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Differences in leaf $\delta^{13}C$ among four dominant species in a secondary succession sere on the Loess Plateau of China

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Abstract

Differences in leaf $\delta^{13}C$ among four dominant species as well as the species-specific response to the fluctuations of either soil moisture or monthly mean temperature were examined along a secondary succession sere with a time scale from 3 to 149 y on the Loess Plateau in north-western China. We used leaf $\delta^{13}C$ as a surrogate for water use efficiency (WUE) of the mentioned dominant species. *Bothrichloa ischaemun* as a dominant species in the final succession stage belongs to C_4 photosynthesis pathway, while the other three dominant species occurring in the first three succession stages belong to C_3 pathway. The overall trend of leaf $\delta^{13}C$ variation among the three C_3 species was *Artemisia gmelinii* (in the third stage) and *Lespedeza davurica* (in the second stage) > *Artemisia scoparia* (in the first stage). This suggests that species with higher WUE (more positive leaf $\delta^{13}C$) would have substantial competitive advantages in the context of vegetation succession. Furthermore, species with highest WUE (*i.e.* C_4 pathway) have great potential to be dominant in the final succession stage in the habitats (such as the study area) undergoing strong water stress in growing season. The evolution of WUE among the dominant species occurring in different succession stages strongly depends on the time scale of given stage since abandonment. The longer the time scale is, the more significant the differences among them in terms of leaf $\delta^{13}C$, hence WUE. Our results support the notions that leaf $\delta^{13}C$ may be more positive when water supply is less favourable.

Additional key words: *Artemisia*; *Bothriochloa*; *Lespedeza*; photosynthesis pathway; semiarid area; species turnover; stable carbon isotope; water use efficiency.

Introduction

In ecological studies, measurements of stable isotopes naturally occurring in biological materials have increased tremendously in recent years (Hobson and Wassenaar 1999, Hultine and Marshall 2000, Su *et al.* 2000, Qu *et al.* 2001). Stable carbon isotope composition, expressed as $\delta^{13}C$, is associated with the ratio of CO_2 partial pressure within the leaves to that outside the leaves (C_i/C_a) (Farquhar *et al.* 1982, Hultine and Marshall 2000). The leaf carbon isotope composition in C_3 plants is related to long-term plant water use efficiency (WUE) (Farquhar *et al.* 1982, Farquhar and Richards 1984, Condon *et al.* 1990, Ehleringer 1993, Stewart *et al.* 1995) and leaf $\delta^{13}C$ and WUE are positively correlated (Silim *et al.* 2001, Warren *et al.* 2001). More negative leaf $\delta^{13}C$ indicates higher C_i/C_a ratios, resulting from either lower chloroplast demand for CO_2 or greater stomatal conductance affecting the supply rate of CO_2 and transpiration (Farquhar *et al.* 1982, 1989). Therefore, the $\delta^{13}C$ signature of plant tissue may be an information-rich signal that provides useful insights into plant performance in the context of ecosystem functions (Warren *et al.* 2001). An integrated measurement of internal plant physiological and external environmental properties influencing photosynthetic gas exchange over the time when carbon is fixed is useful (Smedley *et al.* 1991).

Considerable efforts have gone into the description of sources of variation in $\delta^{13}C$, which varies among co-occurring species (Gower and Richards 1990, Bannister and Strong 2001), genotypes within species (Zhang *et al.* 1993), and plant functional types along an environmental gradient (DeLucia and Schlesinger 1991, Hultine and Marshall 2000). However, few studies were conducted to clarify the inter-specific variation of leaf $\delta^{13}C$ with relation to a succession sequence. Mechanism of plant species replacement during succession has fascinated plant ecologists for decades (Connell and Slatyer 1977, Tilman

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1987, Van Mierlo *et al.* 2000). In most previous studies, mainly comparisons of both species morphology and plant life history between early- and late-succession stages were done. The authors evaluated the underlying mechanisms of species turnover during succession (Noble and Slatyer 1980, Huston and Smith 1987, Walker and Chapin 1987, Prach and Pysek 1999, Wang 2002). Bearing in mind that the large variations of leaf $\delta^{13}C$ within or among species were constantly associated spatially or temporally with the fluctuation of environment, we hypothesise that the inter-species differences in physiological responses to environmental fluctuation may be also one of the major factors shaping the succession pattern. This holds especially for dominant species that play a key role in vegetation succession (Prach and Pysek 1999, Lenssen *et al.* 2000).

