Environ Earth Sci (2013) 68:1099–1105
DOI 10.1007/s12665-012-1811-z

ORIGINAL ARTICLE

Influence of vegetation factors on biological soil crust cover on rehabilitated grassland in the hilly Loess Plateau, China

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Received: 3 April 2011 / Accepted: 18 June 2012 / Published online: 14 July 2012

Abstract Biological soil crusts (BSCs) perform essential ecosystem functions in arid and semi-arid ecosystems worldwide. The formation, development, and distribution of BSCs are influenced by changes in multiple environmental factors, including changes in the vascular plant community. The influence of changes in vegetation factors on BSC cover in 8-, 12-, and 16-year-old rehabilitated grasslands were studied in the hilly area of the Chinese Loess Plateau. The rate of degradation of BSCs underneath litter ($P < 0.01$) and the degradation cover of BSCs ($P < 0.05$) differed significantly between the 8- and 16-year-old successions. Stepwise multiple linear regression analysis showed that the main vegetation factors influencing the dynamics of BSC cover differed among the 8-, 12-, and 16-year-old rehabilitated grasslands. Basal cover, phytomass, and litter cover were the main vegetation factors influencing the dynamics of BSC cover on 8-year-old rehabilitated grassland. Phytomass, litter thickness, and litter cover were the main factors influencing the dynamics of BSC cover on 12-year-old rehabilitated grassland. On 16-year-old rehabilitated grassland, Pielou evenness index, litter thickness, and litter biomass were the main vegetation factors influencing degradation of BSC cover underneath litter, whereas basal cover, litter thickness, and litter biomass were the main vegetation factors influencing the degradation cover of BSCs. At particular stages of herbaceous succession, vegetation factors can have a large influence on changes in the community's basal cover and litter, which are key factors influencing changes in BSC cover. The degradation of BSCs underneath litter may be a result of complicated eco-physiological processes.

Keywords Basal cover · Degradation · Herb · Litter · Moss · Succession

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Introduction

Biological soil crusts (BSCs) are assemblages of bryophytes, lichens, algae, cyanobacteria, and fungi that exist at the soil surface and are a prominent feature of arid and semi-arid ecosystems worldwide (Read et al. 2008). These communities are essential parts of ecosystems (Belnap and Lange 2003), because they influence soil stability (Williams et al. 1995; Belnap and Gillette 1998), soil fertility (Hawkes 2003; Housman et al. 2006), and local hydrology (George et al. 2003; Ram and Aaron 2007), as well as the germination, survival, and nutritional status of vascular plants (Prasse and Bornkamm 2000; Su et al. 2007; Langhans et al. 2009). In deserts, BSCs can completely cover the soil surface in large interplant spaces and are often the dominant living cover (Belnap et al. 2006). BSCs also exist in large areas of the hilly region of the Chinese Loess Plateau (Cai et al. 1998). Implementation of the Grain for Green project in this area is expected to provide conditions suitable for the formation and development of BSCs (the Grain for Green project is a state campaign to restore ecological balance in the country's western parts, including the Loess Plateau region, by converting the low-yielding farmlands on slopes of 25° or more back into forests or pastures). Farmers who participate in the project receive subsidies from the government in the form of grain or money (Zhao et al. 2010a); indeed, BSCs are now developing well over most of this area and are becoming very common in the landscape (Zhao et al. 2006). BSCs will play an important role in the ecosystem in this region.

The formation, development, and distribution of BSCs are influenced mainly by topography, water, soil properties, disturbance, type of vascular plant community, and type of microhabitat (Belnap and Lange 2003; Belnap et al. 2006; Bowker et al. 2005; Chen et al. 2006; Eldridge and Tozer 1997; Muscha and Hild 2006; Rivera-Aguilar et al. 2009; Thompson et al. 2005). In the dry lands of Mexico, BSCs are positively correlated to soil apparent density and lichen is also positively correlated with pH, but is not significantly correlated with sun exposure (Rivera-Aguilar et al. 2009). Rainfall and light intensity are the main factors affecting the biomass of human-made algal crusts in Inner Mongolia, China (Chen et al. 2006). The detrimental effects of grazing livestock on BSCs have been documented in places such as the Great Basin in North America (Marble and Harper 1989) and the deserts of south-western USA (Beymer and Klopatek 1992). Therefore, different key factors may affect the formation, development, and distribution of BSCs in different regions.

