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Can the restoration of natural vegetation be accelerated on the Chinese Loess Plateau? A study of the response of the leaf carbon isotope ratio of dominant species to changing soil carbon and nitrogen levels

Received: 16 May 2005 / Accepted: 15 July 2005 / Published online: 20 August 2005
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Abstract For the heavily degraded ecosystem on the Chinese Loess Plateau, it would be of great significance if vegetation restoration could be accelerated anthropogenically. However, one major concern is that if the late successional species were planted or sown in degraded habitats, would they still be competitive in terms of some critical plant traits associated with specific habitats? Water use efficiency (WUE) is a major plant trait shaping the pattern of species turnover in vegetation secondary succession on the Loess Plateau. We hypothesized that if late successional stage plants could still hold a competitive advantage in terms of WUE, the prospects for an acceleration of succession by sowing these species in newly abandoned fields would be good. We tested this hypothesis by comparing the leaf C isotope ratio ($\delta^{13}\text{C}$) value (a surrogate of WUE) of dominant species from different successional stages at given soil C and N levels. Results indicated that leaf $\delta^{13}\text{C}$ of the two dominant species that co-dominated in the second and third stages were significantly more positive than that of the dominant species from the first stage regardless of changing soil C and N. Yet the dominant species from the climax stage is a C_4 grass assumed to have the highest WUE. In addition, increasing soil nutrition had no effects on leaf $\delta^{13}\text{C}$ of two dominant species in the late successional stage, indicating that dominant species from the late successional stages could still have a competitive advantage in terms of WUE in soil C- and N-poor habitats. Therefore, from the perspective of plant WUE, there are great opportunities for ecosystem restoration by sowing both dominant species and other species that co-occur in late successional stages in newly abandoned fields, for the purpose of enhancing species diversity and optimising species composition.

Keywords Water use efficiency · Semiarid area · Secondary succession · Stable carbon isotope · Abandoned field

Introduction

The Loess Plateau, a cradle of ancient Chinese civilization, has been affected by anthropogenic disturbance for millennia (Liu 1985). During the second half of the twentieth century, habitat fragmentation and environmental degradation on the Loess Plateau were accelerated due to the extensive monocultures (Lu 1997; Liu 1999; Jiang et al. 2003) grown for the increasing population (e.g. the population increased from 37 million to > 100 million). Natural vegetation has been replaced by cultivated crops. Nearly 70% of the total area has suffered from severe soil erosion and water losses (averagely soil losses amount to $3,720 \text{ t km}^{-2} \text{ year}^{-1}$) (Lu 1997; Liu 1999). Soil erosion has not only impoverished the ecosystems, but has also threatened the Yellow River because much of the eroded soil is eventually transported into this river. Consequently, the Loess Plateau has become an extremely degraded area both economically and ecologically, therefore constraining the economic development and ecological sustainability of China (Biological Department, The Chinese Academic of Sciences 2000).

In order to counteract the deterioration of the Loess Plateau ecosystems and recover ecosystem functioning, over the last 5 years, the Chinese central government has launched a nationwide restoration project [Retrieval of the Previously Cultivated Lands into Ecologically Significant Vegetation (Forests and/or Grasslands) Project]. To abandon arable land to secondary succession may be an ecologically sound practice (Brown and Gange 1989; Bazzaz 1996; Olff et al. 1997) but has little potential when coupled with local short-term economic interests. Therefore, some more positive restoration approaches have been adopted, i.e. involving anthropogenic and

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material investments in the context of succession in order to accelerate the restoration processes. However, the extent to which succession can be enhanced depends on many biotic or abiotic factors, prominently the availability of propagules (Bekker et al. 1997; Thompson et al. 1997; Van der Putten et al. 2000) and changes in soil nutrition (Tilman 1986). Planting or sowing late-successional species in the abandoned lands may meet the demand for propagules, as conducted elsewhere (e.g. Stampfli and Zeiter 1999; Van der Putten et al. 2000). However, do these late successional species still have competitive potential as they do in the original successional stages when planted in habitats where soil nutrition has been changed? On the Loess Plateau, due to the densely distributed hillsides and gullies, and the loose loess substrates, the soil has low water retention. Limited total precipitation always occurs as torrential rain. Water deficit is therefore a major stress factor for plant growth (Liu 1985, 1999). Given this, we hypothesized that those species with higher water use efficiency (WUE) should have the advantage in suppressing other species during succession (Wang 2003). We tested the hypothesis by measuring leaf C isotope ratio ($\delta^{13}\text{C}$) (a surrogate for WUE) of dominant species which occurred in different successional stages. The results indicated that species with higher WUE indeed have a substantial competitive advantage in the context of vegetation succession. Species with the highest WUE (i.e. C_4 plants) have a great potential to become dominant in the climax stage (Wang 2003). However, due to the different history of land abandonment, soil nutrition differs with successional stages. Namely, soil N and C in the final successional stage (ca. 150 years after abandonment) were two or threefold higher than that of the newly abandoned lands (Wang 2002). Soil nutrient availability for those species that dominated in different stages, therefore, differed. There is some evidence which indicated that WUE may, to some extent, increase with increased nutrient availability (Farquhar and Richards 1984, and references therein). Thus, the differentiation of leaf $\delta^{13}\text{C}$ among dominant species may be affected by soil C and N. Some questions are therefore raised: Do the dominant species with higher WUE which occurred in soil nutrient-rich habitats still show this trait when planted in soil nutrient-poor habitats (e.g. newly abandoned land)? Hence, to what extent are the practices used to enhance restoration feasible from the perspective of some critical eco-physiological traits, such as WUE?