We designed a field experiment to clarify the underlying mechanisms of species replacement in secondary vegetation succession with the time scale from 3 to 149 y on the Loess Plateau in north-western China. We analysed leaf $\delta^{13}C$ of the dominant species occurring in different succession stages. Our goal was to determine whether some physiological traits, such as WUE, would yield a generalising correlation over a succession sequence. The following questions were asked: (*1*) Do the dominant species in different succession stages differ from each other in terms of leaf $\delta^{13}C$, hence WUE? (*2*) Does leaf $\delta^{13}C$ of different dominant species demonstrate different response to the fluctuation of either soil moisture or monthly mean temperature in the growing season? (*3*) Given the strong water stress in growing season in the study area, does dominant species with higher WUE have any competitive advantage in species turnover during succession?

Materials and methods

Study area and plants: The study area is located in Zhifanggou drainage area (36°44′N, 109°15′E), Ansai County, Shensi Province, north-western China. The drainage area is *ca.* 8.27 km^2. Mean annual temperature is 8.8 °C, mean annual precipitation 549.1 mm (Wang 2002). Due to the loose loess substrates, soil in the study area is poor in water retention. In addition, the limited total precipitation always poured as torrential rain. Thus water deficit is a major stress to plant growth in the study area (Liu 1985, 1999).

In a relatively homogeneous area of upper lands near watersheds (relative gentle slopes from 0° to 15°, altitude 1 303–1 328 m a.s.l.), a secondary vegetation succession sere in abandoned fields was identified (Wang 2002). The first stage is a newly abandoned farmland with low soil N and C contents and high pH. *Artemisia scoparia* as a distinctive dominant species in this stage is characterised by annual life history, root system of taproot, flowering in August, high allocation for aboveground growth, hence large investment in supporting photosynthesis (Table 1). The second stage is previously farmland, *ca.* 26 y after abandonment, with lower soil N and C contents. *Lespedeza davurica*, a legume perennial herb, became the dominant species characterised by fairly higher lateral spread ability and well-developed taproot system; it flowers in August. Underground biomass is much larger than that of aboveground (Table 1), suggesting the small investment in supporting photosynthesis while large proportion in supporting carbon storage. The third stage, *ca.* 46 y after abandonment, is characterised by intermediate soil N and C, highest species richness, diverse life and regeneration strategies, and strong lateral spread ability. The dominant species (*Artemisia gmelinii*) is a perennial with strong clone ability as well as high proportion of investment in supporting underground biomass, flowering in August. The fourth stage is an old graveyard, *ca.* 149 y after abandonment, with highest soil N and C as well as low soil pH value (Wang 2002). *Bothriochloa ischaemun* as a distinct dominant species is characterised by perennial life history, well developed fibre root system; it flowers in early September.

Methods: Among the plots of each succession stage, one of 100 m^2 encompassing four subplots of 5×5 m was sampled. In each plot, a reasonable degree of homogeneity in plant community composition and topography was ensured. In each month from June to September of 2001, leaf samples of the dominant species were collected from different subplots within one plot. In each subplot, leaves were collected from at least five healthy individuals, then pooled into one sample. Samplings for each species were three times replicated. Leaf samples were dried at 65 °C for 24 h, then ground, and passed through 80 mesh-sieve for carbon isotope analysis. Soil was sampled by aggregating three 5-cm-diameter by 20-cm-deep soil cores taken from each plot in a V-shaped pattern. Soil samples were placed in sealed plastic bags for soil moisture analysis, made in the Laboratory of Biological Centre, Institute of Botany of the Chinese Academy of Science. Leaf carbon isotope ratio was determined in the Laboratory of Mass Spectrum, Chinese Agriculture Academy of Science. Leaf sub-samples (3–5 mg) were combusted for 2 h at 850 °C using the sealed quartz methods, and the isotope ratio was measured using a stable isotope mass spectrometer with a dual inlet system (*Finnigan MAT 251*, Bremen, Germany). Carbon isotope ratio [‰] was calculated with respect to the PDB standard:

$$\delta^{13}C = \{[(^{13}C/^{12}C)_{\text{sample}}/(^{13}C/^{12}C)_{\text{standard}}] - 1\} \times 1\,000$$

