N balance and cycling of Inner Mongolia typical steppe: a comprehensive case study of grazing effects

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Abstract. Increasing grazing pressure and climate change affect nitrogen (N) dynamics of grassland ecosystems in the Eurasian steppe belt with unclear consequences for future delivery of essential services such as forage production, C sequestration, and diversity conservation. The identification of key processes responsive to grazing is crucial to optimize grassland management. In this comprehensive case study of a Chinese typical steppe, we present an in-depth analysis of grazing effects on N dynamics, including the balance of N gains and losses, and N cycling. N pools and fluxes were simultaneously quantified on three grassland sites of different long-term grazing intensities.

Dust deposition, wind erosion, and wet deposition were the predominant but most variable processes contributing to N losses and gains. Heavy grazing increased the risk of N losses by wind erosion. Hay-making and sheep excrement export to folds during nighttime keeping were important pathways of N losses from grassland sites. Compared to these fluxes, gaseous N losses (N₂O, NO, N₂, and NH₃) and N losses via export of sheep live mass and wool were of minor relevance. Our N balance calculation indicated mean annual net N losses of 0.9 ± 0.8 g N/m² (mean ± SD) at the heavily grazed site, whereas the long-term ungrazed site was an N sink receiving mean annual inputs of 1.8 ± 1.1 g N/m², mainly due to dust deposition. Heavy grazing reduced pool sizes of topsoil organic N, above- and belowground biomass, and N fluxes with regard to plant N uptake, decomposition, gross microbial N turnover, and immobilization. Most N-related processes were more intensive in seasons of higher water availability, indicating complex interactions between land use intensity and climate variability. The projected increase of atmospheric N depositions and changes in rainfall pattern imposed by land use change will likely affect N sink–source pathways and N flux dynamics, indicating high potential impact on grassland ecosystem functions. Land use practices will be increasingly important for the management of N dynamics in Chinese typical steppe and, therefore, must be considered as key component to maintain, restore or optimize ecosystem services.

Key words: China; climate variability; grassland; land use; N dynamics; N pathways; semiarid; sheep.

INTRODUCTION

Nitrogen (N) availability often limits primary productivity of terrestrial ecosystems (LeBauer and Treseder 2008), with the degree of N limitation differing between biomes and climatic zones and modified by soil...
physicochemical conditions. The functioning of these ecosystems in response to N availability is a key trait in analyzing related fluxes of carbon (C) and water. Agricultural production systems for food, fuel, and fiber dominate the public perception, due to both the substantial resource input (including large amounts of N) into these production systems and the impact on eco-environmental services (Vitousek et al. 1997, Gruber and Galloway 2008). However, the relevance of grasslands is obvious from their central role in global N and C budgets. Due to the close biogeochemical coupling between water and N, most natural grassland systems are co-limited by both resources (Burke et al. 1997, Hooper and Johnson 1999, LeBauer and Treseder 2008). Analyses of grassland responses to N availability are, thus, relevant in the context of (1) potentially increasing N deposition to which natural vegetation is exposed (Galloway et al. 2004, 2008, Reay et al. 2008), (2) the expected changes in climate that exert control over and are feedback by changes in N and C pools (Ojima et al. 1993, Parton et al. 1995, Hungate et al. 2003), and (3) land use practices that potentially bear the strongest impact on N dynamics. Consequently, quantification of grasslands’ N and C pools and related fluxes is of vital importance for analyzing the C sink and source relationships and specifically the global warming potential induced by land use related N and C losses to the atmosphere.

Within global grassland biomes, natural temperate semiarid grasslands represent an important ecosystem covering roughly 10% of the global land surface (excluding Antarctica), of which 50% belongs to the Eurasian steppe belt (Loveland et al. 2000). Since typical steppe climate constrains the decomposition of soil organic matter (SOM; see, e.g., Anderson 1991), N has accumulated for hundreds of years in relatively stable SOM pools (Meentemeyer 1984). As soil N and C pools and their dynamics usually are closely linked (Schimel et al. 1997), N imports and losses will consequently affect the ecosystem’s C storage. Large-scale variation in grassland types and related N pools and dynamics are mainly determined by temperature and precipitation gradients (Burke et al. 1997), while landscape-scale variation is strongly related to topography and soil physical characteristics (Burke et al. 1999, Hook and Burke 2000, Gong et al. 2008).

In addition to these soil physical and climatic factors, land use has pronounced effects on N dynamics and balances. Land use changes are a central concern of global C and N inventories as conversion of vegetation type (e.g., from forest to crop or pasture) has pronounced effects on soil C (Guo and Gifford 2002, Wu et al. 2003) and N (Burke et al. 2002, Zhou et al. 2007) pool sizes. Typical steppe systems are subject to grazing, which, in a historical perspective, has been both highly variable over time and diverse in terms of grazers (Mack and Thompson 1992, Janis 2008).

The most comprehensive overview of grazing effects on the C and N budget of grasslands was given by Milchunas and Lauenroth (1993) who surveyed 236 sites and found no consistent effect of grazing on soil C and N pools. For grasslands in the Eastern part of the Eurasian steppe belt negative effects of grazing on C and N balances were reported. C and N pools in grasslands of Inner Mongolia were larger in exclosures than in grazed sites and decreased with grazing intensity (Su et al. 2005, Wu et al. 2007, Han et al. 2008).

To go beyond simple C and N inventories of grassland’s SOM pool requires a quantification of relevant pools and fluxes. N balancing of non-grazed grasslands is basically simple if the relevant components are measured. These are N inputs by wet and dust deposition and N2 fixation and N outputs by percolation of N below the rooting zone, water and wind erosion, and gaseous N emissions. Information about temporal dynamics of net primary productivity, standing dead biomass and litter, above- and belowground allocation of dry mass, and transport of biomass by mammals into the soil in combination with decay rates of SOM pools would then allow for the prediction of N pools and fluxes under variable climate and land use.

Pastoralism, at first glance, modifies this N balance only by additional N losses via biomass export. However, it adds substantial complexity to N balancing approaches as grazing modifies almost all fluxes and pools. The N cycle of arid and semiarid grasslands is characterized by a slow transfer from the soil organic N pool to the plant available N pool and grazing accelerates N turnover via feces and urine redistribution eventually increasing the productivity by higher N availability and N conservation mechanisms (McNaughton et al. 1997, Frank et al. 2000). However, patches of urine and feces are potentially subject to high rates of N volatilization, reducing the amount of N redistributed to the grazing area. Next to N excretion by feces and urine, grazers have a direct impact on net primary productivity. Grazed areas are characterized by reduced standing biomass and litter and altered shoot–root allocation patterns (Milchunas et al. 2008), increasing the risk of N losses by wind and water erosion. Selective grazing in combination with interannual climate variability affects plant species composition in a complex manner (Adler et al. 2006) and grazing-induced soil compaction increases the risk of surface runoff and, by modifying soil water retention and pore space distribution, as well as gaseous N losses.

In numerous grassland studies, only one or few of the aforementioned components of the N balance were analyzed and compiled data have rarely been reported (Woodmansee 1978, Woodmansee et al. 1978, Lauenroth and Milchunas 1992, Burke et al. 2008). In an attempt to consider all these components, we present data of N gains and losses by wet deposition, wind erosion and dust deposition, gaseous N losses, and N losses through animals combined with measurements of N pools and fluxes related to above- and belowground
biomass and SOM. We constructed detailed N balance sheets of three sites subjected to contrasting land use practices in Inner Mongolia, including (1) a long-term heavily grazed site, typical for large steppe areas where the increasing meat demand encouraged farmers to increase herd sizes, (2) a winter grazed site, additionally used for hay-making, and (3) a long-term grazing exclosure representing ultimate grassland conservation. We quantified most of the relevant N pools and fluxes and compared the relevance of different processes and components of the N cycle in relation to the overall N dynamics.

Climate variability affects N dynamics of ecosystems with complex impact on the various components of the N cycle and balance. As one feature of climate change and with regard to the substantial natural annual fluctuations of precipitation, it is crucial to consider effects of climate variability in relation to those of land use practices. However, in terms of ecosystem overexploitation by land use practices, analysis of critical, resource-limiting periods is required for drawing conclusions in terms of sustainable land use.

Motivation to carry out this study is based on the environmental impact of increasing grazing pressure affecting large areas of the Eurasian steppe belt. This intensified land use during the last decades is well documented for the Inner Mongolian rangeland systems (Tong et al. 2004, Yu et al. 2004, Angerer et al. 2008), which is the most important region in China for grassland-based animal husbandry. The identification of key processes affecting N cycling and balance under contrasting land use practices and climate variability may help to indicate management options in order to improve natural grassland-based land use systems toward an increased resource use efficiency and reduced land degradation. Furthermore it may improve our understanding how delivery of grassland ecosystem services, such as fodder production, C-sequestration, and biodiversity conservation may develop under future conditions shaped by land use and climate dynamics.

Material and Methods

Study area

The study area was located in the Xilin River Catchment of the Inner Mongolia autonomous region in China, nearby the Inner Mongolia Ecosystem Research Station (IMGERS; 43°38′ N, 116°42′ E; Fig. 1). The semiarid continental climate of this typical steppe ecosystem allows for an annual growing season of about five months between early May and late September. In this period, average monthly temperatures are above 5°C (annual mean temperature, −0.4°C) reaching a maximum of 19°C in July. The winter is dry and extremely cold with a mean temperature in January of −21.6°C. Mean annual precipitation (MAP) is 348 mm for the period 1979–2002 and more than 85% of precipitation occurs between May and September with a maximum in July. The three experimental years contrasted each other in terms of rainfall. In 2004, rainfall was typical in terms of amount (325 mm) and seasonal distribution while 2005 was the driest year ever recorded at IMGERS with only 142 mm of rainfall between May and September and an annual total of 166 mm. The year 2006 was a year with nearly normal rainfall amount (304 mm) but no pronounced summer rainfall peak and considerable rainfall at the end of the growing season in September (Fig. 1). Mean annual temperatures in 2004–2006 were between 1.5° and 2.0°C and higher than the long-term mean average temperature of 0.7°C.

Study sites

In order to assess N pool sizes and related fluxes as affected by grazing practices, we selected three sites with different long-term land uses: (1) a 100-ha site subjected to local farming with heavy grazing for more than 30 years (site HG; 43°34′54″ N, 116°40′37″ E); (2) a 42-ha site with moderate summer communal grazing and occasional hay-making and, after fencing in 1999, winter grazing (site WG; 43°32′57″ N, 116°40′04″ E); and (3) a 28-ha fenced site protected from grazing since 1979, representing a benchmark site of grassland conservation (site UG; 43°33′10″ N, 116°40′33″ E; Table 1). Sites UG and WG were 600 m apart; site HG was located about 2.5 km northeast of the other sites. As long-term factorial grazing experiments were not established in this region, and the supply of equipment and personnel power to perform simultaneous measurements on several sites were unrealistic, a pseudoreplicated experimental design was unavoidable. Site selection was done in close cooperation with the Institute of Botany, Chinese Academy of Sciences, providing a long-term experience of experimental fieldwork on these sites of which many results were published. Data of animal-related N pools and fluxes were collected from on-farm feeding and grazing experiments (Glindemann et al. 2009a, b, Wang et al. 2009) adjacent to sites WG and UG. Soils of the study sites were classified as calcic Chernozems (IUSS Working Group WRB 2006) with a sandy loam texture (sand 50–64%, silt 21–38%, and clay 18–27%; Table 2). Groundwater levels in farm wells close to experimental sites were below 8 m from the soil surface, indicating that capillary rise or leaching was most likely not contributing to site water balance. Soil water content was measured at 5 cm depth with three replicates on each site during the growing season at 30-minute intervals with calibrated Theta probes (Type ML2x; Delta-T Devices, Cambridge, UK). Throughout the years 2004–2006, site UG had higher soil water content compared to the grazed sites; the dry year 2005 reduced average soil water content at all sites by around 50% with carry over effects into 2006 (Table 2).

