IMPACT OF MULTIPLE SOIL NUTRIENTS ON DISTRIBUTION PATTERNS OF SHRUBS IN AN ARID VALLEY, IN SOUTHWEST CHINA

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Abstract

Shrubs play key roles in arid regions and multiple interacting resources limit their distribution patterns. Identifying limiting resources and their coupling effects on shrubs is essential for developing restoration theory and practice. A survey of shrub composition, soil properties and topography was conducted in fifty-seven 15-m×15-m plots in an arid valley of the upper Minjiang River, Southwest China. With quantitative classification method and ordination technique, 48 shrubs species were classified into four clusters and two categories along soil gradient. Cluster I and II composed Category I and had a significantly higher percentage of dominant legume shrubs than in Cluster III and Cluster IV, which made up Category II. Correlation analysis indicated that both multi-resource limitation and single resource limitation were coexisting simultaneously in this arid area, the extent of which was functional cluster-specific and also quantified hierarchical structure of multiple resource limitation: soil water played a primary limitation role, available nitrogen the next, and available phosphorus the third at community scale. Moreover, this study affirmed that both soil pH and soil texture could effectively regulate retention of soil moisture and available nutrients, respectively. Distinguishing critical limiting resources and their regulators is very meaningful to clarify couplings and controlling mechanisms in restoration practices. Therefore, decreasing soil pH and increasing soil clay content should be conducted thoroughly in plantation sites to remain abundant soil moisture and available nutrients in native restoration projects.

Key words: Shrub pattern, Multi-resource limitation, Hierarchical limiting structure, Co-limitation, Ecological restoration

Introduction

Human overexploitation of natural resources has caused or accelerated land degradation and desertification in large areas of arid and semiarid ecosystems (Matson et al., 1997; Ashraf et al., 2012). Therefore, ecological restoration has been widely used to reverse the environmental degradation (Benayas et al., 2009). Shrubs are one important functional vegetation cluster in arid natural ecosystems. Being the dominant life form in arid lands, they can improve soil quality and reduce runoff and soil loss (Wilcox, 2002; Xu et al., 2008a; Xu et al., 2009). Moreover, they provide key ecosystem products, such as fodders and medicines (McKell, 1975). They are well suited to drought environment and facilitate the development of fertile islands (Thompson et al., 2005; Song et al., 2010a), thereby remediating the abiotic environment, which can initiate or accelerate the co-evolution process between plant and environment (Hilderbrand et al., 2005). http://www.ecologyandsociety.org/vol10/iss1/art19/. So restoration of shrub vegetation may have an important role to play in the reversal of land degradation and desertification due to their important potential for ecological restoration.

Interactions between multiple limiting resources are widespread across aquatic and terrestrial systems (Harpole et al., 2011), especially where arid ecosystems are resource-poor environments. Multiple resource limitation to shrub distribution and growth in arid lands have been demonstrated (Drenovsky & Richards, 2006; James et al., 2005). Not only does low and infrequent precipitation lead to low water availability, but it also decreases nutrient availability (Drenovsky & Richards, 2006). So both water and nutrients are commonly co-limiting in arid environments (Zhu et al., 2013), and local plants have adapted to condition of multi-resources limitations through numerous eco-physiological mechanisms. So efforts to better understand how shrub species interact with limiting resources should be a high priority, since the information can provide value clues about the correct addition of suitable nutrients and the appropriate selection of feasible management methods in developing restoration practices.

