Temporal and spatial variability and controls of soil respiration in a temperate steppe in northern China

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[1] In this study, soil respiration and environmental variables were examined to explore the temporal and spatial variability and controls of soil respiration in eight plant communities along an east–west transect in a temperate steppe of Inner Mongolia, China. Our results show that there was substantial temporal (coefficient of variation (CV) = 58.6 ± 1.54%, n = 14) and spatial variability (CV = 32.6 ± 2.65%, n = 8) in soil respiration. Soil temperature and moisture were more important than plant growth in controlling the seasonal patterns of within-site soil respiration in all the eight steppe communities. Spatial differences in soil respiration rate could be mainly attributed to the differences in soil moisture and net primary productivity (NPP) among the study sites, whereas soil temperature played a minor role in regulating the spatial pattern of soil respiration. Significantly, positive site-to-site correlations were found between soil respiration and site soil traits such as soil C, N, and clay contents. In contrast, soil respiration was negatively correlated with soil bulk density and sand content. These findings indicate that the relative importance of abiotic and biotic factors in regulating soil respiration differs temporally from spatially. The conclusions drawn from the present study provide valuable information for developing future models of soil respiration driven by site climatic and soil variables, applicable for large-scale estimates of soil respiration in grassland ecosystems.


1. Introduction

[2] Soil respiration is an important component of the carbon cycle and a sensitive indicator for the overall belowground biogeochemical processes in terrestrial ecosystems [Craine and Wedin, 2002; Schimel, 1995]. The total CO2 efflux via soil respiration represents the second largest terrestrial-atmospheric carbon exchanges [Raich and Schlesinger, 1992]. Accurately quantifying CO2 emissions by soil respiration and identifying the environmental controls are still major tasks in assessing the potential impacts of global or regional environmental changes on terrestrial ecosystems [Raich and Tufekcioglu, 2000]. Despite its obvious importance, soil respiration is extremely difficult to be accurately quantified, largely due to its high variability at different temporal and spatial scales [Scott-Denton et al., 2003].

[3] Soil temperature and moisture, which are two major factors controlling soil respiration rate in terrestrial ecosystems [Singh and Gupta, 1977], can affect soil respiration by altering activities of plant roots and soil microbes and by changing plant biomass production and substrate supply [Wan et al., 2007]. Seasonal fluctuations in soil microclimate play an important role in determining seasonal dynamics of soil-CO2 emissions within sites [Raich and Tufekcioglu, 2000], whereas increasing evidence shows that plant growth may also pose a strong effect on the seasonal dynamics of soil respiration, mainly due to the direct dependence of soil respiration on recent plant photosynthesis or growth[Bremer et al., 1998; Dornbush and Raich, 2006; Högberg et al., 2001; Pendall et al., 2001; Verburg et al., 2004]. Distinguishing the individual from interactive impacts of the above factors on seasonal variations in soil respiration would greatly improve our understanding of the seasonal dynamics of soil respiration and carbon cycling in terrestrial ecosystems in response to environmental change [Wan et al., 2007].

[4] Climatic differences in general, and soil moisture in particular, lead to different soil respiration rates among distant sites [Raich and Potter, 1995; Raich and Tufekcioglu, 2000]. At the within-site scale, a large portion of spatial variability in soil respiration can be explained by differences in soil carbon and nitrogen contents, and in soil moisture or temperature [Ohashi et al., 2008; Soe and Buchmann, 2005; Stoyan et al., 2000]. Other factors that potentially influence soil respiration rate in situ include plant root densities and activities [Knohl et al., 2008], soil physical and chemical properties [Boudot et al., 1986]. However, the spatial variations in soil respiration and the accountability of controlling

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factors among close sites within the same vegetation type have rarely been addressed in previous studies [Dornbush and Raich, 2006; Webster et al., 2008].

[5] Clear relationships between soil respiration and aboveground net primary productivity (ANPP) have been reported at the biome scale [Raich and Schlesinger, 1992] and among grasslands worldwide [Raich and Tufekcioglu, 2000]. These analyses and other studies suggest that soil respiration and plant biomass production might be poorly correlated at local scales [Ellis, 1969; Reiners, 1968], yet this argument has been examined insufficiently in field studies. A clear among-site correlation between soil respiration and site variables reflecting site productivity (e.g., leaf area index or ANPP) will provide a useful approach for large-scale estimates of spatially resolved regional soil respiration in terrestrial ecosystems [Reichstein et al., 2003].

