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Consecutive annual mowing reduces soil respiration and increases the proportion of autotrophic component in a meadow steppe

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Abstract

Background Soil respiration (R_s), as the second largest CO_2 emissions of terrestrial ecosystems, is sensitive to disturbance and consequent environmental changes. Mowing is strategically implemented as a management approach and has the potential to influence carbon cycling in meadow steppes. However, it remains unclear how and why R_s and its heterotrophic (R_h) and autotrophic (R_a) components respond to consecutive mowing and associated ecological consequences. Here, we conducted a field mowing experiment in a meadow steppe in 2018 and monitored R_s , R_h , and R_a from 2019 to 2022.

Results We observed a significant reduction in R_s by 4.8% across four years, primarily attributed to a decrease in R_h . This decline in R_s intensified over time, indicating an accumulative effect of mowing. In addition, mowing induced a generally increasing R_a/R_s ratio over the experimental years with a simultaneous increase in the ratio of belowground to aboveground biomass (BGB/AGB). Furthermore, structural equation modeling results revealed that the decline in R_s was largely ascribed to reduced microbial biomass carbon (MBC) under mowing, while the increased R_a/R_s was primarily explained by the enhanced BGB/AGB. Partial regression analysis suggested that the biotic factor of microbial biomass dominated changes in soil respiration induced by mowing rather than abiotic soil temperature.

Conclusions Our findings showed that consecutive mowing decreased R_s and raised R_a/R_s in meadow steppe by decreasing plant biomass and altering the proportion of biomass allocation. This observed decline in R_s would help to reduce CO_2 concentration in atmosphere as well as alleviate global warming. However, considering the concurrent lower microbial biomass, the potential positive impacts of mowing on climate and ecosystem function should be reevaluated in future grassland management practices.

Keywords Carbon allocation, Clipping, Microbial biomass, Microbial respiration, Plant biomass, Root respiration

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Introduction

Grassland covers approximately 40% of the world's land and stores 30% of the world's soil carbon (Raich et al. 2002; Dlamini et al. 2016). The massive soil carbon storage plays an important role in regulating carbon exchange between the atmosphere and the earth's surface (Raich et al. 1992; Carey et al. 2016; Mou et al. 2024). Most of global grasslands have experienced human disturbance and management (Bardgett et al. 2021; Zhang et al. 2024). Mowing, as a common management practice, is strategically implemented to maintain the balance between vegetation growth and herbivore consumption in grasslands and therefore has a potential impact on grassland carbon cycling (Detling 1998; Pykälä 2000; Erb et al. 2017; Gil-mullina et al. 2023). Soil respiration (Rs) is second of the largest carbon fluxes between terrestrial ecosystems and the atmosphere and is sensitive to disturbance (Raich et al. 1992; Lei et al. 2021). Thus, exploring changes in Rs and their underlying mechanisms in response to mowing would improve our understanding of grassland carbon cycling.

Over the past two decades, a growing body of research has demonstrated that mowing has an impact on Rs through abiotic and biotic pathways (Wan et al. 2002; Garavani et al. 2023; Kohler et al. 2024). By harvesting vegetation, mowing generally exposes soils to direct sunlight and increases evaporation, raising soil temperature and reducing soil moisture. However, the effect of mowing on Rs varies inconsistently depending on its impacts on soil temperature and moisture. For example, the removal of vegetation and subsequent increased exposure to sunlight can elevate soil temperature, inhabiting root growth and decreasing Rs in water-limited temperate steppe. Additionally, mowing can enhance soil moisture by decreasing evapotranspiration, leading to increased Rs in semi-arid grassland ecosystems (Wang et al. 2016).

Apart from soil abiotic factors, mowing also affects Rs through biological processes. Specifically, mowing directly removes plant biomass available for decomposition and disrupts the natural decomposition processes, leading to lower Rs rates compared to unmanaged grasslands (Wan et al. 2005; Simpson et al. 2012; Zhang et al. 2023). Moreover, this disruption of decomposition potentially decreases nutrient availability, exerting a negative effect on plant growth and Rs (Heet et al. 2021; Zhang et al. 2022). On the other hand, mowing aids in improving plant biomass, microbial activity and seed germination by enhancing sunlight exposure to promote Rs (Bush and Van Auken 1995; Luo et al. 2021). Moreover, mowing can lead to a reduction in plant diversity (Chiste et al. 2018; Zhao et al. 2022). The reduced plant diversity can decrease Rs because different plant species exhibit

different contributions on CO₂ emission (Busch et al. 2018; Zhu et al. 2020; Moulin et al. 2021). Given these contradictory results and complex ecological processes, it remains unclear how and why mowing influences Rs in grassland ecosystems.

