REVIEW

Biological Soil Crust Rehabilitation in Theory and Practice: An Underexploited Opportunity

Matthew A. Bowker[1,2]

Abstract

Biological soil crusts (BSCs) are ubiquitous lichen–bryophyte microbial communities, which are critical structural and functional components of many ecosystems. However, BSCs are rarely addressed in the restoration literature. The purposes of this review were to examine the ecological roles BSCs play in succession models, the backbone of restoration theory, and to discuss the practical aspects of rehabilitating BSCs to disturbed ecosystems. Most evidence indicates that BSCs facilitate succession to later seres, suggesting that assisted recovery of BSCs could speed up succession. Because BSCs are ecosystem engineers in high abiotic stress systems, loss of BSCs may be synonymous with crossing degradation thresholds. However, assisted recovery of BSCs may allow a transition from a degraded steady state to a more desired alternative steady state. In practice, BSC rehabilitation has three major components: (1) establishment of goals; (2) selection and implementation of rehabilitation techniques; and (3) monitoring. Statistical predictive modeling is a useful method for estimating the potential BSC condition of a rehabilitation site. Various rehabilitation techniques attempt to correct, in decreasing order of difficulty, active soil erosion (e.g., stabilization techniques), resource deficiencies (e.g., moisture and nutrient augmentation), or BSC propagule scarcity (e.g., inoculation). Success will probably be contingent on prior evaluation of site conditions and accurate identification of constraints to BSC reestablishment. Rehabilitation of BSCs is attainable and may be required in the recovery of some ecosystems. The strong influence that BSCs exert on ecosystems is an underexploited opportunity for restorationists to return disturbed ecosystems to a desirable trajectory.

Key words: aridlands, cryptobiotic soil crusts, cryptogams, degradation thresholds, state-and-transition models, succession.

Introduction

Biological soil crusts (BSCs) are communities of diminutive but important organisms that may include lichens, mosses, liverworts, cyanobacteria, and others, which are intimately associated with the mineral soil surface, creating a cohesive thin horizontal layer. These communities are common in ecosystems with high light input at the soil surface, such as the world's drylands (approximately 40% of terrestrial ecosystems), but occur at least as ephemeral successional seres in most other terrestrial ecosystems of the world. In stark contrast to physical crusts (Mando et al. 1994), BSCs enhance soil quality by (1) aggregating soil particles, thereby reducing wind and water erosion (Mazor et al. 1996); (2) increasing soil surface temperature (Gold & Bliss 1995); (3) modifying the water run-off infiltration balance, shuttling run-off to run-on zones in some cases (Kidron & Yair 1997), and increasing infiltration in others (Brotherson & Rushforth 1983); and (4) increasing soil fertility by N and C fixation (Evans & Ehleringer 1993; Lange et al. 1994). Consequently, BSCs are used as an indicator of rangeland or soil health (Tongway & Hindley 1996; Pellant et al. 2000).

Despite thousands of increasingly international studies documenting the important roles of these organisms (Belnap & Lange 2003), BSCs are rarely discussed in the restoration literature. I examined every article and commentary (excluding book reviews, editorials, and introductions to special issues) in *Restoration Ecology* from 1996 to March 2006. During this time, 503 articles were published, of which 8 presented data on BSCs or soil bryophyte–lichen communities, constituting less than 2% of the total and approximately 5% of the dryland studies. Another seven articles mentioned some form of BSC, with no data presented. Four of the studies with data on BSCs (Lukešová 2001; WallisDeVries & Raemakers 2001; Grettarsdottir 2004; Rozé & Lemauviel 2004; Rayfield et al. 2005) were conducted in mesic environments on mine tailings, severely eroded land, coastal dunes, and disturbed forest, respectively. Only three articles with BSC data were from drylands (Li et al. 2004; Maestre & Cortina 2004; Eldridge et al. 2006), despite dryland studies being generally well represented (approximately 12% of the total).

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Why is this important ecosystem component so rarely addressed in the restoration literature? Even a recent book on BSCs devotes only a paragraph to BSC restoration and rehabilitation (Belnap & Lange 2003). One might argue that this is because restoration and rehabilitation are moving away from emphasis on particular ecosystem components and toward emphasis on the whole ecosystem. However, as I argue subsequently, rehabilitation of BSCs should primarily be undertaken to restore ecosystem function rather than BSCs per se. Perhaps, the most important reason for the absence of BSCs in restoration literature is the perception that BSC rehabilitation is unrealistic because the best-known property of BSCs is their slow *unassisted* recovery from disturbance. Unassisted recovery times vary due to biotic and abiotic factors and range from only 6 years for trampling disturbance in cool deserts with fine soils (Belnap & Eldridge 2003), a century for late successional lichens in Australia (Eldridge & Ferris 1999), to millennia for General Patton's tank tracks in the hottest, driest portions of North America (Belnap & Warren 1998). Many estimates are linear extrapolations based on short-term datasets, which may yield gross over-estimates (Belnap & Eldridge 2003). Perhaps, these figures have been discouraging for those who wish to incorporate BSCs in rehabilitation, but there is evidence that *assisted* recovery may reduce this time period to a scale more manageable in the context of a rehabilitation project (Grettarsdottir et al. 2004; Li et al. 2004). Available data show that it is possible to restore BSCs and that it may be necessary in at least some cases.

