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REVIEW

Progress in the study of algae and mosses in biological soil crusts

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Abstract Algae and mosses are not only two of the familiar communities in the process of desert vegetational succession, but also have the highest biomass in biological soil crusts. Meanwhile, being the pioneer plants, algae and mosses are involved in the establishment of biological soil crusts, which have great importance in arid environments and play a major role in desert ecosystems, such as being the indicator of the vegetation type, soil-holding, preventing erosion by water and wind, and sand fixation. This paper reviews the advances in the study of algae and mosses in arid and semi-arid areas. It mainly describes the ecological functions of algae and mosses including their influences on water cycle, circulation of substances, and community succession. In addition, the relationships between algae and mosses are discussed. Finally, some suggestions are proposed for the research orientations of algae and mosses in biological soil crusts. Ecologically, algae and mosses have significant ecological importance in arid areas, especially in those areas where environmental problems are becoming increasingly serious.

Keywords algae, biological soil crusts, mosses

1 Introduction

Biological soil crusts are complex assemblages of non-vascular plants, such as cyanobacteria, green algae, lichens, mosses, fungi and liverworts, which form intimate associations with surface soil (Eldridge and Greene, 1994; Zhang et al., 2005a, 2005b; Zhang, 2005; Zhao et al., 2006). They are found in mesic environments, tropical and temperate deserts and in the polar regions of the globe (Eldridge and Greene, 1994). Ecologically, these kinds of crust are differentiated from other soil surface features such as vesicular horizons and rain-impact and depositional crusts by being organo-genic in nature and by their general effect on infiltration, bulk density, water storage and soil fertility (Nash et al., 1979; Belnap et al., 1994; Hu et al., 2003; Zhang, 2005). Based on the dominant species, biological soil crusts have been classified into three different types: algal crust, lichen crust, and moss crust (Fig. 1). Algae and mosses are integral components of biological soil crusts on the desert surface in many arid and semi-arid regions (Eldridge and Leys, 2003). They are well-known to play a major role in ecosystem functioning, soil stability, and in processes such as nitrogen fixation, biomass production and the regulation of infiltration in desert areas. The occurrences of algae and mosses are common in arid and semi-arid areas and they have such functions in desertification control as preventing soil erosion by water and wind, altering the distribution of water, and the fixation of unconsolidated sand (Durrell and Shields, 1961; Wu et al., 2002; Chen et al., 2003).

2 Research methods and techniques for biological soil crusts

Nowadays, with the development of research methods for biological soil crusts, much progress has been achieved in the extensive studies of biological soil crusts (Eldridge and Greene, 1994; Zhang et al., 2005a, 2005b; Zhang et al., 2005; Zhao et al., 2006). The research methods and techniques mainly refer to sampling, microscopic observation, data analysis and culturing. First of all, soil samples must be collected from the desert. Undamaged crusts are taken with an aseptic ring-knife or sharp shovel, placed in sterilized petri dishes, wrapped in parafilm, and rapidly carried to the laboratory (Hu et al., 2000a, 2000b, 2002; Hu

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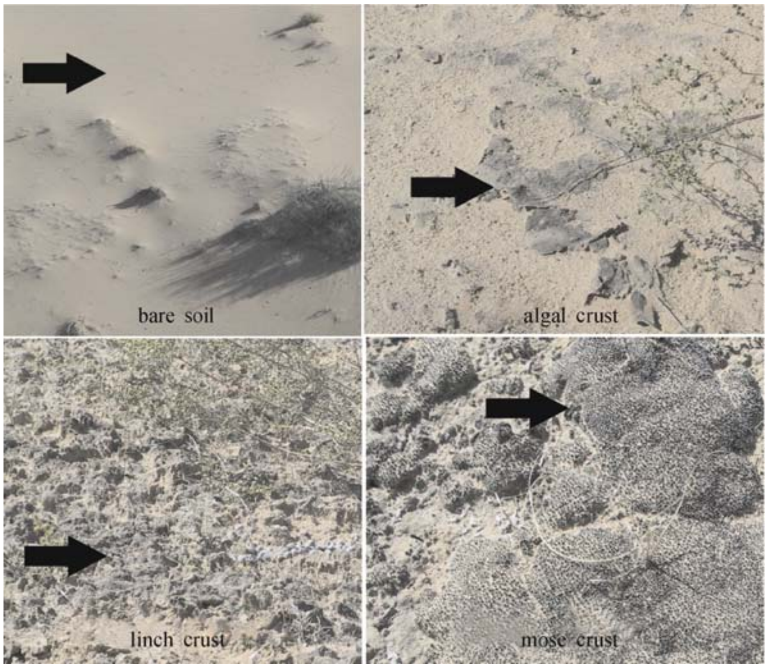

