REVIEW ARTICLE

Research progress on algae of the microbial crusts in arid and semiarid regions*

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Abstract Microbial crusts are attracting much interest in view of their possible uses in environmental conservation and ecological restoration of the arid and semiarid regions. Because algae play an irreplaceable important role in the early formation and the strengthening of microbial crusts, they are paid much more attention to than other cryptogams. In this paper, an overview of the current knowledge on the fine structure and development of microbial crust, focusing on the algal biomass, vertical distribution, succession, influential factors on algae, cohesion of soil stabilization, cementing mechanism for soil particles and the microalgal extracellular polymers is given, with particular emphasis on the authors' researches, and some prospects are put forward as well.

Keywords: microbial crusts, algae, desert, arid and semiarid region.

The microbial crust has a number of effects on the desert ecological system, including soil stabilization, moisture, nutrient, thermal effects of the ground surface, and also on the global climate change. Therefore it is paid much attention to by researchers in the world[1~5]. In the face of quick development, the aim of this paper is to give an overview of the current knowledge on algae in the microbial crust, with particular emphasis on our own results.

1 Fine structure and development

1.1 Fine structure

Desert is thought as terrestrial limits of life, but algae can survive. They do not only depend on their physiological response to all kinds of stresses, but also on the relatively favourable ecological niches they occupy in the extreme environment. For example, the Antarctic terrestrial algal mats have been reported to have fine structure, which means the surface is composed of non-living material; the lower layers are less structured than the upper layer, and include cyanobacteria and eukaryotic algae although still dominated by *Phormidium autumnale*. The lowest layers are composed of dead organic material[6]. The authors found clear structure of algal crust in an arid region at the Shapotou area (Ningxia, China; 37°27′ N, 104°57′E). In our researches, substantial amount of algal crusts were collected from five different desert experimental sites which were aged 42, 34, 17, 8 and 4 years respectively, and the species composition in a micro-scale upon 0.1 mm of depth was determined. It was found that the vertical distribution of cyanobacteria and microalgae in the crusts is distinctly laminated into an inorganic-layer (0.00~0.02 mm, with few algae), an algae-dense-layer (0.02~1.0 mm) and an algae-sparse-layer (1.0~5.0 mm). It was interesting to note that in all crusts *Scytonema javanicum* Born et Flah (or *Nostoc* sp., cyanobacterium), *Desmococcus olivaceus* (Pers ex Ach., green alga) Laundon and *Microcoleus vaginatus* Gom. (cyanobacterium) dominated at the depth of 0.02~0.05, 0.05~0.1 and 0.1~1.0 mm from the surface respectively. *Phormidium tenue* Gom. (or *Lyngbya cryptovaginatus* Schk., cyanobacterium) and *Navicula cryptocephala* Kutz. (or *Hantzschia amphioxys* (Ehr.) Grun. and *N. cryptocephala* together, diatom) dominated at the depth of 1.0~3.0 and 3.5~4.0 mm respectively, of the crusts from the

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42 and 34 year-old sites. Apparently there are more green algae in more developed crusts and the niches of *Nostoc* sp., *Chlorella vulgaris* Beij., *M. vaginatus*, *N. cryptocephala* and fungi are closer to the surface. For algal biovolume, if lichens and mosses accounted for less than 41.5% of the crust surface, it was bigger in the older crusts, but the opposite was true when the cryptogams other than algae covered more than 70% of the surface[7,8].

1.2 Development

In the previous studies, we found that soil physical-chemical properties, composition of minerals and biological character of the crust were different during the process of crust development. (1) Organic matter and nutrient, electric conductivity, silt, clay, secondary minerals are higher and there are more micro-beddings in the older crusts than in the less developed ones. (2) For well-developed crusts algal community structure is much more complex than the young ones, the spatial pattern of algal vertical distribution is much finer; the abundance of cyanobacteria slightly decreased, the abundance of green algae increased, obviously the niches of *Nostoc*, singled-cell green algae (i.e. *D. olivaceus*) and some cyanobacteria, green algae, diatoms and hyphae with weaker resistance to stresses are more near to the surface. (3) At the primary stage algal biomass increases with the developmental progress, but at the later stage, the increase speed is relative slower or basically stable, or even decreases with an apparent appearance of more lichens and mosses. (4) Biomethods (such as fine species distribution and biovolume) that resulted from the above crust developing stages are more precise than mineralogical approaches in judging algal crust development and thus could be a better means to measure the potentiality of algal crusts in desert amelioration[1)].

