Biophysical regulation of the net ecosystem CO₂ exchange over an *Elymus nutans* artificial pasture in the Three-River Source Region of the Qinghai-Tibetan Plateau

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We examined the net ecosystem CO₂ exchange (NEE) in an *Elymus nutans* artificial pasture in the Three-River Source Region of the Qinghai-Tibetan Plateau from January 1, 2008 to December 31, 2008 using the eddy covariance method. The hourly minimum NEE rate was −7.89 μmol CO₂ m⁻² s⁻¹. The hourly maximum ecosystem respiration (Rₑ) in the pasture was 5.03 µmol CO₂ m⁻² s⁻¹. The annual sum of the NEE in the pasture was 140.01 g C m⁻² year⁻¹. For the entire growing period, the apparent quantum yield (α) was −0.0275 µmol µmol⁻¹, and the α values for the pasture’s light response curve varied with the canopy development, the air temperature (Tₐ), the soil water content (SWC), and the vapor pressure deficit (VPD).

Piecewise regression results indicated that the optimum Tₐ and VPD for the daytime NEE were 14.1°C and 0.65 kPa, respectively. During the entire growing period, the daytime NEE decreased as the SWC increased, and the apparent temperature sensitivity of respiration (Q₁₀) in the pasture ecosystem was 3.0 and was obviously controlled by the SWC conditions. The results of linear regression analysis suggested that approximately 32.5% of the variation in the daily NEE can be explained by variation in the leaf area index.

[Keywords: Net ecosystem CO₂ exchange, Ecosystem respiration, Artificial pasture, Eddy covariance, The Three-River Source Region]

Introduction

The grassland ecosystem occupies approximately one-third of the total global land area and is an important component of the earth’s carbon circulation¹. For the past few decades, ecologists have studied the effect of environmental factors (such as radiation, temperature, water, and soil nutrition), biological factors, and management measures on the carbon exchange between the land surface and the atmosphere of the grassland ecosystem by using eddy covariance²⁻³, and these ecologists have noted the significance of human activity on the carbon exchange process⁴. The grassland of China occupies approximately 40% of the nation’s total land area and plays an extremely important role in the regional circulation of carbon⁵. However, because the study of China’s grassland carbon flux started late, the focus of these studies has mainly been on the low-lying regions in China⁶.

The Qinghai-Tibetan Plateau has drawn considerable attention as the “initiation zone”® and the “sensitivity zone”® for China’s weather changes⁷. Although there have been reports on the carbon exchange between the land surface and the atmosphere and on the driving mechanisms underlying the primary natural vegetation types (e.g., alpine meadows and alpine shrubs) over the last several years⁸⁻⁹, there have only been a few reports on the carbon exchange process, the source/sink function of artificial vegetation (e.g., artificial grassland), and the driving mechanisms of the controlling environmental and biological factors.

The Three-River Source Region (TRSR, i.e., the source of the Yangtze, Yellow and Mekong rivers and well known as the —water tower of Asia”) is located in the hinterland of the Qinghai-Tibetan Plateau. In recent years, the grassland in the region has severely degraded. Statistics indicate that the area that is experiencing moderate and severe degradation has already reached 5.7×10⁶ hm², occupying 55.40% of the total usable grassland area¹⁰. To curb grassland degradation in the region, the Chinese government has established a large area of artificial grassland in the Three-River Source Region. By 2005, this artificial grassland area had already reached 160,000 km²¹¹. Establishing artificial grassland on a degraded alpine meadow ecosystem can improve the productivity of the original ecosystem, increase the organic carbon content of the soil, and accelerate the turnover rate of the soil’s nutrients to alleviate the
regional trend toward grassland degradation. We sought to identify the influence of the establishment of the artificial grassland on the ecosystem’s carbon budget. We wanted to know the effects of environmental and biological factors on the carbon budget of the artificial grassland, but there are few reports on these issues. Therefore, we continuously collected observational data in the present study from January 1, 2008 to December 31, 2008 with an eddy covariance system and performed a quantitative analysis of the CO$_2$ flux variations and controlling factors in the TRSR pasture to achieve the following objectives: (1) to quantify the magnitude of the CO$_2$ exchange, (2) to investigate the biophysical regulation of the CO$_2$ flux, and (3) to calculate the carbon budget of the pasture over 2008.