The purposes of this review was to (1) examine the roles of BSCs in facilitation of succession and transitions of ecosystems among alternative steady states; (2) review available literature on the practical aspects of BSC rehabilitation; and (3) advance a conceptual framework for implementing the rehabilitation of BSCs.

Roles of BSCs in Succession

To examine the potential importance of BSCs for ecological rehabilitation, we need a fundamental distinction between high and low abiotic stress systems (Grime 1979; Fig. 1). High abiotic stress systems have open canopies due to various constraints such as severe resource limitations (e.g., water or nutrients), spatial constraints (e.g., shallow rooting depth), or temporal constraints (e.g., short growing seasons). In a low abiotic stress system, BSCs are often among the colonizers in primary succession, and secondary succession may provide a window of opportunity for BSC establishment because light and other resources are suddenly more available. These BSCs are eventually displaced by a closed vascular plant canopy. In contrast, in high abiotic stress systems, BSCs may also play a role in succession but tend to persist as a permanent component of undisturbed steady states, and their loss or addition may trigger transitions between steady states.
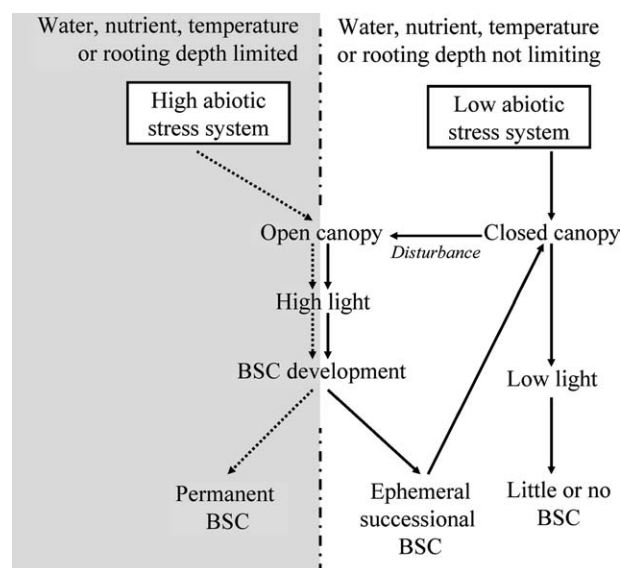

Figure 1. In high abiotic stress ecosystems, BSCs develop as a permanent feature of the undisturbed system, whereas in low abiotic stress systems, BSCs are an ephemeral successional sere.

BSCs as a Successional Sere

Much of the conceptual backbone of restoration ecology derives from ecological succession theory. The presence of lichen–moss microbial communities as an early sere in terrestrial primary succession is widely known (Clements 1916; Rayburn et al. 1982; Wynn-Williams 1993; Kurina & Vitousek 1999; Lukešová 2001) but rarely specifically studied in the primary literature (Worley 1973). The universality of BSCs as early colonizers is not surprising when considering that BSCs may have comprised the earliest terrestrial communities in conditions that must have closely resembled those during primary succession (Campbell 1979; Watanabe et al. 2000; Prave 2002). Collectively, BSCs have several life history traits that enhance their ability to colonize severe environments: (1) wind dispersal of small propagules (Lewis Smith 1993); (2) desiccation tolerance (Oliver et al. 1993); (3) several photoprotective pigments (Bowker et al. 2002); (4) N fixation (Evans & Ehleringer 1993); and (5) C fixation (Lange et al. 1994).

BSCs are potentially important in secondary succession, though this hypothesis has not been extensively studied (Booth 1941; Hunt et al. 1979; Ahti & Oksanen 1990). In tallgrass prairies, fires may stimulate a pulse in the growth and N fixation activity of soil surface cyanobacteria (Eisele et al. 1989). Similarly, in an old field, early N fixation was primarily attributable to cyanobacteria (Kapustka & Rice 1976). Booth (1941) hypothesized that after the cessation of plowing, the soil stabilizing cyanobacterial crusts were a prerequisite for later colonizing plants.

Three studies that have experimentally examined the net effect of BSCs on later successional vascular plant species (Chapin et al. 1994; Elmarsdottir et al. 2003; Hawkes 2004) indicate that the effect generally fits Connell and Slatyer's

(1977) facilitation model, wherein the BSC enhances the probability of colonization and survival of members of later seres. In a severely eroded Icelandic landscape, BSCs were favorable microsites for vascular plant seedings (Elmarsdottir et al. 2003). Similarly, at Glacier Bay, a cyanobacterially dominated "black crust" decreased germination but enhanced survivorship of later successional spruce and alder, resulting in net facilitation (Chapin et al. 1994). In a postfire xeric scrub community of Florida, greenhouse trials suggested that live BSCs enhanced germination of vascular plants, but in the field, effects of BSCs were variable and less important than other factors (Hawkes 2004). The facilitative interpretation is bolstered by observational work in various habitats (Booth 1941; Danin 1978; Danin & Barbour 1982; Van de Ancker 1985; Bliss & Gold 1994). Walker and del Moral (2003) asserted that these instances of indirect facilitation are not obligate for later successional species because plants can colonize barren substrates. Walker and del Moral (2003) also suggested that BSCs may sometimes inhibit the establishment of later seres. In Turkmenistan, the expansion of moss-dominated BSCs decreased the socioeconomical value of grazing land by displacing forage species (Orlovsky 2004). In general, the research on the effects of BSCs on vascular plant germination and establishment produces contradictory results, with BCS acting in facilitative (St. Clair et al. 1984; Eckert et al. 1986) or inhibitory (Prasse & Bornkamm 2000; Hawkes & Menges 2003) roles. One probable source of the contro-