To examine these questions, we conducted a field experiment focusing on the relationship between plant WUE of several dominant plant species and soil nutrient variation (in terms of soil N and C) along a secondary successional sere in the Zhifanggou drainage area on the Loess Plateau where our previous studies were conducted (Wang 2002, 2003). Stable isotope methods have recently emerged as one of the most powerful tools for advancing the understanding of relationships between plants and their environment (Dawson et al. 2002). Leaf C isotope composition in C_3 plants is related to long-

term plant WUE (Farquhar et al. 1982; Farquhar and Richards 1984; Condon et al. 1990; Ehleringer 1993; Stewart et al. 1995). $\delta^{13}\text{C}$ integrates information about how a plant regulates CO_2 and water fluxes as they relate to the ratio of intracellular to ambient CO_2 (Farquhar et al. 1989). In addition, $\delta^{13}\text{C}$ is more stable over time than are absolute fluxes, thereby providing a better indicator of whole plant constraints rather than environmental constraints (Brooks et al. 1997; Hanba et al. 2000). In this paper, we took leaf $\delta^{13}\text{C}$ as a surrogate for WUE as we did in previous work. We attempted to answer three questions:

1. What is the leaf $\delta^{13}\text{C}$ pattern among dominant species at a given soil nutrient level in terms of soil C and N?
2. How does the leaf $\delta^{13}\text{C}$ of dominant species respond to the soil nutrient gradient?
3. From the perspective of WUE in dominant species, could the restoration process be accelerated in the Loess Plateau ecosystem?

These findings may have implications for the recovery and reconstruction of degraded ecosystems on the Loess Plateau of China.

Materials and methods

Study area

We carried out the study in the Zhifanggou drainage area ($36^\circ44'\text{N}$, $109^\circ15'\text{E}$), Ansai County, Shannxi Province, north-western China. The drainage area is ca. 8.27 km^2 , and located in the central part of the Loess Plateau. Topographically, the study area is characterized by hilly gullies with thick loess coverage and altitude ranging from 1,050 to 1,320 m from valley basin to the top of the watershed. The mean annual temperature is 8.8°C , while the mean annual precipitation is 550 mm (1955–2000; data from Ansai Weather Station ca. 20 km from the study sites). A major challenge in examining a successional sere on the Loess Plateau is that most areas have been heavily disturbed by long-term agricultural activities. We set up study sites in the Zhifanggou drainage area because some land use management projects have been conducted in this area since the 1950s (Lu 1997). Thereafter, the most extensive monoculture has been confined to the river basin or flat land, while a large part of the hilly gullies and watersheds has been either abandoned for natural vegetation recovery or has been subjected to anthropogenic restoration efforts (specifically, planting shrubs or grasses on the dry sunny slopes and trees on the shady hilly slopes), which therefore facilitate the attempt to identify a time sequence of vegetation restoration. In previous works, we identified a successional sere with a temporal scale from 3 to nearly 150 years (including four stages, 3, 26, 46 and

149 years old) in a relatively homogeneous area of higher land near watersheds (relatively gentle slopes from 0° to 15°, altitude 1,303–1,328 m a.s.l.) in this area (Wang 2002, 2003). In spite of not being true replicates, these four successional stages are adequate for comparisons because they are situated close together and have a common bedrock and parent material (loess), soil (loess soil) and topography (Wang 2002). Although soil moisture in the study area fluctuates significantly across the growth season, it is quite similar among the successional stages at a given time (Wang 2003). This was also confirmed by a study conducted in the study area. The study examined the difference in soil moisture between loess tableland with a slope of < 15° and loess hilly land with a slope from 15° to 35° (Lu 1997). In their results, the soil moisture of the 0- to 200-cm-deep soil layer showed no significant difference among the sites due to the loose loess substrate characterised by strong vertical seepage loss (Lu 1997). On the other hand, soil total C and N increased with years since abandonment, making it possible to examine the responses of leaf $\delta^{13}\text{C}$ of the dominant species to changing soil nutrition at a given soil moisture level. Although loess soil is generally alkali,

soil pH still demonstrated a decreasing trend with the time sequence (from 8.43 ± 0.015 to 8.24 ± 0.043) (Wang 2002).

