Journal of Arid Environments 94 (2013) 96–104

Contents lists available at SciVerse ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Controls of biological soil crust cover and composition shift with succession in sagebrush shrub-steppe

E. Dettweiler-Robinson [a,*], J.D. Bakker [a], J.B. Grace [b]

[a] School of Environmental and Forest Sciences, University of Washington, Box 354115, Seattle, WA 98195, USA
[b] U. S. Geological Survey, 700 Cajundome Blvd., Lafayette, LA 70506, USA

ARTICLE INFO

Article history:
Received 24 January 2012
Received in revised form
26 January 2013
Accepted 29 January 2013
Available online 9 April 2013

Keywords:
Bromus tectorum
Columbia Basin
Community succession
Indicator Species Analysis
Structural equation modeling

ABSTRACT

Successional stage may determine strength and causal direction of interactions among abiotic and biotic factors; e.g., species that facilitate the establishment of other species may later compete with them. We evaluated multivariate hypotheses about abiotic and biotic factors shaping biological soil crusts (BSCs) in early and late successional stages. We surveyed vegetation and BSC in the shrub-steppe ecosystem of the Columbia Basin. We analyzed the relationships with bryophyte and lichen covers using structural equation models, and analyzed the relationships with BSC composition using Indicator Species Analysis and distance-based linear models. Cover, indicator species, and composition varied with successional stage. Increasing elevation and bryophyte cover had higher lichen cover early in succession; these relationships were negative in the later successional stage. Lichen cover did not appear to impede *B. tectorum* cover, but *B. tectorum* appeared to strongly negatively affect lichen cover in both stages. Biological soil crust composition varied with bunchgrass cover in the early successional stage, but with elevation and *B. tectorum* cover later in succession. Our findings support the hypotheses that as succession progresses, the strength and direction of certain community interactions shift, and *B. tectorum* leads to reductions in biological soil crust cover regardless of successional stage.

1. Introduction

Primary producer communities can change over time because of discrete disturbances, species introductions, or changing resources due to climatic variations or human activities. Disturbances can damage or remove primary producers and may change abiotic properties. The new conditions affect which species can grow, acting as a filter of abiotic stressors that shape early secondary successional community composition. However, remnant or early-establishing individuals may facilitate arriving propagules by mediating the harsh environmental conditions (Bowker et al., 2005), making these organisms disproportionately important to the successional trajectory (del Moral and Lacher, 2005). As succession progresses, the biotic community may alter abiotic characteristics, reducing the stress on the organisms living there. Competition may become the dominant interaction as resources are consumed, resulting in shifts in community composition (Callaway and Walker, 1997). Invasive species arriving soon after a disturbance may prevent recovery of native species, but mature communities may be resilient to the establishment of invasive species (Levine et al., 2004). Invasive species may promote feedbacks between disturbances and expansion, further altering the successional trajectory (Brooks et al., 2004).

In arid and semi-arid lands, mature communities of primary producers include plants and biological soil crusts (BSCs) living on the soil surface. Biological soil crusts are globally distributed and provide important ecosystem functions, including soil stability and the cycling of carbon, nutrients, and water (Bowker, 2007; Evans and Johansen, 1999). Biological soil crust cover and composition vary with landscape position, vegetation type, and microsite characteristics (Ponzetti et al., 2007). Disturbances such as fire or trampling can affect the cover, composition, and physiological functioning of BSCs (Belnap and Eldridge, 2001). The general successional trajectory following disturbance moves from microscopic algae and cyanobacteria to bryophytes and non-crustose lichens to crustose lichens to fruticose and foliose lichens, depending on climate and soils. Mature crusts may take decades to centuries to develop depending on conditions, with moister areas showing faster rates of development than dry areas (Belnap and Eldridge, 2001).

Changing interactions among abiotic factors, biotic factors, and BSC organisms have been studied in primary successional

---

[*] Corresponding author. Present address: Department of Biology, MSC03 2020, 1 University of New Mexico, Albuquerque, NM 87131, USA. Tel.: +1 505 573 4734.
E-mail address: evadr@unm.edu (E. Dettweiler-Robinson).

0140-1963/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jaridenv.2013.01.013

communities. Following glacial retreat, early-arriving soil mosses and lichens colonized the sparse glacial soil and paleomaterial patches. This facilitated the establishment of long-lived plant species during early successional stages by enhancing soil fertility, but soil organisms were over-topped by high vegetation cover at later successional stages (Breen and Levesque, 2006). In secondary succession in arid and semi-arid lands, abiotic and biotic controls on the BSC community are likewise expected to differ across a disturbance chronosequence. Resprouting perennial plants may favor BSCs by creating microsites favorable in terms of reduced erosion potential, increased available nutrients and moisture, and reduced damaging solar radiation due to foliar cover. However, when plant canopy increases and new plants establish, they may out-compete BSCs for space and shade the soil surface.

We investigated the relative importance of abiotic and biotic factors on BSCs in early and late successional sagebrush shrub-steppe communities following wildfire in the Columbia Basin. Early successional vegetation communities tend to be dominated by invasive annuals such as cheatgrass (*B. tectorum*) and perennial species that can resprout following fire (Davies et al., 2012). *B. tectorum* can change the physical and chemical properties of the soil (Norton et al., 2004), reduce the fire return interval (Brooks et al., 2004), and impede BSC development (Belnap et al., 2006). In mature sites, native vegetation and BSC covers are positively correlated (Ponzetti et al., 2007) and may provide resistance to invasion by *B. tectorum* (Chambers et al., 2007; Deines et al., 2007).

We used structural Equation (SE) modeling (Grace, 2006) to investigate relationships among elevation, native bunchgrasses, *B. tectorum*, and BSC cover by fitting separate models for early and late successional stages. We hypothesized that the magnitudes and even causal direction of some relationships might differ with successional stage (as determined by time since fire). We expected that 1) favorable moist environmental conditions would speed recovery in early succession and lead to more productive late successional communities, 2) relationships between native species would be facilitative in early succession but competitive in later stages, and 3) invasive species would hinder BSC recovery in early successional stages but that mature crusts could resist invasion.

We also hypothesized that community composition might respond to similar cues as total cover, or alternatively, species-specific tolerances to abiotic characteristics and vegetation structure might drive composition. Using community analysis methods, we identified indicator species for each successional stage and examined the correlations among BSC composition and abiotic and biotic factors to describe the controls on the BSC community.

2. Materials and methods

2.1. Study site

Our study was conducted in the sagebrush shrub-steppe of the Columbia Basin in south-central Washington state (46.3′ N, 119.4′ E). The region has a semiarid climate with mean annual precipitation of 182 mm, an average January temperature of 1 °C, and an average July temperature of 23 °C. Most precipitation falls during winter (October–March) (Western Region Climate Center, 2011).