versy is that plant–BSC interactions are likely to be highly species specific, dependent on plant traits (such as mucilaginous seeds; Zaady et al. 1997), and physical or chemical traits of the organisms dominating the BSC community (Serpe et al. 2006).

Whether or not BSCs are deemed facilitative or inhibitory for later successional vegetation may depend on how exhaustively the interaction between plants and BSCs is studied. For example, on stabilized dunes, BSCs may in some cases inhibit plant germination (Mitchell et al. 1998), but they also represent the single most important biotic element maintaining stability without which there would probably be very little plant cover (Danin & Barbour 1982). Likewise in southern China, BSCs reduced infiltration (an inhibitory effect) but increased soil stability and served as an N source for surviving and recolonizing trees (facilitative effects; Uchida et al. 2000; Tateno et al. 2003). Only one study has tracked multiple effects of BSCs on vascular plants throughout their life history, and although some effects were inhibitory, the net effect of BSCs on annual plants was facilitative (DeFalco et al. 2001). BSCs and plants may interact with one another *via* several different pathways, and it is the net effect of the various pathways that determines whether BSCs promote or retard plant colonization (Fig. 2).

Whether or not BSC–plant interactions in succession follow Connell and Slatyer's (1977) facilitation or inhibition models, we should be aware of the nature of this
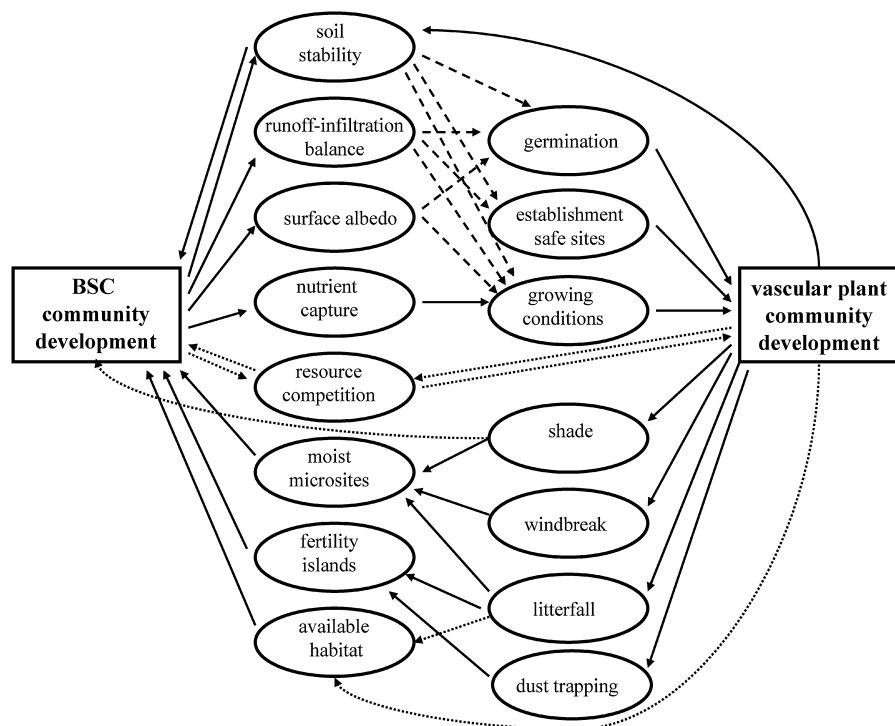

Figure 2. Interactions between BSCs and vascular plants are highly complex. Most past experiments address only one or a few of the many possible pathways; the net effect of all pathways determines whether the relationship is facilitative or inhibitory. Solid arrow, primarily positive effects; dotted arrow, primarily negative effects; dashed arrow, effects are variable.

interaction because properly manipulating it could result in more successful rehabilitation on the ground. For example, under the facilitation scenario, if BSC colonization is assisted, perhaps the rate of succession may increase. Under the inhibition model (e.g., Mitchell et al. 1998; Orlovsky et al. 2004), perhaps microdisturbances to partially disrupt the BSC could be introduced to prevent BSCs from retarding succession. For example, BSCs were strategically removed to shuttle resources to planted trees in Israel (Shachack et al. 1998; Eldridge et al. 2002).

