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Carbon isotope discrimination of C3 vegetation in Central Asian grassland as related to long-term and short-term precipitation patterns

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Abstract. The relationship between carbon isotope discrimination ($^{13}\Delta$) of C3 vegetation and long-term (30 years) and short-term (growing period) precipitation was investigated. Different species of *Stipa*, a dominant grass genus in the (semi-)arid Asian steppes, and other C3 species were collected along aridity gradients in Inner Mongolia in 2005 (11 sites, 71 samples) and in the Republic of Mongolia in 2006 (40 sites, 45 samples). The data set was expanded with published and unpublished data of *Stipa* and other C3 species (11 studies covering 8 years, including 64 observations of *Stipa*, and 103 observations of other C3 species) and C3 community bulk-samples (11 samples). Weather data were geostatistically interpolated for all sampling sites and years. $^{13}\Delta$ of *Stipa* followed different relationships for the individual years when related to mean annual precipitation due to large anomalies between annual and long-term average precipitation patterns. However, the $^{13}\Delta$ response to rainfall converged when the (long-term) mean annual precipitation was replaced by year-specific mean daily precipitation during the growing period ($\overline{P}_G$). Remarkably, the $^{13}\Delta$-response to ($\overline{P}_G$) for C3 species as a whole (including herbaceous dicots, semi-shrubs and grasses) and also the C3 community-level response were virtually identical to that of *Stipa*. The relation was also valid outside the geographical and climatic range where it was developed, giving proof of its robustness.

1 Introduction

The Central Asian grassland is the largest continuous biome of the world and includes the steppes of the Republic of Mongolia (1.3 Mio km^2 of a total land area of 1.6 Mio km^2, Kerven et al., 1996) and of the Inner Mongolia autonomous region (0.8 Mio km^2 of a total land area of 1.2 Mio km^2, Xiao et al., 1995a and citations therein) of the People's Republic of China. This region has a continental climate with most of the rain falling from June to August. By far, the largest part of this grassland is situated in arid and semiarid zones, and the amount and distribution of rainfall is a major factor controlling vegetation composition, functioning and services, such as the quality and availability of herbage for grazing livestock (Xiao et al., 1995a and citations therein). The Central Asian grassland flora contains a large number of C4 species (approx. 20% of the flora; mostly dicots; Pyankov et al., 2000), but the vegetation is generally dominated by C3 species, mostly perennial grasses. In particular, species of the genus *Stipa* are a frequent and often dominant component of most grassland types in the region.

The carbon isotope composition ($\delta^{13}C$) of C3 vegetation generally correlates negatively with water availability. This is primarily attributed to the leaf-level response of ^{13}C discrimination ($^{13}\Delta$) to water availability in C3 plants (Farquhar et al., 1989), which translates to community and higher scales (e.g., Kaplan et al., 2002; Randerson et al., 2002; Schnyder et al., 2006). The carbon isotope composition of plants ($\delta^{13}C_p$) is related to $^{13}\Delta$ as

$$\delta^{13}C_p = (\delta^{13}C_a - {}^{13}\Delta)/(1 + {}^{13}\Delta) \qquad (1)$$
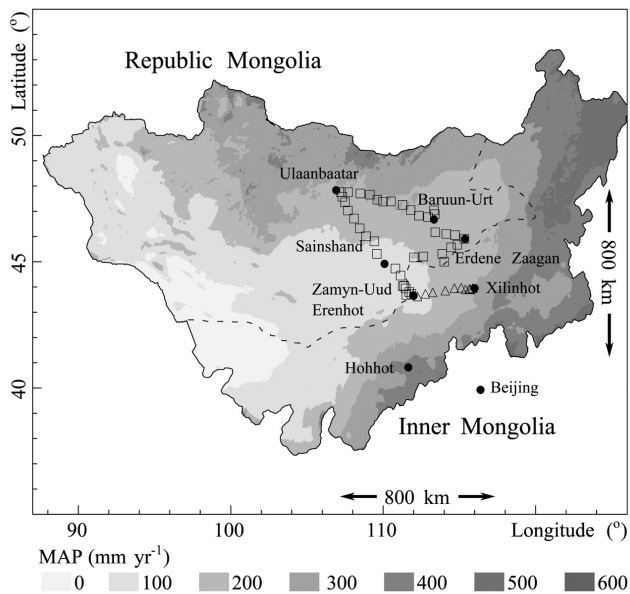
Fig. 1. Mean annual precipitation (MAP, mm yr^{-1}); normal period 1961–1990; data from Climate Source Inc.), major towns and sampling sites (triangles denote the 2005 and squares the 2006 sampling campaign).

where $\delta^{13}C_a$ is the $\delta^{13}C$ of atmospheric CO_2 (Farquhar et al., 1989). Rearranging Eq. (1) leads to $^{13}\Delta=(\delta^{13}C_a-\delta^{13}C_p)/(1+\delta^{13}C_p)$ and shows that $^{13}\Delta$ can be calculated directly from $\delta^{13}C_p$ if $\delta^{13}C_a$ is also known.

Precipitation is highly variable in time and space in the Mongolian grassland. Mean annual precipitation (MAP) varies from several hundred millimeters per year (mm yr^{-1}; mainly in the northern and eastern part of the region) to less than one hundred millimeters per year in the Gobi desert (Fig. 1). But, at a given site, hydrological conditions may differ drastically between years. For example, MAP at Erenhot is 158 mm yr^{-1}, but exceeds 275 mm yr^{-1} or falls below 45 mm yr^{-1} in every second year (NOAA NCDC Climate Data Online, 2007). These factors may exert strong influences on the carbon isotope composition of grassland via (i) effects on the relative abundance of C3 and C4 species (which differ by about 10 to 18‰ in carbon isotope discrimination; O'Leary, 1981; Farquhar et al., 1989), and (ii) variation of $^{13}\Delta$ in C3 plants.

