

Variations in $\delta^{13}\text{C}$ values among major plant community types in the Xilin River Basin, Inner Mongolia, China

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Abstract. The $\delta^{13}\text{C}$ values of 51 plant species selected from eight plant communities along a moisture gradient were measured. Our results showed that all the community types that we investigated are dominated by C_3 species in the Xilin River Basin. Large variations in the average ^{13}C natural abundance of different communities were detected, and the magnitude of $\delta^{13}\text{C}$ values showed the following trend: typical steppe (-23.0‰) > degraded steppe (-23.5‰) > sand dune (-25.0‰) > restoring degraded steppe (-25.8‰) > meadow steppe (-26.4‰) \geq saline meadow (-26.5‰) > swamp meadow (-28.2‰). The major determinants of the biomass-weighted $\delta^{13}\text{C}$ values in a given community were the presence or absence of C_4 plants, the intrinsic variation among species and the variation of the same species growing in different habitats with different soil-moisture regimes and disturbance history. These results suggested that different habitats support dominant species with different water-use efficiencies and a trend in the community-level $\delta^{13}\text{C}$ values was observed, as ascribed by the contribution of C_4 plants and/or the variations among species or the response of water-use efficiency of the same species to different soil moisture conditions.

Introduction

Natural abundance of stable isotopes is used as natural integrators of ecological processes, which allow ecologists to evaluate the net outcome of many processes that vary both spatially and temporally, while not altering the natural activity or behaviour of the element in that system (Dawson *et al.* 2002). Fractionation against $^{13}\text{CO}_2$ of plants during photosynthesis results in depletion of organic material in ^{13}C compared with source CO_2 , with a more negative carbon isotope natural abundance ($\delta^{13}\text{C}$, ‰) than for source CO_2 (Farquhar *et al.* 1982, 1989). Foliar $\delta^{13}\text{C}$ values are influenced by the $\delta^{13}\text{C}$ of ambient CO_2 (the source air for photosynthetic assimilation) and carbon isotope fractionation during photosynthesis (Buchmann *et al.* 2002). Although the stable carbon-isotope technique was originally used to distinguish various photosynthetic pathways (C_3 , C_4 , CAM) (Bender 1968), it had been further developed to evaluate more critically the interactions between water use and C_3 photosynthetic efficiency, because $\delta^{13}\text{C}$ relates directly to ecophysiological traits, such as C_i/C_a , which is the ratio of the internal CO_2 concentration in the mesophyll airspaces (C_i) to the ambient atmospheric concentration of CO_2 (C_a) (Farquhar *et al.* 1989), and ultimately to potential water-use efficiency. In contrast to gas-exchange techniques that provide measurements of photosynthetic rates at a single time, $\delta^{13}\text{C}$ integrates photosynthetic activity throughout the period the leaf tissue is synthesised. Moreover, leaf $\delta^{13}\text{C}$ values reflect the interplay among all aspects of plant carbon and water relations and are therefore more useful than plant gas-exchange measurements as integrators of the whole plant

function (Martin and Thorstenson 1988; Dawson *et al.* 2002; Máguas and Griffiths 2003). $\delta^{13}\text{C}$ has also been instrumental in revealing how species adjust their gas-exchange metabolism and their strategies of resource acquisition and use to ensure competitiveness and survival in a given habitat (Ehleringer and Cooper 1988; Tieszen and Song 1990; Ehleringer 1993a, 1993b; Van de Water *et al.* 2002).

The strong correlation between carbon isotope composition and water-use efficiency (WUE) has led to the generalisation that more water-efficient plants should have more positive $\delta^{13}\text{C}$ values (Farquhar *et al.* 1982; Farquhar and Richards 1984; Devitt *et al.* 1997; Schulze *et al.* 1998; Peñuelas *et al.* 1999). As a consequence, variation in $\delta^{13}\text{C}$ values has been applied to an array of biological and ecological questions related to water use. The analysis of $\delta^{13}\text{C}$ has been used as a means of studying water-using processes at the leaf (Farquhar *et al.* 1982), individual (Su *et al.* 2000; Tsialtas *et al.* 2001), population (Schuster *et al.* 1992; Donovan and Ehleringer 1994), community (Stewart *et al.* 1995; Schulze *et al.* 1998), ecosystem (Ehleringer and Cook 1998; Bowling *et al.* 2002; Fessenden and Ehleringer 2002) and even global (Lloyd and Farquhar 1994; Kloeppel *et al.* 1998) levels in the present time or in the past. Although there is considerable taxonomic variability within a given plant community, the averaged $\delta^{13}\text{C}$ value for that community gives a strong indication of moisture availability (Stewart *et al.* 1995).

