Climate and ecosystem $^{15}$N natural abundance along a transect of Inner Mongolian grasslands: Contrasting regional patterns and global patterns

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Nitrogen isotopes provide integrated information about nitrogen cycling in terrestrial ecosystems. This study explores the regional patterns of ecosystem $^{15}$N abundance along a 1200 km transect in Inner Mongolian grasslands and their relationships with climate. Results indicate that climatic variables control approximately 50% of the variation in ecosystem $^{15}$N abundance along the transect. Ecosystem $^{15}$N abundance decreases as both mean annual precipitation (MAP) and mean annual temperature (MAT) increase. Regional patterns obtained from our study differ from reported global patterns. Ecosystem $^{15}$N abundance is negatively correlated with MAT along the eastern part of the transect, while a positive correlation between MAT and ecosystem $^{15}$N is apparent at the global scale. MAP exerts stronger controls on ecosystem $^{15}$N abundance along the western part of the transect than what is shown in a global regression model. Ecosystem $^{15}$N abundance in the western part of the transect is substantially higher (ca. 3%) than the values projected by a global model. The $\Delta^{15}$N_{soil-plant} (%) (difference in $\delta^{15}$N values between plant and soil) values in Inner Mongolian grasslands are not significantly correlated with either MAP or MAT; but $\Delta^{15}$N_{soil-plant} values are positively correlated with MAT and negatively correlated with MAP at the global scale. These conflicting trends strongly indicate that climatic controls on ecosystem $^{15}$N abundance are scale-dependent. Regional N deposition gradients, grazing-induced ammonia volatilization, and variation in plant-soil types are among the possible causes of these inconsistencies.


1. Introduction

Since the start of industrial revolution, human activities worldwide have increasingly altered the global N cycle, primarily through N fertilization and NOx emissions [Vitousek et al., 1997]. Human alteration of the global N cycle has resulted in a marked increase in active N input to virtually all ecosystems [Schlesinger, 1997]. One of the main components of this enhanced N input is atmospheric N deposition. How ecosystems may respond to this altered N input has become an important global issue because N cycling is a key biogeochemical process itself and is also intimately linked to other biogeochemical cycles. While there is an increasing level of understanding of ecosystem responses to short-term N inputs [Galloway, 1998], it remains a challenge to extend results from short-term, small ecosystem studies to the understanding of long-term changes at regional to global scales.

The natural abundance of N isotopes allows studies of N cycling in response to natural or anthropogenic variables in the long term and at large spatial scales [Handley et al., 1999; Martinelli et al., 1999; Robinson, 2001; Amundson et al., 2003]. The $^{15}$N abundance of vegetation and soil is a function of the rate and isotopic composition of inputs and outputs, and the internal N transformations that occur in a plant-soil system [Mariotti et al., 1982; Nadajnhofer and Fry, 1994]. Different $^{15}$N abundances of coexisting plants may provide information in N2 fixation [Shearer and Kohl, 1993], root depth [Schulze et al., 1994], or levels of mycorrhizal colonization [Michelsen et al., 1998; Hobbie et al., 2000] among species. At the ecosystem scale, measurements of natural $^{15}$N abundance have been informative in exploring the influence of anthropogenic N deposition on forest N cycling [Durka et al., 1994], changes in N cycling in response to disturbance [Evans and Ehleringer, 1993], N cycling and losses in relation to climatic variables [Austin and Vitousek, 1998; Handley and Raven, 1992], and rates of grassland N cycling and retention [Frank et al., 2000].
[4] Published work has indicated that ecosystem $\delta^{15}$N values decrease with increasing precipitation [Shearer et al., 1978; Heaton et al., 1986; Sealy et al., 1987; Vogel et al., 1990; Evans and Ehleringer, 1993, 1994; Aranibar et al., 2004; Swap et al., 2004]. In addition to the influence of mean annual precipitation, mean annual temperature also controls $\delta^{15}$N values in plants and soils. For example, the $\delta^{15}$N values of soils and plants in tropical forests are commonly higher than in temperate forests [Martinelli et al., 1999]. A similar temperature effect was also noted in studies using elevation gradients [Craine and Lee, 2003; Mannel et al., 2007]. However, the effects of nonclimatic variables such as plant-soil type and age of soil substrate on ecosystem $^{15}$N abundance are often not separately assessed from climatic variables in these studies. This is likely one of the major causes of relatively low model accountability of total variation presented in these reports, because nonclimatic variables, especially plant species [Handley et al., 1999, Martinelli et al., 1999] and soil substrate age [Brenner et al., 2001], can substantially influence ecosystem $^{15}$N abundance.

