

Plant functional types regulate non-additive responses of soil respiration to 5-year warming and nitrogen addition in a semi-arid grassland

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Abstract

1. How climate warming interacts with atmospheric nitrogen (N) deposition to affect carbon (C) release from soils remains largely elusive, posing a major challenge in projecting climate change–terrestrial C feedback.
2. As part of a 5-year (2006–2010) field manipulative experiment, this study was designed to examine the effects of 24-hr continuous warming and N addition on soil respiration and explore the underlying mechanisms in a semi-arid grassland on the Mongolian Plateau, China.
3. Across the 5 years and all plots, soil respiration was not changed under the continuous warming, but was decreased by 3.7% under the N addition. The suppression of soil respiration by N addition in the third year and later could be mainly due to the reductions in the forb-to-grass biomass ratios. Moreover, there were interactive effects between continuous warming and N addition on soil respiration. Continuous warming increased soil respiration by 5.8% in the ambient N plots, but reduced it by 6.3% in the enriched N plots. Soil respiration was unaffected by N addition in the ambient temperature plots yet decreased by 9.4% in the elevated temperature plots. Changes of soil moisture and the proportion of legume biomass in the community might be primarily responsible for the non-additive effects of continuous warming and N addition on soil respiration.
4. This study provides empirical evidence for the positive climate warming–soil C feedback in the ambient N condition. However, N deposition reverses the positive warming–soil C feedback into a negative feedback, leading to decreased C loss from soils under a warming climate. Incorporating our findings into C-cycling models could reduce the uncertainties of model projections for land C sink and global C cycling under multifactorial global change scenarios.

KEYWORDS

carbon cycling, climate warming, community composition, global change, nitrogen deposition, plant productivity, water availability

1 | INTRODUCTION

Intensified human activities such as the combustion of fossil fuels and production of nitrogen (N) fertilizers have substantially altered Earth's climate and atmospheric composition. Over the past 136 years (1880–2015), land surface temperature has increased by 0.87°C and is expected to rise continuously in the future (IPCC, 2018). In parallel to climate warming, the rates of atmospheric reactive N deposition have increased threefold to fivefold globally (Galloway et al., 2008). Because temperature and N availability are the two essential factors limiting plant growth and productivity (Duffy et al., 2021; Song et al., 2019a), the unprecedented climate warming and atmospheric N deposition have the tremendous potential to influence carbon (C) cycling of terrestrial ecosystems (Greaver et al., 2016; Reay et al., 2008; Song et al., 2019a). As the second largest C flux between terrestrial biomes and the atmosphere, soil respiration has released up to 98 Pg C to the atmosphere worldwide in 2008, exerting strong controls on terrestrial C balance (Bond-Lamberty & Thomson, 2010; Schlesinger & Andrews, 2000). Therefore, accurately quantifying the individual and interactive effects of warming and N deposition on soil respiration is crucial to reduce the uncertainties of model projections for climate change–terrestrial C feedback and global C cycling (Greaver et al., 2016; Song et al., 2019b).

Over the past two decades, extensive studies using manipulative field experiments (Luo et al., 2001; Nottingham et al., 2020; Xu et al., 2015), long-term observations (Bond-Lamberty & Thomson, 2010) and meta-analyses (Rustad et al., 2001; Song et al., 2019a) have demonstrated that temperature-associated increases in soil respiration primarily arise from the enhancement in C substrate supply related to plant and microbial sources. Several explanations have been proposed. First, warming can stimulate plant photosynthesis and productivity (Högberg et al., 2001; Song et al., 2017; Wan et al., 2009), subsequently resulting in the increases in respiratory loss of soil old C (Chang et al., 2021). Second, elevated temperature could accelerate the decomposition rates of soil organic matter driven by higher soil microbial activity (Allison et al., 2010; Walker et al., 2018). However, responses of soil respiration to warming may strongly depend on local water availability (Song et al., 2019a; Wang et al., 2014). For example, intensified water stress under climate warming may suppress plant growth and further overwhelm the positive influences of elevated temperature on C substrate availability (Reich et al., 2018; Song et al., 2019a), leading to neutral and even negative responses of soil respiration to experimental warming (Liu et al., 2009; Wan et al., 2007).

Nitrogen addition can stimulate plant growth and further enhance the availability of C substrates for soil respiration (Song et al., 2019a; Xia & Wan, 2008). However, it has been well documented that N addition often decreases soil respiration (Janssens et al., 2010; Song et al., 2019a). The suppressions in soil respiration under N addition could be mainly due to soil acidification-induced reductions in both soil microbial activity and rates of organic matter decomposition overwhelming the positive effects of increased plant productivity under N enrichment (Frey et al., 2014; Song

et al., 2019a; Ye et al., 2018). Decreased C allocation and respiration of roots as well as reduced priming of soil organic matter in response to N addition may also be responsible for the suppressions in soil respiration (Fontaine et al., 2011; Janssens et al., 2010; Song et al., 2019a).

Irrespective of the well-defined individual effects, only a few two-factor experiments have manipulated warming and N addition simultaneously (Contosta et al., 2011; Graham et al., 2014; Fang et al., 2017, 2018; Liu et al., 2017; Zhao et al., 2017; see also Table S1) and reached little consensus on the interactive influences of the concurrent increases in temperature and N availability on soil respiration and the underlying mechanisms (Greaver et al., 2016; Song et al., 2019a). Given that warming and N addition generally have additive effects on soil microclimate (e.g. temperature and moisture) and acidity (Liu et al., 2017; Xia et al., 2009), the main factors affecting soil respiration (Liu et al., 2009; Wan et al., 2007; Ye et al., 2018), changes of soil microclimate and acidity may not help explain the non-additive effects of warming and N addition on soil respiration. A growing body of evidence has demonstrated that shifting plant community composition may modulate soil respiration responses to global change driving forces via directly regulating C substrate availability such as community productivity and litter quantity and quality (Chen et al., 2017; Cowles et al., 2016; Wang et al., 2012). For example, a 13-year warming experiment has revealed that increased proportion of C₃ forbs in the community enhances the positive effects of experimental warming on soil respiration after 7 years of treatment in a tallgrass prairie (Xu et al., 2015). In contrast, N addition-induced decreases in the dominance of forbs reduce soil respiration after 1- or 2-year treatments of N application in a semi-arid grassland (Du et al., 2018) and an alpine meadow (Wang et al., 2019). Moreover, other works have reported that the proportion of legumes in the community tends to increase under warming but decrease under N addition (Storkey et al., 2015; Wang et al., 2012), likely further affecting community productivity and ecosystem C cycling (Chen et al., 2017; Cowles et al., 2016). Nevertheless, the roles of plant functional types in controlling the nonlinear responses of soil respiration to warming and N addition remain largely unexplored.

