Primary Succession of Algal Community Structure in Desert Soil

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Abstract: The microbiotic crust study is among new focuses in investigating on the desertification control. Based on determination of algal crusts with different successive ages (4-, 8-, 17-, 34-, 42-year-old) and unconsolidated sand in the desert area, species composition and clustering analyses were carried out in this study. Results on successional orientation revealed that (1) the abundance of Cyanophyta, specially of Scytonema javanicum gradually decreased; (2) the abundance of Chlorophyta, Bacillariophyta and a species of Cyanophyta, Phormidium tenue increased; (3) the biodiversity increased gradually with the community succession; and (4) biomass of microalgae increased at the early stage, but decreased at the later stage due to the abundance of lichens and mosses. But, the speed of natural succession was so slow that the community-building species was still the first dominant species after 42 years, except that its dominant degree decreased just slightly. However, successive speed and trend were affected by water, vegetation coverage, terrain, time and soil physico-chemical properties as well, especially Mn content in the soil appeared to have a threshold effect.

Key words: desert soil; algae; community structure; primary succession

In the arid and semi-arid area, soil microorganisms often form a thin layer in the topsoil, it was called algal crusts in phycology; microbiotic crusts in soil microbiology and cryptogams crusts in cryptogamy. No matter what the difference of nominatum is, the crusts play important roles in the sand dune stabilization and soil melioration. Among various types of organisms, it has long been suggested that microalgae play important and irreplaceable roles in the early formation and strength maintaining of the crusts (Johansen, 1993; Evans and Johansen, 1999). Therefore, algae are particularly paid much more attention in desertification control in Shapotou area of China (Li et al., 2000; 2002; Hu et al., 2002a). In order to explore a new approach in controlling the severe desertification, algal species, community structure, biomass change, fine spatial distribution and cementing mechanism of algal crusts were studied (Zhou et al., 1995; Hu et al., 1999; 2000a; 2000b; 2002a; 2002b; Liu et al., 2001), and we found that the algal crusts were substituted with lichen crusts or moss crusts following their further development. However, the succession is a gradual process, especially in harsh desert environment. There are still few researches documented and explored on this aspect, and the succession mechanism still remains unknown (Brock, 1973; Johansen, 1993; Hu et al., 2002b), even it is thought that terrestrial floristic community succession begins from lichen in most references.

The objective of this study was to investigate in situ the actual change of algal community structure from algal crusts to lichen or moss crusts, to determine which factors affect this process, and to explore its possible mechanism. There are a series of desert algal crusts of different ages spanning up to 42 years (i.e., 4-, 8-, 17-, 34-, 42-year-old) and unconsolidated sand in Shapotou, the experimental area, because researchers made long-term efforts in planting trees, enclosing and protecting the investigations sites continuously (Hu et al., 2000a). This offered the advantageous natural conditions for an ideal research work on primary succession of soil algae. Results of this research would breakthrough the previous old concepts, and may be very important in developing new techniques to control the desertification.

1 Research Area

Shapotou (37°27′ N, 104°57′ E) is located in the southeast of Tengger Desert, Ningxia Hui Autonomous Region, China. Details on its natural conditions were given previously (Hu et al., 2000a; 2000b; Li et al., 2002). ST1, ST2, ST3 and ST4 were non-irrigated sites (ST) and were enclosed respectively in 1956, 1964, 1981 and 1994. ST5 is situated in the small woods (40 m × 2 000 m) of southern area of railway line. It is occasionally irrigated by water from the Yellow

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River, but the soil surface was artificially turned over in 1990, so the present crusts was formed after 1990. ST6 is the area of unconsolidated sand. Table 1 describes the microhabitats of the above-mentioned sites.

2 Methods

2.1 Sampling

Soil samples were collected from the above six sites in four different seasons of 1997 and 1998 according to previous methods (Hu et al., 2000a; 2000b; 2002a). Undamaged crusts were taken with an aseptic ring-knife or sharp shovel, placed in sterilized petri dishes, wrapped in parafilm, and rapidly carried to laboratory.

