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ORIGINAL ARTICLE

Biological soil crusts: An eco-adaptive biological conservative mechanism and implications for ecological restoration

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Abstract
Biological soil crusts (BSCs) are highly complex associations of soil particles with mosses, cyanobacteria, lichens, bacteria, and fungi. BSCs affect many ecological processes, including infiltration and evaporation, soil erosion, vegetation succession, and nutrient cycling, and perform important ecological functions of ecosystems in arid areas. In the past 30 years, many studies on BSCs were conducted by researchers all over the world. This paper reviews the recent research progresses and frontier problems, and discusses the current controversial conclusions. The main ideas are as follows: (1) influenced by many macroclimate and micro-environment factors, BSCs are characterized by developmental complexity, composition diversity, and spatial heterogeneity. In any typical areas where exist all types of BSCs at different succession stages, it is of great significance to conduct comparable studies on BSCs and to explore if there exists a probable zonality for them. (2) BSCs not only exert positive impacts on soil fertility and soil erosion, but they also show controversial influences on the hydrological processes, especially on infiltration, evaporation, soil moisture, and vegetation succession such as survival, germination, emergence, and establishment. To understand the function-performing mechanisms of BSCs is helpful for the revealing of their action patterns and the comprehension of the implications of the patterns on ecological processes and restoration as well as clarification of existing controversial points. It will eventually contribute to the effective management and utilization of BSCs resources in a given region for large-scale ecological engineering.

Keywords: *Biological soil crusts, biological conservation, ecological function, ecological mechanism, biological–soil interactions*

1. Introduction

Biological soil crusts (BSCs) are highly complex associations between soil particles and mosses, cyanobacteria, lichens, bacteria, and fungi (Meeting 1991). BSCs are commonly found in adverse environments such as dry, barren, and high-temperature areas. They are also widely distributed in the frigid and tropical zones. For example, fungi, an important component of BSCs, can exploit natural or xenobiotic resources and can be well adapted to harsh environments due to their ecological plasticity and extreme tolerance (Selbmann et al. 2013). Covering 35% of the continental surface on the earth and even more than 70% in some arid regions (Belnap & Lange 2001), BSCs not only exert great influences on many ecological processes such as rainwater infiltration and evaporation, soil development, soil erosion, and vegetation succession, but they also act as primary producers and indicators of the cycles of carbon, nitrogen, and other main elements (Evans & Lange 2001; Wu et al. 2002; Guo et al. 2008). The occurrence and development of BSCs indicate that deserts transform from shift ones to fixed and semi-fixed ones and thus can be employed as indicators to evaluate whether an ecological environment is healthy or not (Chen 2007). Conversely, habitat destruction or fragmentation of BSCs leads to the reduction of biodiversity (Janisova et al. 2011).

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The international research on BSCs began in 1980s. In the past 10 years, it has become one hot research point in the fields of ecology, biology, and pedology. So far, there have been great numbers of studies done or being done worldwide (Appendix 1), which primarily focused on desert areas located in the middle latitudes (Appendix 2). In China, BSCs researches are mainly carried out in the Loess Plateau and the Gobi deserts, which distribute in the northwest, north, and northeast parts of China.

2. The characteristics of the development of BSCs

2.1 Process and composition

Soil crusts first experience physical soil crusts and then BSCs dominated by algae, lichens, and mosses (Duan et al. 1996; Li et al. 2000). During this process, shifting dunes generally become fixed ones (Xie et al. 2008). However, in irrigated areas, algae-dominated soil crusts can transform into moss crusts without the formation of lichen crusts (Hu et al. 2002). It is found that the color of BSCs was getting darker with their development because of their increased biomass production and higher concentrations of UV protective pigments. Six development levels of cyanobacteria crust are defined based on their soil surface darkness, which was suggested to be effective to assess its development level and soil stability (Belnap et al. 2008). BSCs consist of autotrophic organisms such as mosses, lichens, liverworts, cyanobacteria, chlorophytes or diatoms, and other eukaryotic algae as well as heterotrophic organisms including fungi, protists, bacteria, and archaea. Cyanobacteria, mosses, and lichens are the predominant components of BSCs (Shepherd et al. 2002; Lalley et al. 2006). The biomasses of BSCs are autotroph determined, but the major diversity sources of BSCs are their heterotrophic organisms (Bowker et al. 2009), which have been discussed much less despite their important role in the process of BSCs formation (Perotto et al. 2013).

