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Distribution patterns of shrubby N-fixers and non-N fixers in an arid valley in Southwest China: implications for ecological restoration

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Abstract Shrubs play different key roles in arid regions. Comparisons of shrubs and their site adaptability are essential for correct selection of candidates in developing restoration theory and practice. A survey of topography, soil properties and shrub composition was conducted in fifty-seven 5-m × 5-m plots in an arid valley of the upper Minjiang River, Southwest China. With cluster analysis and critical examinations based on edaphic properties, soil was classified into three groups: dry cinnamon soils (DCS), calcareous cinnamon soils (CCS) and eluvial-accumulation cinnamon soils (EACS). EACS had the highest fertility level, DCS the next and CCS the lowest level. For non-N fixers, soil moisture is the primary limiting factor, and nitrogen the next. However, N-fixers are weakly constrained by soil moisture and nitrogen, the extent of which is species-specific. N-fixers had a significantly higher cumulative relative importance value (44.4%) in CCS than in DCS (34.0%) and EACS (17.3%). The results suggest that it would be reasonable to restore non-N fixers in DCS and EACS and that N-fixers are appropriate for CCS. Compared with grass, shrubs significantly enhanced the availability of nitrogen and phosphorus and soil electric conductivity, and significantly decreased the soil C/N ratio. The median fertility level of soil dominated by N-fixers indicates that N-fixers are suitable driver candidates from grassland to non-N-fixing shrub land. Four native shrubby legumes (*Indigofera amblyantha*, *Sorophora viciifolia*, *Desmodium podocarpum* and *Bauhinia faberivar*) and one soil-con-

serving shrub (*Ajanía potaninii*) are the top-priority pioneers for ecological restoration.

Keywords Arid region · Species distribution · Legume shrub · Restoration species selection · Ecological restoration

Introduction

In the past decades, human overexploitation of natural resources (e.g., deforestation, overcropping and overgrazing) has caused or accelerated land degradation and desertification in large areas of arid and semiarid ecosystems (Matson et al. 1997). Ecosystem degradation is characterized by loss or disturbance of vegetation coverage, increase in soil erosion, loss of biodiversity and soil nutrients, loss of microbial propagules and/or diminution of microbial activities (Duponnois et al. 2005). The establishment of suitable plant cover is known to improve the physicochemical and biological properties of soil (Dobson et al. 1997; Duponnois et al. 2005) and to protect the soil against water erosion (Morgan 2007; Xu et al. 2008). Thus, revegetation is desired in arid zones. To date, a variety of techniques and practices, such as mulching, planting with containerized stock, terracing and contour planting (Eckholm 1975), have been developed to restore and improve regional environments. These techniques have little practical relevance for large parts of the drier areas because their effective management requires high capital and labor inputs (Lamers et al. 1996; Schlecht and Buerkert 2004; Schlecht et al. 2007).

Spatial heterogeneity in soil properties may influence species composition, distribution, performance and possibly ecosystem-level processes in ecosystems on local to region scales (Sperry and Hacke 2002; Fu et al. 2004; Kubota et al. 2004; Lu et al. 2006; Mirkka et al. 2006). Moreover, processes of primary succession involve soil physical and biological activities on a temporal scale (Dobson et al. 1997). If the spatial and temporal distribution of nutrients evolves over many cycles of

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disturbance and recovery, the species composition of secondary forests may continue to change (Lawrence et al. 2005). So, in successions, community development accompanies the development of the habitat (Dobson et al. 1997). Based on the co-evolution law of plants and the environment, the ecological principle of “restoring suitable vegetation in the right place” was put forward for vegetation restoration in the arid valley (Ma et al. 2004).

Shrubs are the dominant life form in arid lands and are well suited to their environment (McKell 1975). Efforts to better understand how they affect the system's functioning should be a high priority. N₂-fixing shrubs are an important functional group in natural ecosystems (Spehn et al. 2000, 2002; Rodríguez-Echeverría et al. 2003; Daudin and Sierra 2008). N-fixers mainly include leguminous and actinorhizal plants in terrestrial ecosystems. Legume species are cosmopolitan, ranging from tropical canopy trees to tiny annual herbs, and are the dominant species in diverse plant communities. Legumes have symbiotic relationships with nitrogen-fixing root nodule bacteria (Matthew 2007), whereas actinorhizal plants, six genera of which (*Alnus*, *Coriaria*, *Elaeagnus*, *Myrica*, *Dryas* and *Casuarinaceae*) are native to China, fix atmospheric nitrogen in root nodules symbiotically formed by an actinomycete (Schwintzer and Tjepkeman 1990; Benson and Silver 1993). Establishment and growth of N-fixers are also likely to be facilitated by their ability to enter into effective symbioses with multiple rhizobium species (Diem and Dommergues 1990; Hibbs and Cromack 1990; Rodríguez-Echeverría et al. 2003). Furthermore, N transfer facilitates plant growth from a N-rich legume to a N-starved non-legume through root-to-root contact, common mycorrhizal networks and root exudates (Høgh-Jensen and Schjoerring 2000; Daudin and Sierra 2008). In addition, N-fixers can affect other key ecological processes, such as the presence of legumes that are commonly increasing primary production in natural systems (Spehn et al. 2000, 2002). Therefore, N-fixers have great potential for the reclamation of degraded land (Safronova et al. 2004).