Plant species

A total of 27 plant species belonging to 23 genera and 12 families were recorded in the four successional stages based on a field survey in 2004, including five annuals (mainly in the first successional stage) and 22 perennial herbs. Nearly half of the total species belong to three families, i.e. Leguminosae (five), Poaceae (five) and Compositae (four). In this study, we focused on the response of dominant species in terms of WUE to a soil nutrient gradient. We identified the dominant species based on the species relative importance value [RIV = (relative height + relative coverage + relative abundance)/3]. Species with a RIV > 0.15 in at least one stage were identified as a dominant species. Using this criterion, a large proportion of the RIV can be ascribed to dominant species in a given stage. This holds true especially for the last three successional stages (73%,

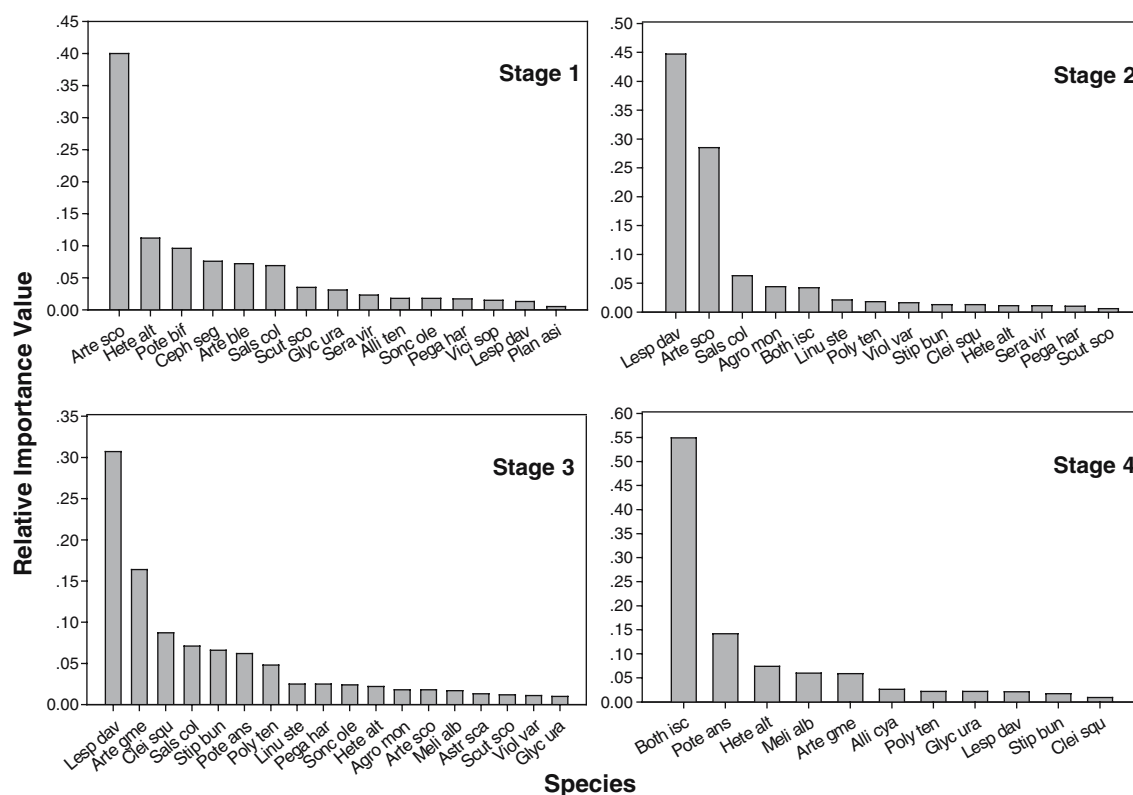


Fig. 1 Relative importance value [RIV = (relative height + relative cover + relative abundance)/3] of species occurring in the four successional stages. Those with RIV > 0.15 were identified as dominant species. *Agro mon* *Agropyron mongolicum*, *Alli cya* *Allium cyanceum*, *Alli ten* *Allium tenuissimum*, *Arte ble* *Artemisia blepharolepis*, *Arte gme* *Artemisia gmelinii*, *Arte sco* *Artemisia scoparia*, *Astr sca* *Astragalus scaberrimus*, *Both isc* *Bothriochloa ischaemum*, *Ceph seg* *Cephalanoplos segetum*, *Clei squ* *Cleistogenes*

squarrosa, *Glyc ura* *Glycyrrhiza uralensis*, *Hete alt* *Heteropappus altaicus*, *Lesp dav* *Lespedeza davurica*, *Linu ste* *Linum stelleroides*, *Meli alb* *Melilotus albus*, *Pega har* *Peganum harmala*, *Plan asi* *Plantago asiatica*, *Poly ten* *Polygala tenuifolia*, *Pote ans* *Potentilla anserina*, *Pote bif* *Potentilla bifurca*, *Sals col* *Salsola collina*, *Scut sco* *Scutellaria scordifolia*, *Sera vir* *Seraria viridis*, *Sonc ole* *Sonchus oleraceus*, *Stip bun* *Stipa bungeana*, *Vici sop* *Vicia sopium*, *Viol var* *Viola variegata*

49% and 55%, respectively, Fig. 1); the dominant species of the later stages are the major concern of this study. Four species were identified as dominant species, i.e. *Artemisia scoparia* dominated in the first stage and co-dominated in the second stage; *Lespedeza davurica* co-dominated in the second and the third stage; *Artemisia gmelinii* co-dominated in the third stage and *Bothriochloa ischaemum* dominated in the last stage (Fig. 1). *A. scoparia*, a C₃ annual herb, is characterised by a taproot, high allocation to above ground growth, and hence a large investment in supporting photosynthesis. *L. davurica*, a leguminous C₃ perennial herb, is characterised by a fairly high lateral spread and well-developed taproot system. Its underground biomass is much higher than its aboveground biomass, suggesting a small investment in supporting photosynthesis and a large investment in supporting C storage. *A. gmelinii* is a C₃ perennial with a strong clonal ability as well as a higher investment in supporting underground biomass. *B. ischaemum* is a C₄ perennial herb characterised by a well-developed fibrous root system (Wang 2002).