BSCs are generally classified into moss, lichen, and cyanobacteria crusts according to their dominating compositions. Cyanobacteria crusts, as pioneer organisms for desert soils, excrete amylase to stabilize soil surface, and thereby to enhance their capacity of resistance to wind or water erosion (Zhou et al. 1995). In China, it is reported that 24 species of algae were found and isolated in the Tengger Desert (Hu et al. 2000), and 121 species, 4 phyla, 21 families, and 49 genera of algae were discovered in the Gurbantunggut Desert (Zhang et al. 2005). Lichens are complexes that algal cells are enveloped inside epiphyte mycelia (Trembley et al. 2002). Therefore, they are able to maintain their vigor in extremely droughty environments and renew their growth with fogs or dews available besides limited rainwater. Thus, soil water is not the key factor that restricts the growth of lichen crust (Feng & Zhang 2005). However, conservation measures are needed because lichens are poorly adapted to human disturbances and environmental changes (Nascimbene et al. 2012). Mosses with stems, leaves, and rhizoids are the lowest plant among high plants and they have relatively strong photosynthetic capacities. Most species of mosses are widely distributed in the cool environment with low trophic load (Ceschin et al. 2012). In the Tengger Desert, up to 16 species of mosses were found, isolated, and classified into two families and seven genera (Xu et al. 2005). Moss-dominated crusts comprise moss crust layer, inorganic sand layer, algae crust layer, and inorganic sand layer (Zhang et al. 2002). In the Loess Plateau, a total of 15 species of mosses were found in BSCs and they were classified into two families and eight genera (Meng 2011). The compositions of BSCs are very different between the Occident and China. In North American deserts, approximately 50 species of cyanobacteria, 52 species of mosses, and 34 species of lichens were described (Rosentreter et al. 2007). In Negev desert, a total of 87 species were identified from the 49 isolated genera (Grishkan et al. 2006). In the Tehuacan deserts of Central Mexico, 7 species of cyanobacteria, 19 species of mosses, and 8 species of lichens were found within the sampled soil crusts (Rivera-Aguilara et al. 2006). Most of the algae, lichens, and mosses are cosmopolitan whereas a few of them are endemic and regional (Belnap & Lange 2001). Although moss, lichen, and algae dominate BSCs organisms, it is difficult to find a crust of a single species because generally all kinds of organisms intermingle in the same field. Meanwhile, the compositions and functional performances of BSCs are very diverse worldwide because hydrothermal factors, soil fertilities, and other environmental factors that act on BSCs differ greatly. Currently, unlike higher plants, little is known on the diversities and functions of micro-organisms of BSCs. Therefore, it is much needed to conduct further studies on the mechanism of the formation of BSCs in order to understand the composition and the development process of BSCs in different areas.

2.2 Spatial distribution and influencing factors

BSCs can occur and expand in the frigid and tropical zones of semiarid and arid regions. Because of the different macroclimates and micro-environments that BSCs face, they present very complex structures and distributions. Continentally, temperature and rainfall exert the greatest influences on BSCs (Rogers 1972).