Plant species composition

The predominant perennial vegetation was classified as a Stipa grandis P. Smirn. and Leymus chinensis (Trin.) Tzvel. dominated steppe community. Species composi-
FIG. 1. (a) Location and (b) climate diagram of the study area, the Xilin River catchment in Inner Mongolia autonomous region, China. The MAGIM project was hosted by the Inner Mongolia Grassland Ecosystem Research Station (IMGERS) located at 43°38'N, 114°42'E, 1200 m above sea level. The site has 346 mm annual mean precipitation and 0.7°C annual mean temperature, both based on 20 years of observation. In panel (b), the striped bar at the bottom of the diagram indicates the period of frost appearance, and the gray bar defines the growing season by monthly mean temperatures >5°C and P > 2T (where P is precipitation in mm and T is temperature in °C). Panels (c)-(e) show the annual climate variability measured at IMGERS from 2004 to 2006. Values on each panel are total annual precipitation and mean temperature.
tion was recorded at peak biomass time in August 2004 and 2006 on 100 sample plots of $1 \times 1$ m, on a regular, orthogonal, grid design (see Steffens et al. [2008] for further details) within each study site. Contrasting land use history affected the botanical composition of the three studied sites (Table 3). Sites UG and HG showed considerable proportions of dicotyledonous species such as *Potentilla acaulis* and *Artemisia frigida* at site HG and *Caragana microphylla*, a chamaephyt legume, at site UG. Site WG was dominated by perennial grasses *Stipa grandis* and *Leymus chinensis*. Grasses dominating at site HG were *Carex korshinskyi* and *Cleistogenes squarrosa*; the most abundant grasses recorded at site UG were *Stipa grandis* and *Achnatherum sibiricum*. For further details, see, e.g., Zhu (1993), Bai et al. (2004), and Yu et al. (2004).

### N gains and losses

**Dust and wet deposition, wind erosion.**—Measurements of dust emissions and deposition are described in detail by Hoffmann et al. (2008a, b). Briefly, wind-driven N fluxes were calculated from dust N content and vertical dust fluxes measured with “modified Wilson and Cooke” catchers and dust deposition samplers (Hoffmann et al. 2008a). The total dust deposition without the dust re-entrainment was measured by the dust deposition sampler. The net dust emission and deposition result from of the upward or downward oriented vertical dust fluxes and were calculated from dust concentration measurements at different heights applying the vertical gradient method. A total of 31 dust storm events were analyzed in 2005 and 2006, which exclusively occurred from March to May, the peak period of dust storm activity driven by strong winds from the North and West. Wet N deposition was calculated from rainfall amount and rainfall N concentration measured during 16 rainfall events in 2005 and 2006.

**Biological N$_2$ fixation.**—Biological N$_2$ fixation by cyanobacteria (*Nostoc* sp.) was measured by using the acetylene reduction technique and $^{15}$N$_2$ fixation experiments at temperatures of $5^\circ$ and $25^\circ$C on samples collected on the three sites in autumn of 2005. Biomass densities of these biological soil crusts were quantified

### Table 1. Size, grazing period, stocking rate, and grazing history of the Inner Mongolia typical steppe experimental sites: heavy grazing (HG), winter grazing (WG), and long-term grazing exclosure (UG).

<table>
<thead>
<tr>
<th>Site characteristic</th>
<th>HG</th>
<th>WG</th>
<th>UG</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size (ha)</td>
<td>100</td>
<td>42</td>
<td>28</td>
</tr>
<tr>
<td>Grazing period</td>
<td>Summer and winter grazing (May–Jan)</td>
<td>Only winter grazing (Oct–Jan)</td>
<td>no grazing</td>
</tr>
<tr>
<td>Stocking rate</td>
<td>2 SU/ha</td>
<td>2 SU/ha</td>
<td></td>
</tr>
<tr>
<td>Grazing history</td>
<td>&gt;30 years heavy grazing</td>
<td>winter grazing since 1999; before, moderate grazing/ hay-making</td>
<td>grazing exclosure since 1979</td>
</tr>
</tbody>
</table>

*Notes:* Stocking rate is calculated during the grazing period. One sheep unit (SU) is a mother sheep with lamb during summer grazing and without lamb during winter grazing.

### Table 2. Topsoil characteristics (0–4 cm depth, except texture [0–10 cm depth]) and average growing season soil water content of Inner Mongolia typical steppe under different land use intensities.

<table>
<thead>
<tr>
<th>Topsoil characteristic</th>
<th>HG</th>
<th>WG</th>
<th>UG</th>
</tr>
</thead>
<tbody>
<tr>
<td>Texture (mg/g)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clay</td>
<td>180 (± 10)</td>
<td>270 (± 10)</td>
<td>220 (± 10)</td>
</tr>
<tr>
<td>Silt</td>
<td>180 (± 20)</td>
<td>230 (± 40)</td>
<td>180 (± 40)</td>
</tr>
<tr>
<td>Sand</td>
<td>640 (± 30)</td>
<td>500 (± 40)</td>
<td>600 (± 41)</td>
</tr>
<tr>
<td>Organic carbon (mg/g)</td>
<td>17.0 (± 4.2)</td>
<td>25.9 (± 4.5)</td>
<td>31.0 (± 5.5)</td>
</tr>
<tr>
<td>Total N (mg/g)</td>
<td>1.74 (± 0.39)</td>
<td>2.72 (± 0.44)</td>
<td>3.15 (± 0.50)</td>
</tr>
<tr>
<td>C:N ratio</td>
<td>9.7 (± 0.4)</td>
<td>9.5 (± 0.4)</td>
<td>9.8 (± 0.3)</td>
</tr>
<tr>
<td>pH (CaCl$_2$)</td>
<td>6.6 (± 0.25)</td>
<td>6.7 (± 0.29)</td>
<td>6.6 (± 0.24)</td>
</tr>
<tr>
<td>Bulk density (g/cm$^3$)</td>
<td>1.28 (± 0.08)</td>
<td>1.09 (± 0.08)</td>
<td>0.94 (± 0.10)</td>
</tr>
<tr>
<td>Topsoil N (g/m$^2$)</td>
<td>89 (± 15)</td>
<td>119 (± 14)</td>
<td>118 (± 10)</td>
</tr>
</tbody>
</table>

**Soil water content (volume%)**

<table>
<thead>
<tr>
<th></th>
<th>2004</th>
<th>2005</th>
<th>2006</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>13.5</td>
<td>6.4</td>
<td>10.4</td>
</tr>
<tr>
<td>Soil water content (volume%)</td>
<td>17.6</td>
<td>9.0</td>
<td>11.6</td>
</tr>
<tr>
<td></td>
<td>18.8</td>
<td>10.2</td>
<td>12.6</td>
</tr>
</tbody>
</table>
Simulated mean NO emissions were 5.8. Season soil temperature and moisture data from our site, on this correlation and by taking the original growing on the fluxes of nitric oxide of typical steppe soils. Based of the combined effects of soil temperature and moisture correlation using multiple nonlinear regression analysis for NO emissions. Yao et al. (2010) found a strong not capture the important freezing and thawing period incubation. On the other hand, Holst et al. (2007) explained by the missing plant N uptake during soil core measurements of Holst et al. (2007) conditions were significantly higher compared to field measurements of Holst et al. (2009). As legumes were rarely found on site HG, biological N2 fixation by legumes was not investigated in this study.

Gaseous N emissions.—N oxide gas fluxes (N2O, NO, and NO2) were measured under field conditions on both the grazing enclosure and the winter-grazed site with a fully automated chamber system during the 2004 and 2005 growing periods (Holst et al. 2007a) and N2O during freezing and thawing cycles in 2006 (Holst et al. 2008). In addition, Yao et al. 2010 incubated intact soil cores to analyze NO emissions. However, measured mean NO emissions from incubation under controlled conditions were significantly higher compared to field measurements of Holst et al. (2007a), which may be explained by the missing plant N uptake during soil core incubation. On the other hand, Holst et al. (2007a) did not capture the important freezing and thawing period for NO emissions. Yao et al. (2010) found a strong correlation using multiple nonlinear regression analysis of the combined effects of soil temperature and moisture on the fluxes of nitric oxide of typical steppe soils. Based on this correlation and by taking the original growing season soil temperature and moisture data from our site, simulated mean NO emissions were 5.8 µg N·m⁻²·h⁻¹ (Yao et al. 2010). This value, integrating both field and soil core incubation results in the laboratory (based on 200 days per year with soil temperatures above 0°C), was used to calculate mean annual NO emissions. N2O gas fluxes at site HG as well as from sheepfolds were measured with a manual system (Holst et al. 2007a) and additional information were collected along topographic transects (May–September 2005), from feces and urine application experiments and by constructing a large chamber for measuring N2O fluxes from entire dung heaps (Holst et al. 2007b). A complete annual cycle of trace gas fluxes was additionally measured on 10 sites of contrasting grazing intensity from August 2007 to August 2008 (Wolf et al. 2010).

Since analyses of N losses due to production of N2 via denitrification were not carried out, we estimated N2 losses by assuming a N2O-N/(N2 + N2O)-N ratio of 0.492 ± 0.066 (mean ± SE) as provided by Schlesinger (2009) on basis of a meta-data analysis for natural and semi-natural soils. This ratio is known to be highly variable over the season and affected by nitrate availability, soil pH, temperature, and water-filled pore space (e.g., Stevens and Laughlin 1998, Müller et al. 2002). Acknowledging the relevance of NH3 losses from urine patches (which were not measured), we estimated this to amount to 30% (with about 10% variability) of the deposited urea-N during summer grazing and, due to low temperatures, to 10% ± 5% during winter grazing period (Sherlock and Goh 1984, Schimel et al. 1986, Frank et al. 2004).

Sheep-related N balance calculations.—Calculations of animal-related N fluxes and pool size estimates are complex and have rarely been reported in detail in from 28 sampling positions at each site (Holst et al. 2009). As legumes were rarely found on site HG, completely absent at site WG, and with only around 5% relative biomass present at site UG (Table 3; see also Gao et al. 2009), biological N2 fixation by legumes was not investigated in this study.

### Table 3. Mean ground cover of major plant species and of bare ground/litter in Inner Mongolia typical steppe under different land use intensities.