Sampling methods

To examine the response of leaf $\delta^{13}\text{C}$ of the dominant species to changing soil nutrients, we need these species to occur in a series of sites with different soil nutrient levels. However, in our previously identified successional stages, we found that not all of the dominant species can occur throughout the entire stages. Given this knowledge, our sampling sites were set in both the four successional stages and other locations where, in most cases, the four dominant species co-occurred and the habitats were similar to those of the previous four successional stages (all on a semi-sunny slope or watershed, full sunlight was guaranteed) within the range of the drainage area. Leaf materials for dominant species and soil samples were taken from 30 sampling sites. Each sampling site encompasses five 1×1-m² quadrats. Of the 30 sites, 16 were set in the four successional stages with quadrat-based quantitative data (plant height, cover and abundance), while 14 sites were set in other locations with only quadrat-based species presence-absence data. A reasonable degree of homogeneity in plant community composition and topography was ensured in each site. Environmental data obtained from the field survey in each site including elevation, latitude and longitude, slope aspect, slope gradient, slope location and soil substrate type. In mid August 2004, plant leaves of dominant species in each site were collected from at least five healthy individuals, then pooled to give one sample. Sampling for each species in each site was replicated 3 times. Leaf samples were dried at 65°C for 24 h, then ground, and passed through a 80-mesh sieve for C isotope analysis. Soil was sampled by aggregating three 5-cm-diameter by 20-cm-deep soil cores taken from each site in a V-shaped pattern. In my previous study, I found that soil C and N in different soil layers (0–10, 20–30,

40–50 cm depth) showed similar trends across the successional stages (Wang 2002). Therefore, soil sampled within 20-cm deep layer could be a good indicator for the deeper soil layer down to 50 cm depth, yet >85% of fine roots of herb plants (in terms of root density, root length and root volume) were distributed within the layer 40 cm deep in the Loess Plateau area (Li et al. 2003). Soil samples were placed in paper bags for soil total C and N analysis. Leaf sub-samples (3–5 mg) were combusted for 2 h at 850°C using the sealed quartz method, and the isotope ratio was measured using a stable isotope mass spectrometer with a dual inlet system (Finnegan MAT 251; Finnegan MAT, Bremen). The precision of the isotope analysis is up to 0.15‰. $\delta^{13}\text{C}$ (‰) was calculated with respect to the Pee Dee Belemnite standard:

$$\delta^{13}\text{C} = \left\{ \left[\left(\frac{^{13}\text{C}}{^{12}\text{C}} \right)_{\text{sample}} / \left(\frac{^{13}\text{C}}{^{12}\text{C}} \right)_{\text{standard}} \right] - 1 \right\} \times 1000$$

Both soil and leaf samples were analysed in the Biological Centre Laboratory, Institute of Botany, Chinese Academy of Sciences.

Statistical analyses

Field survey resulted in a site×species matrix (S×S, presence-absence data) and a site×environment matrix (S×E, including six environmental variables, i.e. altitude, soil C and N, slope location, slope aspect and slope gradient). Two categorical environmental variables were converted to quantitative data (slope aspect, 1 for semi-sunny slopes, 2 for semi-shady slopes; slope location, 1, 2 and 3 for upper, middle and lower position along a slope, respectively). Of the 30 sampling sites, 27 sites with a similar soil substrate (loess) were selected for analysis, while three sites with gravel substrate were omitted. Among the 27 sites, soil C and N range from 1.467 to 8.994 g kg⁻¹ and from 0.289 to 1.070 g kg⁻¹, respectively. We therefore identified three soil nutrition levels, namely, low level, mid level and high level (Tables 1–2, $P < 0.0001$). To clarify the differences in leaf $\delta^{13}\text{C}$ among the dominant species at a given soil nutrition level as well as the species-specific response of leaf $\delta^{13}\text{C}$ to the soil C and N gradient, one-way ANOVA with Duncan's test was used. To demonstrate the distribution pattern of dominant species with relation to the environmental gradients, ordination analysis was used. Detrended correspondence analysis with a S×S matrix indicated that the longest gradient is 2.03; we therefore used linear ordination methods for analysis (ter Braak and Smilauer 1998; Leps and Smilauer 2003). Two data sets (S×S matrix and S×E matrix) were subjected to principal components analysis (PCA). The relation between dominant species and environmental variables were shown as a PCA biplot based on the first two principal components. All statistical procedures were carried out using SPSS software and the critical