Regionally, soil types especially texture predominantly controlBSCs (Belnap & Lange 2001). Locally, BSCs are inhibited by vegetations because they directly compete with each other for light and moisture (Malam et al. 1999). It is suggested that micro-environmental factors including soil moisture, temperature, and organic matter content influenced the developments of BSCs more significantly than macro-environmental factors (Grishkan et al. 2006). Similarly, it is found that the micro-geomorphologies determined BSCs' community structures on a small scale (Li et al. 2010). In addition, soil pH and total potassium content are positively correlated with cyanobacterial and algal colonization in topsoil.

Soil moisture generally improves the development of BSCs. When dews, fogs, or temporary rainfalls happen to act as moisture sources during their wet and cool periods of time, BSCs on sand surface grow and expand fastest (Kidron et al. 2002). It is suggested that the BSCs under the canopy survive most easily due to the favorable conditions (higher soil moisture) produced by the vegetation (Petrou & Milios 2012). The distribution of BSCs correlated with the precipitation in the Gurbantunggut Desert, that is, algae mainly appeared in the northern part with low precipitation, and moss more commonly appeared in the southern part with high precipitation (Chen et al. 2005). For the lichen crust, however, the increase in the summer rainfall frequency had negative effects on their covering and richness in the Mojave Desert (Belnap et al. 2004). The result is similar to what is found in Utah deserts (Ustin et al. 2009). BSCs communities dynamically correspond with the drying-wetting cycles, but the morphologies and types of BSCs do not respond to them (Aguilar et al. 2009). Climatic and land-use changes cause later-succession soil crusts to transform into early – succession soil crusts characterized by lower C and N fixation rates (Housman et al. 2006). It is confirmed that different aridity degrees corresponded with different BSC successional stages (Zaady et al. 2010). Furthermore, it is proposed that the aridity degree could be used as ecosystem function indicators of BSCs in combination with other indicators related to them (Bowker et al. 2008).

BSCs are related to temperature changes. The coverage of nitrogen-fixing lichen *Collema* declined from 19% in 1996 to as low as 2% in 2003 due to an increase in monthly maximum temperature (Belnap et al. 2006). Besides, the distributions of BSCs are site dependent. For example, windward slopes of sand dunes are heavily dominated by cyanobacteria, whereas leeward slopes of them are covered by green algae. Lichen crusts mainly occur in lower slope parts of sand dunes and inter-dune areas. Moss species can only be found under the canopies of vascular plants (Zhang et al. 2007a).

Jointly affected by precipitation, soil properties, temperature, and morphology, the development of BSCs shows process periodicity, composition complexity, regional zonality, and plot scale differentiation. In addition, it is difficult to find BSCs with only moss, lichen, or algae in nature. Therefore, those findings related to the development characteristics and ecological functions of BSCs cannot be extrapolated to other geographic regions (Muscha & Hild 2006). For example, the results on the Wyoming sagebrush steppe differ from those on the Colorado Plateau and the Great Basin (Belnap & Gardner 1993; Muscha & Hild 2006). As to the BSCs in a specific region, a special study should be conducted to find out the mechanism of their formation and ecological functions.

3. Ecological functions

BSCs play a significant role in maintaining normal functions of ecosystems, such as involvement in soil formation, stability and fertility, C and N cycles, water and nutrient retention, preventions of soil erosions by water or wind, and colonization expansion of vascular plants and habitats (Evans & Lange 2001; Belnap et al. 2003; Li et al. 2006; Darby et al. 2007). BSCs can probably serve as a useful model system for differently oriented researches (Bowker et al. 2009). In addition, the morphologies of BSCs organisms are crucially important to investigate their activities and functions (Eldridge & Rosentreter 2000). To systematically study the multi-trophic and multi-function of BSCs enables rapid understanding of the consequences of soil biodiversity losses, and it helps improve a biodiversity-function theory (Bowker et al. 2009). Thus, long-term and spatial studies on BSCs are necessary to get the spatio-temporal dynamics of BSCs communities and the potential functional roles of BSCs in affecting highly biotically and abiotically variable environments.