The dry river valley of the Upper Reach of the Minjiang River watershed, in the Upper Yangtze River basin, represents a transitional landscape from the Tibet Plateau to the Sichuan Basin. The vegetation cover had declined to 5.7% from 50% during the last eight hundred years along the main river. Moreover, Wenchuan Earthquake recently struck the mountain ecosystems and led to further ecological degradation. Now up to 44% of the land in the area has been described as degraded due to frequent natural and anthropogenic disturbances, such as repeated geological disaster, large-scale water and soil erosion. Ecological degradation has sharply decreased the amount of soil water and soil nutrients, threatened the biodiversity and productivity of the ecosystem, and endangered regional ecological safety. It is thus considered one of the most important region for ecological restoration in China. In this area, more field studies on soil water and nutrients pattern (Wang et al., 2003; Ma et al., 2004), biodiversity of shrub and herb (Lu et al., 2006; Xu et al., 2008b), and change of land use (He et al., 2006) have been carried out for many years. Moreover, considerable attention of some studies has been paid to effects of single or two resources limitation to shrub seedling in lab (Li et al., 2008; Wu et al., 2008). Although fertilizer experiment had verified that a strong co-limitation of soil water, nitrogen and phosphorus was
occurred to growth and biomass partitioning of native shrub seedlings (Song et al., 2010b), but no research has been directly focused on the effect of co-limitation on distribution patterns of shrubs under condition of multi-resources limitation in these intensively disturbed environments. Based on field investigations of shrub composition, soil properties and topography, the objectives of this community-level study were to: (1) examine the distribution patterns of shrub species under conditions of multi-resource limitation in a dry deciduous shrubland community; (2) identify the crucial limiting resources and regulating factors of shrubs’ spatial distribution in terms of their dynamics and variations; (3) quantify the multi-resource limitation structure and provide scientific suggestions for ecological restoration in this degraded arid land.

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 in length and has an altitude range of 3,560 m. The upper Minjiang River Basin (30º44'-32º24'N, 102º41'-103º58'E) is a 337-kilometer 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 while the minimum one 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 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.

Regional vegetation mainly consists of small-leaf arid shrubs (\(h_{sb} = 1,300-2,200\) m), such as Sophora viciifolia, Bauhinia faberi, and Indigofera bungeana, and sparse herbs, such as Ajania breviloba, Sedum wenchuanense and Heteropogon contortus.

Data collection: In order to study the characteristics of distribution patterns of various shrubs, field investigation was carried out at three sites (Fig. 1), which were located in the semiarid valley and represented three different vegetation zones, in August 2008. Shida guan, on the upper reaches of the core area, was dominated by short dry herbs and dwarf dry shrubs. Feihong guan is within the central part, whose vegetation consisted only of sparse dwarf dry shrubs and sparse herbs. Wenchuan, only sparse shrubs were found on slopes. At three sites, two transects were placed on opposite (i.e. south- and north-facing) slopes, oriented to make a ‘V’ shape. For each transect, the range of slope degrees values is 25 to 50. Sample plots were established along transects with points at about 20-m intervals between 1,300 and 2,200 m in a semi-arid valley. Sample plots were homogenous and 225 m² (15 m×15 m) in area. A total of 57 plots were examined, and 19, 18 and 20 plots were from Shida guan, Feihong guan and Wenchuan, respectively. In these plots, all shrub 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), slope (SLO), aspect (ASP, degree) and slope position (SLP) and shape (SHA) were obtained. Since soil water content (SWC) varies over time due to 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). Composite surface soil samples (0-20 cm) were collected using cores (5 cm diameter) from five random soil profiles, air-dried, thoroughly mixed, and passed through a 2 mm sieve to remove gravel and debris. Soil finer than 2 mm was kept for further chemical and granulometric analyses. The semimicro-Kjeldahl method (Wang et al., 2003) was employed to determine the total nitrogen (TN). Total phosphorus (TP) was determined colorimetrically after wet digestion with H₂SO₄ plus HClO₄ (Parkinson & Allen, 1975). Available nitrogen (AN) was determined by the Cornfield method (alkaline hydrolysable nitrogen) (Lu et al., 2006). Available potassium (AK) and available phosphorus (AP) were extracted with 3% (NH₄)₂CO₃ solution (Xu et al., 2009). After filtering, the solution was measured by ICP-AES (Song et al., 2010a). Soil organic matter (SOM) was determined by the K₂Cr₂O₇ titration method after digestion (Lu et al., 2006). Total potassium (TK) was determined by atomic absorption spectrometer (Lu et al., 2006). Soil pH was measured in 1 : 2.5 soil-water slurry. Soil clay content (Clay, <0.002 mm, SC) and soil sand content (Sand, 0.02-2 mm, SS) were measured after the digestion of organic matter by laser diffraction technique with Mastersizer 2000 (Malvern Instruments Ltd, UK) (Xu et al., 2009). All samples were replicated three times.

