Patterns in biological soil crust recovery in Conservation Reserve Program fields, Washington State

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ABSTRACT.

KEYWORDS. Biological soil crust, bryophytes, mosses, lichens, shrub-steppe, recovery, Washington State.

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INTRODUCTION

Background and Research Objectives

Historically, shrub-steppe ecosystems dominated over 645,000 km^2 of the western North American landscape, extending from northern California into southern Canada (Rickard *et al*. 1988). This ecosystem is characterized by shrubs, most often species of sagebrush, *Artemisia* spp., perennial bunchgrasses, a diverse forb component, and, in the spaces between the vascular plants, a biological soil crust, also known as a biotic, microbiotic, or cryptogamic crust. Preceding settlement, shrub-steppe was the prevalent habitat type throughout much of eastern Washington (Daubenmire 1970, Vander Haegen *et al*. 2004). Since then, however, mainly through conversion to crop production, over 60% of the shrub-steppe in Washington has been lost (Vander Haegen *et al*. 2004). The remaining shrub-steppe is highly fragmented and usually severely degraded mainly by livestock, invasion by exotic plants, and changes in fire frequency (Vander Haegen *et al*. 2004). Concurrent with these impacts to the shrub-steppe habitats has been the loss and degradation of biological soil crusts in eastern Washington. Biological crusts are fragile and readily disturbed, often degrading before vascular plant assemblages (Belnap *et al.* 2001).

Living soil crusts are important components of healthy shrub-steppe ecosystems. They are comprised of complex associations of organisms that includes lichens, bryophytes (including mosses and a few species of liverworts), single-celled algae, cyanobacteria, and fungal hyphae intermixed with plant roots, litter, and soil (Belnap *et al.* 2001, Belnap 2003). Soil crusts perform a number of ecological functions that contribute to the ecosystem integrity and health of shrub-steppe (Belnap *et al.* 2001, Evans and Johansen 1999, Hilty *et al.* 2004, Jones and Rosentreter 2006, McIntosh 2003, Ponzetti and McCune 2001). They bind soil surfaces increasing soil stability by reducing or eliminating soil displacement (Belnap 2003, Schulten 1985). The complex surficial microtopography of a biological crust creates a boundary of still air and further protects the soil from wind erosion (Eldridge and Kinnell 1997, Lehrsch *et al.* 1988, Leys and Eldridge 1998, Neuman and Maxwell 1999). Crusts have been shown to increase water infiltration rates (Eldridge 1993). The presence of an intact biological crust appears to inhibit the establishment of cheatgrass (*Bromus tectorum* L.) and other invasive species (Belnap *et al.* 2001, Kaltenecker *et al.* 1999, Wicklow-Howard *et al.* 2003). Lichens and cyanobacteria fix atmospheric carbon and nitrogen, contributing to the overall productivity of a plant community (Belnap 2001, Belnap *et al.* 2001, Evans and Belnap 1999). In some cases, vascular plants in areas of well developed crusts have higher accumulations of essential mineral nutrients than in sites that lack crusts (Belnap *et al.* 2001, Ridenour and Callaway 1997). Crusts may enhance the establishment and survival of vascular plant seedlings by increasing the availability of essential mineral nutrients (Harper and Belnap 2001, Pendleton *et al.* 2004). Recent research (Li *et al.* 2006, Zack *et al.* 2003) has shown that the presence of biological soil crusts significantly increases the diversity and abundance of insect species in arid areas.

Because of its ecological importance and the constant threats to both extent and quality, shrub-steppe warrants special management consideration. One initiative is the Conservation Reserve Program (CRP) which is currently the only large-scale effort designed to manage the restoration of shrub-steppe for use by native wildlife in the Columbia Basin. Administered by the US Department of Agriculture (USDA), this voluntary program pays farmers to take agricultural lands out of production in order to achieve conservation objectives that include enhancing wildlife habitat and reducing soil erosion. Through the CRP in Washington, over 400,000 ha of former croplands have been managed, through planting and restricting use, by the CRP. Although CRP fields were planted with a variety of non-native grasses early in the program, an increasing number of fields have been planted with native grasses, forbs, and arid-land shrubs as the program has developed. In some cases, native shrubs, particularly big sage, and some native herbaceous species have seeded into former cultivated areas from adjacent shrub-steppe habitats. Research, in particular by the Washington Department of Fish and Wildlife (WDFW), has been developed to evaluate the potential role of the CRP in long-term shrub-steppe conservation in the Columbia Basin. To date, this research has mainly focused on wildlife, in particular birds, mammals, and reptiles (Vander Haegen *et al.* 2004).

