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Large regional-scale variation in C3/C4 distribution pattern of Inner Mongolia steppe is revealed by grazer wool carbon isotope composition

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Abstract

This work explored the spatial variation of C3/C4 distribution in the Inner Mongolia, China, steppe by geostatistical analysis of carbon isotope data of vegetation and sheep wool. Standing community biomass (n=118) and sheep wool (n=146) were sampled in a ~0.2 Mio km^2 area. Samples from ten consecutive years (1998–2007) were obtained. Community biomass samples represented the carbon isotopic composition of standing vegetation on about 1000 m^2 ("community-scale"), whereas the spatio-temporal scale of wool reflected the isotope composition of the entire area grazed by the herd during a 1-yr period (~5–10 km^2, "farm-scale"). Pair wise sampling of wool and vegetation revealed a ^{13}C-enrichment of 2.7‰ in wool relative to vegetation, but this shift exhibited no apparent relationships with environmental parameters or stocking rate. The proportion of C4 plants in above-ground biomass (P_{C4}, %) was estimated with a two-member mixing model of C3 and C4 ^{13}C discrimination ($^{13}\Delta_3$ and $^{13}\Delta_4$, respectively), in accounting for the effects of changing ^{13}C in atmospheric CO_2 on sample isotope composition, and of altitude and aridity on $^{13}\Delta_3$. P_{C4} averaged 19%, but the variation was enormous: full-scale (0% to 100%) at community-scale, and 0% to 85% at farm-scale. The farm-scale variation of P_{C4} exhibited a clear regional pattern over a range of ~250 km. Importantly P_{C4} was significantly higher above and lower below the 22°C isotherm of the warmest month, which was averaged from high-resolution maps of the sample years. This is consistent with predictions from C3/C4 crossover temperature of quantum yield in C3 and C4 plants. Still, temperature gradients accounted for only 10% of the farm-scale variation of P_{C4}, indicating that additional factors control P_{C4} on this scale.

1   Introduction

The carbon isotope composition (δ^{13}C) of terrestrial ecosystems holds important information on photosynthetic pathways, carbon fluxes and linked biogeochemical cycles

(Schimel, 1995; Ehleringer et al., 2000). In grassland, the ^{13}C signal can vary considerably. This is primarily related to the presence of variable proportions of C3 and C4 photosynthetic types (Tieszen et al., 1997; Bird and Pousai, 1997; Collatz et al., 1998) and the large difference in carbon isotope discrimination ($^{13}\Delta$) between them (Farquhar

5 et al., 1989). Variation in the C3/C4 ratio has wide biogeochemical and land use implications: it affects the magnitude and seasonal distribution of biomass production, soil carbon storage, water use and nutrient cycling (Tieszen et al., 1997; Bird and Pousai, 1997; Epstein et al., 1998; Sage and Kubien, 2003; Semmartin et al., 2004). Hence, as it indicates the C3/C4 ratio, δ^{13}C is a useful proxy of vital functions of grassland.

10 However there exist very few regional-scale investigations on δ^{13}C of C3/C4 mixed grassland.

   There is abundant evidence that the current distribution of C4 plants is primarily controlled by growing season temperature (Ehleringer et al., 1997; Collatz et al., 1998) and that this is related to the higher effective quantum yield of CO_2 fixation (Ehleringer and

15 Bjorkman, 1977) and higher maximum photosynthetic rate of C4 plants at high temperature (Sage and Kubien, 2003). Central East Asia has experienced one of the largest temperature increases on earth during the last decades (Chase et al., 2000; Yu et al., 2003), which should promote C4 plants. On the other hand, rising atmospheric CO_2 stimulates C3 photosynthesis more than C4. Nutrient limitation due to increased photo-

20 synthesis may again favour C4 species (Sage and Kubien, 2003) leading to a complex web of interactions, which makes it difficult to predict the overall effect. Furthermore, the different influences act on different spatio-temporal scales. While CO_2 concentration changes globally, temperature varies regionally and nutrient limitation may differ down to the scale of urine patches. The effects may thus vary regionally or even locally

25 and can only be assessed by taking scales into account. Furthermore, the seasonal distribution of precipitation (Murphy and Bowman, 2007), aridity, and disturbance (for instance by overgrazing) may exert secondary, modifying effects. E.g., predominance of summer rainfalls typically benefits C4 more than C3 (Hattersley, 1983; Paruelo and Lauenroth, 1996). C4 dicots predominate in hot arid, saline or highly disturbed habi-

tats (e.g., Ehleringer et al., 1997). Presumably such secondary controls have their strongest effect on C3/C4 abundance in those regions which have a growing season mean temperature that is near the C3/C4 crossover temperature (i.e. the temperature above which the quantum yield efficiency of C4 plants is higher than that of C3 plants,
5 see Ehleringer et al., 1997). In this respect, the grassland of Inner Mongolia is of particular interest, as the average temperature during the summer months (especially July) when most of the annual precipitation falls is close to the C3/C4 crossover temperature. There are several reports indicating increases in the number and abundance of C4 species with aridity in (Inner) Mongolia grassland (Pyankov et al., 2000; Wang,
10 2004) and desertification (Wang, 2002), although conflicting evidence has also been presented (Wang, 2003; Ni, 2003).