Rs consists of heterotrophic (Rh) and autotrophic (Ra) components according to the differences in mechanism processes and carbon resources (Bhupinderpal-Singh et al. 2003; Ren et al. 2018; Nissan et al. 2023). Rh is involved in microbial decomposition of organic matter, producing CO₂ as a byproduct while Ra is the process by which plants and other photosynthetic organisms release CO₂ during cellular respiration (Hanson et al. 2000; Bond-Lamberty et al. 2004; Han and Zhu 2021). Mowing has been reported to exert different influences on Rh, Ra, as well as the proportion of these two components across various grassland ecosystems. For example, mowing could promote Rh and subsequent Rh/Rs due to the increased soil temperature and microbial activities in alpine meadow (Yan et al. 2022a, b) or tallgrass prairie (Zhou et al. 2007). By contrast, mowing could suppress Rh owing to the reduced substrate supply in semi-arid grassland (Zhang et al. 2022). Moreover, mowing had no effect on Rh and therefore had no effect on Rh/Rs (Li et al. 2013). The differences in Rs response to mowing might associate with mowing practice duration. Specifically, on the one hand, short-term mowing has been reported to not alter soil microenvironment and consequently has no impact on Rs (Francioni et al. 2020). On the other hand, Rs can be changed by alteration in plant biomass or nutrients (Du et al. 2018; Mao et al. 2023) or continuous loss of plant litter owing to long-term mowing (Hassan et al. 2023). However, we still lack an understanding of how Rh and Ra contribute to changes in Rs in response to consecutive mowing and the underlying mechanisms. Hulunbuir grassland is an important part of the Eurasian continent and performs important pastoral and ecological functions. Mowing has become a local management approach to store feed for livestock (Pongratz et al. 2018; Yang et al. 2020). Here, we aim to address the following three questions: (1) How does consecutive annual mowing influence Rs and what are the underlying mechanisms? (2) Whether annual mowing has consistent effects on the two components of Rh and Ra and affects their relative contributions to Rs? (3) Would the impact of annual mowing on Rs change over time?

Materials and methods

Site description and experimental design

This study was conducted at the National Hulunber Grassland Ecosystem Observation and Research Station, Chinese Academy of Agricultural Sciences (49°23'13"N;

120°02′47″E, 628 m a.s.l.). The study site is characterized by a mean annual temperature of 2.4 °C and mean annual precipitation (MAP) of 390 mm, with the growing season from May to September. The soil is classified as Chestnut soil. Vegetation is dominated by *Leymus chinensis*, *Stipa baicalensis*, *Cleistogenes squarrosa*, *Poa pratensis*, and *Vicia amoena*.

The experiment was a part of the multi-factor experiment conducted in the Hulunber Grassland Ecosystem in 2018. Twenty 5 m×6 m blocks were allocated into 4 rows and 5 columns with an interval buffer of 2 m. Each block was split into mowing and control plots with a 1 m buffer zone. Mowing was performed in the middle of August with peak plant biomass each year using a light lawn mower (Yard-Man 160CC, USA). We performed mowing twice on May 30 and August 15, 2018. After that, the mowing was applied once in mid-to-late August each year (Fig. S1). The height of the mowing stubble was 5 cm. In addition to mowing, five simulated precipitation regimes including unchanged precipitation were also applied in every block. Therefore, we had 40 plots with 10 treatments with 4 replicates. We obtained measurements only in the 4 blocks with unchanged precipitation.

Measurements of Rs and its components

Rs was divided into Rh and Ra by the method described by Luo et al. (2001). In each plot, two PVC collars (inner diameter 11 cm, height 5 cm) were permanently inserted into the soil at a depth of 2–3 cm at the two opposite corners to measure soil respiration. In addition, the other two deep PVC collars were inserted into 20 cm to exclude plant roots to measure microbial Rh given that more than 90% of plant roots were distributed in the topsoil of 20 cm (Jobbagy and Jackson 2021). Ra was then calculated by subtracting Rh from Rs. Plants in the collars were clipped to the ground level the day before we measured respiration to eliminate the aboveground plant respiration during the measurement. Rs was measured using a portable, automated soil C flux system (Li-8100A, Li-Cor Biosciences Lincoln, NE, USA) during consecutive four years (2019–2022). The measurements were taken between 8:30 am and 11:30 am (local time). From 2019 to 2022, Rs was measured at least twice a month in June, July, and August during the growing season. The measurement of Rs was lack in June 2022 due to the instrument damage.

Soil temperature and soil moisture

Soil temperature (ST) at 10 cm depth in each plot was measured using a thermocouple probe (Li-8100-201), while the soil volume moisture (SM) at the same depth was measured using a portable SM device (Diviner 2000; Sentek Pty Ltd., Balmain, Australia). All measurements

were performed adjacent to the PVC collars simultaneously with the Rs measurement.

Soil sampling and microbial biomass carbon

Soil samples were collected at 0–10 cm in depth from all the plots in the middle of August of each year. After removing roots and stones by sieving with 2 mm mesh, the soil samples were placed on an icebox and immediately transported to the laboratory. Microbial biomass carbon (MBC) was measured using the chloroform fumigation-extraction method (Vance et al. 1987). Briefly, each fresh sample (10 g dry weight equivalent) was fumigated with chloroform for 24 h along with a control soil sample that was not fumigated. The soils were extracted with 100 ml 0.5 mol L⁻¹ K₂SO₄ after 30 min shaking. Total concentrations of carbon in the extracts were analyzed using an elemental analyzer (liquiTOC, Analysensystem, Germany). MBC was calculated using the differences between extractable C with a conversion factor of 0.45.

