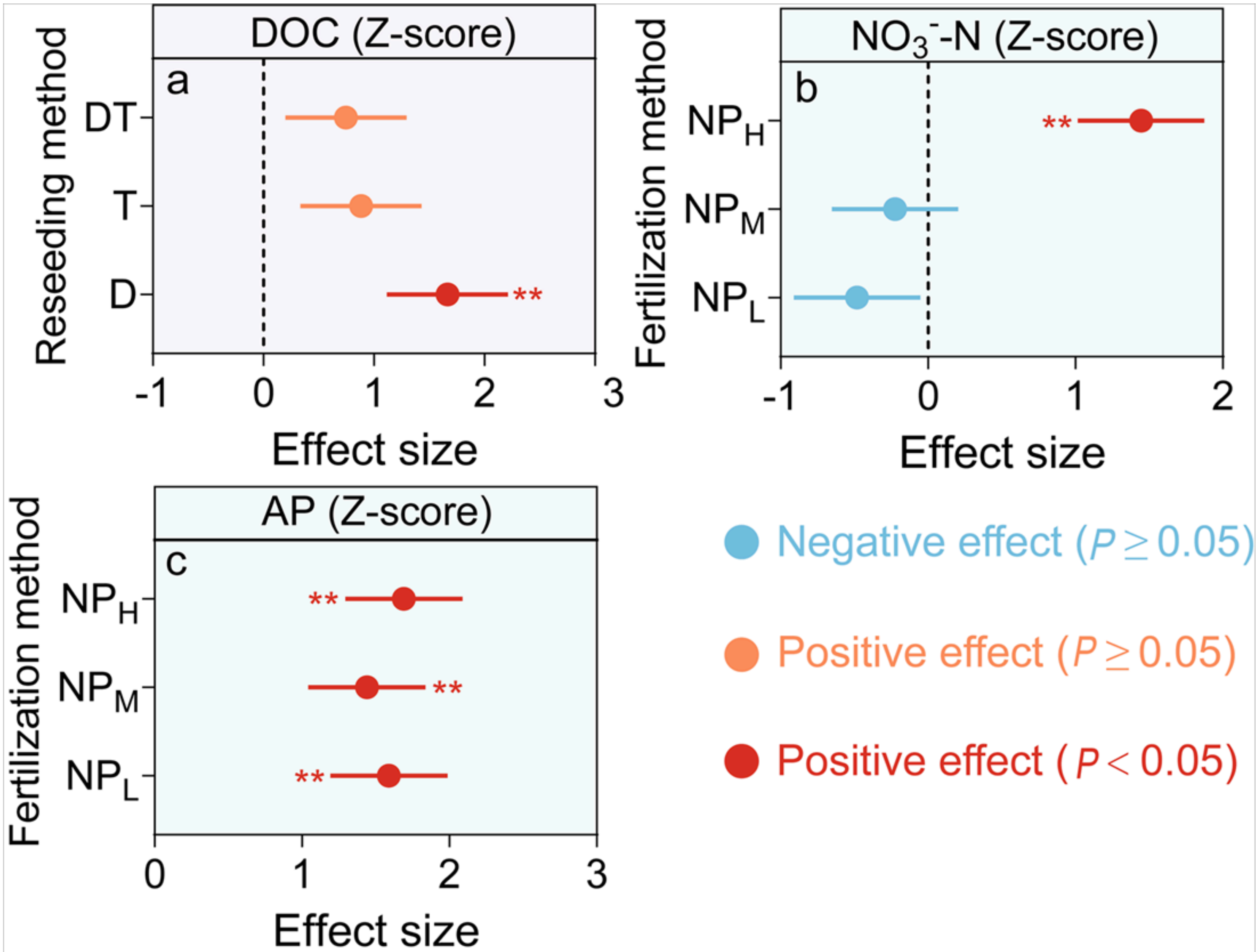

Figure 2

Effects of experimental treatments on Z-Score transformed Soil physicochemical. a, DOC under reseeding b, NO_3^--N under fertilization; c, AP under fertilization. Linear mixed-effects models were applied to calculate the estimated effect size. Wald type II χ2 tests are applied to determine statistical significance. The estimated effect sizes are represented as mean values ± standard errors. Significant effects are denoted by asterisks: * $P < 0.05$, ** $P < 0.01$.

