Effects of temperature and soil water-content on soil respiration of grazed and ungrazed *Leymus chinensis* steppes, Inner Mongolia

B. Jia\(^a,b\), G. Zhou\(^a\), Y. Wang\(^a,\ast\), F. Wang\(^a,b\), X. Wang\(^a\)

\(^a\)Laboratory of Quantitative Vegetation Ecology, Institute of Botany, The Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Haidian District, Beijing 100093, PR China

\(^b\)Graduate School of the Chinese Academy of Sciences, Beijing 100039, PR China

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**Abstract**

The dynamics and the controlling factors of soil respiration measured with a closed static chamber method for continuous 2 years in grazed and ungrazed typical *Leymus chinensis* steppes, Inner Mongolia, PR China were analysed. There were similar diurnal and seasonal dynamics between the grazed and ungrazed plots. The diurnal patterns of soil respiration could be expressed as one-humped curves, reaching to the maximum at 11:00–14:00 and falling to the minimum at 1:00–3:00. During the growing season, the rates of soil respiration increased from the middle of June to the end of July and then gradually decreased. The seasonal changes of soil respiration were mainly influenced by moisture and temperature. When temperature was an independent controlling factor, it played a good role under the conditions of lower temperature (<15 °C) and lower moisture (<12%). However, the temperature models (e.g. linear, quadratic, power, exponential and Arrhenius models) did not reflect the stimulation effect of moisture on soil respiration with increasing temperature and moisture. Moisture was the single best predictor of hourly soil respiration rate in the arid and semi-arid grassland, but the mutual regulation by temperature and moisture did improve the predictive capacity of the models. Linear models could give better simulations than others did, and account for above 82% of the variation in soil respiration at the ungrazed plot. Although there was no further improvement in exponential, exponential-power and exponential-Arrhenius models for the...
simulation at the ungrazed plot, they did enhance the predictive capacity of soil respiration at the grazed plot ($R^2 = 0.87–0.88$).

1. Introduction

Soil organic matter contains a large reservoir of carbon, recently estimated at 1500 Pg C (IPCC, 2001), about twice of the atmospheric CO$_2$-C pool. Changes in the size of the soil C pool therefore can significantly affect atmospheric CO$_2$ concentrations (Raich and Potter, 1995). As a major flux between atmosphere and land, soil respiration is estimated to be 50–78 Pg C yr$^{-1}$ (Raich and Schlesinger, 1992; Raich and Potter, 1995; IPCC, 2001), accounting for about 25% of the global carbon dioxide exchange. Therefore, accurate estimation of soil respiration becomes one of the important issues in the global carbon cycle.

*Leymus chinensis* (Trin.) Tzvel. steppe occupies the largest area ($30 \times 10^4$ ha) in the typical steppe zone of Inner Mongolia, primarily as grazing and mowing lands (Li et al., 1988). Due to human disturbances (mainly overgrazing), the area of degraded grassland in China reached $1.35 \times 10^8$ ha, accounting for one third of the available grassland area and increasing at the speed of $200 \times 10^4$ ha yr$^{-1}$ (Zhou and Wang, 2002). Whether grassland acts as a carbon source or sink for atmospheric CO$_2$ depends on its special land use, grazing intensity and climate (Frank, 2002). However, the effects of grazing management on the biogeochemical processes that control the exchange of carbon between soil and atmosphere are not well understood yet (Reeder and Schuman, 2002). Thus, the studies on soil respiration and its controlling factors in grazed and ungrazed grassland ecosystems would contribute to understanding and accurately evaluating global carbon budget and climate change.

Soil respiration relies on a suite of complex processes contributing to CO$_2$ efflux from soil surface, mainly from plant roots and micro-organisms. Temperature and moisture are usually taken as important factors controlling soil respiration by different relationships, including linear, quadratic, power, exponential and Arrhenius models, etc. (Table 1). Those respiration models were developed based on specific (or multiple) vegetation type(s), representing a single (or synthetic) measurement(s) at a single (or multiple) site(s). However, few studies examine the validation of these models in other regions, especially in grazed and ungrazed grassland ecosystems. In order to improve the simulation accuracy, the comparisons among temperature–based soil respiration models have been done (e.g. Howard and Howard, 1979; Lloyd and Taylor, 1994; Fang and Moncrieff, 2001); however, these among moisture-based or temperature–moisture-based soil respiration models have not been done. A statistical evaluation of the existing models is a useful and necessary step in global carbon budget analyses (Raich and Potter, 1995). This study aims to evaluate the ability of the above-mentioned equations controlled by temperature, moisture and temperature–moisture interaction (Table 1) for predicting soil respiration rate at hourly temporal resolution in grazed and ungrazed *L. chinensis* steppes, Inner Mongolia, based on the residuals analysis method to determine the appropriateness of model fits on these main factors.
Table 1  
Relationships of soil respiration with temperature, moisture and temperature-moisture interaction