[5] Conceptual and simulation models [Handley et al., 1999; Amundson and Baisden, 2000; Brenner et al., 2001] have convincingly shown that the isotopic composition of N leaving the system is the most important determinant of ecosystem $\delta^{15}$N values. Some studies have suggested that ecosystem $\delta^{15}$N values decrease with increasing precipitation possibly because the forms and the isotopic composition of the N leaving the ecosystems change in a systematic way as precipitation increases [Austin and Vitousek, 1998; Handley et al., 1999; Schuur and Matson, 2001]. Virtually all these studies have shown that soil and plant samples are much more enriched in $^{15}$N in arid regions than in moist regions, and that the level of $^{15}$N-enrichment declines with increasing precipitation. One often used explanation for this phenomenon is that N-cycling becomes more open as MAP decreases, resulting in disproportionate loss of inorganic N [Austin and Vitousek, 1998]. This process enriches the remaining organic N with $^{15}$N in the system because inorganic forms of N are often more $^{15}$N-depleted than organic N. However, it is less clear what mechanisms cause the disproportionate loss of inorganic N in arid ecosystems as precipitation decreases. Some studies have shown that N loss through NH$_3$ volatilization, especially grazing-induced NH$_3$ volatilization has the potential to cause significant $^{15}$N enrichment in arid and semiarid ecosystems with high soil pH values [Frank and Evans, 1997; Bouwman et al., 2002; Frank et al., 2004]. However, it remains unclear how grazing-induced NH$_3$ volatilization may influence the relationship between precipitation and ecosystem $^{15}$N enrichment. We propose that grazing by domesticated herds for thousands of years in the Inner Mongolian steppes may have resulted in further ecosystem $^{15}$N enrichment because of the enhanced NH$_3$ volatilization through urine deposition. We test this hypothesis with a case study of varying grazing intensities and by comparing our data with the global model predictions of Amundson et al. [2003].

[6] This study explores $^{15}$N abundance in plants and soils along a transect of approximately 1200 km across Inner Mongolia grasslands from the eastern edge to the western border. This transect covers a MAP gradient from 120 to 450 mm and a MAT gradient from 0.5 to 7.1°C. In order to separate the effects of climatic variables and nonclimatic variables (e.g., plant species and substrate age), we chose to sample two main plant species that occur across the entire transect with the same substrate age. Our main objectives were (1) to seek patterns of $^{15}$N natural abundance in relation to precipitation and temperature, (2) to compare and contrast the regional patterns with global patterns; (3) to explore potential mechanisms that may contribute to these patterns (i.e., NH$_3$ volatilization and N deposition), and (4) to fill the major data gap over Asian grasslands. Our current understanding about global patterns of climate controls on ecosystem $^{15}$N abundance is primarily based on studies in North America, Europe, South America, and Africa. There is an apparent data gap over Mongolian grasslands. Globally, Mongolian grasslands cover a large land area, a size larger than Western Europe, and represent the oldest and the largest existing grassland region in the world [World Resources Institute, 2000]. Filling this data gap and integrating these data into the global data set [e.g., Amundson et al., 2003] may enhance our understanding of the global N cycle.

2. Methods

[7] Plant and soil samples were taken from an east-west transect in Inner Mongolia, China, which was approximately 1200 km long. The longitudinal range of the transect was 112°–124°E, and the latitudinal range was 43.5°–43.9°N (Figure 1). This line transect was laid out within the larger Northeast China Transect of IGBP. There were three main vegetation types along the transect: (1) meadow grassland predominantly in the eastern part of the transect, (2) typical steppe grassland in the central part of the transect, and (3) desert grassland in the western part of the transect. Soils along the transect were predominantly arid, sandy, brown loessial rich in calcium, and belong to Kastanozem soil group in the FAO classification system. The soil pH values in the 0–20 cm layer ranged from 6.2 to 8.5. Detailed information is available in the work of Chen and Wang [2000].

[8] All samplings of plants and soils took place in July of 2004. Sampling locations were GPS referenced with latitude, longitude and elevation (eTrex Venture, Garmin, ±3 m accuracy), with each location being 20–25 km apart along the transect. Plant samples at each location were obtained from three 1 × 1 m squares. Each square was randomly chosen within a larger area that was determined representative of the location by visual observation of the vegetation and soil at each location. Plant species and the number of plants for each species within each square were identified and recorded. All plant materials were air-dried during the sampling trip and oven-dried at 70°C before analysis.

[9] Four soil cores of 2.54 cm diameter were taken within each square to a depth of 40 cm. A total of 12 soil cores were obtained at each sampling location. The top 0–20 cm portion of the 12 soil cores was bulked into one cloth bag, and the 12 cores from 20 to 40 cm depth into another bag. Soil samples were air-dried under shade during sampling trips. Visible roots and other plant materials in each soil sample...
were discarded by handpicking. Fine roots and other coarse materials in soil samples were further removed by sieving through a 2.0 mm screen. After sieving, all soil samples were homogenized and oven-dried at 70°C. After oven-drying, 20 g of soil was ground to pass through 0.177 mm mesh, and stored in a plastic bag for further analysis.