[6] Temperate steppes in Inner Mongolia of northern China constitute a major part of the Eurasian grasslands and play an important role in the global carbon cycle [Li et al., 1997, 1998; Xiao et al., 1997]. Soil respiration rates as well as their seasonal patterns have been studied only for a few communities [Li et al., 2000, 2002a, 2002b; Liu et al., 2007] at the within-site scale. Given the enormous area of the temperate steppe occurring in northern China [Kang et al., 2007], multisite measurements are indispensable for extrapolating our site-based estimates of soil respiration to the regional scale to obtain an overall picture of the carbon cycle in the area. In the present study, we conducted a field experiment in eight steppe communities growing along a transect in the Xilin River Basin of the Inner Mongolian Plateau. Our major objectives were (1) to distinguish between the individual and interactive impacts of soil temperature, moisture and plant growth on the within-site seasonal variations in soil respiration in these communities and (2) to assess the spatial variations in soil respiration and the controlling factors across the sites.

2. Materials and Methods

2.1. Study Sites

[7] This study was conducted in the Xilin River Basin of the Inner Mongolian Plateau (43°26′–44°39′N, 115°32′–117°12′E; 950–1300 m above sea level). The area belongs to the semiarid temperate climate zone. The mean annual temperature is approximately 0.6°C. The coldest mean monthly temperature is −21.4°C in January, while the warmest is 18.5°C in July. Mean annual precipitation is about 350 mm, with the rainy season being between mid-June and mid-September, with approximately 10% falling as snow in winter. Vegetation is dominated by temperate steppes, including three subtypes, i.e., meadow steppe, typical steppe and desert steppe [Li et al., 1988]. The soils studied were Chernozem and Chestnut soils in Chinese soil taxonomy, which are equivalent to Mollisols in U.S. soil taxonomy, with pH values ranging from 7.1 to 8.3 [Zhao et al., 1988]. Plants usually grow from late April to early October.

[8] Eight major steppe communities distributed along a 160 km west–east transect were chosen, located approximately 20 km apart (Figure 1). There is a clear decreasing precipitation gradient with long-term mean annual precipitation varying from 449 mm in the east to 327 mm in the west. In contrast to the precipitation, air temperature differs only slightly (from −1.4°C to 2.0°C) among these sites. At each site, an area of 100 × 100 m with flat ground and comparable vegetation was fenced for various measurements.

2.2. Soil Respiration Measurements

[9] Soil respiration was measured using the alkali absorption technique [Anderson, 1982; Keith et al., 1997]. A container (6.5 cm in diameter, 7 cm in height) with 20 ml of 1 M NaOH solution was put on a wire bracket which was 2 cm above the ground and covered with a zinc-plated iron chamber (25 cm in diameter and 30 cm in height) inserted 2 cm into the soil. After 24 h, absorbed CO2 was precipitated with 3 M BaCl2 and titrated with 1 M HCl using phenolphthalein as indicator to determine the change in color and hence the amount of CO2 absorbed. An identical, closed chamber without soil and vegetation was used as a control chamber, by which CO2 content of the headspace upon closure was measured using the same procedure. Emission of CO2 was calculated according to the formula given by Anderson [1982]. On each measuring occasion, five measurement chambers and two control chambers were randomly distributed on different locations inside the fenced area at each site. Prior to placement of the chambers, all green and standing dead plants covered by the chambers were removed by clipping to the ground level 1 or 2 days in advance. Soil respiration was measured once every 10 days from 5 June to 15 October 2001. Concurrent measurements were made on the same day on each occasion at all the sites.

[10] To assess possible bias by the alkali absorption method, we also conducted concurrent comparative measurements using a Li-Cor 6400 infrared gas analyzer (IRGA) (Li-Cor Incorporated, Lincoln, Nebraska, United States) in several pilot stands and found highly significant linear correlations between the measured values by the two methods, with r2 values ranging from 0.76 for the meadow steppe (y = 0.2941x + 363.4, n = 9, p < 0.001; where y and x are the soil respiration rates measured by the alkali absorption method and IRGA, respectively) to 0.87 for the typical steppe (y = 0.3142x + 320.9, n = 10, p < 0.0001). On average, the actual soil respiration rate measured by the alkali absorption method was 32.5% (for the typical steppe) and 38.6% (for the meadow steppe) lower than that by IRGA (data not shown). Some other studies also confirmed that measurements of soil respiration by alkali absorption method are quantitatively comparable to those by IRGA method in their specifically designed comparative studies [Keith and Wong, 2006; Yang et al., 2004; Zhang et al., 2003]. Therefore, alkali absorption technique-based data were directly used in the various analyses in the present study.