The carbon isotope signal produced by grassland vegetation is imprinted in ecosystem carbon pools (such as soil carbon) and exchange fluxes (such as biosphere atmosphere CO_2 exchange), and is therefore potentially highly useful for biogeochemical studies and ecosystem reconstruction. However, in C3:C4 mixed grassland, the separate effects of C3:C4 abundance and variation of $^{13}\Delta$ in C3 plants on community/ecosystem $^{13}\Delta$ must be known, to allow interpretation of ecosystem or community carbon isotope signals. The present work concentrates on one aspect of this problem, namely the

effect of aridity on $^{13}\Delta$ in C3 plants, and then discusses its implications for C3:C4 mixing models.

The effect of aridity on $^{13}\Delta$ in C3 plants has generally been studied in aridity-transect studies where the $^{13}\Delta$ of species was related to mean annual precipitation at the sampling sites. The responses observed in theses studies were highly variable (e.g., Stewart et al., 1995; Schulze et al., 1991, 1996; Wang et al., 2003; Liu et al., 2005; Zheng and Shangguan, 2007). Here, we test the hypothesis, that the variability of the $^{13}\Delta$-response of C3 plants to MAP in (semi-)arid grasslands is related to interannual variation of weather conditions. To test this prediction, we analysed the relationship between $^{13}\Delta$ of C3 species and short-term (growing period) and long-term (climatic, 30 years) precipitation along aridity gradients in Inner Mongolia in 2005 and in the Republic of Mongolia in 2006. The data set was complemented with published and unpublished (partially own) data, thus expanding the temporal and geographic representation.

2 Material and methods

2.1 Sampling area

Stipa species were sampled in the Republic of Mongolia in 2006 (total transect length of approx. 1650 km) and in Inner Mongolia, People's Republic of China in 2005 (total transect length of approx. 400 km) passing three vegetation zones, forest steppe, typical steppe and desert steppe (Wallis de Vries et al., 1996), with MAP ranging from around 280 mm yr^{-1} near Ulaanbaatar to 125 mm yr^{-1} and less in the Gobi area near Sainshand and Erenhot and rising again to 280 mm yr^{-1} near Xilinhot (Fig. 1).

The mean temperature ranges from about $-23°C$ in winter in Ulaanbaatar to about $23°$ in summer in Zamyn-Uud. The local precipitation is highly variable in space and time (Gong et al., 2004). Even closely vicinal climate stations show remarkable differences: although the distance between Zamyn-Uud (Republic of Mongolia) and Erenhot (Inner Mongolia) is only 10 km, the mean monthly precipitation in August is 0.52 mm day^{-1} for Zamyn-Uud and 1.29 mm day^{-1} for Erenhot (mean for last normal period 1961–1990). Similarly, the MAP is 114 mm yr^{-1} for Zamyn-Uud and 158 mm yr^{-1} for Erenhot, while mean monthly temperatures are similar for both locations (calculated from NOAA NCDC Climate Data Online, 2007).

2.2 Sampling method and the sampled species

Sampling stops were made about every 30 km. Leaves of *Stipa* (if present), and other C3 species were cut with scissors from several plants within an area of about 50×50 m (sometimes there were only one or two specimen of a species at a sampling site). The samples for each site were transferred to separate paper bags and dried behind the front window of

the car. The current position was measured with a mobile outdoor global positioning system (Casio Satellite Navi 2 or Garmin GPS 12). In total 39 *Stipa* samples were taken in the Republic of Mongolia in 2006 and ten *Stipa* samples were taken in Inner Mongolia in 2005 (see Table A1 in supplementary material for original data – http://www.biogeosciences.net/5/913/2008/bg-5-913-2008-supplement.pdf). In a few cases specimens of *Stipa* could not be classified at the species level. The following species were collected: *Stipa krylovii*, *Stipa grandis* and *Stipa glareosa* in Republic of Mongolia, and *Stipa gobica* and *Stipa grandis* in Inner Mongolia. In addition, 61 samples of another 19 C3 species were collected in 2005; and six samples of six C3 species in 2006.

For validation, the data set was expanded with two samples of *Stipa* and 20 samples from 20 C3 species sampled in 2003 in Inner Mongolia, three bulk C3 samples collected in Mongolia in 2006 and eight C3 bulk samples collected in Inner Mongolia in 2007. Sampling procedures were the same as during the 2005 and 2006 sampling campaigns.

2.3 Inclusion of published data and normalization for altitude effect

Published data (Table 1) were included in the validation data base with the primary aim of increasing the temporal (and secondarily the geographic) representation. These data covered a wide range of site conditions, with altitudes extending above 2000 m a.s.l. (especially Ivanov et al., 2007). As altitude affects the δ^{13}C of C3 plants (Körner et al., 1988), all data were normalized to an altitude of 1000 m a.s.l., which is close to the average altitude of our sampling locations (mean: 1160 m a.s.l; SD: 180 m). The altitude effect was corrected for by 1.15‰ per 1000 m following Männel et al. (2007) with a mean absolute correction to $^{13}\Delta$ of 0.26‰. For publications containing no altitude data, this information was obtained with Google Earth$^{®}$ using the coordinates of the sample sites.

2.4 Isotope analysis

Samples were further dried in the laboratory (1 h at 95°C and 48 h at 60°C), ground with a ball mill and then combusted in an elemental analyser (NA 1110; Carlo Erba, Milan) interfaced (ConFlo III; Finnigan MAT, Bremen) to an isotope ratio mass spectrometer (Delta Plus; Finnigan MAT). Carbon isotope data are presented as δ^{13}C relative to the international VPDB standard: $\delta^{13}C=(R_{sample}/R_{standard})-1$; where R_{sample} and $R_{standard}$ are the ratios of ^{13}C/^{12}C in the sample and standard. All samples were measured against laboratory working standard gases, which were previously calibrated against IAEA secondary standards (IAEA CH6 for ^{13}C, accuracy of calibration ±0.06‰ SD). Wheat flour (C/N 21:6) as solid internal laboratory standard (SILS) was calibrated against these references. One SILS was measured after every tenth sample. The precision for sample repeats was better than 0.2‰ for δ^{13}C.

C3 community-mean $^{13}\Delta$ was calculated as the biomass- or ground cover-weighted average of all C3 species in the community. The arithmetic (unweighted) mean $^{13}\Delta$ was calculated if information on ground cover or biomass fraction was missing. In this way C3 community-mean $^{13}\Delta$ was obtained from 35 data sets by Chen et al. (2005), Wang et al. (2005), Liu et al. (2005), Gong et al. (2008) and for 10 data sets obtained by us in 2005. This was complemented by 11 C3 samples collected as bulk samples in our 2006 and 2007 sampling trips.