<table>
<thead>
<tr>
<th>Equation</th>
<th>Example</th>
<th>Vegetation</th>
<th>Method</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Temperature:</strong></td>
<td></td>
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</tr>
<tr>
<td>Linear: $F = a + bT$</td>
<td>$F (g \text{ C m}^{-2} \text{ yr}^{-1}) = 265.9 + 27.7T$, $R^2 = 0.83$</td>
<td>Peatlands</td>
<td>Synthesis</td>
<td>Chimner (2004)</td>
</tr>
<tr>
<td>Quadratic: $F = a + bT + cT^2$</td>
<td>$F (mg \text{CO}_2 \text{ m}^{-2} \text{ h}^{-1}) = 89.78 + 1.54T + 5T^2$, $R^2 = 0.83$</td>
<td>Tundra</td>
<td>IRGA</td>
<td>Peterson and Billings (1975)</td>
</tr>
<tr>
<td>Power: $F = aT^b$</td>
<td>$F (mg \text{ C m}^{-2} \text{ d}^{-1}) = 256.75T^{0.6557}$, $R^2 = 0.58$</td>
<td>Leymus chinensis</td>
<td>Alkali absorption</td>
<td>Li et al. (2000)</td>
</tr>
<tr>
<td>$F = a(T + 10)^b$</td>
<td>$F (mg \text{C m}^{-2} \text{ s}^{-1}) = 1.66 + 2.20 \ln(T+10)$, $R^2 = 0.89$</td>
<td>Tallgrass prairie</td>
<td>IRGA</td>
<td>Kuera and Kirkham (1971)</td>
</tr>
<tr>
<td>Exponential: $F = aT$</td>
<td>$F (\mumol \text{ CO}_2 \text{ m}^{-2} \text{ s}^{-1}) = 0.375e^{0.066T}$, $R^2 = 0.46$</td>
<td>Peatlands</td>
<td>IRGA</td>
<td>Chimner (2004)</td>
</tr>
<tr>
<td>$F = aT^{0.1049T}$</td>
<td>$F (mg \text{ C m}^{-2} \text{ s}^{-1}) = 7.069 + 0.133T$, $R^2 = 0.47$</td>
<td>Forest</td>
<td>Synthesis</td>
<td>Liu and Fang (1997)</td>
</tr>
<tr>
<td>$F (g \text{ CO}_2 \text{ m}^{-2} \text{ h}^{-1}) = 0.14e^{0.0813T}$, $R^2 = 0.75$</td>
<td>Mixed hardwood forest</td>
<td>IRGA</td>
<td>Kang et al. (2003)</td>
<td></td>
</tr>
<tr>
<td>$F = a(T - T_{min})^b$</td>
<td>$F (mg \text{ C m}^{-2} \text{ s}^{-1}) = 1.66 \times 10^{3}(T+26.5)^{0.10}$, $R^2 = 0.90$</td>
<td>Lab incubations</td>
<td>IRGA</td>
<td>Fang and Moncrieff (2001)</td>
</tr>
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<td>IRGA</td>
<td>Chimner (2004)</td>
</tr>
</tbody>
</table>
Moisture:

**Linear:** $F = a + bW$

- $W < 0.12 \text{cm}^3 \text{cm}^{-3}$, $F(\text{mg C m}^{-2} \text{h}^{-1}) = 2852W - 128$ $R^2 = 0.48$
- $W > 0.12 \text{cm}^3 \text{cm}^{-3}$, $F(\text{mg C m}^{-2} \text{h}^{-1}) = -198W + 201$ $R^2 = 0.22$
- $W =$ volumetric water content at 0–15 cm depth (cm$^3$ cm$^{-3}$)
- *Quercus glauca:* $F(\text{mg CO}_2\text{ m}^{-2} \text{h}^{-1}) = 0.005W^2 + 0.122$, $R = 0.46$

**Camellia sinensis:** $F(\text{mg CO}_2\text{ m}^{-2} \text{h}^{-1}) = 0.021W - 0.199$, $R = 0.54$
- $W =$ gravimetric water content at 0–5 cm depth (%)
- $F(\mu\text{mol CO}_2\text{ g}^{-1} \text{h}^{-1}) = 4.35W - 0.148$, $R = 0.96$

- $W =$ gravimetric water content (%)
- $F(\text{mg CO}_2\text{ m}^{-2} \text{h}^{-1}) = 24.29W - 50.59$, $R^2 = 0.80$
- *Leymus:* $F(\text{mg CO}_2\text{ m}^{-2} \text{d}^{-1}) = 126.51W - 6.51$, $R^2 = 0.92$