2.3. Measurements of Plant Biomass and Climatic Variables

[11] Living aboveground plant biomass (AGB) was measured by the harvest method. On each occasion of soil respiration measurement, five 1 m2 squares were randomly chosen at the fenced plot of each site and live plants were clipped at 1 cm above the ground level. ANPP was estimated to be the maximum standing crop of aboveground biomass in
the growing season. Root biomass at 20 cm depth was taken with the soil core method in the same sample squares that were used for determination of canopy biomass. Plant materials were oven-dried at 65°C for 48 h to determine total aboveground and root biomass.

Soil temperature and precipitation were monitored in situ throughout the whole experimental period by installing a temporary meteorological station at each study site. A rain gauge (BME-98, Tianjin Weather Instruments Factory, 20 cm in diameter, 70 cm in height, with resolution of ±2%) was employed to measure rainfall. Soil temperature was measured using a manually inserted soil thermometer (SDM 6310, Tianjin Weather Instruments Factory, with resolution of ±1°C). The moisture content of the topsoil (0–20 cm) \( (n = 5) \) was measured gravimetrically and concurrently with soil respiration [Jackson et al., 2000], with soil samples being taken within 1 m distance from the soil respiration chambers each time.

2.4. Soil Sampling and Laboratory Analyses

In mid-August, the top 20 cm layer of soil was sampled using a 5 cm diameter soil auger adjacent to the locations for soil respiration measurement. All the samples were transported to the laboratory immediately, passed through a 2 mm sieve to remove all visible plant materials, and air-dried for measurements of soil density and texture, C and N contents and pH value. Soil texture was measured by the pipette method [Gee and Bauder, 1986]. Soil organic C concentration was determined using wet combustion as described by Nelson and Sommers [1996]. Soil total N was determined by the Kjeldahl method [Bremner, 1996]. Soil pH (H\(_2\)O) was determined using a 1:5 soil solution ratio.

2.5. Calculations and Statistical Analyses

To quantify the temporal and spatial variability in soil respiration, soil temperature, soil moisture and living aboveground biomass, the coefficient of variation (CV) was calculated as:

\[
CV = \frac{\text{Standard deviation}}{\text{mean}} \times 100\% \tag{1}
\]

Linear regression was performed to examine relationships between soil respiration and soil moisture. An exponential function was used to describe the relationship between

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**Figure 1.** Locations of the eight sites used in this study. The eight communities investigated are numbered in the order of east to west along a transect. Site 1: Filifolium sibiricum meadow steppe; site 2: Artemisia frigida+Potentilla acaulis typical steppe; site 3: Stipa grandis+Leymus chinensis typical steppe; site 4: Artemisia frigida+Cleistogenes squarrosa typical steppe; site 5: Salsola collina desert steppe; site 6: Leymus chinensis typical steppe; site 7: Caragana stenophylla-Salsola collina desert steppe; site 8: Stipa krylovii+Cleistogenes squarrosa typical steppe.
soil respiration and soil temperature [Raich and Potter, 1995; Rey et al., 2002]:

\[ R = a \times e^{\beta T} \]  

where \( T \) is measured soil temperature at 10 cm depth, \( R \) is the soil respiration rate at \( T \), \( \beta \) is the coefficient of temperature sensitivity, and \( a \) is the basal soil respiration. A similar exponential function was also applied to describe the relationship between soil respiration and aboveground biomass (B).

To examine the concordant effects of soil temperature (T), soil moisture (M) and aboveground biomass (B) on soil respiration (R), the following model was used:

\[ R = a e^{\beta T} + c M^d \]  

where \( a, b, c \) and \( d \) are constants.

\[ R = a e^{\beta T} + c M^d \]  

Figure 2. Temporal dynamics of soil temperature (T), soil moisture (M), living aboveground biomass (AGB), and soil respiration (R) in four (sites 1, 3, 5 and 8) out of the eight sites along the transect. Site description is given in Figure 1.

\[ R = a e^{\beta T} + c M^d \]  

where \( T \) is measured soil temperature at 10 cm depth, \( R \) is the soil respiration rate at \( T \), \( \beta \) is the coefficient of temperature sensitivity, and \( a \) is the basal soil respiration. A similar exponential function was also applied to describe the relationship between soil respiration and aboveground biomass (B).

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where \( a, b, c \) and \( d \) are constants.