2.5 Carbon isotope composition of atmospheric CO_2

$\delta^{13}C_a$ of sampling years was estimated with a third order polynomial that was fitted to measured $\delta^{13}C_a$ data of Keeling (1979), Friedli et al. (1986), Conway et al. (1994), Francey et al. (1999), Gat et al. (2001), Allison et al. (2003) and the NOAA data base (NOAA NCDC Climate Data Online, 2007) for the stations Mauna Loa, Siple, Antarctica, Ulan Uul, Shetland Islands, Hegyhatsal and Ochsenkopf (n=62), as in Geist et al. (2005):

$$\delta^{13}C_a = m_1 \times yr^3 + m_2 \times yr^2 + m_3 \times yr + m_4, \qquad (2)$$

where yr is the sampling year and m_1, m_2, m_3 and m_4 are constants (11.70712×10^{-6}; -69.78999×10^{-3}; 138.640104 and -91.785 valid from 1959 to 2006). The standard error of this regression was 0.09‰. $\delta^{13}C_a$ decreased from −8.12‰ in 1996 to −8.48‰ in 2007. The mean $\delta^{13}C_a$ during the growing period was then estimated from the mean $\delta^{13}C_a$ of the year (Eq. 2) by applying a correction for the seasonal departure from the annual mean $\delta^{13}C_a$. This correction was obtained from air samples collected at Ulan Uul (Tans et al., 2005), which is a long-term measuring station located near the center of the sampling area (44°27′ N, 111°05′ E). Average $\delta^{13}C_a$ was less negative by 0.25‰ between April and August as compared to the annual average. Thus a $\delta^{13}C_a$ of −8.17‰ and −8.19‰ resulted for the growing periods in 2005 and 2006 respectively. The mean $\delta^{13}C_a$ during the growing period of other years was estimated accordingly.

2.6 Statistical methods

Linear and linearised regressions were used to evaluate the datasets. The coefficient of determination was tested with a two-sided test for significance of the regression. In addition the 95%-confidence interval for the samples and the 95%-confidence interval for the regression were calculated to allow for comparison between data sets. A pairwise comparison of means was used to test whether the species differed regarding MAP and Δ. These statistical procedures followed standard protocols (Sachs and Hedderich, 2006).

Geostatistical analyses (for theory see Nielsen and Wendroth, 2003; Webster and Oliver, 2004) were conducted

Table 1. Sampling year, region, mean annual precipitation (MAP) and species name of literature references and own data used for validation. Top: *Stipa* data, bottom: other C3 species.

Sampling year	Region	MAP (mm yr^{-1})	Altitude (m a.s.l.)	Number of data	Species	Reference
1996	Mongolia	250	750	1	*Stipa krylovii*	Cerling and Harris (1999)
1999	Northwest China	290	1730	3	*Stipa breviflora*	Wang et al. (2005)
2001	Inner Mongolia	325	1267	1	*Stipa grandis*	Chen et al. (2005)
2001	Mongolia	118	2170	2	*Stipa glaeosa*	Ivanov et al. (2007)
2002	Northwest China	240–670	498–2095	37	*Stipa bungeana*	Liu et al. (2005)
2003	Inner Mongolia	340	1180	2	*Stipa krylovii, Stipa* unidentified	This study
2003–2004	Inner Mongolia	250	1200	3	*Stipa grandis, S. krylovii, S. baicalensis*	Liu et al. (2004)
2004	Inner Mongolia	321	1184	11	*Stipa grandis*	Gao (2004)[1]
2004–2005	Inner Mongolia	323	1267	4	*Stipa grandis*	Gong et al. (2008)
1997	Mongolia	250	1750	4	*Carex rhynchophysa, Agrostis trinii, Leymus chinensis, Ptilogostis mongolica*	Cerling and Harris (1999)
1999	Northwest China	194	1730–1850	15	*Allium polyrhizum, Reaumuria soongorica, Sympegma regelii, Ajania fruticolosa* and others	Wang et al. (2005)
2001	Mongolia	118	2170	5	*Allium polyrhizum, Ephedra sinica*	Ivanov et al. (2007)
2002	Northwest China	240–670	498–2095	31	*Lespedeza davurica, Heteropappus less*	Liu et al. (2005)
2003	Inner Mongolia	323	1180	20	20 different C3 species	This study
2003	Northwest China	50–350	395–1956	21	*Reaumuria soongorica*	Ma et al. (2005)
2004	Inner Mongolia	323	1267	4	*Carex korshinskyi, Leymus chinensis*	Gong et al. (2008)
2005	Inner Mongolia	323	1267	3	*Carex korshinskyi, Leymus chinensis*	Gong et al. (2008)
2005	Inner Mongolia	146–364	951–1204	61	*Leymus* sp., *Caragana* sp., *Agropyron* sp. and others	This study
2006	Mongolia	125–257	1253–1479	6	*Caragana microphylla, Hedysarum pumilum, Astralagus* sp., *Salsola laricifolia*	This study

[1] Gao, Y.: Yinzhi Gao, Institut für Pflanzenernährung, Christian-Albrechts Universität zu Kiel, unpublished data, 2004.

with package geoR (Ribeiro and Diggle, 2001) of the software GNU R 2.6 (R Development Core Team, 2007). The semivariance of a parameter (e.g. precipitation) is defined as the half mean quadratic difference of the parameter values of points which are separated by a certain distance (called lag). For calculation of the latter, the coordinates of sampling points were transformed from geographic coordinates to UTM coordinates using the package PBSmapping (Schnute et al., 2007, UTM zone=50). Semivariances were then grouped by lag classes and semivariances and lags within a group were averaged yielding the empirical semivariogram (x-axis: lag, y-axis: semivariance). A theoretical semivariogram was fitted to minimize weighted least squares, with weights calculated from the ratio of pairs within a class to mean lag. This gives more weight to the classes, which are based on many data pairs and which are more important for interpolation. Maps were constructed by spatial interpolation, which was carried out for a rectangular grid by ordinary point kriging, based on the theoretical semivariogram. The quality of the predictions from the resulting maps is given as the krige standard deviation averaged for the sampling locations.