The arid upper Minjiang River Valley is an extremely degraded landscape in the Hengduan Mountains. Vegetation damage along the Minjiang River has been going on for at least 1,000 years (Editorial Board of Sichuan Vegetation 1980; Zhang 1992). Forest coverage has decreased from about 50% in the 1800s to about 18% at present, and deforestation is especially prevalent in the arid valley (Editorial Board of Sichuan Vegetation 1980; Zhang 1992). It consequently leads to more serious soil erosion and further deterioration of soil, water and nutrient conditions (He et al. 1993; Ma et al. 2004). Ecological degradation has decreased the water quality, threatened the biodiversity and productivity of the ecosystem, and endangered regional ecological safety. For many years, considerable attention has been paid to techniques for establishing vegetation in arid systems. Major emphasis has been placed on investigating tech-

niques for ameliorating soil fertility to allow immediate establishment of a vegetation cover, whereas little attention has been paid to the processes of soil development and natural recruitment in these intensively disturbed environments (Shu et al. 2005). Moreover, most previous studies neglected selection of suitable native species and sites because of insufficient information about the diversity of native shrubby species and their site adaptability, especially woody N-fixers, in the arid upper Minjiang Valley. Based on field investigations of the vegetation, the objectives of this study were to: (1) compare responses concerning the distribution and composition of N₂-fixing and non-fixing species among soil groups in a dry deciduous shrub community; (2) detect crucial factors affecting the N₂-fixing shrub distribution pattern; (3) select pioneer species for revegetation and provide scientific suggestions for ecological restoration in the arid system.

Materials and methods

Study area

The upper Minjiang River is a first-order branch of the Yangtze River (Fig. 1), which is about 735 km long and has an altitude range of 3,560 m. The upper Minjiang River Basin (30°44'–32°24'N, 102°41'–103°58'E) is a 337-km section between the headwaters and Dujiangyan City. It is located in the northwestern corner of Sichuan Province, in a transition zone bounded on the west by the Tibetan Plateau and on the east by the Sichuan Basin. In this area, the maximum elevation is > 3,600 m in the headwaters, and the minimum is < 900 m in Dujiangyan City. The mountainous topography has a large degree of vertical variation in precipitation and air temperature. The arid valley studied is located between 1,300 and 2,200 m elevation in a semi-arid climate. The mean annual precipitation is near 500 mm, the mean annual potential evapo-transpiration is about 1,332 mm, and the mean annual temperature is about 11.2°C.

The soil is classified as calcic cambisols (FAO-UNESCO 1988). Regional vegetation mainly consists of small-leaf arid shrubs ($h_{alt} = 1,300\text{--}2,200$ m), such as *Sorophora viciifolia*, *Indigofera bungeana* and *Bauhinia faberivar*, and sparse grasses, such as *Ajanía breviloba*, *Sedum wenchuanense* and *Heteropogon contortus* (Ma et al. 2004; Lu et al. 2006).

Data collection

The field investigation was carried out in August 2006 at three sites (Fig. 1), which were located in the semiarid valley and represented three different vegetation zones. Shidaguan, on the upper reaches of the core area, is dominated by short dry grasses and dwarf dry shrubs on both the north- and south-facing slopes. Feihongguan is within the central part, whose vegetation consists only of

Fig. 1 Location of the sampling sites along the upper Minjiang River, China

sparse dry dwarf shrubs on north-facing slopes and sparse grasses on south-facing slopes. Within the lower portion, Wenchuan, some small trees are growing on the north-facing slopes, but only sparse shrubs were found on the south-facing slopes. At each site, two transects were placed on opposite (i.e., south- and north-facing) slopes, oriented to make a 'V' shape. Sample plots were established along transects with points at about 20-m intervals. Sample plots were homogenous and 25 m² (5 m × 5 m) in area.

Soils and plants were sampled from 57 plots, and 19, 18 and 20 plots were from Shidaguan, Feihongguan and Wenchuan, respectively. In these plots, all shrub and tree species were identified and separately measured for shrub coverage (Shrubcov), herb coverage (Herbcov), litter coverage (Littercov), gravel coverage (Gravelcov) and total height and frequency. Corresponding to each sample plot, the topography was surveyed, and the elevation (ELE) and slope (SLP) were obtained. Since soil water content (SWC) varies over time because of fluctuations in rainfall and plant water requirements in the summer season, the data collection was conducted on sunny days within a 2-week period. Within each plot, moisture of the surface soil (0–20 cm) was determined at nine points by using a portable time domain reflectometry (TDR) device. Composite surface soil samples (0–20 cm) were collected using cores (5 cm in diameter) from five random soil profiles, air-dried, thoroughly mixed and passed through a 2-mm sieve to remove gravel and debris. Soils finer than 2 mm were kept for further chemical and granulometric analyses. The semimicro-Kjeldahl method was employed to determine the total nitrogen (TN). Total phosphorus (TP) was determined colorimetrically after wet digestion with H₂SO₄ plus HClO₄ (Parkinson and Allen 1975). Available nitrogen (AN) was determined by the Cornfield method (alkaline hydrolysable nitrogen). Available potassium (AK) and available phosphorus (AP) were extracted with 3% (NH₄)₂CO₃ solution. After filtering,

the solution was measured by ICP-AES (Editorial Committee 1996). Soil organic matter (SOM) was determined by the K₂Cr₂O₇ titration method after digestion (Nelson and Sommers 1975). Total potassium (TK) was determined by atomic absorption spectrometer (Editorial Committee 1996). Soil pH and electric conductivity (EC) were measured in 1:2.5 soil-water slurry. Soil clay content (clay, <0.002 mm, SCC) and soil sand content (sand, 0.02–2 mm, SSC) were measured by laser diffraction technique with Mastersizer 2000 (Malvern Instruments Ltd., UK). All samples were replicated three times.