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One-way ANOVA was used to compare differences in the mean values of the coefficient of variation of soil temperature, moisture, living aboveground biomass, and soil respiration across the eight sites. A General Linear Model was used to examine significance of regression analyses. All statistical analyses were conducted using SAS 9.0 (SAS Institute Incorporated, Cary, North Carolina, United States).

3. Results

3.1. Seasonal and Spatial Patterns in Microclimate and Soil Respiration

There were substantial seasonal fluctuations in soil temperature, soil moisture, living aboveground biomass, and soil respiration at all the sites (Figure 2). Soil temperature, living aboveground biomass (AGB) and soil respiration peaked in July and August and declined over time, whereas
seasonal patterns of soil moisture were site-specific. Temporal coefficient of variations (CVs) of soil temperature generally declined from the east to the west along the transect, and CVs of soil moisture and AGB were irregular, while CVs of soil respiration appeared to be greater in the west than in the east (Figure 3a). Across the eight sites, mean temporal variability of living AGB (61.2 ± 7.65%) was significantly greater ($p < 0.01$) than that of soil temperature (46.7 ± 1.04%) and moisture (42.6 ± 3.99%) (Figure 3b). Mean CV of soil respiration (58.6 ± 1.54%) was also greater than that of soil moisture (Figure 3b).

No clear spatial trends of the seasonal means of soil moisture, soil respiration and ANPP were found, while an increasing trend was detected for soil temperature from the east to the west (Table 1). Highest levels of soil moisture, maximum observed AGB (i.e., ANPP), and soil respiration as well as the lowest soil temperature occurred in the meadow steppe in the east. During the whole growing season, spatial variability across the eight sites of soil temperature and moisture generally increased, whereas there was a declining trend in the spatial variability of soil respiration with time (Figure 4a). When averaged over the growing season, spatial CVs of soil moisture (70.3 ± 4.26%) and living AGB (65.7 ± 3.51%) were significantly greater ($p < 0.01$) than those of soil temperature (12.5 ± 2.33%) and soil respiration (32.6 ± 2.65%, Figure 4b).

3.2. Temporal Controls Over Soil Respiration

Over the growing season, soil respiration increased exponentially with soil temperature at all the sites ($p < 0.05$, Table 1). The relationships between soil respiration and temperature were stronger at sites where seasonal mean soil temperatures were higher (Table 1). Relationships between soil respiration and soil moisture differed among the communities. Significantly positive linear correlations between soil respiration and soil moisture were found in six out of the eight sites ($p < 0.05$) where intermediate soil moisture was observed (Table 1). In contrast, seasonal variations in soil respiration were independent of soil moisture at the wettest (site 1) and driest (site 5) sites over the growing season (Table 1). In addition, the effects of soil moisture on soil respiration became weaker at the sites with higher maximum living AGB than those with lower maximum living AGB (Table 1). Significantly positive exponential correlations between soil respiration and AGB were found in four out of the eight sites, tending to become more obvious at the sites with higher ANPP (Table 1).

![Figure 3](https://example.com/figure3.png)

Figure 3. (a) Temporal variability (coefficient of variation (CV)) in soil temperature (T), soil moisture (M), living aboveground biomass (AGB), and soil respiration (R) and (b) their mean values (mean ± 1SE) across the eight sites.

Table 1. Relationships Between R and T, M, AGB, and the Combined Effects of T/M/AGB in the Eight Steppe Communities