[10] Total organic carbon content of all soil and plant samples was determined using the dichromate oxidation method with external heat [Nelson and Sommers, 1982]. Total nitrogen content of plant and soil samples was analyzed using the micro-Kjeldahl digestion method [Bremner and Mulvaney, 1982]. Soil pH was measured using a pH meter in soil water suspension (soil:water = 1:2). The δ15N of plant and soil samples was determined using a continuous flow isotope mass spectrometer (Finnigan Delta Plus XP, Thermal Electron Corporation, Waltham, Massachusetts, USA). By convention, the natural abundance of 15N is expressed using the delta notation [Hoering, 1955]: δ15N(‰) = (Rsample/Rair − 1) × 1000, where Rsample = 15N/14N of a sample and Rair = 15N/14N of the standard atmospheric N2 equal to 0.3663 atom% 15N [Junk and Svec, 1958]. Because of the limitation of available funding, only the δ15N values of two main plant species occurring along the whole transect, Stipa spp and Leymus spp, were determined.

[11] The mean annual precipitation (MAP) and mean annual temperature (MAT) data were original records of past 40 years (1961–2000) for 10 locations evenly distributed along the transect. The MAP and MAT data for the rest of the locations were interpolated on the basis of regression equations using latitude, longitude, and elevation as independent variables. The equations are: MAP(mm) = −3017 + 40.3 L − 35.2 N + 0.178 E, R2 = 0.875; MAT(°C) = 82.0 − 0.167 L − 1.23 N − 0.00585 E, R2 = 0.903; where L is longitude (East), N is latitude (North), and E is elevation (meter above sea level). The latitude, longitude and elevation values for each location were obtained using a GPS system (eTrex Venture, Garmin, with ±3 m accuracy).

[12] The grazing case study was conducted in 2005 at the permanent grazing site of the Inner Mongolia Grassland Ecosystem Research Station, Chinese Academy of Sciences, near the mid point of the transect (43°50’N, 116°34’E). Grazing treatments have been maintained since 1989. There were five grazing intensities of 0, 1.33, 2.67, 4.00 and 5.33 sheep ha−1, with 3 replications. During the entire year of 2005, NH3 volatilization rates were determined for a total of six times at a 2-month interval using the method of H2SO4 solution trapping as described by Billings et al. [2002]. Soil samples (0–10 cm layer) were used for δ15N determination.

3. Results

3.1. Transect Description

[13] Data of the 53 locations along the transect were obtained (see Table S1).1 The longitudinal range of the transect was 112–124°E, and the latitudinal range was relatively narrow, 43.5–43.9°N. The eastern end of the transect had the lowest elevation (approximately 130 m above sea level). The highest elevation (about 1400 m above sea level) was located at the middle of the transect, and the elevation at the western end of the transect was 950 m above sea level. MAP along the line transect ranged from 129 to 444 mm with a mean of 323 mm, and MAT ranged from 0.57 to 7.1°C with a mean of 3.9°C. West of the highest elevation point, MAP increased steadily as longitude increased, which represented most of the MAP gradient (Figure 1). East of the highest elevation point, MAT increased as longitude increased, which accounted for most of the temperature gradient.

[14] The soil C:N ratios at the 0–20 cm depth ranged from 5.42 to 30.6 with a mean of 17.1, but no significant relationship was found between soil C:N ratio and MAP or MAT. The soil pH values of the 0–20 cm layer ranged from 6.3 to 9.2 with a mean of 7.7, and from 6.7 to 9.7 with a mean of 8.0 for the 20–40 cm depth. Soil pH values had a significant (P = 0.0039 and R2 = 0.153) negative correlation with MAP along the whole transect (Figure 2). This is consistent with the general pattern that higher pH values are mostly found in drier environments.

[15] The δ15N values of total soil nitrogen at the 0–20 cm layer along the transect ranged from −2.5% to 7.4% with a

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1Auxiliary materials are available in the HTML. doi:10.1029/2008GB003315.
mean of 4.7%. For the 20–40 cm layer, the δ^15N values ranged from 1.3% to 7.9% with a mean of 5.4%. The deeper layer tended to have significantly (P < 0.0001, paired t test) higher δ^15N value than the surface layer. The δ^15N values of Stipa shoots ranged from −3.0% to 4.4% with a mean of 0.4%. The δ^15N values of Leymus shoots ranged from −3.9 to 5.3% with a mean of 0.8%. According to the results of a paired t test, Leymus shoots had significantly higher δ^15N values (by approximately 0.4%) than Stipa shoots when sampled at the same location. The δ^15N values of aboveground plant tissues (both Leymus and Stipa) were significantly correlated with the δ^15N values of total soil nitrogen at the 0–20 cm layer along the whole transect (Figure 3), indicating the dependence of plant δ^15N on soil δ^15N. On average, the δ^15N values of plant shoots were approximately 4.5% more negative than the soil δ^15N values at the 0–20 cm depth. This difference in δ^15N values between plants and soils was highly significant (P = 0.00001, paired t test).

Figure 2. Soil pH values at the 0–20 cm depth are negatively correlated to mean annual precipitation, P = 0.0039, R^2 = 0.153, n = 53.