Materials and Methods

Study site

The study area is situated in the Geduo pastoral committee grass field 25 km southeast of the town of Dawu in Guoluo Prefecture in Qinghai Province, which is located in the TRSR. The geographical coordinates of the area are 100°26′–100°41′E and 34°17′–34°25′N, and the area lies at an elevation of 3980 m above sea level. The area experiences typical plateau continental weather: the annual average sunshine duration is 2576 h, the radiation is strong, there is no absolute frost, and the annual average temperature is −0.5°C. The monthly average temperature is −12.7°C, the average temperature in July is 9.8°C, and the annual precipitation (PPT) is approximately 500 mm, with 85% of the PPT concentrated between May and September. The soils are mainly an alpine meadow type and an alpine shrub type. The artificial pasture was established in May 2002, and its total area was 2000 hm$^2$. The pasture was sown singly with *Elymus nutans*, and the pasture vegetation height was 40 to 60 cm. The meadow was grazed in winter, and the grazing intensity was medium.

Eddy flux and micrometeorological measurements

A 3.0-m high eddy covariance flux tower was installed at the center of the observation field. The fluxes of CO$_2$ and H$_2$O were measured using the eddy covariance method. The uniform fetch was more than 300 m from the tower in all directions. A three-dimensional ultrasonic wind speed meter, manufactured by Campbell Scientific, Inc. (CSI) (CSAT-3, Logan, UT, USA), was used to measure turbulence. The CO$_2$ and H$_2$O densities and the temperature fluctuations were measured using an open-path CO$_2$/H$_2$O infrared gas analyzer (CS7500, CSI) and an anemometer-thermometer at 10 Hz, respectively. The average value was output once every 15 min, and the data were saved in a data collection device (CR5000, CSI). The CO$_2$/H$_2$O analyzer system was calibrated each year.

At the same time that we measured the CO$_2$ flux, we also performed measurements of other routine weather factors. The system for obtaining the routine measurements was installed on the same flux tower as the eddy measurement system. Among these measurements, the net radiation was measured using a net radiometer (CNR-1, Kipp and Zonen, Delft, South Holland, The Netherlands), and the photosynthetic photon flux density (PPFD) was measured using a quantum sensor (LI-190SB, Li-Cor, Lincoln, NE, USA). Both measurements were recorded at a 150-cm height. The soil temperature was measured using copper-constantan thermocouples (105-T, CSI) at depths of 5, 10, and 30 cm underground. The air temperature (T$_a$) and humidity were measured with a humidity and temperature probe (HUMP45C, CSI) at heights of 110 and 300 cm aboveground. The wind speed and direction were also measured at heights of 110 and 300 cm aboveground using cup anemometers (034A-L and 014A, R. M. Young Co., Traverse, MI, USA). The soil heat flux was measured at a soil depth of 2 cm with heat flux plates (HFT-3, CSI). Altogether, there were three heat flux plates in the test field, and the average soil heat flux value recorded by the three plates was used. The soil moisture was measured using time domain reflectometry sensors (CS615, CSI) at depths of 5, 20, and 30 cm underground. The soil surface temperature was measured with thermometers (107, CSI) at three points in a 1-m$^2$ area. The PPT volume was determined using a tipping bucket (TE525MM, CSI) mounted 70 cm above the ground. The output data consisted of average values calculated every 15 min. These data were stored in the data collector (CR5000, CSI).

Data processing and energy balance closure

The data were obtained from January 1, 2008 to December 31, 2008. All the micrometeorological and...
fluctuations in CO$_2$ fluxes, the turbulence intensity at that time was not strong ($U^* \leq 0.2$ m s$^{-1}$). The nighttime data gaps were filled using the soil temperature increase as follows:

$$Q_{10} = \exp(10b)$$  \hspace{1cm} (2)

The daytime gaps in the CO$_2$ flux ($F_c$) during the growing season were filled through rectangular hyperbolic regression according to Formula (3)$^{15}$ as follows:

$$F_c = F_{\text{max}} \alpha \text{PPFD}/(F_{\text{max}} + \alpha \text{PPFD})$$  \hspace{1cm} (3)

where PPFD is the photosynthetic photon flux density ($\mu$mol m$^{-2}$ s$^{-1}$), $F_{\text{max}}$ is the value of the NEE at a saturating light level ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$), $\alpha$ is the apparent quantum yield ($\mu$mol CO$_2$ $\mu$mol$^{-1}$ photons).