Table 1 Summary of sampling sites surveyed in the study area

Sites	Latitude	Longitude	Altitude (m)	Slope aspect/ gradient	Substrate
1	36°44.255'	109°14.642'	1,261	E, 30°	Loess
2	36°44.299'	109°14.268'	1,324	E, 6°	Loess
3	36°44.687'	109°15.421'	1,259	W, 25°	Loess
4	36°44.288'	109°14.287'	1,309	E, 35°	Loess
5	36°44.765'	109°15.690'	1,288	E, 25°	Loess
6	36°45.585'	109°15.629'	1,065	E, 26°	Loess
7	36°44.821'	109°15.712'	1,296	E, 26°	Loess
8	36°44.273'	109°14.612'	1,290	E, 35°	Loess
9	36°44.842'	109°15.312'	1,280	E, 27°	Loess
10	36°44.789'	109°15.621'	1,298	E, 22°	Loess
11	36°44.873'	109°15.171'	1,140	W, 24°	Loess
12	36°44.654'	109°15.587'	1,300	E, 5°	Loess
13	36°44.800'	109°15.649'	1,298	E, 14°	Loess
14	36°46.099'	109°15.834'	1,053	W, 35°	Loess
15	36°45.143'	109°15.486'	1,100	E, 8°	Loess
16	36°44.765'	109°15.598'	1,298	W, 12°	Loess
17	36°45.044'	109°15.285'	1,105	E, 34°	Loess
18	36°44.512'	109°15.623'	1,315	E, 4°	Loess
19	36°44.723'	109°15.635'	1,325	E, 4°	Loess
20	36°44.495'	109°14.939'	1,160	W, 26°	Loess
21	36°44.545'	109°15.601'	1,310	E, 2°	Loess
22	36°44.238'	109°14.869'	1,184	E, 25°	Loess
23	36°44.815'	109°15.612'	1,305	E, 2°	Loess
24	36°44.596'	109°15.663'	1,320	E, 5°	Loess
25	36°44.239'	109°14.662'	1,243	E, 30°	Loess
26	36°44.824'	109°15.654'	1,305	E, 5°	Loess
27	36°44.839'	109°15.680'	1,305	E, 5°	Loess
28	36°44.387'	109°14.770'	1,193	E, 25°	Gravel
29	36°44.272'	109°14.694'	1,201	E, 5°	Gravel
30	36°44.397'	109°14.896'	1,160	E, 25°	Gravel

Table 2 One-way ANOVA for the three soil C and N levels (g kg⁻¹)

	<i>n</i>	Mean	SD	95% Confidence interval for mean		Minimum	Maximum	<i>F</i>	<i>P</i>
				Lower bound	Upper bound				
Soil C									
Low	12	2.037	0.390	1.789	2.285	1.467	2.958	159.304	0.000
Mid	8	4.123	0.816	3.440	4.805	3.203	5.581		
High	7	7.689	0.847	6.906	8.472	6.381	8.994		
Soil N									
Low	10	0.347	0.028	0.327	0.368	0.290	0.386	64.498	0.000
Mid	10	0.499	0.046	0.466	0.532	0.424	0.558		
High	7	0.805	0.150	0.666	0.944	0.600	1.070		

value of $P < 0.05$ was used to show significant difference. CANOCO for Windows (version 4.0; ter Braak and Smilauer 1998) was used for PCA analysis.

Results

Leaf $\delta^{13}\text{C}$ with relation to soil C and N

At low soil C and N levels, the trends of leaf $\delta^{13}\text{C}$ variation among the three C_3 species are *L. davurica* (dominant species in the second and third successional stages) $>$ *A. gmelinii* (dominant species in the third successional stage) $>$ *A. scoparia* (dominant species in the

newly abandoned stage) (Fig. 2, $P < 0.05$). At mid and high soil C and N levels, there are no significant differences in leaf $\delta^{13}\text{C}$ between *L. davurica* and *A. gmelinii*; both are significantly higher than that of *A. scoparia* (Fig. 2, $P < 0.05$).

On the other hand, for the species-specific response to a changing soil C and N gradient, the leaf $\delta^{13}\text{C}$ of *L. davurica* (Fig. 2) and *B. ischaemum* (dominant species in the climax successional stage; Figs. 3, 4) showed no significant trend with increasing soil C and N. In addition, increasing soil C also has no significant effect on leaf $\delta^{13}\text{C}$ of *A. scoparia*, but significantly affected leaf $\delta^{13}\text{C}$ of *A. gmelinii* because leaf $\delta^{13}\text{C}$ of *A. gmelinii* is significantly higher at a high soil C level than at the low and mid soil C