2.2 Samples analysis

All species grown in culture were identified and counted according to Hu et al. (1999). For cyanobacteria and diatom, the mean volume of each species was obtained from 50 individuals of direct observation, while green algae and Euglena were from culture observation. Analyses of soil physico-chemical properties were all carried out according to the standard methods, and the data were provided by Lanzhou Institute for Desert Research, The Chinese Academy of Sciences.

2.3 Data analysis

Similarity of algal community was estimated using Jaccard index and species diversity was indicated by Margalef index (Odum, 1981). The abundance was expressed as a percentage of total individual volume in total algal volume per gram of soil. Dominant species were determined according to the important value (IV) calculated as follows:

\[ IV = \frac{\text{Relative abundance} \times \text{relative frequency}}{2} \]

Species with \( IV \geq 3.615 \) were considered as dominant species. Succession trend was assessed by the method of clustering analysis. Community ordination was performed by principal component analysis, and they were accomplished in Statistica (6.0).

3 Results

3.1 Species composition

A total of 24 algal taxa were recorded from the studied crusts during the two years' investigation (Table 2), in which cyanobacteria (10 taxa) were the most diverse group, followed by diatom (seven taxa), green algae (five taxa) and Euglena (two taxa). Among the six sites, the 24 species all occurred at ST1, and Chroococcus epiphyticus, Gloeocapsa

<table>
<thead>
<tr>
<th>Table 1 Micro-habitats of all sites (ST)</th>
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<tbody>
<tr>
<td><strong>ST1</strong></td>
</tr>
<tr>
<td>Terrain</td>
</tr>
<tr>
<td>Water source</td>
</tr>
<tr>
<td>Shrub coverage (%)</td>
</tr>
<tr>
<td>Mosses coverage (%)</td>
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<tr>
<td>Lichens coverage (%)</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Table 2 Distribution of algae in the all sites (ST)</th>
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</thead>
<tbody>
<tr>
<td><strong>Cyanophyta</strong></td>
</tr>
<tr>
<td><em>Anabaena azotica</em></td>
</tr>
<tr>
<td><em>Chroococcus epiphyticus</em></td>
</tr>
<tr>
<td><em>Gloeocapsa</em></td>
</tr>
<tr>
<td><em>Lyngbya cryptovaginatus</em></td>
</tr>
<tr>
<td><em>Microcoleus vaginatus</em></td>
</tr>
<tr>
<td><em>Nostoc flagelliforme</em></td>
</tr>
<tr>
<td><em>Nostoc sp.</em></td>
</tr>
<tr>
<td><em>Phormidium tenue</em></td>
</tr>
<tr>
<td><em>Scytonema javanicum</em></td>
</tr>
<tr>
<td><em>Synechocystis pveakezii</em></td>
</tr>
<tr>
<td><strong>Chlorophyta</strong></td>
</tr>
<tr>
<td><em>Chlamydomonas sp.</em></td>
</tr>
<tr>
<td><em>Chlorella vulgaris</em></td>
</tr>
<tr>
<td><em>Chlorococcum humicola</em></td>
</tr>
<tr>
<td><em>Palmelloccus miniatus</em></td>
</tr>
<tr>
<td><em>Desmococcus olivaceus</em></td>
</tr>
</tbody>
</table>

| **Bacillariophyta** |
| *Cryptomonas sp.* | + | + | + | + | + | + |
| *Diatoma vulgar var. ovalis* | + | + | + | + | + | + |
| *Fragilaria intermedia* | + | + | + | + | + | + |
| *Gomphonema constrictum* | + | + | + | + | + | + |
| *Hantzschia amphioxys* | + | + | + | + | + | + |
| *Navicula cryptcephala* | + | + | + | + | + | + |
| *Pinnularia borealis* | + | + | + | + | + | + |