We focused primarily on two regions, the Arid Lands Ecology Reserve and the Horse Heaven Hills (HHH). The Arid Lands Ecology Reserve is managed by the U.S. Fish and Wildlife Service. It has not been cultivated since 1943 and has been fenced to exclude livestock and off-road vehicles since 1962. Low elevation areas were aerially sprayed with herbicide to control *B. tectorum* and other invasive species as recently as 2009. Much of the HHH area is managed by the U.S. Bureau of Land Management and has not been grazed by livestock since 1986. Additionally, we studied several private ranches that have retained native vegetation in rotational livestock pastures.

Elevations range from 100 to 1100 m with a generally northerly aspect. Soil types include Hazel sands, Quincy loamy sands, Esquatzel silt loams, Warden silt loams, Ritzville silt loams, Lickskillet silt loams, and Kiona very stony silt loams (NRCS, 2011).

Native vegetation is characterized by large shrubs (*Artemisia tridentata* ssp. *wyomingensis*, *Artemisia tripartita*) and bunchgrasses (*Pseudoroegneria spicata*, *Poa secunda*, *Festuca idahoensis*), with composition differing as a function of climate (Daubenmire, 1970) and disturbance history (Davies et al., 2012). Mature BSC communities are dominated by bryophytes and lichens (McIntosh, 2003; Ponzetti et al., 2007).

2.2. Sampling design

We sampled 100 transects, each 100 m long, between April and June 2010. Most transects ($n = 89$) overlapped or were adjacent to existing monitoring plots where BSC had been observed in the past (McIntosh, 2003; Evans and Lih, 2005; Ponzetti et al., 2007). The other 11 transects were established in areas with different fire histories. Transects were >300 m apart and distributed across a total study area of ~100,000 ha.

The fire history of each transect was determined using fire maps from 1981 to 2010; fires occurred in 1984, 1986, 1987, 1998, 2000, 2002, 2005, 2007, and 2009. We did not consider fire history prior to 1980 because the spatial information about fire perimeters is unreliable during this period. Transect elevation was estimated from 10 m pixel Digital Elevation Models. Soil texture at each transect was determined from a soil sample (200 g aggregated from the top 1 cm of 7–10 points along the transect) using the hydrometer method (Brookside Laboratories, Inc., New Knoxville, OH). Missing values for each of fourteen transects were estimated as the average values from 2 to 4 nearby transects on the same soil type.

Five quadrats, each 20 × 50 cm, were established 20 m apart along each transect. To ensure that quadrats contained adequate potential growing space for BSC, quadrat position was shifted 5–10 m if the selected location had >20% cover of pebbles, gravel, or rocks >1 cm in diameter.

In each quadrat, vascular plants were identified to the level of species, and the cover of each species was estimated to the nearest percent. Cover values were averaged at the transect level. Litter was removed to observe BSCs. The soil surface was lightly sprayed with water to initiate metabolism and make BSCs more visible. Total lichen and total bryophyte cover were recorded to the nearest percent. Species were identified where possible (Flowers, 1973; McCune and Rosentreter, 2007); when this was not possible they were grouped as genera or morphological groups (Appendix 1) as recommended by Eldridge and Rosentreter (1999). The presence, but not cover, of each 'species group' was recorded for each quadrat. Unidentified species were collected for determination with chemical tests and light microscopy; voucher samples are housed at the University of Washington Burke Herbarium. Species codes follow PLANTS database (USDA, NRCS, 2011).

2.3. Statistical methods

We categorized transects into successional groups based on time since the last recorded fire. Particularly large fires occurred since 2000, so we designated all transects which burned then or more recently as early successional ($n = 78$) and all others as late successional ($n = 22$). The early successional transects spanned a much larger range of environmental conditions than the late successional transects. To permit equitable comparisons amongst these successional groups, we selected the early successional transects with similar soil textures (>50% silt plus clay) and elevations (<700 m) as the late successional transects. In the end, we included 46 early successional and 22 late successional transects for the analyses described in Sections 2.3.1 and 2.3.2.

We examined the importance of abiotic and biotic factors relative to BSC cover (percent) and composition. The abiotic factor was elevation (m). The biotic factors were bunchgrass cover and *B. tectorum* cover, both in percent. Perennial bunchgrasses are the dominant vascular plant life form in these communities, so the summed cover of the large species (*P. secunda* was excluded because it was ubiquitous across transects) served as a surrogate for native vegetation. *B. tectorum* cover served as a surrogate for the degree to which transects were invaded. We compared each factor by successional stage with a two-sided Wilcoxon rank sum test. *Artemisia* spp., though an important structural element to this ecosystem, were only present on 13 transects due to the recent prevalence of fire in this area and therefore shrub cover was not included as a biotic factor in these analyses.

2.3.1. Structural equation modeling of BSC cover

General hypothesized relationships were represented in an *a priori* conceptual model (Fig. 1; Grace and Bollen, 2008), with directed arrows indicating causal relationships based on published studies or reasonable inferences (described in Table 1). We distinguished between bryophyte and lichen covers because they have different documented rates of recovery after disturbance (Belnap and Eldridge, 2001). We subsequently tested for significant effects of elevation, bunchgrass cover, and *B. tectorum* cover on bryophyte and lichen covers in separate models for early and late succession. Our initial models included a reciprocal relationship between *B. tectorum* cover and lichen cover rather than a directed effect because of the possibility for reciprocal effects (Grace, 2006) because *B. tectorum* invasion reduces BSC cover (Belnap et al., 2006), but lichen cover can prevent *B. tectorum* establishment (Deines et al., 2007). On the other hand, we chose to model the net relationship between bunchgrass and *B. tectorum* as a simple correlation, not because their interaction is not reciprocal, but so that we could obtain statistical identification of the reciprocal interaction between *B. tectorum* cover and lichen cover. A key contrast of interest in our analysis was whether relationships differed by successional stage.

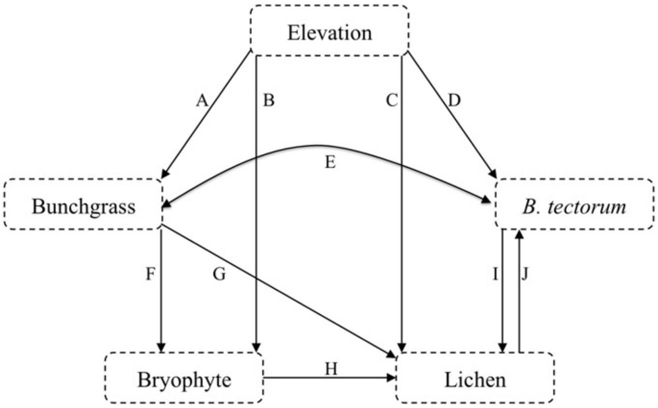

Fig. 1. Initial conceptual model for early successional and late successional groups, each run separately. Straight arrows indicate hypothesized directed relationships between variables, and curved, double-headed arrows indicate undirected correlations between the error terms of two response variables. Letters correspond to interpretations in Table 1.