As part of a 5-year (2006–2010) two-factor manipulative experiment, this study was designed to examine the responses of soil respiration to 24-hr continuous warming, N addition, and their factorial combination and explore the underlying mechanisms in a semi-arid grassland of the Mongolian Plateau, China. The following three hypotheses were specifically tested: (a) experimental warming could decrease soil respiration by reducing soil moisture because soil water availability is the predominant factor in regulating plant growth and C cycling of this semi-arid grassland (Liu et al., 2009), (b) N addition could suppress soil respiration likely through decreasing the growth and biomass of forbs in the community (Du et al., 2018) and (c) experimental warming could interact with N addition to affect soil respiration likely driven by the contrasting responses of forb and legume functional types under elevated temperature and increased N availability (e.g. Storkey et al., 2015; Wang et al., 2012).

2 | MATERIALS AND METHODS

2.1 | Study site

The study site is located in a semi-arid grassland in Duolun County (42°02'N, 116°17'E, 1,324 m a.s.l.), Inner Mongolia, China. Long-term (1953–2019) mean annual temperature and precipitation are 2.4°C and 382 mm, respectively (China Meteorological Data Sharing Service System). The sandy soil is classified as chestnut soils (Chinese classification) and Xeric Haplocalcids according to the US soil taxonomy classification system (Soil Survey Staff, 1999). Plant community at the study site is dominated by perennial species such as *Agropyron cristatum*, *Artemisia frigida*, *Artemisia pubescens*, *Lespedeza davurica* and *Stipa krylovii* (Zheng et al., 2021).

2.2 | Experimental design and manipulations

A randomized complete block design was used in this experiment with four treatments including a control (C; no warming and without N addition), 24-hr continuous warming (W), N addition (N) and continuous warming plus N addition (WN). There were six replicates (block) for each treatment (see also Xia et al., 2009). Twenty-four 3-m × 4-m plots were arranged in 4 × 6 matrix, with a 3-m buffer zone between any two adjacent plots.

The continuous warmed plots were heated continuously using MSR-2420 infrared radiators (Kalglo Electronics Inc.) suspended 2.25 m above the ground from 23 April to 15 November in 2006 and from 15 March to 15 November during 2007–2010. In the unwarmed plots, one 'dummy' heater with the same shape and size as infrared radiators was suspended 2.25 m high to mimic the shading effects of infrared radiators. The level of N addition was set at 10 g N m⁻² year⁻¹ as ecosystem responses to N enrichment in this area could reach the saturation point at a rate of 10.5 g N application m⁻² year⁻¹ (Bai et al., 2010). NH₄NO₃ was applied in the enriched N plots once on 19 July in each of the five experimental years from 2006 to 2010.

2.3 | Soil microclimate and plant biomass measurements

In each growing season from May to October, soil temperature (°C) at 10-cm depth was measured three times per month using a portable temperature probe (LI-8100-201) attached to a LI-8100 Soil CO₂ Flux System (Li-Cor Inc.). Soil volumetric water content (% V/V) at 10-cm depth was measured weekly with a Diviner-2000 Portable Soil Moisture Probe (Sentek Pty Ltd). Both the measurements of soil temperature and moisture were conducted adjacent to collars used for soil respiration measurements on clear and sunny days between 09:00 and 12:00 a.m. (local time).

Peak above-ground biomass (AGB) was estimated using a non-destructive method (see also Wang et al., 2020; Xia et al., 2009). In

brief, 80 1-m × 1-m calibration plots were set close to our experimental plots in May 2006 to develop regression equations between AGB and coverage for each plant species. NH₄NO₃ was added in half of the 80 calibration plots (10 g N m⁻² year⁻¹) on 19 July each year. The percent coverage of each plant species in each calibration plot was recorded by visual estimates in late August each year. At the same time, the percent coverage of each species in two permanent 1-m × 1-m quadrats in each experimental plot was also visually monitored. After the coverage measurements, plant above-ground parts in the 80 calibration plots were clipped, separated into different species, oven-dried at 65°C to constant weight and weighed as AGB of each species. In the ambient and enriched N plots of the experiment, AGB of each plant species was evaluated using the regression equations between AGB and coverage derived from the calibration plots with the ambient and enriched N treatments, respectively. We further classified plant species into forb, grass and legume functional types and calculated the forb-to-grass biomass ratios (hereafter termed 'forb:grass ratios') and the proportion of legume biomass in the experimental community (hereafter termed 'legume proportion').

Below-ground net primary productivity (BNPP) was measured using root ingrowth method. In early May each year, two 50-cm deep cylindrical holes were excavated at two opposite corners in each plot with a 7-cm-diameter soil auger. The soil was refilled to the same hole after removing roots and rocks via 2 mm sieves. Root ingrowth samples were collected in early October each year using a 5-cm-diameter soil auger at the centre of the original root ingrowth holes. The dry mass of roots was determined by oven-drying at 65°C to constant weight and weighed as BNPP.