Statistical analysis

Because of the high spatial heterogeneity in cinnamon soil, K-means cluster analysis was performed using the program SPSS 13.0 to detect soil groups among the sample plots based on soil chemical properties. The Euclidian distance was used for cluster analysis. After graphic assessment of distributions for normality, three groups were classified to reflect different soil fertility levels. Soil texture and fertility were compared among soil groups (at the 0.05 level) with ANOVAs under the general linear model. For those variables with significant differences, Tukey tests were applied for comparisons of means among soil groups. Occurrence of native shrubs and relative importance values (RIV) in corresponding soils were compared. The shrub relative importance values (RIV) for each sample were calculated using the following formula:

$$\text{RIV} = (\text{Relative density} + \text{Relative coverage} + \text{Relative height})/3.$$

We used canonical correspondence analysis (CCA) to investigate the crucial factors affecting the distribution pattern of all shrubs using the program CANOCO. This

method was commonly used to indicate the relationship between species and environmental variables (Ter Braak 1988; Lu et al. 2006). The species abundance matrix consisted of the parceled RIV (Van Tongeren 1995). Only species with more than four individuals in the total samples and RIV more than 1% in every plot (Lu et al. 2006) were included. As recommended by Ter Braak (1995), all abundance values were log-transformed before being entered into the analysis, as their distributions were skewed towards a few very large values. The matrix of environmental variables per plot initially included the coverage of three layers, site elevation, slope (degree) and aspect (ASP, degree), and all chemical and granulometric figures. Slope position (POS) and shape (SHA) were transformed into two dummy variables. The flat SHA or middle POS was operationalized as the excluded category. Then, the dummy variables were coded as

Dummy 1 = 1 if top (convexity), 0 if middle (flat),
0 if bottom (concave)

Dummy 2 = 0 if bottom (concave), 0 if middle (flat),
0 if top (convexity).

After a preliminary CCA analysis, a number of environmental variables were eliminated due to either high redundancy (variance inflation factors > 20 or VIFs of 0) or poor correlation (intraset correlations with axes 1 or 2 < 0.3; Ter Braak 1988, 1995). The Monte-Carlo permutation test (Ter Braak 1988) was performed to assess the significance of the correlations between the species abundance distribution and the environmental variables. The percent of variation of topographical variables (SHA and POS) was only 2.7% for all variations (unpublished data), so these variables were not included in the analysis of shrub ordination. However, in some cases, the second axis of CCA may be the second variant of the first axis, leading to the 'arch effect.' Detrended canonical correspondence analysis (DCCA) can remove the 'arch effect' and thus may improve the robustness of ordination. DCCA was also performed with the species matrix, and the most strongly correlated variables were indicated by CCA (Ter Braak 1995).

With the aim to test the effects of shrubby N-fixers on surface soil fertility at the community scale, plant communities were classified as grassland with no shrub and herb N-fixers (GL), shrub land dominated by N-fixing shrubs (SNF) and shrub land dominated by non-N fixing shrubs (SNNF). GL (total seven plots) was dominated by the *Aremisia argyi*, *Onosma farrerii* and *Caryopteris incana*, SNF (total 36 plots) was dominated or co-dominated by shrubby legumes from *Bauhinia faberivar*, *S. viciifolia*, *Lespedeza formosa*, *Desmodium podocarpum*, *Campylotropis macrocarpa*, *Indigofera amblyantha*, *Lespedeza floribunda* and *Lespedeza davurica*, and the other 14 plots were categorized as SNNF, which was dominated by non-N fixers (such as *Ajania potaninii*, *Spiraea cantoniensis*, *Quercus cocciferoides* and *Cotinus*

coggygia). The SWC, SOM, AN, AP, soil EC and soil C/N ratio were compared in the multi-analysis of covariance (MANCOVA) with plant community type as the main factor. Topographic variables were considered as co-variables in MANCOVA to eliminate the topographic effects on soil fertility. In order to select suitable species for vegetation restoration, Spearman's rank correlation coefficients were also calculated between the species RIV and the 11 environmental variables. Finally, in terms of the soil moisture and fertility levels, appropriate sites were identified for shrub candidates.

Results

Soil properties

The cluster analysis based on the soil chemical properties of the 57 plots distinguished three distinct soil types. SOM, TN, TP, TK, AN, AP, AK and soil pH of group 1 and group 2 corresponded to fertility levels of eluvial-accumulation cinnamon soil (EACS) and calcareous cinnamon soil (CCS), respectively, as described by Guo and Tang (1994) and Wang et al. (2003). Group 1 included 13 plots, with 4 from 1,900- to 2,200-m elevation, 2 from 1,800 to 1,900 m, 6 from 1,500 to 1,600 m and only 1 plot from lower than 15,00 m. Group 2 consisted of 39 plots, of which 20 were distributed from 1,300 to 1,800 m in elevation, 14 from 1,800 to 2,000 m and 5 from 2,000 to 2,200 m. Particularly among the 20 plots from 1,300 to 1,800 m, nine were distributed between 1,300- and 1,500-m elevation. This zone was located at the transition area from dry cinnamon soil (DCS) to yellow cinnamon soil, which was relatively fertile compared to DCS (Zhang 1992). Group 3 comprised three plots located in the lower dry valley (1,300–1,600 m) of the survey area and two isolated plots (1,800–2,000 m). In contrast, levels of SOM of group 3 were significantly higher than those of DCS, while the GC, TN, TP, TK, AN, AP and soil pH of group 3 were not significantly different compared to DCS. The distribution pattern of plots along the elevation gradient displayed high spatial heterogeneity. According to the comprehensive analysis of soil group textures, fertility and distribution elevation, it was tentatively put forward that soil groups 1, 2 and 3 corresponded to EACS, CCS and DCS, respectively (Fig. 2). The relatively larger differences among three soil types were in SOM, SCC, SWC, TP, TK and AK, among which only SOM was significantly different ($P < 0.05$, $n = 57$). CCS had the smallest value of SOM, and DCS had the largest TP and SOM.