2 Biomass

2.1 Expression of algal biomass

The most interesting prospect of microbial crusts is the function of ecological restoration and reconstruction in the arid and semiarid regions, so the algal biology of the early formation of crust, the actual measurement of their biomass is very important. But for a long time the differences in counting methods (direct counting and culture counting), in culture conditions (with different culture media and usages), in the methods of dealing with samples (ground or not, grinding degree, dilution degree, disperse degree etc.), and in the basic ration units used (cell number, individuals number or cell volume of per gram dry soil or per unit area), make the comparison of results quite difficult. Additionally due to the limiting environmental factors, or the changes of developmental degree, the results from various authors are obviously different[9]. Thus, the methods for soil algal biomass measurement have long been in confusion and caused serious practical errors. This has severely retarded the progress in this research area. We conducted direct counts by using acridine orange and 4,6-diamidino-2-phenylindole dyes under a fluorescence microscope, dilution plate techniques with a series of dilution gradients incubated on BBM, BG11, BHB-D1 and Chu' 10 agar culture media, biovolume method by translation of both direct counts and plate counts results into volume for each species of algae. By comparison we put forward a relative standard method to quantify algal biomass in species level, namely biovolume techniques. The detailed biovolume technique is: (1) sampling should be much finer in depths. Normally the vertical samplings are done at serial sections of 0~5, 5~15, 15~50, 50~150, 150~200 mm in depth respectively. In the laboratory, sections of those blocks were firstly scraped clean with a sterile scalpel, then cut into 0~1, 1~2, 2~5, 5~10, 10~15, 15~20, 20~25, 25~50, 50~100, 100~150 and 150~200 mm blocks, whereas soil of clay kinds into 0~5, 5~15, 15~50, 50~150, 150~200 mm blocks; (2) samples should be ground, diluted, shaken and dispersed as much as it can before culturing; (3) the average volume of each species was measured by direct observation (species can be identified without culture) and solid culture observation (species can be identified only under the culture conditions); (4) different culture media and 3~4 replications for each medium should be used; (5) natural community structure and the percentage of dominant species should be determined under direct observation; (6) volume calculation should include both natural and culture community structure. Biomass was expressed as volume per gram dry soil. According to this method the average biovolume was 5.99~8.58 $mm^3\ g^{-1}$ dry soil in the algal crusts of non-irrigation area of Shapotou, and 1.28 $mm^3\ g^{-1}$ dry soil in irrigation area. The maximal biovolume

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was exhibited in August with the highest precipitation; the minimal value in February with the lowest air temperature[9].

2.2 Influential factors on algal biomass

Biomass of desert algae is often positively correlated to local precipitation or available water, negatively correlated to soil pH and organic matter, meanwhile it is affected by soil nutrient level and texture; but the influences of light intensity, soil temperature, moisture degree, changeable sodium, sulphate, Ca, Mg, EC, C/N, S, Mn etc. on biomass of soil algae are a little different[10,11]. The possible reasons would be the following two. One is that the influential factors are really different in different stages of crusts. The other one is that some researches only involved a few environmental factors, and some most important factors were ruled out. Six microclimate factors (wind speed, air and surface temperature, evaporation, precipitation and humidity) and 27 soil microenvironment parameters (total N, P, K, rapidly available N, P, K, C/N, organic matter, moisture, pH, electric conductivity, Ca^{2+}, Mg^{2+}, SO_4^{2+}, Cl^-, Mn, V, Zn, Cu, Fe, Co, coarse sand grains, fine sand grains, coarse silt, fine silt and coarse clay particles) associated with biovolume were considered by the authors in the research. Stepwise multiple regression analysis indicated that biovolume was positively correlated with the amount of local precipitation, total K_2O, soil hydrolysable nitrogen, Fe^{3+} and coarse silt, while negatively correlated with pH, organic matter, Cu and Zn. Meanwhile it was affected by trace element Co[10].

3 Vertical distributions

Although algae are often distributed within the crusts, they also grow in the deeper layers, and the distribution of them is generally asymmetrical. Twenty-six algal taxa were found in the crust layers of Shapotou area, 15 and 10 taxa separately in 0 ~ 50 mm and 50 ~ 100 mm depth below the surface, no algae in the ranges below 100 mm depth. Among them the widespread species were *Nostoc* sp., *M. vaginatus*, *N. cryptocephala*, *C. vulgaris*, *Euglena* sp., *L. cryptovaginatus*, *P. tenue*, *S. javanicum*, *D. olivaceus* and *Chlorococcum humicola* in the crust, and blue-green algae and filamentous species were the most abundant. In the depth of 0 ~ 50 mm and 50 ~ 100 mm diatoms and unicellular species dominated respectively, namely *H. amphioxys*, *N. cryptocephala* and *Diatoma vulgare* var. *ovalis* distributed often in 0 ~ 50 mm depth, while *H. amphioxys* and *N. cryptocephala* in 50 ~ 100 mm ranges. In addition, all species that appeared in the lower layers could be found in the upper ones as well.