**Puccinellia:** $F(\text{mg CO}_2\text{ m}^{-2} \text{d}^{-1}) = 60.43W - 1.70$, $R^2 = 0.98$
- $W =$ gravimetric water content at 0–10 cm depth (%)
- $F(\text{mg CO}_2\text{ m}^{-2} \text{h}^{-1}) = 58.15W - 105.88$, $R^2 = 0.85$

- $W =$ volumetric water content at 0–10 cm depth (%)
- Rice-involved: $F(\text{mg CO}_2\text{ m}^{-2} \text{h}^{-1}) = -35.89W + 1231.8$, $R^2 = 0.55$
- Rice-uninvolved: $F(\text{mg CO}_2\text{ m}^{-2} \text{h}^{-1}) = -6.11W + 135.2$, $R^2 = 0.58$
- $W =$ water level in rice paddy (cm)
- $F(\mu\text{mol CO}_2\text{ m}^{-2} \text{s}^{-1}) = -7487.7 + 34365W - 39391W^2$, $R^2 = 0.40$

**Quadratic:**

$F = a + bW + cW^2$
- $W =$ volumetric water content (%)
- Forest: $F(\text{g C m}^{-2} \text{h}^{-1}) = 1.90W^2 + 0.14$, $R^2 = 0.30$

- $W =$ volumetric water content at 0–30 cm depth (cm$^3$ cm$^{-3}$)
- Pasture: $F(\text{g C m}^{-2} \text{h}^{-1}) = 3.46W^2 + 0.09$, $R^2 = 0.54$

**Exponential:** $F = ae^{bW}$

- $T < 10 \text{ C}$, there was no significant relationship with $W_S$ or $W_L$
- $T > 10 \text{ C}$, $\ln F(\text{mg CO}_2\text{ m}^{-2} \text{h}^{-1}) = -0.019W_S + 5.31$, $R^2 = 0.71$
- $\ln F(\text{mg CO}_2\text{ m}^{-2} \text{h}^{-1}) = -0.005W_L + 5.76$, $R^2 = 0.76$
- $W_S =$ gravimetric water content at 0–20 cm depth (%)
- $W_L =$ litter water content (%)
- *Eucalyptus Pauciflora Forest*:

**Logarithmic:** $F = a + b\log W$

- $F(\text{g C m}^{-2} \text{h}^{-1}) = -0.043 \log(-\Psi) + 0.16$, $R^2 = 0.31$
- Pasture: $F(\text{g C m}^{-2} \text{h}^{-1}) = -0.047 \log(-\Psi) + 0.19$, $R^2 = 0.62$
- $\Psi =$ matric potential (MPa)

- *Forest and Pasture*:

**Results for: Mixed hardwood forest, Evergreen broad leaved forest, Lab incubations, Gas chromatography, Steppe Alkali absorption, Alkali absorption, Tropical forest, Forest and Pasture, Soda lime absorption.**

**References:**
- Davidson et al. (1998)
- Huang et al. (1999)
- Orchard and Cook (1983)
- Cui et al. (2000)
- Wang et al. (2002)
- Jia et al. (2004)
- Zou et al. (2003)
- Sotta et al. (2004)
- Davidson et al. (2000)
- Keith et al. (1997)
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<tbody>
<tr>
<td>$R(g \text{C m}^{-2} \text{d}^{-1}) = 3.467 \log W - 2.053$, $R = 0.92$</td>
<td></td>
<td></td>
<td></td>
<td>Davidson et al. (2000)</td>
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<tr>
<td>$W =$ gravimetric water content at 0–20 cm depth (%)</td>
<td></td>
<td></td>
<td></td>
<td>Chen et al. (1999)</td>
</tr>
<tr>
<td>$F(\mu\text{mol CO}_2 \text{g}^{-1} \text{h}^{-1}) = -0.167 \ln(-\Psi) + 0.95$, $R = 0.99$</td>
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<td></td>
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<td>Orchard and Cook (1983)</td>
</tr>
</tbody>
</table>

### Temperature–moisture: Exponential

- **Linear: $F = a + bT$**
  - $R(g \text{C m}^{-2} \text{d}^{-1}) = 0.88 + 0.013T$, $R^2 = 0.83$
  - $W =$ gravimetric water content at 0–10 cm depth (%) | Stipa grandis steppe | Alkali absorption | Wildung et al. (1975) |

- **Temperature–moisture: Exponential-power**
  - $W < 7.5\%$, $R = 0.90$ | Leymus chinensis steppe | IRGA | Wang et al. (2003) |
  - $W > 7.5\%$, $F(\mu\text{mol CO}_2 \text{g}^{-1} \text{h}^{-1}) = -147.7 + 5.1W + 6.0T + 1.2WT$, $R^2 = 0.81$
  - $T =$ soil temperature at 0 cm depth (°C), $W =$ gravimetric water content at 0–10 cm depth (%) |