Data analysis: Preliminary canonical correspondence analysis (CCA) was used 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 (Lu et al., 2006). The species abundance matrix consisted of the relative importance values (RIV). The species RIV for each sample were calculated using the following formula:

\[
\text{RIV shrub} = \frac{\text{Relative density} + \text{Relative height} + \text{Relative coverage}}{300}
\]

Only species with more than four individuals in the total samples and RIV more than 1% in every plot were included (Lu et al., 2006). Their names are listed in Table 1. The matrix of environmental variables per plot initially included the coverage of three layers and all physicochemical and topographical 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:

\[
\text{Dummy 1} = 1 \text{ if top (convexity), 0 if middle (flat), 0 if bottom (concave)}
\]

\[
\text{Dummy 2} = 0 \text{ if bottom (concave), 0 if middle (flat), 0 if top (convexity)}
\]
We developed a matrix of RIVs of 48 × 57 (species × samples). 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; Song et al., 2010a). The Monte-Carlo permutation test (Ter Braakc, 1995) 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.

Second, two-way indicator-species analysis (TWINSPAN) and detrended canonical correspondence analysis (DCCA) were used to recognize homogenous plots and shrubs because DCCA can remove the ‘arch effect’ and thus may improve the robustness of ordination. Third, Pearson's correlation (PC) was performed to figure out and measured the limiting resources and their regulating factors between soil water or soil nutrients and the main two DCCA axes and soil pH, soil clay sand ratio. As recommended by Ter Braak (1995), all values were log-transformed before entering the analysis, as their distributions were skewed towards a few very large values. 11 variables were selected and included in the analysis of shrubs ordination based on our previous study (see Song et al., 2010a for details). The TWINSPAN analysis was carried out using the default settings of the computer program TWINSPAN, the DCCA analysis was performed with the soft package CANOCO for Windows 4.5 (Lu et al., 2006). The PC analysis was conducted using the SPSS program for Windows 16.0 (SPSS Institute Inc., 2012) and considered significant at 0.05, 0.01 and 0.001 level.

In addition, plant communities were classified as shrubland dominated by legume shrubs (SLS) and shrubland dominated by non-legume shrubs (SNS). SLS (total 36 plots) was dominated or co-dominated by shrubby legumes from B. faberivar, S. viciifolia, Lespedeza formosa, Desmodium podocarpum DC, C. Macrocarpa, Indigofera Amblyantha Craib, Lespedeza floribunda Bunge and Lespedeza davurica (Laxm.) Schindl, and the other twenty one plots were categorized as SNS, which was dominated by non-legume shrubs, such as Ajania potaninii (Krach.) Poljak, Spiraea cantoniensis Lour, Quercus cocciferaoides and Cotinus coggygium var. glaucophylla C.Y.Wu. The number of SLS and dominant shrubby legume and their percentage in four shrub clusters were compared with the aim to test the response difference between shrubby legumes and non-legume shrubs along soil gradient at community scale.

**Results**

**Patterns and properties of plots distribution:**

TWINSPAN analysis was performed on the 57 plots in shrubs, and the stopping point of the group formation was set at the second level based on experience, which could produce up to four groups of 57 plots (Fig. 2).

The four groups of plot were described as follows:

**Group I:** This group of 25 plots (2, 4, 5, 6, 7, 8, 16, 17, 18, 20, 21, 22, 23, 24, 25, 26, 27, 28, 32, 34, 35, 37, 39, 40, 41) was mainly located on sunny slopes from 1,350- to 2,050-m elevation, and was mostly dominated by legume shrubs (B. faberi, S. viciifolia, I. Amblyantha Craib, L. floribunda) and non-legume shrub (A. potaninii). Shrub coverage was typically less than 40%, gravel coverage was typically more than 22%. Percentage of plots dominated with shrubby legumes accounted for over 84% (Fig. 3a), and percentage of shrubby legume highly reached 66.67% for 6 dominant shrubs (Fig. 3b).

**GROUP II:** This group was characterized not only by shrubby legumes (including B. faberi, S. viciifolia, L. floribunda) but also three non-legume shrubs, such as Sageretia pycnophylla Schneid and Q. cocciferaoides, comprising 15 plots (1, 9, 10, 11, 12, 13, 15, 19, 29, 30, 31, 33, 42, 44, 48) from 1,800 m to 2,150 m. Most of the plots were on dry slopes. Shrub coverage varied from
50% to 70%, gravel coverage was from 10% to 12%. Percentage of plots dominated with shrubby legumes almost made up 80% (Fig. 3a), 50% percent of legume shrub species was occurred for 6 dominant shrubs in this group (Fig. 3b).

