Effects of mowing and nitrogen addition on soil respiration in three patches in an oldfield grassland in Inner Mongolia

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Abstract

Aims
Vegetation type is important in determining variations in soil carbon (C) efflux under grassland managements. This study was conducted to examine the effects of mowing and nitrogen (N) addition on soil respiration and their dependences upon vegetation types in an old-field grassland of northern China.

Methods
Soil respiration, temperature, moisture and aboveground net primary productivity (ANPP) and belowground net primary productivity (BNPP) were examined in response to mowing and N addition among the three patches dominated by different species (named as grass, forb and mixed patches, respectively) in the growing seasons (May–October) from 2006 to 2008.

Important Findings
Across the 3 years, soil respiration in the grass patch was greater than those in the forb and mixed patches, which could have been ascribed to the higher soil moisture (SM) in the grass patch. Mowing had no impact on soil respiration due to unaltered SM and plant growth. Soil

respiration was stimulated by 6.53% under N addition, and the enhancement was statistically significant in 2006 but not in 2007 or 2008 because of the limited water availability in the later 2 years. There were no interactive effects between mowing and N addition on soil respiration. Soil respiration showed positive dependence upon SM, ANPP and BNPP across plots. The results suggest that soil water availability and plant growth could be the primary factors in controlling the temporal and spatial variations in soil respiration and its response to different treatments. Our observations indicate that grassland managements (i.e. mowing for hay once a year) may have little influence on soil respiration of the oldfield grassland in northern China.

Keywords: mowing • nitrogen addition • patch • semiarid grassland • soil C flux • soil water availability

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INTRODUCTION

Soil respiration is the second largest carbon (C) flux between terrestrial ecosystems and the atmosphere, which is estimated to be 50–78 Pg C year^{-1} and plays an important role in regulating climate-C feedbacks (Hibbard *et al.* 2005; Luo *et al.* 2001). As a biological process that needs substrate supply, soil

respiratory activities are closely related to plant growth, photosynthetic supply to roots and status of plant litter and soil organic C (Bremer *et al.* 1998; Wan and Luo 2003; Xu and Qi 2001). In addition, microclimate factors, such as soil temperature and soil moisture (SM), also affect both temporal and spatial variations in soil respiration (Borken and Matzner 2009; Knapp *et al.* 1998; Liu *et al.* 2009). Thus, any factor that can

impact C substrate supply, soil temperature and SM is likely to cause changes in soil respiration and therefore climate-C feedbacks.

Spatial heterogeneity is a general phenomenon in arid and semiarid grassland ecosystems (Hook *et al.* 1991; Schlesinger *et al.* 1996) and can lead to spatial variation in species composition and community structure. Differences in species identity and composition have been proved to affect ecosystem function and process (De Boeck *et al.* 2007; Naeem *et al.* 1994). Plant growth or cover can mediate soil respiration via its influences on both belowground C supply and soil microclimate (temperature and moisture). For example, soil respiration has been shown to directly depend on plant growth and root metabolic activity (Bremer *et al.* 1998; Yuste *et al.* 2004). Plant growth could not only directly affect autotrophic respiration (root respiration) but also indirectly influence heterotrophic respiration by altering litter production, root exudates and microbial communities (Phillips *et al.* 2002). Moreover, different vegetation covers could cause variations in both soil temperature and moisture. For example, higher productivity and coverage of plant community lead to lower soil temperature by shading solar radiation during daytime and consequently lesser soil water loss via reducing evaporation (Bremer *et al.* 1998). However, greater plant production may also reduce SM by enhancing transpiration (Bremer *et al.* 1998). Therefore, it is expected that soil respiration could be variational among different patches that are dominated by different species.

Mowing for hay is an important land-use type in grassland ecosystem. The impacts of mowing on soil respiration have been well documented but the results are inconsistent (Antonsen and Olsson 2005; Bremer *et al.* 1998; Wan and Luo 2003; Zhou *et al.* 2007). Mowing may reduce soil respiration by decreasing canopy photosynthesis (Bremer *et al.* 1998; Zhou *et al.* 2007). The loss of C substrate supply from photosynthesis and aboveground litter associated with mowing could reduce soil respiration and its temperature sensitivity (Wan and Luo 2003). In contrast, soil respiration could also be enhanced after mowing by stimulating growth of arbuscular mycorrhizal fungi (Antonsen and Olsson 2005). In addition to its impact on C supply, mowing may affect soil respiration by changing soil microclimate. Bare ground after mowing absorbs more soil-surface irradiance and leads to higher soil temperature, which could stimulate root and microbial respiration. However, mowing-induced higher soil-surface temperature is likely to stimulate evaporation, which is in conjunction with mowing-reduced transpiration to influence SM (Bremer *et al.* 1998). Therefore, the mechanism of mowing effects on soil respiration is complex and will vary with vegetation type and soil texture.

Nitrogen (N) has been recognized as the most important nutrient for plant growth in terrestrial ecosystems, especially in grassland (Niu *et al.* 2010; Xia and Wan 2008). Changes in root and microbial respiration due to stimulation of plant growth (Olsson *et al.* 2005) and alterations of microbial activity and biomass (Allison *et al.* 2008) in response to N addition will affect soil respiration (Neilsen *et al.* 1992). However, the effects of N addition on soil respiration are inconsistent, with positive (Bowden *et al.* 2004), negative (Harpole *et al.* 2007; Mo *et al.* 2008) or neutral effects (Raich and Tufekcioglu 2000) observed in various ecosystems. Therefore, it is reasonable to speculate that the responses of soil respiration to N addition will be variable among different patches due to the variations in interspecific N responses of plant growth. Furthermore, enhanced N availability after N addition may alleviate the negative impact of mowing on soil respiration by decreasing C and N inputs.