- **Marginal fen: $F = a + bT + cW$**
  - $R(g \text{C m}^{-2} \text{d}^{-1}) = -2.07 + 0.07T + 0.03ML$, $R^2 = 0.76$
  - $T =$ soil temperature (°C), $W =$ gravimetric water content at 0–10 cm depth (%) | Cedar swamp | IRGA | Reiners (1968) |
  - $R(g \text{C m}^{-2} \text{d}^{-1}) = -2.06 + 0.08T + 0.04ML$, $R^2 = 0.83$
  - $T =$ soil temperature (°C), $W =$ gravimetric water content at 0–10 cm depth (%) |

- **Cedar swamp: $F = a + bT + cW + dTW$**
  - $R(g \text{C m}^{-2} \text{d}^{-1}) = 0.33W^{0.6}\exp(-0.042T)$, $R^2 = 0.76$
  - $T =$ soil temperature (°C), $W =$ gravimetric water content at 0–10 cm depth (%) | Riparian buffers and crop fields | Soda lime absorption | Tuleckioğlu et al. (2001) |

- **Cedar swamp: $F = a + bT + cW + dTW$**
  - $R(g \text{C m}^{-2} \text{d}^{-1}) = 26.17W^{0.82}\exp(-0.047T)$, $R^2 = 0.95$
  - $T =$ soil temperature (°C), $W =$ gravimetric water content at 0–10 cm depth (%) | Riparian buffers and crop fields | Soda lime absorption | Tuleckioğlu et al. (2001) |
<table>
<thead>
<tr>
<th>Environment</th>
<th>Method</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ponderosa pine</td>
<td>IRGA</td>
<td>Xu and Qi (2001)</td>
</tr>
<tr>
<td>Degraded steppe</td>
<td>Alkali</td>
<td>absorption</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chen et al. (2003)</td>
</tr>
<tr>
<td>Deciduous broad</td>
<td>IRGA</td>
<td>leaved forest</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lee et al. (2002)</td>
</tr>
<tr>
<td>Tundra</td>
<td>IRGA</td>
<td>Oberbauer et al. (1992)</td>
</tr>
</tbody>
</table>

**Equations:**

1. **Ponderosa pine IRGA Xu and Qi (2001):**
   
   \[ F = 5911.65W^{0.91}e^{0.04T}, \quad R^2 = 0.86 \]

2. **Degraded steppe Alkali absorption Chen et al. (2003):**
   
   \[ F = 1.97 \times 10^{-5}e^{0.045T} \times (W-21.42) \times (58.54-W)^{4.46}, \quad R^2 = 0.96 \]

3. **Deciduous broad leaved forest IRGA Lee et al. (2002):**
   
   \[ F = C \times e^{-E/RT} \times e^{Swt} \]

   - \( C \) = constant (\( \mu \)mol m\(^{-2}\)s\(^{-1}\)), \( T \) = soil temperature at 1 cm depth (K), \( R \) = gas constant (8.31 J mol\(^{-1}\)K\(^{-1}\)), \( E \) = apparent activation energy (J mol\(^{-1}\)), \( Swt = AW/(W + B) \), \( W \) = depth to water table below soil surface (cm), \( A \) and \( B \) are fitted parameters.

- \( T \) = soil temperature (°C), \( W \) = volumetric water content at 0-30 cm depth (%).
- \( T \) = air temperature (°C), \( W \) = gravimetric water content at 10-20 cm depth (%).
- \( T \) = soil temperature (°C), \( W \) = volumetric water content at 15 cm depth (%).
- \( T \) = soil temperature at 1 cm depth (K), \( W \) = depth to water table below soil surface (cm), \( A \) and \( B \) are fitted parameters.
2. Materials and methods

2.1. Site description

The study site is located at Baiinxile pasture (lat. 43°55′N, long. 116°31′E, 1201 m above mean sea level), Xilin River Basin, Inner Mongolia, PR China. The climate belongs to semi-arid, continent temperate climate with a mean annual temperature of \(0.4^\circ\text{C}\), ranging from \(-21.4^\circ\text{C}\) in January to \(18.5^\circ\text{C}\) in July. Mean annual precipitation is about 350.43 mm, concentrating from July to September. Chestnut soil is the zonal soil type (Jiang, 1985). The grassland is severely degraded due to continuously high grazing pressure. The ungrazed plot about 2.80 ha with flat terrain had been free from grazing since early June 2001. During the growing season from 2001 to 2002, \(1556\pm135\) and \(1954\pm103\) plants/m\(^2\) in plant densities, \(8.26\pm0.34\) cm and \(18.73\pm2.01\) cm in average plant heights were observed at the grazed and ungrazed plots, respectively. Compared with the ungrazed plot, the plant productivity was significantly lower in the nearby grazed area, and its above-ground biomass was reduced to 51–82% (data not shown), but no differences in species composition were observed. The dominant plant species is \(L.\ chinensis\), with main companions of \(Stipa\ grandis,\ Cleistogenes\ squarrosa,\ Agropyron\ cristatum,\ Artemisia\ frigida\) and \(Carex\ korshinskyi\).