Aboveground biomass and belowground biomass

Aboveground biomass (AGB) was measured using the harvesting method in the middle of August. A sample quadrat of 0.25 m×0.25 m was set and all vegetation tissues above ground in the sample quadrat were sampled in a clockwise direction. The obtained vegetation was oven-dried at 65 °C for more than 72 h and weighed to get biomass. The belowground biomass (BGB) was determined by collecting 0–20 cm depth of roots using a 7-cm diameter soil corer at the end of August in 2021 and 2022. The soil cores were transported to the laboratory immediately and carefully washed on a 60-mesh sieve to separate the roots from the soil. The washed roots were oven-dried at 65 °C for 72 h to constant weight. The unit of AGB and BGB is g m⁻².

Statistical analysis

Repeated measures analysis of variance (ANOVA) was performed to assess the effects of mowing and year on ST, SM, Rs, Rh, and Ra across the four years. Then the mean values of these variables were calculated across the sampling dates for each year. These mean values were used to analyze the effects of mowing and year on MBC, AGB, BGB, and BGB/AGB with two-way ANOVA. Linear regression was used to analyze changes in Rs, Rh, Ra, the proportion of Rh (Rh/Rs) and Ra (Ra/Rs) along the experimental year. To discover the pathways to influence Rs and Ra/Rs, we applied piecewise structural equation modeling (SEM) to reveal the driving factors of Rh and Ra/Rs in response to mowing. Due to the lack of data on plant and soil microbial biomass in 2019 and 2020, we used

the mean data across 2021 and 2022 to perform SEM. The Fisher's *C* statistic (Fisher's *C*), degrees of freedom (*df*), *P* values, and the root mean square errors of approximate (RMSEA) were used to determine the adequacy of the fit of the model. The standardized effects of each factor on *Rh* were calculated by calculating their direct and indirect path effects.

Results

Soil microenvironment and respiration

There were substantial inter-annual variations in *ST*, *SM*, *Rs*, *Rh*, and *Ra* (Figs. 1 and 2). Mowing significantly increased *ST* and *SM* by 1.06 °C and 0.94% across the four years. The effects of mowing on *SM* varied across different years. The main effects of mowing on *Rs*, *Rh*, and *Ra* were significant. On average, mowing decreased *Rs*, *Rh*, and *Ra* by 4.8%, 5.3%, and 0.6%, respectively. In addition, the interaction of mowing and year significantly