Prior to modeling and based on data examinations, we used Box–Cox plots to identify appropriate transformations so that statistical distributions were approximately normal and bivariate relationships were linear (Appendix 2). Bunchgrass cover was square root transformed. All other variables were inverse-square root transformed (Cohen et al., 2003) and then divided by the exponent to recover the rank order of the untransformed data.

Structural Equation model analyses were run in AMOS Version 19.0.0 (Arbuckle, 2010). The development of SE models in this application followed the guidelines presented in Grace (2006) and updated in Grace et al. (2010) and Grace et al. (2012). Because models included reciprocal interactions between *B. tectorum* and lichen cover, attention was paid to parameter identification and the stability of estimates. Parameter significance was judged based on likelihood ratio tests comparing models by freely estimating or setting parameter estimates to zero. Parameters associated with reciprocal interactions (paths I and J in Fig. 1) were “free” (e.g., freely estimated) throughout the model evaluation process to permit a proper test of bidirectional effects.

2.3.2. Indicator species and community composition

We used Indicator Species Analysis to identify BSC species groups that were strongly associated with successional groups. The Indicator Value (*IV*) is calculated independently for each species group i as the product of its relative abundance and relative frequency in each group j (early vs. late successional group) (Bakker, 2008). Indicator values range from 1 to 100. Significance was assessed by permuting group identities 99 times and recalculating IV_{ij}. *IV*s were calculated using the function given in Appendix S1 of Bakker (2008). Significant indicators were those with $P < 0.05$ and $IV_{ij} > 25$ (Dufrêne and Legendre, 1997).

We assessed BSC composition, including both bryophytes and lichens, based on the frequency of each species group along each transect. A ‘dummy’ species group (frequency = 0.1) was added to all transects so that those without BSC, a biologically meaningful scenario, could be included in the analysis (Clarke et al., 2006). Species groups that occurred on <5% of transects were removed, leaving a total of 32 species groups in the compositional matrix. The composition matrix was standardized by species group maxima and site totals and converted to a Bray–Curtis distance matrix. Factors affecting BSC composition were assessed with distance-based linear modeling (Anderson, 2001) using the adonis function in the vegan package of the statistical software R (R Foundation for Statistical Computing, 2009, version 2.10.1). Main effects of successional group, elevation, bunchgrass cover, and *B. tectorum* cover were examined for the entire dataset, and the latter three variables were tested in each successional group separately. For consistency, explanatory variables were transformed as in the SE models. Because the adonis function uses Type 1 Sums of Squares, we removed terms that were non-significant when included as the first term in the model. Non-significant factors were removed in a stepwise manner, beginning with the least significant term. Remaining factors were ordered from highest to lowest R^2 when they were the first term.

Relationships among composition and explanatory variables were visualized with Nonmetric Multidimensional Scaling (NMDS) (Clarke, 1993) using the metaMDS, envfit, and ordisurf functions in the vegan package. We used the results of a Principal Components Analysis as a starting configuration, up to 20 random starts, and 999 permutations. We selected a final solution with three dimensions to balance reductions in stress with ease of visualization. We used the envfit function in the vegan package to display the direction in ordination space of explanatory variables that had the maximal correlation with the ordination configuration. The weighted averages of Indicator Species' scores were calculated with the wascores

Table 1
Pathways, hypotheses, and observations or mechanisms associated with the directionality of arrows in the *a priori* conceptual model for BSC cover in early- and late-successional stages in the Columbia Basin (Fig. 1).

Code	Hypothesis	Observation or potential mechanism
A, B, C, D	The net effect of elevation on vegetation and BSC is likely positive.	i As elevation increases, lower temperatures and higher precipitation may lead to lower water stress for organisms and therefore higher cover.
E	The net relationship between native vegetation and invasive species is likely negative.	i Bunchgrasses may compete with *B. tectorum* that is invading (Beckstead and Augspurger, 2004). ii *B. tectorum* may decrease growth of bunchgrasses by reducing water availability (Melgoza et al., 1990).
F, G	The net effect of native vegetation on BSC is likely positive in early succession and likely negative in late succession.	i Areas of higher vascular plant cover have higher BSC cover (Anderson et al., 1982). ii Vegetation may create favorable microsites for BSC due to enhanced water and nutrient availability and to temperature moderation (Bowker et al., 2005). iii Areas with higher BSC cover are found in areas of lower precipitation where there is less vegetation (Kaltenecker et al., 1999). iv Vegetation may inhibit growth of BSC or compete for resources (Bowker, 2007).
H	The net effect of bryophyte cover on lichen cover is likely positive in early succession and likely negative in late succession.	i Bryophytes may recover quickly after a disturbance and stabilize the soil, facilitating lichen establishment. ii Bryophytes may compete for space and resources with lichens.
I	The effect of invasive species on lichen cover is likely negative.	i Areas previously invaded by cheatgrass show reduced cover of mosses and lichens (Belnap et al., 2006). ii Litter accumulation from invasive species can impede recovery of BSC after fire (Hilty et al., 2004).
J	The effect of lichen cover on invasive species is likely negative.	i *B. tectorum* seedlings grown on crustose lichen crust showed decreased water status and unsuccessful root tip formation (Serpe et al., 2008). ii *B. tectorum* seedlings failed to germinate on lichen crust (Deines et al., 2007).

function in the vegan package to display the centroids of species space on the NMDS ordination. We scaled plot characters by total bryophyte and lichen cover and shaded them according to relative cover of moss out of total BSC cover to explore the relationship between cover and composition.

3. Results

3.1. Differences between successional stages

Late successional transects had significantly higher bunchgrass cover, bryophyte cover, and lichen cover (Table 2). Because we selected for plots spanning similar elevational ranges and soil textures, these did not differ between groups. *B. tectorum* cover also did not differ between groups.