<table>
<thead>
<tr>
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<tbody>
<tr>
<td><strong>Perennial grasses (%)</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><em>Stipa grandis</em></td>
<td>2.4</td>
<td>1.4</td>
<td>21.0</td>
<td>10.7</td>
<td>12.2</td>
<td>7.7</td>
</tr>
<tr>
<td><em>Leymus chinensis</em></td>
<td>1.5</td>
<td>0.8</td>
<td>10.2</td>
<td>5.3</td>
<td>5.0</td>
<td>4.1</td>
</tr>
<tr>
<td><em>Achnatherum sibiricum</em></td>
<td></td>
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<tr>
<td><em>Agropyron michnoin</em></td>
<td>4.3</td>
<td>1.6</td>
<td>2.5</td>
<td>2.4</td>
<td>4.7</td>
<td>4.5</td>
</tr>
<tr>
<td><em>Carex korshinsky</em></td>
<td>12.8</td>
<td>9.3</td>
<td>8.7</td>
<td>4.0</td>
<td>7.3</td>
<td>5.3</td>
</tr>
<tr>
<td><em>Cleistogenes squarrosa (C₄)</em></td>
<td>12.2</td>
<td>1.4</td>
<td>8.6</td>
<td>5.7</td>
<td>5.3</td>
<td>3.5</td>
</tr>
<tr>
<td><strong>Perennial forbs (%)</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td><em>Potentilla acaulis</em></td>
<td>16.7</td>
<td>0.9</td>
<td>0.2</td>
<td>2.4</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td><em>Artemisia frigida</em></td>
<td>11.1</td>
<td>3.7</td>
<td>2.0</td>
<td>0.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Legumes†</td>
<td>0.7</td>
<td>0.2</td>
<td></td>
<td></td>
<td>5.8</td>
<td>6.7</td>
</tr>
<tr>
<td><strong>Annuals</strong></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chenopodium sp.</em></td>
<td>&lt;0.1</td>
<td>7.4</td>
<td>&lt;0.1</td>
<td>1.5</td>
<td>0.2</td>
<td>2.7</td>
</tr>
<tr>
<td><em>Salsola collina</em></td>
<td>&lt;0.1</td>
<td>0.3</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
<td>0.1</td>
<td>0.7</td>
</tr>
<tr>
<td>All other (%)</td>
<td>7.6</td>
<td>2.2</td>
<td>4.1</td>
<td>4.3</td>
<td>20.2</td>
<td>11.7</td>
</tr>
<tr>
<td>All species green biomass</td>
<td>69.5</td>
<td>28.4</td>
<td>60.3</td>
<td>36.1</td>
<td>76.7</td>
<td>56.4</td>
</tr>
<tr>
<td>Litter, bare ground</td>
<td>30.7</td>
<td>71.6</td>
<td>39.7</td>
<td>63.9</td>
<td>23.3</td>
<td>43.6</td>
</tr>
</tbody>
</table>

**Notes:** Measurements were taken at peak biomass time in August 2004 (a year of normal rainfall amount and distribution) and 2006 (a year without pronounced rainfall peak and late rainfall in September, additionally affected by the extreme drought in 2005). Sample plot size is 1×1 m, grid design; HG and UG n = 100 samples, WG n = 124 samples. Empty cells indicate that species is absent.

† Accumulated green biomass ground cover (%) of *Caragana microphylla, Astragalus galactites, Melilotus suavedens, Melisitmus ruthenica, and Thermopsis lanceolata.*
grassland studies. Our calculations were based on measured, estimated, and derived parameters summarized in Table 4. These parameters were used for calculating N-related parameters listed in Table 5. Calculations are explained in the following sections. Not to create the impression of a nonexistent accuracy, values in the text were rounded if appropriate, whereas in the tables decimal places are given to enable reconstruction of calculations.

**Grazing periods and stocking rates.**—Grazing mainly occurs during the vegetation growth period, whereas, during autumn and winter, sheep either have access to standing dead biomass or are supplied with hay. A common feature of herd management in grasslands of Inner Mongolia is that animals are brought to sheepfolds near the farmhouse at night, which needs to be considered for N balance calculations with regard to excrement deposition. Sheep are kept full-time in sheepfolds from February to May for the lambing period and because of governmental regulation to protect grassland during the early growing season (for an overview of issues involving landowner rights and grassland protection, see, e.g., Li et al. [2007]). In order to consider this intra-annual variability in stocking rates in our N balance calculations, we divided the year into three grazing periods: summer grazing from June to September (122 days); winter grazing from October to January (123 days); and a sheepfold time from February to May (120 days; Table 4).

We defined a mother sheep including the lamb (raised from early spring on and sold in late summer or autumn) as one sheep unit (SU). Grazing-related land use effects on the N balance were evaluated by comparing two intensive land use practices: hay-making in combination with winter grazing (site WG) and continuous heavy grazing (site HG) with a stocking rate of 2 SU/ha.

**Sheep live mass gain.**—Live mass of a SU was 43 kg/SU (35-kg mother sheep, 8-kg lamb) at the beginning of the summer grazing period. Live mass gain rate of 130 g SU\(^{-1}\) d\(^{-1}\), was based on determinations from 15-month-old non-pregnant and non-lactating female sheep (Glindemann et al. 2009b). Total live mass gain until end of the summer grazing period (122 days) was about 16 kg/SU (Table 4). As part of the herd (male lambs and older ewes) is sold in late summer, live mass of a SU (now without lambs) during winter grazing period and sheepfold time was assumed to be constant at 35 kg. For the sheepfold time, we estimated a live mass gain rate of 70 g SU\(^{-1}\) d\(^{-1}\) or in total around 8.5 kg live mass gain of the lamb until end of May.

**Feed intake, digestibility, and excrement production.**—Feed organic matter intake (OMI\(_{feed}\)) and feed dry matter intake are central parameters of N balances, but are impossible to measure directly under field conditions. OMI\(_{feed}\) was, therefore, calculated from daily fecal organic matter excretion (OME\(_{fec}\)) and feed organic matter digestibility (DOM\(_{feed}\); Table 4; see also Glindemann et al. 2009b).

OME\(_{fec}\) was determined by oral inert marker (TiO\(_2\)) application and analysis of its concentration in fecal grab samples. Average daily OME\(_{fec}\) of female sheep with an average body mass of 32 kg was 530 g independent of stocking rates ranging from 1.5 to 9 sheep/ha (Glindemann et al. 2009a). Extrapolating to summer-season average SU body mass of about 51 kg/SU at site HG (average of beginning and end-of-season masses of 43 and 59 kg), daily OME\(_{fec}\) was 845 g/SU (Table 4). At site WG (average SU body mass 35 kg), daily OME\(_{fec}\) was 580 g/SU during the winter grazing period.

With 13% dry matter crude ash content of feces (AC\(_{fec}\); Glindemann et al. 2009a), daily dry matter excretion (DM\(_{fec}\)) during the summer and winter grazing periods were around 970 and 670 g/SU, respectively (Table 4).

Feed organic matter digestibility (DOM\(_{feed}\)) was derived from regression equations developed from in-vivo digestibility trials and measurements of fecal organic matter crude protein content (OMPC\(_{fec}\); Wang et al. 2009). This fecal crude protein method allows for estimating DOM\(_{feed}\) without collecting representative feed samples, which is a methodological advantage for heterogeneous grazing sites and animals with selective foraging behavior. The average DOM\(_{feed}\) of the study area was 0.54 during the summer grazing period. OMPC\(_{fec}\) during winter grazing was not experimentally determined. For this period we assumed a lower OMPC\(_{fec}\) (Table 4) since the N content of the litter and standing dead plant material was substantially lower due to translocation of nutrients to plant perennial belowground organs.

Daily OMI\(_{feed}\) was about 1800 and 1100 g/SU for the summer and winter grazing periods, respectively (Table 4). With feed organic matter contents (OMC\(_{feed}\)) of 95% and 90% during summer and winter grazing, respectively (Giese et al. 2009, Schiborra et al. 2009), daily feed dry matter intake (DMI\(_{feed}\)) was around 1900 and 1200 g/SU, respectively.

Since feed intake during the sheepfold time is based on external fodder sources and excrement are not redistributed to the grazing site, this time period is not relevant for grassland N-balance calculations. However, in order to construct sheep-related annual N balances, we calculated the corresponding parameters for the sheepfold period (Table 4).

The sheep-related N balance calculations required information about feed N intake (N\(_{feedIN}\)). N incorporation into the animal body (N\(_{LMG}\)) and wool (N\(_{wool}\)), and N excretion via feces and urine (N\(_{fec}\) and N\(_{urine}\)), and followed the basic assumption

\[
N_{feedIN} = N_{LMG} + N_{wool} + N_{fec} + N_{urine}.
\] (1)

Feed N intake (N\(_{feedIN}\)) during the grazing period was calculated from daily dry matter feed intake, feed dry
Table 4. Parameters of the sheep-related N balance of Inner Mongolia typical steppe under different land use practices: heavy grazing (HG), winter grazing (WG), and sheep fold (SF).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Abbreviation</th>
<th>Equation</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grazing period (G)</td>
<td>GP</td>
<td></td>
<td>d m⁻²</td>
</tr>
<tr>
<td>Grazing/sheep fold area (G)</td>
<td>GA</td>
<td></td>
<td>SU m⁻²</td>
</tr>
<tr>
<td>Number of sheep units (G)</td>
<td>SU</td>
<td></td>
<td>d m⁻¹</td>
</tr>
<tr>
<td>Stocking rate (D)</td>
<td>SR</td>
<td></td>
<td>g FM SU⁻¹ d⁻¹</td>
</tr>
<tr>
<td>Live mass gain rate (MCE)</td>
<td>LMG</td>
<td></td>
<td>g FM SU⁻¹ d⁻¹</td>
</tr>
<tr>
<td>Live mass gain (D)</td>
<td>LMG</td>
<td></td>
<td>g FM SU⁻¹ d⁻¹</td>
</tr>
<tr>
<td>Feces OM crude protein content (M-E)</td>
<td>OMPCfec</td>
<td></td>
<td>g OM SU⁻¹ d⁻¹</td>
</tr>
<tr>
<td>Feed OM digestibility (D)</td>
<td>DOMfeed</td>
<td>DOMfeed = 0.899 – 0.644 × exp(−0.5774 × OMPCfec × 10)</td>
<td>dimensionless</td>
</tr>
<tr>
<td>Feces OM excretion (M-E)</td>
<td>OMEfec</td>
<td></td>
<td>g OM SU⁻¹ d⁻¹</td>
</tr>
<tr>
<td>Feed OM intake (D)</td>
<td>OMIfeed</td>
<td>OMIfeed = OMEfec/(1 − DOMfeed)</td>
<td>g OM SU⁻¹ d⁻¹</td>
</tr>
<tr>
<td>Feed OM content (M)</td>
<td>OMCfeed</td>
<td></td>
<td>g OM SU⁻¹ d⁻¹</td>
</tr>
<tr>
<td>Feed DM intake (D)</td>
<td>DMIfeed</td>
<td>DMIfeed = OMIfeed/OMCfeed</td>
<td>g DM OM</td>
</tr>
<tr>
<td>Feces DM ash content (M)</td>
<td>ACfec</td>
<td></td>
<td>g ash DM</td>
</tr>
<tr>
<td>Feces DM excretion (D)</td>
<td>DMEfec</td>
<td>DMEfec = OMEfec/(1 − ACfec)</td>
<td>g DM SU⁻¹ d⁻¹</td>
</tr>
<tr>
<td>Feces DM crude protein content (D)</td>
<td>DMPCfec</td>
<td>DMPCfec = OMPCfec × (1 ACfec)</td>
<td>g DM SU⁻¹ d⁻¹</td>
</tr>
<tr>
<td>Feces DM N concentration (D)</td>
<td>DMNCfec</td>
<td>DMNCfec = DMPCfec/6.25</td>
<td>g N/g DM</td>
</tr>
<tr>
<td>Feed dry matter N concentration (M)</td>
<td>DMNCfeed</td>
<td></td>
<td>g N/g DM</td>
</tr>
<tr>
<td>Excremen site allocation factor (E)</td>
<td>AFex</td>
<td></td>
<td>dimensionless</td>
</tr>
<tr>
<td>Sheep body N concentration (L)</td>
<td>NCsheep</td>
<td></td>
<td>g N/g DM</td>
</tr>
<tr>
<td>Wool N concentration (L)</td>
<td>NCwool</td>
<td></td>
<td>g N/g DM</td>
</tr>
<tr>
<td>Wool production (E)</td>
<td>Pwool</td>
<td></td>
<td>g SU⁻¹ d⁻¹</td>
</tr>
<tr>
<td>Volatilization loss from urine patches (E)</td>
<td>VUrine</td>
<td></td>
<td>dimensionless</td>
</tr>
<tr>
<td>Hay harvest index (E)</td>
<td>NHay</td>
<td></td>
<td>dimensionless</td>
</tr>
<tr>
<td>Aboveground net primary productivity/</td>
<td>ANPP, AGB</td>
<td></td>
<td>g DM m⁻²</td>
</tr>
<tr>
<td>aboveground biomass (winter) (M)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: Parameters were given (G), derived (D), estimated (E), measured (M), or from literature (L). M-E parameters were measured but not for all land use practices or for all time periods. In order to consider intra-annual variability in stocking rates in our N balance calculations, we divided the year into three grazing periods: summer grazing from June to September; winter grazing from October to January; and a sheepfold period from February to May. Abbreviations are FM, fresh mass; OM, organic matter; DM, dry matter.