2.7 Meteorological data

The growing period in the sampling area starts in April with only one growth cycle (no regrowth after cutting or heavy grazing). Sampled plant material thus included biomass grown in the period of April to mid of July (2005) or April to end of July/beginning of August (2006). This period is termed "growing period" in the following and indexed with "G". Most of the rain usually falls during this period. For 40 meteorological stations in and around the sampling area, long-term mean precipitation from April to September correlated closely with MAP (r^2=0.98) and contributed 74‰ to MAP. Normally only little growth occurs in September, which receives only 10‰ of MAP in an average year. Hence, above-ground living biomass in ungrazed areas generally peaks between late July and late August (Xiao et al., 1995b). The effective water availability for plants in different years and studies was estimated as the mean daily precipitation during the respective growing period ($\overline{P}_G$; mm day^{-1}). This accounted for the fact that sampling did not occur on exactly the same dates in the different studies, but provided a common denominator for comparison of data gathered in different years.

Sampling sites, either own or from literature, were usually not located near meteorological stations. Two data sets were used to estimate meteorological data for the sampling sites. (i) The long-term averages of the last normal period (1961–1990) of precipitation data (monthly and annual means) were taken from high resolution maps obtained from The Climate Source Inc., Corvallis, Oregon. These maps have a pixel resolution of 0.02°×0.02° (approximately 1.5×1.5 km^2, Fig. 1), judged sufficient to locate the sampling sites. These data were created using the PRISM method (parameter-elevation regressions on independent slopes model; Daly et al., 2002), which accounts for topography, rain shadows, lake effects, temperature inversions, and more. (ii) For year-specific data we assumed that the principal causes underlying the PRISM maps were also valid at the small scale but were modified by large-scale trends. Daily precipitation data at 40 climate stations, provided by the NOAA Satellite and Information Service (NOAA NCDC Climate Data Online, 2007) was compiled. These stations were situated inside or just outside the sampling area. The latter were included to improve the geostatistical interpolation at the periphery of the sampling area. To calculate $\overline{P}_G$, the difference between the normal-period mean daily precipitation during the growing period (MPG) and $\overline{P}_G$ was calculated for each meteorological station to quantify the anomaly, $\overline{P}_G$. These anomalies were geostatistically interpolated for the whole sampling area and each year to represent the large-scale spatial pattern of the anomalies. This trend was then superimposed on high-resolution normal-period maps to obtain high-resolution maps for individual years; e.g. for the year 2005 $\overline{P}_G$ was given by:

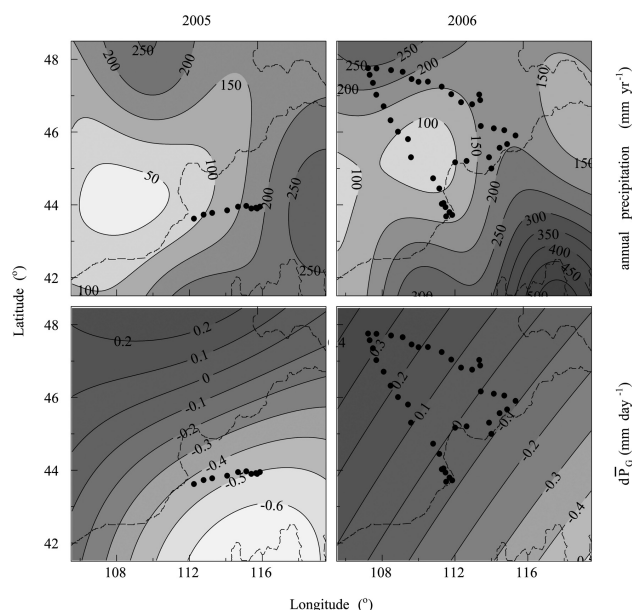$$\overline{P}_G 05 = \text{MGP} + \text{d}\overline{P}_G 05. \tag{3}$$

Fig. 2. Isohyet maps for the annual precipitation in 2005 (top left) and 2006 (top right) and of the anomalies in mean daily precipitation during the growing period (d$\overline{P}_G$) in 2005 (bottom left) and 2006 (bottom right). For details see text. Circles denote sampling sites; dashed lines are the border between the Republic of Mongolia and Inner Mongolia Autonomous Region of China. Mean krige standard deviation is 46 mm yr^{-1} (top left), 52 mm yr^{-1} (top right), 0.32 mm day^{-1} (bottom left) and 0.41 mm day^{-1} (bottom right) for the locations of vegetation sampling.

While annual precipitation was similar in 2005 and 2006, $\overline{P}_G$05/06 differed considerably (Fig. 2). In some locations anomalies in $\overline{P}_G$ between the two years and between MGP and $\overline{P}_G$ were as large as 0.6 mm day^{-1}, which was more than one third of the mean precipitation. The best geostatistical interpolation was obtained by ordinary kriging interpolation with Gaussian models (Fig. 2). In both years there was a trend in the anomaly, which decreased from northwest to southeast. In 2005 the trend differed somewhat in direction, strength, curvature and the position of the zero isohyet compared to 2006. In 2006 the zero isohyet was near the center of the sampling area, the south-eastern part of the sampling area being drier than average and the north-western part wetter. In 2005 the zero isohyet was near the northern border of the sampling area, and most of the area received less precipitation during the vegetation period than in a normal year (Fig. 2).
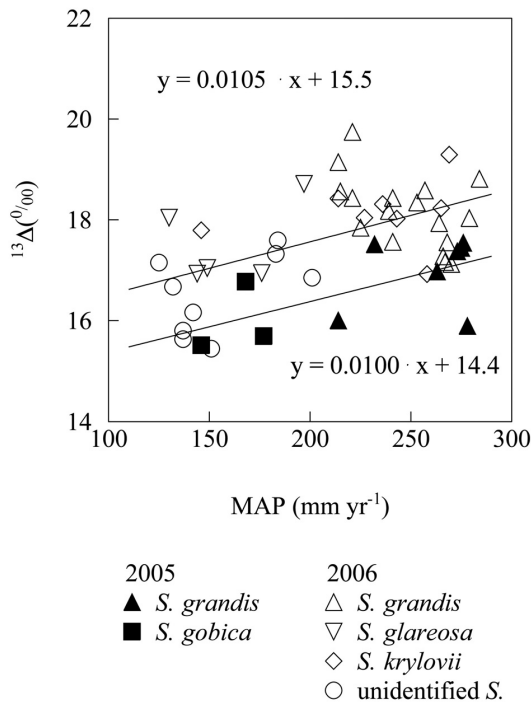
Fig. 3. Carbon isotope discrimination ($^{13}\Delta$) of different *Stipa* species depending on mean annual precipitation (MAP) for samples collected in 2005 (r^2=0.385, P<0.1) and in 2006 (r^2=0.296, P<0.001).