3.2. Climatic Controls of Plant and Soil δ^15N Values Along the Whole Transect

[16] The δ^15N values of Leymus, Stipa, and the surface soil were all significantly and negatively correlated with MAP along the whole transect (Figure 4), indicating that MAP is an important determinant of ecosystem δ^15N values. The correlation between MAP and soil δ^15N values at the 0–20 cm depth accounted for 32% of total variation. The correlation between MAP and δ^15N values of Stipa shoots accounted for 28% of total variation. The correlation between MAP and Leymus δ^15N values accounted for 31% of total variation. The slope value in the equation between MAP and soil δ^15N values was similar to that between MAP and δ^15N values of Stipa shoots, but lower (P = 0.01) than that between MAP and δ^15N values of Leymus shoots. It seemed that the δ^15N values of Leymus shoots were more responsive to changes in MAP.

[17] The δ^15N values of Leymus, Stipa, and the surface soil were also significantly and negatively correlated with MAT along the whole transect (Figure 5). The correlation between MAT and soil δ^15N values at the 0–20 cm depth was highly significant (P < 0.00001) and accounted for 32% of total variation (R^2 = 0.324). The correlation between MAT and δ^15N values of Stipa shoots accounted for 23% of total variation, while for Leymus δ^15N values accounted for 25% of total variation. The slope values in the three equations were similar to each other, indicating that both the soil δ^15N values and the plant δ^15N values had similar temperature sensitivities.

[18] Using unweighted least squares multiple regression, the influences of MAP and MAT on the δ^15N values of Stipa, Leymus, and soil samples along the whole transect were analyzed (Table 1). Again, both MAP and MAT were negatively correlated to the δ^15N values of Stipa, Leymus, and soil samples, respectively. MAP and MAT together were responsible for approximately 50% of the total var-
Fig. 5. Negative correlations between MAT and the $\delta^{15}N$ values (‰) of Leymus (triangles, $\delta^{15}N = -0.55x + 2.73$, $R^2 = 0.25$, $P = 0.002$), Stipa (filled circles, $\delta^{15}N = -0.68x + 2.63$, $R^2 = 0.23$, $P = 0.003$), and the surface soil samples (open circles, $\delta^{15}N = -0.60x + 7.04$, $R^2 = 0.32$, $P < 0.0001$). The slope values of all three regressions are not significantly different from each other. The intercept value for the soil $\delta^{15}N$ values is significantly higher than the other two.

3.3. Different Patterns Between the Eastern and the Western Parts of the Transect

As shown in Figure 1, west of the highest elevation point (at 116.9516°E) along the transect, MAP increased steadily as longitude increases, which represents most of the MAP gradient. East of the highest elevation point, MAT increased as longitude increases, which accounts for most of the temperature gradient. The relationship between MAT and soil $\delta^{15}N$ values for the western part of the transect was different from the eastern part of the transect (Figure 6). Soil $\delta^{15}N$ values for the western part of the transect were positively correlated with MAT. However, soil $\delta^{15}N$ values for the eastern part of the transect were negatively correlated with MAT. The relationship between MAP and soil $\delta^{15}N$ values for the western part of the transect was similar to the eastern part of the transect (Figure 7); both showed negative correlations, even though the range of MAP was wider for the western part than for the eastern part. The relationship between total soil N content and soil $\delta^{15}N$ values for the western part of the transect was also different from the eastern part of the transect (Figure 8). The soil $\delta^{15}N$ values for the eastern part of the transect were positively correlated with soil N content, suggesting that the level of $^{15}N$-enrichment increased as the total soil N stock increased. However, soil $\delta^{15}N$ values for the western part of the transect were negatively correlated with soil N content, indicating that higher $^{15}N$-enrichment was connected to lower levels of total soil N stocks. These results suggest that some N cycling mechanisms of the eastern part were fundamentally different from those of the western part.

Table 1. Summary of Unweighted Least Squares Multiple Regression for Ecosystem $\delta^{15}N$ Values and for the $\Delta^{15}N$ Between Sample Types Using MAP and MAT as Two Independent Variables in Inner Mongolian Grasslands