2.2. Soil respiration

Soil respiration was measured with a closed static chamber method. The closed chamber was made from acrylic material. The surface area of the chamber was 50 cm \(\times\) 50 cm and 15 cm in height. Two air mixture fans (12 V, 0.13 A) and a highly precise temperature and humidity sensors (type: NKHT, Beijing Northking Electronic Technology Development Co., Ltd.) were fitted inside the chamber and connected with a Thermohygrograph (type: 3DD150, Beijing JunFang Technical Institute of Physics and Chemistry). \(\text{CO}_2\) concentration inside the chamber was directly measured by an infrared gas analyser (type: GXH-3010D, Beijing Computer Technology & Application Institute).

Soil respiration was measured with three replicates. Firstly, three stainless steel frames (50 cm \(\times\) 50 cm) were put in the plot randomly and inserted into the soil at the depth of 5 cm. Meanwhile all green and standing-dead plants inside the frames were clipped to ground level and litter was collected. The soil respiration would be measured on the following day. During measurements, the chamber was enclosed outside the stainless steel frame and sealed with sealing tape. Each measurement would continue to 3 min, temperature, humidity and \(\text{CO}_2\) concentration in the closed chamber were logged every 10 s.

Soil respiration rates were computed from the concentration change over the measurement period (Dong et al., 2000):

\[
F = (\Delta m/\Delta t)D(V/A) = hD\Delta m/\Delta t,
\]

where \(F\) refers to soil respiration rate (mg m\(^{-2}\) h\(^{-1}\)), \(\Delta m/\Delta t\) denotes linear slope of concentration change with time over the measurement period, which is thought to be effective only when the correlation coefficient (\(R^2\)) is greater than 0.95, \(D\) the gas density of the chamber (\(D = P/RT\), mol m\(^{-3}\)), \(P\) the atmospheric pressure (Pa), \(T\) the temperature (K) and \(R\) the air constant (8.31 J mol\(^{-1}\) K\(^{-1}\)), \(V\) the chamber volume (m\(^3\)), \(A\) the surface area of the chamber (m\(^2\)), and \(h\) represents the height of the chamber (m).
The field observations were conducted from 2001 (19 June–23 September) to 2002 (1 June–24 September). The soil respiration at the ungrazed plot was measured once every 10–15 days, and it was done on August 29, 2001 and June 20, July 26, August 30–31, September 23, 2002 at the grazed plot. Usually, soil respiration was measured every hour from 6:00 to 18:00. Twenty-four-hour continuous soil respiration measurements were done on August 26–27, 2001 and August 27–28, 2002 at the ungrazed plot and August 30–31, 2002 at the grazed plot.

The volumetric soil water-contents in four layers (0–10, 10–20, 20–30 and 30–40 cm) with three replicates were determined concurrently with soil respiration measurements near the frames with Profile Probe (Type: PR1/4, Delta-T Devices Ltd. CAMBRIDGE CB5 0EJ UK, recorded by HH2-Moisture Meter).

2.3. Statistical analysis

All statistical nonlinear regression analyses were performed using SPSS 10.0 (SPSS for Windows, Version 10.0, Chicago, IL). The Levenberg-Marquardt algorithm was used to determine the parameters that minimize the sum of squares of differences between dependent variable values in the models and the observed values. The three-dimensional smoothed relationships of soil respiration residual with temperature and soil water-content were investigated using local linear regression (smoother function, normal kernel, bandwidth multiplier value \( \lambda = 1 \)).

3. Results and analyses

3.1. Diurnal and seasonal dynamics of soil respiration rate

The diurnal patterns of soil respiration were similar between the grazed and ungrazed plots (Fig. 1), and they could be expressed as one-humped curves. In general, soil respiration rates would reach to the maximum at 11:00–14:00 and fell to the minimum at 1:00–3:00, coinciding with the highest and the lowest air temperatures. Thus, air temperature exerted dominant control over diurnal soil respiration variations. During the whole observation period, daily average CO2 emission rates were close to those at 7:00–8:00 and 17:00–19:00 at the grazed and ungrazed plots. Thus, soil respiration rates around 8:00 could be taken as representatives of mean daily values.