Fig. 4. $^{13}\Delta$ and mean daily precipitation during the growing period (d$\overline{P}_G$) for *Stipa* species sampled in 2005 (triangels) and in 2006 (squares). Closed symbols: *S. grandis*. r^2=0.352, $P\ll0.001$.

3 Results

3.1 Carbon isotope discrimination of *Stipa* as related to mean annual precipitation

The gradient of MAP covered by the sampling transects was similar in the two years, and ranged between approx. 130 and 290 mm yr^{-1} (Fig. 3). $^{13}\Delta$ among *Stipa* increased with MAP in both years, although the increase was only significant in 2006 (P<0.01). The slope of this relationship ($^{13}\Delta$ versus MAP) was very similar in both years (P>0.05), but there was a significant offset between the years, so that $^{13}\Delta$ at a particular MAP was 1.1‰ higher in 2006 than in 2005. In both years, there was no relationship between $^{13}\Delta$ and the C/N ratio of samples suggesting that variation in photosynthetic capacity related to changed nitrogen concentration did not cause the variation in $^{13}\Delta$.

In both years, the effect of MAP on $^{13}\Delta$ coincided at least partially with species replacement along the aridity gradient: *S. gobica* and *S. glareosa* were only present in the most arid part of the transects (MAP<200 mm yr^{-1}) and had lower than average $^{13}\Delta$ (Table 2). Conversely, *S. grandis* and *S. krylovii* had higher than average $^{13}\Delta$ and mainly occurred where MAP was >210 mm yr^{-1}. This was true except for one site with MAP=146 mm yr^{-1} where *S. krylovii* was also found in 2006. It is not known if *S. krylovii* has a wider eco-
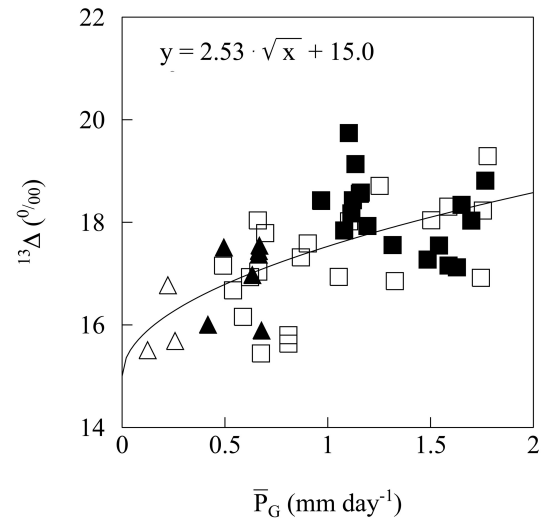
logical range with respect to MAP, or if a local hydrological peculiarity, such as local groundwater or lateral water flow, accounted for its presence. The significant separation between species regarding MAP and $^{13}\Delta$ suggests that species distribution in the area was (at least partially) determined by MAP, whereas species $^{13}\Delta$ was strongly influenced by year-to-year variability in precipitation.

3.2 Carbon isotope discrimination of *Stipa* as related to actual precipitation

Mean daily precipitation during the growing period ranged from 0.1 to 0.7 mm day^{-1} in 2005 and from 0.5 to 1.8 mm day^{-1} in 2006. $^{13}\Delta$ of *Stipa* collected in 2005 and 2006 followed the same relationship with $\overline{P}_G$, with $^{13}\Delta$ (‰)=15.0+2.53 sqrt($\overline{P}_G$) (Fig. 4). Thus, the difference between years (apparent when $^{13}\Delta$ was regressed against MAP) disappeared when $^{13}\Delta$ was regressed against growing period precipitation. This suggested that interannual variations in $^{13}\Delta$ were related to interannual variations in precipitation. The square root expression indicates that the effect was strong when $\overline{P}_G$ was very low and decreased with increasing precipitation.

Species did not differ in the relationship between $^{13}\Delta$ and $\overline{P}_G$ (highlighted for *S. grandis* in Fig. 4). Thus, it seemed that species-replacement was controlled by long-term precipitation patterns, whereas the within-species response to short-term precipitation patterns controlled $^{13}\Delta$.

3.3 Comparison with published *Stipa* data

There were eight data sets (six published and two unpublished; see Table 1) for which the relationship

Table 2. Mean annual precipitation (MAP) at sampling sites and carbon isotope discrimination ($^{13}\Delta$) of different species of *Stipa* in the 2005 and 2006 transect studies. Mean, minimum and maximum, standard deviation (SD), and significance of species separation at $P < 0.05$.

Species	MAP (mm yr^{-1})					$^{13}\delta$ (‰)				
	Mean	Min.	Max.	SD	Significance	Mean	Min.	Max.	SD	Significance
2006										
S. glareosa	160	130	197	27	A	17.5	16.9	18.7	0.81	B
S. krylovii	232	146	269	40	B	18.1	16.9	19.3	0.66	B
S. grandis	246	209	284	25	B	18.2	17.1	19.7	0.71	B
2005										
S. gobica	164	146	177	16	A	16.0	15.5	16.8	0.68	A
S. grandis	259	214	278	25	B	17.0	15.9	17.5	0.72	A

between $^{13}\Delta$ and actual precipitation could be calculated and compared with the results from our transects (see Table A2 in supplementary material for precipitation data – http://www.biogeosciences.net/5/913/2008/bg-5-913-2008-supplement.pdf). These studies reported a total of 62 data for different species of *Stipa*. The data corresponded well with the relation derived from the 2005 and 2006 samples (Fig. 5, top). Notably, this was also true for studies in which *Stipa* experienced higher precipitation than the maximum encountered in our transect studies (Fig. 5, hatched areas denoting $(\overline{P}_G) > 2.2$ mm day^{-1}). Inclusion of data of Liu et al. (2005) reporting $^{13}\Delta$ of *S. bungeana* along a rainfall gradient in Northwest China further expanded the range of precipitation, and also agreed with the relationship derived from the 2005 and 2006 collections of *Stipa*. Overall, these comparisons supported the notion that the relationship presented in Fig. 4 provides a general and unbiased prediction of the $^{13}\Delta$ of *Stipa* in the grasslands of Mongolia.