Although the C3/C4 ratio is the main factor affecting $\delta^{13}C$ of grassland, variation in $^{13}\Delta$ of C3 plants may also contribute, as the $\delta^{13}C$ of C3 plants decreases with precipitation, moisture availability (e.g., Schulze et al., 1998; Liu et al., 2005; Wittmer
15 et al., 2008) and with altitude (Körner et al., 1991; Männel et al., 2007). Variation in the $\delta^{13}C$ of C3 plants has to be taken into account when estimating the C3/C4 ratio from carbon isotope composition.

Another difficulty in regional-scale studies of the ^{13}C signal of grassland is a potentially high spatio-temporal variation: the life-span of the aboveground parts of grass-
20 land plants is short, reflecting growing conditions prevailing in a period of weeks to a few months before sampling. This is aggravated in C3/C4 grassland due to the asynchronous development of C3 and C4 components resulting from their different thermal preferences. One possibility to overcome (integrate) these spatio-temporal variations is to collect representative bulk samples over a large area and to sample several times
25 during the vegetation period. An alternative to this is to take advantage of the "sampling" activity of livestock which are grazing the grassland. Provided that they do not select between photosynthetic types, and eventual post-ingestion fractionation of carbon isotopes is known, the $\delta^{13}C$ of vegetation can be inferred from wool or other animal tissue (e.g., Jones et al., 1981; Schnyder et al., 2006; Norman et al., 2008). Geostatis-

tical analysis can then be used to separate between the regional pattern and the noise of the individual samples, e.g. caused by small-scale peculiarities of individual animals, farms or years.

The aim of this work was to answer the following questions by geostatistical analysis of δ^{13}C derived from wool samples by taking into account the diet-wool shift and environmental influences on the C3 and C4 end-members:

(i) How is the C3/C4 pattern of the grassland of Inner Mongolia?

(ii) How does this pattern relate to driver patterns like (growing period) temperature and/or precipitation?

2 Materials and methods

2.1 Study area

The study area was situated between 111°38′ and 117°49′ E (approximately 500 km) and 41°48′ and 45°46′ N (approximately 450 km) in the Autonomous Region of Inner Mongolia in the Peoples Republic of China (Fig. 1). Sampled altitudes ranged from 800–1700 m above sea level (a.s.l.). Mean annual precipitation (MAP, mm yr^{-1}) increases from 100 mm yr^{-1} in the western part to 400 mm yr^{-1} in the eastern part of the study area. Most of the precipitation (approximately 75%) falls during the growing period (April–September). The spatial variation of temperature follows altitudinal and latitudinal trends. Mean annual temperature and mean temperature of the growing period vary between 0–6°C and 14–19°C, respectively. Almost the whole area is used for small ruminant livestock production (mainly sheep and cashmere goats) with little agriculture, mainly cultivation of maize. In general, animals graze from spring till winter depending on snow cover and availability of herbage. In overgrazed areas grazing is suspended during winter and/or early spring to allow for recovery of vegetation. Animals do not receive supplements on pasture. Pen fodder in the winter and/or spring consists of hay from meadows, supplemented in some cases with small

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amounts (<10% of the ration) of maize and/or industrial pasture from the major towns e.g., Hohhot or Baotou (information obtained from interviewing the local herders).

2.2 Sampling

Samples were collected in August/September 2003, August/September 2004, July 2005, July 2006 and June/July 2007. The sampling area (116°12′ to 118°54′ E and 40°36′ to 47°42′ N) exceeded the study (target) area to evade boundary effects at the periphery of the study area during spatial analysis and interpolation. The current sampling position and altitude was measured with a mobile outdoor global positioning system. Bulked leaves were collected within approximately $1000 \, m^2$ on a reduced scale of apparent species-level contribution to total standing biomass ("community-scale" samples) on 112 sites within the study area and on 6 sites outside the periphery. At some sites (n=52), encompassing the entire aridity gradient in the sampling area, the leaves of the dominant and in parts the co-dominant species (contributing individually >5% to total aboveground biomass) were sampled separately (>3 different plants per sample), to obtain separate estimates of the $\delta^{13}C$ of the C3 and C4 components of plant communities.

The wool samples resulted from the last shearing and therefore reflected the period in between two consecutive shearing (mostly one year), which generally take place in June, and the grazing grounds of one herder ("farm-scale" samples). Wool from 146 sheep dating from 1998–2007 was sampled on 82 sites (2003, 2004 and 2007) within the study area and on ten sites beyond the periphery. Most wool samples were provided by local herders and originated from the recent shearing.