During the growing season, the rates of soil respiration increased from the middle of June to the end of July and then gradually decreased at the grazed and ungrazed plots (Fig. 2a). Soil respiration changed from 47.72 to 438.15 mg CO2 m\(^{-2}\) h\(^{-1}\) and from 42.81 to 561.63 mg CO2 m\(^{-2}\) h\(^{-1}\) in the ungrazed steppe in 2001 and 2002, respectively, and from 36.43 to 196.85 mg CO2 m\(^{-2}\) h\(^{-1}\) in the grazed steppe in 2002. The ungrazed steppe experienced somewhat greater seasonal variation in soil respiration rate than the grazed steppe did. A parallel pattern was observed in soil water content, especially the dramatic rise of soil respiration rate on July 22, 2001 at the ungrazed plot associated with anomalous increase of soil water content (Fig. 2b). During the observed period, soil water content fluctuated in the range of 2.9–14.4% and 5.9–17.4% at the grazed and ungrazed plots, respectively (Fig. 2b). Air temperature exerted dominant control on diurnal soil respiration variations, while it became secondary to soil water content at the seasonal scale at the grazed and ungrazed plots (Figs. 1 and 2).
3.2. Relationship between soil respiration and temperature

Based on the existing models and the observed data at the grazed and ungrazed plots, relationships of soil respiration with temperature, moisture and temperature–moisture interaction were given in Table 2. When temperature was an independent controlling factor, linear, quadratic and original power models of soil respiration gave relatively poor fits (\( R^2 = 0.25–0.26 \)), compared to the improved power, exponential and Arrhenius models (\( R^2 = 0.39–0.40 \)) at the ungrazed plot. The improved power models of soil respiration with an extra parameter (\( F = a(T+10)^b \) and \( F = a(T - T_{\text{min}})^b \)) provided more flexibility, and had a better fit than the original power model. However, all of the above-mentioned soil respiration models gave similar fits at the grazed plot (\( R^2 = 0.42–0.54 \)). Whether grazed or ungrazed plot, analysis of soil respiration residuals on exponential temperature model showed that soil respiration rates were estimated accurately at low temperatures (<15 °C) and overestimated with increasing temperature when soil moisture was lower than about 12%; soil respiration rates were underestimated when soil moisture was higher than about 12% (Fig. 3a). Other temperature models also had similar residual distributions (figures not shown). Soil respiration rate was controlled mainly by temperature under lower temperature and lower moisture; however, these temperature models did not represent the stimulation effect of moisture on soil respiration with increasing temperature and moisture.

3.3. Relationship between soil respiration and moisture

When soil water-content as an independent controlling factor of soil respiration, except exponential model (\( R^2 = 0.60 \)), the others could explain above 72% of soil respiration variation at the ungrazed plot, significantly higher than the correlation coefficients (\( R^2 = 0.42–0.66 \)) at the grazed plot (Table 2). The quadratic model produced better fits for both plots. Compared to exponential temperature models, residual analysis on quadratic

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Fig. 1. Diurnal dynamics of soil respiration rate and air temperature at the ungrazed and grazed plots. Dots are means of three replicates with standard error bars.
moisture models suggested that variations between simulated and measured data were distinctively decreased at the grazed and ungrazed plots (Fig. 3).

3.4. Relationship between soil respiration and temperature–moisture interaction

Table 1 also listed the relationships between soil respiration and temperature–moisture interaction based on different types of the existing models, including linear, exponential, combination of exponential and power or Arrhenius models. Variation in soil respiration rates observed during the growing season (Fig. 2a) could be explained largely by water availability and temperature (Fig. 2b and c). Hourly soil respiration in *L. chinensis* steppe was mainly controlled by soil water-content, and its estimation would improve when the
Table 2
Fitted relationships of soil respiration with temperature, moisture and temperature-moisture interaction