The relation with $\overline{P}_G$ even explained data obtained in 2001 (Table 1), which was an extremely dry year in Inner Mongolia. In that year more than half of the numerous lakes of the province of Qinghai (in the west of Inner Mongolia) disappeared (Reuters, 2001), and in the Republic of Mongolia the herders lost one quarter of their large-animal livestock such as horses and cattle (Retzer, 2007).

3.4 Comparison with other C3 species

"Non-*Stipa*" C3 species included 170 data from a total of 55 species, collected in eight different years (1996, 1999, 2001, 2002, 2003, 2004, 2005 and 2006). Again, the comparison indicated a fair agreement between the precipitation response of $^{13}\Delta$ in *Stipa* and that of the other species, although the scatter was somewhat larger in the latter. Still, 80% (135 out of 170) of all non-*Stipa* data fell inside the 95‰ confidence interval of *Stipa* (Fig. 5, bottom). Subdivison of the whole data set in functional groups (monocots $n=163$ and dicots $n=118$; grasses $n=143$, forbs $n=50$ and shrubs and semi-shrubs $n=68$) also provided no evidence for a different precipitation response at the level of functional groups. However, dicots deviated from monocots insofar as their $^{13}\Delta$ was about 0.5‰ higher on average at a given precipitation level. In particular, leaves of *Reaumuria soongorica*, a short-statured woody shrub, had 1.8‰ higher $^{13}\Delta$ than *Stipa* and other species at the same precipitation level. Yet, even in *R. soongorica*, the slope of the $^{13}\Delta$ versus $\overline{P}_G$ relationship did not deviate from that of *Stipa* or that of the whole of other species.

3.5 The $^{13}\Delta$-response of C3 communities to growing period precipitation

The C3 community-mean $^{13}\Delta$ responded to mean daily growing period precipitation in the same way as $^{13}\Delta$ of *Stipa* (Fig. 6; see Table A3 in supplementary material for main species and biomass data – http://www.biogeosciences.net/5/913/2008/bg-5-913-2008-supplement.pdf) but with less scatter due to an averaging effect, which compressed the 95‰ confidence interval for the data points. The regression for the community data, calculated to obtain a robust relation over the entire range of precipitation, was virtually the same relation as that for *Stipa*, but the confidence interval of the regression remained narrow over the entire range due to the continuous support by data.

3.6 The relationship between precipitation anomalies and $^{13}\Delta$ anomalies

The deviation of growing period precipitation from the long-term mean (precipitation anomaly) was directly related to the deviation between actual $^{13}\Delta$ and $^{13}\Delta$ predicted for mean conditions at the respective sites ($^{13}\Delta$ anomaly). This effect was manifested at the level of C3 communities (Fig. 7), and species (data not shown). The precipitation anomalies modified the community-mean $^{13}\Delta$ by ±1‰. The response at the community level and the large spatial extension of precipitation anomalies imply that this response was also effective at larger scales.
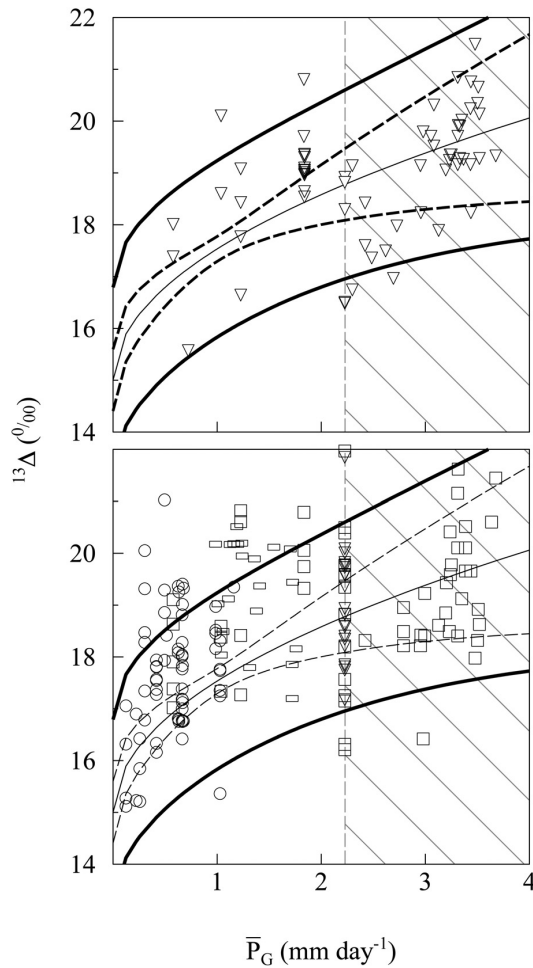
Fig. 5. Validation of the $^{13}\Delta$ *versus* mean daily precipitation relationship of *Stipa* sp. shown in Fig. 4. Top panel: *Stipa* data from nine studies (*n*=64) given in Table 1. Bottom panel: Data from other ("non-*Stipa*") C3 species as taken from literature (squares; *n*=83; see Table 1) or collected in our own 2005 and 2006 transect studies (circles; *n*=87, see Table 1). Data from *Reaumuria soongorica* (from Ma et al., 2005; samples obtained in 2003) are shown as rectangles (*n*=21). In both panels, the lines denote the *Stipa* regression from Fig. 4, which was obtained from the 2005 and 2006 samples (central line), the 95% confidence intervals for the regression (dashed inner lines) and the 95% confidence intervals for the individual *Stipa* samples collected in 2005 and 2006 (thick outer lines). The hatched areas denote the precipitation range that exceeded the range covered by the 2005 and 2006 sampling transects.