In 2004, the WDFW initiated a study designed to evaluate the re-establishment and recovery of biological soil crusts in recovering CRP fields. Although a great deal of research has been completed in other parts of North America and elsewhere on soil crusts, little research has been completed in Washington State. The few regional studies include Daubenmire (1970) who discussed crusts in his seminal work on shrub-steppe, Johansen *et al.* (1993) studying the effects of fire on the algal and cyanobacterial crust components on the Arid Lands Ecology Reserve, Ponzetti and McCune (2001) who studied soil crust community composition in relation to soil chemistry, climate, and livestock activity in the Horse Heaven Hills, and McIntosh (2003) who studied biological crust diversity and community assemblages at the Hanford Reach National Monument.

Although some literature is available that discusses soil crust recovery following fire (e.g., Hilty *et al.* 2004, Johansen *et al.* 1986, 1993) or livestock trampling (e.g., Anderson and Rushforth 1982, Anderson *et al.* 1982, Evans and Belnap 1999, Johansen and St. Clair 1986, Kaltenecker *et al.* 1999), research is lacking that examines the re-establishment of a biological crust from a completely barren environment, in our case following long-term disturbance by plowing and subsequent crop management. The main aim of this paper is to initiate the assessment of patterns of recovery and succession of the biological soil crust in the CRP research program. This study is the first part of a larger study of biological soil crust recovery, succession, and classification in the Columbia Basin.

Research Constraints

An inherent problem with the study of biological soil crusts is the identification of their component lichen and bryophytes species. A concentrated period of training is often necessary before the identity of most of the taxa can be positively confirmed in the field or, if collected, in the laboratory. However, because most of the soil crust research has been undertaken by scientists who are well-trained in lichen taxonomy, a variety of references are available that help in lichen identification. The most comprehensive work is the recent soil lichen monograph by McCune and Rosentreter (2007), although Goward *et al*. (1994), McCune and Rosentreter (1995), and Brodo *et al*. (2001) are also useful. Lichen specimens often need chemical tests to confirm identification so laboratory work or sending specimens to experts is sometimes necessary. Bryophytes pose a more serious problem than lichens because arid land-specific guides are lacking, except for the regional treatments of Flowers (1973) and McIntosh (1986, 1989). Additional references include Lawton (1971) and Rossman (1977). However, the recently published Volume 27 for the Flora of North America (Buck *et al.* 2007) provides keys and some illustrative material for most of the dryland moss taxa likely to be encountered in the study area. In addition to taxonomic difficulties, sterile lichen thalli or juvenile mosses are often observed in plots, and identification is not possible in most of these cases, so some 'lumping' of observations is necessary. However, these taxa usually make up only a small portion of the soil crust.

Difficulties in identification have been noted Rosentreter *et al.* (2001) and Rosentreter and Eldridge (2002) who recommend using morphological groups (that is, grouping lichens or mosses of similar ecological function/response) and measuring the cover of these groups in plots versus individual species. Although this method does allow for a more rapid collection time, easier identification, and some quantification of large-scale trends, it does not allow for fine-grained species by species analyses, an important step considering that there are probably 'response' overlaps within or between the various morphological groups. Further, mosses are often lumped as either tall or short mosses, and this is unsatisfactory with respect to mosses: in many instances, even if lichens dominate the crust cover, the diversity of mosses is relatively high, and, although we are still learning about their successional responses, many of the 'short' mosses are early successional and others are late successional, and some smaller mosses, if environmental conditions are favourable, may be scored as 'tall' mosses.

A further constraint on the present work is the general study design and the restrictions it places on subsequent data analyses. This soil crust study was broad-based and limited in time and scope, and it was necessary to gather within the pre-determined WDFW CRP sampling design (discussed below). Many of the sites that are used for comparison in the CRP project are kilometers apart, and are dissimilar with respect to a number of environmental variables, in particular soils (e.g., stoniness vs. sandiness), but also slope and aspect. Also, the past history (e.g., grazing, fire, seeding treatments) often varies considerably between sites. Thus, at this time and until more work is completed at a more local scale, it was necessary to provide only qualitative and semi-quantitative analyses of the data.