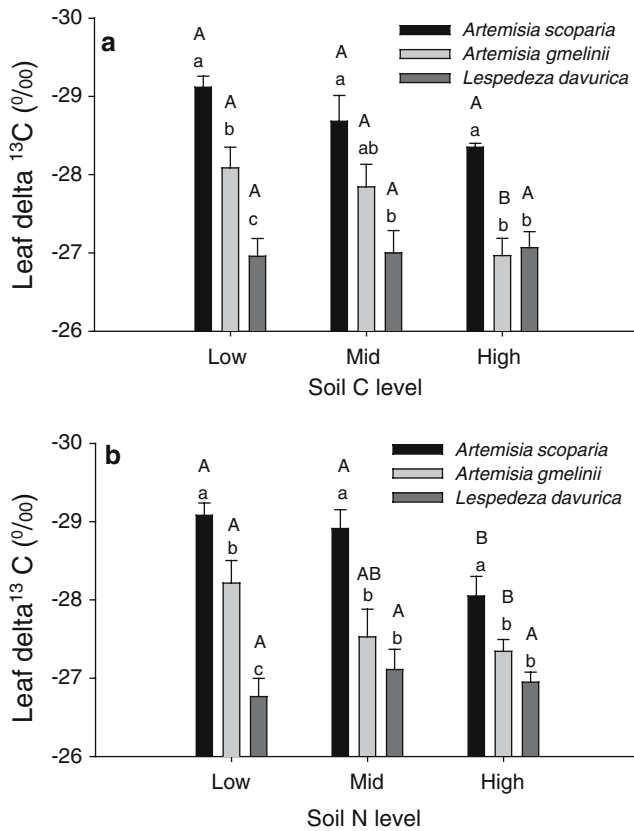


Fig. 2 Differences in leaf $\delta^{13}\text{C}$ among three dominant C_3 species at a given soil C (a) and soil N (b) level (significant differences between means at $P < 0.05$ according to Duncan's test indicated by different lowercase letters) as well as the species-specific response of $\delta^{13}\text{C}$ to the soil C and N gradient from the low, to mid to high level (significant differences between means at $P < 0.05$ according to Duncan's test indicated by different uppercase letters)

level. Along the soil N gradient, leaf $\delta^{13}\text{C}$ of both *A. gmelinii* and *A. scoparia* were significantly higher at a high soil N level than at a low and mid soil N level.

Distribution of the dominant species with relation to environmental gradients

The first two PCA axes (principal components) explain 94.4% of the variability in species data. The eigenvalue for the first axis is larger than that for the second axis (0.85 vs. 0.094), suggesting that the first axis is much more informative than the second axis. Along the first axis from left to the right, the environmental gradient is prominently characterized by decreasing soil C and N. In addition, three topographical factors may also be correlated to some extent with this axis, i.e. semi-shady habitats may have a higher probability of occurrence than semi-sunny slopes, slope location is lower and the gradient steeper. The probability of the occurrence of dominant species from the late successional stages (such as *B. ischaemum* and *A. gmelinii*) is positively correlated with increasing soil C and N, while that of dominant species from the newly abandoned field (*A. scoparia*)