The study of BSCs has come to interest researchers since the implementation of the Grain for Green project on the Chinese Loess Plateau. There have been some studies of the distribution of BSCs (Chen et al. 2005; Jiao et al. 2007) and of the effects of BSCs on soil physicochemical properties in this region (Zhao et al. 2006; Xiao et al. 2008, 2010). However, because BSCs are widespread in the hilly Loess Plateau, concerns have arisen about their degradation and decline (as evidenced by moss tissue necrosis and mortality) underneath litter accumulated in the rehabilitated grassland. What factors have caused this phenomenon? The objective of this research was to examine the relationship between vegetation factors and the degradation of BSCs and also to provide an understanding the process of succession between BSCs and the vascular plant community in this region.

Materials and methods

Study area

The study area was located in the County of Ansai (36°31′–37°20′N and 108°52′–109°26′E) in the middle of the loess plateau in northern Shaanxi Province, China. This area is well known for its high erosion rate. Ansai County has a typical semiarid continental climate with an average temperature of 8.6 °C and an average annual precipitation of 500 mm, with high variability (about 74 % of the rain falls between July and September). The landform is a typical loess hilly-gullied landscape with elevations ranging from 997 to 1,731 m above sea level (most of the land is at 1,200–1,500 m). The soils have developed on wind-deposited loess parent material and are classified as Calcic Cambisols (Wang et al. 2003). They are yellow, with an absence of bedding and a silty texture, with looseness, macroporosity, and wetness-induced collapsibility (Jiao et al. 2008).

Survey methods

To study the relationship between vegetation factors and degradation of BSCs in rehabilitated grasslands, quadrats were set up in successions of three different ages: 8-year-old (Q8, *Heteropappus altaicus* + *Artemisia capillaris*), 12-year-old (Q12, *Potentilla bifurca* + *Lespedeza davurica*), and 16-year-old (Q16, *Stipa bungeana* + *Cleistogenes squarrosa*), respectively. In this region, BSCs gradually form moss from 4 to 8 years after the start of grassland rehabilitation (Zhao et al. 2006). Litter begins to accumulate after this time. We randomly selected twenty 0.5 × 0.5 m quadrats within each succession site. Within each quadrat, plant species name; number of plants; plant height; plant basal cover and cover; aboveground biomass; litter cover, biomass, and thickness; and BSC cover and thickness were measured. All biomass samples were first dried to a constant weight at 60 °C in the laboratory. The basal diameter of each species was measured with calipers.

Calculation of species diversity of vegetation

$$\text{Relative frequency} = (\text{frequency value for a species})/(\text{total off requency for all species}) \times 100 \quad (1)$$

$$\text{Relative density} = (\text{density for a species})/(\text{total of density for all species}) \times 100 \quad (2)$$

$$\text{Relative cover} = (\text{totalofintercept lengths for a species})/(\text{total of intercept lengthsfor all species}) \times 100 \quad (3)$$

$$\text{Importance value (IV)} = (\text{relative frequency} + \text{relative cover} + \text{relative density})/3 \quad (4)$$

Species diversity was calculated from the following formula:

$$\text{Shannon} - \text{Wienerindex}\, H' = -\sum_{i=1}^{s} p_i \ln p_i \quad (5)$$

$$\text{Pielou evenness index}\, J = H'/\ln S \quad (6)$$

$$\text{Margalef richness index}\, D = (S-1)/\ln N \quad (7)$$

In the aforementioned equations, where S is the number of species, N the number of individuals of all species, and p_i is the proportion of the importance value of individuals per species i in the community made up of S species with known proportions p_1, p_2, p_3, …, p_s (Hegazy et al. 1998).

Calculation of BSC degradation indexes

In the rehabilitated grassland of the hilly region of the Loess Plateau, BSCs tend to completely cover the soil in the large interplant spaces in most arid areas (Belnap et al. 2006), and they colonize the soil surface before perennial herbs in the sequence of vegetation succession. To reflect the relationship between BSCs and vegetation factors of around 10-year-old rehabilitated grassland in this region, the three formulas listed below were defined to calculate BSC degradation indicators at the site scale:

$$D_{\text{rate}} = S_{\text{Dr}}/S_{\text{litter}} \times 100\,\% \quad (8)$$

$$C_{\text{litter}} = S_{\text{Dr}}/S \times 100\,\% \quad (9)$$

$$C_{\text{BSCs}} = S_{\text{Bc}} + S_{\text{Dr}} \quad (10)$$

where D_{rate} is the rate of degradation of BSCs underneath litter, S_{Dr} the area of degraded BSCs underneath litter, S_{litter} the area of litter, C_{litter} the cover of degraded BSCs beneath litter within the quadrat, S the quadrat area, C_{BSCs} the total cover of degraded BSCs in the quadrat area, and S_{Bc} is the basal area of the vegetation community in the quadrat. In these equations, D_{rate} reflects the extent of BSC degradation caused by the presence of litter, C_{litter} reflects the proportion of degraded BSCs caused by the presence of litter, and C_{BSCs} reflects the area of BSC degradation influenced by vegetation.