| **Euglenophyta** |
| *Euglena sp.1.* | + | + | + | + | + | + |
| *Euglena sp.2.* | + | + | + | + | + | + |
| Total number | 24 | 19 | 17 | 15 | 19 | 1 |
sp. and Cyamella sp. were unique to this site. Nineteen species were recognized at ST2, from which five belonged to green algae and two to Euglena, cyanobacteria and diatoms accounted for seven and five species respectively. Seventeen species were encountered at ST3, of which six for cyanobacteria, five for green algae, four for diatom and two for Euglena. At ST4, 15 species were identified, in which cyanobacteria, green algae, diatoms and Euglena represented six, four, four and one species, respectively. The ST5 was similar to ST2 both in species number and in percentage of each phylum, but Nostoc flagelliforme and Fragilaria intermedia were only identified at ST2, not at ST5. Synechocystis pevalekii and Gomphoema constrictum were only found at ST5, not at ST2. At ST6, only Microcoleus vaginatus (a cyanobacterium) existed. By comparing ST1, ST2, ST3 and ST4 (with the same water sources) with ST6 (unconsolidated sand area), it was found that the older the algal crust was, the bigger the species number would be. ST5 showed a different trend: it included much more species than ST3 and ST4, and had higher percentage of green algae than ST4. This meant that relatively higher shrub coverage and abundant water triggered off the increment of species number of algae, especially green algae.

3.2 Biomass

Table 3 shows that ST2 had the largest biomass among the six sites. For the other five sites, algal biomass decrease showed the following trend: ST1 > ST4 > ST3 > ST5 > ST6. This reflected that the biomass of ST1 (42-year-old) was lower than that of ST2 (34-year-old), and ST4 (four-year-old, located in the lower area) was higher than that of ST3 (17-year-old, and located in plain area). But for the sites with the same terrain and water source, such as ST2, ST3 and ST6, biomass sequence matched their age sequence.

From the surface to bottom the significant decline of algal biomass with depths was discovered at all sites (Fig. 1), but the decreased speed was relatively slower in older crusts (ST1, ST2) than in relatively younger crusts (ST3, ST4 and ST5).

3.3 Species diversity

Table 3 shows that there was a trend of species diversity sequence among the algal crusts. The diversity indexes were consistent with the crust ages was from high to low as from ST1 to ST5, ST2, ST3, ST4 and ST6. It was obvious that the oldest crusts had the highest species diversity, and the older the crusts were, the higher the diversity could be, except ST5 (with 100% shrub coverage and occasional irrigation). This also indicated that relative abundant water sources and less irradiation benefited to algal diversity, whereas the difference of terrain did not show obvious effect on diversity within a short time.

3.4 Similarity

ST3 displayed a highest similarity with ST2 and ST5 (Table 4), and it was settled near them. ST6 was located far away from all sites, especially from ST1, the oldest one.

3.5 Abundance of dominant species

The dendrogram obtained from the abundance of the five dominant species, M. vaginatus, Scytonema javanicum, Lyngbya cryptovaginatus, Phormidium tenue and Nostoc sp. (Fig.2) showed that two groups could be distinguished: the one including ST4, ST3 and ST2 was a group characterized by a relatively higher abundance of S. javanicum (a highly UV-resistance species) (Garcia-Pichel and

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**Table 3** Community structures of algae in all sites (ST)