**Group III:** It included 14 plots (3, 14, 36, 38, 43, 49, 50, 51, 52, 53, 54, 55, 56, 57) distributed from 1,350 m to 1,750 m. Indicator of legume species for this group were *B. faberi*, *L. floribunda*, *C. macrocarpa*, and non-dominant shrubby legumes were *Abelia macrotera* (Graebn. EtBuchw.) Rehd, *Q. cocciferoides*, *Caryopteris incana* Miq, *Berberis wilsonae*, *A. potaninii*, *Cotinus szechuanensis* A. penzes, *Rosa sweginzowii* Koehne, *Jasminum humile* Linn and *A. macrotera*. Most of the plots were on moisture slopes. Shrub coverage varied from 40% to 60%, average gravel coverage was about 18%. Percentage of plots dominated with shrubby legumes comprised over 25% (Fig. 3a), percentage of legume shrubs reached 21% for 13 dominant shrubs in 14 plots (Fig. 3b).

**Group IV:** It consisted of 3 plots (45, 46, 47) distributed from 2,000 m to 2,200 m. The dominant non-legume shrubs were *S. cantoniensis* Lour, *Rhododendron fargesii*, *B. wilsonae*, *A. macrotera*. Legume dominant shrubs were not found in this group. Most of the plots were on little moisture slopes. Shrub coverage was typically more than 50%, an average gravel coverage was lower than 8% (Fig. 3).

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**Fig. 2.** Dendrogram of the TWINSPAN classification of 57 plots. Note: Dx indicates the number of division; Nx indicates the number of plots.

**Fig. 3.** Analysis of number of plots for shrubland dominated by legume shrubs (SLS) and their percentage (a) and number of dominant legume shrub species and their percentage in total species (b).
Table 1. Occurrence of native shrub species sampled in 57-15m×15m plots in four shrub clusters and their corresponding four plot groups along the upper Minjiang River Valley, China, with their names and abbreviations.

<table>
<thead>
<tr>
<th>Species name</th>
<th>Abbrev.</th>
<th>Shrub cluster</th>
<th>Plot group</th>
<th>Species name</th>
<th>Abbrev.</th>
<th>Shrub cluster</th>
<th>Plot group</th>
<th>Species name</th>
<th>Abbrev.</th>
<th>Shrub cluster</th>
<th>Plot group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spiraea longissima Maxim.</td>
<td>Splo</td>
<td>I</td>
<td>I</td>
<td>Cotinus coggyria var.</td>
<td>Ccocs</td>
<td>I</td>
<td>I, II, III</td>
<td>Campylocarpus micranthum (Bge.) Rehd.</td>
<td>Cama</td>
<td>III</td>
<td>III, IV</td>
</tr>
<tr>
<td>Wilksonia maculata (Rehd.) Domke</td>
<td>Wimo</td>
<td>I</td>
<td>I, II</td>
<td>Cotinus szechuanensis L.</td>
<td>Cosz</td>
<td>I</td>
<td>I, II, III</td>
<td>Dalpine penticus Rehd.</td>
<td>Dape</td>
<td>IV</td>
<td>III, IV</td>
</tr>
<tr>
<td>Daphne tangutica Maxim.</td>
<td>Data</td>
<td>I</td>
<td>I, II</td>
<td>Lespedeza davurica (Laxm.) Schind.</td>
<td>Ledau</td>
<td>I</td>
<td>I, II, III</td>
<td>Spiraea cantoniensis Lour.</td>
<td>Spca</td>
<td>IV</td>
<td>III, IV</td>
</tr>
<tr>
<td>Rhus poirainii</td>
<td>Rhpo</td>
<td>I</td>
<td>I, II</td>
<td>Spiraea salicifolia L.</td>
<td>Sipa</td>
<td>I</td>
<td>I, II, III</td>
<td>Rhus typhina L.</td>
<td>Rhys</td>
<td>IV</td>
<td>IV</td>
</tr>
<tr>
<td>Securidaca suffruticosa Rehd.</td>
<td>Seso</td>
<td>I</td>
<td>I, II</td>
<td>Ostryphus davidii (Baill.) Deane</td>
<td>Qids</td>
<td>I</td>
<td>I, III, IV</td>
<td>Rhododendron falconii</td>
<td>Rhfd</td>
<td>IV</td>
<td>IV</td>
</tr>
</tbody>
</table>

a@Shrubby legumes are in bold.