2.4 | Soil respiration measurements

Two 5-cm tall polyvinyl chloride collars (10 cm in diameter) were permanently inserted 3 cm into the soil at two opposite corners of each plot. A CO₂ flux chamber attached to the LI-8100 Soil CO₂ Flux System was put on each collar for 90 s to measure soil respiration, and then moved to the next collar. To eliminate influences of plant respiration, the above-ground parts of living plants inside collars were cut at least one day prior to the measurement. The above-ground cut materials were left inside the collars. Soil respiration was measured three times per month on clear and sunny days between 09:00 and 12:00 a.m. (local time).

2.5 | Statistical analyses

The two values of soil temperature and moisture, AGB, BNPP and soil respiration measured at the two opposite corners of each experimental plot were averaged as the mean values of each plot. All the measurements of soil temperature, moisture and respiration in the same month were averaged as the monthly mean values, which were further used to calculate the mean values of growing season

(i.e. annual mean values). Two-way repeated-measures analysis of variance (ANOVA) was used to examine the effects of warming, N addition, year, and their interactions on soil temperature and moisture, AGB, BNPP, forb:grass ratios, legume proportion and soil respiration. In the repeated-measures ANOVA, between-subject effects were assessed as warming, N addition, and their interactions and within-subject effects were year and their interactions with warming and N addition. Prior to analysis, the homoscedasticity and normality of the data used in the repeated-measures ANOVA were tested (see Tables S2 and S3). Given that most of the data fit the criteria of homoscedasticity and normality, we did not convert any data in the repeated-measures ANOVA. In addition, the main effects of warming across the ambient and enriched N plots as well as the main effects of N addition across the ambient and elevated temperature plots on AGB, BNPP, forb:grass ratios, legume proportion and soil respiration in each of the six blocks were calculated as: $\frac{W-C+WN-N}{C+N} \times 100\%$ and $\frac{N-C+WN-W}{C+W} \times 100\%$, respectively. If there were significant interactions between warming and N addition, we calculated the warming effects on these variables in the ambient and enriched N plots in each of the six blocks as: $\frac{W-C}{C} \times 100\%$ and $\frac{WN-N}{N} \times 100\%$, respectively. The N addition effects in the ambient and elevated temperature plots were estimated in each of the six blocks as: $\frac{N-C}{C} \times 100\%$ and $\frac{WN-W}{W} \times 100\%$, respectively. Moreover, simple linear regressions were conducted to explore the relationships of soil respiration with the abiotic (i.e. soil temperature and moisture) and biotic factors (i.e. AGB, BNPP, forb:grass ratios and

legume proportion). All the aforementioned statistical analyses were performed using SAS 9.0 (SAS Institute).

On the basis of results of linear regression analyses and the prior knowledge, structural equation model (SEM) linking the abiotic and biotic factors with soil respiration was constructed using AMOS 17.0.2 (Amos Development Corporation). The goodness of model fit was evaluated based on chi-square and RMSEA (root mean square error of approximation) test (Grace & Bollen, 2005). The strength of total, direct and indirect effects of the abiotic and biotic factors on soil respiration was also estimated.

3 | RESULTS

3.1 | Soil microclimate

On average across all the four treatments, both soil temperature and moisture fluctuated substantially among the five experimental years (Figure 1; both $p < 0.001$, Table 1). Warming significantly increased soil temperature by 0.73°C averaged over the 5 years (Figure 1a; $p < 0.001$). However, neither N addition nor its interaction with warming affected soil temperature. In addition, both warming and N addition showed additive effects with year on soil temperature.

Soil moisture was significantly decreased by 0.38% V/V (absolute change) under the warming treatment (Figure 1b; $p < 0.001$; Table 1), but did not change under either the N addition or its interaction with