Most studies on $\delta^{13}\text{C}$ values at the community level have focused on forest and desert ecosystems and there is a dearth of literature on the $\delta^{13}\text{C}$ signature of grassland ecosystems,

especially across communities or ecosystems. The objectives of this study were (1) to evaluate the community-level $\delta^{13}\text{C}$ values on the basis of the foliar $\delta^{13}\text{C}$ values of selected species occurring in different habitats and (2) to investigate the factors that affect community $\delta^{13}\text{C}$ values of different community types, including plant photosynthetic pathways, soil water availability and disturbance history.

Materials and methods

Study site

The Xilin River Basin ($43^{\circ}26'N$ – $44^{\circ}29'N$, $115^{\circ}32'E$ – $117^{\circ}12'E$) is located in the typical steppe zone of Inner Mongolia Plateau, with elevation range from 1500 to 900 m. The Xilin River Basin is semi-arid continental temperate steppe, with dry spring and moist summer. Annual mean temperature increases from south-east to north-west, ranging from 0.5 to 2.1°C. Annual precipitation decreases gradually from 400 mm in the south-east to 250 mm in the north-west and more than 70% of annual precipitation occurs during May–August (Chen 1988). Zonal soil types are chestnut and dark chestnut soils (Wang and Cai 1988).

Plot selection

This study was conducted in the areas adjacent to the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), the Chinese Academy of Sciences, which is located in the middle reach of the Xilin River.

Eight plant communities adjacent to IMGERS were selected. Because the eight communities were located in a relatively small area, within a distance of less than 25 km, they presumably were subjected to similar climatic conditions, such as temperature and precipitation. The eight plant communities differed in floristic composition and soil-water status, representing a soil-moisture gradient dependent on their relative elevation and soil types. We chose swamp-meadow, saline-meadow, meadow-steppe, typical-steppe, degraded typical-steppe and sand-dune communities because they were the most frequently found community types in the region. More

detailed information about the eight communities is shown in Table 1.

Survey of vegetation composition

We surveyed the plant species composition from 93 quadrats (1×1 m in size) sampled in eight communities (5–19 quadrats in each community) between 10 and 12 August 2001 when the maximum aboveground biomass usually appears according to our 22-year monitoring. In the more heterogeneous habitats (sand dunes and meadow steppe) we placed 19 quadrats, whereas in the more homogeneous meadow community we sampled only five quadrats. For the rest of the community types, we sampled 10 quadrats from each type. In each quadrat, the height and number of individuals of each plant species were measured and counted, and the aboveground part of each species was collected and taken back to the laboratory immediately. After weighing the fresh weight of each plant species, the samples were oven-dried at 70°C for ~48 h, and then weighed to determine their aboveground biomass. The plant water content (PWC) was calculated by determining the difference between fresh and dry weight for each species in each plot, by using the following equation:

$$\text{PWC (\%)} = \frac{[(\text{fresh weight of plant} - \text{dry weight of plant}) / \text{fresh weight of plant}] \times 100}{}$$

Sampling and analyses

From 23 to 25 August 2001, 6–12 plant species in each plot were sampled for foliar $\delta^{13}\text{C}$ analysis. The selected species were dominant or common species in their respective community, and represented more than 80% of the total biomass (excluding Plot 1). Fully expanded leaves from at least 10 individuals of each plant species were collected as one sample and five replicates were sampled. The samples were dried at 70°C, and then ground to pass an 80-mesh screen.