† One sheep unit (SU) during summer grazing and sheepfold period consists of one mother sheep with lamb (raised from early spring on and usually sold in late summer or autumn). One SU during the winter grazing period only consists of the mother sheep.

§ No hay-making.

Plant-related N fluxes and pools.—Seasonal dynamics of above- and belowground net primary productivity (ANPP, BNPP) were measured at site UG, WG, and HG on at least five sampling dates during the vegetation growth periods, with five, six, and seven replicates in 2004, 2005, and 2006, respectively. At site HG, grazing effects on ANPP were studied with movable exclosure cages. Root system studies included root in-growth cores until 50 cm depth to quantify BNPP and conventional soil coring until 1 m depth to determine belowground biomass (BGB) and live root fractions (Gao et al. 2008). Shoot and root biomass N concentrations were measured repeatedly from subsamples during vegetation periods 2004–2006 and analyzed by dry combustion with a CN elemental analyzer (EA 1108; Carlo Erba,
Milan, Italy). A common trait of Inner Mongolia typical steppe ecosystems is the relatively low abundance of plant species with perennial aboveground organs (e.g., for our study sites, Caragana microphylla (UG) and Artemisia frigida (HG) with usually less than 10% ground cover). Therefore the perennial aboveground biomass-N pool was of minor relevance with regard to N dynamics in this ecosystem and, thus neither considered for the N-cycling nor taken into account for N-translocation and decomposition calculations.

Based on sequential BGB samplings in 2004–2006, Gao et al. (2008) measured an average living-to-dead root ratio of 0.3. Root biomass-N concentrations (living and dead roots) were around 1% at sites HG and UG and 0.8% at site WG (Table 6; see also Giese et al. 2009). Living root N concentrations of dominating plant species were measured in the range of 0.8–1.2% (data not shown) and did not differ significantly from total root biomass-N concentrations. Therefore, root biomass-N concentrations were taken to calculate root-N pools. We considered the difference between peak belowground biomass and BNPP to reflect the perennial belowground living root biomass. Therefore, we calculated the belowground living root biomass N pool as 0.3(\text{BGB} – \text{BNPP}) \times \text{rootN}_{\text{conc}} and accordingly the dead root N concentration was calculated as 0.7(\text{BGB} – \text{BNPP}) \times \text{rootN}_{\text{conc}}.

A robust approach to determine N resorption efficiency from leaves is based on the difference between leaf N concentrations at peak biomass time and at senescence (Aerts 1996, Yuan et al. 2005). We used this method to quantify the amount of N translocated (\text{Ntrans}) from senescing leaves to perennial belowground plant organs. The remaining N fraction was taken as the annual litter-N input (\text{Nlitter}) subjected to decomposition:

\[
\text{Ntrans} = \text{ANPP-N}_{\text{peak}} \times (1 - \frac{\text{ANPP-N}_{\text{csen}}}{\text{ANPP-N}_{\text{cpeak}}})
\]

\[
\text{Nlitter} = \text{ANPP-N}_{\text{peak}} \times (\frac{\text{ANPP-N}_{\text{csen}}}{\text{ANPP-N}_{\text{cpeak}}})
\]

where ANPP-N_{\text{peak}} is the aboveground N pool size built-up by the current year’s net primary productivity at peak biomass time, ANPP-N_{\text{csen}} is the biomass N concentration at senescence and ANPP-N_{\text{cpeak}} is the N concentration of current year’s net primary productivity at peak biomass time. Mean shoot N concentration measured from senescent leaves at the end of the growing season was approximately 1.0%, which was about half of the mean N concentration measured at peak biomass time (Yuan et al. 2005, Gao 2007). Consequently, we assumed that 50% of peak leaf N was translocated to perennial plant organs.

In order to consider feed-N intake or hay-N (\text{Nfeed}) at sites HG and WG, respectively, both were subtracted from ANPP-N_{\text{peak}} before the remaining N fraction of senescent shoot biomass (\text{Nlitter}) and \text{Ntrans} was calcu-
grazing cessation on the amount, composition, and sampled to 1 m depth analyzing effects of grazing and experimental sites. (2) At each site, three soil pits were added to the litter fraction. Effects of grazing and standing dead was separated from green biomass and ground biomass, litter was collected with a hand rake. Aboveground standing dead and litter biomass simultaneously to ANPP sampling. Before clipping the aboveground biomass, litter was collected with a hand rake. Standing dead was separated from green biomass and added to the litter fraction. Effects of grazing and rainfall variability on shoot and root decomposition dynamics were additionally examined in a litter-bag study (for details see: Gao et al. 2008). Root turnover rates were calculated for 2005 and 2006 as BNPP divided by mean live root biomass (Gao et al. 2008) and compared with decomposition rates from the root litter-bag study.

**Soil-related N pools and fluxes**

Effects of grazing on soil N pools were assessed with two different approaches: (1) bulk density, organic C, and total N were collected from 100 bulked topsoil (0–4 cm) samples from regular, orthogonal grids in the three experimental sites. (2) At each site, three soil pits were sampled to 1 m depth analyzing effects of grazing and grazing cessation on the amount, composition, and turnover of SOM in detail. A combined aggregate size, density, and particle size fractionation procedure was applied to soil samples from three horizons of each pit to separate functional SOM fractions and pools. The horizons were sampled based on diagnostic features, e.g., color, texture, structure, and aggregation. All physical fractions were analyzed for C and N concentrations while the SOM quality of selected fractions was applied to soil samples from three horizons of each pit to separate functional SOM fractions and pools. The horizons were sampled based on diagnostic features, e.g., color, texture, structure, and aggregation. All physical fractions were analyzed for C and N concentrations while the SOM quality of selected fractions was analyzed for neutral sugar and radio carbon content using solid-state $^{13}$C NMR spectroscopy (Steffens et al. 2008, 2009, 2011).

Gross N mineralization and gross nitrification rates of our different grazing sites were determined with the $^{15}$N pool dilution technique from soil cores incubated at in situ soil temperature and moisture conditions (Holst et al. 2007a, Wolf et al. 2010). Mean daily rates (mg N kg soil DM d$^{-1}$) of gross ammonification, gross nitrification, and ammonium and nitrate immobilization were used to estimate gross microbial N turnover rates and immobilization (g N m$^{-2}$) for a four-month growing season (122 days) with site specific bulk densities of 0–5 cm topsoil (Table 2).

**RESULTS**

**N gains and losses**

**Dust and wet deposition, wind erosion.—**N losses by wind erosion and N gains by dust deposition were affected by stocking rates and highly variable between years (Hoffmann et al. 2008, 2009, 2011). Site UG was a dust deposition area with mean N gains of 1.2 g N m$^{-2}$yr$^{-1}$ ranging from 0.4 to 2.0 g N m$^{-2}$yr$^{-1}$. Mean N inputs at site WG were 0.3 g N m$^{-2}$yr$^{-1}$ (range 0.15–0.53), whereas site HG experienced net N losses due to wind
erosion of soil sediments of 0.4 g N m⁻² yr⁻¹ (range 0.04–0.83; Table 7). Notably, a single dust storm event in 2006 contributed 0.93 g N m⁻² or roughly 50% of the 2006 N gain by dust deposition at site UG. Average rainwater-N concentrations in 2005 and 2006 were 1.3 mg/L NH₄⁺-N and 1.1 mg/L NO₃⁻-N. With total annual rainfall amounts of 166–324 mm (2004–2006), the mean annual N gain by wet deposition was 0.64 g N m⁻² yr⁻¹, ranging from 0.40 to 0.78 g N m⁻² yr⁻¹ (Table 7).

Biological N₂ fixation.—N-fixing biological soil crusts were present in our study area including cyanobacteria of the genus Nostoc, whereas the also investigated lichen Xanthoparmelia cantschadalis did not show any N-fixing activity (Holst et al. 2009). Our estimates of annual N₂ fixation by Nostoc, determined by the ¹⁵N₂ technique, varied from 0.002 to 0.007 g N m⁻² for sites HG and WG, since, at site UG, Nostoc crusts were hardly found. However, these rates were calculated rather conservatively assuming that N₂ fixation by Nostoc only happened at days with rainfall, allowing the Nostoc crusts to rewet and become active. Taking into account that actual rates may be higher by a factor of 2–10 (e.g.,

Table 5. Above- and belowground net primary productivity (ANPP, BNPP), belowground biomass (BGB), aboveground annual minimum and maximum litter/standing dead biomass pools, root turnover rates, shoot-/root decomposition, and biomass N concentrations of Inner Mongolia typical steppe.

<table>
<thead>
<tr>
<th>Site</th>
<th>HG</th>
<th>WG</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass (g/m²)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ANPP mean (range)</td>
<td>86ᵃ (75–122)</td>
<td>107ᵇ (96–126)</td>
</tr>
<tr>
<td>BNPP mean (2005, 2006)</td>
<td>124ᵃ (107, 139)</td>
<td>157ᵇ (142, 171)</td>
</tr>
<tr>
<td>BGB mean (range)</td>
<td>1602ᵃ (1487–1666)</td>
<td>2032ᵇ (1866–2179)</td>
</tr>
<tr>
<td>Litter/standing dead</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual min. mean (2005, 2006)</td>
<td>8ᵃ (2, 14)</td>
<td>77ᵇ (79, 76)</td>
</tr>
<tr>
<td>Annual max. mean (2005, 2006)</td>
<td>17ᵇ (6, 28)</td>
<td>148ᵇ (121, 175)</td>
</tr>
<tr>
<td>Root turnover rates (2005, 2006)</td>
<td>0.23, 0.29</td>
<td>0.24, 0.30</td>
</tr>
<tr>
<td>Root decomposition rate, k (2004, 2005; g·g⁻¹·yr⁻¹)</td>
<td>0.28, 0.36</td>
<td>0.24, 0.26</td>
</tr>
<tr>
<td>Root decomposition rate, k (2004, 2005; g·g⁻¹·yr⁻¹)</td>
<td>0.40, 0.20</td>
<td>0.38, 0.23</td>
</tr>
<tr>
<td>Biomass N concentrations (%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aboveground peak green biomass N⁺⁺⁺⁺</td>
<td>2.06ᵃ ± 0.34</td>
<td>1.84ᵃ ± 0.36</td>
</tr>
<tr>
<td>Aboveground litter N⁺⁺⁺⁺</td>
<td>0.85ᵇ ± 0.02</td>
<td>0.30ᵇ ± 0.01</td>
</tr>
<tr>
<td>Belowground root biomass N⁺⁺⁺⁺</td>
<td>1.04ᵇ ± 0.03</td>
<td>0.83ᵇ ± 0.02</td>
</tr>
</tbody>
</table>

Notes: Data were measured between 2004 and 2006 at sites of different land use intensities: heavy grazing (HG), winter grazing (WG), or long-term grazing exclosure (UG). Different superscript letters after means indicate significant difference between sites at P = 0.05. ANPP and BGB are given as mean values (range) from peak biomass samplings in 2004, 2005, and 2006. BNPP was determined by the ingrowth-core method (Gao et al. 2008). The annual minimum (min.) for litter/standing dead was sampled at peak biomass time in August, the annual maximum (max.) was sampled in April. Litter minimum at site UG was most likely underestimated due to the sampling method not capturing fine litter particles originating from forbs substantially contributing to biomass at site UG. Root turnover was calculated as belowground net primary production divided by mean live root biomass (Gao et al. 2008). Root and shoot decomposition rates were calculated from a litter-bag study (Giese et al. 2009).