<table>
<thead>
<tr>
<th>$\delta^{15}N$ value</th>
<th>Intercept</th>
<th>MAP (mm)</th>
<th>MAT (°C)</th>
<th>$R^2$</th>
<th>$n$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A: Stipa</td>
<td>7.07</td>
<td>-0.014</td>
<td>-0.737</td>
<td>0.553</td>
<td>36</td>
<td>0.00001</td>
</tr>
<tr>
<td>B: Leymus</td>
<td>10.31</td>
<td>-0.023</td>
<td>-0.440</td>
<td>0.460</td>
<td>35</td>
<td>0.00001</td>
</tr>
<tr>
<td>C: Soil (0–20 cm)</td>
<td>10.18</td>
<td>-0.011</td>
<td>-0.477</td>
<td>0.510</td>
<td>53</td>
<td>0.00001</td>
</tr>
<tr>
<td>D: Soil (20–40 cm)</td>
<td>7.34</td>
<td>-0.0038</td>
<td>-0.172</td>
<td>0.151</td>
<td>53</td>
<td>0.0163</td>
</tr>
<tr>
<td>C–A</td>
<td>2.51</td>
<td>0.0049</td>
<td>0.279</td>
<td>0.161</td>
<td>34</td>
<td>0.055</td>
</tr>
<tr>
<td>C–B</td>
<td>-0.14</td>
<td>0.0108</td>
<td>0.0706</td>
<td>0.168</td>
<td>34</td>
<td>0.060</td>
</tr>
<tr>
<td>D–C</td>
<td>-2.84</td>
<td>0.0074</td>
<td>0.305</td>
<td>0.285</td>
<td>53</td>
<td>0.0002</td>
</tr>
</tbody>
</table>

Global Model

| Soil (0–10 cm)      | 3.20      | -0.0005  | 0.1340   | 0.11  | 85  |
| Soil (0–50 cm)      | 3.89      | -0.007   | 0.1680   | 0.19  | 47  |
| Soil (0–50 cm)      | 4.33      | -0.0012  | 0.2048   | 0.39  | 29 (climosequence) |
| Plants              | 0.07      | -0.0016  | 0.1548   | 0.34  | 106 |
| $\Delta_{soil-plant}$ (10) | -4.69 | -0.0007  | 0.0911   | 0.13  | 49  |
| $\Delta_{soil-plant}$ (50) | -7.28 | -0.007   | 0.1718   | 0.23  | 30  |
| $\Delta_{soil-plant}$ (50) | -8.40 | 0.1852   | 0.37     | 21 (climosequence) |

*For comparison, results of global regression models [Amundson et al., 2003] are also included here. The units for $\Delta^{15}N$ are %.
3.4. Ammonia Volatilization, Grazing Intensity, and Ecosystem $^{15}N$

In order to elucidate potential mechanisms controlling ecosystem $^{15}N$ abundance, we measured NH$_3$ volatilization rates and soil $^{15}N$ abundance at a grazing intensity study site located near the middle part of the transect in 2005. Compared with the ungrazed treatment, grazing for 16 years slightly increased the soil $^{15}N$ abundance by about 1%, even though the difference was not statistically significant (Figure 9) because of the high variability in soil $^{15}N$ values. Soil $^{15}N$ values were significantly positively correlated with NH$_3$ volatilization rates (Figure 10), indicating that NH$_3$ volatilization is a key mechanism responsible for the level of soil $^{15}N$ enrichment in these grasslands.

4. Discussion

Our results demonstrated that climate imposes significant controls on ecosystem $^{15}N$ abundance, and that within a region, these climatic controls can differ from global patterns. MAP and MAT together accounted for approximately 50% of the variability in ecosystem $^{15}N$ abundance along the whole transect (Table 1). Consistent with published reports [e.g., Austin and Vitousek, 1998; Handley et al., 1999; Schuur and Matson, 2001; Aranibar et al., 2004; Swap et al., 2004], ecosystem $^{15}N$ abundance increased as MAP decreased along the transect. However, in contrast to published results, MAT was negatively correlated with ecosystem $^{15}N$ abundance in our regional study. Comparing our results from this multiple regression model with the global regression model compiled by Amundson et al. [2003], the slope values associated with MAT and MAP in this regional regression model are much higher than those in the global model (0.13–0.20 for MAT in the global model, 0.44–0.74 for MAT in this regional model; 0.0005–0.0016 for MAP in the global model, 0.011–0.023 in this regional model). This apparent difference suggests that ecosystem $^{15}N$ values are more sensitive to climatic
variables at smaller scales than at larger scales when heterogeneity associated with vegetation and parent materials are reduced at the regional scale, or that the climate sensitivity is greater in a more arid environment. This interpretation is further supported by the much higher $R^2$ values in this regional regression model than in the global model ($R^2 = 0.5$ in the regional model as compared to $R^2 = 0.11$ for the soil $\delta^{15}N$ values and 0.34 for the plant $\delta^{15}N$ values). There is one striking difference between the two models: ecosystem $\delta^{15}N$ values are positively correlated with MAT in the global model, but negatively correlated with MAT in this regional model. We will explore the possible causes of this conflicting result in the following section.