4 Discussion

4.1 Interannual variation of $^{13}\Delta$ results from growing period precipitation anomalies

This work reveals strong effects of interannual variation in precipitation on $^{13}\Delta$ of C3 plants in the grasslands of Mongolia. This effect was particularly evident in the genus *Stipa*
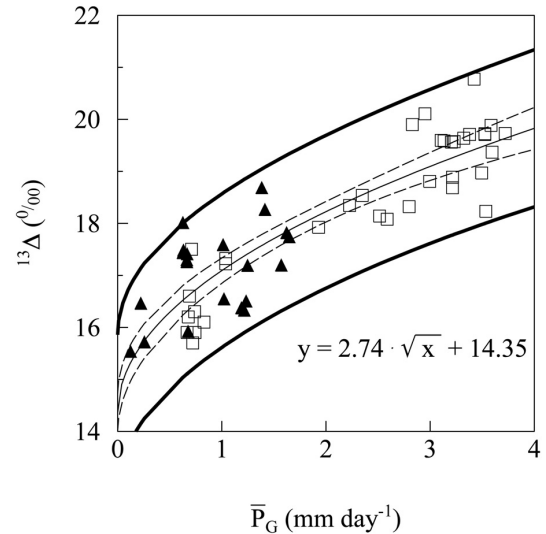

Fig. 6. $^{13}\Delta$ and $\overline{P}_G$ for C3 communities from this study (closed triangles) in 2005 (*n*=10), in 2006 (*n*=3) and in 2007 (*n*=8) and from literature data (squares; *n*=35). All data were adjusted to a common altitude of 1000 m a.s.l. The middle line denotes the square-root regression (r^2=0.753, $P \ll 0.001$), dashed lines the 95%-confidence interval for the regression and outer bold lines the 95%-confidence interval for the data points.

for which a large data set was available from collections along precipitation gradients in two different years, and published data from several years. Moreover, the effect was also apparent at the level of communities and functional groups (grasses other than *Stipa*, perennial forbs, and shrubs and semi-shrubs). An important consequence of the interannual variability of precipitation was that it caused interannual fluctuations in the relationship between (annually determined) $^{13}\Delta$ and MAP. This means, that a stable and unbiased relationship between $^{13}\Delta$ and MAP can only be obtained by relating long-term averaged $^{13}\Delta$ to MAP.

Interannual variation of $^{13}\Delta$ (or δ^{13}C) has been observed before, particularly in trees (Sparks and Ehleringer, 1997; Warren et al., 2001; Li et al., 2007), but also in Grassland taxa (Mole et al., 1994; Tsialtas et al., 2001), and was also explained by rainfall anomalies (Mole et al., 1994; Li et al., 2007) or other weather related factors (e.g. seasonal variation in water vapour deficit as reported by Sparks and Ehleringer (1997), variation in soil water content as reported by Tsialtas et al. (2001) and Schnyder et al. (2006)). However, effects of weather anomalies on $^{13}\Delta$ have generally not been considered in aridity transect studies. It is evident from the present work, that (at least) part of the variation in $^{13}\Delta$ observed in those studies (e.g. compare studies of Gong et al., 2008, or Wang et al., 2005) can be explained by such deviations of growing year weather conditions from long-term mean conditions. This may also include interannual variability of soil moisture and atmospheric vapour pressure, which

exert direct effects on $^{13}\Delta$ (Sparks and Ehleringer, 1997; Tsialtas et al., 2001). However, since these factors are usually (but not always, see Schulze et al., 1996) correlated with precipitation, their effect is (at least partially) included in the relationship of $^{13}\Delta$ with year-specific growing period precipitation.

4.2 Species, functional groups and communities share the same precipitation response of $^{13}\Delta$

The $^{13}\Delta$-response (that is the slope of the relationship between $^{13}\Delta$ and $\overline{P}_G$) of *S. grandis* was the same as that of the other species of *Stipa* in the data base. It was also very similar to the "mean" species response, and the response of C3 communities. Even in *R. soongorica*, which had a comparatively high $^{13}\Delta$ in all rainfall conditions, the slope of the relationship between $^{13}\Delta$ and year-specific growing period precipitation was the same as that of the "mean" species. Although the relationship between $^{13}\Delta$ and growing period precipitation has not been studied in any detail, the uniformity in the $^{13}\Delta$ responses of species' or functional groups to rainfall, as seen here, was not expected: inter-specific differences in the $^{13}\Delta$-response to environmental parameters have been observed before (e.g. Handley et al., 1994), and the adaptive significance of different strategies of water use have been discussed and emphasized (e.g. Golluscio and Oesterheld, 2007). Yet, it is acknowledged that, although the number of species in the data base was relatively large (55 C3 species, including 7 *Stipa* species), it was nevertheless a small fraction of the total flora of the grasslands of Mongolia. Moreover, the data base was dominated by perennial grasses (over 50% of all data). But in this respect the data base reflects the species composition of most Grassland communities of Mongolia. For instance, *Stipa* accounted for more than 40% and perennial grasses (including *Stipa*) for more than 70% of total aboveground biomass in the communities sampled in 2005. Perennial grasses from arid and semi-arid temperate grasslands share great similarities in phenology, leaf structure, and root architecture and placement, which may explain the similarity in their water use (Golluscio and Oesterheld, 2007). Thus, the similarity in the precipitation response of $^{13}\Delta$ by C3 communities was related to the predominance of perennial grasses (particularly *Stipa*) in these communities and the similarity in water use strategies among grasses. These similarities might also explain, why species-replacement along the aridity gradient did not affect the precipitation response of $^{13}\Delta$ (Fig. 4).