**Vegetation measurement**

The biomass and leaf area index (LAI) were measured six times over the whole growth season. The aboveground biomass measurement adopted the harvesting method, with five randomly collected samples, each including the vegetation within a square area covering 0.25 m$^2$. The vegetation was cut off and brought back to the lab with the roots to be dried in a 65°C thermostatic oven. The LAI was determined from measurements taken with a leaf area meter (LI-3100, Li-Cor). Based on plant phenology, the biomass and LAI for the sampling field were both zero before April 20 (DOY111) and after October 18 (DOY292), which marked the beginning and end of the growing season, respectively. LAI gaps were linearly interpolated to daily intervals$^8$.

**Results**

**Meteorological and biological factors**

Figure 1(a) shows that the PPFD peaks occurred between May and August, when the solar elevation angle was higher than in other seasons. Because of the high elevation of the plateau, the PPFD values of the plateau also tended to be high, and the maximum daily values reached 695.9 $\mu$mol m$^{-2}$ s$^{-1}$ (Fig. 1(a)). The vapor pressure deficit (VPD) also showed significant seasonal variation, reaching its highest and lowest values of approximately 1.32 and 0.04 kPa.
respectively, during the growing season and during the winter (Fig. 1(a)). The daily mean $T_a$ and $T_s$ values showed the same seasonal variation trends, ranging from $-17.8$ to $12.1°C$ for $T_a$ and from $-8.4$ to $16.5°C$ for $T_s$. The annual average was $-0.54°C$ for $T_a$ and $4.2°C$ for $T_s$ (Fig. 1(b)). The annual PPT was $628.9$ mm, which was higher than the average PPT across multiple years (approximately $500$ mm), and the PPT during May–September accounted for $66.4%$ of the annual PPT. After October, the PPT was significantly reduced (Fig. 1(c)). The variation in the soil water content (SWC) was strongly dependent on the PPT; the SWC was higher from May–October than at other times of the year and was generally maintained above $20%$ (Fig. 1(c)).

Figure 1(c) shows that the LAI for the field in the sampled pasture started to increase at the end of April, and the maximum LAI ($2.9±0.3$) was reached at the end of August. In September, the LAI decreased rapidly because of leaf aging. The growing season for the pasture in 2008 (DOY 113–292) could be divided into four periods (Table 1): the beginning growing period (I, DOY 113–145), the fast growing period (II, DOY 146–194), the peak growing period (III, DOY 195–252), and the aged growing period (IV, DOY 253–292).

**Diurnal course of carbon dioxide exchange**

Figure 2(d) shows that the daily variation in the NEE was regular during every growth period. This variation was most likely a reflection of daytime absorption and nighttime emission. In the morning, the NEE was converted from a positive value (representing carbon emission) to a negative value (representing carbon absorption). The absorption value reached its maximum before noon (10:00–11:00 h) and then started to diminish. Near evening (approximately 19:00 h), the NEE changed from a negative value to a positive value. The hourly maximum and minimum NEE rates, which were $3.25$ and $-7.89$ μmol CO$_2$ m$^{-2}$ s$^{-1}$, respectively, both occurred during the peak growing period. Figure 2(e) shows that the hourly maximum $R_e$ rate of the pasture, which occurred at approximately 16:00 h during the peak growing period, was $5.03$ μmol CO$_2$ m$^{-2}$ s$^{-1}$.

Fig. 1—Temporal variation during 2008 in the (a) photosynthetic photon flux density (PPFD) and vapor pressure deficit (VPD), (b) daily mean air temperature (Ta) and soil temperature at a depth of...
5 cm (T.), (c) daily precipitation (PPT) and soil water content at a 5-cm depth (SWC), (d) daily net ecosystem CO₂ exchange (NEE) and ecosystem respiration (Re), and (e) leaf area index (LAI).

Fig. 2—Average diurnal cycles of the (a) photosynthetic photon flux density (PPFD), (b) air temperature (T.), (c) vapor pressure deficit (VPD), (d) net ecosystem CO₂ exchange (NEE), and (e) ecosystem respiration (Re) at different growing periods. Bars indicate ± standard error (SE). Time of day is Beijing Standard Time (BST).

Seasonal course of carbon dioxide exchange

Figure 1(d) shows that from January until the end of April, the pasture NEE was greater than 0 because the aboveground vegetation had withered; thus, the ecosystem was exhibiting carbon emissions (NEE>0). Starting May 1 (DOY121), as the vegetation began to appear, the NEE commenced to drop to below 0. The whole ecosystem converted from carbon emission to carbon absorption (NEE<0) and reached peak carbon absorption between July and August. Starting in September, as the vegetation aged, the carbon absorption capability of the pasture gradually degraded. By the end of October, the NEE began to exceed 0, and the whole ecosystem engaged in carbon emission (NEE>0). The maximum daily absorption value, −2.91 g C m⁻² day⁻¹, occurred on August 12 (DOY225). The annual NEE for the pasture in 2008 was −140.04 g C m⁻² year⁻¹. Thus, the pasture was a carbon sink during 2008.