† Mean values (±SD) from 2004 and 2005 sampled at peak biomass time in August.

‡ Mean values (±SD) from 2004 and 2005 sampled at peak biomass time in August.

Table 6. Above- and belowground net primary productivity (ANPP, BNPP), belowground biomass (BGB), aboveground annual minimum and maximum litter/standing dead biomass pools, root turnover rates, shoot-/root decomposition, and biomass N concentrations of Inner Mongolia typical steppe.
because of dew formation), we estimated N₂ fixation by *Nostoc* at 0.05 ± 0.03 g N/m² (mean ± SE) for sites HG and WG. Due to low abundance, legumes were not investigated, however, we assume that N inputs by N₂ fixation were balanced between grazed sites with higher abundance of biological soil crusts and site UG with some legumes present (e.g., *Caragana* sp., Table 3) but almost no soil crusts. At our three sites the annual N gain by biological N₂ fixation is therefore assumed not to exceed 0.08 g N/m² (Table 7).

**Gaseous N.**—N₂O emissions during the vegetation period were 0.003–0.014 g N₂O-N·m⁻²·yr⁻¹, with fluxes close to the detection limit and not affected by grazing (Holst et al. 2007a). N₂O emissions were, however, significantly higher during freezing and thawing periods (Holst et al. 2008, Wolf et al. 2010, Yao et al. 2010) and moreover, in contrast to the main growing season, substantially affected by land use. Including the freeze–thaw cycles, mean annual N₂O emissions from non-grazed sites were 0.022 ± 0.005 g N/m² (mean ± SE) and therefore twice as high compared to heavy and moderate grazed sites with average annual N₂O emissions of 0.011 ± 0.005 g N/m² (Table 7; see also Wolf et al. 2010). Yao et al. (2010) calculated mean NO emissions based on in situ temperature and soil moisture content from the growing season 2004 at site WG to 5.8 ± 1.2 µg N·m⁻²·h⁻¹, which equals an annual NO flux of 0.028 ± 0.006 g N·m⁻²·yr⁻¹ (200 days per year with soil temperatures above 0°C; Table 7). Annual gaseous N₂ losses were approximately in the same range as N₂O fluxes at all sites.

Urine-N deposition is partially subject to N losses via NH₃ and N₂O volatilization. N₂O emissions from urine patches were not investigated prior to our studies for Eurasian steppe ecosystems. Holst et al. (2007a) found no significant stimulating effects of urine application on soil N₂O emission. Estimated annual urine-N volatilization losses from the heavy grazing area were 0.09 ± 0.02 g N/m² and 0.001 g N/m² for site WG (for determinations of urine-N excretion see sheep related N balance calculations).

**Capillary rise, leaching, surface runoff, and organic matter transport by wind and water.**—These parameters were not experimentally quantified during the measurement campaigns. The estimated figures for these fluxes as balanced in Table 7 are elaborated in Discussion.

**Sheep-related N fluxes.**—The total annual feed intake at site HG was 1.26 g N/m² composed of 0.99 and 0.27 g N/m² during summer and winter grazing, respectively (for the corresponding values of site WG, see Table 5). The total amount of N excreted via feces during summer and winter grazing at site HG was 0.49 g N/m². N amounts incorporated into live mass and wool were 0.08 g N/m² and 0.05 g N/m², respectively. The difference between feed N intake and cumulative N pathways via feces, live mass, and wool was 0.64 g N/m², which is considered to reflect N excretion by urine. N excretion by urine during the summer was higher (0.55 g N/m²)
compared to the winter grazing period (0.09 g N/m²). In order to consider deposition of excrement to sheep folds during the night (about half of the total excrement), 0.24 g N/m² of feces N and 0.32 g N/m² of the urine N were excreted to the sheep folds and the other half on the grassland area.

The total annual N losses from the grazing area via sheep excrement, live mass gain, wool production, and N volatilization were 0.78 g N/m² at site HG, the amount of N returned to the grassland site by excrement was 0.48 g N/m² (Tables 5 and 7). Both, losses and regain of N equal the N feed intake of 1.26 g N/m².

Hay-making.—Hay is produced on both ungrazed and moderately grazed areas. In Table 7, we combined N losses by grazing and hay-making on site WG. Based on local hay-making practice with a cutting height of about 6–10 cm (personal observation) and knowledge of the biomass distribution over height (Gao et al. 2009) we estimated a biomass potential for hay-making of roughly 60% of the annual ANPP. With a range of ANPP between 96 and 126 g/m² (mean 107 g/m²) during the experimental years and a mean N concentration in green biomass of 1.8% ± 0.36% (mean ± SD) at site WG (Table 6), mean annual N losses by hay-making were 1.13 ± 0.15 g N m⁻² yr⁻¹ (mean ± SE).

N cycling

Aboveground biomass and related N pools.—N transfer to aboveground biomass is the central interface between soil and aboveground related N fluxes and pools (Fig. 2). Long-term heavy grazing reduced ANPP compared to winter grazing and the grazing exclosure (Table 6). Additionally to grazing, ANPP was markedly affected by seasonal rainfall with 22–39% higher ANPP in 2004, a year of average rainfall amount and distribution, as compared to ANPP realized in the very dry year 2005 and in 2006 (the year with no pronounced summer peak and late rainfall). With the average green biomass N concentrations (Table 6), the mean amount of N allocated aboveground was 1.8 g N m⁻² yr⁻¹ (range 1.6–2.6 g N m⁻² yr⁻¹) at site HG, 1.9 g N m⁻² yr⁻¹ (range 1.7–2.3) at site WG and 2.5 g N m⁻² yr⁻¹ (range 2.1–3.5) at site UG with the upper values representing the year of normal rainfall amount and distribution (2004).

N translocation from senescing leaves to perennial plant organs was substantially lower at sites HG and WG compared to site UG (Fig. 2). Estimates of annual mean N translocation were 0.4 g N/m² (range 0.3–0.8 g N/m²) at site HG and 0.4 g N/m² (range 0.3–0.5) at site WG, while N translocation at site UG was 1.3 g N/m² (range 1.1–1.8) and, therefore, about three times higher compared to the other sites.

Belowground root biomass and related N pools.—BNPP was higher than ANPP at all three sites in our study area and varied from 58% to 66% of the season total net primary productivity. BNPP was lowest at site HG, followed by site WG and site UG (Table 6). Based on root-N concentrations (Table 6), the mean annually produced belowground plant N pool (BNPP-N) was comparable at both grazed sites with 1.2 g N/m² (range 1.1–1.4) at site HG and 1.3 g N/m² (range 1.1–1.4) at site WG, but higher at site UG with 1.9 g N/m² (range 1.8–2.0; Fig. 2). Total mean annual plant N uptake (ANPP-N + BNPP-N, termed root N uptake, see Fig. 2) was in the same range at the grazed sites, HG with 3.0 g N/m² (range 2.7–4.0) and WG with 3.2 g N/m² (range 2.8–3.7), but higher at site UG with 4.4 g N/m² (range 3.9–5.5). The perennial belowground living root biomass N pool was 4.4 g N/m² (range 4.1–4.6) at site HG, 4.5 g N/m² (range 4.1–4.8) at site WG and 7.0 g N/m² (range 6.7–7.4) at site UG. The dead root N pool was 10.4 g N/m² (range 9.7–10.7) at site HG, 10.5 g N/m² (range 9.7–11.3) at site WG, and 16.4 g N/m² (range 15.5–17.3) at site UG.

Decomposition.—Due to 50% N resorption from senescing leaves half of the yearly produced aboveground biomass-N at site UG was transferred to the litter biomass pool. Grazing and hay-making substantially reduced the aboveground biomass N and, thus, litter N production at sites HG and WG compared to site UG (Fig. 2). With a corresponding litter N concentration of 0.8% at sites HG and UG and 0.5% at site WG (Table 6), mean N stored in standing dead and litter measured at peak biomass time (litter minimum) was less than 0.1 g N/m² at site HG, 0.4 g N/m² at site WG, and 0.9 g N/m² at site UG for the years 2005 and 2006 (variability between the years for all sites was less than 0.1 g N/m²). The corresponding amount of N stored at litter maximum time was <0.3 g N/m² at site HG, 0.7 (0.6 in 2005 and 0.9 in 2006) g N/m² at site WG and 2.7 g N/m² (2.5 in 2005 and 2.9 in 2006) at site UG. Sampling litter at the annual maximum and minimum (Table 6) allows for roughly quantifying annual decomposition and respective N release, in which, under grazing, the feed N intake based on litter and standing dead must be considered. The mean annual N amount transferred to the soil organic matter pool via aboveground decomposition was therefore extremely low at site HG and WG, with less than 0.1 g N/m² at site HG and 0.2 g N/m² (range 0.1–0.4) at site WG, whereas at site UG, 1.8 g N/m² (1.7–1.9) were decomposed (Fig. 2).

Belowground litter dynamics were analyzed from data of root turnover rates and root litter-bag decomposition studies. According to Gao et al. (2008), annual root turnover rates were lower in the dry year 2005 (0.23) than in the wetter year 2006 (0.33) whereas differences between grazing sites were not significant (Table 6). Results from the litter-bag study (Giese et al. 2009) supported these findings with decomposition rate, k, of 0.17–0.23 g g⁻¹ yr⁻¹ in the dry year 2005 and no difference between sites. Higher decomposition rates (k = 0.38–0.41 g g⁻¹ yr⁻¹) were found in the wetter year 2004. Based on the measured dead root fraction of BGB and 30% annual N release, we calculated mean annual N
fluxes to the SOM pool via root decomposition of 3.1 g N/m² (range 2.9–3.2 g N/m²) at site HG and 3.2 g N/m² (range 2.9–3.4) at site WG. The larger dead root fraction measured at site UG resulted in higher mean annual belowground N release via decomposition with 4.9 g N/m² (range 4.6–5.2).

Soil organic matter N and microbial N turnover.—Total soil N content to 1 m depth of the three sites ranged from 800 to 1200 g N/m². Land use effects were evident as topsoil N contents (0–4 cm) at sites UG (119 g N/m²) and WG (118 g N/m²) were higher than at site HG (89 g N/m²; Table 2; Steffens et al. 2008).