3.1 *The improvement of soil fertility*

BSCs are capable of C and N fixation, acceleration of soil humus decomposition and soil development. In the past 10 years, the C and N fixations of BSCs have attracted many researchers' attention. It is estimated that the desert BSCs cover $27.7 \times 10^6\,km^2$ and contain 10×10^{15} g C (Saugier et al. 2001). A conservative estimation is provided that the cyanobacterial biomass in the deserts of the USA, which covers an area of $38.7 \times 10^6\,km^2$, consists of 56×10^{12} g C (Garcia-Pichel et al. 2003). On the basis of the simple precipitation-driven activity model, the inter-year variability in BSCs-related net carbon deposition ranges from 7 to 51 $kg\,ha^{-1}\,year^{-1}$ in the northern Negev Desert (BSCs area index of

$0.6\,m^2\,m^{-2}$), Israel (Wilske et al. 2009). Moreover, studies on the Colorado Plateau and Chihuahuan Desert showed that the retrograde of BSCs from their later successional stages to their early successional stages resulted in a sharp decrease in C and N inputs into the ecosystem (Housman et al. 2006).

C and N fixation capabilities of BSCs vary with their abundance, species composition, temperature, and hydration history (Jeffries et al. 1993a, b; Lange et al. 1998). It is estimated that incessant disturbances and climate changes can significantly reduce the contribution of BSCs to C and N fixations (Housman et al. 2006). High soil moisture is much more important to BSCs carbon deposition (Wilske et al. 2008). The net photosynthetic rates of the dark crusts are the highest when the soil water contents range from 40% to 60%. However, they decline at the temperatures >25°C in the frigid desert (Utah) and the temperatures >35°C in the tropical desert (New Mexico) (Grote et al. 2010).

The composition of BSCs is crucial to determine N input in a desert ecosystem. It is suggested that all types of BSCs have the highest nitrogenase activities (NAs) from June to October, and the NAs of algae crusts are higher than those of lichen crusts and moss crusts (Wu et al. 2009). Soil moisture increases probably cause BSCs to transform from complex types to relatively simple types, thus enhancing their ability of nitrogen fixation (Li et al. 2010). The studies on the Colorado Plateau highlands and the Sonoran Desert lowlands compared crusted and non-crusted soils. They found that no matter what climatic and geological scenarios existed, the four biogenic elements (C, N, P, and S) showed a statistically significant enrichment trend in the BSCs layer, and the 21 non-biogenic elements also showed a statistically significant depletion trend underneath BSCs (Beraldi-Campesi et al. 2009). It is proposed that the effects of BSCs and desert plants on soil microfauna are a combination of carbon inputs, microclimate ameliorations, and soil hydrology alterations (Darby et al. 2010). The colors of BSCs, which affect the temperature of the underlying soil due to their differentsurfacealbedo, can influence the decomposition of organic matter and C and N cycling (Cornelissen et al. 2007; Malam et al. 2009).

3.2 The reduction of erosion

At present, all studies show that BSCs can resist erosion by increasing soil stability regardless of their types. However, some researchers assumed that increased run-off probably resulted in rill erosion and caused much more erosion due to BSCs infiltration reduction (Bu et al. 2008). Many researches discussed the erosion control mechanism of BSCs. Chlorophyll *a*, exopolysaccharides (EPS) and the type and shape of organisms of BSCs are the main factors in erosion mitigation. It is proposed that chlorophyll *a* and EPS of BSCs strongly correlate with soil erodibility (Belnap et al. 2008). Other researchers found that chlorophyll *a* was a moderate to excellent soil stability predictor (R^2 0.21–0.75) and it always performed better than EPS in the Revised Universal Soil Loss Equation (RUSLE) (Bowker et al. 2008). Remote sensing techniques for BSCs highly improve soil erosion predictions by RUSLE and other erosion models, and they can even be used to map BSCs dynamic process (Chen et al. 2005). The strong relationship between the spectral signatures and chlorophyll *a* contents of various BSCs makes it feasible to estimate soil erosion by remote sense imagery (Karnieli et al. 1999). The morphologic types and continuities or discontinuities of BSCs organisms are likely to engage in the erosive forces and water redirection, and thus contributing to gains or losses in the sediment and infiltration run-off balance (Cornelissen et al. 2007). A study on the Loess Plateau showed that the proportion of moss in BSCs positively correlated with soil erodibility in a significant degree (Bu et al. 2009).