3.2. Models of BSC cover

Several of the model pathways initially included in Fig. 1 were not supported by the data and subsequently associated parameters were set to zero. Stability of estimates was excellent for both final models based on the stability index presented by Amos (Arbuckle, 2010). The final model for the early successional group (Fig. 2A; $\chi^2 = 2.9$, df = 4, $P = 0.57$) explained 17% of the variation in bunchgrass cover, 55% of the variation in lichen cover, and none of the variation in *B. tectorum* or bryophyte cover. The results imply that elevation had a positive effect on the cover of bunchgrasses and lichens and that elevation had an influence on BSC independent of the differences in vegetation among transects. *B. tectorum* cover and bunchgrass cover were significantly negatively related. Native bunchgrass cover tended to show positive relationships with bryophyte and lichen covers (Appendix 2), but neither relationship was significant in the final model. Bryophyte cover was positively related to lichen cover. Results indicate that *B. tectorum* had a strong negative effect on lichen cover but not *vice versa*.

Table 2
Abiotic, biotic, and BSC variables measured on early ($n = 46$) and late successional ($n = 22$) stage transects. Each variable was tested separately to determine whether it differed between successional stages using a Wilcoxon rank sum test with continuity correction. For each variable, the average ± standard deviation are reported in each group along with the test statistic *W* and the *P*-value for the test.

	Early successional group	Late successional group	*W*, *P*
Elevation (m)	384 ± 114	413 ± 130	436.5, $P = 0.366$
Soil texture (sum of % silt and clay)	60.2 ± 4.93	60.5 ± 4.45	513, $P = 0.932$
Bunchgrass cover (%)	7.0 ± 3.4	9.9 ± 3.7	275.0, $P = 0.002$
B. tectorum cover (%)	2.6 ± 6.7	3.2 ± 4.3	384.5, $P = 0.110$
Bryophyte cover (%)	4.7 ± 5.4	16.9 ± 9.8	91.5, $P < 0.001$
Lichen cover (%)	4.8 ± 6.0	9.2 ± 7.6	263.5, $P = 0.002$

The final model for the late successional group (Fig. 2B; $\chi^2 = 2.2$, df = 5, $P = 0.81$) explained 62% of the variation in lichen cover and none of the variation in *B. tectorum*, bunchgrass, or bryophyte cover. The results imply that elevation, *B. tectorum* cover, and bryophyte cover all had strong negative effects on lichen cover. Bunchgrass cover and *B. tectorum* cover were negatively correlated, but not significantly. There was again evidence that cheatgrass had a strong negative effect on lichen cover but not *vice versa*.

3.3. Indicator species and BSC composition

In total, 41 species groups were documented, including nine bryophytes and 32 lichens (Appendix 1). A moss (*Pterygoneurum ovatum*) and a crustose lichen (*Caloplaca tominii*) were significant indicators of the early successional group (Table 3, Appendix 3). Nine species groups were significant indicators of the late successional group, including a liverwort (*Cephaloziella divaricata*), one moss, and eight lichens, including fruticose and lobate species (Table 3, Appendix 3).

The final distance-based linear model for the entire dataset included bunchgrass cover, successional stage, and *B. tectorum* cover and explained 21% of the variation in BSC composition (Table 4). The final model for the early successional group included bunchgrass cover and explained 13% of the variation in BSC composition. The final model for the late successional group included the main effects of *B. tectorum* cover and elevation and explained 19% of the variation in BSC composition.

The NMDS ordination had a stress of 0.12, and a non-metric fit of $R^2 = 0.98$. There was considerable overlap in the composition between the two groups (Fig. 3). Late successional transects were more similar to one another than were early successional transects. Some early successional transects had very similar compositions to late

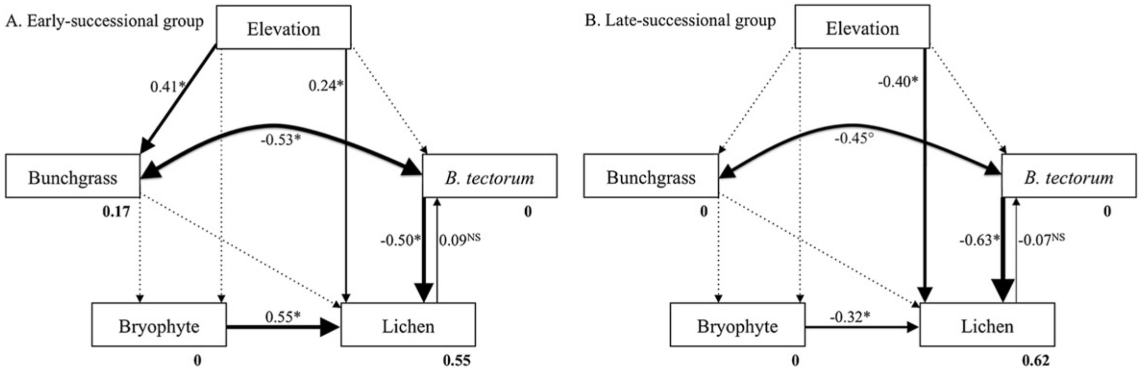

Fig. 2. Final models for (A) early successional and (B) late successional groups. Arrow width is proportional to the magnitude of the path coefficient and the standardized regression weight is listed with "*" indicating significant pathways ($P < 0.05$), "°" indicating marginally significant pathways ($P < 0.10$), or "NS" indicating non-significant pathways. Dotted arrows denote paths that were non-significant and set to 0. R^2 values are in bold below response variables.

successional transects, particularly if they were located at high elevations and/or with high bunchgrass cover. Early successional indicator species *C. tominii* and *P. ovatum* were associated with lower *B. tectorum* and bunchgrass cover. Late successional transects lower in elevation with lower bunchgrass and *B. tectorum* cover were associated with the indicator species *Syntrichia* spp., while fruticose lichens and a liverwort were associated with higher elevations and bunchgrass cover (Fig. 3A and B). In the early successional group, transects with low bunchgrass cover had lower total cover and higher proportion bryophyte than transects with high bunchgrass cover (Fig. 3C). Late successional transects had higher total BSC cover and a range of proportions of bryophyte cover (Fig. 3D).

4. Discussion

4.1. Differences in successional stage and models of BSC cover

Recent fire had significant effects on all native vegetation and BSC variables recorded, decreasing cover of plants and BSC. *B. tectorum* was found across the study area, similar in cover in both recently burned and mature areas. Though fire history was important in structuring both cover and composition, we found abiotic and biotic factors also affected BSC.

Table 3
Significant indicator species groups and group code of early ($n = 46$) and late-successional ($n = 22$) groups. Each species group is characterized by growth form (moss, liverwort, or various lichen morphologies; McCune and Rosentreter, 2007). For each indicator, the number of transects on which it occurred in that group is reported along with its Indicator Value (*IV*), and *P*-value. Complete indicator species information is provided in Appendix 3.