<table>
<thead>
<tr>
<th>Site</th>
<th>Mean Soil T (°C)</th>
<th>Mean Soil M (%)</th>
<th>ANPP (g m⁻² yr⁻¹)</th>
<th>Mean Soil R (mg m⁻² d⁻¹)</th>
<th>$R^2$ T-R</th>
<th>$R^2$ M-R</th>
<th>$R^2$ AGB-R</th>
<th>$R^2$ TM-R</th>
<th>$R^2$ TMB-R</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>15.3</td>
<td>11.6</td>
<td>254.9</td>
<td>952.4a</td>
<td>0.382*</td>
<td>0.0018</td>
<td>0.406**</td>
<td>0.501*</td>
<td>0.564*</td>
</tr>
<tr>
<td>2</td>
<td>16.2</td>
<td>4.0</td>
<td>110.8</td>
<td>785.9ab</td>
<td>0.365*</td>
<td>0.327*</td>
<td>0.033</td>
<td>0.642**</td>
<td>0.690**</td>
</tr>
<tr>
<td>3</td>
<td>17.7</td>
<td>4.4</td>
<td>81.9</td>
<td>767.8ab</td>
<td>0.594***</td>
<td>0.496**</td>
<td>0.614***</td>
<td>0.906***</td>
<td>0.911***</td>
</tr>
<tr>
<td>4</td>
<td>18.6</td>
<td>3.8</td>
<td>105.1</td>
<td>661.3b</td>
<td>0.571**</td>
<td>0.485**</td>
<td>0.258</td>
<td>0.841***</td>
<td>0.863***</td>
</tr>
<tr>
<td>5</td>
<td>19.0</td>
<td>1.9</td>
<td>94.8</td>
<td>565.1b</td>
<td>0.509**</td>
<td>0.185</td>
<td>0.394*</td>
<td>0.597**</td>
<td>0.728**</td>
</tr>
<tr>
<td>6</td>
<td>19.8</td>
<td>6.2</td>
<td>174.4</td>
<td>911.3a</td>
<td>0.553**</td>
<td>0.444**</td>
<td>0.375*</td>
<td>0.783**</td>
<td>0.802**</td>
</tr>
<tr>
<td>7</td>
<td>19.0</td>
<td>4.3</td>
<td>73.0</td>
<td>582.4b</td>
<td>0.527**</td>
<td>0.667***</td>
<td>0.053</td>
<td>0.861**</td>
<td>0.866**</td>
</tr>
<tr>
<td>8</td>
<td>18.0</td>
<td>2.2</td>
<td>126.3</td>
<td>581.7b</td>
<td>0.424**</td>
<td>0.343*</td>
<td>0.135</td>
<td>0.862**</td>
<td>0.884**</td>
</tr>
</tbody>
</table>

*aOne asterisk, $p < 0.05$; two asterisks, $p < 0.01$; three asterisks, $p < 0.001$. R, soil respiration; T, soil temperature; M, soil moisture; AGB, aboveground biomass; ANPP, aboveground net primary productivity.

*bNumbers with the same letter (a, b) are not significantly different at $p = 0.05$.

*TMB refers to soil temperature–soil moisture–aboveground biomass.
Combined effects of soil moisture and soil temperature on the seasonal patterns of soil respiration were significant for all sites (all $p < 0.05$) (Table 1). Compared with the temperature alone, inclusion of soil moisture explained an additional 9–44% of the seasonal variation in soil respiration. The inclusion of the living AGB did not improve significance of the relationships when compared with the combined effects of soil temperature and moisture at all the sites (Table 1).

3.3. Spatial Controls Over Soil Respiration

Across the eight sites, seasonal mean soil temperature tended to be negatively related to the growing-season precipitation, although the correlation was not significant ($r^2 = 0.46$, $p < 0.10$). In contrast, seasonal mean soil moisture ($r^2 = 0.94$, $p < 0.0001$), maximum observed AGB ($r^2 = 0.82$, $p < 0.01$) and seasonal mean soil respiration ($r^2 = 0.65$, $p < 0.05$) were all positively correlated with growing-season precipitation (Figure 5).

No significant correlation between mean soil respiration rate and mean soil temperature ($r^2 = 0.20$, $p = 0.26$) over the growing season was detected across the eight sites (Figure 6a). However, soil respiration was found to be significantly correlated with soil moisture, and about 70% of the spatial variation in soil respiration could be explained by changes in soil moisture (Figure 6b).

Regression analyses between the mean soil respiration and soil traits and the maximum observed AGB among the eight sites identified significant positive relationships between soil respiration rate and soil clay contents ($r^2 = 0.80$, $p < 0.01$; Figure 6c), soil organic C ($r^2 = 0.56$, $p < 0.05$; Figure 6e), total nitrogen ($r^2 = 0.57$, $p < 0.05$; Figure 6f) and maximum AGB ($r^2 = 0.65$, $p < 0.05$; Figure 6h). In contrast, there were negative relationships between soil respiration and soil sand content ($r^2 = 0.83$, $p < 0.01$; Figure 6d) and bulk density ($r^2 = 0.65$, $p < 0.05$; Figure 6g). No significant relationship was detected between soil respiration and soil pH value (data not shown).