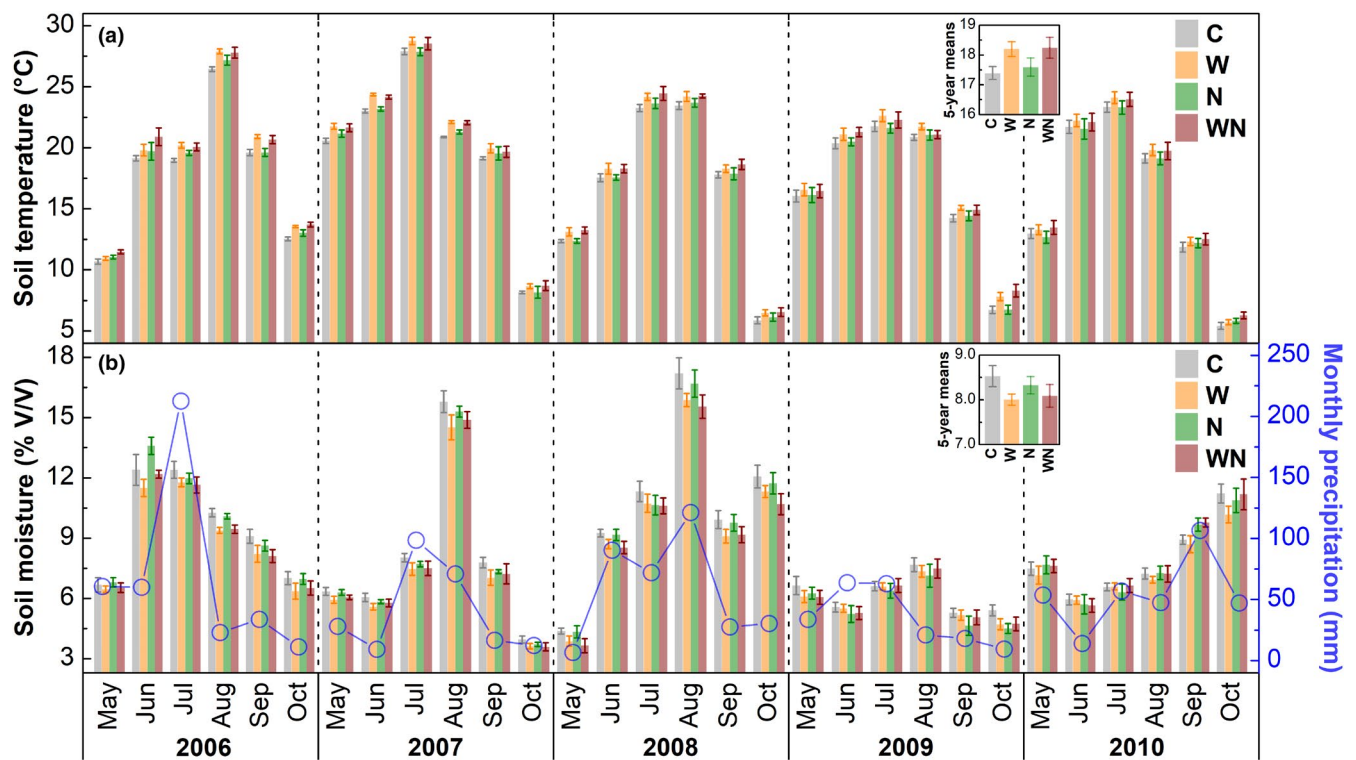


FIGURE 1 Seasonal dynamics of soil temperature (a) and soil moisture (b) and 5-year means (insets). Means \pm 1 SE, $n = 6$. The blue lines in panel (b) show monthly precipitation of the five growing seasons. C, control; N, nitrogen addition; W, warming; WN, warming plus nitrogen addition

TABLE 1 Results (p values) of two-way repeated-measures ANOVAs on the effects of W, N, year and their interactions on ST, SM, AGB, BNPP, forb:grass ratios, legume proportion and SR over the 5 years

Source of variation	ST	SM	AGB	BNPP	forb:grass ratios	Legume proportion	SR
W	<0.001	<0.001	0.995	0.130	0.206	0.008	0.834
N	0.175	0.564	<0.001	0.050	0.010	0.009	0.010
W × N	0.362	0.162	0.927	0.363	0.592	0.021	<0.001
Year	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Year × W	0.825	0.157	0.212	0.409	0.188	0.005	0.739
Year × N	0.745	0.483	<0.001	0.493	0.035	0.131	0.004
Year × W × N	0.936	0.946	0.128	0.617	0.992	0.529	0.912

Note: The bold values highlight the significance at $p < 0.05$.

Abbreviations: AGB, above-ground biomass; BNPP, below-ground net primary productivity; forb:grass ratios, the forb-to-grass biomass ratios; legume proportion, the proportion of legume biomass in the community; N, nitrogen addition; SR, soil respiration; ST and SM, soil temperature and moisture; W, warming.

warming. Additive effects between warming/N addition and year on soil moisture were also detected.

3.2 | Changes in plant biomass

Averaged over the 5 years, warming had no effect on AGB (Figure 2a; Table 1), but N addition significantly increased AGB by 20.6% ($p < 0.001$). There was no interaction between warming and N addition on AGB. In contrast, the effects of N addition on AGB changed with year ($p < 0.001$). Nitrogen addition significantly increased AGB by 19.2% (two-way ANOVAs, $p = 0.002$, see Table S4),

45.4% ($p < 0.001$) and 13.6% ($p = 0.002$) in 2006, 2008 and 2010, respectively. While N addition enhanced BNPP by 14.8% (Figure 2b; $p = 0.050$), BNPP was not affected by warming and its interaction with N addition. Both warming and N addition showed additive effects with year on BNPP.

When analysed separately by plant functional types, the forb:grass ratios were significantly reduced by 24.8% under the N addition averaged over the 5 years (relative change, Figure 2c; $p = 0.010$, Table 1), but were not changed under the warming and its interaction with N addition. The responses of forb:grass ratios to N addition varied with year ($p = 0.035$). Nitrogen addition significantly increased forb:grass ratios by 30.8% in 2006 (two-way ANOVAs, $p = 0.011$, see

FIGURE 2 Changes in above-ground biomass (AGB, a), below-ground net primary productivity (BNPP, b), the forb-to-grass biomass ratios (forb:grass ratios, c), and the proportion of legume biomass in the community (legume proportion, d) induced by warming (W-induced main effects, dark red circles) and N addition (N-induced main effects, dark green circles). The insets in panel d show the interactions between warming and N addition, that is, changes in legume proportion (LP) under warming in the ambient (aN, dark red triangles) and enriched N plots (eN, dark green triangles; the upper inset) as well as changes in LP under N addition in the ambient (aT, inverted dark red triangles) and elevated temperature plots (eT, inverted dark green triangles; the lower inset). Means ± 1 SE, $n = 6$. C, control; N, nitrogen addition; W, warming; WN, warming plus nitrogen addition