The vertical distribution of algal biomass dramatically decreased with the soil depths from the surface to the lower levels, and more than 99% of biomass was concentrated in the crust layer. Within the crust 78% of biomass was distributed in the 0.1 mm upper depth, 96% in the 1.0 mm upper depth. It was obvious that there was not enough oxygen and light illumination for algal growth in the depth below 1.0 mm. Seasonal variance of species number in the crust layers and 0 ~ 50 mm ranges was closely related to local precipitation, and the highest value occurred in the most abundant rainy season (August), but it was basically stable in the deeper layer (50 ~ 100 mm depth). This was attributed to the rainwater seeping. In the rainfall those species, which are small in size and could be easily oozed down from the upper layers, were concentrated in the deeper layer. After their long-term metabolic activities the soil of deeper layer will be improved in structure and characteristics[12].

4 Successions

4.1 Colonization succession

As a kind of pioneer organism, algae often first occur in the harsh environments where other organisms are difficult to survive, and they gradually affect and change the surrounding conditions so that other organisms can live at later stages. As for the relationship between algal colonization and the environmental factors including the soil matrix, Davey et al. thought that it only occasionally exists[13], Pluis did not find obvious pattern in this aspect[14], and we did not discover a clear relationship neither[1]. However, we observed that the process could be divided into six stages in the Shapotou area, of which *M. vaginatus*, *S. javanicum*, *D. olivaceus*, *C. humicola* and *M. vaginatus* dominate respectively at 5 different stages, *N. cryptocephala*, *H. amphioxys* and *M. vaginatus* take nearly equal advantage over other

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species at another stage. *M. vaginatus* is a species that always first colonizes in all desert microenvironments and it is remarkable over other algae in most stable algal crusts. Water content, nutrient level and shade degree all affect the process. Among them, water shortage is the most important factor that limits algal growth. Under the irrigation condition in the relative flat area, where the steep degree is lower than 45°, a succession of dominant species could be accomplished within 1~2 months. When nutrient level is low, the stage at which *S. javanicum* dominates occurs necessarily in the process, and shade degree does not affect the succession. On the contrary, in case of a relatively high level of nutrient, the stage at which *D. olivaceus* is dominant is indispensable, and shade degree affects the succession. The stage dominated by *C. humicola* does not occur until shade degree and nutrition level is relatively high. But in unconsolidated sand of Laarder Wasmeer, the first colonizing species is *Oscillatoria* sp., and then in turn are the species of *Klebsormidium*, *Synechococcus*, *Zygogonium*[14]. We suggest that the algal species differences in colonization are related to the local climate, species from air-borne resources and other factors in terms of both pedology and biology.

4.2 Primary succession

When stable algal crusts form in the naked land, after several years' development, many of them will be substituted by the lichen crusts (except Sahara Desert). During the process of primary succession, the succession orientation was discovered as that: the abundance of Cyanophytes, specially of *S. javanicum* decreased gradually; the abundance of Chlorophytes, Bacillariophytes and a species of Cyanophyta, *P. tenue* increased; the biodiversity increased gradually along with community succession; biomass of microalgae increased at the early stage, decreased at the later stage due to the appearance of more lichens and mosses. But the speed of natural succession is so slow that the community-building species is still the first dominant species after 42 years except that its dominant degree just decreased slightly. However, the successive speed and trend could be affected by water, vegetation coverage, terrain, time and soil physicochemical properties as well, and especially the Mn content in the soil appears to have a threshold effect[15].

Due to the obvious spatial heterogeneity of the surface, the succession is not in the same phase even for the same sites. Nevertheless, the biological primary succession is still obvious and clear, and the algal crusts are definitely the first stage of the succession process in the Shapotou area. The algal crusts can form on the basis of physical crusts, and directly on the shifting sand as well. In the non-irrigated sites of Shapotou, algal crusts gradually change into lichen crusts (crustose lichens) with ascension of the *Nostoc* niche and the increase of green algal number. So lichen crusts are the secondary succession stage in this area. The third phase is the moss crusts that lichen crusts further developed (This stage is obvious, but the detailed process is unknown). Therefore, the succession sequence is approximately the same with Eldridge and Greene's statement[16]. The recovery experiment of the crusts also further proves the above order[17]. However, algal crusts can jump over lichen stage, and become directly moss crusts in the artificial irrigation area with a relatively high coverage of shrub[15].