Statistical analyses: To clarify the species specific response of variation of leaf $\delta^{13}C$ to the fluctuations of soil moisture and mean monthly temperature from June to September, we related leaf $\delta^{13}C$ of the four dominant species to these two environmental factors with either linear or quadratic model. In addition, one way *ANOVA* was used to demonstrate the inter-specific differences among the three C_3 pathway dominant species within each month or through the whole growing season. All statistical procedures were carried out using *SPSS* software and the critical value of $p<0.05$ was used for significant difference.

Results

Differences in leaf δ^{13}C among the dominant species: According to leaf δ^{13}C, *B. ischaemun* as a dominant species in the final succession stage is a C_4 photosynthesis pathway plant, while the other three species occurring in the first three succession stages belong to C_3 pathway (Table 1). In the growing season from June to September, the overall trend of leaf δ^{13}C variation among the three C_3 species was *A. gmelinii* and *L. davurica* (significantly) > *A. scoparia* (Table 1, $p<0.05$). On the other hand, inter-species differences of leaf δ^{13}C were also different in individual months (Table 2). In June 2001, soil moisture was fairly lower while monthly temperature was higher (Fig. 1), and leaf δ^{13}C of *A. gmelinii* in the third succession stage was significantly higher than that of the dominant species from first and second stages. Also leaf δ^{13}C of *L. davurica* (in the second stage) was more positive than that of *A. scoparia* (in the first stage) (Table 2, $p<0.05$). In July 2001, highest monthly temperature accompanied with lowest soil moisture might pose a strong water stress (Fig. 1). Therefore leaf δ^{13}C of the dominant species from the first (*A. scoparia*) and the second stage (*L. davurica*) was more positive than that of the species from the third stage (*A. gmelinii*). From August to September, soil moisture became more preferable while monthly temperature was lower (Fig. 1). Thus leaf δ^{13}C of the dominant species from both the second stage (*L. davurica*) and the third stage (*A. gmelinii*) was more positive than that of the species from the first stage (*A. scoparia*) (Table 2, $p<0.05$). This shows that although leaf δ^{13}C of *A. scoparia* from the first stage was more positive than that of other species in June, its overall leaf δ^{13}C (refers to the mean δ^{13}C in the four months) was significantly lower than that of the other two dominant species from the second and third stages. Thus dominant species from late succession stages (*e.g.* the second and the third stage) generally have higher WUE than the pioneer dominant species occurring in newly abandoned field.

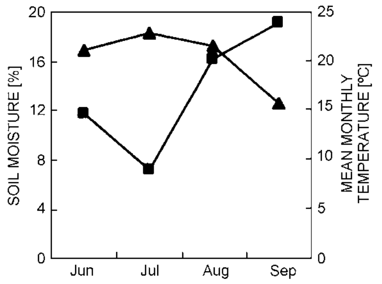

Fig. 1. Seasonal dynamics of soil moisture (■) and mean monthly temperature (▲) in the study area.

Table 1. General features of the four dominant species identified in the four succession stages from the study area. Ratio of root/canopy (in biomass), root depth, and leaf δ^{13}C value marked with different letters mean their differences are significant at $p<0.05$. Number of succession stages of each dominant species is indicated in brackets.

Dominant species	Life form	Root type	Root depth [cm]	Root/canopy	Leaf δ^{13}C [‰]
Artemisia scoparia (1)	Annual herb	Taproot	34.00±15.38^{b}	0.26±0.12^{d}	-26.89±0.66^{b}
Lespedeza davurica (2)	Perennial legume	Taproot	59.00±29.69^{a}	1.28±0.63^{a}	-26.24±0.48^{a}
Artemisia gmelinii (3)	Perennial forb	Taproot	78.33±20.21^{a}	0.71±0.42^{b}	-26.21±0.49^{a}
Bothriochloa ischaemun (4)	Perennial grass	Fibre	24.43± 6.06^{b}	0.51±0.22^{c}	-15.81±1.79

Table 2. Differences in leaf δ^{13}C [‰] among the three dominant species with C_3 pathway. Leaf δ^{13}C value within each column marked with different letters means difference significant at $p<0.05$.