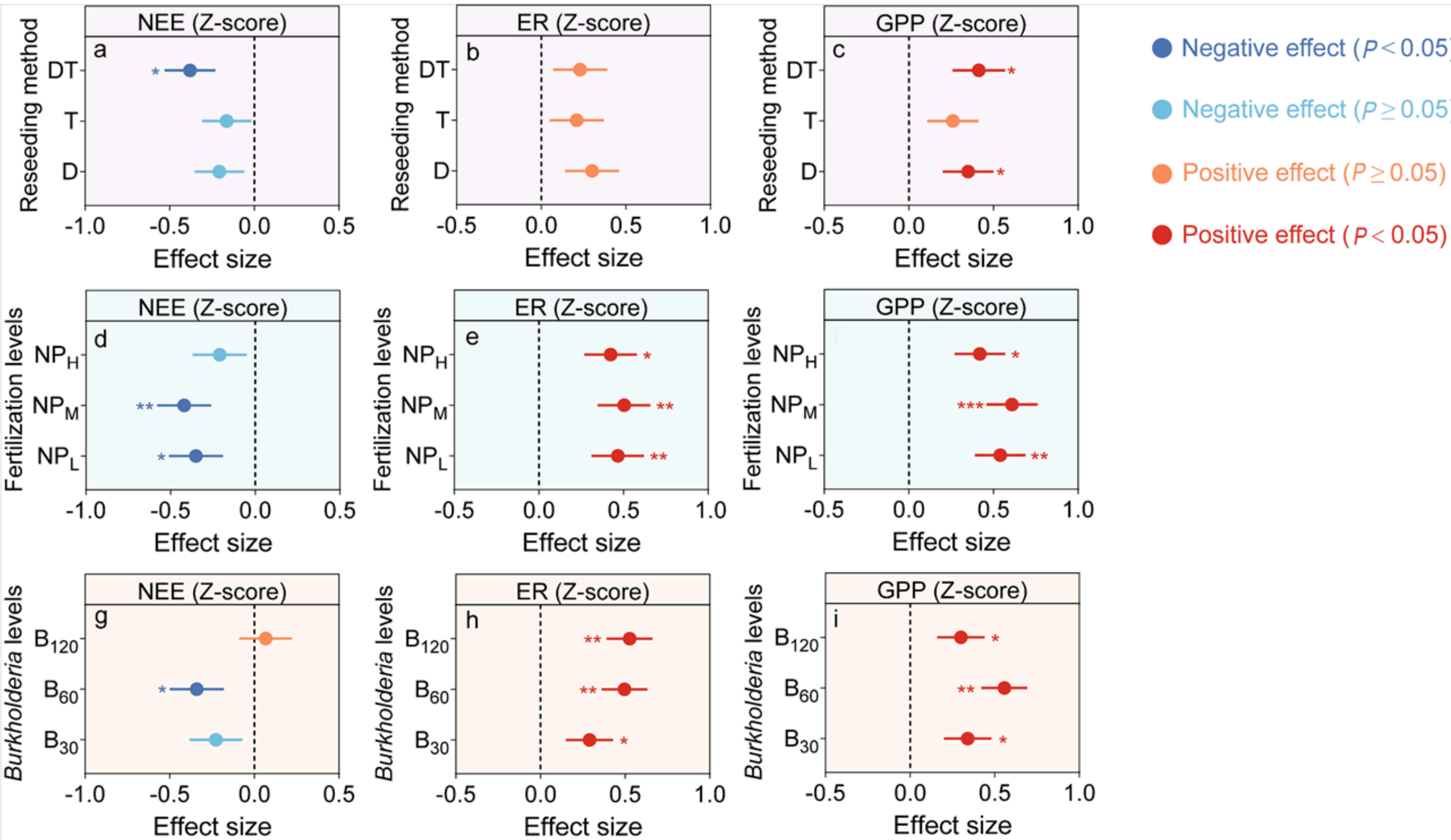

Figure 3

Effects of experimental treatments on Z-Score transformed NEE, ER, and GPP. a, NEE under reseeding; b, ER under reseeding; c, GPP under reseeding; d, NEE under fertilization; e, ER under fertilization; f, GPP under fertilization; g, NEE under *Burkholderia* sp. addition; h, ER under *Burkholderia* sp. addition; i, GPP under *Burkholderia* sp. addition. Linear mixed-effects models were applied to calculate the estimated effect size. Wald type II χ2 tests are applied to determine statistical significance. The estimated effect sizes are represented as mean values ± standard errors. Significant effects are denoted by asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

