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The response of soil respiration to different N compounds addition in a saline–alkaline grassland of northern China

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Abstract

The increase in atmospheric nitrogen (N) deposition has profound effects on soil respiration (SR). However, the responses of SR to the addition of different N compounds, particularly in saline–alkaline grasslands remain unclear. A 3-year controlled field experiment was conducted to investigate the responses of SR to different N compounds (NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3) during the growing seasons in a saline–alkaline grassland located in the agro-pastoral ecotone of northern China. Our results demonstrated that SR showed a bimodal pattern and a significant interannual difference that was regulated by air or soil temperature and precipitation. Nitrogen addition had a significant effect on SR, and the effect of N addition on SR varied yearly, which was related to seasonal precipitation. The mean SR across 3 years (2017–2019) was increased by 19.9%, 13.0% and 16.6% with the addition of NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3, respectively. The highest effect of NH_4NO_3 addition on SR across 3 years was ascribed to the highest aboveground net primary production, belowground net primary production (BNPP) and soil NO_3^- concentrations. SR (C loss) was significantly increased while plant productivity (C input) did not significantly change under NH_4HCO_3 addition, indicating a decrease in C sequestration. In addition, BNPP was the main direct factor influencing SR in this saline–alkaline grassland, and soil salinization (e.g. soil base cations and pH) indirectly affected SR through soil microorganisms. Notably, NH_4NO_3 addition overestimated the response of SR to N addition, and different N compounds should be considered, especially in saline–alkaline grassland.

Keywords nitrogen compounds, soil respiration, soil microorganism, plant biomass, saline–alkaline grassland

不同形态氮化合物添加对中国北方盐渍化草地土壤呼吸的影响

摘要：持续增加的氮沉降在提高陆地生态系统生产力的同时也会对土壤微生物产生显著影响；土壤呼吸由植物根系呼吸和土壤微生物呼吸组成，因此影响植物生产力和微生物的因子都会影响到土壤呼吸。以往氮富集对土壤呼吸的研究主要在土壤中性的草地生态系统开展，而对于盐渍化草地土壤呼吸是如何响应氮沉降的研究尚不多见，这限制了全球变化陆地生态系统土壤呼吸模型预测的准确性和完整

性。本研究以中国北方农牧交错带盐渍化草地为研究对象，通过3年(2017–2019年)野外监测土壤呼吸及相关生物和非生物因子的变化，探讨了不同形态氮化合物添加(NH_4NO_3、$(NH_4)_2SO_4$和NH_4HCO_3)对盐渍化草地土壤呼吸的影响及其调控机制。结果表明：(i)土壤呼吸受大气温度、土壤温度及降水的调控，呈现双峰的季节动态变化趋势和显著的年际差异。(ii)与对照相比，经过3年的处理，土壤呼吸在NH_4NO_3、$(NH_4)_2SO_4$和NH_4HCO_3添加处理下分别提高了19.9%、13.0%和16.6%。(iii)NH_4NO_3添加对土壤呼吸较高的促进作用与较高的地上生物量、地下生物量以及土壤NO_3^-含量有关。(iv)在NH_4HCO_3添加处理下，土壤碳排放(土壤呼吸)显著增加而碳输入(净生产力)无显著改变，表明NH_4HCO_3添加会降低土壤碳的固持。(v)净地下生产力(BNPP)是盐渍化草地土壤呼吸的最主要调控因子，并且土壤阳离子浓度和pH值通过影响土壤微生物间接影响土壤呼吸。上述研究结果表明，草地添加NH_4NO_3的研究高估了氮沉降对土壤呼吸的影响，并且在碳循环预测模型中应充分考虑盐渍化草地土壤碳动态。

关键词：氮化合物，土壤呼吸，土壤微生物，植物生产力，盐渍化草地

INTRODUCTION

With the continuous increase in atmospheric nitrogen (N) deposition (Gruber and Galloway 2008; Kanakidou *et al.* 2016), the additional N inputs have a large potential effect on ecosystem carbon (C) cycling processes (Neff *et al.* 2002; Zhou *et al.* 2014) and consequently feedback to climate changes (Kirschbaum 2000; Melillo *et al.* 2002). Soil respiration (SR) is the second-largest C flux between soil and atmosphere and plays an essential role in regulating terrestrial C cycles (Bond-Lamberty and Thomson 2010; Schimel 1995).

To date, there is no consistent consequence relevant to the effects of N addition on SR. N addition showed positive (Feng *et al.* 2017; Zhang *et al.* 2014; Zhou *et al.* 2016), negative (Du *et al.* 2018; Ward *et al.* 2017; Wei *et al.* 2018) or neutral effects (Zhang *et al.* 2017) on SR in different ecosystems. These inconsistent results may attribute to the different responses of root growth and soil microorganisms, which regulated the variations of soil autotrophic and heterotrophic respiration, respectively (Du *et al.* 2018; Wei *et al.* 2018; Yan *et al.* 2010). Nitrogen deposition promotes root growth in N-restricted regions and reduces root biomass when N reaches saturation by the experiment of N gradient addition (Peng *et al.* 2017; Zeng *et al.* 2018). Therefore, the response of root-dominated autotrophic respiration to N addition was uncertain yet. The consistent results indicate that the soil heterotrophic respiration driven by soil microorganisms was inhibited under N addition due to the decrease in microbial biomass (Wei *et al.* 2018; Zhang *et al.* 2018), the change in the microbial community (Liu *et al.* 2018; Zhang *et al.* 2018), the decrease in soil enzyme activity (Widdig *et al.* 2020) and the changes in soil substrate quality and quantity (Shahbaz *et al.* 2018). To sum up, inconsistent or even opposite responses of SR to N addition related to climate zones, grassland types, the quantity of N addition and soil N availability, which still need a further study for accurately predict the terrestrial ecosystem C flux.

Generally, atmospheric N deposition contains various N forms (NH_4-N and NO_3-N) (Liu *et al.* 2013). Soil microorganisms and N transformation were affected by the addition of different N compounds (NH_4^+-N or NO_3^--N) (Ying *et al.* 2017), and soil microbial respiration presented different responses to N addition when different N compounds were used (Ramirez *et al.* 2010; Wang *et al.* 2018; Zeng 2017). The uptake and utilization strategies of different N sources by plants are different (Diao *et al.* 2021; Högberg 1997), and the branching and elongation of lateral roots were enhanced under the combination of NH_4^+-N and NO_3^--N addition (Takushi and Hitoshi 2016). Therefore, the effect of N addition on SR was related to N forms owing to different responses of plant and soil microorganisms. However, most studies focused on a single N compound in the field study, and thus the accurate understanding of the effects of atmospheric N deposition on SR was limited.

Moreover, the area of saline–alkaline land worldwide reached 11.7 M km^{-2} (Hassani *et al.* 2020), which is one of the major environmental challenges of next century. Soil salinization (salinity and pH) is a crucial factor affecting SR through microbial community and plant growth (Rath and Rousk 2015; Yan and Marschner 2013; Yang *et al.* 2018). Most studies revealed a negative relationship between soil salinity and SR (Setia *et al.* 2011; Yang *et al.* 2019a). This is due to that higher soil salinity was often accompanied with lower osmotic potential of the soil solution and imbalanced of ions, which inhibited plant growth and soil microbial activity (Rath and Rousk 2015; Yang *et al.* 2018). Besides, the changes in soil pH induced by N addition were also a main factor affecting microbial community structure and then regulating SR (Du *et al.* 2018; Rousk *et al.* 2010). While soil base cations play a vital role in alleviating soil acidification (Cai *et al.* 2017; Tian and Niu 2015). Thus, the response of soil pH and exchangeable base cations (Na^+, Ca^{2+}, Mg^{2+} and K^+) to N addition would then affect plants and soil microorganisms and then affect SR. However, it is still unclear whether N addition of different compounds would affect SR through soil base cations and pH in saline–alkaline grassland.