5 Effect of fixing-soil

Many researches have confirmed that microbial crusts can increase the stability of soil aggregates in water[18,19]. For wind stability, Belnap and Gillette measured the threshold friction velocity of the natural crusts[20]. However, the natural aged microbial crusts often intermix with lichens, fungi and mosses. It is long disputed as to which kinds of cryptogams really stabilize soil, or which one is more important in the sand stabilization[11]. McKenna Neuman et al. measured the sand stabilization capacity of *Nostoc*, *Chlmydomonas*, *Lyngbya* and three fungi (*Aureobasidium pullulans*, *Trichoderma harzianum*, *Absidia corymbifera*)[21,22]. But because the biomass indices of algae and fungi are different, other factors are also not uniform, it is difficult to compare each other. In our studies, four filamentous cyanobacteria, *M. vaginatus*, *P. tenue*, *S. javanicum* (Kutz.) and *Nostoc* sp., and a single-celled green alga, *D. olivaceus*, were batch cultured and inoculated onto unconsolidated sand in a greenhouse or a field experimental plot. Their ability of reducing the wind erosion was quantified by using special equipments in a wind tunnel laboratory. The major parameters related to the cohesion of algal crusts, such as biomass, species, species combinations, bioactivity, niche, growth phase of algae, moisture, thickness of the crusts, dust accretion (including dust content and manner of dust added) and other cryptogams (lichens, fungi and mosses) were studied. The best of the five species were *M. vaginatus*. and *P. tenue*, while the best combination was a blend of 80% *M. vaginatus* and 5% each of *P. tenue*, *S. javanicum*, *Nostoc* sp. and *D. olivaceus*. The threshold friction velocity was significantly increased by the presence of all of the cyanobacterial species, while the threshold impact velocity was notably increased only by the filamentous species. Thick crusts were less easily eroded than thin crusts, while the biomass of algae was more effective in preventing the erosion than that by the crust thickness. Dust was incorporated best into *Microcoleus* crust when added in small amounts over time, and appeared to increase the growth of the cyanobacterium as well as strengthen the cohesion of the crust. Microbial crust cohesion was mainly attributed to algal aggregation, while lichens, fungi and mosses affected more the soil structure and physico-chemical properties[23,24].

6 Cementing mechanisms

Gillette and Dobrowoski thought that the formation of microbial crusts was composed of both cryptogam and dust[25]. The cementing mechanism has long been suggested both to be binding of trichomes, hyphae or root and adhesion of their metabolism secretion. Most validate experiments on the role of algae in the formation of microbial crust have focused on the number, size, water stability of soil aggregates. But in the harsh environment there is less clay mineral in unconsolidated sand when cyanobacteria early stabilized the shifting sand, even if the old crusts with relatively high clay minerals have not any aggregates[8]. In our researches, a series of natural algal crusts of 34, 17, 4 and 1.5 years old were collected from Shapotou, and 40 day-old field and artificial algal crusts produced in the greenhouse were developed *in situ* in the same sandy soil at the same sites. Cohesions of the crusts against both wind force and pressure were measured respectively in a sandy wind-tunnel experiment and with a penetrometer. On the basis of these algal crusts, cementing mechanism was revealed with the following evidence. In the indoor artificial crusts, of which the cohesion was the weakest, with bunchy algal filaments in the surface and few extracellular polymers (EPS) produced, the binding capacity of the crusts was just accomplished by mechanical bundle of algal filaments. For the field crusts, most filaments grew toward the deeper layers of the sandy soil, secreted much more EPS, and when organic matter content was more than 2.4 times that of chlorophyll a, too much organic matter (primarily the EPS) began to gather onto the surface of the crusts and formed an organic layer in the relatively lower micro-section, and this made the crust cohesion increase 2.5-fold. When the organic layer adsorbed and intercepted a certain amount of dusts, soil particles and sand grains scattered down from wind, and it changed gradually into an inorganic layer where inorganic matter dominated, and this made the crusts cohesion enhance 2~6-fold further[26]. So the spatial heterogeneity of intensity mainly depends on whether an inorganic layer exists or not, because the inorganic layer is a little similar to the firm physical soil crusts that absorb, intercepte silt and clay by electrostatic attraction. The new inorganic layer forms continuously, and the old one is buried by the new one with the development of the algal crusts. The dusts of the old crust gradually move into the deeper layer, rearranged, and deposit with occasional currents. Algae often grow in the relatively stable depth due to phototaxis motion except when the crusts are watered[27]. Thus, the thickness of the crusts gradually increases, and the inorganic layer of the surface and deposited dust particles clog the pores between the larger soil particles and sand granules, sealing water from the surface to deep, and causing runoff. But because parts of the micro-sections of the surface do not form the inorganic layer, these micro-sections cannot be sealed. This is just the complexity being long disputed whether microbial crusts bring out runoff or not. Additionally, the cryptogams meliorate soil structure to which the organic substance excreted and decomposed makes soil crack into certain sizes of soil aggregates. These aggregates lead to the increase of soil porosity and extension of plant root system. Therefore, these organic matters do not only bind soil particles together but also balance the binding and breakage.