4. Discussion

4.1. Temporal Controls of Microclimate Over Soil Respiration

Temperature can influence soil respiration mainly by affecting root activities, decomposition of plant litter and soil organic matter and plant biomass production, leading to changes in C substrate availability for plant roots and soil microbes [Wan and Luo, 2003; Xu et al., 2004]. Our findings...
show that temperature was the major controlling factor for the seasonal patterns of within‐site soil respiration in the study area. The exponential dependence of seasonal dynamics of soil respiration upon soil temperature observed in this study (Table 1) is consistent with relationships reported from many other grassland ecosystems [Dornbush and Raich, 2006; Singh and Gupta, 1977; Wan et al., 2007]. However, changes in other abiotic (soil water availability) and biotic (plant growth and soil microbial activities) factors may also contribute to temporal variations in soil respiration, thus leading to differences in the temperature controls over soil respiration among different vegetation types and regions in different climate zones [Raich and Tufekcioglu, 2000]. Our findings reveal that temperature controls over seasonal patterns of soil respiration varied substantially among sites even within the same community type (e.g., sites 2 and 4) at the regional scale. The magnitude of seasonal variation in soil respiration (Figures 2 and 3) due to soil temperature varied from 36.5% at site 2 to 57.1% at site 4 (Table 1). In addition, the dependence of soil respiration on soil temperature tended to be stronger at sites with higher mean soil temperature (Table 1).

[26] Positive correlations between soil respiration and soil moisture observed in this study are in accordance with those in grassland ecosystems [Chen et al., 1999; Holt et al., 1990; Li et al., 2000] and other terrestrial ecosystems [Singh and Gupta, 1977]. However, we found that the influence of soil water availability on seasonal dynamics of soil respiration was closely dependent upon the overall site‐specific soil water regimes. For example, at the sites with intermediate mean soil moisture, soil moisture exerted strong impacts on the seasonal changes in soil respiration, whereas it had no effects at the sites with the highest (site 1) and lowest (site 5) mean soil moisture levels (Table 1). Even at moderate soil moisture levels, the contribution of soil moisture to soil respiration varied greatly, ranging from 34.3% at site 8 to 66.7% at site 7. In addition, at low to moderate mean soil moisture levels, the correlation coefficient of soil respiration and soil moisture tended to increase with mean soil water contents (Table 1). These findings suggest that seasonal dynamics of soil respiration is under the control of other factors rather than soil moisture when soil water availability is not a limiting factor. Soil water availability may constrain root and microbial activities at high and low water contents [Liu et al., 2002; Scott‐Denton et al., 2003; Wan et al., 2007]. For instance, at an old‐field grassland with very high mean soil moisture content, a negative relationship between soil respiration and soil moisture was observed [Wan et al., 2007]. This response may largely result from reduction in oxygen availability for both microbial decomposition and autotrophic activities [Davidson et al., 1998; Rey et al., 2002; Xu and Qi, 2001].

[27] Interestingly, we observed that the dependence of soil respiration upon soil moisture over the growing season became weaker with increasing maximum aboveground biomass among the sites (Table 1). With increases in the maximum observed aboveground biomass across the communities, the contribution of plant growth to total soil respiration may have increased by enhanced root respiration, for instance in response to inputs of soil active carbon from canopy and the consequent priming effects on SOM decomposition, leading to a weaker relationship between soil respiration and soil moisture was observed [Wan et al., 2007]. This response may largely result from reduction in oxygen availability for both microbial decomposition and autotrophic activities [Davidson et al., 1998; Rey et al., 2002; Xu and Qi, 2001].

4.2. Temporal Controls of Plant Growth Over Soil Respiration

[28] A number of studies have suggested that soil respiration is directly related to recent plant photosynthesis or growth [Bremer et al., 1998; Dornbush and Raich, 2006; Högberg et al., 2001]. Temporal changes in plant growth can impact soil respiration by affecting C substrate supply for plant roots and soil microbes in rhizosphere. Consequently, seasonal variations in soil respiration generally display good
correlation with plant growth in many terrestrial ecosystems [Högberg et al., 2001; Verburg et al., 2004; Verburg et al., 2005; Wan et al., 2007; Curiel Yuste et al., 2004; Zhang, 2002]. Canopy characteristics such as aboveground biomass and leaf area index have been used to relate the control of plant growth to soil respiration in a number of studies [Janssens et al., 2001; Li et al., 2000, 2002b; Pendall et al., 2001; Reichstein et al., 2003; Verburg et al., 2004; Curiel Yuste et al., 2004]. However, in the present study, we only found significant correlations between soil respiration and aboveground biomass over the growing season in four out of the eight sites (Table 1). In addition, with exception of one location (site 7) did inclusion of aboveground biomass as an additional factor in the modeling not affect explanation of soil respiration variation greatly (Table 1). These findings suggest less importance of plant growth in regulating seasonal dynamics of soil respiration than other factors (temperature and water availability) in the temperate steppe.