Figure 1(e) shows that from January until the end of March, Re slightly exceeded 0 and did not change significantly. As the temperature began to increase in April, Re also started to rise. In 2008, the daily maximum Re for the pasture was 5.04 g C m⁻² day⁻¹ on July 28 (DOY 210). The annual Re was 403.57 g C m⁻² year⁻¹ in 2008.

The relationship between the daytime NEE and the PPFD

We used Formula (3) to depict the relationship between the daytime NEE and the PPFD. The NEE data were averaged using PPFD bins of 100 µmol m⁻² s⁻¹. As shown in Fig. 3, at PPFD<1600 µmol m⁻² s⁻¹, the daytime NEE decreased as the PPFD increased. However, for PPFD>1600 µmol m⁻² s⁻¹, the daytime NEE increased as the PPFD increased (Fig. 4). Therefore, Formula (3) was only valid for depicting the relationship between the NEE and the PPFD for PPFD<1600 µmol⁻¹ m² s⁻¹. During the entire growing season, the model-derived α and Fmax values in the pasture increased as the canopy developed, and their maximum values occurred during the peak growing period, reaching −0.0358 µmol CO₂ µmol⁻¹ photons and −8.69 µmol CO₂ m⁻² s⁻¹, respectively.
During the entire growing season, the $\alpha$ and $F_{\text{max}}$ values in the pasture were $-0.0275 \, \text{µmol CO}_2 \, \text{µmol}^{-1} \, \text{photons}$ and $-7.86 \, \text{µmol CO}_2 \, \text{m}^{-2} \, \text{s}^{-1}$, respectively.

To further study the influence of environmental factors on the NEE-PPFD curve, we inspected the NEE-PPFD curves generated under different $T_a$ conditions ($T_a \leq 5^\circ \text{C}$, $5^\circ \text{C} < T_a \leq 15^\circ \text{C}$, and $T_a > 15^\circ \text{C}$), SWC conditions ($\text{SWC} \leq 25\%$, $25\% < \text{SWC} \leq 30\%$, and $\text{SWC} > 30\%$), and VPD conditions ($\text{VPD} \leq 0.6 \, \text{kPa}$ and $\text{VPD} > 0.6 \, \text{kPa}$). Under the aforementioned micro-meteorological conditions, the NEE could be further subdivided based on the PPFD (using $100 \, \text{µmol m}^{-2} \, \text{s}^{-1}$ PPFD subdivisions), and the NEE was then averaged for each PPFD level. Statistically, this method can reduce or offset the errors that occurred during measurement.

In the pasture, the $F_{\text{max}}$ and $\alpha$ values for the NEE-PPFD curve were under the influence of the SWC, $T_a$, and the VPD. Both $F_{\text{max}}$ and $\alpha$ increased as the SWC increased, and at a SWC$<20\%$, $F_{\text{max}}$ and $\alpha$ were significantly lower than they were when the SWC$>30\%$. $F_{\text{max}}$ and $\alpha$ were highest when $5^\circ \text{C} < T_a \leq 15^\circ \text{C}$. $F_{\text{max}}$ and $\alpha$ decreased as the VPD increased, and at a VPD$>0.6 \, \text{kPa}$, $F_{\text{max}}$ and $\alpha$ were 93\% and 38\%, respectively, of their values at a VPD$\leq 0.6 \, \text{kPa}$ (Table 1).

The relationship between the daytime NEE and $T_a$, the VPD, and the SWC
For statistical purposes, the daytime NEE data were averaged by abiotic controls into bins, with bin widths of 1°C for $T_a$, 1% for the SWC and 0.1 kPa for the VPD over all the PPFD values. Figures 5(a) and (b) show that the relationship between the daytime NEE and $T_a$ and the VPD can be depicted by a quadratic function, and the stepwise regression analysis results indicated that the $T_a$ and VPD values optimal for the pasture ecosystem were $14.1^\circ \text{C}$ and $0.65 \, \text{kPa}$. The daytime NEE diminished as the SWC increased (Fig. 5(c)).