The semiarid steppe in northern China, which accounts for >30% of the national land area (Kang *et al.* 2007), has been disturbed greatly by human activities (tillage, mowing and atmospheric N deposition). The policy of Grain for Green in China has led to a large area of oldfield grassland in Inner Mongolia since the beginning of this century. Changes in land-use patterns may cause subsequent impacts on ecosystem C processes in the grassland in northern China. To investigate effects of mowing, N addition and their potential interactions on soil respiration, we conducted an experiment in three patches dominated by different plant species in an oldfield grassland in northern China since 2005. Given the co-limitation of soil water availability (Liu *et al.* 2009) and C substrate (Xia *et al.* 2009) on soil respiration in this ecosystem, we hypothesized that (i) grass patches have greater soil respiration than other vegetation types because of higher production and soil water availability (Sebastiá 2007) and (ii) the effects of mowing and N addition on soil respiration will be mediated by their influences on plant growth and SM.

MATERIALS AND METHODS

Site description

The experimental site is located in a semiarid grassland in Duolun County (42°02′N, 116°17′E, 1 324 m above sea level) in Inner Mongolia, China. The long-term mean annual temperature in the area is 2.1°C, with minimum and maximum monthly mean temperatures of −17.5°C in January and 18.9°C in July, respectively. Mean annual precipitation is 383 mm with 90% concentrated from May to October. N deposition in this area was estimated at ~20 kg ha^{-1} year^{-1} in 2005–06 (Zhang *et al.* 2008). The sandy soil could be classified as chestnut soils (Chinese classification) or Haplic Calcisols according to the *Food and Agriculture Organization* classification.

Experimental design

The experimental site was abandoned in 2001. Mosaic patterns were formed in the oldfield with the restoration of natural vegetation. There were three patches dominated by different plant species, including a grass-dominated patch occupied by *Pennisetum centrasiaticum* Tzvel, a forb-dominated patch occupied by *Artemisia frigida* Willd and a mixed patch dominated by a mixture of the above two species. Soil texture in the three patches was homogeneous ($P > 0.05$), with sand, silt and clay contents

in soils as 66.06 ± 0.25%, 23.61 ± 0.20% and 10.34 ± 0.11%, respectively. The experiment was set up in late August 2005. Within each patch, there were four treatments including control, mowing, N addition (10 g N m^{-2} year^{-1} as NH$_4$NO$_3$) and mowing plus N addition with a full factorial design and six replicates for each treatment. Therefore, there are totally seventy-two 4 × 4 m^2 plots in the three patches. Mowing was carried out at the beginning of the experiment on 3 May 2006 and then done once a year on 8 September 2006, 7 September 2007 and 6 September 2008. The plots were mowed at the height of 10 cm above the soil surface, and the harvested plant material was removed from the plots. Nitrogen addition treatments were conducted annually on 19 July 2006, 10 July 2007 and 11 July 2008. The measurements in this study were conducted in the growing season (May–October) from 2006 to 2008.

Soil respiration

A PVC soil collar (11 cm in diameter and 5 cm in height) was permanently installed 2–3 cm into the soil in each plot for the measurement of soil respiration. Living plants inside the collar were removed by hand frequently and left into the collar to avoid autotrophic respiration from the aboveground parts of plants. Soil respiration was measured once a week using an Li-8100 portable soil CO$_2$ fluxes system (Li-Cor Inc., Lincoln, NE, USA) between 9:00 AM and 12:00 PM (local time). In each measurement, the chamber was sealed on the PVC collar for 90 s at each plot.

Soil microclimate

Soil temperature (°C) was measured by a thermocouple probe (Li-8100-201) connected to the Li-8100. The probe was inserted into the soil at the depth of 10 cm adjacent to the PVC collar at the same time when soil respiration was measured. Volumetric SM content (0–10 cm) was measured using a portable SM device (Diviner 2000; Sentek Pty Ltd, Balmain, Australia) concurrent with the measurements of soil temperature.

Aboveground and belowground net primary productivity

Aboveground net primary productivity (ANPP) was determined by clipping aboveground live plants from two 1 × 0.15 m^2 quadrats in each plot at the peak growing season. All living plant tissues were collected, then oven-dried at 65°C for at least 48 h and then weighed.

Belowground net primary productivity (BNPP) was estimated by root in-growth core method (Xu and Wan 2008). In early May of the 3 years from 2006 to 2008, we excavated two 50-cm-deep cylindrical holes in each plot using 8-cm-diameter soil augers. Roots in the soil cores were taken out from the soils by 1-mm sieves and the root-free soil was refilled in the same hole. We excavated the soil again in late October using 6-cm-diameter soil augers at the center of the original root in-growth holes. The root

in-growing samples were collected, washed and weighed after oven-drying at 65°C for at least 48 h.

Statistical analysis

Four-way analysis of variance was used to examine the main effects of year, patch, mowing, N addition and their possible interactions on the seasonal mean values of soil respiration, soil temperature, SM, ANPP and BNPP. Repeat-measurement analysis of variance was used to determine the main and interactive effects of patch, mowing and N addition on soil respiration, soil temperature as well as SM in each year. Simple linear, stepwise multiple linear and nonlinear regression analyses were used to determine relationships of soil respiration with soil temperature, SM, ANPP and BNPP at temporal and spatial scales. All statistical analyses were performed using SAS V.8.1 (SAS Institute Inc., Cary, NC, USA).