<table>
<thead>
<tr>
<th></th>
<th>ST1</th>
<th>ST2</th>
<th>ST3</th>
<th>ST4</th>
<th>ST5</th>
<th>ST6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species number</td>
<td>24</td>
<td>19</td>
<td>17</td>
<td>15</td>
<td>19</td>
<td>1</td>
</tr>
<tr>
<td>Biomass (mm³/g dry soil)</td>
<td>7.085</td>
<td>8.576</td>
<td>5.990</td>
<td>6.263</td>
<td>1.278</td>
<td>0.082</td>
</tr>
<tr>
<td>Diversity index of species</td>
<td>1.275</td>
<td>1.153</td>
<td>1.122</td>
<td>0.932</td>
<td>1.233</td>
<td>0.142</td>
</tr>
<tr>
<td>Abundance of Lyngbya cryptovaginatus (%)</td>
<td>3.520</td>
<td>6.070</td>
<td>2.520</td>
<td>4.740</td>
<td>0.150</td>
<td>0.000</td>
</tr>
<tr>
<td>Abundance of Microcoleus vaginatus (%)</td>
<td>72.260</td>
<td>65.610</td>
<td>61.260</td>
<td>64.640</td>
<td>83.190</td>
<td>100.000</td>
</tr>
<tr>
<td>Abundance of Nostoc sp. (%)</td>
<td>3.400</td>
<td>5.140</td>
<td>3.590</td>
<td>1.560</td>
<td>0.510</td>
<td>0.000</td>
</tr>
<tr>
<td>Abundance of Phormidium tenue (%)</td>
<td>11.800</td>
<td>0.450</td>
<td>0.820</td>
<td>1.180</td>
<td>0.830</td>
<td>0.000</td>
</tr>
<tr>
<td>Abundance of Scytonema javanicum (%)</td>
<td>3.520</td>
<td>16.980</td>
<td>28.610</td>
<td>26.210</td>
<td>1.370</td>
<td>0.000</td>
</tr>
<tr>
<td>Abundance of Cyanophyta (%)</td>
<td>94.550</td>
<td>97.050</td>
<td>97.320</td>
<td>98.870</td>
<td>90.060</td>
<td>100.000</td>
</tr>
<tr>
<td>Abundance of Chlorophyta (%)</td>
<td>3.940</td>
<td>1.690</td>
<td>1.580</td>
<td>0.600</td>
<td>8.700</td>
<td>0.000</td>
</tr>
<tr>
<td>Abundance of Bacillariophyta (%)</td>
<td>1.510</td>
<td>1.260</td>
<td>1.100</td>
<td>0.530</td>
<td>1.240</td>
<td>0.000</td>
</tr>
</tbody>
</table>
Table 4  Similarities of the six sites (ST)  

<table>
<thead>
<tr>
<th></th>
<th>ST1</th>
<th>ST2</th>
<th>ST3</th>
<th>ST4</th>
<th>ST5</th>
<th>ST6</th>
</tr>
</thead>
<tbody>
<tr>
<td>ST1</td>
<td>0.792</td>
<td>0.708</td>
<td>0.625</td>
<td>0.792</td>
<td>0.042</td>
<td></td>
</tr>
<tr>
<td>ST2</td>
<td>0.895</td>
<td>0.700</td>
<td>0.810</td>
<td>0.053</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ST3</td>
<td>0.778</td>
<td>0.895</td>
<td>0.059</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ST4</td>
<td>0.789</td>
<td>0.067</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ST5</td>
<td>0.052</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig.2. Cluster dendrogram of the abundance of dominant species at all sites (ST).

Castenholz, 1991; Liu et al., 2001); the second comprised ST6, ST5 and ST1, and was a group featured by a lack or low percentage of S. javanicum. We inferred that the relative integrity of the crust structure had reduced relatively far from the effect of solar irradiation, especially UV irradiation. Thus, the requirement for screening radiation decreased correspondingly in well-developed old crusts. On the contrary, the requirement of S. javanicum crust was much more obvious for whose shrub coverage was low and young. This result indicates the succession of community structure went along the trend that the abundance of S. javanicum gradually decreased.

Clustering analysis of algal crusts based on the total abundance, the abundance of dominant species, the species number and the biomass, it was shown (Fig.3) that ST6 was a separate group, which was mostly far away from the other five sites. At the linkage distance 19, three large groups were distinguishable: ST1 and ST5 belonged to a group presenting a relatively high similarity in the species number, an abundance of S. javanicum, and a total abundance of cyanobacteria and green algae; ST6 was still a separate group because the value for all variables was obviously low; ST2, ST4 and ST3 belonged to another group because the abundance of M. vaginatus, S. javanicum, L. cryptovaginatus, Nostoc sp. and the total abundance of cyanobacteria, green algae and diatoms were in between the above-mentioned two groups. This result of analysis would be helpful to reveal the primary succession of algal community structure in desert crust, which developed towards a trend of increasing the species number, the abundance of green algae and diatoms, declining the abundance of Cyanobacteria especially of the dominant species, S. javanicum.