<table>
<thead>
<tr>
<th>Equation</th>
<th>Ungrazed plot ((N = 246))</th>
<th>Grazed plot ((N = 73))</th>
<th>(R^2)</th>
<th>(F) value</th>
<th>(F) value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\text{Temperature})</td>
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</tr>
<tr>
<td>Linear</td>
<td></td>
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<tr>
<td>(F = a + bT)</td>
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<tr>
<td></td>
<td>(a = -76.91^*, b = 16.59^{**})</td>
<td></td>
<td>0.25</td>
<td>80.49</td>
<td>0.42</td>
</tr>
<tr>
<td>Quadratic</td>
<td></td>
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<td></td>
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<tr>
<td>(F = a + bT + cT^2)</td>
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<tr>
<td></td>
<td>(a = -47.51, b = 12.79, c = 0.11)</td>
<td></td>
<td>0.25</td>
<td>40.23</td>
<td>0.46</td>
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<tr>
<td>Power</td>
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<tr>
<td>(F = aT^b)</td>
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<tr>
<td>(F = a(T + 10)^b)</td>
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<tr>
<td>(F = a(T - T_{\text{min}})^b)</td>
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<tr>
<td>Exponential</td>
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<tr>
<td>(F = ae^{bT})</td>
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<tr>
<td>(F = a \exp(bT + cT^2))</td>
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<tr>
<td>Exponential</td>
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<td>(F = ae^{bT})</td>
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<tr>
<td>(F = a \exp(bT + cT^2))</td>
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<tr>
<td>Arrhenius</td>
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<tr>
<td>(F = a \exp(-E / (R(T + 273.2))))</td>
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<tr>
<td>(F = a \exp(-E_0 / (T + 273.2 - T_0)))</td>
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<tr>
<td>Moisture</td>
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<tr>
<td>Linear</td>
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<tr>
<td>(F = a + bW)</td>
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<tr>
<td>Quadratic</td>
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<tr>
<td>(F = a + bW + cW^2)</td>
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<tr>
<td>Cubic</td>
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<tr>
<td>(F = aW^3)</td>
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<tr>
<td>Exponential</td>
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<td></td>
</tr>
<tr>
<td>(F = ae^{bW})</td>
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</tbody>
</table>

Note: * significant at \(p < 0.05\), ** significant at \(p < 0.01\), *** significant at \(p < 0.001\)
Logarithmic: \( F = a + b \log W \)

\[
a = -933.41^{**}, \ b = 1191.04^{**}
\]

\[
F = a + bTW
\]

\[
a = -109.17^{**}, \ b = 1.68^{**}
\]

\[
F = a + bT + cW
\]

\[
a = -381.83^{**}, \ b = 8.85^{**}, \ c = 43.63^{**}
\]

\[
F = a + bT + cW + dTW
\]

\[
a = 75.80, \ b = -13.40^{**}, \ c = -7.54, \ d = 2.42^{**}
\]

Exponential

\[
\ln F = a + bT + cW
\]

\[
a = 2.33^{**}, \ b = 0.06^{**}, \ c = 0.15^{**}
\]

\[
\ln F = a + bT + cW + dTW
\]

\[
a = 2.79^{**}, \ b = 0.04^{**}, \ c = 0.10^{**}, \ d = 0.002
\]

Exponential-power

\[
F = a e^{b T + c W}
\]

\[
a = 1.19, \ b = 0.06^{**}, \ c = 1.65^{**}
\]

\[
F = a e^{b T} (W - c)(d - W)
\]

\[
a = 1.63 \times 10^5, \ b = 0.06^{**}, \ c = -1.89 \times 10^6, \ d = 45.16, \ f = -5.06
\]

Exponential-Arrhenius: \( F = a e^{(E/V) \left( 1/T - 273.2 \right)} \)

\[
a = 6.14 \times 10^{-6^{**}}, \ E = 3.34 \times 10^4^{**}, \ b = 0.15^{**}, \ R = 8.31 \text{ J mol}^{-1} \text{ K}^{-1}
\]

*significant at 95% confidence by \( t \)-test; ** significant at 99% confidence by \( t \)-test. All \( F \) values are significant at 99.9% probability.
effect of temperature was included in the models (Table 2). Linear models provided better fits than the others, accounting for above 82% of the variation in soil respiration at the ungrazed plot. The combined linear model of other two simple ones ($F = a + bT + cW + dTW$) is more flexible. There was no further improvement in exponential, exponential-power and exponential-Arrhenius models for the ungrazed plot; however, which did enhance the predictive capacity for the grazed plot, especially the exponential-power function ($R^2 = 0.88$). Despite of extra parameters, the improved exponential, exponential-power and exponential-Arrhenius models did not differ much from the original ones at the grazed and ungrazed plots. Residual analysis on linear and exponential-power models did not show a systematic variation at the ungrazed and grazed plots, respectively (Fig. 3). Both models could estimate accurately most of the measured data except those at high temperature and high moisture.

Fig. 3. Residuals between measured soil respiration rates and simulated ones with the representative models at the ungrazed (a) and grazed plots (b).
4. Discussions

4.1. Temperature-based soil respiration models

The relationships between soil respiration and temperature vary among sites, including linear, quadratic, power, exponential and Arrhenius models (Table 1). Among them, an exponential model is most commonly used and Arrhenius \( F = a \exp(-E/RT) \) and power \( F = a(T - T_{\text{min}})^b \) models have theoretical bases.