RESULTS

Soil microclimate

Interannual variations in both soil temperature and moisture (both $P < 0.001$) were found from 2006 to 2008 (21.0°C and 14.3% in 2006, 17.4°C and 8.7% in 2007 and 16.9°C and 10.8% in 2008, respectively; Fig. 1; Table 1). Both soil temperature and moisture showed strongly seasonal variations (all $P < 0.001$) from 2006 to 2008 (Fig. 1; Table 2), with the highest values occurring in late July or early August. Soil microclimates were different among the grass, forb and mixed patches in the 3 years (all $P < 0.001$) except for soil temperature in 2008 ($P > 0.05$; Table 2). Seasonal mean soil temperature in the grass patch (17.6°C) was lower than those in the forb (19.1°C) and mixed patches (18.5°C) across the 3 years. In contrary, seasonal mean SM was higher in the grass patch (13.1%, absolute difference) comparing with those in the forb (10.3%) and mixed (10.4%) patches. Across the 3 years, mowing significantly affected soil temperature ($P < 0.001$) but not SM ($P > 0.05$; Table 1) over the three patches. Neither soil temperature nor moisture was influenced by N addition across the 3 years (all $P > 0.05$; Table 2).

Mowing enhanced soil temperature by 0.8°C in both 2006 and 2007 (both $P < 0.01$) but showed no impact on soil temperature in 2008 ($P > 0.05$; Table 2). Mowing did not affect SM in any year (all $P > 0.05$; Table 2). The effects of mowing on soil temperature varied with patch ($P < 0.05$; Table 2) in 2006. Mowing increased soil temperature by 1.5°C and 1.2°C in the grass and mixed patches, respectively, but did not affect it in the forb patch in 2006. Similarly, the effects of mowing on SM varied among patches in both 2007 and 2008 (both $P < 0.05$; Table 2). In 2007, mowing slightly increased SM in the forb patch (+4.9%; $P = 0.084$) but decreased that in the mixed patch (−8.9%; $P < 0.05$). In 2008, mowing reduced SM by 5.8% and 10.8% (both $P < 0.05$) in the grass and mixed patches, respectively, whereas enhanced it by 6.3% ($P < 0.05$) in the forb patch. Nitrogen addition had no impact on soil temperature or

moisture across the three patches from 2006 to 2008 (all $P >$ 0.05; Table 2). In addition, no interactive effect between mowing and N addition on soil temperature or moisture was observed across the 3 years (all $P > 0.05$; Table 2).

Table 1: results (F values) of four-way ANOVA for SM, ST, ANPP, BNPP and SR from 2006 to 2008

Source of variation	ST	SM	SR
Year (Y)	347.65***	266.33***	677.91***
Patch (P)	40.60***	82.02***	96.49***
Mowing (M)	23.32***	0.00ns	0.00ns
N addition (N)	0.06ns	0.62ns	15.69***
Y × P	6.30***	2.54*	0.91ns
Y × M	1.05ns	2.30ns	1.31ns
Y × N	0.68ns	0.15ns	4.99**
P × M	8.13***	4.49**	4.88**
P × N	0.14ns	2.05ns	1.26ns
M × N	1.98ns	0.50ns	3.24ns
P × M × N	0.18ns	11.58***	4.91**
Y × P × M	1.05ns	0.24ns	1.13ns
Y × P × N	0.19ns	1.01ns	0.32ns
Y × M × N	0.07ns	0.56ns	0.01ns
Y × P × M × N	0.20ns	13.06***	0.38ns

*, ** and *** indicate statistically significant at $P < 0.05$, 0.01 and 0.001, respectively; ns indicates statistically insignificant at $P < 0.05$. ANOVA = analysis of variance, SR = soil respiration, SM = soil moisture, ST = soil temperature.

Soil respiration

There was substantially interannual variability of soil respiration across the 3 years from 2006 to 2008 ($P < 0.001$), with the highest value in 2006 (3.42 μmol m^{-2} s^{-1}), the intermediate value in 2008 (2.58 μmol m^{-2} s^{-1}) and the lowest value in 2007 (1.60 μmol m^{-2} s^{-1}; Fig. 2; Table 1). Strong seasonal variations in soil respiration were detected (all $P < 0.001$) in all the 3 years from 2006 to 2008, with the highest values occurring in July and August (Fig. 1; Table 2). Soil respiration was significantly different among patches across the 3 years (all $P < 0.001$; Figs 2 and 3, upper panel; Table 1). Across the 3 years, soil respiration in the grass patch (2.88 μmol m^{-2} s^{-1}) was 31.4% and 13.8% greater than that in the forb (2.19 μmol m^{-2} s^{-1}) and mixed (2.53 μmol m^{-2} s^{-1}) patches, respectively. Mowing did not influence soil respiration (all $P > 0.05$) across the 3 years (Figs 2 and 3, middle panel; Table 1). Nitrogen addition significantly increased soil respiration by 6.5% ($P < 0.001$) from 2006 to 2008 (Figs 2 and 3, lower panel; Table 1). In addition, the impacts of N addition on soil respiration also showed interannual variation ($P < 0.01$), with an enhancement of 10.3% ($P < 0.001$) in 2006 but no change in 2007 or 2008 (both $P > 0.05$; Fig. 3, lower panel; Table 2).