At the same time, soil samples from 0–20-cm depth in each plot were collected and divided into two subsamples (10–15 replicates were sampled in each plot). One subsample was used to determine the soil water content (SWC) by calculating the difference between wet and oven-

Table 1. General condition of the study plots in the Xilin River Basin, Inner Mongolia

Data within columns are mean \pm s.d. ($n = 15$ or $n = 10$). Significant difference between plots was determined by one-way ANOVA ($P < 0.05$). Values followed by the same letters are not significantly different at $P = 0.05$ according to the Duncan's multiple comparisons test

Plot no.	Vegetation type	Location	Altitude (m)	Soil type	Soil water content (0–20 cm, %)	Soil N content (0–20 cm, %)	Land-use type
1	Swamp meadow	$43^{\circ}37.460'N$, $116^{\circ}40.347'E$	1150	Swamp meadow soil	$135.34 \pm 54.75a$	$0.74 \pm 0.30a$	Fenced plot
2	Saline meadow	$43^{\circ}44.925'N$, $116^{\circ}40.629'E$	1190	Saline meadow soil	$16.65 \pm 2.89b$	$0.16 \pm 0.04bc$	Grazing pasture
3	Meadow steppe	$43^{\circ}29.418'N$, $116^{\circ}49.643'E$	1380	Dark chestnut soil	$15.55 \pm 1.23b$	$0.20 \pm 0.08bc$	Mowing field
4	Typical steppe	$43^{\circ}32.895'N$, $116^{\circ}40.708'E$	1250	Chestnut soil	$11.40 \pm 1.40c$	$0.17 \pm 0.03b$	Fenced plot
5	Typical steppe	$43^{\circ}32.322'N$, $116^{\circ}33.117'E$	1180	Chestnut soil	$9.49 \pm 0.67d$	$0.16 \pm 0.02bcd$	Fenced plot
6	Restoring degraded steppe	$43^{\circ}35.748'N$, $116^{\circ}44.419'E$	1210	Chestnut soil	$7.75 \pm 2.75de$	$0.13 \pm 0.03cd$	Fenced plot
7	Degraded steppe	$43^{\circ}37.967'N$, $116^{\circ}39.397'E$	1180	Chestnut soil	$7.14 \pm 0.61e$	$0.14 \pm 0.03cd$	Heavily grazed
8	Fixed sand dune complex	$43^{\circ}39.189'N$, $116^{\circ}39.892'E$	1220	Sandy soil	$4.44 \pm 2.42f$	$0.09 \pm 0.07d$	Fenced plot

dried (105°C to constant weight) soils, according to the following equation:

$$\text{SWC (\%)} = [(\text{wet weight of soil} - \text{dry weight of soil}) / \text{dry weight of soil}] \times 100.$$

The second subsample was wind-dried, and ground to pass a 100-mesh screen for a total N content (TNC) analysis. About 0.5–1-g subsamples were used to determine soil TNC by the Auto-Kjeldahl method (Kjeltec System 1026 Distilling Unit, Sweden) at the Research Center of Plant Ecology and Biodiversity Conservation, Institute of Botany, the Chinese Academy of Sciences. Soil TNC (%) was expressed as the amount of total soil N per unit dry mass.

Carbon isotope composition of leaf samples was measured by a Finnigan MAT 251 mass spectrometer (Thermo Finnigan, Bremen, Germany) in the Center of Soil and Environment Analysis, Institute of Soil Science, the Chinese Academy of Sciences. The stable isotopic ratios of the leaves were expressed as follows:

$$\delta^{13}\text{C}(\text{‰}) = [(^{13}\text{C}/^{12}\text{C})_l - (^{13}\text{C}/^{12}\text{C})_s] / (^{13}\text{C}/^{12}\text{C})_s \times 1000,$$

where $\delta^{13}\text{C}$ is the foliar $\delta^{13}\text{C}$ value, $(^{13}\text{C}/^{12}\text{C})_l$ and $(^{13}\text{C}/^{12}\text{C})_s$ are the carbon abundance ratios of the leaf and the standard Pee Dee Belemnite (PDB), respectively.

Mean $\delta^{13}\text{C}$ of a community was calculated by weighting $\delta^{13}\text{C}$ each plant species according to its relative biomass in the community as follows (Tsialtas *et al.* 2001):

$$\text{Community } \delta^{13}\text{C}(\text{‰}) = \sum [B_i \times \delta^{13}\text{C}_i] / \sum B_i,$$

where B_i is the relative biomass of the Species i in a community, and $\delta^{13}\text{C}_i$ is the $\delta^{13}\text{C}$ value of Species i .

Statistical analysis

Statistical analyses were performed by using SPSS 10.0 procedures. Multiple comparisons among different plots were made on the average height, density, aboveground biomass, SWC and TNC. The significance of differences was tested by one-way ANOVA (Duncan's test) at $P = 0.05$. Correlation analysis was performed to investigate relationships between community $\delta^{13}\text{C}$ values and the relative biomass of C_4 plants, SWC, SNC, PWC, the number of species and aboveground biomass in different plots.