Distribution pattern of N-fixer and non-N fixer along soil gradients

The results of the community survey are summarized in the Appendix. A total of 2,613 individual shrubs were registered in the 57 plots with a total area of 2.5 ha in

Fig. 2 Chemical characteristics of soils of three groups along the upper Minjiang River Valley, China. Means for the same nutrients followed by the different case letters showed differences ($P < 0.05$)

the dry upper valley. A total of 62 shrub species from 25 families was recorded in the inventory of shrub species, including 9 *Leguminosae* species and 1 actinorhizal plant (*Coriaria nepalensis*). *Rosaceae* (12 species) and *Leguminosae* (9) were the most important families. *Compositae* (5), *Anacardiaceae* (4), *Betulaceae* (3), *Thymelaeaceae* (3) and *Verbenaceae* (4) were also commonly represented in the arid valley of the upper Minjiang River. *A. potaninii* (391), *B. faberiva* (324), *Caryopteris incana* (265), *S. viciifolia* (242), *L. formosa* (233), *L. floribunda* (183), *Berberis wilsonae* (151) and *D. podocarpum* (146), with the highest densities, accounted for over 53.6% of all specimens, and shrubby legumes made up 58.3% of these 8 highest densities. N-fixers comprised over 35.0% of all species individuals. Particularly shrubby N-fixers comprised over 41.2% of the total number of specimens in DCS, 40.1% in CCS and 22.1% in EACS. Species with the largest number of specimens in CCS were *A. potaninii*, *B. faberivar*, *S. viciifolia*, *L. formosa* and *Cotinus szechuanensis*, which together accounted for 52.0% of the total value in this soil group. The importance value demonstrated by *B. faberivar*, *C. incana*, *B. wilsonae*, *C. szechuanensis*, *Q. cocciferoides* and *Rosa hugonis* was 47.9% in DCS. *A. potaninii*, *S. viciifolia*, *L. floribunda*, *Spiraea salicifolia*, *Sageretia pycnophylla* and *Periploca sepium* showed a preference for EACS, with an importance value of 71.46%. Ecological dominance of shrubby N-fixers accounted for 34.0% in DCS, 44.4% in CCS and 17.3% in EACS (see [Appendix](#)). The legumes *S. viciifolia* and

I. amblyantha were common to three soil groups; no N_2 -fixing shrubs were only common to EACS and DCS, six shrubby legumes (*B. faberivar*, *L. formosa*, *D. podocarpum*, *C. macrocarpa*, *Robinia pseudoacacia*) only to EACS and CCS, and one leguminous shrub (*L. floribunda*) only to DCS and CCS.

Site adaptability of N-fixer and non-N fixer

Eleven comprehensive variables were selected from the results of CCA and DCCA by using shrub importance value data for the more common species (Table 1). This procedure resulted in very high eigenvalues (> 0.35) for the first two axes (Table 1), indicating very “long” gradients. Moreover, CCA resulted in an insignificant negative correlation between the occurrence of N-fixer and soil properties. Despite the differences, the variances of species data summarized by both CCA and DCCA axes were still small, which indicated that considerable “noise” remained unexplained. In fact, CCA produced considerably high values for both species-environment correlations and respective cumulative percentage variances. In addition, the Monte-Carlo permutation test indicated that the species abundances and environmental variables were significantly correlated ($F = 4.83$, $P < 0.01$, first axis; $F = 2.10$, $P < 0.01$, overall test).

Soil, topographical and vegetation variables eliminated because of poor correlations coincided with those with no significant differences among the soil groups,

Table 1 Summary of canonical correspondence analysis (CCA) and detrended canonical correspondence analysis (DCCA) for the shrub community in 57 plots along the upper Mingjiaing River Valley, China

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
CCA					
Eigenvalues	0.55	0.41	0.31	0.21	5.62
Species–environment correlations	0.93	0.90	0.84	0.83	
Cumulative percentage variance					
Of species data	9.70	17.00	22.40	26.20	
Of species–environment relation	28.60	50.10	66.10	77.20	
Sum of all canonical eigenvalues					1.91
DCCA					
Eigenvalues	0.55	0.37	0.19	0.06	5.62
Species–environment correlations	0.90	0.87	0.79	0.76	
Cumulative percentage variance					
Of species data	9.70	16.30	19.70	20.70	
Of species–environment relation	24.00	42.30	0.00	0.00	
Sum of all canonical eigenvalues					1.91

Table 2 Canonical correspondence analysis (CCA): intraset correlations on the first two ordination axes and weighted correlation matrix for the environmental variables supplied in the analysis

	VIF	Intraset correlations												
	Axis 1	Axis 1	Axis 2	SWC	SCC	ELE	Shrubcov	AK	AN	TN	SSC	pH	Gravelcov	TK
SWC	4.25	0.86	0.00	–										
SCC	4.91	0.82	0.08	0.83	–									
ELE	2.34	0.15	0.65	0.23	0.16	–								
Shrubcov	1.73	0.17	0.62	0.26	0.28	0.26	–							
AK	2.48	0.44	0.16	0.64	0.70	0.14	0.38	–						
AN	3.52	0.13	0.56	0.10	0.25	0.54	0.38	0.31	–					
TN	1.72	0.06	0.33	0.02	0.16	0.29	–0.06	0.19	0.55	–				
SSC	1.97	–0.38	–0.31	–0.32	–0.33	–0.48	0.08	–0.17	–0.14	–0.18	–			
pH	1.52	–0.06	–0.33	0.03	0.00	–0.37	–0.03	0.09	–0.48	–0.30	0.18	–		
Gravelcov	1.54	–0.29	–0.40	–0.19	–0.26	–0.24	–0.32	–0.21	–0.50	–0.32	0.19	0.14	–	
TK	1.58	–0.30	–0.12	–0.28	–0.37	0.07	–0.33	–0.29	–0.25	–0.09	–0.27	0.04	0.12	–

VIFs Variance inflation factors

Correlations with absolute values > 0.3 and 0 < VIFs < 20 are in bold

and 11 variables were selected (Table 2). The first canonical axis was significantly and positively correlated with SWC and SCC, whose correlation vectors formed the smallest angle with the first canonical axis, followed to a much lesser extent by AK, and was distinctly negatively correlated with SSC, TK and Gravelcov (Fig. 3). The second canonical axis showed significant correlations with ELE, Shrubcov and AN, followed by TN, and particularly a negative correlation with the soil pH and Gravelcov. The first and second canonical axes showed mostly the effect of edaphic physiochemical properties. The results showed that soil moisture and nitrogen availability significantly co-constrained shrub distribution and growth.