Fig. 1 Types of biological soil crusts

and Liu, 2003; Eldridge and Leys, 2003). The inner microstructure of biological soil crusts are generally observed by microscopy. For surface microscopic observations, the samples are freeze-dried overnight and glued onto aluminum stubs with the exposed vertical natural section facing upward and coated with gold. Observations of the microstructures of soil crusts are performed using a scanning electron microscope (Zhang et al., 2005). Similarity of algal communities is estimated using the Jaccard index and species diversity. The research data are analyzed using STATISTIC or SPSS software (Belnap et al., 1994; Hu and Liu, 2003).

3 Desert algae and algal crust

Desert algae are involved in the establishment of biological soil crusts, which have great ecological importance in preventing wind and fixing sand dunes. Different factors such as climate, soil physico-chemical properties, and the disturbance history of habitats may influence species composition and the external morphology of biological soil crusts. It has been confirmed that the algal flora of the soil includes Cyanophyta, Chlorophyta, Bacillariophyta and Euglenophyta (Hu et al., 1999; Chen et al., 2003; Zhang et al., 2005b). Additionally, the species diversity of Cyanophyta is the most abundant, Chlorophyta is the second, and Bacillariophyta and Euglenophyta are the least. Generally speaking, the filamentous cyanobacteria are the dominant species, especially *Microcoleus vaginatus*. However, the green algae are mainly composed of unicellular coccoid species. Previously, studies on desert algae were mainly conducted in the Shapotou area of Ningxia Province and the Gurbantunggut Desert in Xinjiang Uigur Autonomous Region (Zhou et al., 1995; Duan et al., 1996; Hu et al., 1999, 2000a; Zhang et al., 2005a, 2005b; Zhao et al., 2006). Correlative studies indicate that the species diversity of algae in the Gurbantunggut Desert is more abundant than in the Shapotou area. There are 121 and 40 species of algae in the Gurbantunggut Desert and the Shapotou region, respectively. In addition, cyanobacteria dominate in the two regions (Hu et al., 1999; Zhang et al., 2005a).

Being the pioneer plants of the ecosystem in desert and semi-desert areas, algae increase the availability of essential elements, such as carbon and nitrogen in the soil, and resist soil erosion by wind and water. Thus, algae play a critical role in the soil succession and also contribute organic matter toward soil formation. Moreover, algae provide the favored conditions for further colonization by plants such as lichens, mosses and vascular plants.

3.1 Cementing mechanism of algal crust

In the arid and semi-arid environment, soil microorganisms often form a thin layer in the topsoil, which is called the algal crust in phycology; the microbeotic crust in soil microbiology, and the crytogams crust in cryptogamy. No matter what the difference of the nominatum is, the algal crust plays a substantial role in sand dune stabilization and soil melioration. Up to now, among various types of organisms, it has long been acknowledged that microalgae play an irreplaceable role in the early formation and strength maintenance of the crusts. Therefore, algae have attracted much attention in desertification control (Hu et al., 1999, 2000b, 2002; Chen et al., 2002, 2003; Zhang et al., 2005).

With regard to the formation of the algal crust, Schulten (1985) suggested that there are two major mechanisms in this process, including the wrapping and bonding effect of filamentous species. In addition, Zhang also indicated that biological crusts result from the colonization of the soil surface by communities of filamentous cyanobacteria, which are mainly dominated by *Microcoleus*, which occurs as a cluster of filaments surrounded by a gelatinous sheath. At this stage, the main contributors to sand fixation change from bacteria to filamentous cyanobacteria (Issa et al., 1999; Zhang, 2005). The coccoid algae can also produce extracellular secretion to cohere to sand particles as a group. In spite of this, it is clear that the wrapping and cohering effects of filamentous and coccoid algae are the deciding factors in sand fixation (Zhang, 2005).