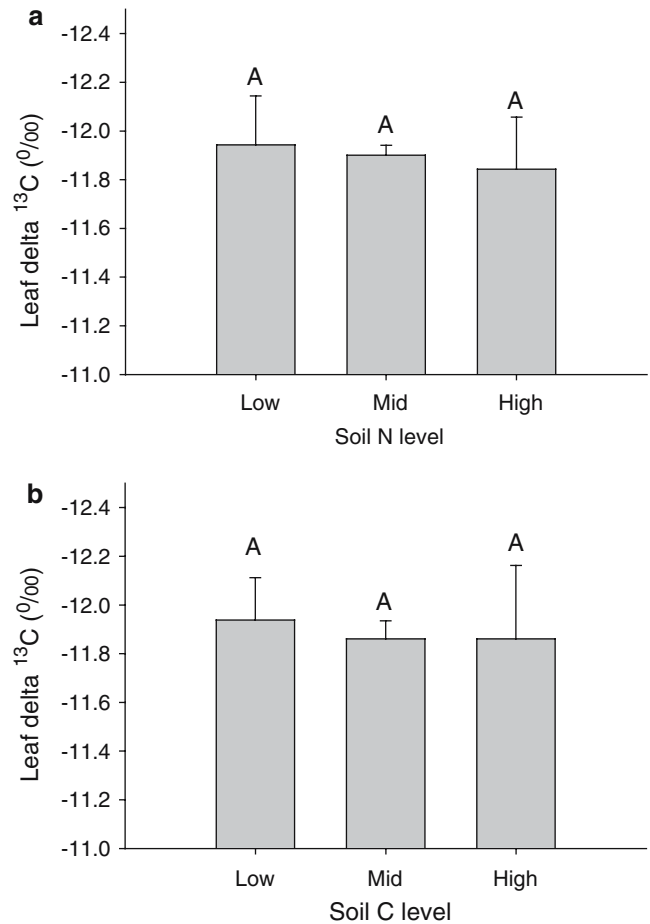


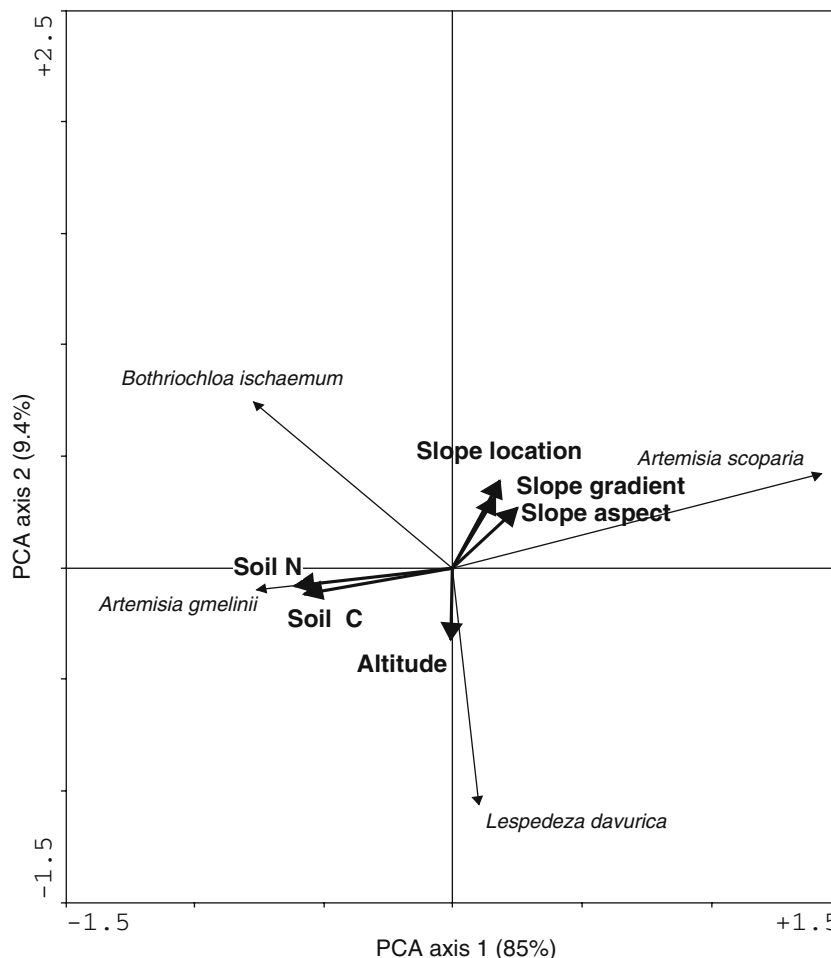
Fig. 3 Leaf $\delta^{13}\text{C}$ response of *Bothriochloa ischaemum* (a dominant C_4 species in the climax successional stage) to the soil C and N gradients from the low, to mid to high level (Different uppercase letters indicate means are significantly different at $P < 0.05$)

decreased with increasing soil C and N levels. The probability of occurrence of *L. davurica* as a dominant species in the second and third successional stages seems to have no relationship with habitat soil C and N level. The second principal component is mainly an altitudinal gradient associated with changes in slope location, slope gradient and slope aspect. From the bottom to the top in the PCA biplot, altitude decreases while slope becomes steeper. Habitats on semi-shady slopes and lower slope locations may have a higher probability of occurrence. *B. ischaemum* and *A. scoparia* tend to have a higher probability of occurrence at lower elevations, while the probability of the occurrence of *L. davurica* in habitats of higher elevations increases. The occurrence of *A. gmelinii* seems to show little correlation with the environmental gradient according to PCA axis 2.

Discussion

For the heavily degraded ecosystem on the Loess Plateau, it would be of great significance if its restoration

Fig. 4 Species–environment principal components analysis with environmental variables passively projected. The increase in both species and environmental gradients (shown in **bold**) are shown by **arrow heads**, while the **length** of arrow heads shows the magnitude of a particular environmental variable. Arrows pointing in the **same direction** correspond to species and environmental variables that are predicted to have a positive correlation, whereas those predicted to have a large negative correlation are indicated by arrows pointing in **opposite directions**. As the arrows for two variables meet nearly at right angles, the variables are predicted to have a low correlation (nearly 0) (Leps and Smilauer 2003)



could be enhanced anthropogenically. With respect to this issue, one major concern is that if late successional species were planted or sown in degraded habitats, would they still be competitive in terms of some critical plant traits, such as WUE in this case? In our previous study (Wang 2003), we found that the overall trend of leaf $\delta^{13}\text{C}$ variation among the three C_3 dominant species was as follows: *A. gmelinii* (in the third stage) and *L. davurica* (in the second stage) > *A. scoparia* (in the first stage). However, this pattern may be affected by site factors such as soil C and N content, because the sites where these dominant species occurred are quite different from each other in terms of soil nutrition level, due mainly to their different history of abandonment (Wang 2002).

The sampling regime conducted in this present study makes it possible to compare leaf $\delta^{13}\text{C}$ values among the dominant species at given soil C and N levels. It should be noted that leaf $\delta^{13}\text{C}$ was supposed to be associated with the ratio of CO_2 partial pressure within the leaves to that outside the leaves (Farquhar et al. 1982). Our sampling regime (all sites were within a relatively small area and had similar topography) also guaranteed the smallest differences in environmental conditions among study sites. Therefore, the ^{13}C in the ambient CO_2 could

be assumed to be the same at all sites studied. Results from this paper indicated that leaf $\delta^{13}\text{C}$ of the two dominant species that co-dominated in the second and third stages were unchangeably significantly more positive than that of the dominant species from the first stage (*A. scoparia*) regardless of changing soil C and N, suggesting that the pattern of leaf $\delta^{13}\text{C}$ among the dominant species is less affected by soil C and N content. On the other hand, as for the species-specific response of leaf $\delta^{13}\text{C}$ of the dominant species to the soil C and N gradient, increasing soil nutrition would enhance WUE of the early successional species (soil N for *A. scoparia*) and a co-dominant species in late successional species (both soil C and N for *A. gmelinii*) yet have no effect on that of other two dominant species in the late successional stages, i.e. *L. davurica* in the second and the third stages and *B. ischaemum* in the climax stage. *B. ischaemum*, a dominant species in the final succession stage, is a C_4 plant. C_4 plants show a high WUE due to the more efficient CO_2 fixation by phosphoenolpyruvate carboxylase, and lack of photorespiration (Farquhar et al. 1982; Henderson et al. 1992, 1998). Results from this paper indicated that the dynamics of leaf $\delta^{13}\text{C}$ of *B. ischaemum* is less affected by changing soil C and N. These findings strongly support the idea that dominant