Additional samples were taken between late June and mid of September in 2005 and 2006 from a long term grazing experiment at 116°40′ E, 43°34′ N. The grazing experiment allowed comparing vegetation and wool directly and to assess selective grazing because it covered a large gradient in stocking densities between 1.5 sheep per hectare, which allowed for selection, and 9.0 sheep per hectare, where the total aboveground biomass was grazed leaving bare soil. For further information on the

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grazing experiment see Zhao et al. (2007). On 14 plots vegetation samples were taken and the wool from 90 sheep. For the latter, the sheep were shorn before they were moved to the pasture (mid of July 2005 and 2006, respectively) and at the end of pasturing (mid of September 2005 and 2006, respectively).

2.3 Sample preparation

The plant samples for each site were transferred to separate paper bags and dried behind the front window of the car. In addition plant samples were dried for 48 h at 60°C and then were ground to homogeneity with a ball mill. 0.7–0.8 mg plant material in tin cups was analyzed for their isotopic composition. The wool samples were cleaned by the procedure of Schwertl et al. (2003) and 0.2–0.4 mg wool were then packed into tin cups for isotope analysis. For the wool originating from the years 2003, 2004 and 2005 an additional segmentation was carried out. The wool was cut into cm pieces, which were analyzed separately to quantify an isotopic shift between the summer wool segments and summer vegetation (n=14 for the grazing experiment; n=62 for repeated regional samplings).

2.4 Isotope and elemental analysis

The carbon isotope composition and carbon and nitrogen content of each sample was determined with an elemental analyzer (NA 1110; Carlo Erba, Milan) interfaced (ConFlo III; Finnigan MAT, Bremen) to an isotope ratio mass spectrometer (Delta Plus; Finnigan MAT). Carbon isotopic data are presented as $\delta^{13}C$, with $\delta^{13}C=(R_{sample}/R_{standard})-1$, where R is the $^{13}C/^{12}C$ ratio and standard is the Vienna Pee Dee Belemnite standard. Each sample was measured against a laboratory working standard CO_2 gas, which was previously calibrated against an IAEA secondary standard (IAEA-CH6, accuracy of calibration 0.06‰ SD). After every tenth sample a solid internal lab standard (SILS) with similar C/N ratio as the sample material (fine ground wheat flour for plant samples; protein powder for wool) was run as a blind

control. The SILS were previously calibrated against an international standard (IAEA-CH6). The precision for sample repeats (SD) was 0.06‰ for plant samples and 0.11‰ for wool samples.

2.5 Carbon isotope discrimination of plants

The $\delta^{13}C$ of plants ($\delta^{13}C_P$) differs from the $\delta^{13}C$ of air ($\delta^{13}C_a$) depending on the discrimination $^{13}\Delta$ (Farquhar et al., 1989):

$$^{13}\Delta = \frac{\delta^{13}C_a - \delta^{13}C_P}{1 + \delta^{13}C_P} \tag{1}$$

with $\delta^{13}C_a$ continuously decreasing over time. Mean annual $\delta^{13}C_a$ was predicted applying a third order polynomial and corrected for seasonal variation in $\delta^{13}C_a$ following Wittmer et al. (2008).

2.6 Meteorological data

For year-specific data on precipitation and temperature we followed the procedure by Wittmer et al. (2008) and corrected long-term average high resolution (2 km×2 km) maps (The Climate Source LLC, 2002) obtained by the PRISM method (parameter-elevation regressions on independent slopes model; Daly et al., 2002) for the deviation of an individual year, which was geostatistically interpolated between meteorological stations. Daily precipitation and temperature data of 46 climate stations, provided by the NOAA Satellite and Information Service (NOAA NCDC Climate Data Online 2008) were used. The annual maps were then averaged for the research period 1998–2007.

2.7 Estimation of C4 fraction

The relative contribution of C4 plants (P_{C4}) to aboveground biomass at each site was estimated from $^{13}\Delta$ of the community using a two-member mixing model:

$$P_{C4} = \frac{^{13}\Delta_c - ^{13}\Delta_3}{^{13}\Delta_3 - ^{13}\Delta_4} \quad (2)$$

where $^{13}\Delta_c$ denotes community, and $^{13}\Delta_3$ and $^{13}\Delta_4$ are the end-members of the mixing model (local $^{13}\Delta$ of pure C3 and C4 vegetation communities, respectively). Regionalized estimates of $^{13}\Delta_4$ (see Results) were obtained from $\delta^{13}C$ of C4 vegetation samples, whereas $^{13}\Delta_3$ was derived from study-area specific data accounting for precipitation during the growing period as reported by Wittmer et al. (2008 and citations therein) and for altitude following Männel et al. (2007). Combining the equations of both studies yielded an estimate for $^{13}\Delta_3$:

$$^{13}\Delta_3 = 14.4\text{‰} + 1.1\text{‰} \cdot \frac{A - 1000}{1000} + 2.7\text{‰} \cdot \sqrt{P} \quad (3)$$

with A denoting altitude (m a.s.l.) and P denoting the mean precipitation (mm day^{-1}) during the growing period. The constant 14.4‰ is the minimal reference $^{13}\Delta_3$ as reported by Wittmer et al. (2008) for 1000 m a.s.l.