With respect to the compressive strength of the algal crust, Hu et al. (2002) suggested that the upper thin inorganic layer of the soil profile is a main factor in enhancing the compressive strength of the algal crust. However, the microstructure of crusts shows that the thin inorganic layer is not the main contributor to sand surface stability compared to the subsurface filamentous network formed by cyanobacteria. Meanwhile, microscopic examination of biological soil crusts has revealed that an intricate structure binds mineral particles on the sandy soil surface. In this regard, the network of filamentous cyanobacteria serves as the main agent in the stabilization of the soil surface. Additionally, the living filaments can migrate through the soil, leaving abandoned sheath material to stabilize the soil surface (Zhang, 2005). In the meantime, these sheathes can also cohere to and wrap sands together to enhance the ability of resisting soil erosion by wind and water (Zhang et al., 2005b).

In a word, the inorganic layer and organic layer on the surface of biological crusts can not only stabilize and fertilize the desert soil but also reduce the effect of erosion by wind and water. Meanwhile, the bonding function of filamentous species and the cohering effect of coccoid algae have great importance in the formation and strength maintenance of biological soil crusts.

3.2 Ecological function of desert algae

Being the pioneer plant in the community succession, the desert algae play a key role in the circulation of substances, the water cycle, and even the environmental succession of the desert ecosystem (Zhang et al., 2002a, 2005b).

3.2.1 Influence on circulation of substances

In biological soil crusts, the colonization of algae not only changes the circulation of substances of desert soil but also increases the quantity of nitrogen and carbon of desert soil (Zhou et al., 1995; Wu et al., 2002; Chen et al., 2003). As a result, it promotes the mineralization of mineral matter and maturation of the soil. Generally speaking, there is little integrated nitrogen in the desert soil. However, the growth of some algae provides an abundant source of nitrogen and carbon for the desert soil, especially the nitrogen fixed by nitrogen-fixing algae (Wu et al., 2002). Ecologically, desert soil is the local habitat of nitrogen-fixing algae. Therefore, algae increase organic matter and improve the environmental conditions to a certain extent by photosynthesis and nitrogen fixation (Chen et al., 2003). Otherwise, the nitrogen-fixing algae and other microorganic communities can increase soil enzymes and accelerate the process of soil succession (Guan, 1991).

3.2.2 Influences on water cycle

As dominant or co-dominant organisms in cold and hot deserts, and on aerial substrates in all latitudes on earth, soil algae, especially the blue-green algae, are well adapted for existence in climatic zones and local microenvironments where available water is the primary limiting factor. Many desert algae have thick cellular walls and sheaths, which can keep water when the environment is arid, and absorb abundant water when the conditions are humid (Zhang et al., 2005b). Therefore, this structure can provide moist and comfortable circumstances for algae. It has been confirmed that the exopolysaccharide always easily combines with temporary rainfall and dew, and water participates in the photosynthesis of many microorganisms on the surface of biological crusts. Thus, they can accumulate energy and organic matter as the foundation substance of the desert ecosystem (Chen et al., 2002).

Much evidence suggests that the reticulated structure, made up of *Microcoleus, Phormidium* and *Tolypothrix*, can absorb water quickly in times of rainfall (Chen et al., 2003; Zhang et al., 2005b). The algae absorb so much water that their bulk increases about 4–5 times more than previous and blocks soil interspaces by about 40%. This process can influence water infiltration in the soil, which leads to the death of vascular plants (Wu et al., 2002; Zhang et al., 2005a).

3.2.3 Influences on community succession

The community succession in the desert is a process wherein species composition changes from lower plants to higher plants and the biodiversity increases gradually (Zhou et al., 1995; Wu et al., 2002). In the process of soil maturation, algae are an important component in the desert ecosystem and are even the first colonizers of crusts, which enhances the stability of the soil surface. Dominant species vary in different stages of the community succession (Zhang et al., 2002a; Xu et al., 2003, 2005). According to the different succession stages, biological soil crusts can be classified into three types: algal crust, lichen crust and moss crust. With the development of biological soil crusts, the algal crust is substituted by the lichen crust or moss crust. However, the succession is a gradual process, especially in harsh desert environments (Booth, 1941; Anderson, 1982; Guan, 1991; Dodds et al., 1995; Garcin-pichel, 1996; Wang et al., 2001; Hu et al., 2000a, 2002; Wu et al., 2002).