$R_e$ in response to $T_s$ and the SWC
For the entire growing season, the nighttime NEE data were bin averaged using $T_s$ bins of 1°C. Figure 6 shows that $R_e$ increased exponentially as the temperature increased, and the $Q_{10}$ for the pasture during the entire growth season was 3.0 (Table 2), with values of 1.9, 2.9, 1.8, and 2.7 for the beginning, fast, peak, and aged growing periods, respectively (Table 2).

To further investigate the effect of the SWC on $T_s$ and $R_e$, we investigated the $T_s-R_e$ relation under different SWC conditions ($\text{SWC} \leq 25\%$, $25\% < \text{SWC} \leq 30\%$, and $\text{SWC} > 30\%$). The results showed that the $Q_{10}$ of the artificial grassland reached its maximum at $25\% < \text{SWC} \leq 30\%$.

The relationship between the daily NEE and the LAI
Figure 7 indicates that during the whole growth season, the artificial grassland’s daily integrated NEE and LAI showed a linear relationship in which $\text{NEE} = (-0.449 \pm 0.005) \times \text{LAI} - (0.291 \pm 0.008)$, $n=175$, adjusted $R^2=0.325$, and $F=84.8$. Therefore, 32.5\% of the variation in the NEE could be explained by variation in the LAI.
## Table 1—Parameters describing characteristics of the relationship between daytime NEE and incident PPFD (Formula (3)).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>DOY</th>
<th>LAI (m² m⁻²)</th>
<th>SWC (%)</th>
<th>T (°C)</th>
<th>VPD (kPa)</th>
<th>α (µmol µmol⁻¹)</th>
<th>Fmax (µmol CO₂ m⁻² s⁻¹)</th>
<th>Re (µmol CO₂ m⁻² s⁻¹)</th>
<th>n</th>
<th>R²</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beginning growing period</td>
<td>113–145</td>
<td>0.35±0.06</td>
<td>22.88±3.59</td>
<td>4.02±1.86</td>
<td>0.52±0.29</td>
<td>−0.0022±0.0008</td>
<td>−5.22±0.34</td>
<td>0.21±0.04</td>
<td>16</td>
<td>0.93</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Fast growing period</td>
<td>146–194</td>
<td>0.97±0.16</td>
<td>25.50±2.55</td>
<td>7.08±2.19</td>
<td>0.46±0.23</td>
<td>−0.0185±0.0053</td>
<td>−6.97±0.24</td>
<td>0.80±0.18</td>
<td>16</td>
<td>0.97</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Peak growing period</td>
<td>195–252</td>
<td>1.92±0.25</td>
<td>35.01±2.47</td>
<td>9.59±2.95</td>
<td>0.46±0.12</td>
<td>−0.0358±0.0091</td>
<td>−8.69±0.66</td>
<td>1.51±0.23</td>
<td>16</td>
<td>0.98</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Aged growing period</td>
<td>253–292</td>
<td>1.38±0.35</td>
<td>37.03±3.63</td>
<td>7.32±1.16</td>
<td>0.56±0.23</td>
<td>−0.0122±0.0047</td>
<td>−6.95±0.53</td>
<td>0.66±0.12</td>
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<td>0.96</td>
<td>&lt;0.0001</td>
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<tr>
<td>Entire growing season</td>
<td>113–292</td>
<td>1.51±0.45</td>
<td>31.72±2.73</td>
<td>7.38±2.41</td>
<td>0.49±0.24</td>
<td>−0.0275±0.0048</td>
<td>−7.86±0.73</td>
<td>1.79±0.28</td>
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<td>0.98</td>
<td>&lt;0.0001</td>
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<tr>
<td>SWC≤25%</td>
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<td></td>
<td></td>
<td></td>
<td>−0.0092±0.0022</td>
<td>−4.28±0.66</td>
<td>0.94±0.18</td>
<td>16</td>
<td>0.96</td>
<td>&lt;0.0001</td>
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<tr>
<td>25%&lt;SWC≤30%</td>
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<td></td>
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<td></td>
<td>−0.0258±0.0046</td>
<td>−5.81±0.82</td>