The effects of mowing on soil respiration varied among patches in 2006 ($P < 0.01$; Table 2). Mowing increased soil respiration by 7.4% and 4.3% in the grass and forb patches, respectively, but decreased it by 7.9% in the mixed patch. The N effects on soil respiration did not change with patches in any of the 3 years from 2006 to 2008 (all $P > 0.05$). No interactive effect between mowing and N addition on soil respiration was observed in any of the 3 years either (all $P > 0.05$).

Table 2: results (F values) of repeated-measures ANOVA for ST, SM and SR in 2006, 2007 and 2008

Source of variation	ST			SM			SR		
	2006	2007	2008	2006	2007	2008	2006	2007	2008
Date (D)	1 655.65***	2 857.05***	1 241.19***	392.10***	2 522.00***	1 156.02***	694.39***	441.76***	407.36***
Patch (P)	99.95***	9.02***	1.83ns	13.06***	62.41***	91.52**	46.24***	43.99***	31.20***
Mowing (M)	34.62***	7.76**	2.54ns	1.24ns	0.75ns	2.10ns	0.27ns	3.04ns	0.44ns
N addition (N)	3.20ns	0.02ns	0.03ns	0.16ns	0.20ns	2.18ns	28.15***	0.49ns	1.74ns
P × M	13.71***	1.57ns	1.45ns	0.83ns	3.80*	6.34**	5.26**	2.02ns	0.30ns
P × N	0.23ns	0.09ns	0.16ns	1.44ns	0.41ns	0.03ns	0.08ns	0.23ns	1.14ns
M × N	1.37ns	1.01ns	0.36ns	0.79ns	0.39ns	0.68ns	1.35ns	1.97ns	0.63ns
P × M × N	0.45ns	0.00ns	0.34ns	17.17***	0.95ns	0.83ns	4.86*	2.07ns	0.72ns
D × P	13.50***	7.01***	5.03***	4.95***	20.68***	7.53***	14.43***	10.97***	6.69***
D × M	6.89***	4.40***	2.41***	0.72ns	1.10ns	5.28***	1.80*	2.28***	1.52ns
D × N	2.56***	1.89**	0.45ns	1.51ns	2.96***	10.41***	6.27***	3.59***	4.16***
D × P × M	2.48***	1.85***	0.87ns	2.15***	1.18ns	1.20ns	3.05***	1.65**	2.42***
D × P × N	0.81ns	0.81ns	0.63ns	3.06***	0.90ns	0.99ns	1.13ns	1.34ns	1.90***
D × M × N	0.34ns	1.53ns	0.47ns	1.17ns	0.51ns	1.93**	3.31***	3.59***	1.17ns
D × P × M × N	0.91ns	0.85ns	0.82ns	10.07***	0.83ns	0.58ns	1.96***	0.68ns	1.07ns

*, ** and *** indicate statistically significant at $P < 0.05$, 0.01 and 0.001, respectively; ns indicates statistically insignificant at $P < 0.05$. ANOVA = analysis of variance, SR = soil respiration, SM = soil moisture, ST = soil temperature.
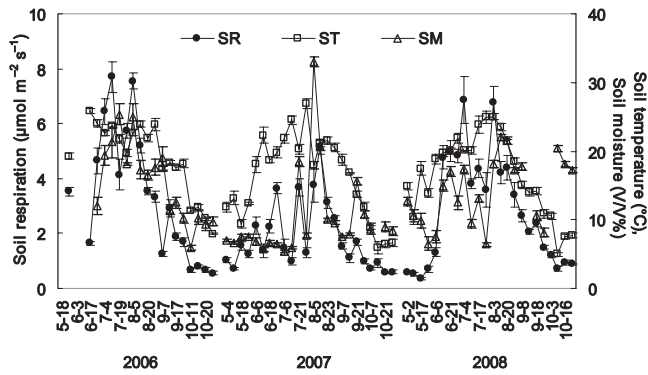
Figure 1: seasonal variations in SR, ST, and SM in the ambient plots in grass patch from 2006 to 2008. SR = soil respiration, ST = soil temperature, SM = soil moisture.

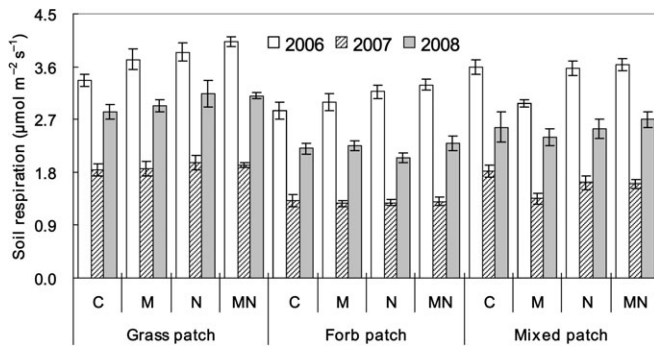**Figure 2:** effects of mowing and N addition on seasonal mean soil respiration (mean ± SE) in the three patches from 2006 to 2008. C: control; M: mowing; N: N addition; MN: mowing plus N addition.