The agro-pastoral ecotone in northern China covers about 6.5 × 10^5 km^2 and is a transitional region from farmland to natural grassland (Yang *et al.* 2019b). The grassland in this area has suffered different degrees of salinization, and is extremely sensitive to nutrient input and environmental changes. Hence, the responses of SR to N addition in the saline–alkaline grassland could be different from previous studies conducted in non-saline–alkaline grassland; the response of SR could vary with the addition of different N compounds ascribed to the different transformation and utilization processes (Takushi and Hitoshi 2016; Ying *et al.* 2017). In this study, the responses of SR to different N compounds (NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3) in this saline–alkaline grassland during the growing seasons were investigated by performing a 3-year controlled field experiment. Specifically, the following two major questions were addressed: (i) Whether soil respiration varied with the addition of different N compounds in saline–alkaline grassland? (ii) Which is the main factor affecting soil respiration under the addition of different N compounds in the saline–alkaline grassland?

MATERIALS AND METHODS

Site description

This study was performed at Youyu Loess Plateau Grassland Ecosystem Research Station, Shanxi Province, China (112°19′39″ E, 39°59′48″ N, 1348 m a.s.l.), which located in agro-pastoral ecotone of northern China and the soil is seriously saline alkalined. The mean annual precipitation is 426 mm, of which the rainfall from June to August exceeds 60%–75% (1991–2019); the mean annual temperature is 4.6 °C in this area according to local weather data records, and the maximum and minimum mean monthly temperature occurs in July and January, respectively (1991–2019). The growing season is from May to September. A weather station (HOBO U30-NRC, USA) was established near the study site to record air temperature and precipitation. The dominated species are *Leymus secalinus* (Georgi) Tzvel., *Puccinellia distans* (Linn.) Parl. and *Saussurea amara* (Linn.) DC. The soil in this site was chestnut soil (Chinese classification) or Calcic Luvisol. Soil pH value in the topsoil (0–10 cm) is between 9 and 10. Exchangeable base cations of potassium (K^+), calcium (Ca^{2+}), sodium (Na^+) and magnesium (Mg^{2+}) before treatments were 94 ± 3, 1452 ± 25, 410 ± 17 and 307 ± 22 mg kg^{-1} dry soil, respectively.

Experimental design

The experiment was conducted in April 2017 based on a randomized block design. Three types of N compounds (NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3) were added as the experimental treatment group; no N addition was set as the control (CK). Six blocks were selected represent six replicates in this experiment, and each block consists of four plots. The area of each plot was 7 m × 9 m, and plots were separated by 2 m buffer zone in each block. The amount of N addition is 10 g N m^{-2} y^{-1} for each N compounds (NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3); and N addition was applied by broadcast at the beginning of May once a year. In order to simulate the general management of grassland in agro-pastoral ecotone of northern China, mowing was carried out in all plots once a year in mid-August.

SR, soil moisture and soil temperature measurements

In April 2017, 48 PVC collars (20 cm in diameter and 5 cm in height) were inserted into 3 cm soil with an interval of 1 m from the edge in each plot. The plants in the PVC collars were removed before the measurement day to avoid the aboveground plant respiration. Soil CO_2 flux was measured using LI-840 System (Li-Cor, Lincoln, NE, USA) connected to the SR chamber between 9:00 a.m. and 12:00 a.m. (local time) by twice a month from May to September in 2017, 2018 and 2019. During the measurements, the covering chamber was tightly buttoned on the PVC collar. Each measurement was recorded about 2–3 min.

The soil temperature (ST, thermometer, China) and soil moisture (SM, TDR-300 probe, Spectrum, USA) were measured at 10 cm soil depth once a week as well as the same time when SR was monitored.

Plant and soil sampling and measurements

Aboveground net primary productivity (ANPP) was measured by clipping all living plants above the soil surface within a quadrat (0.2 m × 1 m) in each plot at mid-August each year (2017, 2018 and 2019). Meanwhile, root in-growth core method was used to estimate the belowground net primary productivity (BNPP) in 2017, 2018 and 2019. A 40-cm deep cylindrical holes were excavated using 10-cm diameter soil augers in each plot in late April; and the hole was refilled by the same soils after removing roots through 2 mm sieves. Soil samples (0–40 cm) were collected at the original root in-growth holes using 7-cm diameter soil augers and washed using a 0.45-mm mesh bag in late October. All plant samples of above- and belowground biomass were dried immediately at 65 °C for 72 h and weighed as ANPP and BNPP.

In the middle of August each year (2017, 2018 and 2019), three soil cores with a diameter of 5 cm and a depth of 10 cm were collected in each plot, mixed as one soil sample, passed through a 2 mm sieve, and then transported to the laboratory for next analyses. The soil bulk density (BD) was measured with the ring knife method, and the oven-drying method was then used to measure the soil water content. Soil pH values were determined with a ratio of soil to the water of 1:5 (w/v); then, the soil was shaken for 30 min, and a pH meter was used to determined soil pH values. Ammonia (NH_4^+) and nitrate (NO_3^-) of 10 g soil were extracted with 50 mL of 0.5 mol L^{-1} K_2SO_4 solution and then analyzed using Auto Analyzer (Continuous-Flow Analysis-CFA, SEAL, Germany). The fumigation-extraction method was adopted to determine microbial biomass carbon (MBC) and nitrogen (MBN), and TOC elemental analyzer was employed (Elementar TOC, Elementar Co., Hanau, Germany) after 0.5 mol L^{-1} K_2SO_4 solution. Ammonium acetate extract method with an atomic absorption spectrometer (AAS, Shimadzu, Japan) was used to determine soil exchangeable potassium (K^+), calcium (Ca^{2+}), sodium (Na^+) and magnesium (Mg^{2+}), and sum of this exchangeable base cations (SEB) was then calculated.

Statistical analysis

Two-way ANOVA was used to test the effects of year, N compounds and their interactions on SR, ST and SM. The effects of N addition of different compounds (NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3) on SR, ST and SM were also analyzed by repeated measurements in each year. One-way ANOVA was conducted to determine the response of seasonal mean SR across 3 years (2017, 2018 and 2019) to different treatments (CK, NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3), and multiple comparisons were performed among treatments. Linear or nonlinear simple regression was conducted to determine the relationships of SR with ST, SM, pH, base cations, ANPP and BNPP in 2017, 2018 and 2019, respectively. The mentioned statistical analyses were conducted by the SPSS version 25 (SPSS Inc., Chicago, IL, USA). Principal component analysis (PCA) was conducted to present the relationship among SR and relevant factors (ANPP, BNPP, ST, SM, BD, NH_4^+, NO_3^-, MBC, MBN, pH, K^+, Ca^{2+}, Na^+, Mg^{2+}, SEB). Redundancy analysis (RDA) was also conducted to quantify the contributions of relevant factors to the variations in SR. PCA and RDA analysis were conducted by Canoco 5.0. A conceptual diagram based on structural equation modeling (SEM) was conducted to illustrating the direct and indirect effect of N addition on SR through pathways of soil environment (ST, SM, BD), plant biomass (ANPP, BNPP), soil available N (NH_4^+, NO_3^-), soil salinization (pH, K^+, Ca^{2+}, Na^+, Mg^{2+}) and soil microbial biomass (MBC, MBN, MBC/MBN). The path coefficients were reported as standardized effect sizes. The SEM was adopted using the Amos version 21.0 (Amos Development Corporation, Chicago, IL, USA). Sigma Plot 12.5 (Systat Software Inc., San Jose, CA, USA) was used to create figures.