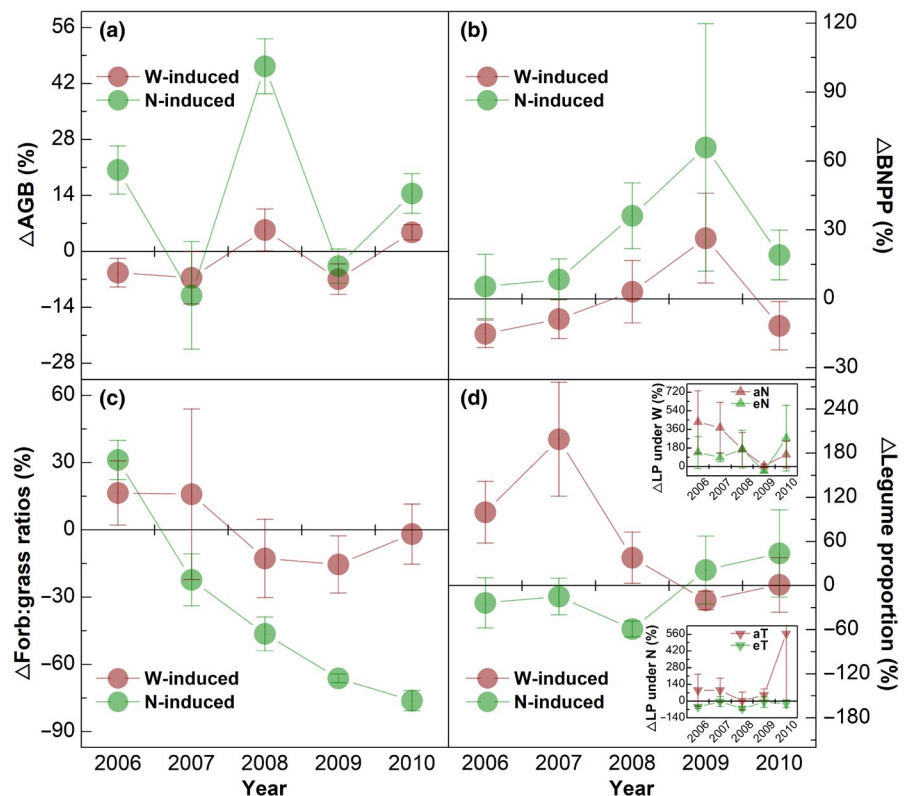


Table S4), but decreased it by 47.4% ($p < 0.001$), 65.9% ($p < 0.001$) and 80.6% ($p = 0.001$) in 2008, 2009 and 2010, respectively. The legume proportion was enhanced by 50.7% under the warming (Figure 2d; $p = 0.008$) but reduced by 33.0% under the N addition ($p = 0.009$). Warming also interacted with N addition to influence legume proportion ($p = 0.021$). Warming significantly increased legume proportion by 91.6% in the ambient N plots (Figure 2d insets; $p = 0.002$, see Table S5), but had no effect in the enriched N plots. In contrast, N addition did not affect legume proportion in the ambient temperature plots, but significantly decreased it by 47.2% in the elevated temperature plots ($p = 0.004$).

3.3 | Soil respiration

Soil respiration showed strong interannual variability during the 5 years (Figure 3a; $p < 0.001$, Table 1), with the lowest ($1.18 \mu\text{mol m}^{-2} \text{s}^{-1}$) and highest ($2.45 \mu\text{mol m}^{-2} \text{s}^{-1}$) values appeared in 2007 and 2008, respectively, averaged across all of the 24 plots. Over the 5 years, soil respiration was not affected by warming, but reduced by 3.7% by N addition ($p = 0.010$). In addition, significant interactions between warming and N addition on soil respiration were detected ($p < 0.001$). Warming significantly increased soil respiration by 5.8% in the ambient N plots (Figure 3b; repeated-measures ANOVAs, $p < 0.001$, see Table S5), but decreased it by 6.3% in the enriched N plots ($p = 0.002$). Nitrogen addition did not change soil respiration in the ambient temperature plots (Figure 3c), whereas significantly reduced it by 9.4% in the elevated temperature plots ($p < 0.001$). Moreover, the effects of N addition on soil respiration significantly varied with year ($p = 0.004$). Nitrogen addition significantly suppressed soil respiration by 5.0% (two-way repeated-measures ANOVAs, $p = 0.011$, see Table S4), 14.3% ($p < 0.001$) and 4.5% ($p = 0.013$) in 2008, 2009 and 2010, respectively.

3.4 | Controls of abiotic and biotic factors on soil respiration

Across the 5 years, there were no spatial relationships of soil respiration with soil temperature (Figure 4a), AGB (Figure 5a) or BNPP (Figure 5b). However, soil respiration showed positive and linear dependences on soil moisture (Figure 4b; $R^2 = 0.18$, $p = 0.042$), forb:grass ratios (Figure 5c; $R^2 = 0.21$, $p = 0.025$) and legume proportion (Figure 5d; $R^2 = 0.25$, $p = 0.013$). The best SEM could explain 51% of the spatial variations in soil respiration (Figure 6). Standardized total effect coefficients of continuous warming and N addition on soil respiration were -0.082 and -0.172 , respectively (see Table S6), which could be attributed to indirect rather than direct influences (see Tables S7 and S8). The effects of continuous warming on soil respiration were determined by the trade-off between decreased soil moisture and increased legume proportion in the community associated with elevated soil temperature. By contrast, N addition suppressed soil respiration primarily through

decreasing both forb:grass ratios and legume proportion in the community.

4 | DISCUSSION

4.1 | Effects of continuous warming

Our result that 24-hr continuous warming did not affect soil respiration is inconsistent with the findings of numerous previous warming studies (Song et al., 2019a). Most studies found increased soil respiration associated with elevated temperature. Those works have demonstrated that higher soil microbial activity and stimulated plant growth and productivity under elevated temperature accelerate the decomposition rates of soil organic matter and old C and consequently increase C release from soils (Chang et al., 2021; Högberg et al., 2001; Song et al., 2017; Walker et al., 2018; Wan et al., 2009). Irrespective of the widely accepted hypothesis of elevated temperature stimulating soil respiration (Bond-Lamberty & Thomson, 2010), there is an increasing evidence that local water availability may play an important role in controlling soil respiration responses to climate warming (Song et al., 2019a; Wang et al., 2014). In this study, no positive effect of experimental warming on either plant above-ground biomass or root productivity was detected, probably due to the fact that our experimental grassland is a water-limited temperate steppe (Liu et al., 2009). Water stress caused by experimental warming may overwhelm the positive effects of elevated temperature on plant photosynthesis and growth (Reich et al., 2018). Although continuous warming significantly decreased soil water availability of this experimental grassland, our findings of the neutral warming effects on soil respiration do not agree with our hypothesis 1 and the results of two previous studies that reported experimental warming-induced soil desiccation reduces soil respiration in grasslands (Liu et al., 2009; Wan et al., 2007).