At the experimental sites mean values of gross microbial N turnover rates of topsoil (0–5 cm) during a vegetation period of four months varied for gross ammonification between 0.6–4.1 and for gross nitrification between 0.5–3.1 mg N/kg soil DM⁻¹·d⁻¹. NH₄⁺ and NO₃⁻ immobilization rates were in the range of 0.6–4.9 and 0.5–1.2 mg N/kg soil DM⁻¹·d⁻¹, respectively (Holst et al. 2007a). Both gross ammonification and gross nitrification rates were significantly higher in the ungrazed plot. Mean daily rates (±SE) were used to estimate gross microbial N turnover rates for a four-month growing season (122 days) in relation to NH₄⁺ and NO₃⁻ immobilization rates for the same time period. Estimated seasonal gross microbial N turnover (39.5 ± 8.8 g N/m²) and immobilization (33.5 ± 3.3 g N/m²) were highest at site UG and significantly lower at the grazed sites with gross microbial N turnover of 10.7 ± 3.7 (WG) and 11.9 ± 7.9 (HG) g N/m² and immobilization of 9.4 ± 1.7 (WG) and 15.1 ± 3.2 (HG) g N/m² (Fig. 2).

**DISCUSSION**

**N gains and losses**

*Dust deposition and wind erosion.*—Compared to other N fluxes measured in this grassland ecosystem, N losses by wind erosion (up to 0.8 g N/m²·yr⁻¹ for site HG) and N gains by dust deposition (up to 2.0 g N/m²·yr⁻¹ for site UG) were substantial, affected by stocking rates and highly variable between years (Hoffmann et al. 2008a, b). Other studies from degraded areas in north-eastern China measured dust emissions with even higher annual net N losses in the range of 0.5–9.0 g N/m²·yr⁻¹ (Wang et al. 2006b). Our results indicate that grazing effects on matter gain and loss by dust storms are highly relevant for the N balance in grasslands of Inner Mongolia. The effect of grazers on wind deposition and erosion of sediments is related to the reduction of canopy height and the vegetation ground cover following grazing. Both parameters affect roughness characteristics of the vegetation surface. In a sandy steppe system of Inner Mongolia, wind erosion rates decreased linearly with increasing vegetation cover, canopy height, and plant density (Li et al. 2005). Hoffman et al. (2008b) estimated that the critical vegetation height, which establishes an equilibrium between dust deposition and wind erosion, was 4–9 cm. Averaged over three years, vegetation height was 9 cm at site HG compared to 24 and 26 cm at sites WG and UG, respectively (Gao et al. 2009). However, dust storms occur to a certain extent at times when the vegetation growth period has not yet begun and, in that instance, litter and standing dead biomass may be more relevant in terms of defining areas as sink or (local) source of wind-driven N transport.

Relevance of wind erosion for the local nutrient balance is determined by the distance of dust source areas, which are degraded drylands and far distant deserts (e.g., Gobi Desert; Xuan et al. 2000). The substantially lower N inputs by dust deposition of 0.15–0.25 g N/m²·yr⁻¹ in North American steppe ecosystems (Lauenroth and Milchunas 1992) suggest a far greater source area for dust transport in grasslands of Inner Mongolia. The high C and N contents (average 35.1–39.1 mg/g C and 0.32–0.36 mg/g N, respectively) of the trapped dust at our study sites (Hofmann et al. 2008a) however, may indicate that the main source areas were degraded soils in the west and northwest of the grassland system and less likely long-distance desert material. This would underline the relevance of anthropogenic pressure on land and climatic factors as a main driver of wind erosion (see e.g., Wang et al. 2006b, Shi et al. 2007, Zhao et al. 2009). Further research is required to address the question how dust sink-source relation change along the central Asian precipitation gradient from the dryer areas of the desert steppe in the North and West to the wetter grassland types located in the south and east, and how land use modifies the N balance across locations of potentially predominant matter losses by wind erosion and aeolian matter gain by dust deposition, respectively.

*Wet deposition.*—The relatively high rates of NH₄-N input may at least partly originate from local livestock farming and NH₃ volatilization from strong point sources such as sheepfolds, while the oxidized wet N deposition compound is likely to be the result of long-range transport from industrialized regions in the south, with, e.g., Beijing being only 500 km away. Our results are somewhat higher compared to N inputs by wet deposition (0.1–0.5 g N/m²·yr⁻¹) observed in the North American grassland ecosystems with comparable rainfall amount (NADP 2009). Compared to other N inputs, wet deposition is a significant component of the N balance in this grassland system and projections suggest that wet N deposition will increase during the next decades (Galloway et al. 2004). Long-term implications are difficult to predict but short-term experiments with N addition rates realistic for future increases in wet N deposition (2–5 g N/m²·yr⁻¹) indicated substantial effects on plant species composition (Li et al. 2011), net primary productivity (Bai et al. 2008, Li et al. 2011), and plant biomass allocation between shoot and root (Gao et al. 2011, Li et al. 2011), although a strong interaction with water availability must be considered.

*Biological N₂ fixation.*—Annual rates of N₂ fixation resulting from activities of cyanobacteria, lichen, and
FIG. 2. Flow chart of the N cycle and balance for Inner Mongolia typical steppe as influenced by different grazing intensities: (a) long-term heavy grazing (HG), (b) winter grazing and hay-making (WG), and (c) and long-term grazing exclosure (UG). Annual mean N fluxes and pool sizes were calculated in g N/m². The range of values for single components of the N cycle and balance indicate minimum and maximum pool sizes and intensities of annual processes observed during 2004–2006, years with average and very low rainfall amounts. Biomass-related N pools and fluxes were calculated based on dry matter and N concentrations shown in Table 6. The accuracy of fit among pool sizes and fluxes compiled in these flow charts vary according to results and calculations based on the respective field measurements. Abbreviations are: ANPP, aboveground net primary productivity; BNPP, belowground net primary productivity (ingrowth-core method); SOM, soil organic matter; dep., deposition; fix., fixation; denit., denitrification; em., emission; vol., volatilization; org., organic. For “Standing dead, litter” litter minimum (min.) was measured at peak biomass time (August), litter maximum (max.) is based on early-spring measurements. Immobilization and gross microbial N turnover are given as mean value (±SE) based on topsoil measurements (0–5 cm).
leagues were estimated not to exceed 0.05 ± 0.03 g N/m²·yr⁻¹ (mean ± SE) for all experimental sites. These values are at the lower end of previous estimates for comparable grassland systems (0.1–1.3 g N/m²; Evans and Belnap 1999, Belnap 2002, Neff et al. 2005) due to lower fixation rates and a comparatively low crust cover. Effects of trampling (site HG and WG) and reduced light penetration (site UG) may be causal factors explaining site differences in Nostoc abundance. Additionally to such grazing-related disturbances (Barger et al. 2006), human impact on Nostoc spread must not be underestimated as Nostoc serves as a traditional dish. Due to the very low abundance of legumes in the plant community (Table 3; Gao et al. 2009) and low N₂ fixation rates by soil crusts within these grasslands (Holst et al. 2009), the relevance of biological N₂ fixation for the total N balance is of minor importance.

**Gaseous N losses.**—Total annual gaseous N losses (N₂O, NO, and N₂) of the grassland sites were below 0.07 g N/m² with negligible differences between grazing treatments except increased N₂O emissions of ungrazed sites during freezing and thawing pulses. From the same study area Xu et al. (2008) reported a cumulative growing season N₂O production between 0.03 and 0.07 g N/m², not affected by different grazing intensities. Annual gaseous N losses by N₂O, NO, and N₂ from other grassland ecosystems with values up to 0.06 g N/m² (Davidson and Kingerlee 1997, Mosier et al. 2008) were of similar magnitude. These rather low values compared to other components of the N balance underline the supposedly minor relevance of gaseous N losses in terms of the overall N budget.

Measurements of N₂O emission from point sources by Holst et al. (2007b) indicate that urine and feces depositions on grassland sites are of minor relevance in this dry climate while sheepfolds are potential emission hotspots (Chen et al. 2011b) responsible for approximately 50% of total regional N₂O emissions at livestock stocking rates of 2 sheep/ha (Holst et al. 2007b). However, human intervention by livestock keeping has the potential to reduce natural N₂O background emissions significantly from grazing areas (Wolf et al. 2010).

The extent of N loss via NH₃ volatilization is high from sheepfolds but assumed to be negligible from grazed pasture (Holst et al. 2007b). This is supported by studies in comparable grassland systems that found rather low emission rates of NH₃ (Schimel et al. 1986, Schlesinger and Hartley 1992, Burke et al. 2008).

**Leaching, surface runoff, and biological N₂ fixation.**—Permanent logging of soil moisture dynamics to 60 cm depth over more than two years indicated that percolation of water below the rooting zone did not occur at any of the sites (Zhao et al. 2010) and, therefore, N leaching was set to zero in our N balance calculation, similar to balance approaches in other steppe ecosystems (e.g., Woodmansee 1978).

We are unsure about the significance of surface runoff. We assume that surface runoff and related N matter fluxes occur during rainfalls of high intensities particularly on heavily grazed areas where soil is compacted by trampling (Table 2) and soil vegetation cover is very low (Table 3). In order to take into account such putative grazing effects, and assuming that 10% of the annual precipitation occurs in heavy rainfall events inducing overland flow, 10% of the annual N wet deposition was lost by surface runoff (0.06 ± 0.02 g N/m²; Table 7). Sites WG and UG were characterized by lower bulk densities and more dense vegetation and litter cover. We are uncertain about the amounts of litter and organic matter transported from grassland sites during such extreme rainfall events at site HG, but suspect that these fluxes may be significant. Based on knowledge about the amount of accumulated sheep droppings and the observed litter dynamics on site HG we estimated the amount of N lost by surface runoff (and wind erosion of litter) at 0.3 ± 0.1 g N/m². However, the N transport in most cases is only of local significance, enhancing the fertility of downhill sites (Burke et al. 1999).

**Sheep-related N fluxes.**—N losses by feces, urine, and sheep body mass are one of the key components that can be managed in terms of sustainable land use. Mainly due to the common management practice of overnight fencing, grasslands of Inner Mongolia experience substantial N losses of 62% of the annual feed N intake, whereas only 38% were redistributed to the grazing area via feces and urine (Fig. 3a). Fencing is part of the traditional management to protect the herd and to collect feces, which are used in households for cooking and heating purposes, resulting in an allocation of around 40% of the annual feed N intake to the sheep fold; 7% of the annual feed N intake is lost by N volatilization from urine patches at the grazing site (and at least another 7% from the folds) and only 10% is attributed to live mass and wool export. N losses from the grazing site could be reduced by about 60% if sheep excrement were redistributed to the grassland area (Fig. 3b).

Live mass gain of sheep in this semiarid grassland system depends on fodder availability and organic matter digestibility, which, in turn, are affected by the annual rainfall amount and distribution, species composition, and soil fertility. The annual N balance of grassland sites, therefore, is interactively affected by the number of animals herded and the climatic conditions such that the grazing pressure (proportion of ANPP consumed) will increase in dry years.

The availability of data about animal-related N budgets of extensively used grassland systems is surprisingly poor. In extensive prairie ecosystems...
(stocking rates between 0.06–0.17 cows/ha), N losses via animal export between 0.06 and 0.11 g N/m² were reported (Dean et al. 1975, Parton and Risser 1980, Lauenroth and Milchunas 1992). These values of typical cattle-based ranching systems are comparable to estimates of this sheep-based grazing system with regard to live mass and wool export, however taking the N losses via excrement export and ammonia volatilization into account, Inner Mongolia grasslands lose up to 10 times more N losses by hay-making.