Further analysis indicated that N-fixers and non-N-fixers (≥ 3 species in the corresponding family) showed distinctly different environmental preferences. All shrubs occupied three different groups as shown in Fig. 3. For N-fixers, five shrubby legumes (*L. floribunda*, *S. viciifolia*, *I. amblyantha*, *D. podocarpum* and *B. faberivar*) had marked negative correlations with SWC, SCC, AN, TN, ELE and Shrubcov, being

strongly positive with TK, Gravelcov and SSC. In contrast, three leguminous shrubs (*L. davurica*, *C. macrocarpa* and *R. pseudoacacia*) positively correlated with SCC, SWC and AK. Only one legume (*L. formosa*) occurred with higher frequency in plots that had higher TN, AN, ELE and Shrubcov (Fig. 3). For non-N fixers, *Compositae* (*A. potaninii* and *Clematis florida*), *Verbenaceae* (*Caryopteris odorata* and *Caryopteris terniflora*) and *Rosaceae* (*Spiraea longigemmis*, *Rosa banksiae*, *Spiraea henryi* and *S. salicifolia*) and two species of *Thymelaeaceae* (*Daphne tangutica* and *Wikstroemia modesta*) occurred more frequently in plots with higher pH, Gravelcov, SSC, TK, lower SWC and soil nutrient levels (lower TN, lower AN and AK). Five species of *Rosaceae* (*S. cantoniensis*, *Cotoneaster multiflorus*, *Contoneaster acutifolius*, *Rosa sweginowii* and *Rosa bella*), all species of *Betulaceae* plant (*Corylus ferox*, *Carpinus turczaninowii* and *O. davidiantii*) and two *Thymelaeaceae* species (*Daphne penicillata*, *Wikstroemia stenophylla*) occurred with higher frequency in plots with higher SWC, AK and clay-rich soils, which also held true for *Pertya sinensis* and *C. incana*. Several

Fig. 3 Canonical correspondence analysis: ordination biplots showing the distribution of species in different families ($\diamond$ Leguminosae, $\triangleleft$ Verbenaceae, $\circ$ Betulaceae, $\square$ Rosaceae, $\triangle$ Anacardiaceae, $\diamond$ Compositae, $\triangleright$ Thymelaeaceae) on the first two ordination axes. Species names are abbreviated (scaled $\times 3$); full names are given in the Appendix; environmental variables are given as arrows; 26 species (≤ 2 species) are unmarked

species, including *Clematis intricata*, *C. coggygia*, *Rhus potaninii* and *Cotoneaster ambiguous*, occupied plots that had similar habitats, with *L. formosa* being strongly influenced by TN, AN, ELE and Shrubcov variables (Fig. 3). *Betulaceae* species demanded even higher levels of SWC and SCC. Moreover, preference of the other 25 species to sites responded weakly to the selected environmental variables.

The distribution of soil fertility and moisture in different functional community types

Figure 4 shows that the soil SWC, AN, AP, EC and soil C/N ratio are significantly different among the three community types, and there were no significant differences in SOM among them. AN, AP and EC were significantly higher in SNNF than in GL, and the soil C/N ratio was significantly lower in SNNF. AN and EC were the highest in SNNF and the lowest in GL. GL showed the lowest AP and the highest soil C/N, and there were no differences between SNF and SNNF in these two soil properties. SWC was the lowest in SNF and the highest in SNNF. The soil C/N ratio in shrub land significantly decreased by over 58% compared to GL (Fig. 4). Although SWC beneath SNF and SNNF (shrub land) was relatively and insignificantly lower than that beneath GL, the variance of SWC beneath shrub land was smaller.

Suitable candidates and site identification

Ordination of the five species by CCA strongly agreed with their rank correlation coefficients with 11 particular environmental variables (Table 3). Interestingly, not all N-fixers were enrolled as candidates. Only four shrubby legumes had a negative correlation with SCC, SWC, AN, AK and soil pH. Some correlation coefficients between fertility variables and candidates species reached a significant level (Table 3). For instance, *I. amblyantha* and *S. viciifolia* correlated significantly and negatively with SWC and SCC. This confirmed that these two shrubby legumes have stronger capacities for drought and nutrient deficiency resistance than *D. podocarpum* and *B. faberivar*. Interestingly, *A. potaninii* (non-N₂ fixing) can tolerate drier and potassium-rich sites on CCS.