Species	Jun	Jul	Aug	Sep
Artemisia scoparia	-26.69±0.10^{c}	-26.33±0.14^{a}	-26.84±0.16^{b}	-27.58±0.50^{b}
Lespedeza davurica	-26.05±0.06^{b}	-26.14±0.06^{a}	-25.87±0.48^{a}	-26.78±0.36^{a}
Artemisia gmelinii	-25.69±0.10^{a}	-26.50±0.04^{b}	-25.92±0.51^{a}	-26.68±0.31^{a}

Species specific response of leaf δ^{13}C to soil moisture fluctuation: Soil moisture varied from 7.20±0.83 to 19.00±0.76 % during the growing season from June to September. Leaf δ^{13}C of *A. scoparia* (in the first stage) decreased significantly with increasing soil moisture (Fig. 2*A*). *L. davurica* as a dominant species in the second stage showed a fairly distinctive uni-modal pattern (Fig. 2*B*, $p = 0.054$), while the dominant plants from the third stage (*A. gmelinii,* Fig. 2*C*) and the fourth stage (*B. ischaemun,* Fig. 2*D*) demonstrated significant uni-modal trend with increased soil moisture ($p<0.01$). In detail, leaf $\delta^{13}C$ of these dominant species increased when soil moisture increased from 7.20±0.83 to 11.70±0.94 %, then decreased with soil moisture increase from 11.70±0.94 to 19.00±0.76 %.

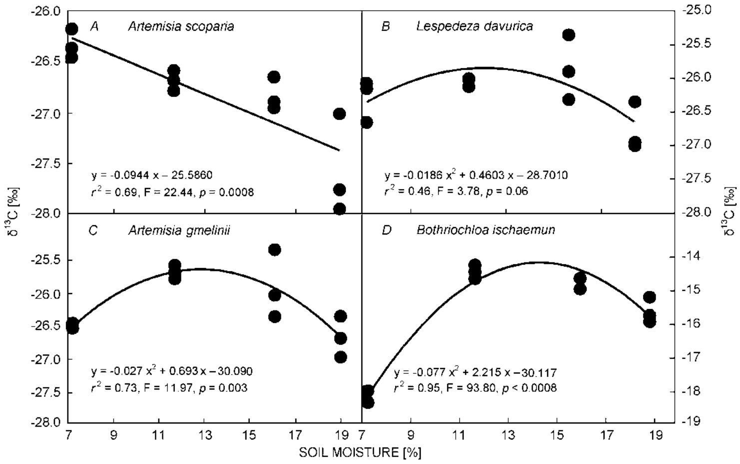

Fig. 2. Relationships between leaf $\delta^{13}C$ of dominant species and soil moisture seasonal fluctuation in growing season.