In order to further compare this regional gradient with the global pattern described by Amundson et al. [2003], we derived soil $\delta^{15}N$ values using the global regression equation, MAT and MAP, and plotted the projected data together with our measured data along the transect (Figure 11). This comparison indicates that the global model predicts much lower soil $\delta^{15}N$ values for the western part of the transect and higher values for the eastern part of the transect. Soil $\delta^{15}N$ values for the western part of the transect were positively correlated with MAT, which is consistent with reported results [e.g., Martinelli et al., 1999; Amundson et al., 2003]. However, soil $\delta^{15}N$ values for the eastern part of the transect were negatively correlated with MAT, which is in conflict with published results. The regression slope value for the western part of the transect is also much higher than the slope value in the global model (1.15 versus 0.13) [Amundson et al., 2003]. We hypothesize that NH$_3$ volatilization is an important contributor to the pattern for the western part and anthropogenically enhanced N deposition is a key factor for the pattern in the eastern part. The relationship between MAP and soil $\delta^{15}N$ values for the western part of the transect was similar to the eastern part of the transect (Figure 7); both showed negative correlations. The slope

**Figure 8.** Relationship between soil total N (%) and soil $\delta^{15}N$ values (%) (0–20 cm) for the western part and the eastern part of the transect. The regression equation for the western part: soil $\delta^{15}N = 7.03 - 8.65 N_{soil}$, $R^2 = 0.28$, $P = 0.0043$, $n = 27$; for the eastern part: soil $\delta^{15}N = 1.52 - 22.1 N_{soil}$, $R^2 = 0.27$, $P = 0.0050$, $n = 27$.

**Figure 9.** Changes in soil $\delta^{15}N$ (%) under different grazing intensities. Grazing intensities G0, G1, G2, G3, and G4 represent 0, 1.33, 2.67, 4.00, and 5.33 sheep equivalents per hectare, respectively. Each column is the mean of three replicated subplots. Error bars represent ± standard error.

**Figure 10.** Relationship between soil $\delta^{15}N$ (%) and NH$_3$ volatilization (g N ha$^{-1}$ a$^{-1}$). The regression line was calculated using values across 15 subplots.
values (0.0054 and 0.0227) for both parts of the transect were higher than the slope value (0.0005) for soils from the 0–10 cm depth in the global model [Amundson et al., 2003]. The soil $\delta^{15}$N values along the western part of the transect were negatively correlated with soil N content, which indicated that higher $^{15}$N-enrichment was associated with a lower level of total soil N content. In contrast, the soil $\delta^{15}$N values along the eastern part of the transect were positively correlated with soil N content (Figure 8), or the level of $^{15}$N-enrichment increased as the total soil N stock increased, which is similar to the results from a fertilization study in a forest [Johannisson and Högbäck, 1994] and from a study of agricultural soils [Shearer et al., 1978]. This “west-east” comparison suggests that N cycling in the eastern part has been profoundly altered possibly by some external disturbances. The actual causes of these conflicting trends between the west and the east need to be further investigated.

[25] The $^{15}$N natural abundance in plant tissues was clearly linked to the $^{15}$N natural abundance in the topsoil across the whole transect. Our data showed that the $\delta^{15}$N values of aboveground plant tissues (both Leymus and Stipa) were significantly correlated with the $\delta^{15}$N values of total soil nitrogen along the whole transect (Figure 3). On average, the difference in $\delta^{15}$N values between plant tissues and the topsoil was approximately 4.5%, indicating that soil N was more enriched in $^{15}$N than plant tissues which had $\delta^{15}$N values of 0.4% and 0.8% for Stipa and Leymus, respectively. This difference between plant and soil $\delta^{15}$N values was relatively constant along the whole transect and was marginally positively correlated with both MAP and MAT (Table 1). This is in contrast with the results of the global regression model of Amundson et al. [2003], which showed that the difference between plant and soil $\delta^{15}$N values is significantly positively correlated with MAT and, to a lesser degree, negatively with MAP. The relatively narrow MAT range along our Inner Mongolian transect as compared to the global scale may have caused this inconsistency. Shifts in N cycling from organic or ammonium-dominated status (e.g., cool temperate ecosystems) to nitrate-dominated status (e.g., tropical ecosystems) have been hypothesized as the potential control of the difference between plant and soil $\delta^{15}$N values [Amundson et al., 2003]. It is possible that the relatively narrow MAT range along our Inner Mongolian transect is insufficient to cause a large shift in N dynamics. However, because $^{15}$N abundance of different plant species and soil types varied widely [Martinelli et al., 1999; Swap et al., 2004], this inconsistency may stem from the fact that our sampling approach largely separated the effects of plant species and soil types on ecosystem $^{15}$N abundance from climate controls, while changes of plant and soil types are an integral part of the global model. Accordingly, this result may indicate that the significant global correlation between $\Delta^{15}$Nsoil-plant values (%) and climatic variables is largely from the effects of changes in plant-soil type together with climate on $\Delta^{15}$Nsoil-plant values, but not so much by climate alone.