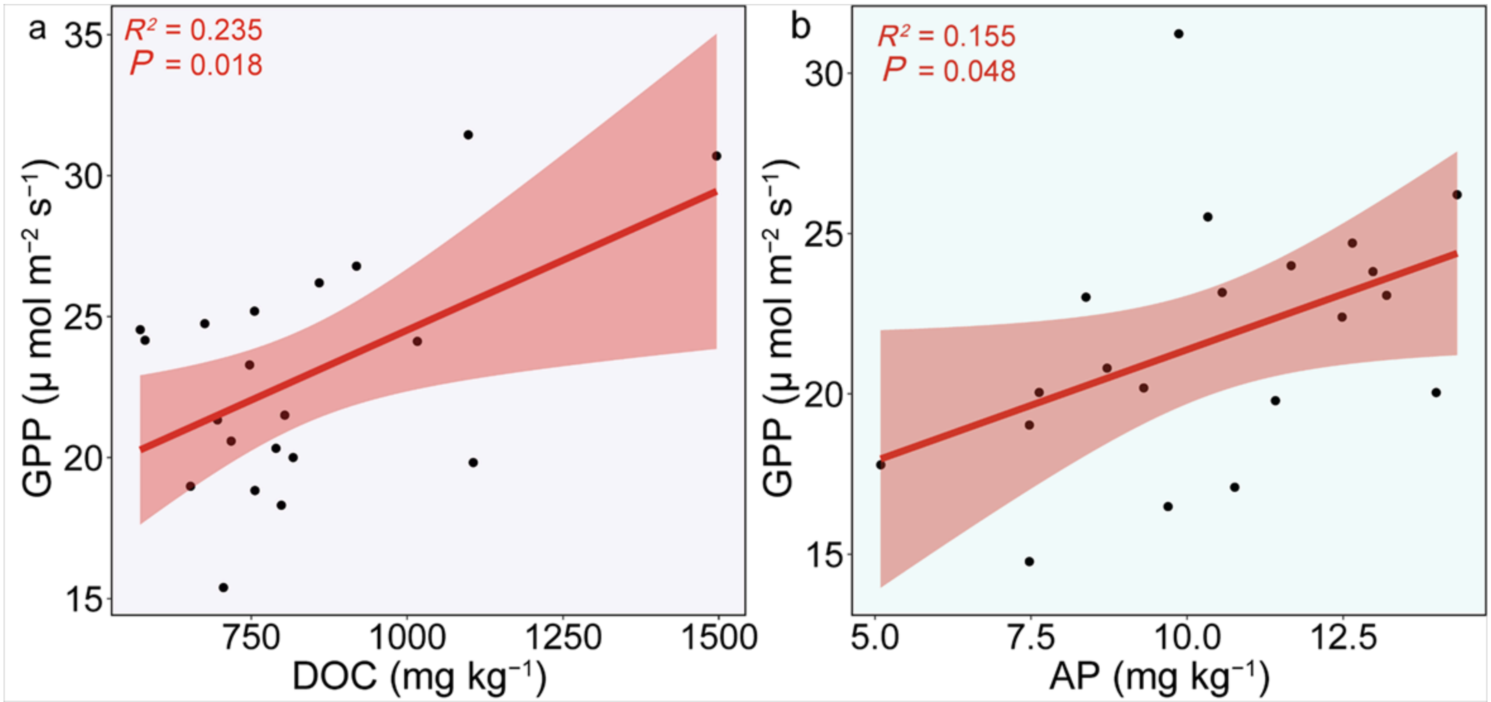

Figure 4

Relationships between ecosystem carbon fluxes with soil physicochemical factors under different experimental treatments. a, Regression analysis of GPP and DOC under reseeding; b, Regression analysis of GPP and AP under fertilization. The grey area represents the 95% confidence interval.