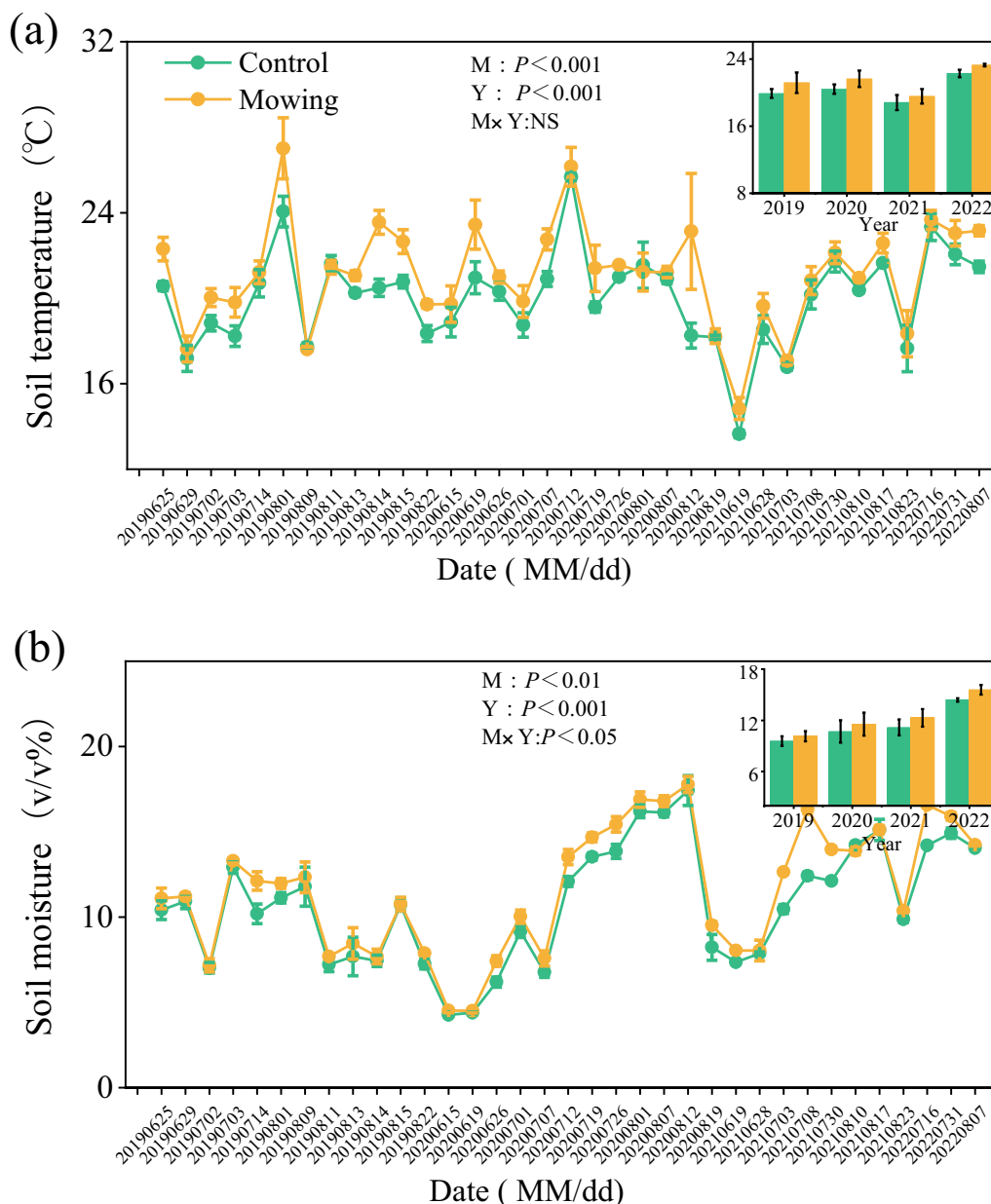


Fig. 1 Seasonal dynamics of soil temperature (a) and soil moisture (b) in 2019, 2020, 2021, and 2022. Each data point represents the mean value of the four replicates. Insets represent the seasonal mean values. *M* mowing; *Y* year. *NS* means insignificant

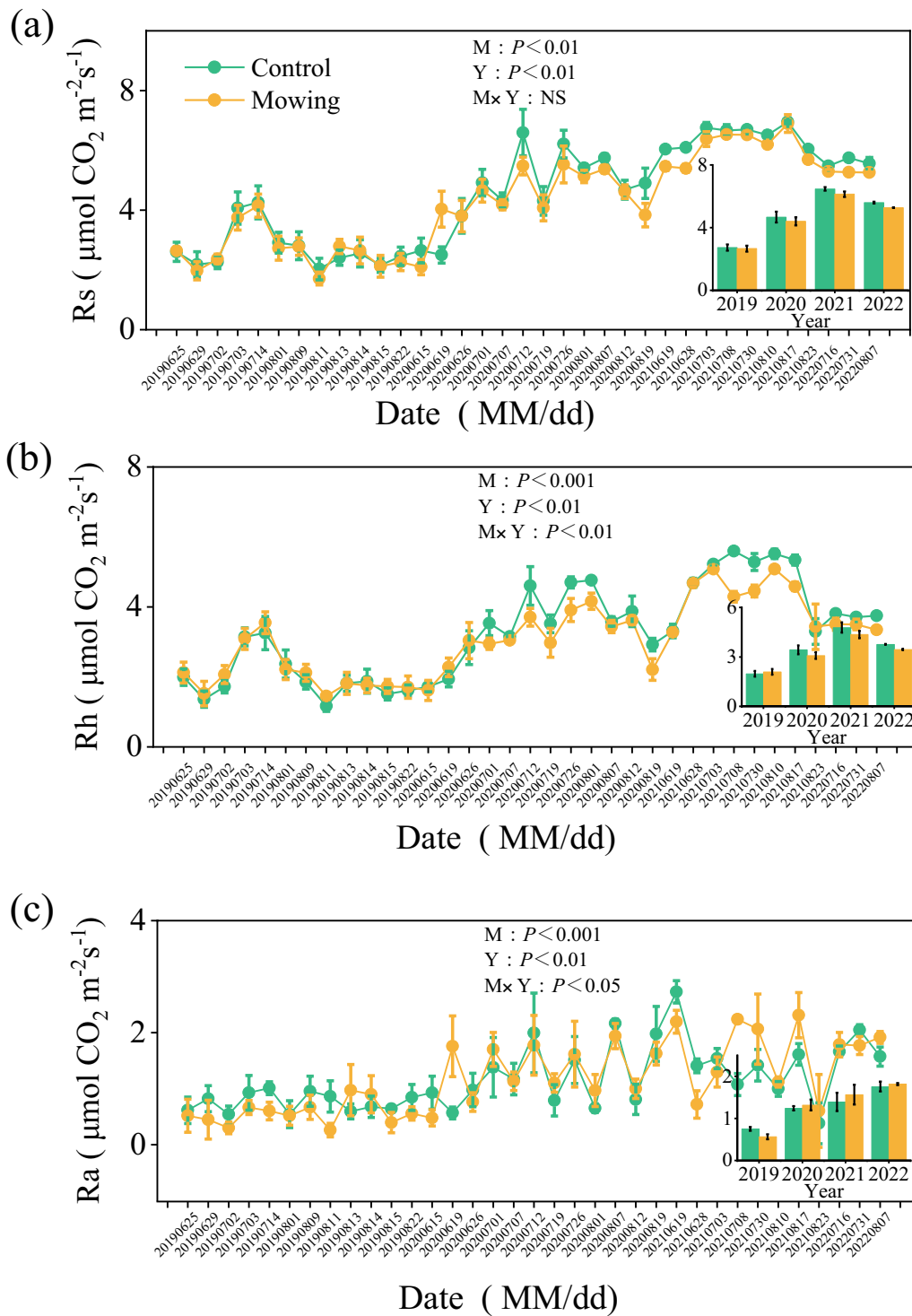


Fig. 2 Seasonal dynamics of R_s (a), R_h (b), and R_a (c) in 2019, 2020, 2021, and 2022. Each data point represents the mean value of the four replicates. Insets represent the seasonal mean values. M mowing; Y year. NS means insignificant. R_s soil respiration; R_h heterotrophic respiration; R_a autotrophic respiration