Results

The SWC of the eight community types decreased from Plot 1 to Plot 8, which could represent a soil-moisture gradient from extremely wet (seasonally waterlogged) to dry conditions (Table 1). Soil N content was the highest in Plot 1 and the lowest in Plot 8. Swamp had the highest species richness and aboveground biomass, compared with the other communities (Table 2).

The stable carbon isotopic composition ($\delta^{13}\text{C}$) of the 372 plant samples, which represented 17 families, 43 genera and 51 species, was determined. Most of these species were C_3 plants on the basis of their $\delta^{13}\text{C}$ values, ranging from -29.8 to -25.0‰ (mean \pm s.e.: $-27.1\text{‰} \pm 1.1$) and only two plant species, *Cleistogenes squarrosa* (a perennial grass) and *Kochia prostrata* (a shrub), had C_4 pathways (mean \pm s.e.: $-15.0\text{‰} \pm 0.3$) (Fig. 1).

There were large variations in the biomass-weighted means of the $\delta^{13}\text{C}$ value in different communities, following a descending order of typical steppe > degraded steppe > sand dune > restoring degraded steppe > meadow steppe > saline meadow > marsh meadow (Fig. 2). The magnitude of variation in the mean $\delta^{13}\text{C}$ values decreased when C_4 plants were excluded from the calculation. A significant positive linear relationship existed between the community $\delta^{13}\text{C}$ values and the relative biomass of C_4 plants (Fig. 3).

With increasing of soil water and N content, the community $\delta^{13}\text{C}$ values tended to decrease significantly (Fig. 4). Significant negative relationships were also found between the community $\delta^{13}\text{C}$ values and the plant water content, the number of species and the aboveground biomass in different plots (Fig. 4).

Discussion

C_3 and C_4 plants have distinct isotopic composition owing to the difference in their primary carboxylating enzymes (Rubisco and PEP carboxylases for C_3 and C_4 plants, respectively). The $\delta^{13}\text{C}$ values of C_3 plants are approximately -28‰ , whereas those of C_4 plants are approximately -14‰ (O'Leary 1988; Farquhar *et al.* 1989). It is clear that all of the eight communities we examined were overwhelmingly dominated by C_3 species, with only two species having C_4 photosynthetic pathway. These results are consistent with the carbon metabolism pathways of the plants found in the Inner Mongolian steppe

Table 2. Main characteristics of eight plant communities in the Xilin River Basin

Data within columns are mean \pm s.d. ($n = 15$ or $n = 10$). Significant difference between plots was determined by one-way ANOVA ($P < 0.05$). Values with any letter in common are not significantly different at $P < 0.05$ according to the Duncan multiple comparisons test. n.d., not determined

Plot no.	Average height (cm)	Density (individual m^{-2})	No. of species	Aboveground biomass (g DW m^{-2})	Dominant species
1	28.37	2218 \pm 315a	47	558.9 \pm 24.4a	<i>Blysmus sinocompressus</i> , <i>Carex</i> spp., <i>Agrostideae</i> spp.
2	18.42 \pm 6.25ab	596 \pm 323bc	18	148.4 \pm 56.2c	<i>Achnatherum splendens</i> , <i>Leymus chinensis</i>
3	16.28 \pm 1.66b	738 \pm 128b	54	159.9 \pm 26.3c	<i>Filifolium sibiricum</i> , <i>Stipa baicalensis</i>
4	22.48 \pm 2.43a	480 \pm 126c	16	150.2 \pm 23.2c	<i>Leymus chinensis</i> , <i>Stipa grandis</i>
5	16.28 \pm 2.09b	374 \pm 105c	24	81.5 \pm 14.0d	<i>Stipa grandis</i> , <i>Leymus chinensis</i>
6	22.69 \pm 3.84a	542 \pm 127c	33	240.2 \pm 34.2b	<i>Caragana microphylla</i> , <i>Leymus chinensis</i>
7	8.97 \pm 2.10c	438 \pm 104c	19	113.4 \pm 15.1cd	<i>Artemisia frigida</i> , <i>Potentilla acaulis</i>
8	n.d.	n.d.	45	264.1 \pm 144.7b	<i>Ulmus pumila</i> , <i>Armeniaca sibirica</i> , <i>Cleistogenes polyphylla</i>