Table 2. Correlations on the first two ordination axes for species, 26 species in both Cluster I and Cluster II, 22 species in both Cluster II and Cluster III, and weighted correlation matrix for the soil variables supplied in the analysis.

<table>
<thead>
<tr>
<th>Shrub cluster</th>
<th>DCCA axis</th>
<th>SWC</th>
<th>SOM</th>
<th>TN</th>
<th>AN</th>
<th>TP</th>
<th>AP</th>
<th>TK</th>
<th>AK</th>
<th>TN/TP</th>
<th>AN/AP</th>
<th>TC/TN/TP</th>
</tr>
</thead>
<tbody>
<tr>
<td>I+II+III+IV</td>
<td>DCCA1</td>
<td>-0.87**</td>
<td>0.15</td>
<td>0.09</td>
<td>0.18</td>
<td>0.14</td>
<td>0.07</td>
<td>-0.46**</td>
<td>0.45**</td>
<td>0.02</td>
<td>0.21</td>
<td>-0.11</td>
</tr>
<tr>
<td></td>
<td>DCCA2</td>
<td>-0.09</td>
<td>0.33**</td>
<td>0.40**</td>
<td>0.59**</td>
<td>0.01</td>
<td>0.41**</td>
<td>-0.21</td>
<td>0.35**</td>
<td>0.19</td>
<td>-0.19</td>
<td></td>
</tr>
<tr>
<td></td>
<td>DCCA1</td>
<td>0.50**</td>
<td>0.58**</td>
<td>0.50**</td>
<td>0.69**</td>
<td>0.33**</td>
<td>0.41**</td>
<td>-0.58**</td>
<td>0.29</td>
<td>0.32*</td>
<td>-0.29</td>
<td></td>
</tr>
<tr>
<td>I+II</td>
<td>DCCA2</td>
<td>0.32*</td>
<td>0.41**</td>
<td>0.42**</td>
<td>0.69**</td>
<td>0.13</td>
<td>0.47**</td>
<td>-0.47**</td>
<td>0.36*</td>
<td>0.25</td>
<td>-0.22</td>
<td></td>
</tr>
<tr>
<td>III+IV</td>
<td>DCCA1</td>
<td>0.87**</td>
<td>0.17</td>
<td>0.32</td>
<td>0.27</td>
<td>0.34</td>
<td>0.24</td>
<td>-0.31</td>
<td>0.28</td>
<td>0.21</td>
<td>0.13</td>
<td>-0.27</td>
</tr>
<tr>
<td></td>
<td>DCCA2</td>
<td>0.22</td>
<td>0.37</td>
<td>0.25</td>
<td>0.27</td>
<td>0.18</td>
<td>0.06</td>
<td>-0.06</td>
<td>0.66**</td>
<td>0.11</td>
<td>0.20</td>
<td>-0.11</td>
</tr>
</tbody>
</table>

*p<0.05, **p<0.01, ***p<0.001

Table 3. Correlations between variables of soil variables and both soil pH and soil clay sand ratio (SC/SS), and weighted correlation matrix for the soil variables supplied in the analysis.

<table>
<thead>
<tr>
<th>Soil pH</th>
<th>SC/SC</th>
<th>SWC</th>
<th>SOM</th>
<th>TN</th>
<th>AN</th>
<th>TP</th>
<th>AP</th>
<th>TK</th>
<th>AK</th>
<th>TN/TP</th>
<th>AN/AP</th>
<th>C/N/P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil pH</td>
<td>1.00</td>
<td>-0.16</td>
<td>-0.03</td>
<td>-0.39**</td>
<td>-0.35**</td>
<td>0.05</td>
<td>1.18</td>
<td>-0.06</td>
<td>0.56</td>
<td>-0.37**</td>
<td>-0.21</td>
<td>0.03</td>
</tr>
<tr>
<td>SC/SS</td>
<td>1.00</td>
<td>0.79**</td>
<td>0.20</td>
<td>0.14</td>
<td>0.22</td>
<td>0.06</td>
<td>0.11</td>
<td>0.18</td>
<td>0.14</td>
<td>0.18</td>
<td>-0.13</td>
<td></td>
</tr>
</tbody>
</table>
Distribution patterns of shrubs along soil gradients: A total of 2,413 individual shrubs in 55 species were registered in the 57 plots in the dry upper valley. 48 species with more than 4 individuals in the total samples are listed in Table 1. Total of 55 shrub species from 25 families was recorded in the inventory of shrub species, including 9 Leguminosae species. The results obtained from shrub ordination were summarized as identified by DCCA.