BSCs in State-and-Transition Models

In high abiotic stress ecosystems (including but not limited to drylands), BSCs are common features of the "natural" or "undisturbed" state, and their removal or reestablishment may shift the state of the ecosystem (e.g., loss of soil fertility and N fixation, Belnap 1995; loss of erosion resistance and microbial activity, Maestre et al. 2005). In these environments, BSCs are usually quite vulnerable to disturbances. In some aridlands, passive rehabilitation techniques such as livestock exclusion or restriction of off-road vehicles can allow the reestablishment of BSCs (Anderson et al. 1982) and return to a state similar to the preexisting ecosystem (Anderson et al. 1982). However, in some systems, recovery does not occur passively (Belnap & Warren 1998). These systems are perhaps better understood using state-and-transition models (Westoby et al. 1989). In various generalized state-and-transition models (e.g., Aronson et al. 1993; Hobbs & Norton 1996), the undisturbed ecosystem may progress to one of multiple degraded steady states when a disturbance occurs. Thresholds are likely to exist along this degradation pathway such that on one side of a threshold, a degraded state will return to an alternative steady state or predisturbance state with cessation of the disturbance (e.g., passive restoration) and on the other side of the threshold, a degraded ecosystem may not be restorable to the preexisting ecosystem state and may be shifted to an alternate steady state only with costly and intensive active restoration treatments (Aronson et al. 1993; Hobbs & Norton 1996).

Transitions across thresholds require triggers (Briske et al. 2006). Loss or degradation of BSCs can act as a trigger. Miller (2005) advanced a state-and-transition model for aridlands, in which, of seven transitions, loss of BSCs can be very important triggers in two (reference state or woody-dominated state → severely eroded state) and are of lesser importance in two more (annualized state or invaded state → severely eroded state). Similarly, loss of soil cryptogams is a component of transitions toward more degraded states in Eucalypt woodlands (Yates & Hobbs 1997).

Briske et al. (2006) proposed that thresholds are crossed in the following sequence: structural, species loss, functional. I propose that loss of BSCs can trigger a transition across structural and functional thresholds because they occupy a unique spatial portion of the landscape (Fig. 3) and contribute strongly to the capture and retention of energy and materials. Aronson et al. (1993) advanced 18 measurable vital ecosystem attributes to describe the structure and function of arid ecosystems. BSCs are strong contributors to or components of at least 11 of these (Fig. 3; Brotherson &
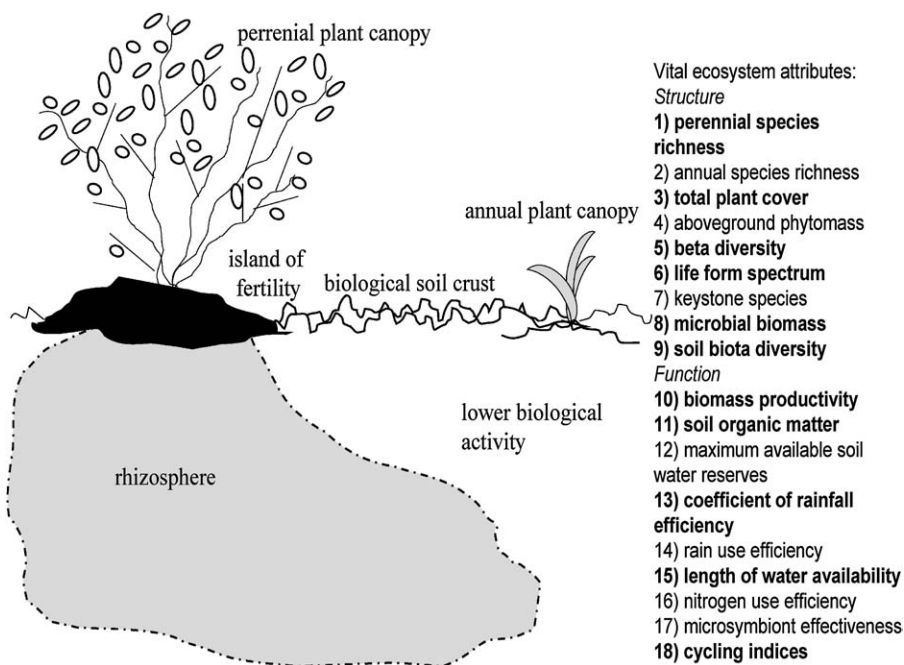

Figure 3. BSCs are one of the key structural and functional components of high abiotic stress ecosystems. They occupy a unique spatial portion of the ecosystem: the soil surface between plant canopies. Vital ecosystem attributes (sensu Aronson et al. 1993) influenced by BSCs are indicated in bold face.

Rushforth 1983; Alexander & Calvo 1990; Evans & Ehleringer 1993; Lange et al. 1994). Loss or degradation of BSCs could trigger transition across functional thresholds via several mechanisms: lower surface albedo (Karnieli & Tsoar 1995), altered water redistribution (Eldridge et al. 2002), decreased fertility (Belnap 1995), increased invasibility by exotics (Serpe et al. 2006), and, most importantly, increased soil erosion (Belnap & Gillette 1998).