	Code	Growth form	Number of transects	*IV*	*P*
Early-successional group					
Pterygoneurum ovatum	PTOV	Moss	26	47.9	0.01
Caloplaca tominii	CATO18	Crustose lichen	21	32.4	0.02
Late-successional group					
Cladonia spp.	CLADO3	Squamulose lichen	21	69.0	0.01
c.f. *Syntrichia*	TORU70	Moss	22	65.6	0.01
Diploschistes muscorum	DIMU7	Crustose lichen	16	60.8	0.01
Leptochidium albociliatum	LEAL20	Lobate lichen	15	56.0	0.01
Leptogium sp.	LEPTO14	Foliose lichen	17	54.0	0.02
Small black crustose lichens	Smblk	Crustose lichen	17	50.6	0.02
c.f. *Buellia*	BUELL	Crustose lichen	12	43.7	0.02
Cladonia pocillum	CLPO60	Fruticose lichen	8	36.4	0.01
Cephaloziella divaricata	CEDI11	Liverwort	8	31.4	0.01

The results support the hypotheses that the lichen component of BSC cover is controlled by both abiotic and biotic factors, and that these relationships vary with successional stage. We found that vegetation type affects BSC, with native perennials having a different kind of effect (neutral) compared to the invasive annual, whose effect appears to be strongly negative. The network of relationships affecting BSC cover in this study supports separate reports of effects of disturbance history (Belnap and Eldridge, 2001), topography (Ponzetti et al., 2007), and vegetation community (Bowker et al., 2005) on BSC cover (Table 1).

Elevation had a strong positive effect on bunchgrass and lichen cover in the early successional group, whereas it had no effect and a negative effect, respectively, in the late successional group. The positive relationships in the early successional group may indicate that recovery of native vegetation and BSC occurs faster under cooler and moister conditions (Belnap and Eldridge, 2001) or that disturbances were less severe or more patchy under these conditions (Davies et al., 2012). However, we did not have data to quantify this, so further studies of this mechanism are warranted. In late successional transects, the decrease in lichen cover with increasing elevation may indicate that the highest elevation areas were less suitable, perhaps because they have exposed lithosol soils or steep slopes which may not retain sufficient available nutrients or water (Sackschewsky and Downs, 2001) to support mature BSC. Factors correlated with elevation, such as moisture availability and soil characteristics, determine the response to disturbance and the potential mature vegetation and BSC communities.

Table 4
Results of distance-based linear models for BSC community composition. Separate models were developed for the full dataset (68 transects), early successional group (46 transects), and late successional group (22 transects). Variables are reported in the order that they were included in each model.

	df	SS	Pseudo-*F*	Partial R^2	*P*
Full dataset					
Bunchgrass cover	1	1.06	9.67	0.12	0.002
Successional stage	1	0.51	4.65	0.06	0.002
B. tectorum cover	1	0.30	2.76	0.03	0.020
Residual	64	7.01		0.79	
Total	67	8.88			
Early successional group					
Bunchgrass cover	1	0.81	6.52	0.13	0.002
Residual	44	5.47		0.87	
Total	45	6.28			
Late successional group					
B. tectorum cover	1	0.24	2.63	0.11	0.006
Elevation	1	0.18	1.92	0.08	0.028
Residual	19	1.76		0.81	
Total	21	2.18			

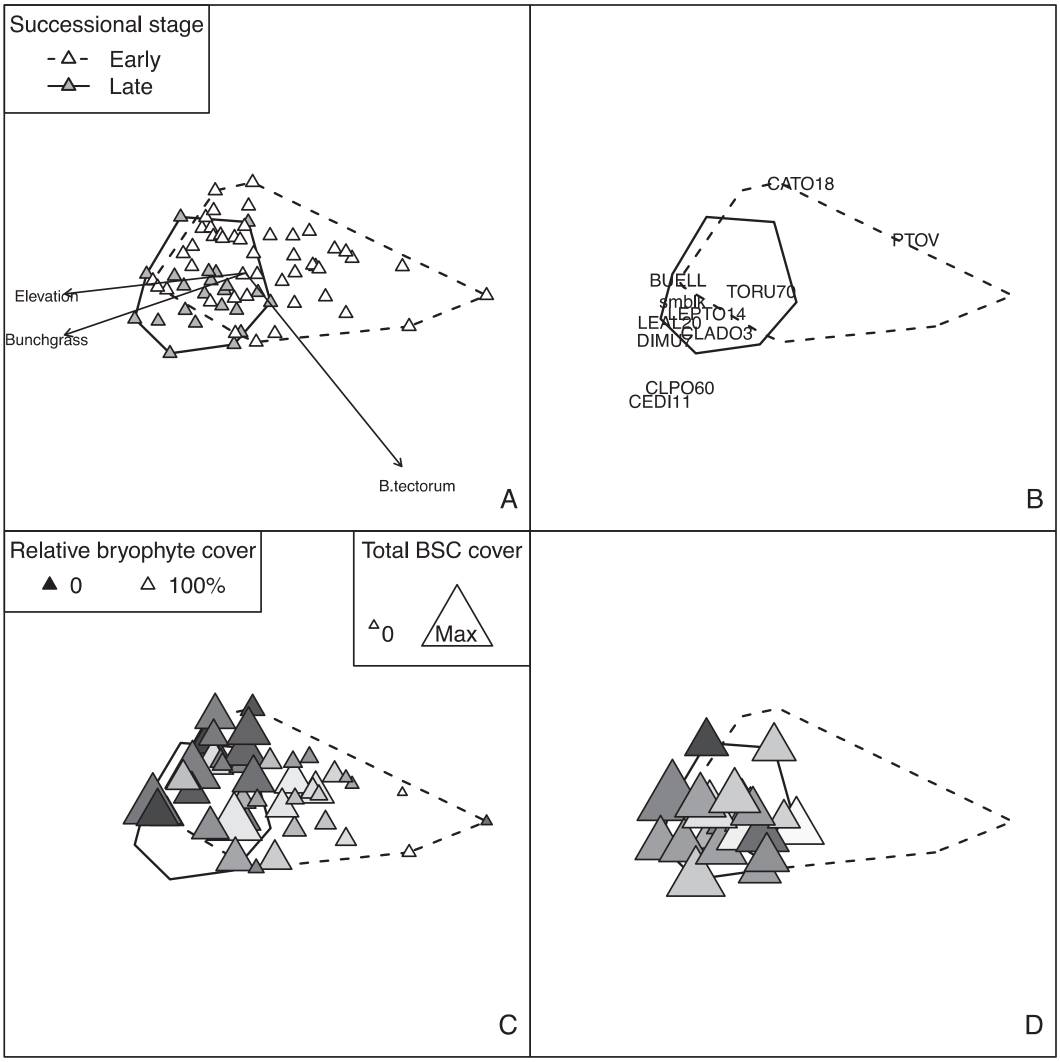

Fig. 3. First two of three dimensions of an NMDS ordination of BSC composition on 68 transects. The ordination had a stress of 0.12. Transects are coded by successional group and the space bounding all plots in each successional group is denoted with a polygon. Environmental variables were transformed as per Section 2.3.1. In A, the linear fits of elevation, bunchgrass and *Bromus tectorum* covers are overlaid on the ordination. In B, species centroids of indicator species for each successional group are indicated by the species group codes (Appendix 1). In C and D, symbol size is proportional to total average BSC cover on each transect and the symbol color is proportional to relative cover of bryophyte cover out of total BSC cover, with the legends in C applicable for both.