RESULTS

Abiotic and biotic factors

The rainfall during the growing season (May–September) was 282, 460 and 255 mm in 2017, 2018 and 2019, respectively, and the most amount of rainfall happened in July and August (Fig. 1a and b). There was a severe precipitation event (54 mm) in later April 2019, lead to the higher soil water content in the early growing season (Fig. 1e). The mean air temperature (May–September) was 17.5, 16.8 and 16.0 °C in 2017, 2018 and 2019, respectively. The mean value of ST and SM during growing seasons in control plots was 20.5 ± 0.2 °C and 22.4% ± 2.7%, 20.1 ± 0.2 °C and 23.5% ± 1.9%, 21.1 ± 0.1°C and 30.1% ± 3.2% in 2017, 2018 and 2019, respectively (Fig. 1c–f). Compared with control, NH_4NO_3 addition significantly reduced ST by 0.9 and 1.5 °C in 2018

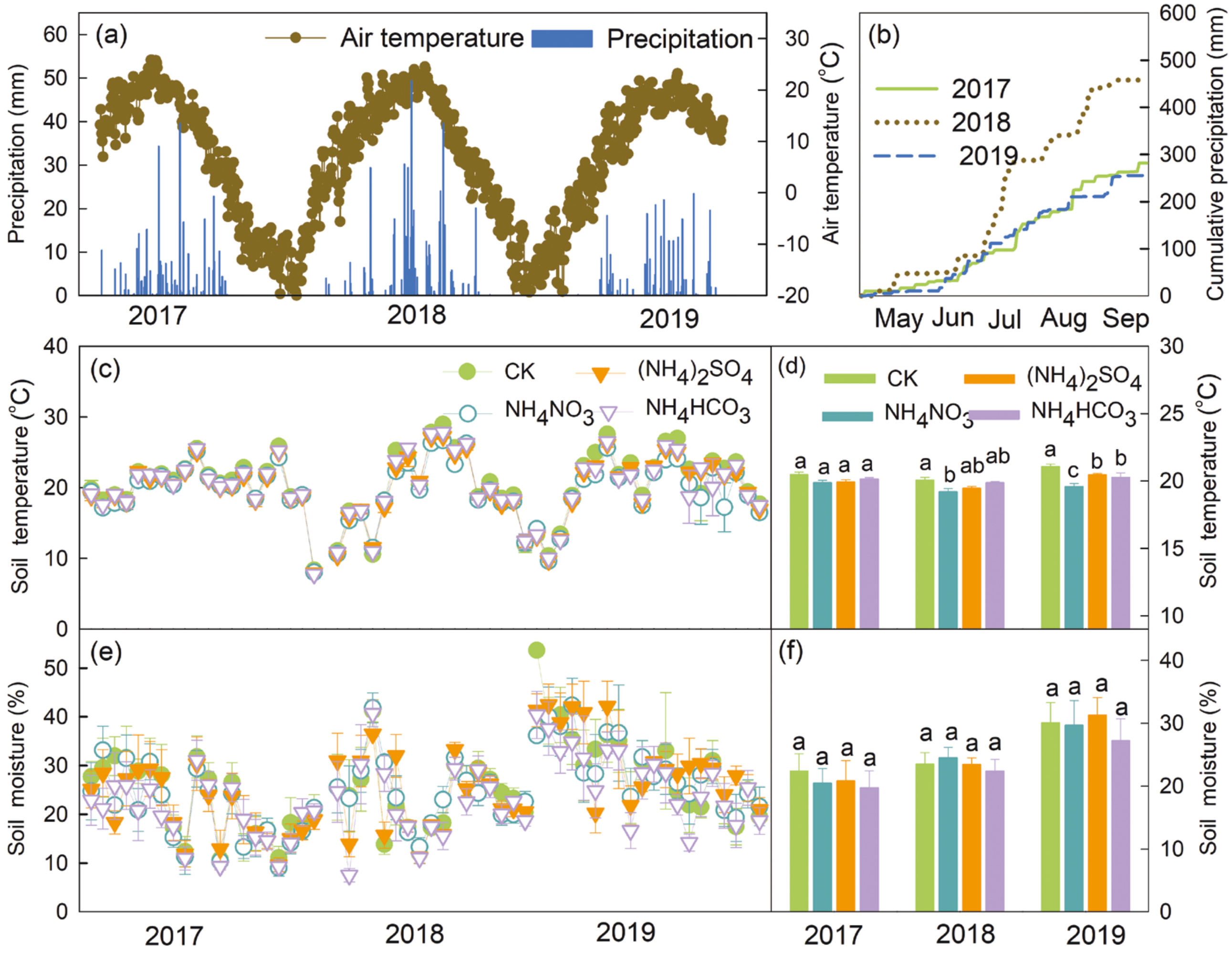

Figure 1: Daily average air temperature and the cumulative precipitation during growing seasons at the study site from 2017 to 2019 (**a**, **b**). Seasonal variations and mean values of ST (**c**, **d**) and SM (**e**, **f**) under different treatments (CK, NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3) at depth of 10 cm in 2017, 2018 and 2019, respectively. Different letters in the bar chart indicate significant differences among treatments ($P < 0.05$).

and 2019, respectively (Fig. 1d), while $(NH_4)_2SO_4$ and NH_4HCO_3 addition significantly lowered ST by 0.6 and 0.8 °C in 2019, respectively (Fig. 1d). However, N addition of different compounds had no significant effect on SM in 2017, 2018 and 2019 (Fig. 1e and f).

The addition of different N compounds had no significant effect on soil exchangeable K^+, Ca^{2+}, Na^+, Mg^{2+} and sum of these base cations (SEB) across 3 years (2017–2019) ($P > 0.05$, Fig. 2), except that soil Mg^{2+} concentration was significantly decreased udder the addition of NH_4NO_3 and $(NH_4)_2SO_4$ treatment in 2019 ($P < 0.05$, Supplementary Table S1). There was no significant difference among treatments of soil pH in 2017, 2018 and 2019 (Fig. 2). While NH_4NO_3 addition significantly decreased soil pH in 2019 compare with control based on one-way ANOVA ($P < 0.05$, Supplementary Table S1). Nitrogen addition of different compounds had no significant effect on soil pH values ($P > 0.05$, Supplementary Table S1).