[29] Several possible explanations may account for the lack of close relationships between soil respiration and aboveground biomass in our study. First, root respiration accounts for only 30–40% of the total soil respiration in temperate grasslands [Subke et al., 2006; Wan et al., 2007]. Heterotrophic respiration (decomposition of soil organic matter and surface litter) in the temperate steppe accounts for the majority of total soil respiration [Li et al., 2002a, 2002b; Liu et al., 2007] and may have different seasonal dynamics from root respiration [Cisneros-Dozal et al., 2006; Subke et al., 2006]. Root respiration is more related to plants’ phenology [Högberg et al., 2001; Janssens et al., 2001; Reichstein et al., 2003; Curiel Yuste et al., 2004], and surface litter decomposition is primarily moisture-dependent, while decomposition of soil organic matter is more closely dependent on temperature. Therefore, the overall temporal patterns of soil respiration are largely dependent on the relative proportions of the different components in total soil respiration. In the study area reported in this paper, decomposition of aboveground litter accounted for a minor fraction of total soil respiration [Chen et al., 1999], and root respiration accounts for 20–35% of the total soil respiration in various steppe communities [Li et al., 2002a, 2002b; Liu et al., 2007], whereas decomposition of soil organic matter is a dominant source for soil respiration. This would lead to poor temporal correlation between total soil respiration and living aboveground biomass in some communities (Table 1).

[30] Second, temporal effects of temperature, soil moisture, and plant growth on soil respiration are mutually inclusive. In addition, plant growth itself is also under the influence of temporal changes in soil temperature and moisture, which are likely to mask the effects of plant growth on soil respiration. Dornbush and Raich [2006] also did not find a clear within-site correlation between soil respiration and ANPP in an American grassland. They argued that soils usually contain excessive C substrate, and soil respiration therefore may not be substrate limited, but climatically limited in most cases.

4.3. Spatial Controls of Climate and ANPP Over Soil Respiration

[31] Strong spatial variability in soil respiration, soil moisture, maximum living aboveground biomass (ANPP), and soil temperature illustrated in this study (Figure 4) necessitates multisite measurements in simulation and projection of ecosystem C cycling involving soil respiration. Our findings show that soil moisture (Figure 6b), rather than temperature (Figure 6a), is the critical climatic factor determining spatial variations in soil respiration at the local scale. Similar results have been reported by Reichstein et al. [2003] in an analysis of the site-to-site variability of soil respiration at forest and shrubland sites and by Janssens et al. [2001] among a collection of colder sites of European forests at regional scale. The mechanism could be that soil moisture poses direct influence on soil respiration through water limitation of soil microbes as well as indirect influence via site plant biomass productivity [Reichstein et al., 2003]. It can be seen that maximum aboveground biomass and soil respiration were all closely related to the growing-season precipitation (Figures 5a and 5b). In contrast to soil moisture, temperature usually is not a strong limiting factor for site productivity [Flanagan and Johnson, 2005; Janssens et al., 2001].

[32] There was also a strong spatial dependence of soil respiration upon the maximum aboveground biomass (Figure 6h) at site to site scale, which does not support conclusions from previous studies that soil respiration are poorly correlated to ANPP at local scales [Ellis, 1969; Reiners, 1968]. Plant biomass production can influence soil respiration mainly in less direct and a longer-term manner by affecting soil C pool size derived from canopy litter input, root biomass and soil organic matter [Raich and Tufekcioglu, 2000; Reichstein et al., 2003], and by affecting the release from these pools, via either respiration or decomposition. Significant among-site correlation between root biomass, instead of ANPP, and soil respiration was found across four Iowa grassland stands, mainly due to the inconsistency of shoot and root dynamics [Dornbush and Raich, 2006].

4.4. Spatial Controls of Soil Traits Over Soil Respiration

[33] We found that seasonal mean soil respiration rate was positively correlated with soil organic C content, total N and clay contents, but was negatively correlated with sand content and bulk density at the among-site scale. Since soil respiration involves the conversion of organic C into inorganic C, soil respiration rate is ultimately controlled by the supply of C substrate [Wan et al., 2007]. The significant positive correlation between soil respiration rate and total N content in our study can be explained by the direct dependence of plant growth and root activities and indirect dependence of ANPP on soil N availability [Pastor et al., 1984; Raich et al., 1997]. At within-site scale, spatial variations in soil respiration in forests have been ascribed to differences in soil C and N contents in a number of studies [Buchmann, 2000; Davidson et al., 1998; Saiz et al., 2006; Soe and Buchmann, 2005; Xu and Qi, 2001]. However, at regional scale, Reichstein et al. [2003] found no significant correlations between soil respiration and site properties such as carbon pool variables and nitrogen stocks among distant sites.