7 Extracellular polymers

Terrestrial algae are known to secrete a variety of extracellular substances comprising polysaccharides, amino acids, amides, vitamins, growth regulators and scytonemin typed pigment into the soil matrix around them. These polymers protect algae from detrimental influence (desiccation, antibiotics, ultraviolet radiation etc.)[28,29], and promote the absorbed dust to form the inorganic layer of the surface of the crusts to increase their cohesion[26]. Painter et al. thought that extracellular polymers conduced to the formation of soil aggregates, the effective utilization of phosphor and release of trace elements, which would be green manure to amend desert soil[30]. Mazor et al. further confirmed their function in nutrients supply of microbial crusts and increase of humidity[31]. Chen and Liu found the function of extracellular polymers in desert soil formation and algal tolerance to salt and alkali[32] 1). Due to the interesting prospects the research on the exopolysaccharides of terrestrial algae has been paid much more attention to in the recent years. But because of the poor water solubility, the structure analysis on that is rare[33~35]. By amelioration in the authors' studies, extracellular polymeric substances (EPS) from five species of algae, *M. vaginatus*, *S. javanicum*, *P. tenue*, *Nostoc* sp. and *D. olivaceus*, were investigated for their chemical composition, structure and physical properties. The EPS contained 7.5% ~ 50.3% protein (in polymers ranging from 14 to more than 200 kD) and 16.2% ~ 40.5% carbohydrate (110 ~ 460 kD). A total of 6 ~ 12 kinds of monosaccharides, including 2-O-methyl rhamnose, 2-O-methyl glucose and N-acetyl glucosamine have been found. For the crust-building species *M. vaginatus*, 88.5% of EPS is the acidic components, 78% is the acidic proteglycan of 380 kD. The uronic acid (galacturonic acid and glucuronic acid) content accounts for 8% of proteglycan, and their free carboxyls are the main sites of binding with metal cations from surrounding matrix[27,28]. All in all, the structure of the proteglycan is novel, complex, and the main chain much branched. Some monosaccharides are present both in β-pyranose and -furanose forms2).

8 Conclusions

Although many new developments have been achieved in the recent years, the following aspects need further studies: (1) The species composition changes obviously with the development and succession stages of microbial crusts, and the dominant species are different in different soil texture, but very few studies have been devoted to species diversity[36~38], especially the diversity in reports from the traditional classification is far lower than that from 16s rRNA and 16s rDNA gene sequence analysis[39]. (2) With the development of the microalgal technology, it is possible to accelerate algal utilization in ecological reconstruction, soil melioration, nutrient supplement and to use algae as a kind of environment monitor for the arid and semiarid regions. To develop new approaches to stabilizing soil, such as the theoretical basis and technology of using algae, algae and grasses, algae, grasses and shrubs, or algae, grasses, shrubs and arbors, and to select better species for soil stabilization and a better match for portions of microbial crusts and higher plants, need to be extensively studied[40]. (3) The particularity of the extracellular polymers of the terrestrial algae in structure and function shows that they have great values both in basic and applied research. The lack of information in molecular structure, biological activity, ecological function, adaptive mechanism to extreme environment has limited their exploitative application in industry, agriculture, medicine, and environment. (4) Microbial crusts cover more than 70% of the arid and semiarid regions, with 50% of photosynthesis rate in higher plants[38]. However, their contribution to the carbon circle is still unknown, so it seriously affects the reliable prediction of the global carbon dioxide, nitrogen, trace gases, and so on.

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