N addition had no effect on ANPP in 2017 and 2018, while ANPP was increased by 142.4%, 47.8% and 39.7% under NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3 addition, respectively, in 2019 ($P < 0.05$, Supplementary Table S1). The main effect of N addition significantly affected BNPP during 3 years ($P = 0.05$, Supplementary Table S1). $(NH_4)_2SO_4$ addition significantly increased BNPP by 107.7% in 2019, while NH_4NO_3 and NH_4HCO_3 addition had no significant effect on BNPP during 3 years (Supplementary Table S1). However, across 3 years (2017–2019), NH_4NO_3 addition had the highest promotion effect on ANPP and BNPP than that of $(NH_4)_2SO_4$ and NH_4HCO_3 addition (Supplementary Fig. S1). The addition

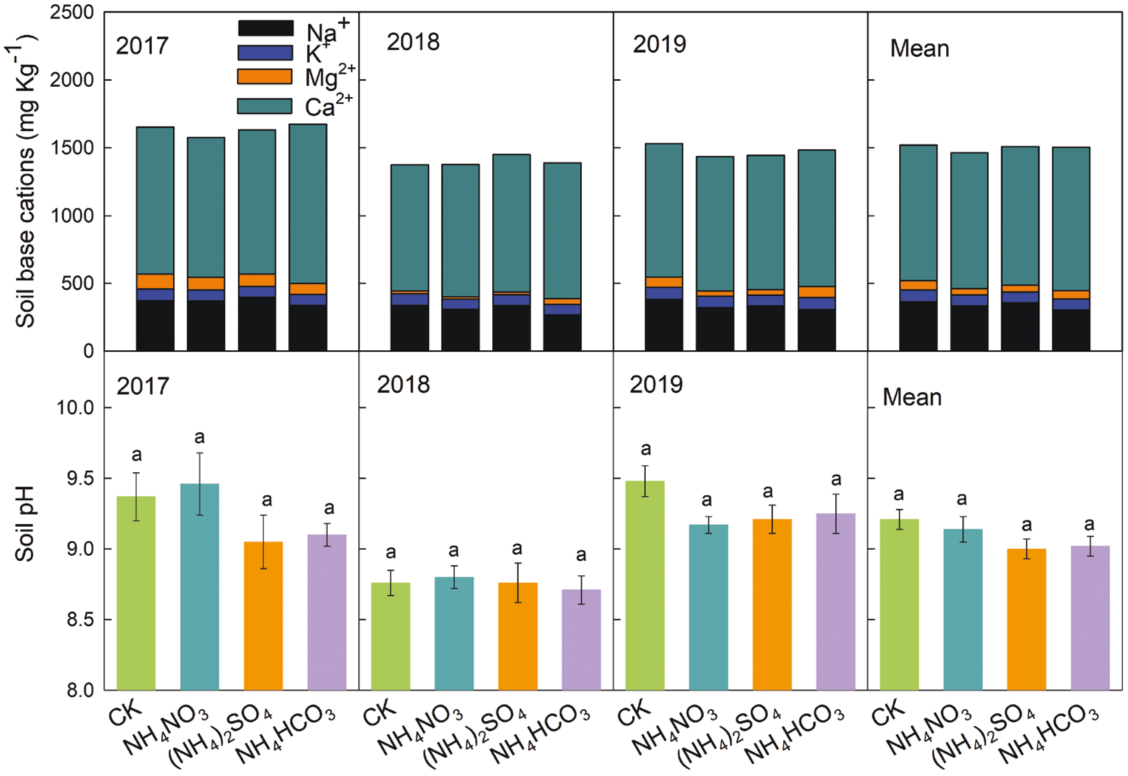

Figure 2: Effects of different N compounds addition (NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3) on soil exchangeable base cations (K^+, Ca^{2+}, Na^+, Mg^{2+}; 10 cm in depth) and soil pH (10 cm in depth) in 2017, 2018 and 2019, respectively. Different letters in the bar chart indicate significant differences among treatments ($P < 0.05$).

of different N compounds had no significant effect on MBC during 3 years, while NH_4NO_3 addition significantly reduced MBN by 48.4% in 2018 and by 29.4% across 3 years ($P < 0.05$). Under NH_4NO_3 addition, soil NO_3^- concentration was significantly increased by 32.6% in 2018, and by 27.3% across 3 years ($P < 0.05$), while NH_4^+ concentration remained unchanged in 2017, 2018 and 2019 ($P > 0.05$, Supplementary Table S1 and Fig. S1). NH_4NO_3 addition significantly decreased soil BD by 7.4% and7.9% in 2018 and 2019, respectively ($P < 0.05$); $(NH_4)_2SO_4$ addition only significantly decreased soil BD by 7.4% in 2019 ($P < 0.05$); while NH_4HCO_3 addition had no effect on soil BD during 3 years ($P > 0.05$). The mean value of soil BD across 3 years (2017–2019) was significantly lowered by 6.0%, and 4.6% with NH_4NO_3 and $(NH_4)_2SO_4$ addition, respectively ($P < 0.05$, Supplementary Table S1 and Fig. S1).

Response of SR to different N compound addition (NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3)

There was a significantly interannual variability in seasonal SR during the three measurement years ($P < 0.001$, Table 1). The mean value of SR in 2017, 2018 and 2019 was 2.81 ± 0.14, 2.36 ± 0.15, 3.16 ± 0.11 μmol m^{-2} s^{-1}, respectively. The sampling date had the main effect on SR in all three experimental years ($P < 0.001$, Table 2). Throughout the growing season of the three measurement years, the seasonal dynamics of SR followed a bimodal pattern, with the highest values in early July and early August (Fig. 3). The mean value of SR across 3 years under the control, NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3 treatment was 2.50 ± 0.15, 2.96 ± 0.16, 2.79 ± 0.10 and 2.87 ± 0.11 μmol m^{-2} s^{-1}, respectively.

The main effect of N addition significantly affected SR across three sampling years ($P < 0.05$, Table 1).

Table 1: Results (*F* values) of two-way ANOVA testing the effects of year, N addition of different compounds and their interactions on SR, ST and SM across 3 years (2017–2019)

	SR	ST	SM
Year (Y)	32.87***	12.39***	10.86***
N addition (N)	6.05**	12.35***	0.43
Y × N	1.32	1.36	0.12

** and *** indicate statistically significant at $P < 0.01$ and $P < 0.001$, respectively.

Table 2: Results (*F* values) of repeated-measures ANOVA for testing the effects of sampling date, N addition of different compounds and their interactions on SR, ST and SM in 2017, 2018 and 2019, respectively

	SR			ST			SM		
	2017	**2018**	**2019**	**2017**	**2018**	**2019**	**2017**	**2018**	**2019**
Date (D)	62.93***	28.20***	86.18***	299.22***	489.30***	74.82***	24.26***	21.67***	15.72***
N addition (N)	0.75	3.90*	4.82*	2.30	4.51*	6.91**	0.16	0.26	0.25
D × N	1.17	1.69*	0.66	0.44	1.18	0.95	0.89	1.58*	0.97

*, ** and *** indicate statistically significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