**Losses by hay-making**

Hay-making is a common and essential land use practice in Inner Mongolia, ensuring the survival of the herd during winter. Compared to other N pathways, hay-making obviously is of high significance for the overall N budget. Hay production is of substantial economic relevance for the farmers, both in terms of herd management and as product to sell or buy. Although the hay demand cannot be met by local production, a substantial amount of hay is transported over long distances and sold to dairy farms requiring high quality feed for milk production. In turn, (low quality) maize straw from grassland-agriculture transition zones receiving more rainfall is frequently imported to typical steppe systems to feed the less demanding livestock during winter time. Information available related to C and N dynamics of hay-making areas or mixed grazing/hay-making systems are still rare compared to pure grazing or exclosure sites, but are essential to assess and improve land use systems having these practices as a substantial component. Hay-making areas offer a certain potential for intensification or increased efficiency, e.g., toward a sustainable N balance, which, however, must be carefully evaluated since the often-remote hay-making sites are presumably core areas of steppe plant and animal diversity.

**N cycling**

**Aboveground biomass and related N pools.—**Grazing-induced reduction of ANPP in this grassland ecosystem is in line with results of a meta-analysis of 28 case studies from North and South America and Africa by Ferraro and Oesterheld (2002). Factors that may explain the reduced annually produced aboveground N pool under heavy grazing are manifold. Site differences in species composition (Gao et al. 2009) may have induced inherently lower productivity of plants at the heavily grazed site. Grazing effects on topsoil bulk density (Steffens et al. 2008) and related changes in water availability (Krummelbein et al. 2009), in combination with a higher relative portion of roots allocated to the topsoil (Gao et al. 2009), lowered ground cover with increases in unproductive water loss by bare soil evaporation (Zhao et al. 2010) and less snow allocation during the winter (Wolf et al. 2010) all may have pushed plants on the heavily grazed site in direction of more frequent drought stress during the vegetation period. In addition to these effects, the long-term depletion of N may have resulted in lower N availability of the heavily grazed site (Giese et al. 2011). Relevance of grazing-induced effects on species composition, water and N availability, and ANPP in this grassland ecosystem were analyzed with factorial experiments with short-term...
manipulation of resource availability (see, e.g., Bai et al. 2010, Brueck et al. 2010, Gao et al. 2011, Gong et al. 2011) or grassland management experiments (Schönbach et al. 2011), which were conducted additionally to the survey of long-term grazing effects at sites UG, WG, and HG summarized in this study. From these studies it can be concluded that productivity is primarily limited by water availability and additionally by N if water is not limiting throughout the growing season. However, N limitation is not restricted to heavily grazed sites but inherent to all different types of land use (including exclosure sites).

**Belowground root biomass and related N pools.**—N and water fluxes from below- to aboveground are realized via the root system, which is considered as the by far dominating source of SOM. A balanced growth of shoot and root organs with a delicate, yet not fully understood, regulatory pattern of C and N partitioning and cycling between both plant compartments is a central feature of plant adaptation to abiotic conditions in general (Farrar and Jones 2000) and certainly in response to grazing as well. In contrast to annual cropping systems in which the seasonal root production can be quantified comparatively straightforward, grassland ecology is confronted with a considerable portion of perennial root biomass. Estimation of annual root production can be based on turn-over rates (Gill et al. 2002a) in order to assess the C balance of grassland systems across climatic gradients (e.g., Gill et al. 2002b); however these estimates of root turnover may change between years (Gill and Jackson 2000) and in response to different land use. Experimental estimates of annual belowground productivity (BNPP) have been compiled for a wide range of grasslands and related to climatic factors (Hui and Jackson 2006), but BNPP for typical Eurasian steppe ecosystems has been rarely reported.

C allocation to belowground organs is known to be highly influenced by resource availability, namely water and N. This effect was nicely reflected in factorial experiments on these sites. A study conducted in a resource manipulation experiment indicated that BNPP as a portion of total net primary productivity varied substantially between a dry year (Gao et al. 2011) with 43–60% and a wet year (Chen et al. 2011a, Li et al. 2011) with 15–40%.

The BNPP-related N pool is only one facet of the grassland's C and N pool. Since root turnover is rather low in this semiarid continental climate, belowground biomass (BGB), including perennial root organs, was substantially larger than BNPP. Our BGB calculations indicate that the standing root biomass N pool is substantially larger than that of ANPP and BNPP. However, negative grazing effects on BNPP are ultimately reflected in BGB. This is indicated by substantially lower BGB at site HG compared to sites WG and UG during 2004–2006 (Table 6; Gao et al. 2008). This finding is in line with results of Turner et al. (1993) who showed that repeated removal of aboveground biomass exhausted the root N pool and finally root system size. The compensatory reaction of grasses, which reallocate C and N from the root system to the shoot in response to recurrent removal of photosynthesizing tissue results in a depletion of the root N pool (Volenec et al. 1996), ultimately weakening the resilience of species to abiotic stressors and directly affecting the SOM pool. Such mid- to long-term effects on C allocation imply negative effects of overgrazing on C sequestration in grasslands. Superimposed are climate change effects, which add substantial complexity to response pattern and, in our opinion, constrain simple generalization of grazing responses in terms of C and N allocation. Altogether our data indicate that interactive effects of grazing history and climate have pronounced effects on the relative allocation of dry mass between root and shoot and consequently the long-term size of the SOM and soil N pool in this steppe system. However, grazing effects are apparently system specific as indicated by contrasting results in U.S. grassland systems (Schuman et al. 1999) and a comprehensive review given by Milchunas and Lauenroth (1993).

**N translocation from senescing leaves to perennial plant organs.**—N resorption from senescing leaves is acknowledged as an important process of N conservation in many ecosystems (Aerts 1996, Eckstein et al. 1999). The plant internal N translocation from senescing leaves to perennial plant organs is a major aspect of N dynamics in steppe ecosystems. N incorporated in shoot biomass during the growth period is either transferred to the standing dead biomass pool and subjected to decomposition or translocated from the shoot system to perennial plant organs. Our estimate of 50% N translocation to perennial plant organs is consistent with average values reported from different species and plant functional groups worldwide (Aerts 1996) and results obtained from in total 28 Inner Mongolian grassland plant species from different functional groups with an average N resorption efficiency from leaves of 48% (Yuan et al. 2005). Hemicyryptophytes and geophytes are the dominating perennial plant functional groups of this steppe ecosystem, storing N in roots, rhizomes, bulbs, and the renewing buds. This N translocation to belowground organs is of high significance for early-season green up, which at least partially relies on the root N reservoir, as low soil temperature constrains soil N mineralization during early spring.

Indeed, we recorded increased abundance and ground cover of annuals in 2006 compared to 2004 on all three sites (Table 3), which was likely a result of the extended drought in 2005. At the same time abundance and cover of perennial species decreased but to a lesser extent at site UG, where, due to higher N translocation, perennials might have been better stocked with nutrient resources and, thus, were more resilient to stress. Consequentially, land use practices allowing plants to translocate more N to perennial organs improve the ecosystem’s stress resistance and may, therefore, support
a more sustainable and less variable productivity. Effects of grazing on plant internal cycling and competitiveness interact with seasonal water availability. In years of favorable rainfall, grazing induced reduction of N translocation will potentially have less impact on related ecosystem functions. However, the expected temperature increase and more frequent drought spells in combination with the current land use practices might increasingly threat typical steppe ecosystems characterized by perennial plants and even exceed thresholds of irreversible disturbances pushing the system into unknown alternative (stable) states (e.g., increasing bush encroachment, C₄ species, and annuals).

**Litter biomass pools and decomposition.**—Above- and belowground litter represents a continuum from recently dead above- and belowground plant tissue to organic particles not smaller than 2 mm, because the latter belong, by definition, to the SOM fraction (Cambardella and Elliott 1993, Six et al. 1998).

Decomposition is considered to be a key process of C and N cycling in ecosystems (Facelli and Picket 1991, Aerts et al. 2003) and, in temperate semiarid climates, predominantly driven by temperature, water availability, and to a certain extent by UV-B radiation, while the chemical composition of the plant material is obviously of minor relevance for steppe ecosystems (Parton et al. 2007, Giese et al. 2009). Additionally, intensive bio-turbation is a typical phenomenon of steppe soils and one major reason for the deep humus-rich molic horizon of these soils (FAO/ISRIC/ISSS 1998, Driessen et al. 2001). Studies quantifying the effects of rodent (and ants) activity on litter dynamics are rare and with regard to presumably substantial impact on C and N dynamics, more attention should be paid to this process in Eurasian steppe ecosystems.

Grassland sites subjected to land use practices were characterized by substantially reduced N recycling via aboveground biomass decomposition. While at site HG, the N taken up by sheep was at least partially redistributed to the grazing area by feces and urine (Fig. 2a), the amount of N removed by hay production is lost for site WG. Thus, at intensively used grassland sites, N pathways via belowground decomposition and soil biochemical processes affecting decay rates (mainly soil water content and temperature) gain relatively more importance. Comparing the three sites, decomposition of shoot litter and dead roots appears to be sufficiently high to meet the plant N demand at all sites.

**N in the SOM pool and microbial turnover.**—The N pool in SOM of temperate semiarid grasslands is usually large compared to the biomass-N pools and annual N fluxes (Burke et al. 2008). We found a decreased topsoil N content at site HG compared to site WG and UG. Our findings are in line with other reports of grazing-related decreases of soil N pool size in Eurasian steppe systems (e.g., Wang et al. 2006a, Zhou et al. 2007), whereas studies from the United States (e.g., Frank et al. 1995, Schuman et al. 1999) and the world-wide survey by Milchunas and Lauenroth (1993) illustrated no clear trend of grazing effects on soil N pool size. Explanations for this discrepancy in response to grazing between the Eurasian steppe and other semiarid grasslands remain speculative, but differences between grassland systems via N losses through leaching and gaseous emission are obviously of minor relevance. It is tempting to speculate that grazer effects (sheep vs. cattle, bison) in terms of intensity of biomass removal may contribute to differences. This hypothesis can only be tested by comparing long-term effects of different grazers on soil N pools. Additionally, N losses by wind erosion contributed to negative N budgets in this typical steppe system, implying either that, in the North American grassland systems, wind erosion is less frequent, erodibility of soils is in general lower, or that vegetation height and canopy cover are less severely affected. One possible explanation is the grazing practice of overnight fencing, which is not common for prairie ranching systems and induces considerable annual losses of N (0.56 g N·m⁻²·yr⁻¹) via excrement export to sheep folds.

Mean root N uptake required for sustaining annual NPP at the three sites varied between 3.0 and 4.4 g N/m² (Fig. 2). This N amount is delivered via net N mineralization of SOM, which is interactively affected by abiotic (microclimate) factors and biotic (microbial) activity. Complexity in analyses of N availability arises from spatial and temporal variability in release of N from the SOM pool (gross mineralization) and subsequent immobilization reactions by microbial activity. Additionally, competitive advantages and strategies for N uptake of plants and microbes are generally accepted as key factors of ecosystems’ N cycling (Schimel and Bennett 2004). Temporal dynamics in species composition of grasslands (long-term responses to climate variability and grazing), microbial amount and composition (short-term responses to freeze-thaw cycles, soil water tension, grazers) and patchiness of nutrient availability by urine and feces droppings are acknowledged modulators of N availability (Day and Detling 1990, Bardgett and Wardle 2003, Schimel and Bennett 2004, Booth et al. 2005).