Correspondingly, all shrubs species occupied four clusters as shown in Fig. 4. Cluster I consisted of 18 shrub species, of which B. faberi, S. vicifolia, L. floribunda, and L. amblyantha were legume species. Cluster II included 9 shrub species, of which Lespedeza floribunda Bunge, S. vicifolia, I. amblyantha and B. faberi Oliver were shrubby legumes. Cluster III included 33 shrub species, of which 8 of 33 were legume species, they were L. floribunda, S. vicifolia, I. amblyantha, B. faberi, L. davurica, Ostryopsis davidii (Baill.) Deene, D. Podocarpum DC and Campylotropis macrocarpa (Bge.) Rehd. Cluster IV included 12 shrub species, L. floribunda, Q. davidianti, C. macrocarpa, Corylus ferox Wall were shrubby legumes.

Relationships between soil properties and first two DCCA axis: The correlation between soil properties and the first two DCCA axis was summarized with respect to the most important edaphic factors as identified by PC analysis (Table 2). For 48 shrubs species, the DCCA Axis 1 was positively correlated to SWC and soil nutrient factors, of which only correlation coefficient between SWC and the DCCA Axis 1(r=0.87) was statistically significant. The Axis 2 was un-significantly negative with SWC, yet significantly positive with most of soil nutrients, such as SOM (r=0.33), TN (r=0.40), AN (r=0.59), AP (0.41) and N:P stoichiometry (TN/TP, r=0.35). For 25 shrubs species from Cluster I and Cluster II, both DCCA Axis 2 had the markedly positive correlation with SWC (r=0.50), SOM (r=0.58), TN (r=0.50), AN (r=0.69) and AP (r=0.41). However, the Axis 1 was significantly correlated positively with N:P stoichiometry (AN/AP, r=0.32), the Axis 2 were obviously correlated positively with N:P stoichiometry (TN/TP, r=0.36). For 23 shrubs from Cluster III and Cluster IV, both DCCA Axis 1 and Axis 2 were positive with SWC and soil other nutrient variables, of which only correlation of SWC with the Axis 1 was significant (r=0.87).

Further analysis indicated that both SWC and soil nutrient variables had directly interactive effects with soil pH and soil clay sand ratio. Table 3 clearly showed that soil pH was negative with SWC and all soil nutrient variables. Soil pH was significantly and negatively correlated with SOM (r=-0.39), TN (r=-0.42), AN (r=-0.50) and TN/TP (r=-0.37). Soil clay sand ratio was positive with most of soil nutrient variables and significantly positive with SWC (r=0.79). However, the weak correlation coefficient (r=-0.16) between soil pH and soil clay sand ratio implied that the two variables were independent.
Discussion

Natural distribution patterns of shrubs: Understanding of the natural distribution patterns of shrub species would be very important for ecosystem restoration and management efforts in the dry valleys of the Hengduan Mountainous Region. Information of shrub distribution patterns along different soil gradient can provide valuable clues about the shrub potential development and their site adaptability (Zhang, 1992). Here, distribution data of shrub species was analyzed using the quantitative classification method (TWINSPAN) and the ordination technique (DCCA). Thirteen shrubs of all shrubs of Cluster I appeared in Group I, having an 81% percentage. All 9 shrubs of Cluster II absolutely appeared in Group II. 94 percent of 15 shrubs in Cluster III occurred in Group III and 86 percent of 7 shrubs in Cluster IV appeared in Group IV (Table 1). Therefore, the results of the TWINSPAN classification showed a series of plots groups changing along soil gradient, which was similar to ordination patterns of the DCCA results. Species richness of Cluster I, Cluster II, Cluster III and Cluster IV were 8.12, 9.10, 11.12 and 12.00 respectively (unpublished data). Shannon-Wiener heterogeneity of four Clusters were 1.73, 1.93, 2.17 and 2.46 respectively (unpublished data). The composition of shrub species varied greatly during the process of distribution, which indicated that species heterogeneity increased gradually along the soil moisture and nutrient gradient.