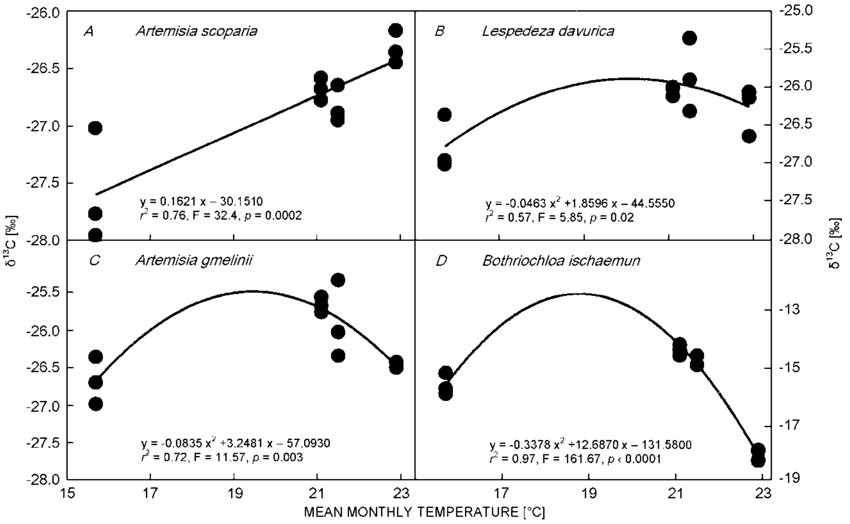

Fig. 3. Relationships between leaf $\delta^{13}C$ of dominant species and mean monthly temperature in growing season.

Species specific response of leaf $\delta^{13}C$ to monthly mean temperature variation (MMT): MMT during the growing season from June to September was 15.7–22.9 °C in 2001. Leaf $\delta^{13}C$ of *A. scoparia* (in the first stage) increased significantly with increase in MMT (Fig. 3*A*). In contrast, the dominant species from the second stage (*L. davurica,* Fig. 3*B*), the third stage (*A. gmelinii,* Fig. 3*C*), and the last stage (*B. ischaemun,* Fig. 3*D*) demonstrated significant uni-modal trend with increased MMT ($p<0.005$). Hence, their $\delta^{13}C$ increased when MMT increased from 15.7 to 21.1 °C, then decreased with MMT increase from 21.1 to 22.9 °C.

Discussion

Our results indicate that *B. ischaemun* as a dominant species in the final succession stage is a C_4 photosynthesis pathway plant, while the other three species occurring in the first three succession stages have the C_3 pathway. C_4 plants show a high WUE due to the more efficient CO_2 fixation by phospho*enol*pyruvate carboxylase, lack photorespiration, and exhibit a better N use efficiency (Cronquist 1982, Farquhar *et al*. 1982, Henderson *et al.* 1992, 1998). Based on our results, we conclude that in habitats that underwent water stress in growing season, such as those of the Loess Plateau ecosystem, species with highest WUE (*e.g.* C_4 pathway) have greater potential to be a dominant species in the final succession stage. On the other hand, δ^{13}C values used as a proxy for WUE for C_3 plants have been fully confirmed (Farquhar *et al.* 1982, Farquhar and Richards 1984, Silim *et al*. 2001). The overall trend of leaf δ^{13}C variation among the three C_3 species was *A. gmelinii* (in the third stage) and *L. davurica* (in the second stage) > *A. scoparia* (in the first stage), suggesting that species with higher WUE would have substantial competitive advantages in vegetation succession.

In this study, the four succession stages were identified basically with subjective approaches due mainly to the availability of plots with different history of abandonment, hence different time scale for restoration (Wang 2002). Our results indicate that the evolution of WUE among the dominant species strongly depended on the time scale of given stage since abandonment. In detail, the longer the time scale is, the more significant the difference between them will be in terms of leaf δ^{13}C, hence WUE. For example, the plot dominated by *B. ischaemun* had undergone a nearly 150 y restoration. Consequently, there is strong differentiation in both photosynthesis pathway and WUE between *B. ischaemun* and the dominant species from the first three stages characterised by relative short-term restoration history (3 to 46 y). Although leaf δ^{13}C of *A. gmelinii* from the third succession stage is significantly higher than that of the dominant species (*L. davurica*) from the second stage in June 2001, there do not exist significant differences between them in terms of the mean leaf δ^{13}C. In correspondence to this pattern, the time interval between them is fairly small (*ca*. 20 y). Furthermore, the mean leaf δ^{13}C values of both *A. gmelinii* and *L. davurica* were significantly more positive than that of the dominant species from the newly abandoned field. This was obviously associated with the relative longer temporal interval (ranging from 26 to 46 y, average 36 y) between the pioneer stage and the late stages (the second and third stages).