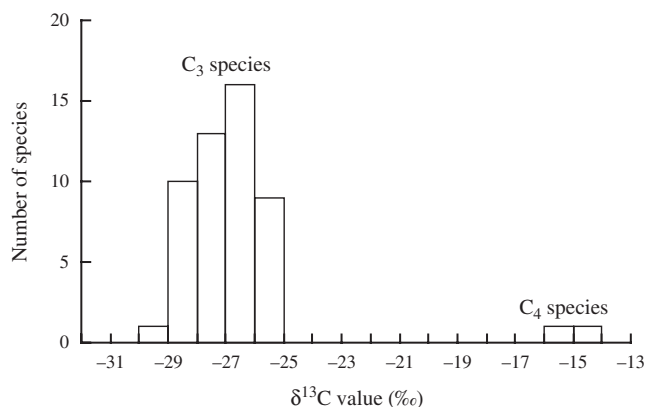


Fig. 1. Frequency distributions of the number of species by $\delta^{13}\text{C}$ class for the main plant species in the Xilin River Basin.

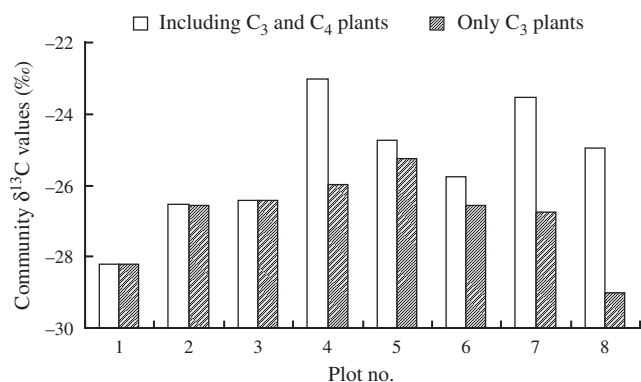


Fig. 2. Biomass-weighted mean $\delta^{13}\text{C}$ values of different communities along a soil moisture gradient.

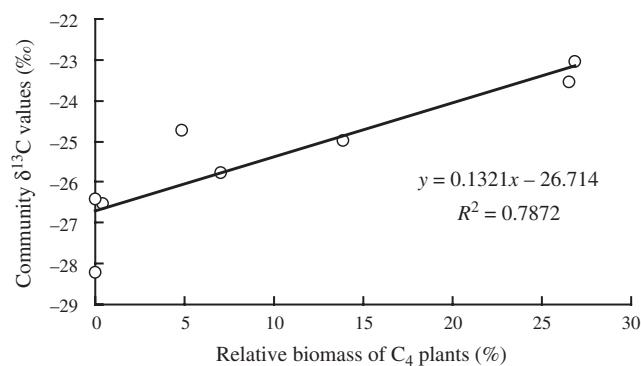


Fig. 3. A relationship between mean community $\delta^{13}\text{C}$ and relative biomass of C_4 plants in different plots ($n = 8$, $P < 0.01$).

(Tieszen and Song 1990; Su *et al.* 2000; Ni 2003). In other similar geographical regions, Pyankov *et al.* (2000) surveyed geographical distribution of C_4 plants in the vegetation of Mongolia and found that the percentage of C_4 species in the total Mongolian flora was only $\sim 3.5\%$, with a strong dominance by Chenopodiaceae. Whereas in some areas of North America with similar latitude, C_4 species were more abundant and had become predominant in some temperate grassland communities

(Tieszen *et al.* 1997; Paruelo *et al.* 1998; Epstein *et al.* 2002). In addition chenopods with C_4 photosynthesis were not abundant in North America (Ehleringer *et al.* 1997).