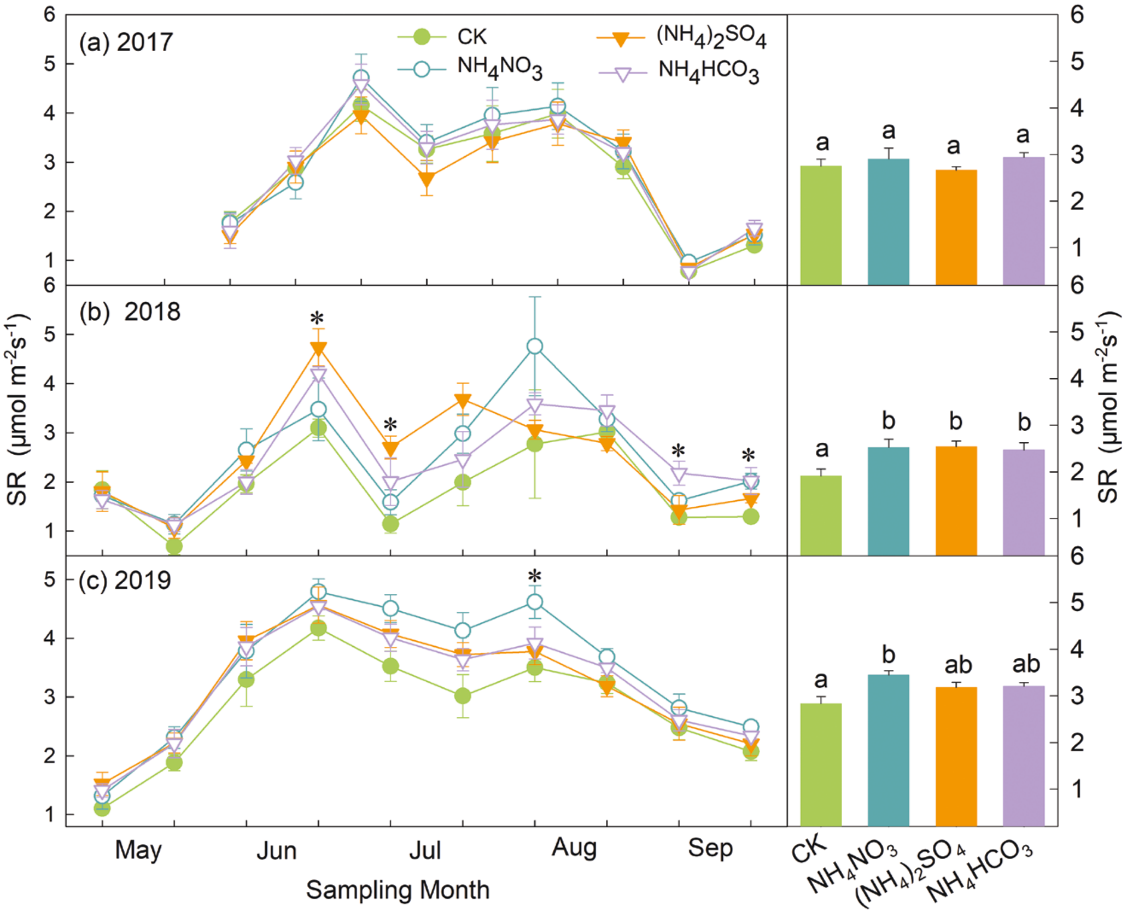

Figure 3: Seasonal variations of SR and their mean values under different treatments (CK, NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3) in 2017 (**a**), 2018 (**b**) and 2019 (**c**). Data with '*' represent that the differences among treatments is significant with $P < 0.05$; and different letters in the bar chart indicate significant differences among treatments ($P < 0.05$).

In 2017, no significant effect of different N compound addition on SR was observed (Table 2; Fig. 3a). In 2018, SR was significantly increased by 37.1%, 38.6% and 35.5% under NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3 addition compared with the control, respectively (Table 2; Fig. 3b). During the growing season of 2019, SR was significantly increased by 23.6% with NH_4NO_3 addition ($P < 0.05$, Fig. 3c); NH_4HCO_3 addition had a marginally effect on SR with an increase by 15.3% compared to control ($P = 0.06$, Fig. 3c); while $(NH_4)_2SO_4$ addition had no significant effect on SR ($P > 0.1$, Fig. 3c). The mean promoting effect of the mean SR across 3 years of NH_4NO_3 addition (by 19.9%, $P < 0.05$) was greater than that of $(NH_4)_2SO_4$ (by 13.0%, $P > 0.05$) and NH_4HCO_3 addition (by 16.6%, $P < 0.05$, Supplementary Fig. S2). The cumulative C emissions from soil during the growing season were calculated by interpolation method between each measurement, and the difference among treatment was significant after

July in 2018 and 2019 (Supplementary Fig. S3). Compared with control, the mean soil cumulative C emission across 3 years (2017–2019) was also significantly increased under NH_4NO_3 and NH_4HCO_3 addition ($P < 0.05$, Fig. 4).

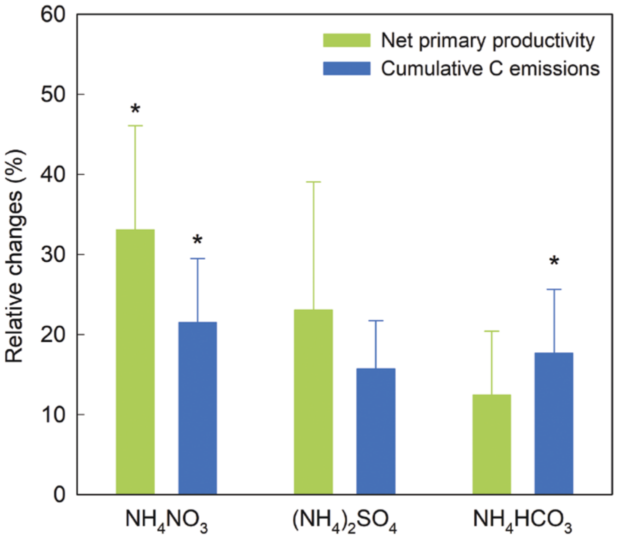

Figure 4: Relative changes of the net primary productivity (NPP, ANPP + BNPP) and the cumulative soil C emissions during growing season to N addition of different compounds (NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3) across 3 years (2017, 2018 and 2019). Data with '*' represent that the differences among treatments is significant with $P < 0.05$.

Relationships between SR and abiotic/biotic factors

During the growing seasons, monthly mean SR was positively correlated with monthly mean air temperature (Fig. 5a), while presenting a first increasing and then decreasing trend with monthly precipitation (Fig. 5b). Besides, annual mean SR also first increased and then decreased with annual precipitation (Fig. 5c). The relative changes in SR induced by the addition of different N compounds showed a significant positive correlation with annual precipitation (Fig. 5d). There was a positive relationship between SR and ST in 2017, 2018 and 2019 (Supplementary Fig. S4a–c), while no significant correlation between SR and SM in 2017 and 2018, and SR was even negatively correlated with SM in 2019 (Supplementary Fig. S4d–f). There was a positive correlation between SR and ANPP in 2019, while a positive correlation between SR and BNPP was found in 2018 and 2019 (Fig. 6a and b). No significant correlation between SR and soil pH and soil base cations was found during 3 years (2017–2019) (Fig. 6c and d). Results of PCA analysis demonstrated that seasonal mean values of SR were positively correlated with BNPP, ANPP and MBC/MBN, and negatively correlated with ST, SEB and BD (Fig. 7a). BNPP had the highest explanation for the variation of seasonal mean SR according to RDA