Controlling factors over soil respiration

The seasonal dynamics of soil respiration produced a one-peak pattern with highest values in July and August in all the three patches in the 3 years. Across the three growing seasons, soil respiration increased exponentially with soil temperature ($R^2 = 0.49$, $P < 0.001$; $R^2 = 0.17$, $P < 0.001$ and $R^2 = 0.58$, $P < 0.001$ in 2006, 2007 and 2008, respectively; Fig. 4a), and the second-order polynomial functions described the relationships between soil respiration and SM in the 3 years ($R^2 = 0.80$, $P < 0.01$; $R^2 = 0.65$, $P < 0.01$ and $R^2 = 0.24$, $P = 0.08$ in 2006, 2007 and 2008, respectively; Fig. 4b). Therefore, the exponential and second-order polynomial functions were combined to describe the interactive effects of soil temperature (T) and SM on soil respiration: $\left(SR = ae^{bT}\frac{cSM^2 + dSM + e}{cSM_0^2 + dSM + e}\right)$, where SM_0 was the SM content at which soil respiration was the highest, and a, b, c, d and e are constant coefficients. The combination of soil temperature and moisture explained 83.7%, 76.9% and 86.8% (all $P < 0.001$) of temporal changes in soil respiration in 2006, 2007 and 2008, respectively (see the fitted information in online Supplementary Table S1).

Across the 72 plots, seasonal mean soil respiration was linearly correlated with soil temperature, SM, ANPP and BNPP from 2006 to 2008 (all $P < 0.01$; Fig. 5). Stepwise multiple regression analyses showed that the changes in soil temperature (partial $R^2 = 0.29$, $P < 0.001$) and ANPP (partial $R^2 = 0.08$, $P < 0.001$) together explained 37% of the spatial variation in soil respiration in 2006. In 2007, 51% of the spatial changes in soil respiration can be explained by the combination of ANPP (partial $R^2 = 0.38$, $P < 0.001$) and SM (partial $R^2 = 0.13$, $P < 0.001$). In 2008, SM (partial $R^2 = 0.29$, $P < 0.001$), ANPP (partial $R^2 = 0.04$, $P < 0.05$) and soil temperature (partial $R^2 = 0.05$, $P < 0.05$) accounted for 38% of the spatial variation in soil respiration.

At the patch level, stepwise multiple regression analyses showed that 70% of spatial variations in soil respiration in the grass patch was explained by SM (partial $R^2 = 0.53$, $P < 0.001$; Fig. 6a), BNPP (partial $R^2 = 0.09$, $P < 0.001$; Fig. 6c) and soil temperature (partial $R^2 = 0.08$, $P < 0.001$; Fig. 6b) across the 3 years. SM (partial $R^2 = 0.55$, $P < 0.001$; Fig. 6d), soil temperature (partial $R^2 = 0.10$, $P < 0.001$; Fig. 6e) and BNPP (partial $R^2 = 0.08$, $P < 0.001$; Fig. 6f) accounted for 73% of spatial changes in soil respiration in the forb patch across the 3 years. In the mixed patch, the combinations of SM (partial $R^2 = 0.61$, $P < 0.001$; Fig. 6g), ANPP (partial $R^2 = 0.10$, $P < 0.001$) and soil temperature (partial $R^2 = 0.05$, $P < 0.01$; Fig. 6h) explained 76% of spatial variations in soil respiration from 2006 to 2008.

DISCUSSION

Soil temperature, moisture and C substrate have been well documented to affect soil respiration in various ecosystems (Davidson *et al.* 1998; Stoy *et al.* 2008; Wan and Luo 2003; Wan *et al.* 2007; Yan *et al.* 2009). It is supported by our observations that soil respiration was strongly correlated with soil temperature, moisture and BNPP at both temporal (Fig. 4) and spatial (Fig. 5) scales. In this semiarid grassland, soil water availability has been proved to be the primary limiting factor for plant growth and ecosystem C processes (Liu *et al.* 2009; Niu *et al.* 2008). Raich and Schlesinger (1992) have reported a positive relationship between precipitation and soil respiration for all climate regions. The strong interannual variations in soil respiration and precipitation in the growing season (May–October; 387.2, 185.6 and 318.0 mm in 2006, 2007 and 2008, respectively) observed in this study are consistent with their results and suggest the regulation of water availability on interannual variation in soil respiration.