<td>1.59±0.22</td>
<td>16</td>
<td>0.98</td>
<td>&lt;0.0001</td>
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<td>SWC&gt;30%</td>
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<td></td>
<td></td>
<td></td>
<td>−0.0329±0.0058</td>
<td>−9.51±0.31</td>
<td>2.08±0.18</td>
<td>16</td>
<td>0.99</td>
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<tr>
<td>Ta≤5°C</td>
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<td></td>
<td></td>
<td>−0.0220±0.0039</td>
<td>−5.89±0.41</td>
<td>1.25±0.16</td>
<td>16</td>
<td>0.97</td>
<td>&lt;0.0001</td>
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<td>5°C&lt;Ta≤15°C</td>
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<td>−0.0289±0.0202</td>
<td>−8.02±1.80</td>
<td>1.69±0.26</td>
<td>16</td>
<td>0.97</td>
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<td>Ta&gt;15°C</td>
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<td></td>
<td>−0.0174±0.0054</td>
<td>−6.87±0.50</td>
<td>1.26±2.16</td>
<td>16</td>
<td>0.99</td>
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<td>VPD≤0.6 kPa</td>
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<td>−0.0291±0.0058</td>
<td>−8.85±1.26</td>
<td>1.85±0.11</td>
<td>16</td>
<td>0.99</td>
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<tr>
<td>VPD&gt;0.6 kPa</td>
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<td></td>
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<td></td>
<td>−0.0112±0.0045</td>
<td>−8.20±0.43</td>
<td>1.23±0.38</td>
<td>16</td>
<td>0.97</td>
<td>&lt;0.0001</td>
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## Table 2. Parameters describing characteristics of the relationship between nighttime NEE and T (Formulas (1) and (2)).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>DOY</th>
<th>SWC</th>
<th>a</th>
<th>b</th>
<th>R²</th>
<th>Q₁₀</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beginning growing period</td>
<td>113–145</td>
<td>23.17±2.13</td>
<td>0.4661</td>
<td>0.0664</td>
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<tr>
<td>Fast growing period</td>
<td>146–194</td>
<td>26.08±1.74</td>
<td>0.4809</td>
<td>0.1068</td>
<td>0.94</td>
<td>2.9096</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Peak growing period</td>
<td>195–252</td>
<td>35.62±2.23</td>
<td>1.2801</td>
<td>0.0583</td>
<td>0.83</td>
<td>1.7914</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Aged growing period</td>
<td>253–292</td>
<td>37.63±3.02</td>
<td>0.6434</td>
<td>0.0992</td>
<td>0.89</td>
<td>2.6966</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Entire growing season</td>
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<td>32.41±2.25</td>
<td>0.5551</td>
<td>0.1088</td>
<td>0.95</td>
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<td>SWC≤25%</td>
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<td>0.96</td>
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<tr>
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<td>0.91</td>
<td>2.6117</td>
<td>&lt;0.0001</td>
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Fig. 4—Relationship between the net ecosystem CO₂ exchange (NEE) and PPFD for different (a) air temperatures (Ta), (b) soil water contents (SWC), and (c) vapor pressure deficits (VPD). The daytime NEE data were averaged over PPFD bins of 100 µmol m⁻² s⁻¹. Bars indicate ±SE. Formula (3) was used to fit the data when the PPFD was below 1,600 µmol m⁻² s⁻¹; the regression coefficients are presented in Table 1.