We found evidence that the sign of the relationship between native bryophytes and lichens switched with successional stage. Bryophyte cover had a strong positive effect on lichen cover in early successional transects in our model. In the time soon after a disturbance, remnant and recovering bryophytes may have a disproportionate impact on the successional trajectory of the BSC communities by stabilizing the soil and increasing productivity. In late successional transects, the model indicates that there were negative interactions between bryophyte and lichen cover, evidence of competition becoming stronger among BSC groups once total cover was high.

The final models did not support our *a priori* hypotheses that mechanisms involving *B. tectorum* in these communities vary with successional stage. We expected to find the relative strengths of effects between *B. tectorum* and lichen to switch between early and later successional stage. Instead, *B. tectorum* appears to negatively affect lichen cover in both stages. Fire and herbicide may have reduced the cover of *B. tectorum* initially in early-successional transects, but *B. tectorum* can increase in abundance again thereafter (Chambers et al., 2007), perhaps with a priority effect over slow-recovering BSC. In late successional stages, *B. tectorum* was still negatively related to BSC. Serpe et al. (2008) found that *B. tectorum* germination was reduced by *Diploschistes* crust which was as an indicator in our late successional group, but the presence of *B. tectorum* in the late successional transects demonstrates that it can successfully invade. This indicates that at this large scale, lichen cover may be insufficient to prevent *B. tectorum* invasion, and instead that *B. tectorum* can degrade native communities even in the absence of fire by competing for space and resources or exploiting other disturbances (Section 4.3) that remove vegetation and BSC.

Several other relationships were the same in both early and late successional stages. Elevation had no significant effect on *B. tectorum* cover. This likely reflects ongoing land management activities, particularly herbicide applications targeted at *B. tectorum* in lower elevations, because *B. tectorum* had reached high percent cover in many areas prior to and after some of the fires (Evans and Lih, 2005). Unfortunately, we did not have sufficient replication of unsprayed transects at comparable elevations to examine the effects of this herbicide treatment. Bunchgrasses and *B. tectorum* had negative relationships in both successional stages, indicating that at both low and high total vegetation cover (Table 2), perennial native species are competing with *B. tectorum*.

Bryophyte cover did not show a significant response to any measured variable. Bryophytes can colonize and grow more rapidly than can many lichens, so perhaps as little as three years (the time from the most recent fire to our observations) was sufficient for bryophytes to colonize and begin to grow in all suitable habitats. Several species of moss were found on nearly every transect (Fig. 3C and D, Appendix 3), indicating that there was habitat to support bryophyte growth at all locations sampled.

In contrast to our results showing no relationship between perennial bunchgrasses and BSC and negative relationships between *B. tectorum* and BSC, Chaudhary et al. (2009) found a negative relationship between total vegetation cover and BSC cover in the cool desert in Utah. The differences in scale may account for the differences in the net relationships because we averaged across transects whereas Chaudhary et al. (2009) examined individual quadrats where dense vegetation cover would compete with BSC for soil resources and could shade the soil surface. Our results demonstrate that at broad scales, functional groups can determine the relationship with BSC cover. Bunchgrasses provide discontinuous fuel so fire may travel slowly without damaging the soil surface, whereas high *B. tectorum* cover and litter accumulation enable direct contact between flames and the soil surface; the fire behavior in these two types of vegetation would therefore differentially affect BSCs present. The appropriate plant functional groups to examine may depend on their structure, life history, phenology, litter deposition patterns, and other traits. This study indicates that plant identity may be important to consider for BSC response to vegetation community changes and fire.

4.2. *Indicator species and BSC composition at different successional stages*

Species groups responded differentially to effects of fire, elevation, and vegetation, leading to different drivers for composition than cover. Early successional transects showed a gradient of cover and composition from areas with high *B. tectorum* cover to high elevation, high bunchgrass cover sites, whereas late successional transects did not have a clear trend (Fig. 3C and D). Many species groups occurred in both successional groups (Appendix 1), and relatively few were significant indicators of one successional stage over the other.

Indicator species at our transects were similar to species identified as early or late successional species in other studies. We found *P. ovatum* as an indicator in the early successional group, and mosses such as *P. ovatum* and small mosses including *Bryum* spp., *Encalypta vulgaris*, and *Ceratodon* spp. have been found soon after disturbance (Evans and Johansen, 1999; Hilty et al., 2004). We identified *C. tominii*, a crustose lichen with vegetative diaspores, as an indicator in early successional transects, and it has been shown to reinvade within two years following fire (Johansen et al., 1984). A tall moss, *Syntrichia* spp, and fruticose and foliose lichens such as *Cladonia pocillum* and *Leptochidium albociliatum* were associated with late successional transects, as previously observed in this area (Ponzetti et al., 2007).

Biological soil crust composition varied between successional stages (Table 4), but there was considerable overlap (Fig. 3), indicating that while cover of BSC was strongly affected by successional stage, the species composition did not respond as strongly. Due to small-scale disturbances (Section 4.3), a patchwork of early successional and late successional species were found within most of the transects. Overall variation in composition was driven primarily by bunchgrass cover (Table 4), indicating differences in BSC species tolerance the conditions created by large bunchgrasses. *B. tectorum* cover was also important in explaining variation within the late-successional community, indicating species group-specific tolerances to vegetation functional type and cover. Elevation also affected late successional composition, perhaps reflecting the effect of stonier soils at the highest elevations.

The recovering plant community structure could be indicative of the recovery of BSC composition. Bunchgrass cover was significantly related to BSC composition in the early successional group. Bunchgrasses are presumed to have resprouted after fire rather than having germinated and established. Early successional transects with high bunchgrass cover and low *B. tectorum* cover were more similar in composition to late successional transects (Fig. 3). Pre-fire conditions or fire behavior may have differed at transects where we found high bunchgrass cover and low *B. tectorum cover*, or recovering bunchgrasses may have facilitated the recovery of certain species of BSC, but we do not have sufficient information to suggest which of these is the mechanism.