[34] Clay content can affect soil respiration indirectly via several aspects. First, soils with higher clay content have a higher soil water holding capacity [Knohl et al., 2008]. Greater soil water availability in turn would affect root and
microbial respiratory activities by stimulating plant growth, belowground C input, decomposition of plant litter and soil organic C. Significant positive correlations between clay content and soil moisture and maximum observed aboveground biomass across the eight sites (Table 2) support this reasoning. Second, a higher soil clay content would enhance soil nutrient availability, thus contributing to greater plant productivity and C substrate for respiratory processes. Positive dependence of total soil N upon clay content (Table 2) is in line with this argument. Finally, more clayey soils could store more soil organic C, and supply more C substrate for heterotrophic respiration [Reichstein et al., 2003]. Across the spatial gradient, soil organic C increased linearly with clay content (Table 2). Clay and sand, which are two of the three texture components of soils, usually exhibit negative correlations (Table 2). This may account for the negative impacts of sand content on soil respiration. Greater soil bulk density contributes to lower soil porosity, thus resulting in lower oxygen availability in soils. This in turn may constrain microbial activities, leading to the observed decrease in soil respiration in the present study.

[35] Among the abiotic and biotic factors, the best single factor explaining the site-to-site variations of soil respiration was soil texture traits such as clay or sand contents (Figure 6). Stepwise multiple regression analyses revealed that the inclusion of other variables (including soil C and N contents, bulk density, pH value, as well as climatic factors) made little improvement on the accountability of the spatial variations in soil respiration among the sites. This finding may be accounted for by the fact that most of these site variables were highly autocorrelated with each other (Table 2).

[36] In summary, we found that substantial temporal and spatial variability in soil respiration exists in the temperate steppe in northern China. Our results indicate that abiotic factors (temperature and moisture) are more important than biotic factors (plant growth) in regulating the seasonal patterns of within-site soil respiration in the steppe. In contrast, spatial differences in soil respiration could be primarily accounted for by the differences in soil moisture and plant biomass productivity among the study sites. These findings suggest that the relative importance of temperature, water availability and plant growth in determining soil respiration depends upon spatial or temporal scales. Moreover, soil texture also has strong impacts on soil respiration by affecting soil moisture, indirectly influencing plant biomass production and substrate availability. Our findings indicate that temporally and spatially continuous measurements of soil temperature and moisture and plant production are of great importance, and should be considered differently in the temperate steppe for better understanding the responses of soil respiration to the changes in climate patterns.

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References


Table 2. Correlation Coefficients of the Soil Parameters Among the Eight Sites

<table>
<thead>
<tr>
<th></th>
<th>Bulk Density</th>
<th>Clay Content</th>
<th>Sand Content</th>
<th>Soil T</th>
<th>Soil M</th>
<th>TN</th>
<th>TOC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clay content</td>
<td>-0.877***</td>
<td>-0.748**</td>
<td>-0.909***</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand content</td>
<td>+0.405&lt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil T</td>
<td></td>
<td></td>
<td></td>
<td>-0.950***</td>
<td>+0.924***</td>
<td>-0.856***</td>
<td>+0.897***</td>
</tr>
<tr>
<td>TN</td>
<td>-0.902***</td>
<td>+0.759**</td>
<td>-0.627*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOC</td>
<td>-0.932***</td>
<td>+0.804**</td>
<td>-0.653*</td>
<td>-0.441^</td>
<td>+0.914***</td>
<td>-0.982***</td>
<td>+0.985***</td>
</tr>
<tr>
<td>AGB</td>
<td>-0.712**</td>
<td>+0.885*</td>
<td>-0.727**</td>
<td>-0.387&lt;</td>
<td>+0.687*</td>
<td>+0.534*</td>
<td>+0.616*</td>
</tr>
</tbody>
</table>

*Plus and minus signs refer to positive and negative correlations, respectively. The symbols are as follows: carat, $p < 0.10$; one asterisk, $p < 0.05$; two asterisks, $p < 0.01$; and three asterisks, $p < 0.001$. TN, total nitrogen; TOC, total organic carbon.