species from late successional stages generally have higher WUE than the pioneer dominant species occurring in newly abandoned fields. Hence, species with higher WUE would have substantial competitive advantages in the context of vegetation succession in the semiarid ecosystem on the Loess Plateau (Wang 2003). In addition, based on the observations in the study area over the last few years (2001–2004), the four dominant species can complete their life cycle within the growing season regardless of habitat types (data not shown).

Although dominant species from late successional stages can still have competitive advantages and fulfil their life cycle in habitats with different soil C and N contents, results from this paper indicated that dominant species from the late successional stages (such as *B. ischaemum* and *A. gmelinii*) naturally tend to have a higher probability of occurrence in habitats with higher soil C and N levels, while dominant species from the newly abandoned field (*A. scoparia*) tend to occur in habitats with lower soil C and N contents. Whereas the occurrence of *L. davurica* (a dominant in the second and third successional stage) seems to show little discrimination with respect to habitat soil C and N level. The dynamic of propagule availability in different habitats may be a major mechanism underlying the observed patterns (Bekker et al. 1997; Thompson et al. 1997; Van der Putten et al. 2000). In the Loess Plateau ecosystem, habitats with lower soil nutrition are highly associated with heavy anthropogenic disturbance, prominently cultivation. The long-term agricultural activities have not only led to a deterioration of soil nutrients but also thoroughly destroyed modules for the proliferation of perennials. Those with a stable soil seed pool, such as *A. scoparia* in this case, therefore have a higher probability of occupying the newly abandoned habitats than those with clonal modules as the major reproductive propagules. As the time since abandonment increased, soil C and N were observed to increase. Meanwhile, the relative importance of the soil seed bank may gradually give way to clonal modules for vegetation recruitment due to the increasing availability of the latter. Annual species are therefore inevitably replaced by perennials (Wang 2002). The distribution pattern of *L. davurica* in the PCA space suggests its special role as a transition species linking the pioneer species and the climax species in the context of vegetation succession on the Loess Plateau.

Due to the loose loess substrates, soil in the study area shows poor water retention. Meanwhile, limited total precipitation always occurred as torrential rain. Thus water deficit is a major stress for plant growth in the study area (Liu 1985, 1999). Given this knowledge, in a previous study we hypothesized that plants with higher WUE (more positive leaf $\delta^{13}\text{C}$ value and/or C_4 pathway) have greater competitive advantages in succession. We tested this hypothesis by comparing leaf $\delta^{13}\text{C}$ of dominant species from different successional stages characterised by different soil C and N contents. The present

study further confirmed that dominant species from the late successional stages (e.g. the second and the third stage) generally have higher WUE than the pioneer dominant species occurring in newly abandoned fields regardless of variation in soil nutrients. These findings therefore indicate good prospects for attempts to accelerate the successional process by sowing the late successional species in newly abandoned fields. However, whether or not this project could be realized may also depend on other factors, prominently, species composition and diversity (e.g. Stampfli and Zeiter 1999; Van der Putten et al. 2000). It was reported that diverse plant species mixtures were more effective at reducing the number of natural colonizers (mainly weeds from the seed bank) than the average low-diversity treatment. In addition, the effect of the low-diversity treatment on weed suppression depended on the composition of the species mixture (Van der Putten et al. 2000). In this case, although dominant species in late successional stages had high RIVs, i.e. 73%, 49%, and 55% for the second, third and climax stage, respectively (Fig. 1), it is suggested that, in addition to dominant species, other species that co-occurred with these in late successional stages should be taken into account for the purpose of enhancing species diversity and optimising species composition.

In summary, three conclusions can be reached from this paper:

1. Leaf $\delta^{13}\text{C}$ of the two dominant species that co-dominated in the second and third stages were significantly more positive than that of the dominant species from the first stage, regardless of changing soil C and N levels.
2. In terms of the species-specific response of leaf $\delta^{13}\text{C}$ to the soil nutrient gradient, increasing soil nutrition would enhance WUE of the early successional species (soil N for *A. scoparia*) and a co-dominant species in the late successional stage (both soil C and N for *A. gmelinii*) yet have no effect on that of the other two dominant species in the late successional stage, i.e. *L. davurica* in the second and the third stages and *B. ischaemum* in the climax stage. This indicates that dominant species from the late successional stages could still have a competitive advantage in terms of WUE in soil C- and N-poor habitats, such as newly abandoned fields.
3. Therefore, from the perspective of plant WUE, there is a great potential for anthropogenic ecosystem restoration in the Loess Plateau ecosystem by sowing dominant and co-occurring late successional species in newly abandoned fields.

Acknowledgements I would like to thank Defeng Li for his help during the fieldwork. This research was funded by the State Key Basic Research and Development Plan of China (G2000018607) and the National Natural Science Foundation of China (NSFC 30270263, 30370251).

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