The principal component analysis (PCA) performed on the basis of the 10 independent variables (given in Table 3) showed that the principal component 1 covered 97.19% of the total variance (Fig.4), and was significantly influenced by the abundance of Cyanophyta and M. vaginatus (2.19, 1.52, respectively). The principal component 2 accounted for only 2.15% of the variance, and largely reflected the effect of the abundance of S. javanicum. Also, the loading on this factor was negative (−2.05). The figure meant that the community structure of ST2 had been at the most flourishing stage among the six sites; ST3 and ST4 were at early stage, ST1 and ST5 were at later stage due to the decline of biomass and high percentage of lichen and moss. This also greatly reflected their transitional characters before being replaced by other cryptogams (Table 1). Thus, the crucial factor that affected the community structure was the abundance of Cyanophyta, whereas enough water and higher shrub coverage enhanced the speed of succession.

3.6 Community structure and soil physico-chemical properties

Clustering analysis of the 10 independent variables of community structure and the 45 parameters of soil
physico-chemical properties showed that the site ST6 displayed the lowest crust incidence compared to the remaining sites (Table 5; Fig.5). ST5 formed an intermediary cluster, whereas ST1, ST2, ST3 and ST4 were characterized by a relatively high crust abundance. Among the later four sites, ST3 and ST4 formed a group, ST1 and ST2 formed another group respectively. This meant that the succession of algal community and the changes of soil physico-chemical properties were crust age-dependent: the larger the difference in age of the crusts were, the farther the distance of biological and non-biological performance would be.

In order to more obviously make the ordination of the successional sequence in the six sites, and to find out the main factors that affected the succession, a PCA (Fig.6) was performed according to the independent variables given in Tables 3 and 5. Results show that the principal