Statistical analysis

One-way ANOVA and LSD multiple comparisons of means were performed to determine significant differences among the variables measured at the different sites. Stepwise multiple linear regression models were used to determine correlations among dependent variables (BSCs degradation indicators) and independent variables (vegetation factors). A path analysis was used to infer the direct and indirect impacts of the various factors on the indicators of BSCs degradation. All statistical analyses were performed using the software program SPSS 12.0.

Results

Dynamics of vegetation factors

During the secondary succession on the rehabilitated grassland, BSC succession was accompanied by the succession of herbaceous communities under the same site conditions. The interaction between BSCs and herbaceous communities was complex and multifaceted. Table 1 shows the differences at 8, 12, and 16 years in the vegetation and BSC factors of the rehabilitated grasslands. The change in herbaceous communities was significant in this succession process. Most of vegetation factors were continuing to increase with early stages of succession process, including Shannon–Wiener index, Pielou evenness index, basal cover, vegetation cover, phytomass, and litter cover. BSC thickness was increasing with stand age, but BSC cover has a significantly decreasing. During this succession process, D_{rate} (the rate of degradation of BSCs underneath litter) was significantly lower at Q16 than at Q12 ($P < 0.01$). The difference in D_{rate} may be related to different environmental condition of the plants and litter in different periods.

Factors influencing degradation of BSCs

From the stepwise multiple linear regression analysis, three explanatory variables were selected from a total of 11 vegetation factors that were significantly associated with the indicators of BSCs degradation (namely C_{litter} and C_{BSCs}), excluding highly correlated ones [i.e. with an R^2 close to 1 and an adjusted coefficient of determination value (R_a) close to 1]. Variance analysis of the optimal regression equation for each site showed that the F value was significant at $P < 0.01$ in all equations. The results (Table 2) showed that (1) at Q8, basal cover, phytomass, and litter cover were the main factors influencing C_{litter} and C_{BSCs}; (2) at Q12, phytomass, litter cover, and litter thickness were the main factors influencing C_{litter} and C_{BSCs}; and (3) at Q16, Pielou evenness index, litter thickness, and litter biomass were the main factors influencing C_{litter}, and basal cover, litter thickness, and litter biomass were the main factors influencing C_{BSCs}.

Correlation among factors influencing degradation of BSCs

The results of a path analysis (Fig. 1) showed that the effects of the explanatory variables on the indicators of BSC degradation could be divided into direct and indirect effect coefficients. This reveals the relative importance of the variables in explaining indicators of BSC degradation (namely, C_{litter} and C_{BSCs}). The results showed that (1) at Q8, basal cover was negatively correlated with C_{litter} and

Table 1 Environmental factors (independent variables X1–X11) potentially related to the indexes of degradation of biological soil crust cover (dependent variables Y1 and Y2) for rehabilitated grassland successions of three different ages (8, 12, and 16 years) on the hilly Loess Plateau, China

Factors	Variable	Site		
		Q8	Q12	Q16
Vegetation factors				
Shannon–Wiener index (H')	X1	0.547 (0.12)^{A}	0.568 (0.18)^{A}	0.700 (0.13)^{B}
Pielou evenness index (J)	X2	0.641 (0.14)^{A}	0.743 (0.14)^{B}	0.798 (0.08)^{B}
Margalef richness index (D)	X3	4.253 (1.26)^{ab}	3.995 (1.35)^{a}	4.871 (1.23)^{b}
Basal cover (%)	X4	2.10 (1.11)^{A}	2.82 (2.78)^{A}	9.61 (5.29)^{B}
Vegetation cover (%)	X5	14.35 (10.17)^{A}	20.96 (6.88)^{AB}	25.78 (17.47)^{B}
Phytomass (g/m^2)	X6	46.46 (17.55)^{A}	85.93 (94.28)^{AB}	105.20 (33.66)^{B}
Litter cover (%)	X7	13.47 (6.99)^{A}	19.59 (15.16)^{AB}	24.53 (11.27)^{B}
Litter thickness (mm)	X8	12.50 (5.11)^{ab}	13.96 (6.34)^{a}	11.13 (4.04)^{b}
Litter biomass (g/m^2)	X9	77.36 (25.11)	90.99 (50.34)	88.21 (34.04)
BSC thickness (mm)	X10	11.31 (2.91)	11.52 (2.07)	12.03 (1.85)
BSC cover (%)	X11	88.60 (1.91)^{a}	81.49 (2.77)^{ab}	79.14 (5.56)^{b}
BSC degradation indicators				
D_{rate}		55.00 (23.83)^{AB}	70.15 (20.45)^{B}	46.65 (27.16)^{A}
C_{litter} (%)	Y1	7.98 (6.04)	14.41 (12.79)	10.32 (10.91)
C_{BSCs} (%)	Y2	10.08 (6.39)^{a}	17.23 (13.82)^{ab}	19.67 (12.98)^{b}