In principle, recent P_{C4} can be estimated from wool considering the isotopic offset with respect to vegetation: in studies with pure or mixed C3 or C4 diets the $\delta^{13}C$ of hair was 2 to 3‰ enriched with ^{13}C relative to diet (Jones et al., 1981; Sponheimer et al., 2003a; Männel et al., 2007). This offset is termed "vegetation-wool shift", S_{VW} ($S_{VW} = \delta^{13}C_{wool} - \delta^{13}C_{vegetation}$), and results from ^{13}C fractionation during digestion or metabolism of animals (De Niro and Epstein, 1978). Hence, the $^{13}\Delta$ of the community can be estimated from Eq. (1) from $\delta^{13}C_c$ or from $\delta^{13}C_c = \delta^{13}C_{wool} - S_{VW}$ if the shift is known. So far published estimates of the shift for wool for mixed C3/C4 diets are

missing as the shift of sheep wool from Männel et al. (2007) was established for pure C3 grassland, with considerably higher digestibility than that found in Inner Mongolia (Wang et al., 2008). In consequence, we assessed S_{VW} by paired sampling across the study area and in the grazing experiment. We compared the $\delta^{13}C$ of vegetation with
5 that of the most-recently grown 1-cm long wool segment from the sheep actually grazing this vegetation. From the grazing experiment, the whole wool was used, which was grown while a sheep was grazing on an individual plot but the first cm was discarded to account for metabolic turnover of body carbon originating from the prior winter period.

2.8 Statistical methods and geostatistical analysis

10 Linear regressions were used to evaluate the datasets. The coefficient of determination was tested with a two-sided test for significance of the regression. Hypothesis testing on equal means of groups were carried out using Student's t-test, customarily performed against a 95% confidence interval if not stated otherwise. Kernel densities (Silverman, 1986) were calculated using Gaussian kernels to yield estimates of the
15 density distribution. Bandwidth of density estimation of different sized data sets was defined via Silverman's "rule of thumb". To allow for comparison of differently sized data sets integral density was adjusted to unity. Statistical spread is denoted as standard deviation (SD) or 95% confidence interval ($CI_{95\%}$). All these procedures followed standard protocols (Sachs and Hedderich, 2006) and were carried out using GNU R
20 2.7.2 (R Development Core Team, 2008).

Geostatistical analyses (see Rossi et al., 1992 and citations therein) were conducted with the auxiliary packages geoR (Ribeiro and Diggle, 2001) and gstat (Pebesma, 2004). The semivariance (γ) of a parameter under consideration is the half mean quadratic difference of the parameter values of points which are separated by a certain
25 distance (called lag) yielding the empirical semivariogram (x-axis: lag, y-axis: semivariance). For calculation of the lag, the coordinates of sampling points had to be transformed from geographic coordinates to UTM coordinates with the package PBS-mapping (Schnute et al., 2008; UTM zone=50). A theoretical semivariogram was fitted

to minimize weighted least squares, with weights calculated from the ratio of pairs (at least 30) within a class to mean lag. This gives more weight to those classes, which are based on many data pairs and which are more important for interpolation. The theoretical semivariogram delivers three parameters, the nugget effect, the sill and the range.

The nugget effect quantifies the small-scale variation including data uncertainty. The sill quantifies the total variation caused by the nugget effect and the variation due to the spatial pattern. The nugget to sill ratio hence reflects the ratio of random (unexplained) to total variation. The range quantifies the distance of autocorrelation caused by the extension of the pattern elements. The quality of the fit between the experimental and the theoretical semivariogram is expressed as root mean squared error (RMSE).

Spatial interpolation to construct maps was then carried out for a uniform rectangular grid (200×200 nodes) by ordinary block kriging for $5{\times}5\,km^2$ blocks, using the theoretical semivariogram. Samples beyond the periphery of the study area were included because this greatly reduces the error at the margins of the study area. The quality of the predictions from the resulting maps is given as the (block) krige standard deviation averaged for the study area.

3   Results

3.1   The $\delta^{13}C$ of vegetation and hair

The isotopic composition of carbon pools varied greatly in the sampling area. Furthermore, the range differed strongly between types of pools: the $\delta^{13}C$ of whole vegetation varied between −12.5‰ and −28.4‰ (Fig. 2a), whereas the site-means for wool ranged between −13.1‰ and −23.7‰ (Fig. 2b). The $\delta^{13}C$ of the C3 components varied between −23.3‰ and −28.5‰ (mean: −25.0‰), the $\delta^{13}C$ of the C4 components of vegetation between −12.5‰ and −15.8‰ (mean: −14.2‰). Evidently, the $\delta^{13}C$ of the C3 and C4 components exhibited variations three to four times smaller than that of whole vegetation (Fig. 2a) indicating a variation in the C3/C4 ratio (see below).