Currently, state-and-transition models have not been used in the context of ecosystem rehabilitation via BSC reestablishment. The two key questions that need to be addressed are (1) which transitions can be triggered by loss or degradation of BSCs? and (2) can reestablishment of BSCs reverse these same transitions? Li et al. (2004) and Grettarsdottir et al. (2004) both recount situations where BSCs may have contributed to reversing transitions. When functional thresholds have been crossed, positive feedbacks reinforce degradation (Briske et al. 2006) and physical rather than biotic processes predominate (Whisenant 1999). This constitutes desertification (Whisenant 1999). Perhaps assisted recovery of BSCs can be a major tool for reversal of desertification, and state-and-transition models may provide the conceptual framework for this application.

Rehabilitation of BSCs

Outside the restoration literature, there is a surprisingly large amount of information relevant to rehabilitation of BSCs. However, the practice of BSC rehabilitation lacks a cohesive conceptual framework. I propose that implementation of a rehabilitation project incorporating BSCs involves (1) establishment of rehabilitation goals; (2) selection, implementation, and integration of methods; and (3) monitoring the response of BSC communities. The purposes of this portion of the review were synthesis of disparate literature and to discuss the first two components in a single document; monitoring has been recently reviewed (Belnap et al. 2001; Rosentreter & Eldridge 2002; Rosentreter et al. 2003).

Establishment of Rehabilitation Goals for BSCs

Any rehabilitation effort requires knowledge of less degraded ecosystem states or some other form of benchmark (Moore et al. 1999). The composition, structure, pattern, heterogeneity, function, dynamics, and resilience of these states serve as an ultimate target for restoration and rehabilitation and as a standard against which to measure success (Hobbs & Norton 1996). According to SER, strict-sense ecological restoration is assisted recovery of a degraded, damaged, or destroyed ecosystem and attempts to return an ecosystem to its historic trajectory (SER 2004). In practice, the historic trajectory is nearly impossible to establish for BSCs because scientists did not give BSCs serious attention until the latter half of the twentieth century. Thus, BSCs are simply not mentioned in historical data sources, with a few exceptions such as historical photo-

graphs recording the presence of BSCs (Webb et al. 2004), and ethnography regarding culturally important taxa (Rieske 1994; Qiu & Gao 1999).

A more practical approach to developing an ultimate target for BSC rehabilitation is establishment of "potential conditions" based on extant areas that have experienced light disturbance regimens or have had time to recover. Potential condition as used here is not a strict-sense reference condition but is rather a sustainable condition that is likely to be stable (Andreasen et al. 2001). The condition of these areas may be closer to what is possible under future climate scenarios because they presumably have responded to climate change in the past century. True relicts are exceedingly rare but can be found in extremely remote or difficult-to-access areas including mesa tops, rimmed canyons, and roadless areas. Exclosures can be very useful if the history is known but are limited because they are rarely maintained on long time scales.

When no true relicts or exclosures are available, low disturbance "islands" can be located among more highly used landscape. Livestock, the most widespread agents of BSC disturbance, tend not to travel long distances from water or high-quality forage and tend to avoid energy expenditures in traveling in variable topography. Sites that are distant from water or forage and are difficult to access will often exhibit lower disturbance. Although these sites generally bear some disturbance legacy, they are often the only option from which to estimate potential BSC conditions. In the situation where no physical sites may be found, expert panels may need to be relied on to estimate potential BSC conditions.

The simplest means of using potential conditions involves a space-for-time replacement, whereby a degraded area is compared to a nearby, ecologically similar area that is at or near its potential. This method is useful, particularly when the site contains a mosaic of disturbed and undisturbed microsites (e.g., Belnap 1993), but in some cases, may ignore the fact that undisturbed systems are naturally variable. The natural variability refers to the range of states and processes that an undegraded site may reflect (Landres et al. 1999). To capture the natural variability of potential conditions, I suggest sampling numerous less degraded sites and statistically modeling the data. Various biotic and abiotic data can be used as predictor variables, and spatially explicit input data and subsequent mapping of model outputs are especially desirable. These input data allow the matching of a site of interest to sites in potential condition based on ecological similarity (e.g., similar climates and soils). Rogers (1972; updated in Eldridge 2003) advanced a spatial model of the presence–absence of Australian lichen-dominated BSCs based on the amount and timing of precipitation and soil characters. Rosentreter and Pellant (unpublished data) created a semiquantitative predictive model based on vascular plant community, precipitation, and soil texture for southern Idaho rangelands that have been used by the Bureau of Land Management for 12 years. A qualitative multiscale predictive model was advanced for the Colorado Plateau based on soil texture

and nutrient and moisture availability (Bowker et al. 2006*a*). Bowker et al. (2006*b*) used precipitation, elevation, and soil type to quantitatively and spatially model the cover and richness of several crust types in semiarid Utah (Fig. 4). Quantitative predictive models can be used to calculate descriptive statistics, e.g., mean and variance, of a parameter (e.g., total lichen cover) to assist comparisons among the potential and actual condition of rehabilitation sites.

Rehabilitation Methods for BSCs

The approaches to assisted BSC recovery are creative and diverse. They are addressed in widely dispersed literature from fields related to restoration (e.g., ecological engineering, reclamation), agriculture, and in the general ecological literature. These techniques can be grouped under three broad classifications: (1) artificial soil stabilization; (2) resource augmentation; and (3) inoculation.