Other works further suggest that plant functional types may be a key mediator of soil respiration responses to climate warming (Chen et al., 2017; Cowles et al., 2016). For example, a tallgrass prairie study has revealed that increased proportion of C_3 forbs in the community under elevated temperature enhances the magnitude of the warming-induced stimulations in soil respiration (Xu et al., 2015). However, we found that continuous warming had no effect on the forb-to-grass biomass ratios yet enhanced the proportion of legume biomass in the community. Our findings are similar to the observations of greater legume abundance, cover and biomass in a warmer climate, as revealed in several previous studies (Chen et al., 2017; Cowles et al., 2016; Wang et al., 2012). In this semi-arid grassland, legumes are more sensitive to soil temperature than soil moisture (see Figure S1), resulting in an increase in the legume proportion with increasing temperature even under the drought conditions created by experimental warming.

Stimulated growth and biomass of legumes under elevated temperature in this study might enhance soil respiration as there was a positive dependence of soil respiration on the proportion of legume

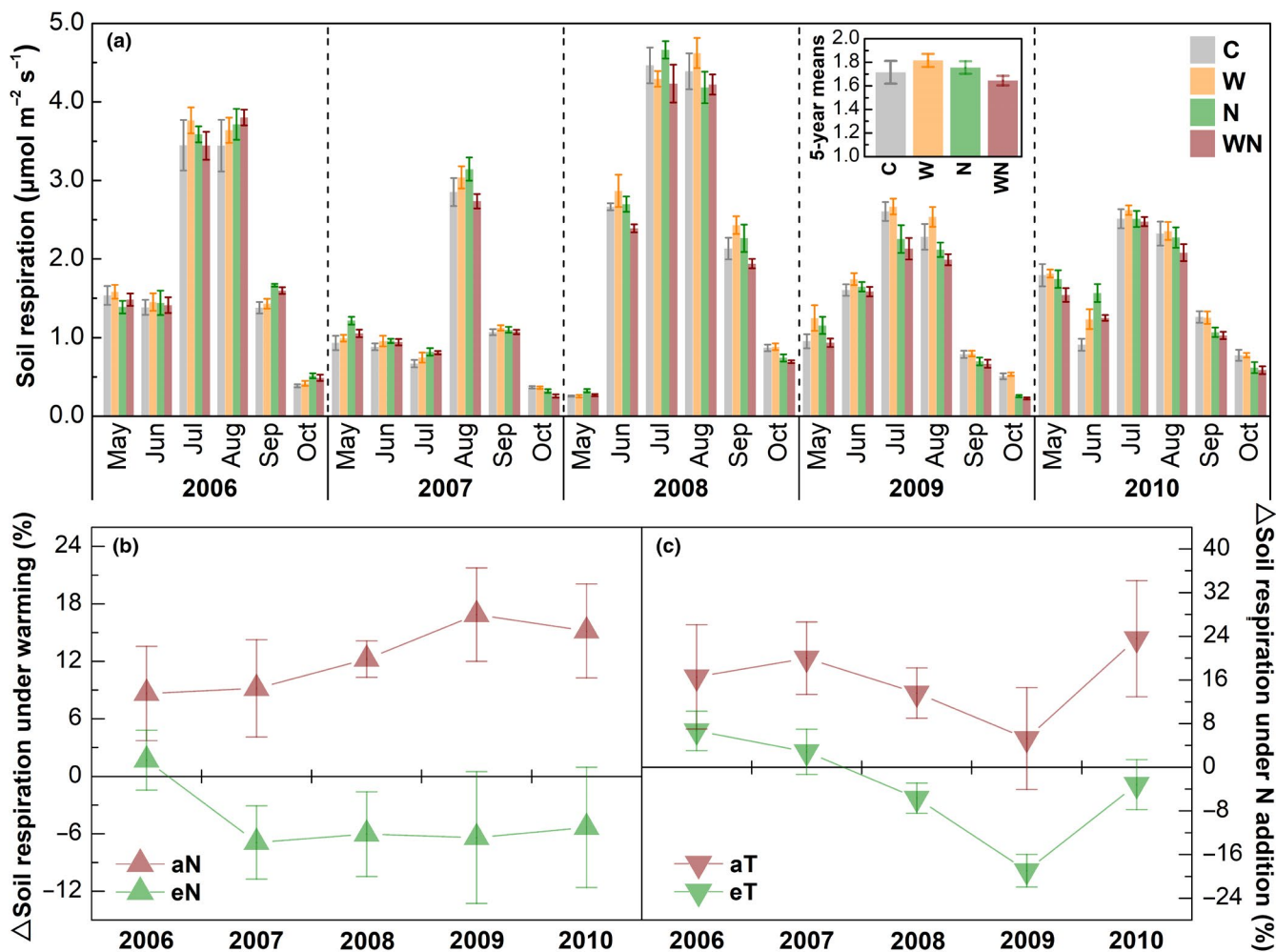
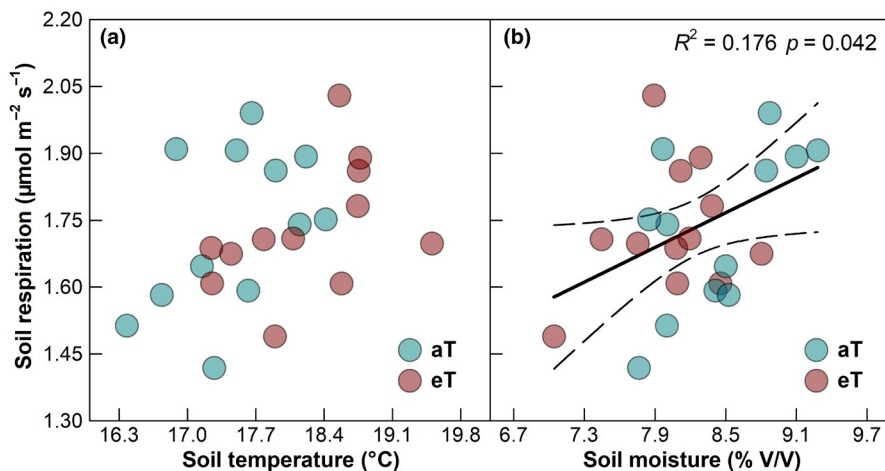