Notably, for site UG the calculated plant available N matches the plant N demand estimated from NPP measurements (root N uptake), whereas figures for site HG and WG indicate an insufficient release of plant available N from the topsoil SOM pool. We speculate that this was due to the extremely low soil water availability in topsoil layers (in particular at site HG) during the year 2005 and plants may have recruited the additional N from deeper soil horizons.

Grazing intensity negatively affected gross microbial N turnover rates, indicating higher potential plant N availability at ungrazed sites. In line with this finding, Giese et al. (2011) found higher in-situ N availability (measured by installing resin capsules) on ungrazed than grazed sites in a year of average rainfall but not during the very dry year 2005. Grazing effects on gross N
mineralization do not necessarily translate to higher net N mineralization rates. Wang et al. (2006a) and Wu et al. (2011) found higher net N mineralization rates of grazed compared to ungrazed sites in this grassland, thereby confirming previous findings that showed increases in net N mineralization under grazing disturbance. Experimental evidence of herbivore effects on soil N availability are not consistent and illustrate decreases, no effects or increases (see e.g., Bardgett and Wardle 2003) of N availability. This is partially due to the complexity of grazer–plant interactions, which operate over larger time scales and are convoluted by short-term microclimate variability. Short-term (within one year) grazing effects such as removal of biomass, changes in C allocation between shoot and root (Table 6), increases in bulk density (Table 2) and increases in fine root dynamics and root exudation all modify C substrate availability and, thereby, likely net N mineralization rate (Janssen 1996). This effect has been indirectly illustrated by an intact plant-soil microcosm study on this grassland in which grazing increased the dissolved organic C content (Wu et al. 2011).

Complexity in analysis arises from the chemico-physical heterogeneity of SOM. A straightforward approach to analyze N dynamics aims at quantifying specific SOM pools. These pools are conceptually defined due to their turnover times, which vary from years (active SOM) and decades (slow, intermediate SOM, often termed particular organic matter, POM) to centuries (passive, recalcitrant SOM, sometimes termed chemically stabilized organic matter, COM [Jenkinson and Rayner 1977, Parton et al. 1987, Gill et al. 1999]). The size of active SOM fractions in temperate grassland ecosystems differ substantially, but are generally >10% of total soil C while 35% to <60% are present in the passive pool (Parton et al. 1993).

Analysis of dynamics of these SOM fractions in response to grazing and grassland management is of great importance for an improved understanding of the long-term stability of SOM and, thus, the C sink and source performance of grassland ecosystems. The identification of a labile SOM fraction that is indicative of over-grazing and declining total SOM would be ideal (Accoe et al. 2004). Steffens et al. (2009) reported that SOM was surprisingly young at site UG (e.g., approximately 60 years for OM associated with clay-sized particles) indicating shorter turnover times compared to the same fractions at grazed sites (375 ± 20 yr [mean and CI]). These shorter turnover times were explained by the higher net primary above- and belowground productivity and the subsequently increased supply of organic matter (Table 6) triggering an increased turnover of the whole soil system. This was also reflected by higher SOM contents of the coarse and medium aggregate size classes at site UG compared to grazed sites. Litter input at site UG was predominantly sequestered in the readily decomposable light fraction, whereas the long-term pool of organo-mineral associations appeared to be close to saturation. Thus, higher SOM contents resulting from decreased grazing intensities or grazing cessation, respectively, did not translate into stabilized SOM fractions and are therefore potentially sensitive to climate and land use changes, which should be taken into account when assessing the C and N sequestration potentials of typical steppe soils.

The N balance as outlined for the three studied grassland sites in Inner Mongolia indicates that moderate grazing is not reducing total N stocks in the long-term. In fact, large N stocks of steppe soils developed under a long evolutionary history of moderate grazing during the last centuries. However, the potential ecosystem fertility does not necessarily guarantee permanent plant N availability and it must be conceded that processes of N mineralization and availability in semiarid grassland in interaction with rainfall variation and wet-dry cycles are poorly understood (Yahdjijan et al. 2006, Burke et al. 2008). In grasslands of Inner Mongolia, variable rainfall was more relevant than grazing to affect N availability (Giese et al. 2011) and system productivity (Gao et al. 2008). Rainfall amount and distribution during the vegetation growth period are the predominant drivers of N availability via soil moisture effects on N turnover processes (Schimel and Parton 1986, Burke et al. 1997, Hook and Burke 2000, McCully et al. 2009). The impact of rainfall variability on N dynamics is likely related to a general threshold and pulse behavior of semiarid ecosystems (Sala et al. 1992, Austin et al. 2004, Schwinning and Sala 2004) and the seasonal N mineralization pattern can follow single precipitation events (Hook and Burke 2000). Not at least for these reasons, prediction of both net primary production (with allocation above- and belowground) and dynamics of SOM (with identification of rapidly responding SOM fractions), and C sink-source relationship in response to grazing and climate variability are extremely difficult (Barrett et al. 2002). However, by providing a comprehensive overview on N-balance and cycling in this typical steppe ecosystem as affected by grazing and contrasting rainfall pattern, this study may have contributed to the understanding of some processes sensitive to climate variability with regard to N (and C) sink–source dynamics.

**Synthesis**

For large areas of Inner Mongolian grasslands, as for many regions of the Eurasian steppe belt, substantial land degradation was reported as a consequence of excessive overgrazing during the last decades. N is considered as a key element for ecosystem functions and, therefore a comprehensive analysis of the system’s N pathways as affected by land use change and climate variability is of fundamental importance to maintain, improve or restore ecosystem services such as forage production, C sequestration and diversity conservation.

Our N balances indicate the ungrazed site as N sink mainly due to N input by dust deposition, whereas the
heavily grazed site must be considered as N source. Major N losses occurred via dust emissions and excrement export from grazing sites, the latter as a consequence of the common practice of keeping sheep in paddocks overnight. If sheep excrement were redistributed to grazing areas, the annual N losses related to animal feed intake could be reduced by around 60% on heavily grazed sites. However, since dried dung is still often the only energy source for cooking and heating, this will require some fundamental changes in regional energy supply. N losses due to export of live mass and wool were relatively small and could be sustainable in terms of N balances as soon as stocking rates are reduced to a level at which the remaining aboveground biomass prevents wind erosion. However, the system’s N gains and losses by aeolian transport were subjected to high interannual fluctuations compared to other N pathways and, thus, are not reliable components of the (annual) N balance. Further, the question arises how this grassland system, relying on external N input by dust deposition to a certain extent, would be affected if dust storm activity decreases due to successful reduction of land degradation in the dust emission areas.

Hay-making contributed to substantial N losses (even more than heavy grazing if related to biomass N export), but is an essential part of the farm management. The establishment of hay-making sites ameliorated by e.g., the cultivation of legumes adapted to steppe environments may be part of a solution to improve regional N balances. The application of comparable small amounts of mineral N fertilizer that covers the N losses by hay-making and dung export can further contribute to a sustainable land use with regard to the N balance and forage production.

In the long-run increased atmospheric N wet deposition may play an important role for the N balance of the steppe ecosystems, specifically in China. The projected global biosphere N enrichment for 2050 (Galloway et al. 2004) will likely exceed the system’s current magnitude of the overall N gains and losses and many of the system internal N pools and fluxes. This additional N import by atmospheric wet deposition will therefore most likely affect grassland ecosystems functions and services. Atmospheric dry deposition of reactive N as gas or aerosol (NO\(_x\) and NH\(_3\)) were not considered in our N balance calculation, but estimated to be around 0.5 ± 0.2 g N m\(^{-2}\) yr\(^{-1}\) (mean ± SE) for our study area in the frame of a global assessment (Reay et al. 2008). Therefore, N dry deposition is a potentially significant component of the N-balance, however, uncertainties mainly resulting from insufficient typical steppe grassland field data need to be considered. Since N dry deposition rates are strongly depending on area surface roughness and wind speed, ungrazed sites are supposed to receive larger N loads compared to heavy grazed areas with low aboveground biomass pools, which finally would amplify the contrast in N balances among these sites. Increasing N depositions in general may compensate for N export from heavy grazed sites, accelerate the restoration process of currently overexploited sites, and may even increase animal carrying capacity by increased grassland productivity, and by this farmer’s income. On the other hand, one might expect negative effects of increased N depositions on plant community structure and diversity. Here grazing might be an important management tool to reduce N pools and mitigate effects of increased N deposition and thus might help to maintain grassland ecosystem services with regard to species diversity conversation. However, effects of N addition will always interact with water availability and therefore need to be carefully evaluated.

The largest uncertainties within our N balance and cycle analysis exist for the N losses assumed for heavy grazing sites via overland flow (transport of SOM, litter, and sheep droppings) and wind-blown dispersal of litter. Results of gaseous N losses were strongly influenced by the timing of measurements (e.g., during freeze-thaw period) and methods applied (in situ vs. laboratory). Some processes such as N mineralization were subjected to high fluctuations triggered by typical semiarid climate wet-dry pulses that may mask long-term land use effects. Therefore, methods and sample intervals should carefully consider the temporal dynamics of the particular parameter.

During our studies we have analyzed three growing seasons of average and very low annual precipitation. However, we did not experience the situation of a wet year, which most likely intensifies N-related matter fluxes relative to fluxes affected by grazing and land use practice. Due to the extreme dry growing season in 2005, we collected a data set representing the extreme low of N dynamics in this semiarid grassland ecosystem. In this situation, grazing and land use systems are definitely more critical to the ecosystem processes since resources are more limited. Since our experimental sites were not replicated during this comprehensive case study, strictly spoken, site differences cannot be stated as pure grazing effects. We cannot exclude influences resulting from a natural spatial variability of e.g., soil properties and plant communities in this grassland ecosystem. However, the comparison of sites subjected to long-term extremes of grazing intensities (UG vs. HG) provides information reflecting, to a certain extent, the upper and lower limits of N response to grazing. Considering that processes were not measured over a wider range of climatic conditions, the validity of up-scaling from this N balance to regional scales must be carefully considered. More information from less well researched grassland ecosystems across the Eurasian steppe belt are essential to improve our understanding how N and C dynamics of this zonal biome respond to land use change and climate variability or change.

A joint effort of diverse disciplines and a system-wide approach as embedded in the MAGIM project allowed us to extract information in a synergistic manner and we want to point out that a detailed analysis of animal
functioning and metabolism is, additionally to data generated with focus on grassland performance and soil status, rather important. Slightly provocatively stated, animals (and the farmers by controlling them) are prime actors shaping vegetation cover characteristics and C and N allocation patterns and should not be seen as ‘noise/interference’ in the botanical and catena focused research continuum. Integrating ecological knowledge with understanding of the social and economic constraints is essential for future successful and sustainable management practices of grasslands.

Acknowledgments
This publication is dedicated to the late Burkhard Sattelmacher who initiated the MAGIM project. Data presented in this paper were obtained from the Sino-German Research Group MAGIM “Matter Fluxes in Grassland Ecosystems of Inner Mongolia”. The MAGIM project was funded by the German Science Foundation (Deutsche Forschungsgemeinschaft, DFG, Research Group 536) with additional support from the National Science Foundation of China (NSFC). We are grateful to the German Academic Exchange Service (DAAD) for enabling the continuation of data analysis and the completion of this manuscript in the frame of the “GrassNet” project. We thank Martin Wiesmeier, TUM, Munich, Germany for providing map material. Finally we thank the people working at the Inner Mongolia Ecology Research Station (IMGERS) for support of the MAGIM project.

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SUPPLEMENTAL MATERIAL

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.s903c