Artificial Soil Stabilization Techniques. Artificial stabilization of the soil surface has successfully resulted in BSC rehabilitation. There are three primary variations: polyacrilimide application, coarse litter application (such as straw), and use of stabilizing vascular plants. Polyacrilimide application was shown to have either no effect or, in combination with other treatments, a negative effect on chlorophyll fluorescence or nitrogenase activity of transplanted *Collema* (Collemataceae) lichens (Davidson et al. 2002). Therefore, this means of soil stabilization appears to have little rehabilitation value for lichens; however, effects on other BSC organisms are unknown.

Recent work in an arid region of China has examined the straw checkerboard technique for dune stabilization and subsequently BSC establishment (Fearnehough et al. 1998; Hu et al. 2002; Li et al. 2004). Straw is vertically

half-buried in a series of lines in a grid pattern, usually spaced 1 m apart. Sometimes, vascular plants are also planted. A succession of a physical crust, cyanobacteria, chlorophytes, and finally the mosses gradually colonize, forming a cohesive and species-rich BSC. Potentially, similar methods could be applied to any sandy area where BSCs and vegetation would naturally stabilize the dunes (Van de Ancker et al. 1985; Maxwell & McKenna-Neuman 1994; Danin 1996; Danin et al. 1998). The only flaw of this remarkably successful method is that there must be a considerable economic incentive (such as preventing railroad burial; Li et al. 2004) to invest the labor resources needed to execute and maintain it on large scales.

Danin et al. (1998) recount the introduction of European beach grass (*Ammophila arenaria*) to stabilize degraded northern California coastal dunes and reduce the need for dredging dune sand from a harbor. This exotic plant spread rapidly, stabilizing the dunes. An unanticipated effect was the development of a moss-dominated BSC in the understory, which further stabilized the dunes. Similarly, trees planted near an unstable sandy area resulted in reduced wind velocity and initiated a succession of shrubs and BSCs, which stabilized the dunes and created a more productive, diverse community (Danin 1978). Planting native and exotic grasses on highly eroded and unstable soils of Iceland coupled with fertilization often resulted in the formation of BSCs in addition to vascular plant vegetation (Aradóttir et al. 2000), though another study in Iceland found fertilization without seeding to be a more successful treatment (Elmarsdottir et al. 2003) In a postfire rehabilitation project in a sagebrush steppe, Hilty et al. (2003) found that the seeding of bunchgrasses increased the proportion of favorable surfaces for BSC establishment.

Resource Augmentation Techniques. Modification of nutrients and moisture to promote BSC establishment in disturbed areas has not been extensively studied. A previous study used earthen water catchments during India's monsoon season to encourage cyanobacterial growth and render highly alkaline infertile soils suitable for agriculture (Singh 1950). Observational evidence often suggests that BSC growth is favored in somewhat shaded, cooler, and wetter microsites (Belnap & Warren 1998; Maestre & Cortina 2002; Bowker et al. 2005). In contrast, supplemental watering negatively affected transplanted lichens by generating erosion (Davidson et al. 2002). However, the strongest pattern in this study was the superior performance of lichens transplanted to the more mesic and cool microaspects of small, upraised ridges in the BSC surface. Similarly, mosses fared better in experimental depressions, particularly when polar oriented (Csotonyi & Addicott 2004). These results suggest that mesic microsites could potentially favor BSC reestablishment as they can for vascular plants (Maestre et al. 2001). Possible rehabilitation methods include seeding with fast-growing perennial plants to create partial shade or creation of artificial soil microtopography. Some authors (Tongway & Ludwig

Potential moss cover (%)

- 0
- 1.9 (2.5)
- 3.6 (2.4)
- 7.2 (4.2)
- 12.3 (2.8)
- 15.0 (9.2)
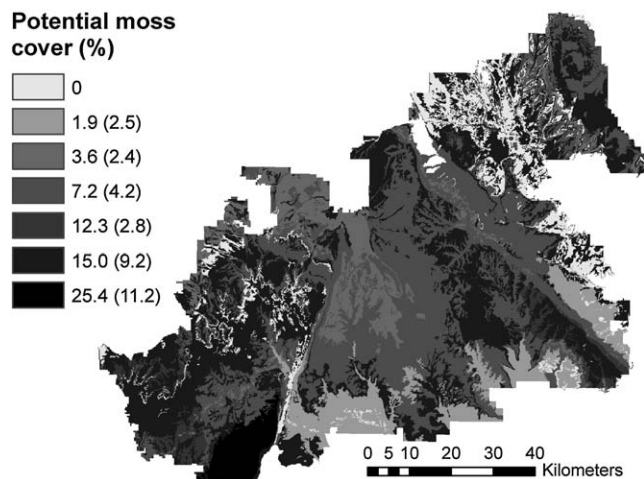- 25.4 (11.2)

0 5 10 20 30 40 Kilometers

Figure 4. An example of a spatial model depicting potential cover of one BSC cover type over a large area, based on sampling of several low disturbance sites (after Bowker et al. 2006*b*).

1996; Maestre & Cortina 2004) suggest the use of brush piles to generate favorable microsites for vascular plant germination. Brush piles would likely favor vascular plants over BSCs, but perhaps this concept could be extended to BSCs by strategically placing smaller amounts of course woody debris to create partial shade.