Values are given as means of 20 replicates in each point. Values in parenthesis are standard deviation. Different capital letters and lowercase letters within a row indicate significant difference at $P < 0.01$ and $P < 0.05$, respectively

Table 2 Multiple linear regression equations for the prediction of degradation indicators of biological soil crusts from vegetation factors at three sites of different age since the start of rehabilitation of grassland on the Loess Plateau, China

Site	Stepwise multiple linear regression equation	Adjusted R^2 R_a	Coefficient of determination R^2	F value	Durbin–Watson statistic (d)
Q8	$C_{litter} = -4.9617 - 2.4978$ X4 $+ 0.2239$ X6 $+ 0.5782$ X7	0.9740**	0.9568	118.1204**	2.3683**
	$C_{BSCs} = -4.9617 - 1.4978$ X4 $+ 0.2239$ X6 $+ 0.5782$ X7	0.9768**	0.9614	132.9093**	2.3683**
Q12	$C_{litter} = -7.9495 + 0.0479$ X6 $+ 0.4905$ X7 $+ 2.1830$ X8	0.9658**	0.9433	88.7644**	1.8600**
	$C_{BSCs} = -2.5112 + 0.0588$ X6 $+ 0.4273$ X7 $+ 0.0694$ X8	0.9612**	0.9359	77.9131**	2.2753**
Q16	$C_{litter} = -39.7541 + 25.7180$ X2 $+ 4.5571$ X8 $+ 0.1787$ X9	0.9121**	0.8585	32.3582**	1.5250**
	$C_{BSCs} = -21.5484 + 1.2504$ X4 $+ 3.55095$ X8 $+ 0.2092$ X9	0.9193**	0.8696	77.9131**	1.6185**

** $P < 0.01$

C_{BSCs}, and phytomass and litter cover were positively correlated with C_{litter} and C_{BSCs} (Fig. 1a, b); (2) at Q12, phytomass, litter cover, and litter thickness were positively correlated with C_{litter} and C_{BSCs}(Fig. 1c, d); and (3) at Q16, the Pielou evenness index, litter thickness, and litter biomass were positively correlated with C_{litter}, and basal cover, litter thickness, and litter biomass were positively correlated with C_{BSCs} (Fig. 1e, f).

Discussion

BSCs perform vital ecosystem functions in the process of vegetation secondary succession on the Grain for Green land of the loess region of China. These services include soil stabilization and reduction of soil erosion; nitrogen and carbon fixation; supply of nutrients for vascular plants; filling of vacant niches; and ecosystem enrichment (Belnap and Gillette 1998; Cai et al. 1998; Housman et al. 2006; Williams et al. 1995; Zhao et al. 2006). However, the formation, development, and distribution of BSCs are influenced by changes in multiple environmental factors, and these changes affect the rate and type of BSCs ecosystem services. We demonstrated here that the cover dynamics of BSCs are influenced by vegetation factors in the process of vegetation secondary succession. The degradation or degeneration of BSCs underneath the litter is also of concern.