Discussion

Water, N and P limitations to shrub distribution and growth in arid lands have been demonstrated (Marschner 1995; Drenovsky and Richards 2004; James et al. 2005). Similar to other arid systems, the combination of a low, unpredictable water supply and nutrient status limited seedling establishment and plant growth in the arid valley. The results of CCA indicated that soil moisture and N co-constrained growth of non-N fixers weakly limit that of N-fixers. Our results are consistent with

Fig. 4 Six key soil nutrient variables for three vegetation patterns along the upper Minjiang River, China (GL grassland; SNF and SNNF are shrublands dominated by N-fixers and non-N fixers, respectively). Different letters indicate significant differences across three vegetation patterns according to Tukey test ($P < 0.05$)

Table 3 Spearman's rank correlation coefficients and their significance for the relative importance values of 7 species used in the 11 environmental variables for CCA

Function	Candidate species	Texture		Soil fertility						Coverage		ELE
		SSC	SCC	SWC	AN	AK	pH	TN	TK	Shrubcov	Gravelcov	
Leguminosae	<i>I. amblyantha</i>	0.19	-0.40*	-0.44*	-0.16	-0.26	-0.01	-0.50*	0.64**	-0.16	0.22	-0.03
Leguminosae	<i>S. viciifolia</i>	-0.04	-0.34*	-0.43**	-0.01	-0.11	-0.02	0.20	0.28	-0.51**	0.05	0.44*
Leguminosae	<i>B. faberivar</i>	-0.44*	-0.14	-0.09	0.66**	0.24	-0.54**	0.48*	-0.08	-0.15	-0.35*	0.52*
Leguminosae	<i>D. podocarpum</i>	0.43	-0.67	-0.60	-0.90*	-0.94*	0.43	-0.54	-0.66	0.18	-0.09	-0.71
Non-N fixer	<i>A. potaninii</i>	-0.28	-0.40**	-0.61**	-0.22	-0.14	0.08	-0.09	0.62**	-0.26	0.42*	0.40*

* $P < 0.05$, ** $P < 0.01$. Species ranked by their coefficient of SWC and SCC

water and N limitations to non-N fixers and demonstrate two comprehensive additional limitations of Gravelcov and soil pH mainly affecting N-fixers (Fig. 3). In fact, increasing alkalinity is expected to further reduce N availability through volatilization of mineralized ammonium (Marschner 1995; James et al. 2005). Surprisingly, limitation of P was not found in this study. However, the significant negative correlation between ELE and N-fixers (Fig. 3) implied a strong limitation of P in relation to them because soil at high elevations contained lower TP (such as EACS vs. DCS, Fig. 2).

Until now, many restoration efforts have been implemented, but have had poor results in the study area (Ma et al. 2004; Li et al. 2005, 2006; Xu et al. 2008). Many introduced woody species have had difficulties becoming established and have become “small old trees” under the conditions of water and nutrition deficiency. Surprisingly, field observations showed that the secondary successional process of shrubs naturally occurred in the arid valley's barren land, forest clear-cutting areas and abandoned land. This region is very unfavorable for the

regeneration of tree species (Ma et al. 2004); revegetating with native shrubs may be ecologically reasonable. In fact, natural recovery of vegetation is gaining increasing attention in various restoration projects (Karel and Petr 2001; Miyawaki 2004; Li et al. 2008b). Therefore, we urgently need to enhance the present restoration methods and theories following the community succession principles, for example, selecting suitable native species from the potential natural vegetation.

Correct selection of suitable species is crucial for ecological restoration (Rosales et al. 1997; Miyawaki 2004). It is desirable to use drought- and leanness-resistant native species instead of exotic species in restoration efforts if these native species are available and can grow well in the region, since they can facilitate and enhance shrub regeneration habitats for later successional species (Montagnini 2006). Tree and shrubby legumes are the most appropriate candidates for revegetation of arid and/or disturbed ecosystems because of their ability to establish tripartite symbiotic associations with nitrogen-fixing rhizobia and mycorrhizal fungi

(Herrera et al. 1993; Zaharan 1999; Quatrini et al. 2003). N-fixing plants can improve the soil structure and nutrient status through the production of leaf debris, root action, formation of humus and stimulation of soil faunal activity, as well as reduced leaching and erosion losses at specific levels in arid ecosystems (Tian et al. 2003; Baets et al. 2007). This view was confirmed by the distribution patterns of N-fixers in the environmental variables in the present study. The weak correlation with nitrogen elements and water of most legumes indicated that they had great potential for tolerance to drought and nitrogen deficiency (Fig. 3). Especially four N-fixers showed a strong 'broad-spectrum' tolerance capacity for the physiochemical properties of soil (Table 3). For example, *B. faberivar* is naturally predominant on south-facing slopes, which have lower soil moisture and nutrient levels (Ma et al. 2004). It is likely that the lower availability of phosphorus in EACS at higher elevations inhibits the process of nitrogen fixing (Fig. 2). Native N-fixers are well developed and can extend avenues of their own seed dispersal. In addition, shrubby legumes have been found to be particularly effective nurse plants in arid lands (Shearer et al. 1983; Lajtha and Schlesinger 1986); they can effectively enhance seedling survival and growth in nutrient-island soils. Furthermore, N-fixers are used for fodder, firewood and even medicines by the local people (Tian et al. 2003; Schlecht et al. 2007; Li et al. 2008a). However, not all shrubby legumes are suitable for revegetation, such as the legume *L. formosa*, which demands higher soil nitrogen, but some non-N fixers have the potential for restoration (Table 3). For example, *A. potaninii* (*Compositae*) cannot tolerate nitrogen and moisture stress, but it reduced runoff production by 66.6% and soil loss by 59.3% (Xu et al. 2008). Thus, potential species should not be overlooked. Therefore, it is fundamental that existing shrub populations and their communities, especially N-fixers, should be protected and preserved, and secondly, those that have been destroyed by human impact should be restored and reconstructed.