affected Rh and Ra. Ra was decreased by mowing only in 2019. Note that the lack of Rs in June in 2022 may result in the overestimation of absolute Rs.

Soil microbial and plant biomass

Across years 2021 and 2022, mowing promoted MBC and AGB by 24.7% and 9.14%, respectively (Fig. 3a, b). Mowing did not significantly influence BGB (Fig. 3c), but increased BGB/AGB (Fig. 3d). There was a positive relationship between Rs and MBC (Fig. 3e). Rh positively correlated with both MBC and AGB (Fig. 3f, g), while Ra positively correlated with BGB/AGB (Fig. 3h).

Changes in respiration and the proportions over the experimental years

The magnitude of decrease in Rs increased along the mowing years (Fig. 4a). However, there were no significant relationships between changes in Rh or Ra with the years (Fig. 4b, c). The relative contribution of Rh to Rs (Rh/Rs) was higher in mowed than control plots in 2019, while it was lower in mowed than control plots in 2022. Rh/Rs negatively declined along with the experimental years under mowing plots (Fig. 5a). Correspondingly, Ra/Rs positively increased along with the experimental years under mowing plots (Fig. 5b). However, neither Rh/Rs nor Ra/Rs changed along with the experimental years.

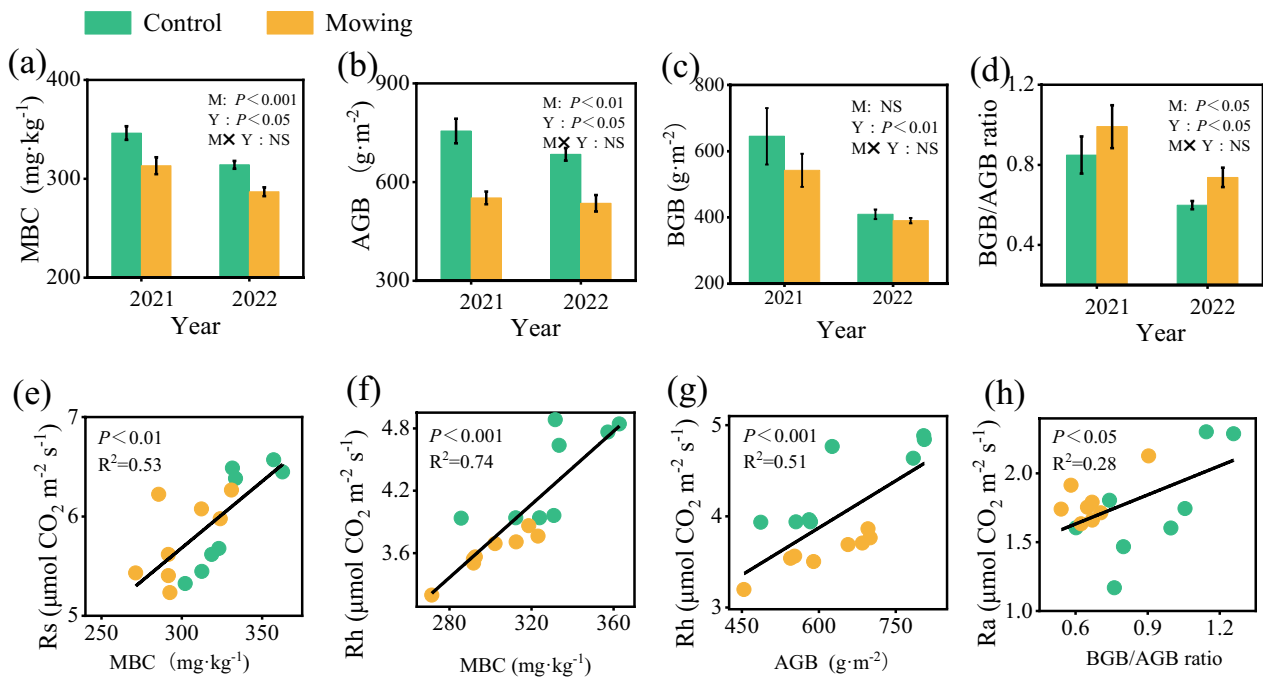


Fig. 3 Effects of mowing on MBC (a), AGB (b), BGB (c), and BGB/AGB (d) in 2021 and 2022, and the linear regressions of Rs vs MBC (e), Rh vs MBC (f), Rh vs AGB (g), Ra vs BGB/AGB (h) across 2021 and 2022. *MBC* microbial biomass carbon; *AGB* aboveground biomass; *BGB* belowground biomass. See Fig. 2 for abbreviations of Rs, Rh, and Ra