Soil respiration in different patches

Greater soil respiration in the grass patch than the forb and mixed patches (Fig. 3) observed in this study is consistent with the assumption that soil respiration varies with vegetation type (Bremer *et al.* 1998; Jenkins and Adams 2010). However, our study demonstrated small-scale variation in soil respiration with patches dominated by different plant species and microclimate in the oldfield grassland (identical soil texture). The difference in soil respiration among patches and vegetation
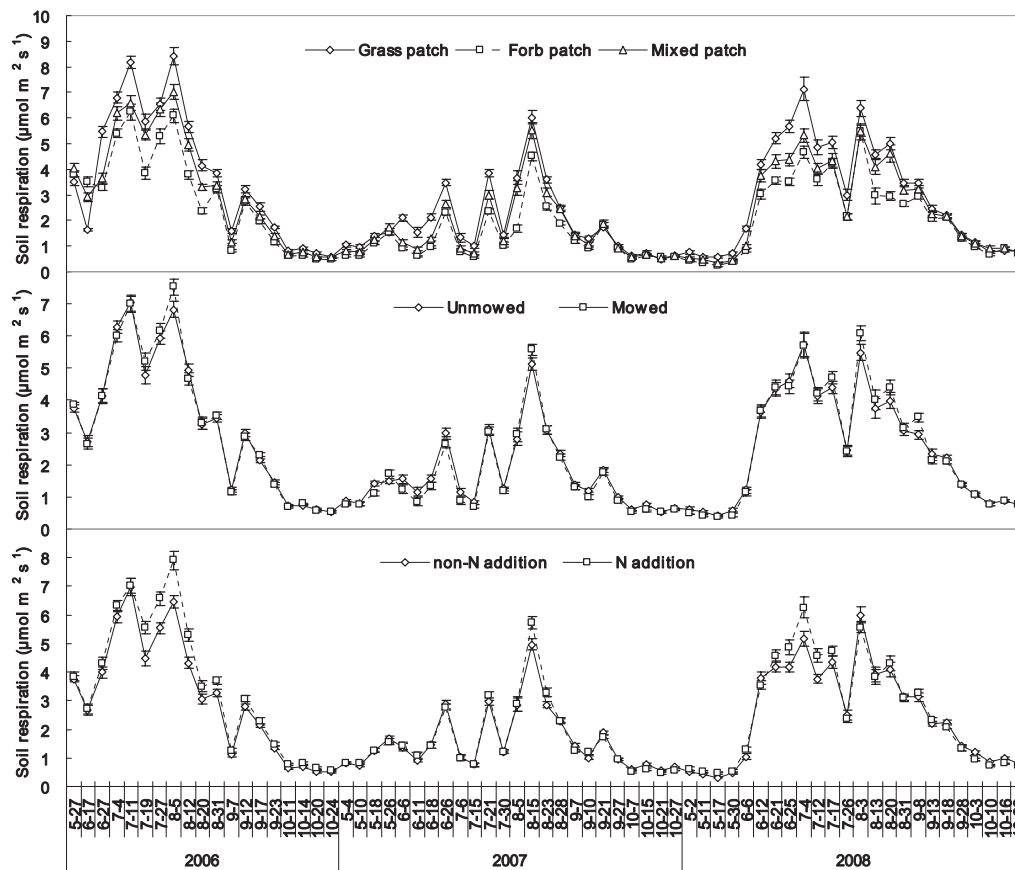
Figure 3: variations in soil respiration in the three patches (upper panel) and its response to mowing (middle panel) and N addition (lower panel) from 2006 to 2008.
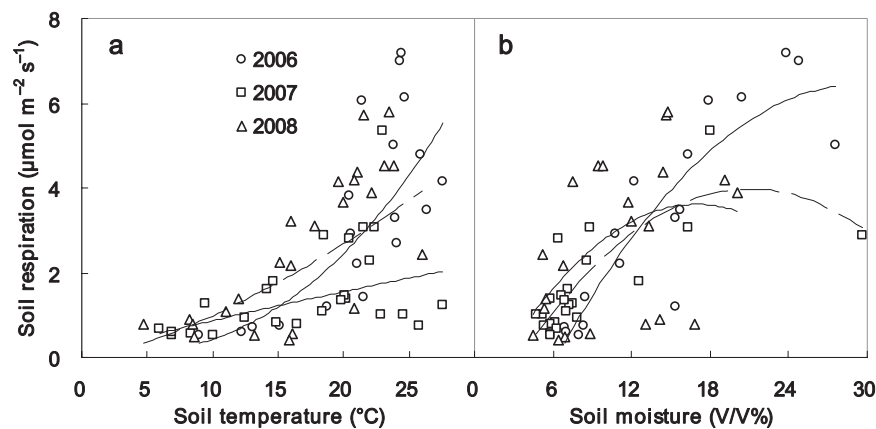

Figure 4: correlations of soil respiration with soil temperature (**a**) and soil moisture (**b**) in the growing seasons from 2006 to 2008. Solid, dashed and dotted lines represent the relationships in 2006, 2007 and 2008, respectively.

types could have been attributed to the divergence in C substrate, soil temperature and soil moisture (Raich and Schlesinger 1992; Stoy *et al.* 2008; Wohlfahrt *et al.* 2008). Considering the strong relationships between soil respiration and SM in all the three patches (Fig. 6), higher SM in the grass patch than the forb and mixed patches may largely contribute

to the higher soil respiration in the grass patch (Fig. 3). The greater BNPP in the grass patch (633.6 g m^{-2}) relative to the forb (435.7 g m^{-2}) and mixed patches (527.9 g m^{-2}) across the 3 years may also lead to greater soil respiration due to higher root respiration. This speculation is supported by the correlations of soil respiration with BNPP across the plots
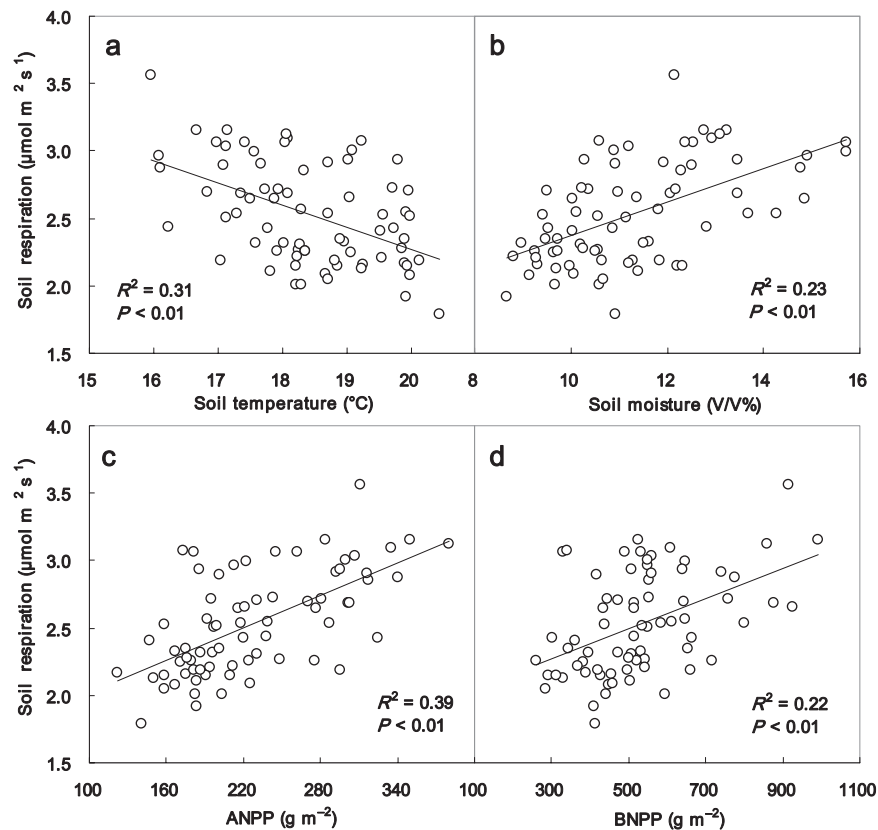
Figure 5: correlations of seasonal mean soil respiration with soil temperature (**a**), soil moisture (**b**), ANPP (**c**) and BNPP (**d**) across different plots from 2006 to 2008.