Similarly, BSCs decrease wind erosion depending on their types, structures, and development levels. BSCs could significantly increase the starting wind speed. No wind erosion was observed under BSCs coverage even if the wind speed ranged from 25 to $30\,m\,s^{-1}$, while the threshold of starting speed of wind erosion for the non-crusted soil was only $8.42\,m\,s^{-1}$. The effects of different types of BSCs on the threshold of starting speed of wind erosion are ranked as follows: moss > lichen > algae (Wang et al. 2004). In the wind tunnel experimentation, it was found that BSCs also increased friction wind velocity and aerodynamic roughness length of soil besides the starting threshold (Zhang et al. 2008). BSCs reduce wind erosion by binding small particles together into larger ones and then they form a consolidated layer (Hu et al. 2002). The mechanisms can be explained in three aspects: physical binding of soil particles and entangling filaments, adhesion to mucilaginous sheaths or slime layers excreted by cyanobacterial trichomes, and attachments of particles to sites along cell walls of cyanobacteria (Danin et al. 1989).

4. The points of controversy

4.1 The relationship between BSCs and vegetation

BSCs significantly affect seed dispersal, germination, and the establishment of vascular plants, and the effects are observed to be either beneficial or inhibitory (Serpe et al. 2006).

BSCs facilitate seedling emergences by increasing soil moisture (Li et al. 2005; Nie et al. 2009), organic matter, and nutrient contents (Belnap & Gardner 1993). Studies suggested that BSCs accelerated seed germination and thereby benefiting vegetation succession (Boeken et al. 2004). A little disturbance of BSCs in the abandoned land causes an increase in the height and richness of vegetation (Vassilev et al. 2011). The greenhouse experiment showed that BSCs, regardless of their ages or conditions, promoted seed germinations of three native species in the hyper-arid region of the Tengger Desert in China (Su et al. 2009). However, more field and laboratory experiments were still needed to determine the factors responsible for these positive effects.

Conversely, the inhibitory effects of BSCs on vascular plant species are reported in arid regions and temperate areas because BSCs generally lead to the absence of suitable micro-relief structures of mechanical stability and insufficient moisture for seed germination (Beyschlag et al. 2008). The inhibitory effects of BSCs are species dependent, and late succession BSCs are less favorable for plant compared with early succession BSCs (Langhans et al. 2009). Under certain circumstances, shrub canopies can protect BSCs from disturbance and create shades for them, and thus enhancing their growth (Belnap et al. 2003). For example, in the Wyoming sagebrush steppe, moss and lichen covers are more abundant under shrub canopies than between the canopies (Belnap & Gardner 1993; Muscha & Hild 2006). Similarly, BSCs under grasses develop three times as much as those in the interspace of grass plants because grasses can provide favorable micro-sites to facilitate crust establishment and development (Jimenez et al. 2009). Microcracks and fissures on BSCs surface are believed to provide seeds with safe sites to be lodged and trapped (Boeken et al. 2004).

Many researchers studied allelopathic effects between plants and BSCs in order to understand the underlying mechanisms. For example, cyanobacteria can produce a few secondary products that have negative allelopathic effects on seed germination (Zaady et al. 1997; Prasse & Bornkamm 2000). Some studies inferred that the effects of mosses on seed germinations of two grass species were compromised by allelopathic compounds, whereas others found an opposite phenomenon that those products encouraged seed germinations (Van Tooren 1990; Hu et al. 2002). There are significantly more seeds of *Artemisia ordosica* and *Bassia dasyphylla* germinating in living moss crusts than in dead moss crusts and it is probably because of the secondary products of mosses (Equihua & Usher 1993). Due to the complex relationship between BSCs and vegetation, the combination of diverse approaches that takes into account various groups of organisms in the ecosystem is needed (Janisova et al. 2011).