| Table 5 Soil physico-chemical properties of all sites (ST) |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                 | ST1             | ST2             | ST3             | ST4             | ST5             | ST6             |
| Water (%)       | 0.569           | 0.604           | 0.459           | 0.645           | 1.220           | 0.181           |
| HCO₃⁻ (g/kg)    | 0.097           | 0.101           | 0.093           | 0.086           | 0.111           | 0.045           |
| Cl⁻ (g/kg)      | 0.007           | 0.010           | 0.010           | 0.006           | 0.016           | 0.003           |
| SO₄²⁻ (g/kg)    | 0.064           | 0.059           | 0.073           | 0.059           | 0.131           | 0.013           |
| CO₂⁻ (g/kg)     | 0.020           | 0.000           | 0.000           | 0.000           | 0.000           | 0.000           |
| Ion (mol/kg)    | 0.238           | 0.236           | 0.231           | 0.204           | 0.365           | 0.083           |
| Ca²⁺ (g/kg)     | 0.047           | 0.044           | 0.042           | 0.038           | 0.052           | 0.012           |
| Mg²⁺ (g/kg)     | 0.009           | 0.008           | 0.026           | 0.006           | 0.012           | 0.004           |
| Na⁺ (g/kg)      | 0.004           | 0.007           | 0.006           | 0.004           | 0.021           | 0.004           |
| K⁺ (g/kg)       | 0.008           | 0.173           | 0.007           | 0.004           | 0.021           | 0.004           |
| Cation (mol/kg) | 0.840           | 0.712           | 0.690           | 0.667           | 1.045           | 0.252           |
| pH              | 8.333           | 7.902           | 7.970           | 7.985           | 7.997           | 7.757           |
| EC (ms/cm)      | 0.173           | 0.147           | 0.143           | 0.141           | 0.212           | 0.052           |
| Organic matter (g/kg) | 17.640      | 14.158          | 10.256          | 11.445          | 31.958          | 0.538           |
| Complete N (g/kg) | 0.705         | 0.648           | 0.445           | 0.512           | 0.762           | 0.037           |
| Complete P₂O₅ (g/kg) | 0.897        | 0.832           | 0.678           | 0.713           | 0.910           | 0.307           |
| Complete K₂O (g/kg) | 24.416        | 24.417          | 24.416          | 24.800          | 24.000          | 22.333          |
| Available N (mg/kg) | 46.983       | 39.283          | 34.516          | 36.780          | 35.883          | 14.783          |
| Available P₂O₅ (mg/kg) | 14.510       | 14.283          | 10.000          | 9.380           | 18.033          | 2.717           |
| Available K₂O (mg/kg) | 181.500       | 148.833         | 155.000         | 152.166         | 266.500         | 99.834          |
| V (mg/kg)       | 57.800          | 56.083          | 46.550          | 48.867          | 56.697          | 33.633          |
| Cr (mg/kg)      | 65.016          | 70.866          | 60.300          | 61.600          | 62.333          | 52.033          |
| Mn (mg/kg)      | 441.330         | 438.866         | 381.750         | 381.916         | 458.333         | 279.733          |
| Co (mg/kg)      | 7.900           | 7.950           | 6.533           | 6.717           | 7.783           | 4.583           |
| Ni (mg/kg)      | 23.283          | 23.383          | 18.566          | 19.700          | 21.533          | 13.833          |
| Cu (mg/kg)      | 14.016          | 13.366          | 11.233          | 11.567          | 17.233          | 6.983           |
| Zn (mg/kg)      | 44.900          | 45.430          | 36.652          | 36.867          | 52.533          | 22.866          |
| Pb (mg/kg)      | 16.367          | 18.750          | 15.967          | 16.350          | 20.733          | 10.600          |
| As (mg/kg)      | 8.100           | 7.417           | 6.067           | 7.300           | 8.617           | 4.733           |
| SiO₂ (mg/kg)    | 72.692          | 72.710          | 76.403          | 76.423          | 69.443          | 81.723          |
| AL₂O₃ (mg/kg)   | 9.243           | 9.260           | 8.603           | 8.666           | 9.205           | 7.737           |
| Fe₂O₃ (mg/kg)   | 3.232           | 3.262           | 2.846           | 2.897           | 3.355           | 2.237           |
| CaO (mg/kg)     | 2.633           | 2.602           | 1.817           | 1.735           | 3.602           | 0.792           |
| MgO (mg/kg)     | 1.530           | 1.373           | 1.188           | 1.185           | 1.538           | 0.645           |
| Gravel (%)      | 0.000           | 0.000           | 0.000           | 0.000           | 0.343           | 0.000           |
| Coarse sand (%) | 0.942           | 0.918           | 3.525           | 1.647           | 3.735           | 4.788           |
| Fine sand (%)   | 75.278          | 77.278          | 80.590          | 83.843          | 63.353          | 94.983          |
| Coarse silt (%) | 19.830          | 16.185          | 13.378          | 12.028          | 22.738          | 0.000           |
| Fine silt (%)   | 1.717           | 1.100           | 1.137           | 0.732           | 3.078           | 0.000           |
| Coarse clay (%) | 2.228           | 1.747           | 1.357           | 1.730           | 3.635           | 0.000           |
| Primary minerals (%)  | 50.000         | 65.000          | 65.000          | 75.000          | 55.000          | 90.000          |
| Secondary minerals (%) | 4.000         | 4.000           | 3.000           | 0.000           | 9.500           | 0.000           |
| Clay minerals (%) | 45.000         | 30.000          | 30.000          | 25.000          | 30.000          | 10.000          |
| Thickness (mm)  | 5.167           | 3.370           | 1.567           | 3.330           | 2.330           | 0.000           |
component 1 mainly represents the changes of Mn (6.19), available K (2.3) and the abundance of Cyanophyta (1.2), and could be interpreted as a successional gradient because it explained 98.21% of the total variance. The principal component 2 mainly reflected available K (−3.4), primary minerals (3.3), fine sand (3.0) and the abundance of *M. vaginatus* (2.9), and explained only 1.34% of the variance in the data. As a whole, ST1, ST2, ST3, ST4 were basically at the close places, but the first principal component showed that ST2 and ST3 were at the transitional position between ST1 and ST4. Moreover, ST1 and ST2, ST3 and ST4 were much more similar to each other. ST5 represented another type of environmental conditions that were relatively favorable for algae. This result meant that, under the same water source condition, the ordination of community succession at the above six sites was fully consistent with the crust age, the older the crusts were, the higher the succession degree of microbial community, soil development and mineralization would be. Shrub coverage and water supply were the main factors affecting the succession direction.