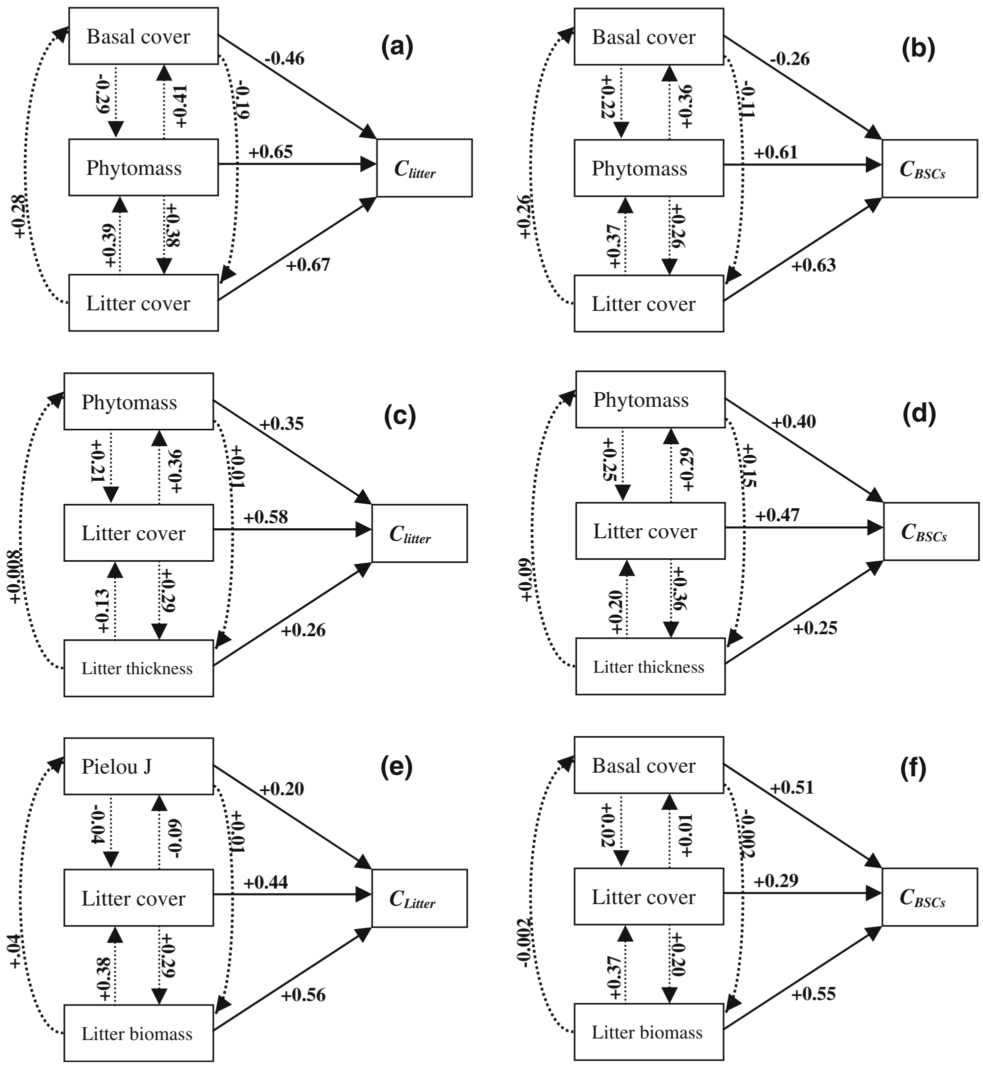

Fig. 1 Results of a path analysis of the influence of vegetation factors on indicators of BSC degradation. Direct and indirect impacts of three explanatory variables on **a** C_{litter} and **b** C_{BSCs} at site Q8, **c** C_{litter} and **d** C_{BSCs} at site Q12, and **e** C_{litter} and **f** C_{BSCs} at site Q16 are shown. *Solid arrows* direct effects, *dotted arrows* indirect effects; *numbers* are correlation coefficients between the two variables joined by an arrow, with the variable at the base of the arrow being the independent variable

The process of secondary succession on rehabilitated grasslands

During the early stage of secondary succession on the rehabilitated grasslands, the change of community composition is very remarkable, and plant traits are diverse. In this region, the vegetation at Q8 was composed of annual (*Artemisia scoparia*) and perennial herbs (*H. altaicus*), which by Q12 had given way to perennial herbs (*P. bifurca* and *L. davurica*); at Q16 the vegetation in turn had changed to a herbaceous perennial Poaceae association (*S. bungeana* and *C. squarrosa*). Many aspects of the vegetation environment of the BSCs therefore changed. Perennial herbage species gradually took advantage of communities and the Shannon–Wiener index and Pielou evenness index gradually increased, although the *Margalef* richness index showed a V-shaped change. Basal cover increased at Q16 because the perennial *Gramineae* herbage association became the dominant species in this community. Vegetation cover and phytomass also increased with time, as did litter cover. The composition and amount of litter changed vastly because of the changes in the community composition. The thickness and biomass of litter first increased and then declined with time (Table 1).