The ^{13}C natural abundance of C_3 plants also provides a useful measure of the integrated carbon–water balance in plants over a longer time interval, and is generally well correlated with plant WUE (Farquhar *et al.* 1982, 1989). The Xilin River Basin is a typical semi-arid grassland area and has an annual average rainfall of ~ 350 mm. In the semi-arid grasslands, water availability is the limiting factor for plant growth, which in turn simultaneously restricts the acquisition of N and P (Johnson and Asay 1993). Variation in the competitive ability to take up water among co-existing species could largely determine the species composition of a community (Vilà and Sardans 1999). Plants that utilise water efficiently may have a competitive advantage, which allows them to dominate the vegetation biomass (Ehleringer 1993b). From swamp to typical steppe, C_3 plants showed significantly more positive $\delta^{13}\text{C}$ values and more efficient water-use strategies with decreasing soil water availability in different community types (Fig. 2). However, $\delta^{13}\text{C}$ values of C_3 plants decreased in degraded steppe (Plot 7) and in two shrub-dominant communities (Plots 6 and 8). Ehleringer and Cooper (1988) found that the average carbon isotope ratio, weighted by abundance of each species, increased along a soil-moisture gradient from relatively wetter wash to the relatively drier slope. Stewart *et al.* (1995) showed a linear increase in community-averaged carbon isotope composition with decreasing annual rainfall in south-eastern Queensland, Australia. In our study, large variations in the biomass-weighted mean ^{13}C natural abundance existed among different community types. Community $\delta^{13}\text{C}$ value gradually increased with decreasing SWC, which indicated that WUE increased as soil water availability decreased. Plant communities had a higher WUE and employed a more conservative water-use strategy to allow plants to grow, survive and maintain a relatively stable productivity in dryer habitats; whereas in wetter habitats, lower WUE and prodigal water-use patterns enable communities to achieve higher productivity.

However, Schulze *et al.* (1996) observed that the simple average $\delta^{13}\text{C}$ values (sun leaves) of all species collected from a given region remained constant (at -27%) along an aridity gradient (rainfall range 770–125 mm) in Patagonia. In three lowland rainforest stands in French Guiana, Bonal *et al.* (2000) also found that basal area-weighted average $\delta^{13}\text{C}$ values were similar in the three stands, despite the large differences in floristic composition among the stands and high interspecific variability in $\delta^{13}\text{C}$. They considered that the change in species composition in these highly diverse communities was the major cause for maintaining the relative importance of the different $\delta^{13}\text{C}$ -contrasted groups and ultimately for maintaining community $\delta^{13}\text{C}$ almost stable (Schulze *et al.* 1996, 1998; Bonal *et al.* 2000). We argue that (1) water may not be the most limiting factor for the growth of plants in the habitats reported in the literature above, because the stable-community $\delta^{13}\text{C}$ values indicate that no water stress occurred in any of the habitats investigated during the time of foliage growth. The study of Schulze *et al.* (1998) along a rainfall gradient in northern Australia supports this argument. They found that simple community-averaged $\delta^{13}\text{C}$ value was almost constant in areas with rainfall