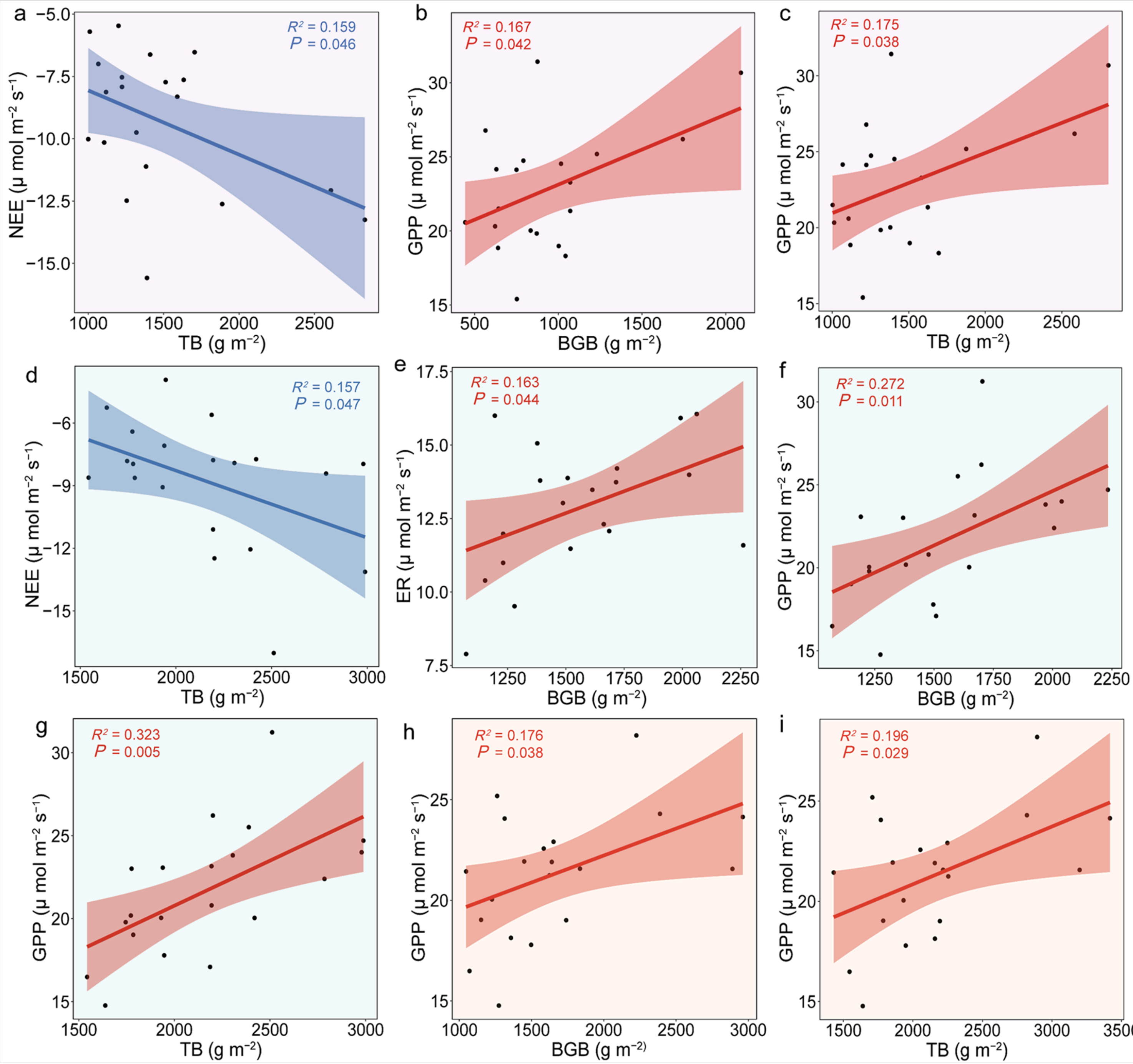

Figure 5

Relationship between ecosystem carbon fluxes with grassland biomass under different experiment treatments. a, Regression analysis of NEE and TB under reseeding; b, Regression analysis of GPP and BGB under reseeding; c, Regression analysis of GPP and TB under reseeding; d, Regression analysis of NEE and TB under fertilization; e, Regression analysis of ER and BGB under fertilization; f, Regression analysis of GPP and BGB under fertilization; g, Regression analysis of GPP and TB under fertilization; h, Regression analysis of GPP and BGB under *Burkholderia* sp. addition; i, Regression analysis of GPP and TB under *Burkholderia* sp. addition. The grey area represents the 95% confidence interval.

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