Nevertheless, there was significant scatter in the overall relationship between $^{13}\Delta$ and growing period precipitation. Although there was no difference between functional groups, the scatter may partly be due to differences between species within groups. Differences between species have been interpreted in terms of differences in intrinsic water use efficiency (e.g. Condon et al., 1990; Ehleringer et al., 1992; Meinzer et al., 1992) and may be related to differences in phenol-
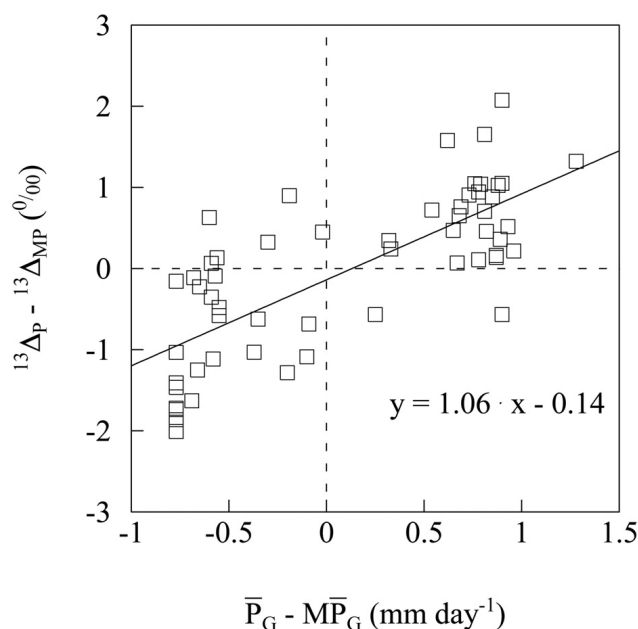

Fig. 7. Relation of the anomalies in C3 community mean $^{13}\Delta$ and growing period precipitation (r^2=0.556, $P\ll0.001$; same communities as in Fig. 6). Both anomalies are expressed as the difference between the annual and the long-term value. The long-term average discrimination, $^{13}\Delta_{MP}$, was calculated from the equation shown in Fig. 6. Year-specific precipitation for the sites of other studies was obtained by geostatistical interpolation analogously to our own data.

ogy (e.g. Smedley et al., 1991), rooting pattern/depth (Golluscio and Oesterheld, 2007) and leaf anatomy (including leaf thickness and nitrogen content) (Farquhar et al., 1989; Schulze et al., 2006). Mechanisms also include special adaptations to arid conditions such as leaf shedding in response to drought as expressed in *R. soongorica* (Ma et al., 2005) and phreatophyte lifestyle. This also explains, why the precipitation response at the community level was associated with much less scatter than that at the species level (cf. Figs. 4 and 6): communities include species with a range of functional attributes which are related to differences in $^{13}\Delta$.

Finally, there exists large short-term, small-scale variability in precipitation in the region, which is not represented entirely when interpolating precipitation at collection sites from weather station data. For instance, the Erenhot and Zamyn-Uud weather stations are separated by approximately 10 km but differ by an average of 15 mm in the monthly precipitation during the growing period. Therefore, errors in precipitation estimates are probably substantial and explain some of the scatter in the $^{13}\Delta$ versus precipitation relationship.

4.3 A stable and unbiased relationship between $^{13}\Delta$ and precipitation for use in C3:C4 mixing models

The findings of this work are useful for estimation of the relative abundance of C3 and C4 vegetation in community biomass from community $^{13}\Delta$ ($^{13}\Delta_{community}$), which requires knowledge of the $^{13}\Delta$ of the C3 ($^{13}\Delta_3$) and C4 ($^{13}\Delta_4$) members in a two-component mixing model (e.g. Still et al., 2003). Evidently, errors in the assessment of $^{13}\Delta_3$ and $^{13}\Delta_4$ cause errors in the estimation of C3:C4 abundance. In general, neglect of variation of $^{13}\Delta_3$ or $^{13}\Delta_4$ overestimates the true variation of the fraction of C3 (and C4) vegetation in communities, because all variation of $^{13}\Delta_{community}$ is attributed to variation in the relative abundances of C3 and C4 plants. If variation of $^{13}\Delta_3$ (or $^{13}\Delta_4$) is systematic, then neglect of this variation provokes a biased variation of the relative abundances of C3 and C4 plants. For instance, neglect of the effect of aridity on $^{13}\Delta$ of C3 plants would underestimate the relative abundance of C3 plants in the dry section of the transect. As shown above the potential variation of $^{13}\Delta_3$ is large in semi-arid and arid Grassland, creating opportunities for large errors in estimation of the relative abundance of C3 and C4 plants from $^{13}\Delta_{community}$. In the present study aridity caused a variation of $^{13}\Delta_3$ of up to ~5‰ (Fig. 6). This is about one third to one half of the difference in $^{13}\Delta$ between C3 and C4 plants in arid and semiarid Grassland (Schulze et al., 1996; Wang et al., 2005). Accordingly, the shift from the wet to the dry end of the aridity gradient has the same effect on $^{13}\Delta_{community}$, as a 33–50% replacement by C4 plants. A possible systematic variation of $^{13}\Delta_3$ must also be considered when interpreting long-term records such as soil organic matter or sediments in terms of the C3:C4 abundance. Variation of $^{13}\Delta_4$ would have a similar effect, although, variation in $^{13}\Delta_4$ is generally smaller (e.g. Liu et al., 2005; Wang et al., 2005) than that of C3 plants and communities as observed here, and $^{13}\Delta_4$ responds much less to drought (Schulze et al., 1996; Ghannoum et al., 2002). Yet, systematic differences in $^{13}\Delta$ between C4 metabolic types exist (e.g. Schulze et al., 1996; Ghannoum et al., 2002) and the relative abundance of metabolic types may change with aridity (Schulze et al., 1996).

5 Conclusions

This work demonstrates that rainfall anomalies cause large variations of the $^{13}\Delta$ versus MAP relationship, which are greatly reduced when $^{13}\Delta$ is related to actual rainfall during the growing period. Significantly, the $^{13}\Delta$-response to growing period rainfall was stable across years, and it was very similar for dominant taxa (*Stipa* members), functional groups (including herbaceous dicots, semi-shrubs and grasses), and C3 communities. Moreover, the relation was also valid outside the geographical and climatic range where it was developed, giving proof of its robustness. Because of its generality

and stability, the relationship between $^{13}\Delta$ and growing period rainfall allows an unbiased estimation of $^{13}\Delta$ of the C3 member for use in C3:C4 mixing models based on community C isotope composition.

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