In the process of ecological succession, the number of community dominant shrubby legumes was decreasing, as was their percentage. This result was consistent with previously published studies in the same study area (Song et al., 2010a). It was worth noting that 8 legume species number increased from four species in Cluster I, five species in Cluster II and eight species in Cluster III, and then decreased to four in Cluster IV. The potential succession series of shrub communities along the main Minjiang River could be as follows: Form. S. viciifolia & A. potaninnii → Form. B. faberi → Form. C. incana & C. szechuanensis → Form. S. cantoniensis. It was viewed as a general model of shrub community recovery on the arid valley along the Upper Minjiang River watershed (Guan et al., 2004; Zhou et al., 2008). This model was similar to that found in other neighbor places of the Hengduan Mountainous Region (Zhang, 1992), despite the ecological differences.

The development of shrub communities in the fields has taken more than 30-40 years in this area. Although shrub communities might not be the climax according to Clements’ definition, but they have developed into a stable stage, thereby being the goal of vegetation restoration. It indicated that native legume shrubs stimulated the co-evolution process in degraded arid land, thereby promoting the ecological restoration, with the increasing of shrubby legume biodiversity and the decreasing of dominant shrubby legumes. This result agreed with most research (Bellingham et al., 2001; Uliaissi & Russ, 2002; Walker et al., 2003; Padilla et al., 2009) and confirmed that native N-fixers were suitable driver candidates from N-fixing shrubland to non-N-fixing shrubland, such as B. faberi, A. potaninnii and I. amblyantha.

Multi-resource limitation of soil moisture and nutrients: Vegetation damage along the upper Minjiang River had taken place for at least a thousand years (Ma et al., 2004; Zhang 1992), and serious soil erosion and soil heterogeneity had occurred, degrading soil water and nutrient conditions (Ma et al., 2004; Xu et al., 2009). In this harsh habitat, the apparent structural simplicity of both shrub communities and the relationship of vegetation and environment provide an excellent model system to study shrub response to multiple resources limitation at species and communities level. Furthermore, since this habitat requires restoration, the information of selecting key limiting resources and main regulating factors could help to identify finite measures that would improve restoration succession.

Although multiple-factor limitations have long been recognized, few studies have investigated functional group or community responses to such limitations. This lack of information may be related to the laborious and lengthy fertilizer experiments and needed to evaluate responses to both single resource limitation and their interactions with other resources. In this study, TWINSPAN classification and DCCA ordination were employed for the quantitative analysis of the shrub species, soil water and soil nutrients. This study is the first to relate the distribution of shrub species to a multiple suite of both soil water and soil nutrients at community spatial scale. We observed a highly significantly positive correlation between soil water and the DCCA Axis 1 for 48 shrubs and found that the DCCA Axis 2 had a notable positive correlation with four soil nutrient variables (including SOM, TN, AN and AP) and N:P stoichiometry (TN/TP). The sequences of correlation coefficients of 11 soil nutrient variables from high to low was SWC > AN > AP > TN > TN/TP > SOM. The results obviously showed that SWC was the primary limiting resource and soil nutrient variables (including AN, AP, TN, TN/TP, SOM) were secondary limiting resources. Similar to other arid systems, the combination of a low, unpredictable water supply and nutrient status limited seedling establishment, plant growth and distribution patterns in an arid environment (Bowker et al., 2005; James et al., 2005; Song et al., 2010b). Moreover, presence and variance of shrub species on the DCCA Axis 1 were stronger than that of the DCCA Axis 2 according to distribution patterns (Fig. 4). These findings further affirmed that soil water played a primary limitation role and nutrient availability was only secondary limiting resources at community scale. Studies in several desert systems have shown that soil N, soil P or soil N/P can limit growth and composition of vegetation once water limitation is removed (Drenovsky & Richards 2004). Studies in several other arid systems have shown the similar hierarchical resource limitation structure in both lab and field experiments (James et al., 2005; Perring et al., 2008; Song et al., 2010b). This hierarchical limitation structure not only demonstrated that soil moisture and available nutrients had the determined various forces, but also indicated that soil nutrients variables also had the difference effects on distribution patterns of shrubs.
To further clarify the effects of limiting resources, four shrub clusters were categorized two Categories based on shrub distribution pattern (Fig. 4). We observed that both soil moisture and soil nutrients variables were simultaneously and significantly co-constrained distribution pattern of shrubs from Cluster I and Cluster II. The sequences of correlation coefficients of 11 soil variables with the DCCA Axis 1 and the DCCA Axis 2 from high to low were AN > SOM > TN > SWC > AP > TP > AN/AP and AN > AP > TN > SOM > TN/TP > SWC. The higher correlation coefficients between first two DCCA axes and soil nutrients than that of between first two DCCA axes and soil water illustrated that soil nutrient variables (mainly including AN, AP and SOM) played a primary decisive roles and both soil water and soil N:P stoichiometry (TN/TP and AN/AP) played a sub-primary roles on distribution patterns of shrubs in Cluster I and Cluster II. Moreover, only soil moisture obviously and positively correlated with the DCCA Axis 1 on distributions of shrubs in Cluster III and Cluster IV (Table 2). Therefore, the results confirmed that effects of both single and multiple resource limitation were coexisting simultaneously in study area.