FIGURE 3 Seasonal dynamics of soil respiration and 5-year means (insets; a). The interactions between warming and N addition, that is, changes in soil respiration under warming in the ambient (aN, dark red triangles) and enriched N plots (eN, dark green triangles; b) as well as changes in soil respiration under N addition in the ambient (aT, inverted dark red triangles) and elevated temperature plots (eT, inverted dark green triangles; c). Means ± 1 SE, $n = 6$. C, control; N, nitrogen addition; W, warming; WN, warming plus nitrogen addition

FIGURE 4 Spatial relationships of soil respiration with soil temperature (a) and soil moisture (b). Each data point represents the 5-year mean value of each of the 12 ambient (aT, dark green circles) and 12 elevated temperature plots (eT, dark red circles). Solid and dashed lines describe linear regressions and 95% CIs, respectively



biomass in the community. The increased soil respiration might offset the potential decrease in soil respiration resulted from the warming-driven water stress, consequently leading to the neutral response of soil respiration to continuous warming. Results of our best

structural equation model further supported the above arguments. In combination with the findings of greater net ecosystem productivity with increasing biomass of legumes and grasses revealed in another grassland study (Chen et al., 2017), this study supports that

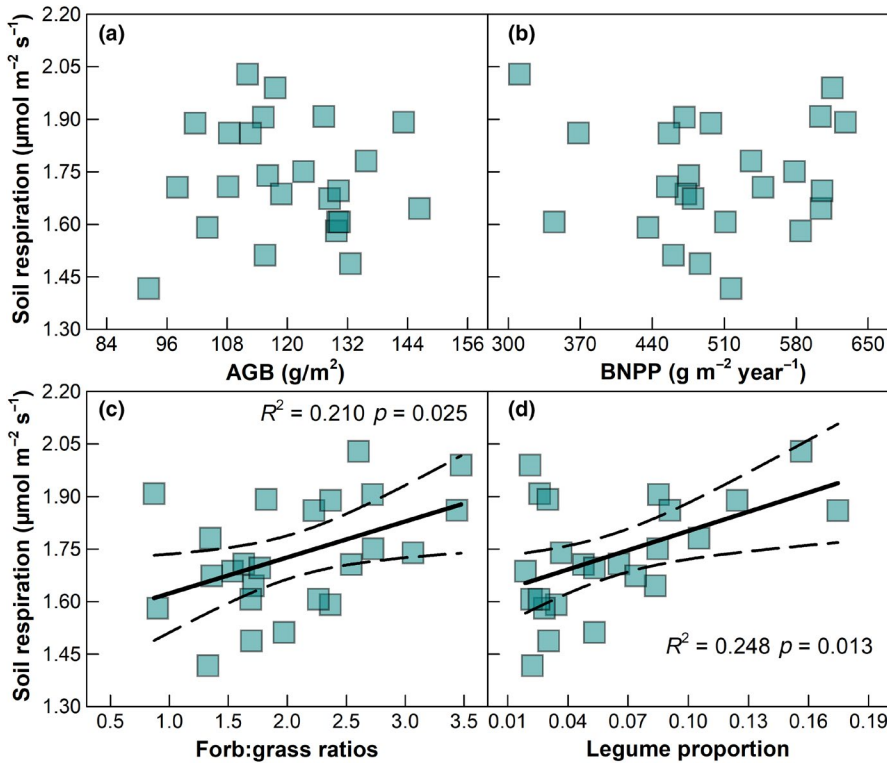


FIGURE 5 Linear dependences of soil respiration on AGB (a), BNPP (b), forb:grass ratios (c) and legume proportion (d). Each data point represents the 5-year mean value of each of the 24 plots. Solid and dashed lines describe linear regressions and 95% CIs, respectively. AGB, above-ground biomass; BNPP, below-ground net primary productivity; forb:grass ratios, the forb-to-grass biomass ratios; legume proportion, the proportion of legume biomass in the community

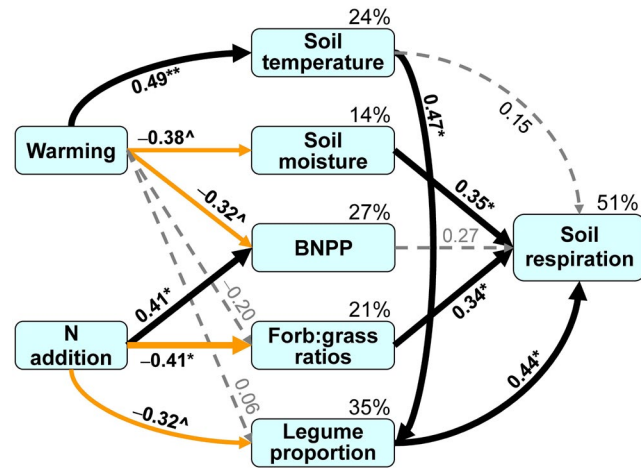


FIGURE 6 Structural equation model (SEM) shows all plausible pathways through which continuous warming and N addition influencing soil respiration. The final model fits the data well based on the chi-square and RMSEA tests ($\chi^2 = 14.6$, $p = 0.406$, $RMSEA = 0.043$, $df = 14$). Grey dashed arrows represent non-significant pathways. Orange and black solid arrows indicate significant negative and positive pathways, respectively. Numbers adjacent to the arrows are standardized path coefficients with different significance levels: $^{\wedge}p < 0.10$, $^*p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$. Percentage value for each dependent variable refers to the proportion of variance explained by the model. BNPP, below-ground net primary productivity; forb:grass ratios, the forb-to-grass biomass ratios; legume proportion, the proportion of legume biomass in the community

legumes, despite with relatively low biomass proportion in grassland plant communities (e.g. <13.4% in the control plots of this experiment), have disproportionately large effects on grassland C cycling.