[26] More over, our results indicate that the level of $^{15}$N enrichment in the 20–40 cm soil layer as compared to the 0–20 cm soil layer increased as both MAP and MAT increased (Table 1). This relationship is in direct contrast to the relationship between ecosystem $^{15}$N abundance and both MAP and MAT along the whole transect. The latter shows that plant and soil $\delta^{15}$N values decreased as both MAP and MAT increased. These opposing trends partially explain why the $\delta^{15}$N value of the deeper soil layer was relatively less sensitive to MAP or MAT (Table 1). This is because the enrichment of $^{15}$N at the deeper soil layer relative to the surface layer counterbalances the depletion of $^{15}$N at the whole system level as both MAP and MAT increase. Furthermore, $^{15}$N enrichment associated with NH$_3$ volatilization from the surface layer may play an important role in reducing the difference in $\delta^{15}$N values between the two soil layers in drier parts of the transect than in the wetter parts, because higher pH values in the drier parts permit larger NH$_3$ volatilization than in the wetter parts.

[27] Along the east-west transect in Inner Mongolian grasslands, MAT was negatively correlated with ecosystem

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**Figure 11.** Longitudinal changes of soil $\delta^{15}$N along the transect based on actual measurements (open circles) and projected values using the global regression model of Amundson et al. [2003] (triangles).
δ¹⁵N values over the whole transect in our study. In contrast, other studies showed positive correlations [Martinelli et al., 1999; Amundson et al., 2003]. The opposing trend was mostly caused by the eastern part of the transect (Figures 8, 9, and 10). The eastern part of Inner Mongolian grasslands has been exposed to a higher level of N deposition than the western part during the past few decades because of air pollution from nearby northern China urban centers and heavy N fertilization in bordering agricultural regions (Table 2). Annual N deposition rates can be as high as 50 kg N ha⁻¹ a⁻¹ near Beijing southeast of the transect and some Northeastern urban locations (L. H. Li, unpublished data, 2006). The trade winds in this region are predominantly southeast during the summer when wet deposition rates peak, which can carry N-containing pollutants to the eastern part of Inner Mongolian grassland. This intensified N deposition has the potential to shift N-cycling to a nonsteady state and significantly alter the pattern of ¹⁵N abundance in the grassland region as δ¹⁵N values of atmospherically deposited N may range from −10% to +5% depending on N sources [Hübner, 1986; Handley et al., 1999]. Although the exact causes of the apparent opposing trend in the relationship between MAT and ecosystem ¹⁵N abundance in the eastern part of the transect as compared to the Western part and other studies are yet to be explored, the differences in N deposition gradient are likely one of the main causes.

In addition to N deposition, several other processes can also determine ecosystem ¹⁵N abundance. As suggested in a steady state model [Amundson et al., 2003], the magnitude of ¹⁵N-enrichment compared to the ¹⁵N abundance in total N entering the system largely depends on the level of ¹⁵N fractionation in all processes that control N loss from the system such as NH₃ volatilization, denitrification, leaching and fire. Because of the often limited water availability, N loss through leaching and denitrification is usually much less important than N loss through fire and NH₃ volatilization in arid and semiarid systems [Xu, 2007]. N loss through fire has similar ¹⁵N abundance as N in the burnt vegetation, therefore, does not necessarily result in significant ¹⁵N fractionation [Herman and Rundel, 1989; Mordelet et al., 1996; Grogan et al., 2000; Cook, 2001; Aranibar et al., 2003]. However, N loss through NH₃ volatilization is known to have a much higher potential for ¹⁵N fractionation than N loss through fire [Frank et al., 2004], because volatilized NH₃ can be depleted in ¹⁵N as much as 60% compared to the remaining NH₃ left in the soil [Högberg, 1997]. It is known that soil pH is the most important factor in controlling NH₃ volatilization. The pH values along the Inner Mongolian transect are certainly high enough for substantial NH₃ volatilization to occur (Figure 2). Some studies have also shown that animal grazing accelerates N-loss by way of NH₃ volatilization and other processes, especially in ecosystems with higher soil pH values [Frank and Evans, 1997; Bouwman et al., 2002; Frank et al., 2004]. A large proportion of the annual N budget of grasslands can cycle through herbivores [Wang et al., 2003]. For example, migratory herds of ungulates in temperate grassland and tropical savanna ecosystems graze as much as 45% and 65% of the aboveground plant production, respectively [Frank et al., 1998], and in rangeland with livestock, consumption ranges between 20% and 75% [Oesterheld et al., 1992]. Thus grazers can function as a conduit for a substantial amount of the biologically active N that is annually cycled in grassland ecosystems. Because 65% or more of the N ingested by grazers is excreted in urine [Mould and Robbins, 1981; Russ, 1987], NH₃ volatilization from urine deposits can represent a major loss of N in grasslands that support abundant herbivores [McNaughton et al., 1988; Hobbs, 1996]. Our results at one intensive study site also indicate that soil ¹⁵N enrichment increases as rates of NH₃ volatilization increase (Figure 10). More over, ¹⁵N fractionation also occurs in animal product removal because relatively less ¹⁵N is in animal products than in animal wastes [Ambrose and Deniro, 1986]. Because of ¹⁵N fractionation linked to N loss associated with herbivores, grazing by domesticated herds for thousands of years on Inner Mongolian grasslands may have contributed to the ¹⁵N-enrichment in the ecosystem.