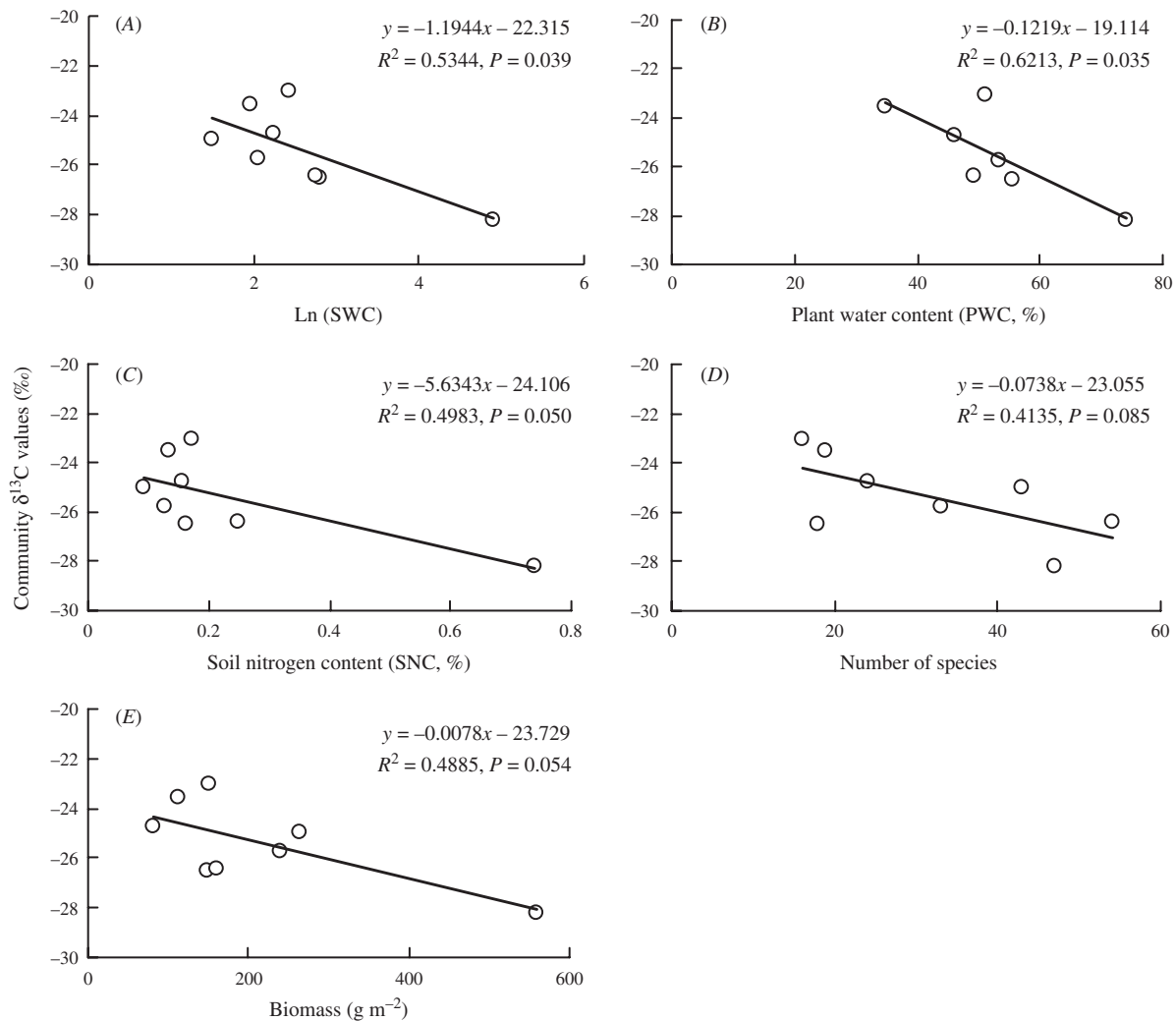


Fig. 4. Relationships between mean community $\delta^{13}\text{C}$ values (excluding C_4 species) and (A) soil water content, (B) plant water content (PWC), (C) soil N content (SNC), (D) the number of species and (E) aboveground biomass of different plots in the Xilin River Basin, Inner Mongolia.

above 475 mm, whereas $\delta^{13}\text{C}$ value increased with decreasing rainfall in areas where annual rainfall was between ~ 450 and 200 mm; that is, water would affect community $\delta^{13}\text{C}$ value when it became a limiting factor. (2) The studies of Schulze *et al.* (1998) and Bonal *et al.* (2000) focused mainly on trees, and other deep-rooted plants such as shrubs, which had more stable and negative $\delta^{13}\text{C}$ because the moisture content in the deep soil layers is more stable and abundant than in the surface layers. In our study, two shrub-dominant communities (Plots 6 and 8) also showed more negative $\delta^{13}\text{C}$ values than did other communities.

Lloyd and Farquhar (1994) suggested that differences in isotope discrimination on a global scale arise because of (1) differences between different C_3 and C_4 species in the extent of discrimination against $^{13}\text{CO}_2$ during photosynthesis, (2) differences between different C_3 plant types in stomatal response to vapor mole fraction difference and (3) spatial and seasonal variation in vapor mole fraction differences. Our results indicated that the differences among community $\delta^{13}\text{C}$ values

could be attributed to the presence or absence of C_4 plants, because exclusion of the C_4 species from our dataset diminished the range of differences in the $\delta^{13}\text{C}$ values. Significant positive linear relationships between community $\delta^{13}\text{C}$ values and the relative biomass of C_4 plants suggest that the most important contribution to the variation in the community $\delta^{13}\text{C}$ values is due to the presence of C_4 plants, as well as their increased proportion in the biomass of different communities. The C_4 species in general are more water-use efficient than C_3 species (Percy and Ehleringer 1984) and tend to dominate warm, dry grasslands (Epstein *et al.* 2002). It has been widely accepted that temperature, precipitation and the seasonal distribution of precipitation are the principal controls on the distribution of C_3 and C_4 species (Ehleringer *et al.* 1997; Ni 2003). In our study, the biomass of C_4 species distinctly increased with decreasing soil-water availability of different community types. For example, *Cleistogenes squarrosa*, a C_4 perennial grass, constituted 12.3% of the biomass of the community in the sand land. Additionally, grazing intensity is also an important factor