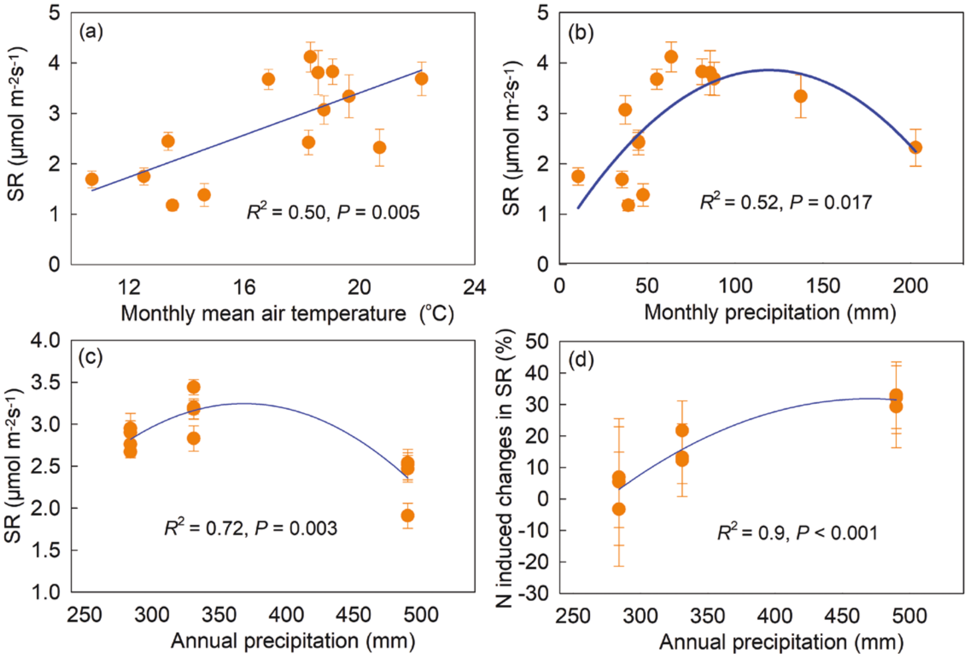

Figure 5: Relationships between monthly SR and monthly air temperature, monthly precipitation and annual precipitation (**a**–**c**); and the relationship between N-induced changes in SR and annual precipitation (**d**). r^2 represents the correlation coefficient.

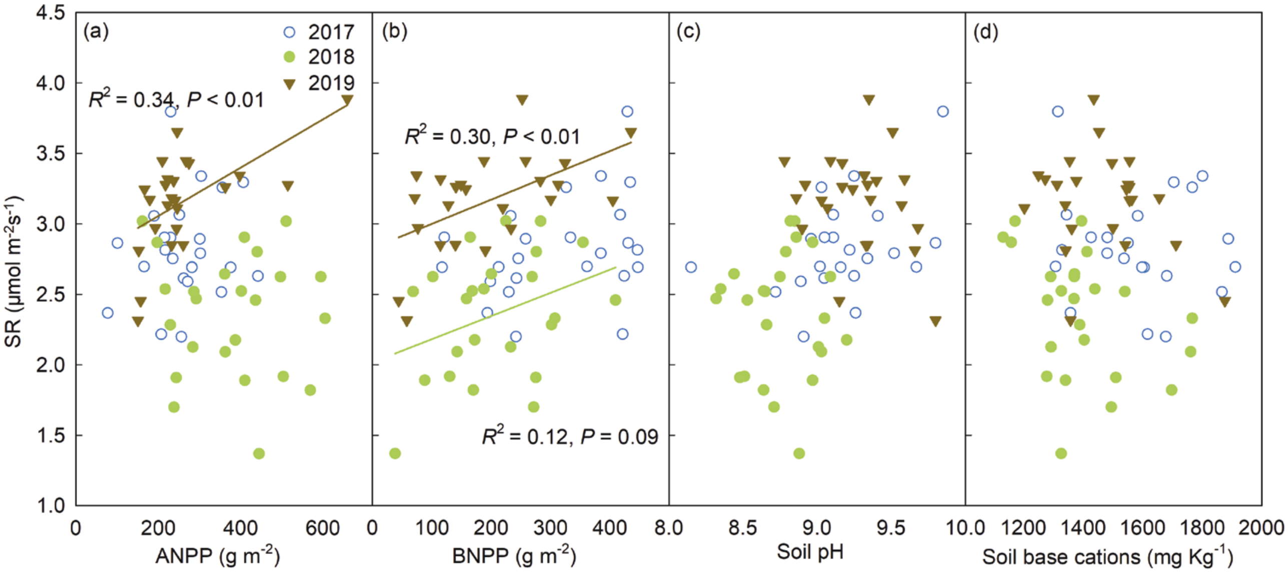

Figure 6: Relationships of SR with ANPP (**a**), BNPP (**b**), soil pH (**c**) and soil base cations (**d**) in 2017, 2018 and 2019, respectively. r^2 represents the correlation coefficient.

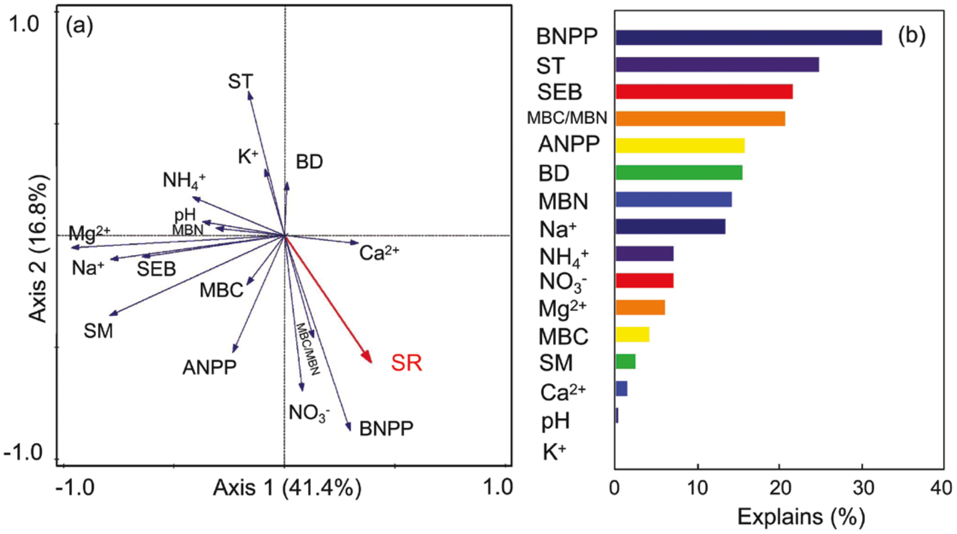

Figure 7: PCA of SR and relevant factors (ANPP, BNPP, ST, SM, BD, NH_4^+, NO_3^-, MBC, MBN, pH, K^+, Ca^{2+}, Na^+, Mg^{2+}, SEB) (**a**); and percentage of variation in SR explained by relevant factors based on RDA (**b**). ANPP (gm^{-2}), BNPP (g m^{-2}), ST (°C), SM (%), soil BD (g (cm^3) $^{-1}$), MBC (mg kg^{-1}), MBN (mgkg^{-1}) and SEB (mg kg^{-1}).

analysis (Fig. 7b). Soil MBC was positively correlated with Ca^{2+} and the sum of base cations, and negatively correlated with soil pH (Supplementary Fig. S5). According to the conceptual diagram and SEM analysis (Fig. 8; Supplementary Fig. S6), SR was mainly directly affected by plants and microorganisms; soil inorganic N promoted plant productivity and then indirectly affected SR; soil salinization (base cations and pH) indirectly regulated SR through modulating soil microorganisms.