4.2 The effects of BSCs to evaporation

The evaporation of BSCs can be divided into two stages: the stable stage at which BSCs increase soil evaporation and the evaporation-decreasing stage at which BSCs restrain soil evaporation (Zhang et al. 2007b). Similar findings indicated that the maximum water absorption and withering humidity of BSCs were higher than those of the bare soil, as a result the soil evaporation rate reduced (Brotherson & Rushforth 1983). It is proposed that BSCs will not change soil evaporation tremendously because their initial decreasing effects are counterbalanced by their final increasing effects (Xiao et al. 2010). Although the evaporation rate of BSCs significantly decreased at the beginning of evaporation, it kept at a high value for a long time later. The “evaporation promotion” mainly resulted from the increase in potential evaporation heat on soil surface due to BSCs’ darker colors (Li et al. 2005). Furthermore, BSCs can easily intercept 10–40% of precipitation and prevent rainwater from penetrating into soil, and thereby it can increase the possibility of evaporation (Li et al. 2002). In addition, soil water consumption contains BSCs transpiration besides soil evaporation. But so far, few studies have been conducted on BSCs transpiration yet.

4.3 The influences of BSCs on infiltration/runoff

The BSCs are observed to have positive, negative, and neutral effects on infiltration and run-off in the fields. In some cases, BSCs covering soils have lower infiltration rates than those of bare soils (Eldridge et al. 2000; Li et al. 2002). On the other hand, BSCs produce positive or no effect on water infiltration into soil (Belnap & Gardner 1993; Williams et al. 1999). For example, it was found that BSCs significantly restrained water infiltration, caused soil drought and accelerated vegetation degeneration, so that appropriate disturbance measures should be taken to improve soil water environments (Lv & Yang 2004; Ma et al. 2007).

Most recent studies indicated that the discrepancies of BSCs’ effects on infiltration and evaporation resulted from the interactions of methodological approaches, rainfall characteristics, soil factors, and the biological composition of BSCs (Warren 2001; Yair 2001; Belnap 2006). Bacterial filaments including polymers of hydrophilic and hydrophobic molecules with adhesive properties, and number of microbial pores, the micro-morphologies and spectacular pores of cyanobacterial crust should play a significant role in the soil water regime (Malam et al.

2009). 2D porosity study showed that BSCs had better developed pore-systems characterized by specific meso-macropore morphologies with BSCs lower infiltration (Miralles-Melladoa et al. 2011). It was found that in the Loess Plateau, the water-storage capacities of different BSCs were ranked in the order of moss > lichen > algae > non-crusted soil (Wang et al. 2009). A similar phenomenon was also reported in the Horqin Desert (Guo et al. 2008).

Run-off amount is adversely related to infiltration amount in a slope plot. For the cyanobacteria crust with abundant hydrophobic polymers to prevent from quick wetting, the final run-offs increased with the thickness of BSCs (Malam et al. 2009). Although the run-off-repelling effect of the polymers ceased while BSCs became wet, the water-holding capacities of cyanobacterial polysaccharides still lead to more run-off (Malam et al. 2009).

4.4 *The effects of BSCs on dew condensation*

In the Negev Desert of Israel, BSCs adapt themselves to exploit dew and fog water to form nearly mature sexual organs (Kidron et al. 2002). Moss crust with complex morphologies and high roughness can capture dew and water vapor from atmosphere at lower temperatures in the night (Zhang et al. 2009).