Bulk vegetation and wool differed markedly in their density distributions of δ^{13}C (Fig. 2a, b). These differences corresponded almost exactly to the isotopic shift, which was observed by paired sampling: on average, wool was enriched by 2.7‰ (n=76, CI$_{95\%}$=0.7‰) relative to vegetation sampled at the same location. There was no indica-
tion of preferential grazing in the grazing experiment, when the shift was regressed either against stocking densities or against P_{C4} derived from vegetation analysis (P>0.05 and P>0.75, respectively). Correcting for this independently derived shift lead to similar density distributions for vegetation derived from either vegetation itself or from wool (Fig. 2b). The main difference between the density distributions then is that the ex-
tremes were lost when using wool, reflecting the larger temporal and spatial integration as compared to the sampling area area of vegetation. The density peak for δ^{13}C of vegetation derived from wool (−23.4‰) was close to the median (−23.6‰) and the mean (−22.8‰) of δ^{13}C from bulk vegetation.

3.2   The relationship between δ^{13}C and environmental gradients

The response of δ^{13}C to the environmental variables was the same for vegetation and wool with no significant differences in slope of the regression, which were very highly significant for mean July temperature, MAP and altitude (Table 1) with similar strength. However, the correlations were rather weak and effects were not independent, since there were also close correlations between the mean July temperature and MAP (R^2=0.75, P≪0.001) as well as between mean July temperature and altitude (R^2=0.41, P≪0.001) and MAP and altitude (R^2=0.26, P≪0.001). As a result, the effects of environmental variables on δ^{13}C of vegetation could not be separated, and each response function of δ^{13}C to an environmental variable included direct and indirect effects.

3.3 $^{13}\Delta$ of C4 vegetation and C4 abundance

Mean $^{13}\Delta_4$ was 6.0‰ (n=46; SD±0.9‰). Within the C4 plants there was a highly signif-
icant difference of 1.1‰ ($P \ll 0.0001$, α=0.01) between *Cleistogenes squarrosa* (mean
6.6‰; n=19), a common perennial xerophytic C4 grass in Inner Mongolia grassland,
and other C4 species (mean 5.5‰; n=27; see also the two shoulders in the density
distribution of δ^{13}C of C4 component in Fig. 2a). However, no significant relationship
between $^{13}\Delta_4$ and normal-period (P>0.60) or annual precipitation (P>0.75), normal-
period (P>0.80) or annual temperature (P>0.10), or plant available soil water (P>0.23,
calculated after Allen et al., 1998 and Schnyder et al., 2006) was found. As no indica-
tion for a relevant regional variation was evident the mean $^{13}\Delta_4$ was used to calculate
P_{C4} from ^{13}C of wool samples considering the isotopic shift between vegetation and
wool.

On average of all wool samples, C4 plants accounted for 19% of aboveground plant
biomass, but P_{C4} varied widely between sites (0 to 85%). C4 abundance increased
by 6% with an increase of 1°C of mean July temperature (normal period, P≪0.001),
decreased by 6% for each 100 mm yr^{-1} increase in MAP (P<0.05). Although all these
relationships were significant, the scatter was large in all of them (R^2 between 0.04
and 0.10).

3.4 Geographic variation of C4 abundance

The theoretical semivariogram followed a spherical model for P_{C4} (Fig. 3). The range
was approximately 260 km and the nugget-to-sill ratio was 0.4. Hence the nugget effect
corresponds to an uncertainty of approximately 16% for P_{C4}. The nugget/sill ratio indi-
cates further that 60% of the variation was caused by a spatial pattern (Table 2). This is
much more than what could be explained with regression analysis (Table 1) assuming
linear relationships to isolated environmental variables.

The map of P_{C4} as reflected in δ^{13}C of wool generated by ordinary block kriging
ranged only between 0 and 40% because block kriging separates the local variation

(noise) from the pattern (regional variation). The map (Fig. 4) is characterized by an increase of P_{C4} from 0% in the south-eastern part to around 40% in the western part of the study area near the Gobi desert and also by a "C3 favoring valley" with P_{C4}<20% from south-east to north-east. From Collatz et al. (1998) a crossover temperature for
5 C3/C4 distribution of 22°C for the warmest month follows for a CO_2 partial pressure of 37 Pa. This theoretical threshold greatly agreed with our estimated distribution of C4 plants, which followed the 22°C July isotherm averaged for the years 1998–2007 ($MJulT_{98-07}$). Separated into two areas, $MJulT_{98-07}$ below and above 22°C, P_{C4} differed significantly (P<0.001, α=0.01) by approximately 13% with sample site mean
10 P_{C4}=23% above 22°C (mean $MJulT_{98-07}$=22.9°C) and sample site mean P_{C4}=10% below 22°C (mean $MJulT_{98-07}$=21.5°C). This indicates a substantial change in a narrow range of temperature.