(Figs 5 and 6) and consistent with previous studies that found the positive dependence of root respiration upon BNPP (Bai *et al.* 2010; Pregitzer *et al.* 2008). Comparing to the forb and mixed patches, the greatest ANPP in the grass patch may also stimulate soil respiration by providing more C substrate for microbial activity and respiration (Lagomarsino *et al.* 2009; St Clair *et al.* 2009). In addition, the higher soil respiration in the mixed patch than that in the forb patch could also be mainly explained by the greater BNPP in the mixed patch given similar soil water availability in the two patches. The negative dependence of soil respiration upon soil temperature in this study (Fig. 5a) could be ascribed to the covariation of SM with soil temperature. For example, highest SM and BNPP but lowest soil temperature occurred in grass patch, while lowest SM and BNPP but highest soil temperature were found in forb patch in this study.

Mowing effects

Mowing and clipping have been reported to reduce soil respiration (Bremer *et al.* 1998; Wan and Luo 2003) by changing soil microclimate and the availability of C substrate for root and microorganisms. However, soil respiration did not respond to mowing across the 3 years from 2006 to 2008 in this system. Two possible reasons could help to explain the little changes in soil respiration under mowing observed in this study. Mowing

is expected to change soil water availability via affecting both transpiration and evaporation. However, both increased (Owensby *et al.* 1970) and reduced (Bremer *et al.* 1998; Wan *et al.* 2002) SM have been reported in response to mowing in the previous studies. Inconsistent with their results, the unaltered SM after mowing in this system could have been resulted from the offset of enhanced evaporation by decreased transpiration. Given the strong regulation of soil water availability on root and microbial activity and respiration in this system (Liu *et al.* 2009; Xu and Wan 2008), no response of soil respiration to mowing observed in this study may be accounted for by the unchanged SM. Mowing is also expected to affect soil respiration through its influence on C substrate (Wan and Luo 2003). Consistent with the results of Antonsen and Olsson (2005), no change in ANPP, BNPP or net ecosystem CO_2 exchange (NEE) in response to mowing was observed in this study (Y Han and C Wang, unpublished data). Therefore, the supply of C substrate to soil microorganisms might not be altered during the period in this study.

N addition effects

Increased soil respiration in response to N addition observed in this study is consistent with a previous study conducted in another site that is ~50 km from our site (Xu and Wan 2008), whereas no change or decrease in soil respiration
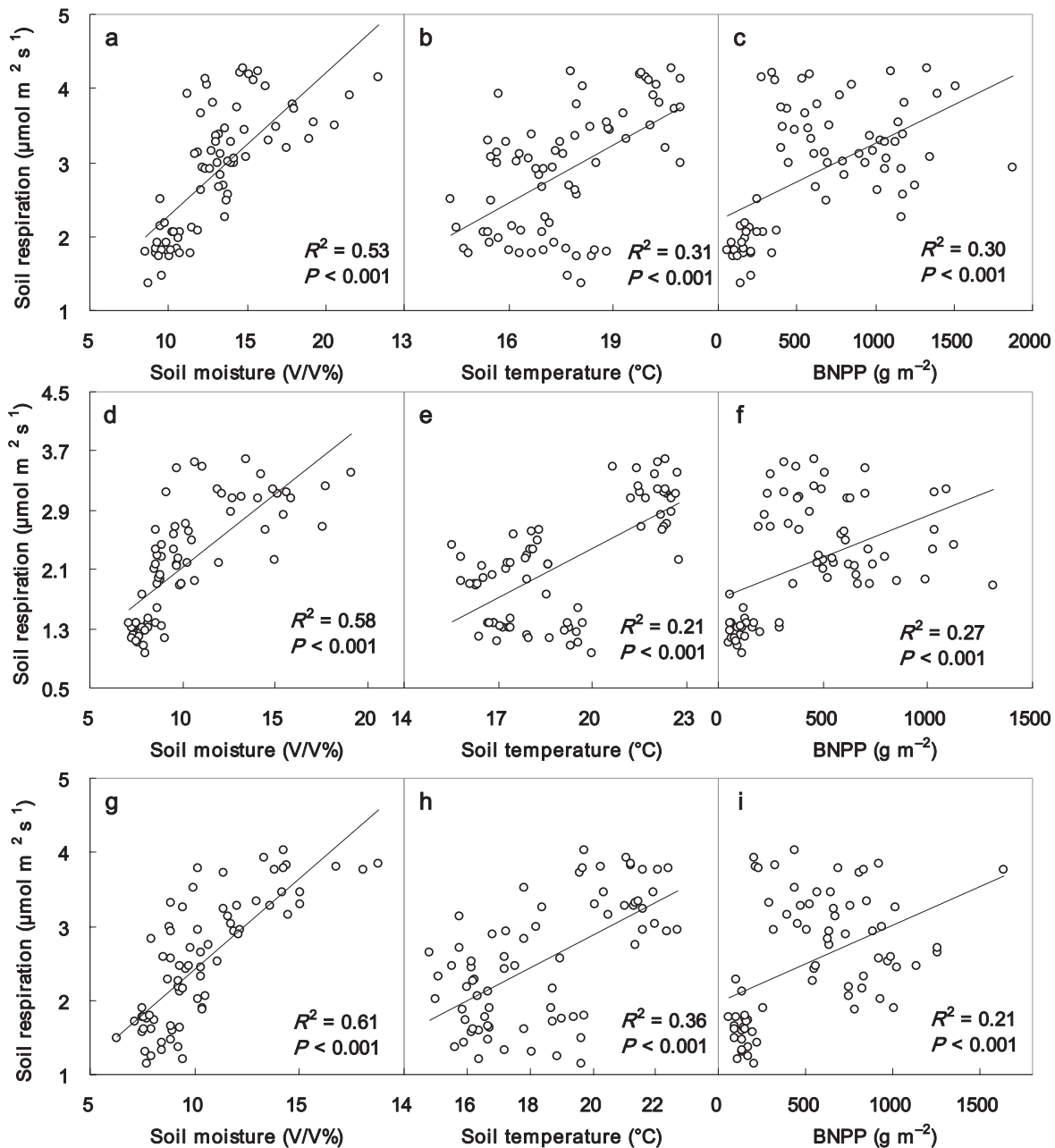
Figure 6: linear correlations of soil respiration with soil moisture, temperature and BNPP in the grass (**a**, **b** and **c**, respectively), forb (**d**, **e** and **f**, respectively) and mixed (**g**, **h** and **i**, respectively) patches across the 3 years from 2006 to 2008.