Once candidate seedlings have been established, it is not climate conditions but soil conditions that matter (Miyawaki 2004). The distribution pattern of nutrients showed the lowest fertility level in CCS, a medium level in EACS and the highest rate in DCS. The results suggest that it would be reasonable and easier to restore DCS and EACS than CCS. At the individual plant level, the presence or absence of N-fixers, such as legumes, may be complementary to nitrogen usage with non-fixing species, and they can also interact positively with other species by increasing soil nitrogen pools and nitrogen supply rates for other plants (Scherer-Lorenzen 2008). At the community level, N-fixers significantly affect the key ecosystem processes, such as biomass production, resource use and decomposition (Maron and Jefferies 1999; Stöcklin and Körner 1999; Scherer-Lorenzen 2008). Compared with GL, significant improvement in nutrient availability, such as AN, AP, soil EC and soil C/N ratio, beneath SNNF and SNF

indicated that the presence of shrubs strongly affected soil fertility, irrespective of EACS, CCS and DCS (Fig. 4). This result is consistent with other studies (Maron and Jefferies 1999; Scherer-Lorenzen 2008). Some tree species were investigated in SNNF plots, such as *Cupressus chengiana*, *P. sepium* and *Pittosporum tor-ira* (Appendix). Therefore, we tentatively put forward that the amelioration of soil fertility stemmed from the facilitative effects of vegetation succession, especially those of N-fixers. In fact, shrubby legumes are widely distributed in regions with a Mediterranean-type climate (Del Pozo and Aronson 2000; Rodríguez-Echeverría et al. 2003). Actinorhizal species also have been considered as pioneer species in pasture ecosystems (Croat 1978; Delagrangue et al. 2007). In the arid valley, there are other actinorhizal plants (*C. nepalensis* and *Myrica rubra*). Therefore, potential candidates can be found from families of *Coriariaceae* and *Myrica*. The non-N₂ fixing species effective in controlling soil and water erosion were suitable for ecosystem restoration.

Conclusion

Our study of the early stages of invasion by N-fixers in an arid valley supports the traditional facilitative role that has long been assumed for N-fixers in secondary succession. We also demonstrate that legume establishment is facilitated by the presence of earlier herb species. From a management perspective, it is pertinent to distinguish N-fixers from non-N fixers considering the key function of leguminous and actinorhizal species in arid systems. Dominant shrubby legumes should have high priority in restoration projects. It is of great benefit to select pioneer species for revegetation and to speed up the community succession process effectively. N-fixing shrubs and trees may be hand-planted directly into grassland, or their seeds and seedlings can be directly sown and planted under shrub canopies. The distribution pattern of N-fixers in arid ecosystems may offer a simple and effective avenue to ecological restoration. For non-N fixers, soil moisture is the primary limiting factor, and nitrogen is next. N-fixers are weakly constrained by soil moisture and nitrogen, the extent of which is species-specific. The proposed pioneer species are four native shrubby legumes (*I. amblyantha*, *S. vicifolia*, *D. podocarpum* and *B. faberivar*) in this zone.

Our empirical study was focally concerned with the site distribution and adaptability of N-fixing shrubs. However, little is known about N-fixing herbaceous and tree species in the arid zone. In addition, appropriate native *Rhizobium* and *Frankia* are crucial for successful nodulation of N-fixers. Further study is necessary to isolate strongly ineffective and effective microorganisms in native natural systems.

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Appendix

See Table 4.

Table 4 Occurrence of native shrub species sampled in 57-15 × 15-m plots in three soils along the upper Minjiang River Valley, China, with their families and quantitative parameters