4 Desiccation tolerance and ecological functions of mosses

Mosses are found over extensive arid and semi-arid areas (Zhang et al., 2002a, 2002b; Xu et al., 2005). Usually, the common habitat of mosses is restricted to humid environments, but some mosses, such as the species of the families Pottiacea, Grimmiacea and Bryaceae, are grown well on loose dune soil. This is probably due to their ability to produce dense networks of underground stems, which make them important soil stabilizing agents. Ecologically, a number of environmental factors influence the survival of mosses in arid and semi-arid areas. Due to their poikilohydric nature, one of the most critical of these factors is external water. In the absence of water, photosynthesis ceases and the plants become dormant. Apart from the influence of water, the distribution of mosses in arid areas is related to total annual rainfall, soil pH, calcium carbonate level, plant cover, texture, organic carbon and soil texture. Rainfall is a primary determinant factor of plant cover, which in turn affects light, nutrient availability and therefore the distribution of mosses. It can also be inferred from literature that the diversity and density of moss populations are much lower in deserts than in mountainous areas at higher elevations. As the dominant species of the biological soil crusts, mosses play key roles in the incrassation of the crusts, moisture maintenance, nutrient retention and so on (Zhang et al., 2002a).

4.1 Desiccation tolerance of mosses

In the desert environment, mosses have formed a number of morphological structures and physiological properties in order to adapt to the arid conditions during the long evolutional process (Wu, 1998; Zhang et al., 2002a).

4.1.1 Morphological adaptation of mosses to arid conditions

In arid and semi-arid areas, the moss crust is a common phenomenon all over the world. Under pressure from extreme desiccation, mosses have developed some morphological and ecological characteristics to adapt to drought conditions (Wu, 1998; Zhang et al., 2002a, 2002b). They grow in tufts or cushion forms which enable them to have a high capacity for water retention and the ability to reduce the loss of water. As a result, evaporation can be decreased. Their leaves curve intensely and attach to stems when environmental conditions become dry so that they can avoid great evaporation and prevent themselves from being damaged by strong sunlight (Zhang et al., 2002a). Additionally, they have white seta on top of the leaves, through which the plant can reflex strong sunshine (Wu, 1998; Zhang et al., 2002a, 2002b; Tian et al., 2005).

4.1.2 Physiological properties of mosses

Since mosses have many important physiological characteristics, they are able to survive in arid and semi-arid areas (Hu, 1985; Wu et al., 2004). Generally speaking, the cytoplasm of mosses has developed altitudinal characteristics of drought tolerance in desert conditions (Zhang et al., 2005). It has been confirmed that the drought species of mosses have a strong ability to repair the damaged cell membrane system. They can repair damage in the cell, even in the whole plant, in harsh environments (Wu et al., 2004). In addition, the drought tolerance characteristics of mosses are also related to the low water potential in the cells (Wu, 1998). Species with strong drought tolerance always have the same water potential as the desert soil. Accordingly, once the environment changes to wetness, water potential grades build up between plant cells and the environment immediately. So the cells of moss can absorb abundant water to maintain their normal water potential (Hu, 1985). Some other researchers have observed the phenomenon that the protoplasm is separated from the cell wall in *Tortula ruralis* to endure drought environments. The protoplasm concentrates to empty the central portion, and is connected by the cytoplast bridge. At the same time, the chloroplast becomes round and smaller. However, if the *Tortula ruralis* is rehydrated, the concentrated protoplasm can expand quickly and abound in the whole cell antrum, and the chloroplast also enlarges in several minutes. This physiological mechanism maintains the integrity of the cell and makes them adapt to drought and the harsh environmental conditions (Wu, 1998; Wu et al., 2004).

4.2 Ecological functions of mosses

Being the pioneer plants, mosses are involved in the process of establishment of soil crust, which has great importance in arid environments. They play a vital role in desert ecosystems, such as being indicators of the vegetation type as well as stabilizing and fertilizing the soil, preventing erosion by water and wind, and being responsible for the stabilization of sand dunes (Xu et al., 2003; Tian et al., 2005). In arid and semi-arid areas, the soil surface may become steady and form a softer and more permeable layer that acts as a basis for colonization of higher plants due to the participation of these mosses and other organisms (Zhang et al., 2002a, 2002b, 2004; Tian et al., 2005).

4.2.1 Influences on the formation of soil crusts

On the incompact sand dunes, mosses have a number of rhizoids which can tightly bond sand particles together. They then gradually develop to be the dominant species of the biological soil crusts. Therefore, in this aspect, mosses have much ecological value in arid and semi-arid areas (Xu et al., 2003; Zhang et al., 2004). Mosses, such as Pottiacea, Grimmiaceae and Buyaceae, are not only involved in the formation of soil crusts to stabilize and fertilize soil and prevent erosion by water and wind, but also increase the possibility of vascular plant colonization. Moreover, they have important functions in holding water, stabilizing the soil surface, reducing erosion by water and wind, and increasing nutrient in the desert soil (Zhang et al., 2002a; Tian et al., 2005).