4 Discussion

4.1 Variation of $\delta^{13}C$ of Inner Mongolia grassland at differing spatio-temporal scales

15 Individual vegetation samples give the mean isotopic composition of aboveground biomass grown in a period of weeks to months in an area of approximately 1000 m^2. The short temporal integration of vegetation samples likely leads to a bias of the results by the time of sampling as C4 develops considerably later than C3 in this area (Bai et al., 2004). This causes a high variability in $\delta^{13}C$ of vegetation samples leading
20 to a semivariance about five times as high as for wool samples (nugget: 690%^{2} versus 130%^{2}) and a semivariogram being almost a complete nugget (nugget/sill ratio of 73%) with a large RMSE (Table 2), which does not allow to retrieve a spatial pattern from vegetation analyses. Whole wool, however, integrates the isotopic signal of feed ingested between two successive shearing (one year) on an area that encompasses
25 the grazing grounds and the haymaking areas of an entire farm (several km^2).
  Despite the large spatio-temporal integration of wool its inter-annual variation may

be large. Inter-annual weather variability (e.g., dry years versus wet years; Wittmer et al., 2008) and a semi-arid situation, where moisture availability is almost entirely driven by precipitation but not by the spatially varying storage capacity of soil, certainly can alter the spatial patterns between years. Theoretically, inter-annual variations can be

5 excluded by pooling the data (Schuurmans et al., 2007) by years prior to the calculation of the empirical semivariogram. Though, this procedure neither improved the semivariogram (actually the nugget and the nugget/sill ratio were higher) nor the kriging prediction (all not shown). The main random variability hence mainly resulted from the intra-annual variation of the C3/C4 ratio but not from the inter-annual variation and

10 this intra-annual variability was excluded by using wool instead of vegetation.

4.2 Isotopic shift between vegetation and wool

Preferential grazing is one mechanism by which grazers can affect vegetation composition (Caswell et al., 1973), and hence carbon pools, fluxes and their isotopic composition. Yet, the present data indicated no preferential grazing of one photosynthetic type

15 (C3 relative to C4, or vice versa). This was suggested by the fact that the observed vegetation-wool shift (+2.7‰) was similar as shifts with pure C3 or C4 diets (average shift: +2.6‰±0.6‰ SD for hairs of different animal species in the studies of Minson et al., 1975; Jones et al., 1981; Sponheimer et al., 2003a; Ayliffe et al., 2004; Schwertl et al., 2005). If animals had grazed preferentially one component of vegetation, then

20 the apparent shift should deviate with a shift <2.7‰, if the sheep preferentially grazed the C3 component, and a shift >2.7‰ for preferential grazing of the C4 component. Preferential grazing would also result in an either right (=more negative; C3 preferred) or left (=less negative; C4 preferred) skewed density distribution of wool compared to vegetation. This was not the case as the density distributions for wool with applied shift

25 and for vegetation apparently were centered (Fig. 2b). In the density distribution of wool, however, the extremes on both sides of the vegetation density distribution were clipped due to the spatio-temporal integration by the animals. And finally, preferential grazing should cause a correlation between the shift and either stocking densities or

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P_{C4}, which both determine the chance for selective grazing. Such relations were not found in the grazing experiment. Furthermore, if selection would happen opportunities would be small on an annual basis with only one growth cycle due to the high grazing pressure caused by the high stocking rate in the study area (Sneath, 1998).

Differences in digestibility between C3 and C3 species can displace the signal in the wool and thus influence the vegetation-wool shift. Nonetheless several studies reported that the nutritional quality and/or digestibility of C4 species is inferior to that of C3 species (e.g., Sponheimer et al., 2003b; Barbehenn et al., 2004) the opposite was also reported (Scheirs et al., 2000). Digestibility decreases strongly with age of the plant material (Fick et al., 1994). An alternating ranking of the digestibility can thus be expected from the asynchronous growth of both photosynthetic types where the greening of the C4 species starts when the some aboveground parts of the C3 species are almost two months old. For that reason, further investigation on individual and combined digestibility of C3 and C4 species are needed. However, this has only minor influences on our results, as the reported differences in digestibility between C3 and C4 species rarely exceed 10–15% (e.g., Sponheimer et al., 2003b; Norman et al., 2008) and the overall C4 abundance in our study area is not higher than 40%. Postulating a direct effect of digestibility on the pattern of C4 abundance, this would lead to maximum error in the estimation of 6%. Anyhow, this would not have the potential to distinctly alter the C4 abundance pattern as derived from wool.

4.3 Variation in C4 end-member ($^{13}\Delta_4$) of C3/C4 mixing model

Several studies reported variations of $^{13}\Delta_4$ along environmental gradients e.g., a decrease in $^{13}\Delta_4$ with increasing precipitation (Schulze et al., 1996) or, in contrast, an increase of $^{13}\Delta_4$ with increasing soil water content (Chen et al., 2002). The absence of any relationship to climatic gradients (temperature, precipitation and soil water parameters) in our data set may thus be caused by compensating effects. Furthermore, C4 species of different metabolic types (see Pyankov et al., 2000) can differ significantly