Leaf δ^{13}C may be affected by many abiotic factors, such as soil moisture (Sun *et al.* 1996), air temperature (Panek and Waring 1995), precipitation dynamics (Leffler and Evans 1999, Warren *et al.* 2001), and atmospheric CO_2 concentration (Ehleringer and Cerling 1995, Marshall and Monserud 1996). Warren *et al.* (2001) argued that δ^{13}C might well be a useful indicator of drought stress, but only in seasonally dry climates and where variation in other environmental factors is minimal. In the present study, the strong homogeneity in topography of the four plots (referring to the four succession stages) ensured lest difference in those mentioned abiotic factors among plots, but they fluctuated seasonally. This would inevitably affect leaf δ^{13}C of a given species in the growing season. We focused on the species-specific response of leaf δ^{13}C to two environmental factors, *i.e.* soil moisture and monthly mean temperature, which demonstrated strong seasonality.

Leaf δ^{13}C of C_3 plants may depend on variations either in stomatal conductance or photosynthetic capacity or both (Farquhar *et al.* 1982, 1989, Farquhar and Richards 1984). Henderson *et al.* (1998) demonstrated a relationship between WUE and carbon isotope discrimination in C_4 species, although C_4 species typically have lower C_i/C_a than that commonly observed for C_3 species. We therefore related leaf δ^{13}C of the four dominant species (both C_3 and C_4) to soil moisture and air temperature to clarify the species-specific response of leaf δ^{13}C. Leaf δ^{13}C was expected to be more positive under drier habitats (Farquhar and Richards 1984, Leffler and Evans 1999, Warren *et al.* 2001). This notion was confirmed by the pioneer dominant species in the first succession stage whose leaf δ^{13}C decreased significantly with increased soil moisture ($p<0.0001$). Partial confirmation was also made by the dominant species from second, third, and the final stages: leaf δ^{13}C of these dominant species demonstrated significant uni-modal trend with increased soil moisture ($p<0.01$). The reason underlying the observed pattern may partly result from the different root system among the dominant species. For example, *A. scoparia* is an annual herb with shallow root system that usually relies on the soil moisture in the upper parts of the soil profile. It may be more sensitive to the fluctuation of soil moisture in upper layer (in this case, 0–20 cm) by means of instantly increasing the stomatal closure when facing strong water stress. Other dominant species from the second and the third stages are all perennials with deep root system that enables access to soil moisture in deeper soil layers, which may be less sensitive to the fluctuation of soil moisture in upper layer. Nonetheless, leaf δ^{13}C of all four dominant species uniformly decreases at continuous increase of soil moisture, which is consistent with the notion that leaf δ^{13}C is more positive when water supply is less favourable (Warren *et al.* 2001).

A. scoparia (the dominant species from the first succession stage) also showed a specific pattern in terms of the response of leaf δ^{13}C to increasing MMT, while the other three dominant species from the second stage (*L. davurica*), the third stage (*A. gmelinii*), and the final stage (*B. ischaemun*) demonstrated uniform (uni-modal) trend with increase in MMT. This indicated that *A. scoparia* can also close stomata more when facing higher temperature, which leads to a decrease in transpiration rate and increase in WUE, while other three dominant species can not constantly increase stomata closure in the face of continuous increase in air temperature. Although further study on this issue is needed, the responses of dominant species in terms of leaf δ^{13}C to either soil moisture fluctuation and MMT were not subject to simple regimes, but varied with different species dominating in different succession stages. The fluctuation of either soil moisture or air temperature would directly influence the dynamic of stomatal conductance, hence the C_i/C_a ratios (Panek and Waring 1995, Sun *et al.* 1996). Therefore the different response pattern of leaf δ^{13}C demonstrated by different dominant species actually reflected the specific physiological strategies to changing environment, which may be one of the major reasons responsible for the observed pattern of species turnover during the succession.

In summary, the dominant species from newly abandoned field in the study area demonstrated specific strategy in the face of the fluctuation of soil moisture or MMT. Due to its relatively lower WUE, however, it was replaced eventually by other species with higher WUE during vegetation succession, while the climax dominant species was a C_4 photosynthesis pathway plant with highest WUE. We thus conclude that from the perspective of species turnover during succession in semi-arid habitats, species with higher WUE have substantial advantages in inter-specific competition, although other plant traits were also supposed to be critical for supporting them to become dominant (Wang 2002).

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