4.2.2 Influences on water storage and soil holding

In the arid and semi-arid areas, mosses enhance sand surface stabilization and increase the biodiversity of biological soil crusts, especially functioning in keeping water and soil. Thus, it has been suggested that mosses play an important role in improving the soil physico-chemical properties, increasing the availability of organic matter and retaining the water of biological soil crusts (Wu et al., 2003; Xu et al., 2003, 2005). Mosses can grow quickly in the arid desert soil surface, which can reduce wind and water erosion in the field. Ecologically, the moss crust has great importance in stabilization of sand surfaces and soil fertility (West 1990; Metting, 1991). In short, mosses have significant ecological importance in arid areas, especially in those areas where environmental problems have become increasingly serious. That is why many bryologists and ecologists focus on desert mosses, especially those species involved in crust formation.

4.2.3 Influences on community succession

Biological soil crusts are widespread throughout the arid and semi-arid regions of the world. The community composition of biological soil crusts is strongly influenced by soil surface biogeochemistry (e.g. surface texture, pH, plant cover, mineral content), land use (e.g. forestry, farming), and available light and moisture (West, 1990; Metting, 1991). After settling down on the desert soil surface, mosses grow quickly to be the dominant species of biological soil crusts (Tian et al., 2005). It has been shown that mosses accumulate large amounts of elements for plant growth, which increases the process of soil formation. As a result, mosses gradually increase the utilization of nutrients and carbon in the desert soil. Therefore, when the organic layer reaches sufficient thickness, vascular plants can colonize in the desert soil (Zhang et al., 2002a; Xu et al., 2003; Wu et al., 2004). Studies on the ecological functions of biological soil crusts indicate that mosses are the pioneer plant in the desert vegetational succession in that they could improve the desert environmental conditions and promote the growth of vascular plants (Wu et al., 2003).

5 Ecological relations between algae and mosses

Cyanobacteria can form associations with species of mosses. The taxonomy of algae growing as epiphytes on mosses in Antarctica has been studied in great detail (Broady, 1987; Ohtani and Kanda, 1987; Fumanti et al., 1997; Alfinito et al., 1998). Only a limited number of cyanobacterial taxa were found, of which only two, *Phormidium frigidum* and *Nostoc commune*,were abundant; frequently, *Microcystis parasitica* was also found (Alfinito et al., 1998). Jordan et al. (1978) also found *Nostoc* sp. to be dominant on leaves of mosses in the Arctic, although *Anabena* sp. and *Oscillatoria* sp. were also observed. Ecologically, algae and mosses are the two types of pioneer plants in the succession of desert vegetation. They play a vital role in stabilizing the sand surface, preventing soil erosion, and fixing the unconsolidated dunes. Meanwhile, being the two important components of biological soil crusts, algae and mosses are involved in the process of establishment of soil crusts, and reduce erosion by wind and water (Zhang et al., 2002a, 2002b; Bai et al., 2003; Zhang et al., 2005a, 2005b).

5.1 Symbiotic relationships between algae and mosses

Algae and mosses are the two main communities of biological soil crusts in arid and semi-arid areas (Hu and Liu, 2003; Tian et al., 2005). In the long evolutional process, algae and mosses have built a symbiotic relationship. Generally, the large community of mosses on the desert soil surface provides a comfortable environment for algae. Meanwhile, the growth of algae contributes organic matter to mosses directly. While algae and mosses occur in association with surficial soils, the carbon and nitrogen fixed by them can make soil fertile, providing energy sources for soil microbial populations. Therefore, algae and mosses can also be regarded as indicators of ecological health.

The existing evidence suggests that algae provide nutrients for the growth of mosses (Hu, 1985). Furthermore, extracellular polymeric substances are always excreted by desert algae. Therefore, filamentous cyanobacteria and moss rhizoids can adhere and bind together tightly to stabilize the soil surface. This structure increases the cubage, mass and proportion of the soil so that wind and rain cannot move it easily. In this sense, a compact layer resisting erosion has formed that enhances the ability to resist draw and increases the stabilization of the soil surface (Duan et al., 1996; Zhang et al., 2002a; Wu et al., 2002, 2003).