Addition of P and K together was studied in a full-factorial field experiment, with five additional factors (Davidson et al. 2002). Phosphorous and K addition had no effect on nitrogenase activity or condition of lichen transplants. Fertilization had variable effects on chlorophyll fluorescence of the transplants, contingent on study site and whether cyanobacteria were also inoculated. Microtopographical aspect was the most influential variable in the study. In a laboratory study of the cyanobacterium *Nostoc flagelliforme*, K was found to promote photosynthetic recovery after desiccation (Qiu & Gao 1999). Two recent studies found that Mn, Zn, K, and Mg were repeatedly positively correlated with BSC mosses and lichens at multiple spatial scales (Bowker et al. 2005, 2006*a*). Additional research is necessary to determine the effects of various fertilization regimens on BSC organisms and on exotic invasive plant species that could potentially benefit from enhanced resource availability.

Perhaps, the most promising research in fertilization-based BSC rehabilitation techniques comes from highly eroded "deserts" of Iceland. There is an approximately 95-year history of efforts to slow soil loss and promote revegetation, including NPK fertilization. One marked effect of fertilization was BSC development, which in turn stabilized soil and provided safe sites for plant seeds via soil warming and N fixation. The altered ecosystem facilitates woody vegetation establishment and succession toward predisturbance states as cool, humid woodlands, heath, and tundra (Aradóttir & Arnalds 2001; Elmarsdottir et al. 2003; Grettarsdottir et al. 2004).

Inoculation-Based Techniques. Inoculation assists BSC development by removing propagule dispersal limitations and may consist of introduction of crust material from another location or mass-cultured crust organisms. Inoculation has a history in polluted soil reclamation (e.g., Ashley & Rushforth 1984) and improvement of agricultural lands (Venkataraman 1972; Metting & Rayburn 1983; Rao & Burns 1990; Rogers & Burns 1994; Falchini et al. 1996). Cyanobacterial amendments were investigated for their benefits in forested ecosystems, either postfire (increased soil fertility and biological activity in a laboratory setting; Acea et al. 2001) or as an N source in a tree plantation (no effects of a commercial inoculum on plant N; Tiedemann et al. 1980). Experiments of this nature in drylands involve the translocation of crushed BSC material, dry (Belnap 1993) or in a slurry (St. Clair et al. 1986; Scarlett 1994) form, to the disturbed area. Both treatments clearly showed enhanced recovery of BSCs but had far less BSC development than undisturbed controls, suggesting a full recovery time much longer than these short duration studies. Scarlett

(1994) and Bowler (1999) discussed successful transplanting methods for establishing founder populations of particular taxa. Cyanobacterial addition had seemingly idiosyncratic effects on transplanted *Collema* lichens, dependent on complex interactions with watering, polyacrilimide, or nutrient additions (Davidson et al. 2002). Despite some encouraging results, methods such as these are limited because they rely on a "sacrifice area" where inoculum material can be removed. Thus, they are probably only suitable on small scales. The great strength of such methods is that BSC material can be salvaged from sacrifice areas and stored for long periods of time while retaining inoculum potential (e.g., 12 years for a desert moss; Stark et al. 2004). Dependency of recovery time on actual propagule density in inoculants is currently unstudied.

The next logical extension of the BSC inoculation approach is ex situ mass culturing of target BSC organisms for reintroduction to field sites. The cyanobacterium *Microcoleus vaginatus* (Oscillatoriaceae) was mass cultured and embedded in alginate pellets (Johansen & St. Clair 1993, 1994). The cyanobacteria could survive pelletization and escape from the pellets in the laboratory and measures of crusts abundance and function with application (Buttars et al. 1998), but this result was not supported under field conditions (Buttars et al. 1994). Addition of cyanobacteria grown on hemp cloth produced short-term promotion of cyanobacterial growth at one of the five sites (Kubecková et al. 2003). Lichen photobionts were cultured and applied in the field to enhance lichen establishment (Davidson et al. 2002). It was determined that mycobiont spores limited new lichen starts rather than photobionts (Davidson et al. 2002).