DISCUSSION

The effect of different N compound addition on SR

Nitrogen addition had a main effect on SR across 3 years (2017–2019) (Table 1). However, different responses of SR to N addition were observed when different N compounds were added (Fig. 3). It was revealed that NH_4NO_3 addition had the highest promotion effect compared with $(NH_4)_2SO_4$ and NH_4HCO_3 addition

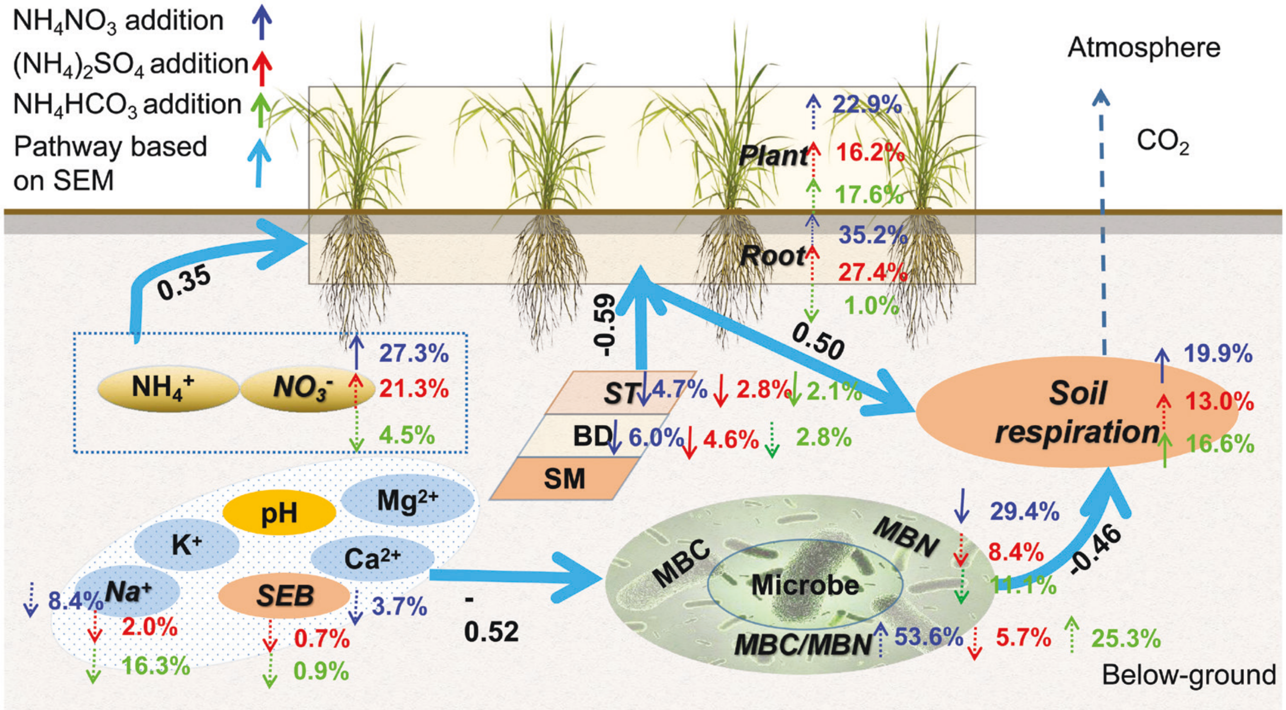

Figure 8: A conceptual diagram illustrating the main factors that affect SR in response to N addition of different compounds (NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3). Blue, red and green arrows or numbers represent the response of SR and related indicators to NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3 addition, respectively. Solid arrows indicate significant effect ($P < 0.05$). Up arrows indicate the positive effect, while the down arrows indicate the negative response of SR and related indicators to N addition. Thicker arrows indicate pathways between factors, and values associated with these arrows represent standardized coefficients according to SEM (see Supplementary Fig. S5). ANPP (gm^{-2}), BNPP ($g\ m^{-2}$), ST (°C), SM (%), soil BD ($g\ (cm^3)^{-1}$), MBC ($mg\ kg^{-1}$), MBN ($mg\ kg^{-1}$) and SEB ($mg\ kg^{-1}$).

in 2019 and across 3 years though there was no significant difference among N compounds.

As demonstrate in the study, N addition had a significant positive effect on SR whatever N compounds were used, consistent with previous experimental studies (Peng *et al.* 2011; Zhang *et al.* 2014) and some meta-analysis results (Feng *et al.* 2017; Zhou *et al.* 2014, 2016). Generally, N addition promoted SR in N-restricted regions by improving plant biomass while inhibiting SR in N-saturated regions (Chen *et al.* 2015; Janssens *et al.* 2010; Yue *et al.* 2021). In our study, N addition caused a significant increase in both ANPP and BNPP in 2019 (the third year of experimental treatment), lead to an increase in SR due to the positive correlation between SR and plant biomass (Han *et al.* 2012; Wei *et al.* 2018; Yan *et al.* 2010). Most studies indicated that N addition inhibited microbial respiration in field or laboratory culture experiments (Ramirez *et al.* 2010; Wei *et al.* 2018; Yan *et al.* 2010). However, soil MBC was not significantly changed under N addition in our study, suggesting that the plants rather than microorganisms respond to N addition and then affect SR.

Moreover, the response of SR was different when different N compounds were used (NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3) and NH_4NO_3 addition presented the highest positive effect across 3 years (2017–2019). This can be explained as follows. Firstly, plants are the direct factors affecting SR (Fig. 8), and the fine root biomass (BNPP) had the highest explanations to the variation of SR (Fig. 7b); the promotion effect of NH_4NO_3 addition on ANPP and BNPP was higher than that of $(NH_4)_2SO_4$ and NH_4HCO_3 addition across 3 years (2017–2019) (Fig. 4). Generally, NO_3^- had a higher diffusion coefficient in the soil compared with NH_4^+ (Miller and Cramer 2004), and the combined application of NO_3^- and NH_4^+ can stimulate lateral roots branching and elongation to optimize N absorption from the soil (Takushi and Hitoshi 2016), resulting in the highest promotion effect on plant growth under NH_4NO_3 addition and the highest promotion effect on SR under NH_4NO_3 addition. Secondly, the mean soil NO_3^- was significant increased under NH_4NO_3 addition across 3 years, and a positive relationship between SR and NO_3^- was revealed, consistent with the previous study

(Luo *et al.* 2016). Ying *et al.* (2017) also suggested that the addition of NO_3^--N could be caused a significant increase in NO_3^- accumulation compared with NH_4^+ addition. SR comprises both autotrophic and heterotrophic respiration, which was driven by plants and soil microorganisms (Li *et al.* 2018). On the one hand, the increased of NO_3^- could mitigate the effects of N limitation on the plants, and thereby increased plant growth, which in turn promote soil autotrophic respiration (Luo *et al.* 2016). On the other hand, the higher NO_3^- availability indicates the higher nitrification rate. However, the soil MBC was unchanged, suggesting that soil microbial composition changes with increased activity, thus accelerated soil heterotrophic respiration. Above all, the response of SR to N deposition cannot be accurately assessed in the previous experiment of adding single form of N compound, and experiments that with NH_4NO_3 addition alone would overestimate the effect of N deposition on SR.

In addition, we found that the effect of N addition on SR was significant in 2018 and 2019, while was not significant in 2017 (Table 2; Fig. 3). The substantially interannual variability was regulated by the difference of annual precipitation (You *et al.* 2022). SR was generally increased with precipitation (Feng *et al.* 2017; Zhang *et al.* 2019) according to the positive correlation between SR and soil water content (Du *et al.* 2018; Orchard and Cook 1983; Ren *et al.* 2017; Yan *et al.* 2010; Zhang *et al.* 2017). However, a saturation relationship between SR and soil water content has been identified (Felton *et al.* 2019; Miao *et al.* 2017; Zhang *et al.* 2019; Yao *et al.* 2022), as well as a negative correlation between SR and a continuous increase in soil water content since excessive water inhibits root growth and soil microbial activity (Han *et al.* 2018; Mielnick and Dugas 2000). The first increasing and then decreasing trend of SR with monthly precipitation and annual precipitation was also found in our study (Fig. 5). However, the changes in SR induced by N addition increased with precipitation, suggesting that water and N are jointly limited in our study site, and N input could weaken the inhibition effect of excessive precipitation on SR. Therefore, the higher precipitation and soil water content in 2018 and 2019 lead to the significant effect of N addition on SR.