under N enhancement has also been reported in other ecosystems (Harpole *et al.* 2007; Mo *et al.* 2008). Nitrogen is one of the most important limiting factors for plant growth (LeBauer and Treseder 2008). Stimulation of plant growth after N addition will enhance soil respiration (Craine *et al.* 2001). This is supported by our observations that soil respiration was increased by 6.5% in response to N addition, while ANPP and BNPP were enhanced by 37.0% and 25.1%, respectively. The stimulation of plant growth by N addition could cause increased litter productions and below-

ground C input, which stimulates soil respiration (Bremer *et al.* 1998; Wan and Luo 2003). No change in soil temperature and moisture associated with N addition observed in this study is consistent with the results reported by Xu and Wan (2008). However, N addition increased soil respiration only under the conditions of no water limitation on plant growth (Johnson *et al.* 2000). In this study, N addition is observed to stimulate soil respiration in 2006 with higher precipitation but had no effect in the dry year of 2007 and the relatively dry year of 2008. The increased soil respiration

(10.3%) under N addition is consistent with the enhanced BNPP (44.8%) in 2006 when greater soil water availability did not constrain plant growth. In contrary, BNPP did not change in the dry year of 2007 ($P > 0.05$) or little increased (19.8%, $P < 0.01$) in 2008, under N addition treatment. Therefore, the interannual variation of N effects on soil respiration was primarily due to the large increase of BNPP in rainy 2006 but little changes in 2007 and 2008 under drought condition. Our results are in accordance with the result from a recent study in the same area (Yan *et al.* 2010), which found that N addition increased soil respiration in a wet year (2006) but reduced it in a dry year (2007). The observations in this and previous studies (Yan *et al.* 2010) indicate that the positive effects of N addition on soil respiration due to enhanced plant growth are limited by soil water availability in this semiarid grassland. However, in this study, we found that N addition increased both ANPP and BNPP in all the three growing seasons except for a neutral influence on BNPP in 2007. It could have been ascribed to the greater N effects on ecosystem photosynthesis than respiration in both dry and wet growing seasons in this ecosystem (Xia *et al.* 2009). These results suggest that the C balance at ecosystem level under N addition may not always be in accordance with the N responses of soil respiration. In fact, we also found that N addition increased NEE in all the three patches (data not shown), suggesting that N addition will enhance the C sink strength in this ecosystem. Though the amount of N input in this study was greater than the natural N deposition in this area, the findings indicate that the N effects on ecosystem C cycling cannot be fully evaluated without taking into consideration of both C uptake and release processes.

CONCLUSIONS

Soil temperature, SM and the availability of C substrate are important factors in regulating spatial and temporal variations in soil respiration in the semiarid grassland of northern China. Various patterns of soil respiration among different plant patches in this study suggest that the prediction of regional and global C cycling should take into consideration of the vegetation dynamics. Mowing once a year, one of the widespread land-use patterns in Inner Mongolia grassland, can provide sustainable biofuel production without increasing ecosystem C release. The stimulation of N addition on soil respiration by stimulating plant growth is limited by soil water availability, suggesting that changes in N input and precipitation patterns under global change may together influence ecosystem C cycling via their impacts on plant growth and C substrate supply. The regulation of water availability and plant growth on soil respiration in response to mowing and N addition among different patches will help to clarify the temporal and spatial variation in soil respiration under grassland managements and various vegetation types in northern China.

SUPPLEMENTARY MATERIAL

Supplementary Table S1 is available at *Journal of Plant Ecology* online.

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