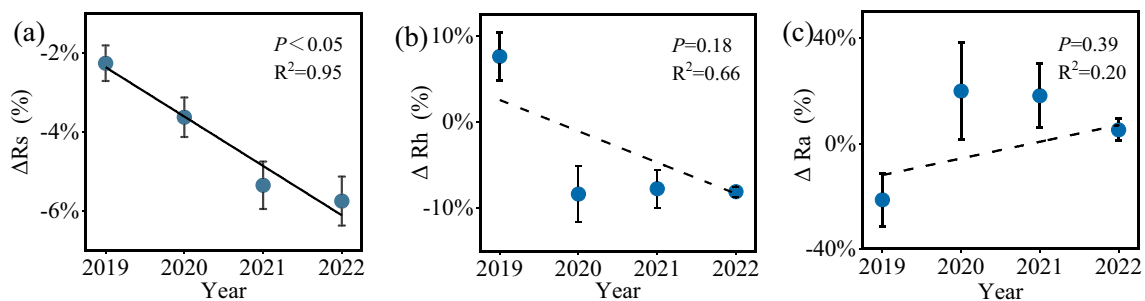


Fig. 4 Linear regressions between mowing-induced changes in Rs (a), Rh (b), and Ra (c) with experiment years. A solid line indicates statistically significant ($P < 0.05$), and dotted lines indicate statistically insignificant ($P > 0.05$)

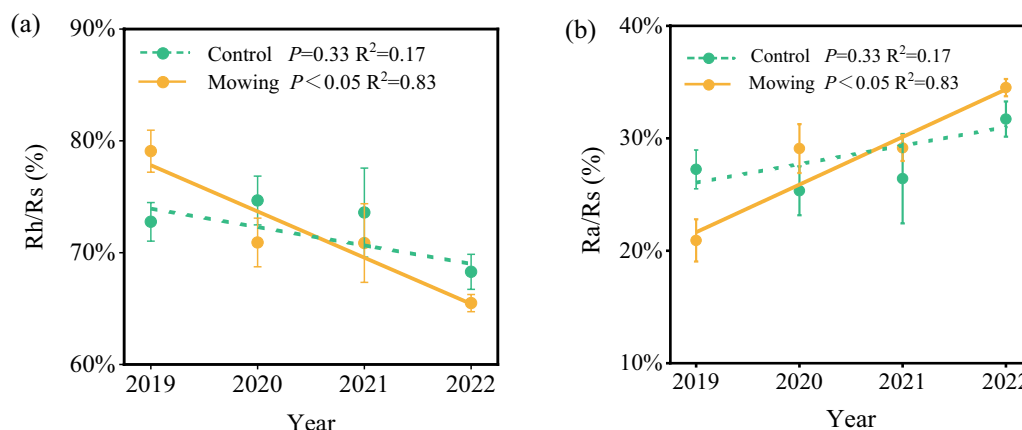


Fig. 5 Linear regression between the relative contributions of Rh (Rh/Rs, **a**) and Ra (Ra/Rs, **b**) to Rs with experimental years, respectively. Solid line indicates statistical significance ($P < 0.05$), while dotted lines indicate statistical insignificance ($P > 0.05$)

Explanations to Rs and Ra/Rs

The SEM results showed that mowing had a direct negative effect on AGB (Fig. 6a, $P < 0.0001$). AGB had a direct positive effect on MBC ($P < 0.01$), while ST had a direct negative effect on MBC. AGB did not directly affect Rs. ST directly affected Rs ($P < 0.05$). MBC had a significant direct influence on Rs ($P < 0.05$). Together, MBC and ST accounted for 65% of the variation in Rs. The standardized total effects exhibited that the decreased Rs induced by mowing was mainly attributable to the negative effects of mowing on MBC.

Mowing had a positive effect on BGB/AGB (Fig. 6c, $P < 0.05$). Both BGB/AGB and MBC positively affected Ra/Rs ($P < 0.05$). Together, BGB/AGB account for 43% of the variation in Ra/Rs under mowing (Fig. 6d). The standardized total effects exhibited that the increased Ra/Rs induced by mowing was mainly ascribed to the positive effects of mowing on BGB/AGB.

Discussion

The response of Rs and its components to mowing and the underlying mechanisms

Consistent with the results from a tallgrass prairie in North America (Zhou et al. 2007) and a natural grassland in India (Mukhopadhyay and Maiti 2014), our results show that continuous annual mowing reduced Rs in the meadow steppe. The observed decrease in Rs can be attributed to a concomitant decrease in Rh rather than Ra, given that mowing did not affect Ra in all the four years except 2019. This reduction in Rs and Rh could be predominantly linked to diminished carbon input and the subsequent attenuation of microbial activity. Indeed, various studies have documented the suppressive effect of mowing on plant growth, attributing it to nutrient loss and insufficient nutrient supply (Simpson et al. 2012).