We predict that the couplings between multiple limiting resources may be instrumental in shaping shrub community and species distributions along soil gradients and are potentially important in defining ecotonal areas between major communities in resource-poor ecosystems. The prominent and repeated co-existing of both single and multiple resource limitation between soil nutrients and shrubs distributions was particularly novel and unexpected. The results may be meaningful in developing restoration methods in many arid regions worldwide. The interactive effects between soil moisture and soil nutrient suggested that applying more fertilizer was practical to recovery of shrubs in Cluster I and Cluster II, yet storing more water was feasible to restoration of shrubs in Cluster I and Cluster II.

Soil texture had a strongly affect on soil water and soil pH significantly influenced on soil fertility. The sequences of absolute correlation coefficients of soil pH and other 11 nutrient variables from high to low was AN > TN > SOM > TN/TP. The significant negative correlation between soil pH and AN, TN, SOM, TN/TP implied that high soil pH constrained the providing of soil nutrient. In fact, increasing alkalinity is expected to further reduce SOM and N availability through volatilization of mineralized ammonium (Marschner 1995; James et al., 2005). In addition, the positive correlation between soil clay sand ratio and soil water was highly marked (Table 3). This meant that soil clay sand ratio was one of determinant factors of water holding capacity of the soil in study area. This result was also consistent with other studies (Xu et al., 2009). Clay soils have the lowest water infiltration rate among silt, loam or sand soils so that they could have the higher capacity to hold water than sand soils. Surprisingly, both soil pH and soil clay sand ratio had no obviously correlations, and both variables had no significantly correlation with either TP or AP, which needed further analysis.

Conclusion

Multiple resource limitation hypotheses that test whether single- or multi-resource constrains growth and primary production of vegetation can be critical for understanding process of ecological restoration. The results from this study were different from previous studies in that this study quantified and hierarchied structure of multiple resource limitation: soil water played a primary limitation role, available nitrogen the next, and available phosphorus the third at community scale. Another unexpected result was that both multi-resource limitation and single resource limitation were coexisting simultaneously in study area by quantitative analysis, the extent of which was functional cluster-specific. Furthermore, this study affirmed that both soil pH and soil texture could effectively regulate retention of soil moisture and available nutrients, respectively. We suggest that it was urgent and necessary to trace out patterns of soil water, available nutrients (especially nitrogen and phosphorus) and N:P stoichiometry. Further longer lab and field investigations will be required in the future to verify the hierarchical limitation structure.

Acknowledgments

This study was supported by the National Natural Science Foundation of China (No. 41101270 and No. 31170581) and the Innovation Group Program of the National Natural Science Foundation of China (No. 40621061). Thanks are due to FangLan Li, MinSheng Ye, Hui Yin and Liang Ge from Beijing Forestry University for their assistance with the constructive suggestion and field survey. Our gratitude also goes to Maoxian Mountain Ecosystem Research Station of Chengdu Institute of Biology (Chinese Academy of Sciences) for their support with laboratory facilities. We also appreciate the help of Dr. Kate He from the Murry State University, USA for improvement in English.

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(Received for publication 10 March 2013)