4 Discussion

It seems clear that, the algal biomass *in situ* indicated the 42-year-old crusts being at a well-developed later stage, 34-year-old crusts at the flourishing stage, four-year-old crusts at a pre-flourishing stage in early stage, whereas 17-year-old crusts at a pre-flourishing stage in the between-ness of the above early and flourishing ones. Crust development at ST5 showed a special successional sequence, which directly evolved from algal to moss stage due to the site position of wood coverage. Change of vertical biomass showed that algal community gradually developed from the surface of the crusts to the deeper layers following the time course. Additionally, at early developmental stage fungi were not present or grew only at the bottom layer of the algal crusts, later they gradually moved up to the relatively shallow layer with the development of the crusts (Hu *et al.*, 2000a), and to some degree the relatively abundant *Nostoc* and green algae of the old crusts much more facilitate the combination of algae and fungi to form lichen, and to promote the transformation from algal crust to lichen crusts. In the present study the lichen coverage of all sites was in full agreement with this inference, whereas the coverage of algae, lichen and mosses of 42-year-old crusts was nearly equal, so it was still at the transient stage between algal and lichen crusts.

The species diversity reflected that all sites were at the transient stage before lichen crusts and moss crusts. No matter what situation the old algal crusts or the moss crusts was, all the diversity indexes were all relatively high, the abundance of the dominant species low, and the abundance of green algae and diatoms (non-dominant species) high. These were different from the succession pattern of high plants (Huang *et al.*, 2000).

The primary succession of plant community was a dissimilation process at the early stage. The dissimilation reflected in both species competition and adaptation to environmental conditions (Odum, 1969). But, the natural succession speed was so slow that the first dominant species of all crusts was still the community-building species, except that its dominant degree slightly decreased before the algal crusts were replaced by lichen or moss crusts. The likely reason is that other species were not able to compete with *M. vaginatus* due to their inferiority in stabilization sand and UV-resistance when the wind force was still the first limited factor of the algal crusts formation (Hu, 1999).

According to the algae tolerance to their environment and resource we inferred that the substitution of the first dominant species could not be accomplished until wind force was not the first stressful factor (McCormick and Stevenson, 1991). Of course, the wind force can be weakened by the increase of water. Therefore, in the environment where wind force was relatively weak and solar irradiation low, *P. temue* or *L. cryptovaginatus* might be the
first dominant species. However, the possibility for single-celled green algae to become the first dominant species was the least unless the microenvironment of desert changed into under vegetation of higher plants or with a forestational climate, and the soil was not alkaline (Liu and Ley, 1993).