The suppression of plant growth could diminish the supply of photosynthetic products to support microbial growth and inhibit microbial activities (Yang et al. 2023). Consistent with these observations, our study reveals a reduction in both plant biomass and microbial biomass under mowed plots (Fig. 3a, b). The structural equation model showed that the lower MBC and positive relationship with Rs further supports the above explanation (Fig. 6a).

The empirical function is commonly used to describe the relationship between Rs and temperature, which means that Rs increases with increasing temperature (Luo et al. 2021; Davidson et al. 2006; Liu et al. 2009; Moinet et al. 2019; Oestmann et al. 2024). Accordingly, mowing-induced stimulation of microbial respiration was observed in Mediterranean grassland and was attributed to increased sunlight exposure and elevated soil temperature (Gavrichkova et al. 2010). In our study, we also found elevated soil temperature induced by mowing. However, we found a reduction in Rs and its negative relationship with soil temperature did not conform to the empirical function. This discrepancy may be ascribed to a simultaneous reduction in substrate quantity and microbial biomass, indicating that the positive effects of mowing-induced increased temperature on Rs could be counteracted and impeded by the negative effects of decreased plant and microbial biomass. Indeed, when accounting for MBC, the partial correlations exhibited significant positive associations between both Rs (Fig. S2) and Rh (Fig. S3) with soil temperature. This finding emphasizes that the positive effects of mowing-induced elevation of temperature on Rs are contingent upon the concurrent dynamics of substrate quantity and microbial biomass.

SM has been shown to substantially affect Rs potentially via influencing either the growth of soil microbes

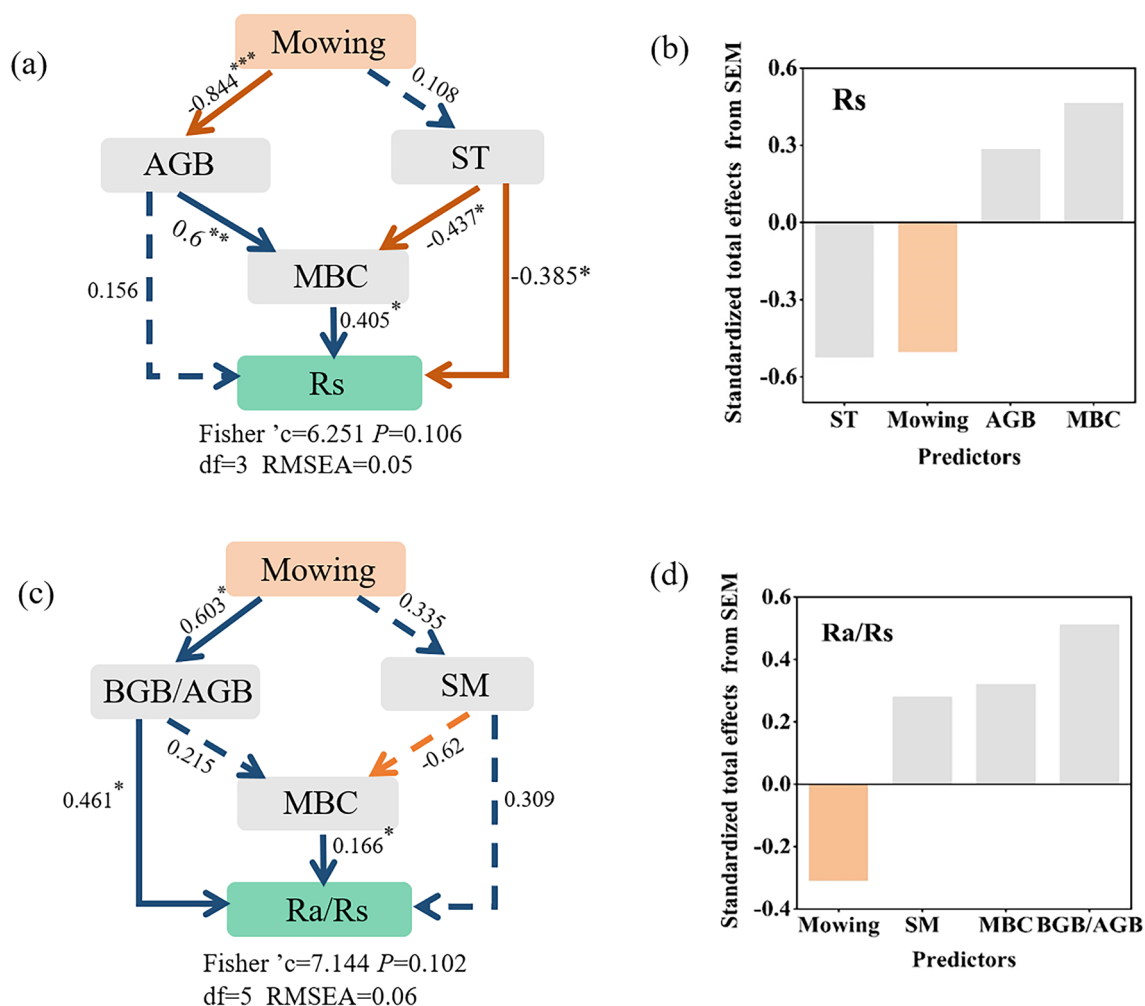


Fig. 6 Piecewise structural equation modeling showing the effects of mowing on soil respiration (Rs) (a) and Ra/Rs (c), and the standardized effects on Rs (b) and Ra/Rs (d). Numbers above the arrows indicate the standardized path coefficients, the width of the path indicates the strength of the causal relationship, and R^2 values denote the proportion of variation explained. Blue and orange arrows indicate positive and negative paths, respectively. Solid and dashed arrows indicate significant and non-significant relationships with asterisks representing the significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. *RMSEA* root mean square error of approximation. *ST* soil temperature. The other abbreviations follow Fig. 3