Notably, NH_4HCO_3 addition had a higher promotion effect on SR than that of $(NH_4)_2SO_4$ addition, though they were all input N by the form of NH_4^+. Thus, the different responses of SR to NH_4HCO_3 and $(NH_4)_2SO_4$ addition may be related to the different inputs of anions (HCO_3^- or SO_4^{2-}). In our study, there was a lower promotion effect on fine root biomass (BNPP) and a higher stimulation effect on soil microorganism (MBC/MBN) under NH_4HCO_3 addition compared with $(NH_4)_2SO_4$ addition. This indicates that the input of HCO_3^- could weaken the promotion effect of N addition on root growth while enhancing the promotion effect of N addition on soil microorganisms (soil MBC/MBN). Besides, there was a dynamic equilibrium between CO_2 and HCO_3^- due to hydrolysis in the soil (De Vries and Breeuwsma 1987), and the addition of HCO_3^- would lead this reaction to the direction of producing CO_2, resulting in higher CO_2 emission in the soil.

Regulation mechanisms of SR in saline–alkaline grassland

The seasonal mean SR in this saline–alkaline grassland ranged from 1.9 to 2.8 μmol m^{-2} s^{-1}, which was close to the results of the research conducted in Loess Plateau (2.1–2.7 μmol m^{-2} s^{-1}) (Wei *et al.* 2018) and Inner Mongolia (1.6–3.4 μmol m^{-2} s^{-1}) (Han *et al.* 2012). This confirmed that there is little difference of soil C loss between saline–alkaline and non-saline–alkaline grassland. However, this result, in turn, suggested that the grassland with higher salinization had a lower C sequestration capacity owing to the limitation of plant productivity (C input) under higher saline–alkaline stress.

SR presents a first increasing and then decreasing trend with monthly and annual precipitation in our study, which demonstrating that the extreme precipitation would inhibit SR in this saline–alkaline grassland (Han *et al.* 2018; Mielnick and Dugas 2000). However, N addition-induced changes of SR were increased with precipitation (Wang *et al.* 2019). Hence, seasonal precipitation plays an important role in regulated the response of SR to N deposition. Besides, plant productivity, especially fine root biomass, was the main factor that regulated SR (Peng *et al.* 2017; Wei *et al.* 2018; Wang *et al.* 2020). However, soil MBC had lower explanation for the variation of SR. These results suggest that soil C emissions in saline–alkaline grassland are mainly dominated by plants rather than soil microorganisms.

No significant effect of N addition on soil MBC was found, inconsistent with previous studies (Ramirez *et al.* 2010; Zhou *et al.* 2017). This revealed that soil microorganisms were less sensitive to N addition in saline–alkaline grassland. Studies showed that soil salinization was a main factor affecting soil microorganisms (Rath and Rousk 2015;

Yang *et al.* 2018), then influencing soil heterotrophic respiration. Our study also showed that there was a significant relationship of MBC with soil pH and base cations (Supplementary Fig. S5). Therefore, the changes in soil salinization (e.g. base cations or pH) induced by N addition would indirectly affect SR through soil microorganisms (Rath and Rousk 2015; Setia *et al.* 2011; Yang *et al.* 2019a). Generally, N addition could cause a decrease in soil pH (Cai *et al.* 2017; Lucas *et al.* 2011). While the higher soil exchange base cations in our study site could alleviated the change in pH due to the higher buffering capacity (Bowman *et al.* 2008; Tian and Niu 2015). Hence, N addition had no significant effect on soil pH and base cations in our study, thus lead to insensitivity of soil microorganisms to N addition, which also reflecting that the plants rather than soil microorganisms that respond to N addition and then affect SR.

NH_4NO_3 addition significant increased plant productivity (ANPP + BNPP) and cumulative C emissions in growing season (Fig. 4). However, the relative changes of plant productivity induced by NH_4NO_3 addition were higher than that of cumulative C emissions, indicating that the addition of NH_4NO_3 would increase the ecosystem C flux and C sequestration. NH_4HCO_3 addition significant increased cumulative C emissions while had no effect on plant productivity (Fig. 4), suggesting that the increase in C input (plant productivity) induced by NH_4HCO_3 addition was lower than that of C loss (cumulative C emissions) in this saline–alkaline grassland. Therefore, the addition of NH_4HCO_3 would accelerate the loss of soil C and decrease soil C sequestration compared with NH_4NO_3 and $(NH_4)_2SO_4$ addition.

Above all, it is found that SR is mainly regulated by plants rather than microorganisms in saline–alkaline grassland due to the insensitivity of MBC to N addition. This also indicates that the addition of N does not alleviated soil salinization, and the saline–alkaline stress of soil microorganisms did not disappear under N addition of 3 years. N addition of different compounds showed asymmetric effects on net primary productivity (C input) and cumulative carbon emissions (C release), which could lead to the difference in C sequestration under N addition of different compounds.

CONCLUSIONS

Throughout the three experimental years, nitrogen addition manifested a promotion effect on SR, and the promotion effect of N addition on SR was higher with more rainfall. The effect of N addition on SR varied with N compounds and exhibited the highest effect size under NH_4NO_3 addition across 3 years. The different responses of SR to different N compounds depend on the variation in plant productivity and the variation of soil MBC/MBN in saline–alkaline grassland. Compared with $(NH_4)_2SO_4$, the greater positive effect of NH_4HCO_3 addition on SR related to the higher variation of MBC/MBN and the transformation of HCO_3^- in the soil. We highlight that researches with NH_4NO_3 addition would overestimate the response of SR to N deposition, and various forms of N compounds should be considered in the future field study, especially in saline–alkaline grassland.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Results (*F* values) of two-way ANOVA testing the effects of year (Y), N addition (N) and their interaction on abiotic and biotic factors.

Figure S1: Relative changes of soil respiration (SR) and relevant factors to the addition of NH_4NO_3 (**a**), $(NH_4)_2SO_4$ (**b**) and NH_4HCO_3 (**c**), respectively, across 3 years (2017, 2018 and 2019).

Figure S2: Relative changes of seasonal mean soil respiration (SR) to the addition of NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3 in 2017, 2018 and 2019, and the mean values across 3 years.

Figure S3: Cumulative soil CO_2 efflux from during growing season in 2017 (**a**), 2018 (**b**) and 2019 (**c**) under the addition of different N compounds (CK, NH_4NO_3, $(NH_4)_2SO_4$ and NH_4HCO_3).

Figure S4: Relationships of soil respiration (SR) with soil temperature (ST) and soil moisture (SM) from 2017 to 2019.

Figure S5: Relationships of the mean of soil exchangeable base cations (K^+, Ca^{2+}, Na^+, Mg^{2+}, SEB) and soil pH with MBC, MBN and MBC/MBN across 3 years (2017–2019).

Figure S6: Structural equation model (SEM) of the effects of N addition on soil respiration through pathways of soil environment (ST, SM, BD), plant biomass (ANPP, BNPP), soil available N (NH_4^+, NO_3^-), soil salinization (pH, K^+, Ca^{2+}, Na^+, Mg^{2+}), soil microbial biomass (MBC, MBN, MBC/MBN), which are the PC1 score using principal component analysis.

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