Although numerous studies have been conducted on BSCs, the hydrologic processes that occur on the surfaces of BSCs still remain unclear (Belnap 2006). At least three aspects are involved in the mixed research on BSCs, which are soil factors (e.g. texture, aggregate stability, and porosity), the feature of BSCs (e.g. type, biomass, surface roughness, hydrophilic, or hydrophobic characteristics), and the research methods. More experiments are needed in the future to find out when these factors have positive, negative, or neutral effects and to further clarify the mechanism of BSCs.

5. The conclusions and perspectives

BSCs, with a number of biotic or abiotic factors affecting them, are characterized by developmental complexity and spatial heterogeneity. They are widely distributed in the arid and semiarid areas, and perform important ecological functions in the ecosystems. BSCs not only have positive effects such as preventing soil erosion and improving soil fertility, but they also have probable negative influences such as promoting soil evaporation, restraining rainwater infiltration, and eventually reducing soil moisture. Meanwhile, the relations between BSCs and vegetations appear much more complex in nature. On the basis of the review above, the following research aspects of BSCs need to be highlighted:

(1) To promote BSCs researches in different climatic regions of the world and to understand the developmental characteristics and formation mechanisms of BSCs in all the typical BSC-distributing areas are important supplements to the global BSCs researches. Both in the tropical and frigid zones of the arid and semiarid regions, to comprehend the development and formation mechanism of BSCs at different succession stages in all typical BSC-distributing areas will help find out the influence of BSCs on the ecosystems and explore if there exist a probable zonality for them, and eventually clarify the existing controversial points.

(2) To determine what impacts BSCs have on erosion, soil moisture, and plants in different environments, and how they respond to disturbances will allow BSCs resources to be properly managed. BSCs can perform positive ecological function and probably also have negative influences on soil moisture and vegetation succession. Under this circumstance, exploring the responses of BSCs to anthropogenic disturbances and global climate change is crucial to utilize BSCs resources effectively, reduce their negative effects, and improve their positive effects.

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Appendix 1

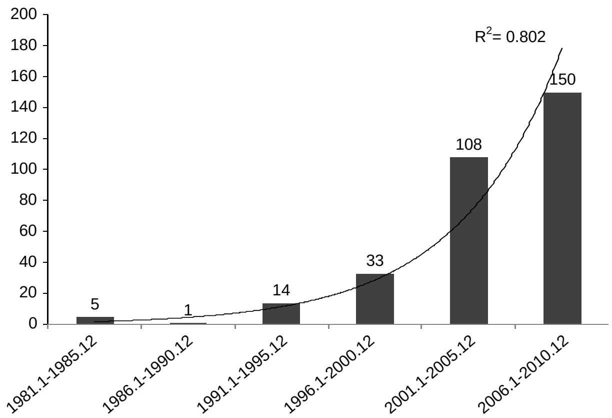

Figure A1. The amounts of journal articles published relating BSCs during 1981–2010

Note: Papers with cyanobacterial soil crust, biotic crust, BSC, soil microbial crust, biogenic soil crust, microbiological soil crust, cryptobiotic soil crust within the title were searched from the Arizona State University Library in the USA in November 2011.

Appendix 2

Table A2. Major BSCs study areas in different countries around the world from 1991 to 2010

Continent	Country	Study area	Continent	Country	Study area
Asia	China	Loess plateau	North America	USA	Colorado plateau
		Gurbantunggut desert			Sonoran desert
		Tengger desert			Mojave desert
		Horqin desert			Chihuahuan desert
		Inner Mongolian steppe			Great Basin desert
		Mu Us desert			Florida shrubland,
Europe	Israel	Negev desert			Massachusetts
	Spain	Southeast Spain			seashore, Oregon
Oceania	Australia	West desert			prairies, Wyoming
Africa	Namibia	Namib desert			steppe, Ohio,
	Botswana	Kalahari desert			Michigan sand,
Antarctica		Glacier foreland			New Mexico