Elevation and *B. tectorum* cover were significantly related to late successional composition. Species distributions have been shown to differ by landscape strata such as ridges, draws, and slopes of warm or cool aspects (Ponzetti et al., 2007), so elevation, with correlated moisture availability, affects the potential species composition. *B. tectorum* may invade sites already altered by some disturbance other than fire (Section 4.3), and the densely growing individuals and accumulation of litter may block light from BSC. Biological soil crust species that tolerate reduced light may persist while others are removed, thereby shifting composition in late successional plots that have higher *B. tectorum* cover.

4.3. *Other factors affecting BSC cover and composition*

Although the models of BSC cover and composition fit statistically, there was considerable unexplained variation in all models. Factors we did not include in the models, including fire regime details, herbivory and other disturbance history, soil chemistry and physical properties, ground cover (litter, vegetation, rock), and microtopography, may be important in this context.

Although this study occurred in the sagebrush shrub-steppe, shrubs were absent from many of the transects due to previous fire. The relationships of BSC with this functional group may be different than with bunchgrass-dominated native vegetation. Biological soil crusts can grow under the canopy of shrubs but are destroyed by the higher intensity fire associated with burning woody material and hence require longer recovery times (Hilty et al., 2004; Muscha and Hild, 2006). The nature of the fire regimes experienced by these transects may therefore have affected BSC cover and composition. For example, all of the early successional transects burned in or after 2000. Where those fires were the first after a long fire-free interval, they removed the shrubs, burned more severely, and therefore had an extensive effect on the vegetation (Davies et al., 2012) and BSC. In contrast, where those fires were re-burns of areas whose shrubs had already been removed in prior fires, they might not have had as large an effect on the BSC. The return interval of repeated fires may alter the trajectory of the recovering community (Davies et al., 2012). However, the relationships between shrub cover and BSC and questions about fire regimes were beyond the scope of this study.

Previous studies have found that large herbivores can severely damage BSC through trampling (Marble and Harper, 1989). Sheep and cattle had been present on nearly all transects in the past, and several transects were located in active pastures. Additionally, we found fresh hoof prints or dung of native herbivores (deer or elk) on every transect indicating that there is current herbivore disturbance.

Small-scale disturbances such as mounds created by burrowing mammals were commonly observed on the landscape. These patches of bare mineral soil could enable early successional BSC to persist within the matrix of a mature BSC community. Because we averaged across quadrats within each transect, we did not examine local disturbances with quadrats; these may help explain the overlap in BSC composition between early and late successional stages.

4.4. Conclusions

The loss of BSCs may trigger transitions across structural and functional thresholds in arid lands because their loss affects diversity, biomass, and nutrient cycling. Once thresholds are crossed, recovery often does not occur passively (Bowker, 2007), so although cyanobacteria may be present and active, mature bryophytes and lichens may not be maintained. If fires burn frequently and over large spatial scales, there may not be time or remaining source populations allowing recovery to occur, and the system may change to an invasive-dominated state (Davies et al., 2012) with concurrent loss of late successional BSC species. Additionally, functions such as nitrogen fixation may take longer to recover than species richness and cover (Evans and Johansen, 1999); the loss of these functions may create further feedbacks leading to degradation.

These results can be used to prioritize actions by managers seeking to prevent the degradation of or to restore BSC communities for purposes of preventing erosion, increasing nutrient cycling, or increasing biodiversity. For example, protection could focus on areas with low relative *B. tectorum* cover, as these have the highest BSC cover and most mature BSC composition. Following disturbance, bunchgrasses could be planted to compete with invasive species or herbicide could be applied, but the effect of herbicide on non-target plants and BSC organisms must be considered. Finally, this study supports previous designations of some BSC species as indicators of early and late successional states; monitoring could focus on these species to gain insight into the successional stage of the BSC community.

This study supports the hypothesis that relationships between biotic communities and their environment change with successional stage (Callaway and Walker, 1997). Early in succession, native bryophytes and moderate environmental conditions were associated with higher lichen cover, while later in succession competitive relationships between these two groups dominated. These data also imply that *B. tectorum* leads to reductions in BSC cover whenever it invades. Results also indicate that cover and composition of BSC respond to different environmental and abiotic factors. It appears that time since fire has a dramatic effect on the cover and composition of vegetation and BSC communities in the sagebrush shrub-steppe.

Acknowledgements

G. Matt Davies assisted with the design of the study and with vegetation surveys. Katherine Glew, Roger Rosentreter, Heather Root, Jeanne Ponzetti, and Terry McIntosh assisted with lichen and bryophyte identification. Heidi Newsome and staff at U.S. Fish and Wildlife Service Hanford Reach National Monument and Barbara Benner and staff at the U.S. Bureau of Land Management provided site history and other assistance relating to the study sites. We thank the private landowners who allowed access to their property. Jean Caldwell assisted with GIS analysis. Scott Batiuk assisted with field work. We thank the reviewers of the manuscript, including Matthew Bowker and Matthew Whalen, as well as D.A. Ravetta and David Eldridge for valuable feedback on earlier versions of the manuscript. Funding was provided by the Joint Fire Science Program under Project JFSP 08-1-5-20. Support for Jim Grace provided by the USGS Ecosystems and Climate Change Programs. The use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2013.01.013.

References

Anderson, D.C., Harper, K.T., Holmgren, R.C., 1982. Factors influencing development of cryptogamic soil crusts in Utah deserts. Journal of Range Management 35, 180–185.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32–46.

Arbuckle, J.L., 2010. IBM SPSS AMOS 19 Users Guide. Amos Development Corporation, Crawfordville, FL.

Bakker, J.D., 2008. Increasing the utility of indicator species analysis. Journal of Applied Ecology 45, 1829–1835.

Beckstead, J., Augspurger, C.K., 2004. An experimental test of resistance to cheatgrass invasion: limiting resources at different life stages. Biological Invasions 6, 417–432.

Belnap, J., Eldridge, D., 2001. Disturbance and recovery of biological soil crusts. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function, and Management. Springer-Verlag, Berlin, pp. 363–383.

Belnap, J., Phillips, S.L., Troxler, T., 2006. Soil lichen and moss cover and species richness can be highly dynamic: the effects of invasion by the annual exotic grass *Bromus tectorum*, precipitation, and temperature on biological soil crusts in SE Utah. Applied Soil Ecology 32, 63–76.