Integration of Multiple BSC Rehabilitation Techniques. Selection of a technique that is likely to be effective is contingent on site conditions. I present a conceptual model that may be useful in guiding rehabilitation design because it illustrates the barriers to successful rehabilitation in order of difficulty to overcome (Fig. 5). Addressing a higher level barrier is unlikely to succeed if a lower level barrier still exists on site. Addressing the lowest level barrier present may allow recolonization faster than no action; but to speed up recovery further, additional barriers may need to be removed. The most difficult barrier is actively eroding soils. This condition may be diagnosed using aggregate stability measures, field observations of rills, or evidence of overland flow. A second barrier is resource limitation. Nutrient limitations may be occurring if soils bear $CaCO_3$ and Fe oxides; have been disturbed for a long time period, resulting in loss of organic matter and fine soil particles; or were infertile prior to disturbance. Despite generally bearing the characteristics of "sun plants" (Lange et al. 1994), most BSC organisms appear to benefit from at least some shade and hence increased soil moisture; if perennial plant cover is poor, or if soil surface microtopography is lacking, addition of favorable microsites may encourage BSC establishment.
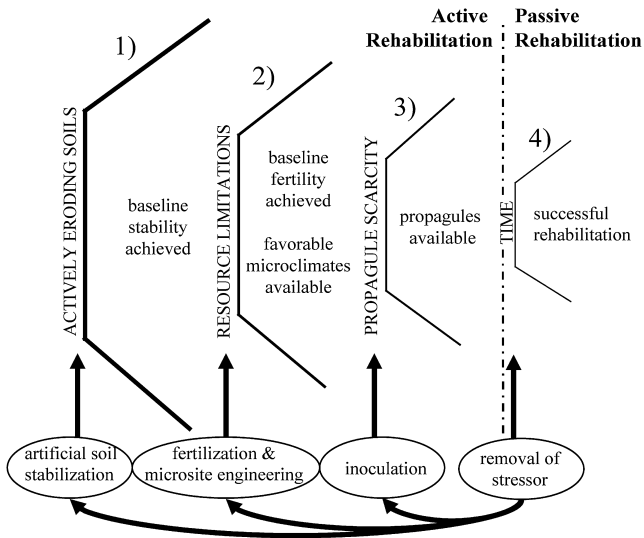
Figure 5. A conceptual model of barriers (denoted vertically in uppercase letters) to BSC reestablishment. Lower numbered barriers are more difficult to overcome. Entries in ovals represent potential actions that may help overcome a barrier.

Propagule scarcity may be ascertained if there are large distances between the rehabilitation site and the intact crust patches. If all these barriers have been surpassed, the final barrier is time. As previously mentioned, BSCs are often slow growing; thus, even successful BSC rehabilitation may take decades to attain potential conditions under some scenarios. Full recovery time of more than a decade is rather typical of arid lands in general (Allen 1995); thus, this should not be viewed as a deterrent unique to BSC rehabilitation. Recovery time is partially dependent on precipitation, thus will be shorter in relatively mesic systems (Belnap & Eldridge 2003).

Rehabilitation of BSCs is still in its infancy, and we are simply learning how to promote faster recovery of BSCs in general or of key taxa within them. When these technological hurdles are surpassed, we will need to focus on what particular BSC characteristics we would like to rehabilitate to best promote recovery of ecosystem functions of interest. In support of this consideration, recent research has shown that different attributes of BSC communities (cover, richness, evenness, spatial clustering) affect indicators of ecosytem functions (erosion resistance, infiltration, microbial respiration, and nutrient cycling) differently (Maestre et al. 2005).

Conclusions

A large number of studies suggest that because BSCs provide important ecosystem functions, their reestablishment is a necessary component of the rehabilitation of numerous terrestrial ecosystems worldwide. In low abiotic stress sites, assisted recovery of ephemeral BSCs may facilitate the establishment of later successional species. In arid and other high abiotic stress systems, loss or addition of BSCs may induce a transition from one steady state to another because BSCs contain key functional components that may not be replicated in the vascular plant community. A much smaller number of studies suggest that BSCs can retard succession in certain circumstances and could perhaps be manipulated with strategic microdisturbances. Regardless of the role of BSCs in succession, their pervasive influence should be viewed as an opportunity to modify the trajectory of the whole system by focusing some effort on this ecosystem component.

Appropriate incorporation of BSCs in rehabilitation requires an estimate of site potential to aid in goal development. I suggest statistical predictive modeling whenever possible to capture the natural variability of potential BSC conditions. To shift the BSC community toward the potential conditions, the key is analysis of factors limiting natural recovery of BSCs. Barriers to recolonization differ in severity and difficulty of correction. Conceptualizing which barriers must be overcome and in what order they must be overcome will divert the selection of techniques away from activities likely to fail. Despite the large number of pertinent studies in development of methodologies, key knowledge gaps remain, which should be studied in the future, particularly in resource manipulation.

Implications for Practice

- BSCs, soil cryptogam–lichen microbial communities, protect the soil surface from erosion and build soil fertility. However, these BSCs are quite susceptible to surface disturbance and may require decades for full recovery if unassisted.
- Development or loss of BSCs may trigger transitions between ecosystem states; thus, rehabilitation of BSCs could potentially be used to rehabilitate damaged ecosystems.
- Rehabilitation involves estimating the potential for BSCs at a particular site to aid in setting goals, choosing an appropriate technique or combination of techniques, and monitoring.
- Inoculation is the best-studied approach to BSC rehabilitation and is frequently successful. However, it may not be appropriate and effective in all situations. Artificial soil stabilization may first be needed if active soil erosion is a problem, and resource limitations may need to be addressed with fertilization or creation of favorable microsites.
- Important future research directions in BSC rehabilitation include (1) trials of different methods of soil stabilization for nonsandy soils; (2) trials of fertilization regimens to promote BSC recovery without also promoting exotic plants; (3) trials of different methods for creating mesic microsites; and (4) effects of propagule density in inoculants.

- When these technical problems have been addressed, the effects of particular community properties of rehabilitated BCSs on the recovery of ecosystem functions will become a more important research focus. BSC rehabilitation efforts could potentially be tailored to recover a specific lost ecosystem process.

Acknowledgments

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