Precipitation may control ¹⁵N abundance in arid and semiarid ecosystems by influencing NH₃ volatilization which enriches soil N with ¹⁵N. Precipitation effects leaching of alkaline cations in soils, therefore determining surface soil pH values. Indeed, there was a negative correlation between MAP and soil pH values across Inner Mongolian grasslands (Figure 2). Because of this, soils in arid and semiarid ecosystems often have high pH values, and for Inner Mongolian grasslands soil pH values in the 0–20 cm depth ranged from 6.3 to 9.2 with a mean of 7.7. It is commonly known that pH values of surface soils significantly influence NH₃ volatilization. The amount and frequency of precipitation also affect NH₃ volatilization from urine patches because water from precipitation can dilute urine and leach solutes into deeper soil layers, thereby reducing NH₃ volatilization from urine patches. Precipitation is one of the most important factors that determine plant production and nitrogen uptake and assimilation in arid and semiarid ecosystems [Chen and Wang, 2000]. More productive ecosystems, in general, have a higher capability to immobilize available N sources, and thereby remove more N from the environment before NH₃ volatilization can occur. Studies also indicate that vegetation can take up NH₃ in the air so that the net loss of N through NH₃

<table>
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<th>Location</th>
<th>Longitude, E</th>
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<th>kg N ha⁻¹ a⁻¹</th>
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<td>44.70</td>
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References

Aranibar et al., 1992. Grazers can also determine ecosystem ¹⁵N abundance. As suggested in a steady state model [Amundson et al., 2003], the magnitude of ¹⁵N-enrichment compared to the ¹⁵N abundance in total N entering the system largely depends on the level of ¹⁵N fractionation in all processes that control N loss from the system such as NH₃ volatilization, denitrification, leaching and fire. Because of the often limited water availability, N loss through leaching and denitrification is usually much less important than N loss through fire and NH₃ volatilization in arid and semiarid systems [Xu, 2007]. N loss through fire has similar ¹⁵N abundance as N in the burnt vegetation, therefore, does not necessarily result in significant ¹⁵N fractionation [Herman and Rundel, 1989; Mordelet et al., 1996; Grogan et al., 2000; Cook, 2001; Aranibar et al., 2003]. However, N loss through NH₃ volatilization is known to have a much higher potential for ¹⁵N fractionation than N loss through fire [Frank et al., 2004], because volatilized NH₃ can be depleted in ¹⁵N as much as 60% compared to the remaining NH₃ left in the soil [Högberg, 1997]. It is known that soil pH is the most important factor in controlling NH₃ volatilization. The pH values along the Inner Mongolian transect are certainly high enough for substantial NH₃ volatilization to occur (Figure 2). Some studies have also shown that animal grazing accelerates N-loss by way of NH₃ volatilization and other
volatilization can be reduced where there is dense vegetation [Frank et al., 2004]. If these mechanisms are predominant in arid and semiarid grasslands in Inner Mongolia, and if NH$_3$ volatilization is the key process responsible for $^{15}$N enrichment, $^{15}$N values of plants and surface soils should decrease as precipitation increases. This can potentially explain the high degree of negative correlation between MAP and $^{15}$N values of plants and surface soils along the whole transect (Table 1), especially in the western part of the transect where the slope of the correlation was much larger than in the global regression model of Amundson et al. [2003].

[30] In summary, the results of ecosystem $^{15}$N abundance and climate from our study filled an apparent global data gap over Inner Mongolian grasslands. The data clearly indicated that climate exerts strong controls on ecosystem $^{15}$N abundance along the transect with similar plant-soil types. Along the whole transect, ecosystem $^{15}$N values decreased as both MAP and MAT increased. This regional pattern differed from the global pattern reported by Amundson et al. [2003] in several aspects. First, temperature control on ecosystem $^{15}$N natural abundance along the eastern part of the transect was in the opposite direction of the global relationship. Second, ecosystem $^{15}$N abundance was significantly more sensitive to MAP along the western part of the transect than in the global relationship. Third, ecosystem $^{15}$N abundance values in the western part of the transect were significantly higher than the values projected by the global model. Fourth, the difference in $^{15}$N values between plants and soils in Inner Mongolian grasslands showed weak relationships with either MAP or MAT; this difference tended to decrease with increasing MAT and with decreasing MAP at the global scale. The much narrower climatic range and plant-soil types encompassed by the transect as compared to the global model may have prevented us from detecting any significant relationship between climatic variables and the difference in plant and soil $^{15}$N values. We suggest that anthropogenic $N$ deposition may have caused the opposing trend in terms of the relationship between MAT and ecosystem $^{15}$N abundance in the eastern part of the transect. Intensive grazing by domesticated animals for thousands of years in these Inner Mongolian steppes may have kept ammonia volatilization at a high rate, and therefore caused $^{15}$N enrichment and a higher sensitivity to MAP changes in the western part of the transect. Further studies are needed to ascertain these suggested mechanisms.

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