or the diffusion of substrates (Tang et al. 2020; Wang et al. 2020). Different from the positive effects of SM on Rs in some manipulative experiments (Steenwerth et al. 2010) or spatial investigation (Boonriam et al. 2021) across grassland ecosystems, we found the greater SM but the lower Rs under mowing. On the one hand, the removal of vegetation and lower plant biomass could weaken transpiration and maintain greater moisture in soils, stimulating Rs under mowing (Gong et al. 2014). On the other hand, the reduced plant biomass suppresses microbial activity and inhibits Rs (Koncz et al. 2015), offsetting the positive effects of moisture on Rs. The contrary responses of SM and Rs to mowing implies the importance of carbon inputs in regulating Rs under mowing.

The accumulative effects of mowing and the proportion of Rh and Ra

Our results revealed that the magnitude of reduction in Rs amplified with increasing experimental years, suggesting an accumulative effect of annual mowing on Rs. We speculate that this accumulative effect on Rs may be due to an exacerbation of the negative effects of sequential plant removal on plant and microbial biomass. We acknowledge that we could not verify this assumption due to the lack of biomass in 2019. However, previous research has shown that Rs remains unaffected by low-frequency mowing (Han et al. 2012), while high-frequency mowing inhibits Rs due to reduced photosynthetic carbon inputs (Francioni et al. 2020). This discrepancy related to the frequency of mowing may partially support our above speculation regarding the

accumulative effect of mowing on Rs. Note that the lack of measurement for June in 2022 would lead to an over-estimation of the absolute value of Rs. To eliminate the impact of missing data on the results of accumulative effect, we analyzed the data from July to August across four years and found the same pattern (Figs. S5, S6), demonstrating the accumulative effect of mowing on Rs.

We found that Rh contributed approximately 70% to Rs in this meadow steppe. The proportion of Rh was promoted by mowing in 2019, primarily driven by decreased Ra this year. This aligns with the findings of Yan et al. (2022a, b), who reported that mowing-induced promotion of Rh/Rs was due to the reduction of Ra associated with diminished belowground biomass. However, the proportion of Rh was decreased by mowing in 2022 indicating a progressive decline in the relative contribution of Rh to Rs over time. This decreasing trend suggests that mowing alters the proportions of Rs components toward decreasing the contribution of Rh as well as increasing the contribution of Ra over time. Given that continuous annual mowing results in nutrient limitation due to plant and litter removal, plants would allocate more carbon to root growth to acquire nutrients to meet their demands (Prescott et al. 2020). The higher ratios of BGB/AGB indicated a higher distribution of carbon to belowground (Figs. 3 and S4), supporting the above explanation. As Ra is associated with belowground carbon allocation in terrestrial ecosystems (Högberg et al. 2001; Gao et al. 2020; Tang et al. 2020), the increased belowground carbon allocation would facilitate the proportionally larger Ra caused by mowing, resulting in higher Ra/Rs (Fig. 6).

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00537-1>.

Supplementary Material 1. Fig. S1: The picture of the field mowing experiment conducted mowing in August 2018. Fig. S2: The univariate regressions between MBC and AGB, Rs and MBC, soil ST, and partial regression between Rs and ST after controlling for MBC. MBC: microbial biomass carbon; AGB: aboveground biomass; Rs: soil respiration; ST: soil temperature. Fig. S3: The univariate regressions between Rh and MBC, ST, and partial regression between Rh and ST after controlling for MBC. Rh: soil heterotrophic respiration; MBC: microbial biomass carbon; ST: soil temperature. Fig. S4: The ratio of belowground biomass distribution in the depth of 30–50 cm to the depth of 0–30 cm in 2021. Fig. S5: Linear regressions between mowing-induced changes in Rs, Rh, and Ra with experimental years. A solid line indicates statistically significant, and dotted lines indicate statistically insignificant. Fig. S6: Linear regression between the relative contributions of Rh and Ra to Rs with experimental years, while dotted lines indicate statistical insignificance.

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Author contributions

Weixing Liu conceived the idea and supervised the study. Changliang Shao, Wen Zhu, Tsegaye Gemechu Legesse, Xiaobing Dong and Qi Tong performed the experiment. Wen Zhu, Aogui Li, and Ziyue Shi analyzed the data. Wen Zhu and Weixing Liu wrote the manuscript with input from all authors.

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Availability of data and material

The data sets used in the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors agreed and approved the manuscript for publication in *Ecological Processes*.

Competing interests

The authors declare that they have no competing interests.

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