Abbre.	Scientific name	Family	Group 1 (EACS)		Group 2 (CCS)		Group 3 (DCS)	
			N ^a	RIV	N	RIV	N	RIV
Bafa^b	<i>Bauhinia faberivar microphylla</i> Oliver.	Leguminosae	96	6.75	228	19.05	0	0
Sovi^b	<i>Sophora viciifolia</i> Hance	Leguminosae	5	0.72	211	11.60	26	9.79
Ajpo	<i>Ajania potaninii</i> (Krasch.) Poljak.	Compositae	52	3.72	265	9.17	74	13.63
Lefo^b	<i>Lespedeza formosa</i> (Vog.) Koehne	Leguminosae	31	2.17	202	8.01	0	0
Cosz	<i>Cotinus szechuanensis</i> A.Penzes	Anacardiaceae	47	5.96	89	4.18	0	0
Sapy	<i>Sageretia pycnophylla</i> Schneid.	Chenopodiaceae	5	1.02	84	3.81	14	6.14
Depo^b	<i>Desmodium podocarpum</i> DC.	Leguminosae	3	0.18	143	3.62	0	0
Cain	<i>Caryopteris incana</i> Miq.	Verbenaceae	182	9.41	83	3.36	0	0
Rohu	<i>Rosa hugonis</i> Hemsl.	Rosaceae	28	4.21	45	3.27	3	1.55
Bewi	<i>Berberis wilsonae</i> Hemsl.	Berberidaceae	42	4.99	90	3.20	19	3.70
Losz	<i>Lonicera szechuanica</i> Batal.	Caprifoliaceae	2	0.20	82	3.00	0	0
Catu	<i>Carpinus turczaninowii</i> Hance	Betulaceae	1	0.23	64	2.23	0	0
Jahu	<i>Jasminum humile</i> Linn.	Oleaceae	23	1.84	28	2.01	2	1.24
Spsa	<i>Spiraea salicifolia</i> L.	Rosaceae	35	3.73	55	1.78	39	6.28
Cafo	<i>Caryopteris forrestii</i> Diels.	Verbenaceae	0	0	36	1.47	6	1.52
Quco	<i>Quercus cocciferoides</i> Hand.-Mazz.	Fagaceae	94	16.57	15	1.41	2	1.05
Pese	<i>Periploca sepium</i> Bge.	Asclepiadaceae	6	0.53	29	1.31	62	8.77
Abma	<i>Abelia macrotera</i> (Graebn. Et Buchw.) Rehd.	Caprifoliaceae	28	2.79	19	1.24	7	1.74
Robe	<i>Rosa bella</i> Rehd. et Wils.	Rosaceae	9	1.16	19	1.24	0	0
Coco	<i>Cotinus coggygia</i> var. <i>glaucohylla</i> C.Y. Wu	Anacardiaceae	0	0	30	1.24	0	0
Rhor	<i>Rhododendron oreodoxa</i> Franch. var. <i>fargesii</i>	Ericaceae	5	0.57	14	1.03	0	0
Cama^b	<i>Campylotropis macrocarpa</i> (Bge.) Rehd.	Leguminosae	29	1.72	29	0.99	0	0
Rhro	<i>Rhamnus rosthornii</i> Pritz.	Rhamnaceae	0	0	11	0.99	0	0
Sphe	<i>Spiraea henryi</i> Hemsl.	Rosaceae	0	0	11	0.91	11	3.87
Osma	<i>Osmanthus marginatus</i> Var. <i>pachyphyllus</i>	Oleaceae	18	0.97	30	0.89	0	0
Cofe	<i>Corylus ferox</i> Wall.	Betulaceae	4	0.32	12	0.89	0	0
Clfl	<i>Clematis florida</i> Bge.	Compositae	4	0.59	23	0.88	2	0.63
Roba	<i>Rosa banksiae</i> Aiton	Rosaceae	0	0	10	0.72	0	0
Spsa	<i>Spiraea cantoniensis</i> Lour.	Rosaceae	31	3.69	5	0.55	0	0
Inam^b	<i>Indigofera amblyantha</i> Craib.	Leguminosae	7	0.69	2	0.54	8	1.79
Dape	<i>Daphne penicillata</i> Rehd.	Thymelaeaceae	0	0	10	0.54	0	0
Coac	<i>Contoneaster acutifolius</i> Turcz.	Rosaceae	4	0.43	4	0.46	0	0
Splo	<i>Spiraea longigemma</i> Maxim.	Rosaceae	0	0	6	0.45	0	0
Wimo	<i>Wikstroemia modesta</i> (Rehd.) Domke	Thymelaeaceae	6	0.48	6	0.43	12	3.64
Left^b	<i>Lespedeza floribunda</i> Bunge	Leguminosae	0	0	10	0.41	173	22.38
Sesu	<i>Securinega suffruticosa</i> (Pall.) Rehd.	Euphorbiaceae	13	2.25	3	0.37	0	0
Pito	<i>Pittosporum tobira</i> (Thunb.) Ait.	Pittosporaceae	12	0.59	12	0.35	0	0
Clin	<i>Clematis intricata</i> Bge.	Ranunculaceae	2	0.21	5	0.31	0	0
Rosw	<i>Rosa sweginowii</i> Koehne	Rosaceae	5	0.78	5	0.29	3	1.22
Coam	<i>Cotoneaster ambiguus</i> Rehd. et Wils.	Rosaceae	2	0.57	3	0.26	0	0
Cysi	<i>Cynanchum sibiricum</i> Willd.	Asclepiadaceae	0	0	6	0.25	0	0
Osda	<i>Ostryopsis davidiana</i> Decne	Betulaceae	27	2.54	5	0.2	0	0
Cuch	<i>Cupressus chengiana</i> S. Y. Hu	Cupressaceae	8	0.66	5	0.19	0	0
Caod	<i>Caryopteris odorata</i> (D. Don) B.L.R.L. Robinson	Verbenaceae	0	0	5	0.19	20	4.47
Rops^b	<i>Robinia pseudoacacia</i> L.	Leguminosae	16	1.28	2	0.18	0	0
Aspo	<i>Aster poliothamnus</i> Diels.	Compositae	0	0	3	0.17	0	0
Cate	<i>Caryopteris terniflora</i> Maxim.	Verbenaceae	40	2.04	3	0.14	6	1.30
Diru	<i>Discocleidia rufescens</i> (Franch.) Paxet Hoffm.	Euphorbiaceae	0	0	2	0.13	0	0
Ajra	<i>Ajania ramosa</i> (Chang) Shih	Compositae	0	0	1	0.09	0	0
Rhpo	<i>Rhus potaninii</i> Maxim.	Anacardiaceae	16	3.21	0	0	0	0

Table 4 continued

Abbre.	Scientific name	Family	Group 1 (EACS)		Group 2 (CCS)		Group 3 (DCS)	
			N ^a	RIV	N	RIV	N	RIV
Leda^b	<i>Lespedeza davurica</i> (Laxm.) Schindl.	Leguminosae	43	2.86	0	0	0	0
Rhty	<i>Rhus typhina</i> L.	Anacardiaceae	21	1.89	0	0	0	0
Data	<i>Daphne tangutica</i> Maxim.	Thymelaeaceae	28	1.76	0	0	8	1.95
Cone^b	<i>Coriaria nepalensis</i> Wall.	Coriariaceae	2	0.88	0	0	0	0
Aial	<i>Ailanthus altissima</i> (Mill.) Swingle	Simaroubaceae	2	0.61	0	0	0	0
Comu	<i>Cotoneaster multiflorus</i> Bge.	Rosaceae	4	0.51	0	0	5	2.79
Eual	<i>Euonymus alatus</i> (Thunb.) Sieb.	Celastraceae	2	0.48	0	0	0	0
Zasi	<i>Zanthoxylum simulans</i> Hance	Rutaceae	2	0.35	0	0	1	0.55
Pesi	<i>Pertya sinensis</i> Oliv.	Compositae	3	0.25	0	0	0	0
Ruco	<i>Rubus corchorifolius</i> L.f.	Rosaceae	3	0.24	0	0	0	0
Stch	<i>Stachyurus chinensis</i> Magpie	Stachyuraceae	1	0.23	0	0	0	0
Acse	<i>Acanthopanax senticosus</i> (Rupr.et Maxim.) Harms	Araliaceae	1	0.17	0	0	0	0
Total N-fixers			232	17.25	827	44.40	207	33.96
Total non-N fixers			818	82.75	1233	55.60	296	66.04
Total			1,050	100	2,060	100	503	100

^a N number of individuals. RIV relative importance value. Species are ranked by descending RIV in CCS

^b N-fixers are in *bold*

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