Fig. 5—Relationship between the daytime NEE and (a) air temperature (Tₐ), (b) vapor pressure deficit (VPD), and (c) soil water content at a 5-cm depth (SWC). The daytime NEE data were averaged over a bin width of 1°C for Tₐ, 0.1 kPa for VPD and 1% for SWC. Bars indicate ±SE. The dotted lines in (a) and (b) were fitted by a piecewise regression model.
Fig. 6—Relationship between the nighttime net ecosystem CO₂ exchange (NEE) and soil temperature (Tₛ) for the (a) entire growing season, (b) different growing periods, and (c) different soil water contents (SWC). The nighttime NEE data were averaged over a bin width of 1°C for Tₛ. Bars indicate ±SE. Formula (1) was used to fit the data; the regression coefficients are presented in Table 2.

Fig. 7—Relationship between the daily net ecosystem CO₂ exchange (NEE) and leaf area index (LAI) from April 20 until October 18, 2008.

Discussion

The effect of biotic and abiotic controls on the NEE

The maximum $F_{max}$ for the pasture ecosystem occurred during the peak growing stage (−8.69 μmol CO₂ m⁻² s⁻¹) (Table 1) and was nearly identical to the $F_{max}$ for a steppe-Kobresia meadow during the peak growing season (−8.7 μmol CO₂ m⁻² s⁻¹). However, the pasture maximum $F_{max}$ was lower than the values reported for other grassland ecosystems (from −9.6 to −40.2 μmol CO₂ m⁻² s⁻¹). For the entire growing season, the $\alpha$ value for the pasture was 0.02754 μmol CO₂ μmol⁻¹ photons, which was higher than that for the steppe-Kobresia meadow (−0.0159 μmol CO₂ μmol⁻¹ photons). However, the $\alpha$ for the pasture for the entire growing period was at a middle to low level compared with the values for other grassland and cropland ecosystems, as reported by Li et al. (2005). These findings indicate that the light use efficiency of the pasture was low. This low efficiency was related to the use of C₃ vegetation to establish the pasture and to the high elevation and low temperatures of the pasture ecosystem.

Under low $T_a$ values ($T_a$≤5°C), the $F_{max}$ and $\alpha$ of the NEE-PPFD curve for the pasture were relatively low (Table 1), mainly because low temperature can suppress the activity of photosynthesis-related enzymes. This situation was also found in the desert steppe of Inner Mongolia. At SWC<20%, the $F_{max}$ and $\alpha$ values of the NEE-PPFD curve for the pasture were relatively low (Table 1), primarily because the low SWC can constrain plant growth. A similar situation also occurred for the steppe. During the aged growing period, the $F_{max}$ and $\alpha$ values of the NEE-PPFD curve for the pasture decreased significantly. This finding is related to the reduced
chlorophyll content of older plants, and the activity of their photosynthesis-related enzymes is also decreased. Similar results also occur with a fenced steppe.

The optimal $T_a$ for CO$_2$ uptake in the pasture was 14.1°C, which was quite close to that of an alpine meadow (15°C). $T_a$ had notable effects on the NEE in our study. The NEE decrease at lower temperatures was most likely caused by the slow growth rate during the early and late stages of the growing season, whereas the depression of the NEE at relatively higher temperatures could be ascribed primarily to enhanced respiration and depressed plant photosynthesis in response to high temperatures and high radiation levels.

In many ecosystems, moisture is an important factor that influences the daytime NEE. The daytime NEE for the pasture declined with increases in the soil moisture (Fig. 4). This trend indicated that increased soil moisture can improve the carbon absorption capability of the pasture. Similar results have been found for a Mongolian steppe. Early studies demonstrated that a lack of moisture could result in the closure of plant stomata, further reducing plant CO$_2$ absorption. In addition, stomatal closure had a significant effect on leaves. An increasing leaf temperature can enhance leaf photorespiration, which further reduces CO$_2$ acquisition by the plants.

In the present study, the daytime NEE and the VPD of the pasture were quadratically related (Fig. 5), and similar results were observed for a temperate desert steppe. The daytime suppression of the NEE by a high VPD could primarily be attributed to the physical relationship between the temperature and the VPD (Fig. 2). Because this relation can affect the hydraulic status of plants and leaves, leading to leaf closure, it can affect the acquisition of CO$_2$ by plants.

The process of carbon exchange between plants and the atmosphere is under the joint regulation of multiple environmental factors (such as the PPFD, $T_a$, SWC, and VPD); thus, it is difficult to identify a specific effect on the NEE by a single factor, especially between $T_a$ and the VPD because a rising $T_a$ is always associated with an increased VPD. Therefore, to study the response mechanisms of the NEE to environmental factors in the future, both modeling and multivariate analysis should be exploited.

**The effect of Ts and the SWC on the nighttime NEE**

$R_e$ is affected by multiple environmental and biological factors, and $T_s$ and the SWC can be regarded as controls.

$R_e$ demonstrates an exponential function with increasing temperature. During the entire growing season in the present study, the Q10 for the pasture was 3.0 (Fig. 6(a) and Table 2), which was higher than the Q10 value for low-elevation grassland ecosystems around the world (2.1). Early studies showed that the Q10 value for $R_e$ decreases as the temperature increases. Here, the relatively high $Q_{10}$ value for the TRSR could result from the low temperature on the plateau. Therefore, the results of the current study indicated that in the context of global warming, the TRSR pasture has a relatively strong carbon emission potential.