Bowker, M.A., 2007. Biological soil crust rehabilitation in theory and practice: an underexploited opportunity. Restoration Ecology 15, 13–23.

Bowker, M.A., Belnap, J., Davidson, D.W., Phillips, S.L., 2005. Evidence for micronutrient limitation of biological soil crusts: importance to arid-lands restoration. Ecological Applications 15, 1941–1951.

Breen, K., Levesque, E., 2006. Proglacial succession of biological soil crusts and vascular plants: biotic interactions in the high Arctic. Botany 84, 1714–1729.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D.A., 2004. Effects of invasive alien plants on fire regimes. Bioscience 54, 677–688.

Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78, 1958–1965.

Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whittaker, A., 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77, 117–145.

Chaudhary, V.B., Bowker, M.A., O'Dell, T.E., Grace, J.B., Redman, A.E., Rillig, M.C., Johnson, N.C., 2009. Untangling the biological contributions to soil stability in semiarid shrublands. Ecological Applications 19, 110–122.

Clarke, K.R., 1993. Non-parametric multivariate analyses of change in community structure. Australian Journal of Ecology 18, 117–143.

Clarke, R.K., Somerfield, P.J., Chapman, M.G., 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. Journal of Experimental Marine Biology and Ecology 330, 55–80.

Cohen, J., Cohen, P., West, S.G., Aiken, L.S., 2003. Applied Multiple Regression/correlation Analysis for the Behavioral Sciences, third ed. Routledge Press, New York.

Daubenmire, R., 1970. Steppe Vegetation in Washington. In: Technical Bulletin 62. Washington Agricultural Experimental Station, pp. 1–131.

Davies, G.M., Bakker, J.D., Dettweiler-Robinson, E., Dunwiddie, P., Hall, S.A., Downs, J., Evans, J.R., 2012. Trajectories of change in sagebrush-steppe vegetation communities in relation to multiple wildfires. Ecological Applications 22, 1562–1577.

Deines, L., Rosentreter, R., Eldridge, D.J., Serpe, M.D., 2007. Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. Plant and Soil 295, 23–35.

del Moral, R., Lacher, I.L., 2005. Vegetation patterns 25 years after the eruption of Mount St. Helens, Washington, USA. American Journal of Botany 92, 1948–1956.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366.

Eldridge, D.J., Rosentreter, R., 1999. Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. Journal of Arid Environment 41, 11–25.

Evans, J.R., Lih, M.P., 2005. Recovery and Rehabilitation of Vegetation on the Fitzner-Eberhardt Arid Lands Ecology Reserve, Hanford Reach National Monument, Following the 24 Command Fire. The Nature Conservancy, Seattle, Washington.

Evans, R.D., Johansen, J.R., 1999. Microbiotic crusts and ecosystem processes. Critical Reviews in Plant Science 18, 183–225.

Flowers, S., 1973. Mosses: Utah and the West. Brigham Young University Press, Provo, UT.

Grace, J.B., 2006. Structural Equation Modeling and Natural Systems. Cambridge University Press.

Grace, J.B., Bollen, K.A., 2008. Representing general theoretical concepts in structural equation models: the role of composite variables. Environmental and Ecological Statistics 15, 191–213.

Grace, J.B., Anderson, T.M., Olff, H., Scheiner, S.M., 2010. On the specification of structural equation models for ecological systems. Ecological Monographs 80, 67–87.

Grace, J.B., Schoolmaster Jr., D.R., Guntenspergen, G.R., Little, A.M., Mitchell, B.R., Miller, K.M., Schweiger, E.W., 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. Ecosphere 3, 44. article 73.

Hilty, J.H., Eldridge, D.J., Rosentreter, R., Wicklow-Howard, M.C., Pellant, M., 2004. Recovery of biological soil crusts following wildfire in Idaho. Journal of Range Management 57, 89–96.

Johansen, J.R., St. Clair, L.L., Webb, B.L., Nebeker, G.T., 1984. Recovery patterns of cryptogamic soil crusts in desert rangelands following fire disturbance. The Bryologist 87, 238–243.

Kaltenecker, J.H., Wicklow-Howard, M.C., Rosentreter, R., 1999. Biological soil crusts in three sagebrush communities recovering from a century of livestock trampling. USDA Forest Service Proceedings RMRS-P-11, 222–226.

Levine, J.M., Adler, P.B., Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecological Letters 7, 975–989.

Marble, J.R., Harper, K.T., 1989. Effect of timing of grazing on soil-surface cryptogamic communities in a Great Basin low-shrub desert: a preliminary report. Great Basin Naturalist 49, 104–107.

McCune, B., Rosentreter, R., 2007. Biotic soil crust lichens of the Columbia Basin. Monographs in North American Lichenology 1, 1–105.

McIntosh, T.T., 2003. Biological soil crusts of the Hanford Reach National Monument. In: Biodiversity Studies of the Hanford Site. Final Report: 2002–2003. The Nature Conservancy of Washington, Seattle, WA. www.pnl.gov/ecomon/Docs/Doc.html (accessed 12.05.11.).

Melgoza, G., Nowak, R.S., Tausch, R.J., 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. Oecologia 83, 7–13.

Muscha, J.M.A., Hild, A.L., 2006. Biological soil crusts in grazed and ungrazed Wyoming sagebrush steppe. Journal of Arid Environments 67, 195–207.

Norton, J.B., Monaco, T.A., Norton, J.M., Johnson, D.A., Jones, T.A., 2004. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. Journal of Arid Environments 57, 445–466.

NRCS, 2011. Natural Resources Conservation Service. United States Department of Agriculture. Web Soil Survey. http://websoilsurvey.nrcs.usda.gov/ (accessed 6.06.11.).

Ponzetti, J.M., McCune, B., Pyke, D.A., 2007. Biotic soil crusts in relation to topography, cheatgrass and fire in the Columbia Basin, Washington. The Bryologist 110, 706–722.

Sackschewsky, M.R., Downs, J.L., 2001. Vascular Plants of the Hanford Site. Pacific Northwest National Laboratory, Richland, WA.

Serpe, M.D., Zimmerman, S.J., Deines, L., Rosentreter, R., 2008. Seed water status and root tip characteristics of two annual grasses on lichen-dominated biological soil crusts. Plant and Soil 303, 191–205.

USDA, NRCS, 2011. The PLANTS Database. National Plant Data Team, Greensborough, NC (accessed 15.10.11.). http://plants.usda.gov.

Western Regional Climate Center, 2001. Prosser 4 NE, Washington: Period of Record Monthly Climate Summary 1981–2010. http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wa6768 (accessed 6.06.11.).