in $^{13}\Delta$ (e.g., Schulze et al., 1996). This was apparent in our data, as *C. squarrosa* (NAD-ME metabolic type, Pyankov et al., 2000) had a 1.1‰ higher $^{13}\Delta$ than other metabolic types (mainly NADP-ME). Several studies reported that the abundances of different metabolic types are related to precipitation gradients with abundance of
5 NADP-ME plants increasing with increasing precipitation at the expense of NAD-ME plants (Wang et al., 2003; Cabido et al., 2008; Osborne, 2008). This should lead to an increase of $^{13}\Delta_4$ with precipitation. This was not obvious in our data as *C. squarrosa* was a component of the C4 community all over the sampling area. Additionally, there was no apparent pattern in the occurrence of the different metabolic types (data not
10 shown) with the exception of *Chloris virgata*, an annual grass of the PEP-CK metabolic type, which was restricted to the drier (western) part of the sampling area. However, *C. virgata* was never a dominant component the C4 community. Importantly, the present estimates of P_{C4} did not change very much when we varied the C4 end-member value of the C3-C4 mixing equation. If $^{13}\Delta_4$ was set to 5.5‰ (100% NADP-ME species in C4
15 community), then the resulting mean P_{C4} was 18.2%. Conversely, if $^{13}\Delta_4$ was set to 6.5‰ (assuming that the C4 community consisted entirely of NAD-ME species, such as *C. squarrosa*), then the mean P_{C4} was 19.8%. So, any reasonable error in estimation of $^{13}\Delta_4$ had a negligible effect on the spatial variation of P_{C4} (Fig. 4).

4.4   Regional variation in C3/C4 composition is related to temperature gradients

20 Competition between C3 and C4 photosynthetic types is controlled by ambient CO_2 concentration and temperature during the growing period (Ehleringer et al., 1997) with high CO_2 concentrations favoring C3 plants and high temperatures favoring C4 plants. The latter agrees with the conclusions of Pyankov et al. (2000) regarding the temperature-dependent distribution of C4 grasses in (Republic of) Mongolia. Due to
25 the simultaneous increase in temperature and precipitation during the growing season (Xiao et al., 1995) the temperature of the warmest month is effective for this competition. The warmest-month isotherm for the predicted crossover temperature follow-

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ing Collatz et al. (1998) essentially explained the spatial pattern. This was only true, however, if the isotherm was derived from the conditions during the study period because the study area has undergone major changes, which had to be accounted for. A pronounced warming of +2°C has increase in mean annual temperature in the last 30 years (NOAA NCDC Climate Data Online, 2008). Thus, the 22°C isotherm has shifted by about 250 km to the east. The 22°C isotherm for 1998–2007 matches the C3/C4 pattern of the same period while the 22°C of the last normal period does not. On the other hand, for the lower CO_2 concentration 30 years ago the crossover temperature was about 2°C lower according to Collatz et al. (1998). Although on average both effects seem to compensate each other numerically, this was not the case for the spatial pattern. The 20°C crossover isotherm of the last normal period did not differentiate between areas of significantly different P_{C4} (means 19 vs. 14%) while the mean difference in P_{C4} between the areas above and below the present crossover isotherm of 22°C was 13% (23 vs. 10%) and highly significant. Hence, the C4 abundance followed the crossover temperature isotherm calculated for the conditions during the sampling period. The good agreement even despite a flat gradient in summer temperature indicates the dominant influence of differences in quantum yield on the regional pattern while the large variation found on smaller scales are hence likely to be caused by controls acting on smaller scales. To our knowledge, this is the first proof on a regional scale for the predicted crossover temperature following Collatz et al. (1998). It shows that the present community reflects present conditions despite large changes in CO_2 concentration and temperature in the past.

5 Conclusions

This work demonstrates that wool is qualified for assessing the abundance of C4 plants in the Inner Mongolia grassland on the regional scale. This is advantageous because it allows covering the whole growth cycle, many years and large areas within short sampling campaigns. An enormous variation on P_{C4} occurred despite the integration

by wool over a 1-yr period and the grazing area. The regional pattern of P_{C4} followed predictions from C3/C4 crossover temperature of quantum yield in C3 and C4 plants. A significant difference was only obtained if the crossover temperature calculated for the conditions during the sampling period was used due to the large changes in CO_2 concentration and regional temperature.

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Interactive Discussion

Table 1. Effect of the environmental variables mean annual precipitation (MAP), mean precipitation during the growing period of the actual year (P), mean annual temperature (MAT), mean July temperature (MJulT) and mean July temperature 1998–2007 (MJulT$_{98-07}$) on δ^{13}C of Inner Mongolia grassland quantified by linear regressions; climate means apply for the last normal period 1961–1990 if not stated otherwise; data from vegetation and wool were combined after applying the appropriate shift for wool.

Parameter	Range	δ^{13}C response	SE	R^2	n
Altitude	840–1692 m a.s.l.	−2.4/1000 m a.s.l.	±0.001	0.02[*]	264
MAP	136–389 mm yr^{-1}	−1.3/100 mm yr^{-1}	±0.002	0.10[***]	264
P	0.4–2.3 mm day^{-1}	0.6/1 mm day^{-1}	±0.403	0.01 n.s.	264
MAT	1.1–7.9°C	0.3/1°C	±0.098	0.03[**]	264
MJulT	18.5–25.2°C	0.5/1°C	±0.108	0.09[***]	264
MJulT$_{98-07}$	20.5–25.0°C	0.8/1°C	±0.151	0.10[***]	264

[*], [**], [***] denote error probability smaller than 0.05, 0.01 and 0.001, respectively.