BSCs are potentially important in secondary succession in arid and semi-arid ecosystems worldwide (Bowker 2007). At our study sites, cyanobacteria-dominated crusts (light gray and less than 1 mm thick) form quickly (within 1 year) after rehabilitation starts (Zhao et al. 2010a). By about the third year, BSCs gradually develop from algaedominated crusts to moss and lichen crusts (increasing in color, height, and species richness). Mosses become dominant by about the 10th year. After 10 years, the thickness of BSCs stabilizes but species composition may gradually continue to become more complex. Eventually, BSC cover declines as vegetation succession progresses (Zhao et al. 2006).

Vegetation factors influence on BSC cover

The interaction between BSCs and vascular plants may be a very complex and dynamic ecological process during succession (Bowker 2007). The dynamics of BSC cover are probably related to plant community composition, plant traits, and litter accumulation (Belnap and Lange 2003; Bowker 2007). Because the biological properties of plants differ from species to species, the different vegetation communities at different stages of succession may have very different effects on the BSC cover. Our stepwise multiple linear regression analysis showed that the main vegetation factors influencing the BSC cover differed between the different successional stages. Basal cover increased from 2.1 % at the Q8 site to 9.6 % at the Q16 site and was negatively related to the BSC degradation indexes (C_{litter} and C_{BSCs}) at Q8 site but positively related to C_{BSC} at the Q16 site. Basal cover is usually increased by the presence of species such as *Sonchus arvensis*, *Lxeris denticulata*, and *Viola philippica.* At the Q8 site, those species were present with a relatively large basal diameter and more individuals per square meter but smaller phytomass than the dominant species, *A. scoparia* and *H. altaicus*. Therefore, an increase in basal cover is likely to mean an increase in the proportion of these species and a decrease in phytomass, which will contribute to litter accumulation (80 % of the degradation of BSC cover was associated with degraded BSC cover underneath litter at the Q8 site). At the Q16 site, the perennial Poaceae herbage (*S. bungeana* and *C. squarrosa*) had clearly increased in basal cover, which accounted for nearly 50 % of the degradation of BSC cover. Although the presence of BSCs modifies soils in ways that can affect the germination, emergence, and survival of vascular plants (Belnap and Lange 2003), the effect of vascular plants on BSC cover may be more obvious among different vegetation communities (Zhao et al. 2010b), including those undergoing succession.

Litter cover may affect the growth of underlying BSCs and lead to a change in BSC cover. Previous studies have reported that litter acts as a historical factor linking interactions across successive generations (Facelli and Pickett 1991), affecting species composition and diversity during succession (Facelli and Pickett 1991; Xiong and Nilsson 1999; Jensen and Gutekunst 2003), and is negatively related to BSC cover (Belnap et al. 2006; Eldridge et al. 2006; Briggs and Morgan 2008). The phenomenon of degradation of BSCs underneath litter may be the result of complex physiological and ecological processes in this study area. The microhabitat of BSCs may change with litter accumulation as follows: microclimate may be affected by physical obstruction, light interception, and changes in soil temperature and moisture (Facelli and Pickett 1991; Xiong and Nilsson 1999; Jensen and Gutekunst 2003); soil properties can be affected by the release of phytotoxic compounds from decomposing litter (Facelli and Pickett 1991; Xiong and Nilsson 1999); and microbial composition and structure may change. However, elucidation of the relative roles of such detailed mechanisms is beyond the scope of this study. In this region, the degradation of BSC cover underneath litter did not differ significantly between the different successional stages, but litter cover accounted for about 50–80 % of the degradation of BSC cover. Therefore, litter accumulation on the areas between plants may be an important factor, not only for development of the plant community (Xiong and Nilsson 1999), but also for the dynamics of the BSCs underneath the litter.

Conclusions

Changes in the types of herbaceous species and their projected cover, basal cover, and biomass, as well as in the composition, biomass, and cover of litter, all influence the dynamics of BSC cover during the process of herbaceous community succession on the Loess Plateau in China. At any particular stage of vegetation succession, vegetation factors have a major influence on the community basal cover and litter, which in turn are key factors influencing BSC cover. Degradation of BSCs underneath litter may occur through complicated eco-physiological processes that influence the dynamics of BSC cover.

Acknowledgments The authors thank the Strategic Technology Project of CAS (XDA05060300) for funding this research, and acknowledge the assistance of the Ansai Ecological Experimental Station of Soil and Water Conservation, CAS. The authors also thank Dr. Takeshi Taniguchi and two anonymous referees who gave valuable comments on early versions of the manuscript.

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