affecting C_4 species distribution in the Xilin River Basin. In degraded steppe, the biomass of C_4 species made up to 35.8% of the biomass of the community, with *Cleistogenes squarrosa* accounting for 22.9% of the entire community, or ~64% of the C_4 plant biomass. Previous studies in this area have shown that the proportion of C_4 plants increases with degradation of grassland caused by over-grazing (Li 1989; Tang 1999), which could be attributed to the adaptability of C_4 species to arid habitat. Moreover, the qualitative nutritional differences between C_3 and C_4 plants also indicate that much of the protein in C_4 leaves is enclosed within the thicker cell walls of the bundle-sheath cells, leading to a lower digestibility by some grazers (Ehleringer *et al.* 1997). Thus, in the relatively small spatial scale such as the Xilin River Basin, the distribution of C_4 species was influenced more by soil water availability and grazing intensity than was that of C_3 species.

Remarkable variation, however, still existed in the community $\delta^{13}\text{C}$ value when only C_3 plants were considered. The variation in plant $\delta^{13}\text{C}$ values among C_3 plant species and habitats with different soil-water availability could explain the variation in the community $\delta^{13}\text{C}$ value without C_4 plants. There was a variation of ~5% in the foliar $\delta^{13}\text{C}$ values among the C_3 species in our study, suggesting that significant differences existed in the WUE and water-use strategy among C_3 species in the Xilin River Basin. Average $\delta^{13}\text{C}$ values of C_3 plants increased with decreasing soil water content, indicating that the WUE of plants was likely to be enhanced (more positive) and/or species with lower WUE might have been substituted by species with higher WUE. Consequently, the WUE of a community would increase. The correlation between the community $\delta^{13}\text{C}$ value and the soil water content further suggested that the WUE of the community was enhanced with decreasing water availability. Our results on the change in floral composition clearly indicated that the proportion of perennial grass species increased, whereas that of perennial forbs decreased along decreasing soil water gradient (Chen *et al.* 2005). The $\delta^{13}\text{C}$ value of perennial grasses ($-26.17\% \pm 0.72$) is significantly more positive than that of perennial forbs ($-26.80\% \pm 1.19$), suggesting that perennial grasses use water more efficiently, and may be more conservative in their water-use patterns. This is consistent with the results of Lloyd and Farquhar (1994) who analysed data at a global scale. These authors concluded that in an environment with periodic water supply, the most successful plants are those that have a non-conservative water-use strategy. On the other hand, where water use is episodic, plants with a conservative water-use strategy seem to be the most successful. Our study conducted in the same area also showed that C_3 plant species could increase their WUE and adopt more conservative water-use patterns with decreasing water supply (Chen *et al.* 2002). *Leymus chinensis*, one of the dominant species in the Inner Mongolia Steppe, had increasing foliar $\delta^{13}\text{C}$ values with decreasing soil water content, indicating that this plant species could change its WUE according to soil-water availability.

Conclusions

Our study has provided evidence that C_4 plants, although rare in the Inner Mongolian steppe, could be important contributors to the overall variation of $\delta^{13}\text{C}$ values among different community

types. This variation could be explained by the presence or absence of C_4 plants, as well as their relative abundance and biomass in a given community. Soil water availability and grazing intensity were the two principal factors affecting the distribution of C_4 species in our study area. Some researchers predicted that global climate change, e.g. global warming and the change of precipitation pattern, would increase the abundance of C_4 plants (Epstein *et al.* 2002) and result in substantial variations in the $\delta^{13}\text{C}$ values at the community level. However, variations in the species composition among communities of different habitat conditions (soil water content, soil types) and disturbance regimes were important components of the observed inter-community variations in $\delta^{13}\text{C}$ values and also an important part of the variation in biomass-weighted $\delta^{13}\text{C}$ values of different community types. C_3 plants of different water-use strategies and their differential abilities to adapt to water-stressed environment might co-exist owing to their niche differentiation in resource use (such as water). In arid habitats, C_3 species have more positive $\delta^{13}\text{C}$ values, whereas more negative $\delta^{13}\text{C}$ values occur in wetter habitat. This suggests that in habitats where water is limited, the most successful plants would be, those having a conservative water-use strategy. On the other hand, where water supply is abundant, plants with a non-conservative water-use strategy seemed to be the most successful.

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