Table 2. Semivariogram parameters for spherical models of P_{C4} derived from δ^{13}C of wool or vegetation. Nugget uncertainty of P_{C4} is the square root of twice the nugget.

Semivariogram parameter	Wool semivariogram	Vegetation semivariogram
nugget (%^{2})	130	690
sill (%^{2})	300	950
range (km)	260	305
nugget/sill ratio (%)	43	73
nugget uncertainty (%)	16	37
RMSE (%^{2})	24.9	86.5
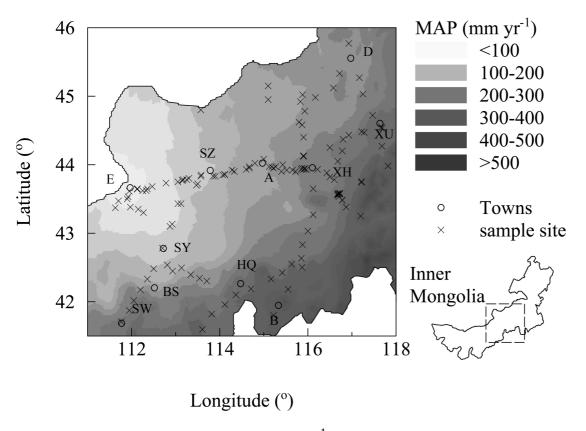
Fig. 1. Mean annual precipitation (MAP, $mm\,yr^{-1}$, normal period 1961–1990) and sampling sites within the study area in Inner Mongolia, People's Republic of China. Towns are A=Abag Qi, B=Baochang, BS=Bayan Sum, D=Dong Ujimqin Qi, E=Erenhot, HQ=Huang Qi, SW=Siziwang, SY=Sonid Youqi, SZ=Sonid Zuoqi, XH=Xilinhot, XU=Xi Ujimqin Qi.
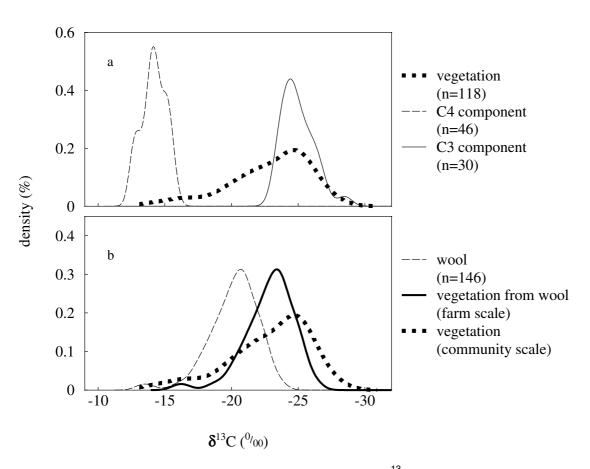
Fig. 2. Density distribution of carbon isotope composition ($\delta^{13}C$) of carbon pools in Inner Mongolia grassland: **(a)** standing vegetation, C4 component and C3 component; **(b)** site mean of wool, whole vegetation and wool with applied shift (data from the grazing experiment are not included).
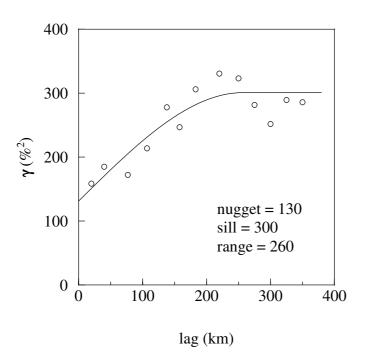
Fig. 3. Empirical (circles) and theoretical (line) semivariogram of percent C4 in above-ground biomass (in %) calculated from isotopic signatures of wool.
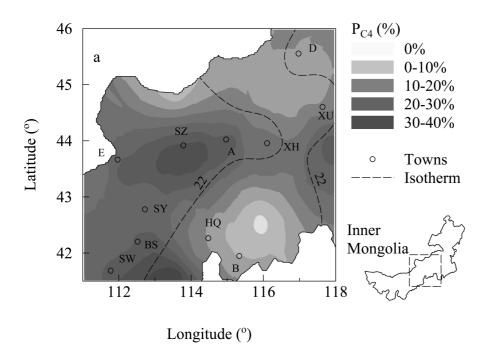
Fig. 4. Regional P_{C4} developed via kriging, estimated from wool originating from 1998–2007. Mean krige standard deviation for the study area is 9.4%. Towns are the same as in Fig. 1. The 22°C isotherm reflects meteorological conditions during the period 1998–2007 and it is equivalent to the predicted crossover temperature for the CO_2 concentration during this period.