The enhancement of the legume proportion increased soil respiration likely in two main ways. First, legume litter with low C-to-N ratios would decompose faster than litter of forbs and grasses (Epihov et al., 2017; Milcu et al., 2008). Second, the increase in the proportion of legume litter could further accelerate the decomposition rate of the whole litter layer on the ground (Kohmann et al., 2018; Song et al., 2020).

4.2 | Effects of N addition

The observations of decreased soil respiration under N addition in this study agree with our hypothesis 2 and the widely accepted consensus that N additions suppress soil respiration (e.g. Janssens et al., 2010; Song et al., 2019a). Irrespective of the positive effects of N enrichment on plant growth and productivity and thus C substrates for soil respiration (Song et al., 2019a; Xia & Wan, 2008), two potential mechanisms have been proposed to account for the N addition-induced reductions in soil respiration. First, soil acidification due to N enrichment could decrease soil microbial activity and rates of organic matter decomposition (Frey et al., 2014; Song et al., 2019a; Ye et al., 2018). Second, N addition could suppress the priming of soil organic matter (Fontaine et al., 2011). In addition, the reductions of root C allocation and root respiration have been documented to be responsible for the N addition-induced suppressions in soil respiration (Janssens et al., 2010; Song et al., 2019a). However, our finding that N addition increased below-ground net primary productivity does not support the above argument, further confirming that our experimental grassland is N-limited (Niu et al., 2010).

The regulatory effects of shifting plant functional types on soil respiration responses to N addition can represent another potential mechanism. For example, soil respiration is decreased with reducing dominance of forbs in plant communities after 1 or 2 years of N addition in grasslands (Du et al., 2018; Wang et al., 2019). Therefore, we expected that N addition would suppress soil respiration by decreasing growth of forbs in this semi-arid grassland (hypothesis 2). Indeed, the positive relationships between the main treatment effects (i.e. changes induced by the continuous warming and N addition) on soil respiration and the forb-to-grass biomass ratios support our hypothesis 2 (see Figure S2; $R^2 = 0.53$, $p = 0.017$). These observations suggest that the reductions in soil respiration under N addition after the third experimental year may be related to the decreased forb-to-grass biomass ratios after 2-year treatments of N application. In addition, our best structural equation model revealed a decreased legume proportion in the plots with high N availability, a result similar to the finding of a previous study (Storkey et al., 2015), could contribute to the N addition-induced reductions in soil respiration, further highlighting the important role of legumes in regulating C cycling of this semi-arid grassland.

4.3 | Interactive effects of continuous warming and N addition

Both additive and interactive effects between warming and N addition on soil respiration have been reported in several previous warming and N addition experiments, but the underlying mechanisms have not been well explored (Contosta et al., 2011; Fang et al., 2017, 2018; Graham et al., 2014; Liu et al., 2017; Zhao et al., 2017). In this study, we hypothesized that warming and N addition would interactively influence soil respiration (hypothesis 3) on the basis that different plant functional types would respond differently to the increases in temperature and N availability. For example, warming stimulates growth and biomass of forbs and legumes but N addition suppresses them (Du et al., 2018; Storkey et al., 2015; Wang et al., 2012, 2019; Xu et al., 2015). Our result of the nonlinear responses of soil respiration to continuous warming and N addition over the five experimental years is consistent with our hypothesis 3. In addition, our observations of the additive effects of warming and N addition on soil microclimate are similar to the findings of two previous studies (Liu et al., 2017; Xia et al., 2009), suggesting that the changes in soil temperature or moisture could not account for the interactions between warming and N addition on soil respiration.

The finding of the significantly positive effects of continuous warming on soil respiration in the ambient N plots in this study is similar to the results of numerous previous studies (Song et al., 2019a) and could be attributed to the stimulation of legume growth in response to elevated temperature. In the enriched N plots, however, no change in the legume proportion and decreased soil moisture under elevated temperature might largely account for the warming-induced suppressions in soil respiration, partly supporting our hypothesis 1 and further confirming the predominant role of

soil water availability in controlling C cycling in this semi-arid grassland (Liu et al., 2009; Xia et al., 2009). However, our result that the proportion change of legume biomass was one of the main factors regulating the effects of climate warming on soil respiration is different from a previous study that reported greater dominance of forbs enhances soil respiration under experimental warming in a tallgrass prairie (Xu et al., 2015). The aforementioned finding also highlights the importance of conducting more manipulative experiments in different ecosystems in the future, which can substantially improve our mechanistic understanding on soil respiration responses to climate warming at regional and global scales (Qiu, 2014; Song et al., 2019a).

The reductions in soil respiration under the N addition treatment only being observed in the elevated temperature plots in this study may be attributed to the decreased proportion of legume biomass in the community, consistent with the widely accepted consensus that the competitive advantage of legumes could decline with increasing N availability in terrestrial ecosystems (Storkey et al., 2015). Overall, this study has revealed that interactive effects of the concurrent increases in temperature and N availability were mainly driven by the shifts of plant community composition—a result supporting our hypothesis 3. Our findings indicate that N deposition may reverse the positive feedback between climate warming and C loss from soils into a negative feedback in this semi-arid grassland and potentially slow down the processes of climate warming. Given the great significance of arid and semi-arid ecosystems in land C sink estimation and global C cycling (Ahlström et al., 2015), incorporating our findings into biogeochemical and ecosystem models could generate more accurate assessment of climate change–terrestrial C feedback and global C cycling (Greaver et al., 2016).

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHORS' CONTRIBUTIONS

S.W. designed the experiment; J.X. performed the experiment; J.S. analysed the experimental data and wrote the first draft of the manuscript; D.H., M.Z. and J.W. contributed substantially to data analyses and manuscript revisions. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.t76hdr81t> (Song et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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