The parameter \( E \) in Arrhenius model represents the activation energy for the chemical reaction. \( E \) equalled 70.2 and 63.1 kJ mol\(^{-1}\) for the grazed and ungrazed sites, respectively (Table 2), close to 61.4 kJ mol\(^{-1}\) for farmland and 83.6 kJ mol\(^{-1}\) for forest (Fang and Moncrieff, 2001) and 53 kJ mol\(^{-1}\) for major ecosystem types worldwide (Lloyd and Taylor, 1994). Parker et al. (1983) reported that the activation energy decreased from 84.9 to 39.5 kJ mol\(^{-1}\) when a desert soil was wetted. Compared to the grazed plot, the decreased activation energy for the ungrazed plot might also be induced by the increase of moisture in this study (Fig. 2b). In an attempt to give better simulation for the dynamics of respiration rates, Lloyd and Taylor (1994) suggested an improved Arrhenius type model (Table 1). However, fitted with our data, the Lloyd and Taylor function did not provide a significantly better fit than the Arrhenius model (Table 2).

Based on \( F = a(T + 10)^b \) proposed by Kucera and Kirkham (1971) and \( F = a(T - T_{\text{min}})^2 \) by Lomander et al. (1998), Fang and Moncrieff (2001) established an improved power function \( F = a(T - T_{\text{min}})^b \). Taken as a temperature when soil respiration totally stops, \( T_{\text{min}} \) was \(-26.5^\circ C\) for farmland and \(-13.4^\circ C\) for forest (Fang and Moncrieff, 2001). Fitted \( T_{\text{min}} \) \((-22.02^\circ C\) was within the above-mentioned range at the ungrazed plot. Although the improved power function gave a better fit \( R^2 = 0.54 \) for the grazed plot, the fitted \( T_{\text{min}} \) \((-112.61^\circ C\) lost its original feature of soil respiration response to minimal temperature.

4.2. Moisture-based soil respiration models

Many studies have indicated that the temperature effect was manifested only when there was sufficient soil water to permit significant root and microbial \( \text{CO}_2 \) production, whereas soil respiration was significantly correlated with moisture or temperature–moisture interaction effect if water was limited in arid and semi-arid regions (Wildung et al., 1975; Buyanovsky et al., 1986; Liu and Fang, 1997). Moisture status could be expressed by gravimetric and volumetric water-contents, precipitation, water potential, moisture index and so on (Table 1). Among them, near-surface soil water-content was commonly used; however, no standardized sample depth was defined (e.g. 0–5, 0–10 or 0–20 cm, etc.). This study presented soil water-content at the depth of 0–10 cm as a surrogate for moisture status.

The relationships between soil respiration and soil water-content are mostly described by simple empirical equations, few formulated mechanistically (Table 1). A linear function is most commonly used to describe the relationship in various ecosystem types. In addition, quadratic, cubic, exponential and logarithmic functions have been found occasionally in some literatures.

Soil respiration originates mainly from root and microbial activity. Howard and Howard (1993) indicated that the both components were strongly influenced by available
soil moisture. In general, three phases of moisture effects on soil biota could be identified (Raich and Potter, 1995): At low moisture levels, metabolic activity increases with increasing moisture availability; there follows a broad region over which moisture has little effect. At high moisture levels, changes of the diffusion of gases in soil and deficiencies of oxygen inhibit aerobic respiration. The second phase occurs generally when soils are 50–80% saturated (Linn and Doran, 1984). Some models included the three phases (Schlentner and Van Cleve, 1985) or the first two (Raich and Potter, 1995). A maximum volumetric water holding capacity of 36% was determined for the depth of 0–30 cm by wetting of undisturbed cores in this study area. Thus, all parameterized models included only the first phase in this study (Table 2), which might disaccord with the original applicable range of some models and limit their predictive capacities.

4.3. Effects of spatial and temporal scales

Soil respiration has been measured with different methods (e.g. alkali absorption, soda lime absorption, gas chromatography, IRGA) in different vegetation types (Table 1). Thus, these models were established based on the corresponding local environment, which increased the uncertainties in upscaling and quantitatively understanding of global carbon sources and sinks at regional scale. To produce consistent and accurate estimates of global CO₂ efflux, data fusion (or data assimilation) and a widely applicable model are currently key issues. We established only one ungrazed plot in this study, thus the validity of the results should be restricted to the area in which our data was gathered and be verified by subsequent studies.

Air temperature exerted dominant control over diurnal soil respiration variations (Fig. 1), and moisture played a more important role at seasonal scale (Fig. 2). There were different main controlling factors at different temporal scales. With the temporal scaling up, the roles of other biotic factors (e.g. above-ground biomass, belowground biomass, leaf area index, photosynthetic rate) might become more important, which will require further research. In conclusion, the interaction of temperature and moisture did improve the predictive capacity of the models in this paper. Among the tested models, linear models ($R^2 = 0.82–0.88$) and related exponential models ($R^2 = 0.87–0.88$) better fitted to the observed data and explained the rates of soil respiration at the ungrazed and grazed plots, respectively (Table 2).

Acknowledgements

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References