The floristic succession was also a process with continuous adaptation of inhabitants to the surrounding environment. The composition of algal species in the desert crust continuously adapted to the changing soil. Thus, the soil property at the initiating point of succession was greatly important. During the secondary succession of algae, some species were allowed to colonize only when the favorable changes occurred such as P, N, Mg, Cd, Al, Si, Fe increased and Cu, Cl, Na and Ca decreased (Starks et al., 1981). The dominant cyanobacteria were substituted by unicellular green algae and mosses after 10 years during the primary succession of Surtsey (ice land) (Brock, 1973). Concerning the colonization process of algae, most studies showed that, it was stochastic, the substitution speed of dominant species was relatively quick (Hu, 1999), and soil physico-chemical properties had not actual effect (Carson and Brown, 1978; Davey and Rothery, 1993; Pluis, 1994; Rayburn et al., 1982). However, we found that Mn and available K obviously affected the primary succession, especially the former. It is known that (1) Mn is an activating element of many enzymes in fatty acid metabolism, DNA, RNA synthesis and Krebs circle, and directly takes part in photosynthesis, Mn also plays extraordinarily important role in nitric acid deoxidization and chlorophyll synthesis; (2) Starks and Shubert (1981) thought that Mn content could adjust and control the secondary succession of revegetation in abandoned soil, when it is higher than 550 mg/kg, the growth of algae was restrained, lower than 350 mg/kg then was accelerated; and (3) in the present study, Mn content was the highest at the irrigated site ST3, but there was the lowest algal biomass (458.33 mg/kg). For sites ST1, ST2, ST3 and ST4 with the same water source, ST1 with the second highest biomass had the higher content of Mn (441.33 mg/kg), ST2 with the highest biomass had Mn of 438.87 mg/kg, ST3 and ST4 of lower biomass, had Mn respectively of 381.75 mg/kg and 381.92 mg/kg. Thus, the present research obviously support, the threshold value effect of Mn content, although we can not affirm the actual threshold value was 438.87 mg/kg currently. In addition, the available K is an essential nutrition of plant, it is one of the necessary components in carbohydrate formation, transportation, protein and nucleic acid synthesis, particularly it increases the hydration degree and drought-resistant of protoplasm. This is specially important in desert environment. Therefore, we thought it could facilitate the whole succession process through their influence on algal adaptation, although it had not obviously effect on the seasonal change of algal biomass (Hu, 1999).

The primary successions of algae often go with the original process of soil formation. Along with the algal growth and the age increase of algal crust, the primary minerals content decrease and the clay minerals increase due to the long-term algal absorption, intercept and mineralization. Also, the thickness and spatial heterogeneity of the crusts increase (Hu et al., 2002a). Consequently, the niches accrue in the desert area where crust-forming organisms can grow. While the biological crusts provide favorable conditions to fungi, lichens and mosses, it synchronously facilitates the further development of algal crusts. At the early stage, water supply, shrub coverage, terrain and time course all play an important role in the primary succession of algal crusts except the soil factors (Hu, 1999). Under the same terrain, water source and shrub coverage, the succession of community structure was positively correlated with time, the longer the time, the higher the biomass. Under different conditions of the above parameters, larger shrub coverage and more water supply were propitious to the increase of the growth of green algae and mosses. In the lower locations of the sand dune area, the increase of algal biomass was relatively fast because the wind force was relatively weak and the nutrient level was high, whereas algal diversity did not obviously change. No matter what conditions of the microhabitat has, the influence of water and terrain on the succession speed and trend revealed that, it was possible to artificially accelerate the process of algal primary succession, and a rapid reconstitution of microbiological crusts can also proceed from these connections.

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荒漠土壤藻群落结构的原生演替

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摘 要：微生物结皮是荒漠化治理中新的热点之一，但其关键形成生物——微型藻类如何通过群落结构的变化向地衣结皮、藓类结皮转变的机理仍是未知的。本文以时空替代法，将沙坡头流沙、4、8、17、34及42龄结皮当作同一群落演替进程中的6个阶段，通过系统聚类、主分量分析的方法首次对这一问题进行了研究，结果显示该地荒漠藻群落的原生演替朝着篮藻总丰度和爪哇丝状藻（Seytonema javanicum）丰度逐渐下降，纤细席藻（Phormidium tenue）和绿藻、硅藻丰度逐渐增加的方向进行；多样性随群落演替的发展而增高；生物量在初期呈正向演替，后期随地衣、藓类的入侵逐渐下降；演替速度非常缓慢，高龄结皮中的优势种仍是建群种，只是优势度略有下降；水分、植被覆盖率、地形、时间、土壤理化性质都影响演替过程和速度，特别是Mn含量对演替有重要的阈值作用。

关 键 词：荒漠土壤；藻类；群落结构；原生演替

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