The $Q_{10}$ value reached its maximum at a medium SWC (Fig. 6(c) and Table 2). This situation also occurred in a *Stipa krylovii* steppe. At a high SWC, the soil moisture can hinder the diffusion of O$_2$. Therefore, a high SWC can suppress the decomposition of organic matter and the microbial respiration rate. Under these conditions, the CO$_2$ release and temperature are not sensitive, and the $Q_{10}$ value is relatively low. However, at a low SWC, the primary component, composed of $R_e$, derives from the more recalcitrant carbon material, and the $Q_{10}$ of this material is low. The situations discussed above cannot explain the high $Q_{10}$ value during the aged growing period (SWC>30%). This result indicated that plant phenology was another factor affecting the $Q_{10}$. A similar result also occurred in a desert steppe.

**The effect of the LAI on the daily NEE**

The structure of the plant canopy, especially the leaf area and light interception capability, determine the quantity of radiation absorbed and reflected by the plant canopy. Therefore, these factors can have a direct influence on plant photosynthesis. For the pasture ecosystem, the LAI could explain 32.5% of the NEE variation (Fig. 7), and this percentage of explained variation was higher than that found for a desert steppe (26%). This finding could be attributed to the additional PPT received during the plant growing season by the pasture ecosystem.

**Diurnal and seasonal variation in the NEE**

At various stages during the growing season, the carbon absorption of the pasture ecosystem was
significantly stronger at noon than before noon, indicating that the daily NEE is significantly suppressed around noon (Fig. 2(d)). Fu et al. (2006) also obtained a similar asymmetrical distribution of the NEE in a study of an alpine shrub. Because of photosynthetic depression at high temperatures, as well as stomatal closure at high PPFD levels, the carbon assimilation was seriously restricted at noon and during the early afternoon. For most plants on the Qinghai-Tibetan Plateau, the photosynthetic depression at noon is a common phenomenon. This response of the plants is primarily due to enhanced respiration and depressed photosynthesis at high temperatures under high radiation conditions.

For the pasture ecosystem, the magnitude of the maximum hourly NEE was $-7.89 \mu$mol CO$_2$ m$^{-2}$ s$^{-1}$, and this value was lower than that of other grassland ecosystems located at similar latitudes, for example, the tall prairie grassland native to North America ($-23 \mu$mol CO$_2$ m$^{-2}$ s$^{-1}$)\textsuperscript{33}, the prairie plains in the USA ($-19.5 \mu$mol CO$_2$ m$^{-2}$ s$^{-1}$)\textsuperscript{34}, and the alpine meadow at Haibei station ($-10.8 \mu$mol CO$_2$ m$^{-2}$ s$^{-1}$)\textsuperscript{35}. This lower magnitude of the NEE in the current study could be attributed to the relatively low temperature of the pasture ecosystem and to the C3 composition of most of the pasture vegetation.

For the pasture ecosystem, the magnitude of the maximum daily NEE was $-2.91$ g C m$^{-2}$ day$^{-1}$, which is at the lower end of the maximum daily NEE variation range (from $-1.91$ to $-9.3$ g C m$^{-2}$ day$^{-1}$)\textsuperscript{36} for other grassland ecosystems. This relatively low value was related to the practice of single-species sowing, which greatly reduces the plant diversity.\textsuperscript{12} Naeem et al. (1994)\textsuperscript{37} found that a reduction in plant diversity can cause a simplification in the canopy structures and a reduction in the light acquisition and utilization efficiency of a plant colony, thereby reducing the CO$_2$ uptake of the overall ecosystem.

The annual NEE of the pasture in 2008 indicated that the pasture acted as a medium-strength carbon sink compared with other grassland ecosystems (from $-18$ to $-274$ g C m$^{-2}$ year$^{-1}$)\textsuperscript{38}. The low air temperature environment and the matching traits of the cool-adapted plants (e.g., the depression of the NEE at relatively higher temperatures) might have operated as important environmental restrictions on the carbon sink potential of the pasture.

**Conclusion**

We have adopted eddy covariance to investigate the net ecosystem CO$_2$ exchange (NEE) for a single-sowed artificial pasture of *Elymus nutans* in the Sanjiangyuan Region in 2008. The results show that for the pasture, the maximum daily NEE was $-2.91$ g C m$^{-2}$ day$^{-1}$, and the NEE for the whole year was $140.01$ g C m$^{-2}$ year$^{-1}$. Therefore, the artificial grassland was a carbon sink during 2008. During the daytime, the NEE was primarily regulated by the PPFD; at night, the NEE was mainly regulated by the $T_s$. A relatively higher temperature can suppress the photosynthesis of the pasture, and it can reduce the carbon absorption capability of the pasture ecosystem. The daily NEE and LAI have a linear relation, and 32.5% of the NEE variation can be interpreted by the LAI variation.

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