Since the ability to prevent disturbance is weak, the algae crust may change into bare soil gradually under several circumstances such as wind and water erosion and animal trampling. Nevertheless, once the moss crust has formed, the complex assemblages of algae and mosses have a stronger ability to resist wind and water erosion than the algal crust alone. Wu et al. also found that moss rhizoids can interact with the filamentous cyanobacteria, which fix soil particles and stabilize the sand surface (Bai et al., 2003; Xu et al., 2005). Based on the different compositions of the biological and physical factors, the moss crust, from the surface to bottom, can be divided into four layers, including the moss layer, inorganic sand layer I, algae crust and inorganic sand layer II. This stratified phenomenon may indicate that mosses are involved in the establishment of biological crusts with their rhizoids (Zhang et al., 2002, 2004). Algae can fix nitrogen for the growth of mosses in the crusts. At the same time, the large coverage of mosses can also protect the algae from strong sunshine and irradiation by ultraviolet light (Zhang et al., 2002b).

5.2 Ecological relationships between algae and mosses in the community succession

In arid and semi-arid areas, algae and mosses serve as two predominant biological factors contributing to sand fixation (Wu et al., 2002). In the early stage of the crusts, algae present firstly on the root of the plants (e.g. small trees, shrubs and herbaceous plants) and then they gradually develop into the algal crust. However, this crust is extremely fragile and susceptible to erosion by wind and water. Subsequently, the mosses directly grow on the basis of the algal crust. So the simple algal crust gradually develops into complex crusts consisting of algae and mosses (Wu et al., 2003). Furthermore, results of some research also indicate that algae are the dominant species in the initial stages of biological soil crusts. With the increasing thickness and coverage of the crusts, mosses gradually develop to become the dominant species. It has been revealed that mosses play a major role in strengthening and stabilizing crusts by their dynamic change of coverage, biomass and sand fixation capacity over the years. Thus, the settlement of the mosses determines the developing orientations of biological soil crusts (Xu et al., 2003). As the pioneer plants, desert algae provide favorable habitats for the establishment of mosses. When mosses settle on the soil surface, algae would escape and occupy new habitats with poorer environments.

6 Applications of desert algae and mosses

The applications of desert algae and mosses are mainly in the restoration and reconstruction of desert vegetation. They can stabilize the topsoil, reduce soil erosion, and enhance the nitrogen pools by nitrogen fixation (Venkataraman and Neelakantan, 1967; Venkataraman, 1972). In arid and semi-arid regions, extremes of moisture, insolation, and temperature are the influential factors in cryptogams. Mosses and desert algae, however, can survive in these areas on account of their special morphological and structural properties. Therefore, mosses and algae, especially the xerophic species, have been cultured and planted into desert soil to prevent erosion from water and wind (West, 1990). In short, the applications of biological soil crusts are important for the rehabilitation of desertified arid and semi-arid lands and provide a natural protective soil surface cover.

7 Future prospects

Algae and mosses are involved in the establishment of biological soil crusts on the desert soil surface. They show significant ecological value in arid and semi-arid areas, especially considering the increasingly serious problem of desertification today. Though many studies of algae and mosses in biological crusts have been conducted, we have little knowledge of the association between desert algae and mosses in biological soil crusts. Due to the pivotal roles of algae and mosses in biological soil crusts, the authors suggest that the research on algae and mosses face several challenges as follows.

Although some studies have been conducted on the species composition in the Shapotou region of the Ningxia Hui Autonomic Region and Gurbantunggut Desert in the Xinjiang Uygur Autonomous Region, due to the limitation of available data and technology as well as the biodiversity of algae and mosses, more research on the species com-position and biodiversity of algae and mosses in the desert areas are needed which will enrich our knowledge of the biodiversity, especially the biodiversity of mosses in xeric conditions. Furthermore, it will also provide basic data for the study of the ecological functions of algae and mosses.

At present, the study on the relationships between algae and mosses in desert is almost a blank. It is known that there are lots of mosses and algae living together in biological crusts. Yet we have not understood the algal species living with the mosses in the crusts clearly, i.e. whether algae have symbiotic species in the moss crust, and if so, what the symbiotic mechanism is. The authors suggest that algologists and bryologists work together to explore the relationship between algae and mosses in the desert, which will help to develop cross-disciplinary and interdisciplinary areas.

Despite studies on the physiological and ecological characteristics of the dominant species of algae and mosses that have been reported, large-scale cultivation of the desert algae and mosses under laboratory conditions has not been achieved yet. Therefore, we should carry out research on the physiological characteristics and the best living conditions of the dominant species. Moreover, studies of the best habitats of algae and mosses under field conditions are also needed.

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