STUDY AREA

The study was undertaken in a series of eight CRP research areas, or clusters, to the east and west of Coulee City in east-central Washington State. These sites stretch across an approximate 90km diagonal (Fig. 1).

METHODS

Study Design

Research was completed during three field sessions, from July 21 to 22, and from September 21 to 23, 2004, and from July 13 to 16, 2006. For our soil crust study, we incorporated the CRP study design implemented in 2000 by the WDFW (Vander Haegen *et al*. 2004). Each of the eight CRP research areas (in the Black Rock, Chester Butte, Coyote Canyon, Jameson Lake, Pine Canyon, Pacific Lake, Swanson Lake, and Tracy Rock areas) is comprised of a matrix of shrub-steppe, recently planted CRP fields (planted between 1998-2000), older CRP fields (planted between 1986-1988), and fields that are presently in cultivation. Six treatments were delineated within each of the eight research areas that would show changes or differences in wildlife between sites with different associated habitats (totaling 48 treatments). These treatments, where permanent large plots were established, are (followed by the acronym that has been assigned to each treatment):

1. new CRP fields surrounded by cultivated fields (NC)
2. new CRP fields surrounded by shrub-steppe (NS; Fig. 2)
3. old CRP fields surrounded by cultivated fields (OC; Fig. 3)
4. old CRP fields surrounded by shrub-steppe (OS)

5. shrub-steppe surrounded by cultivated fields (SC; Fig. 4)
6. shrub-steppe surrounded by shrub-steppe (SS)

Figure 2. Typical new CRP field (Coyote Canyon: CCNS).

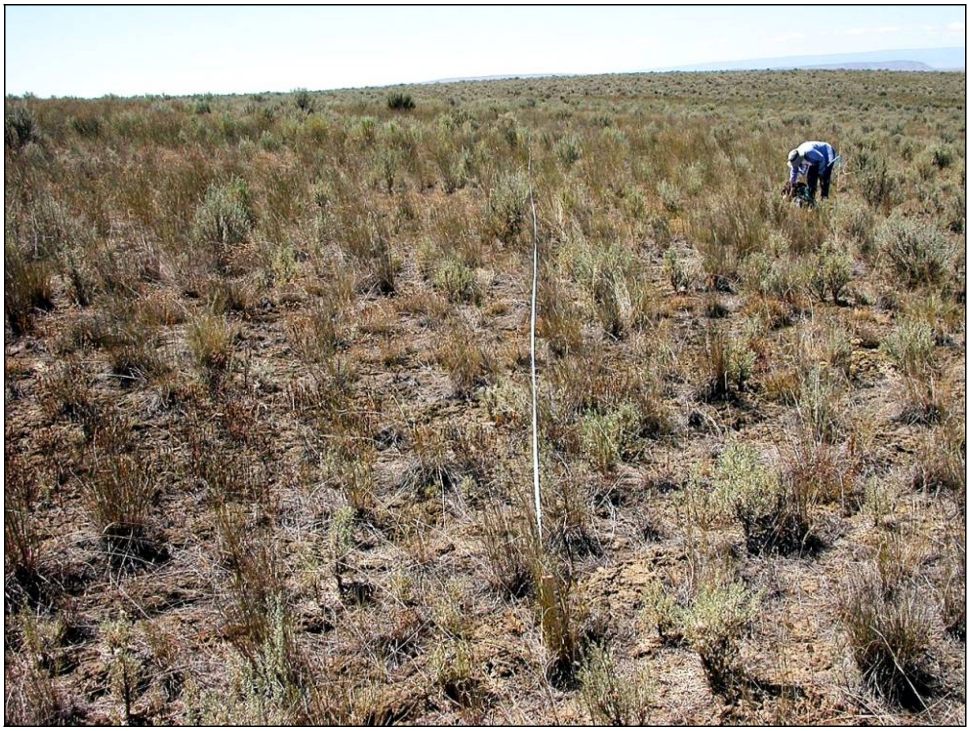

Figure 3. Typical old CRP field (Coyote Canyon: CCOC).

Figure 4. Typical shrub-steppe site (Coyote Canyon: CCSC).

Field Work

At each research area, we first randomly placed a 50m transect as close to an area center post as possible and within a habitat that best represented the habitat as a whole. Transects were laid parallel to a slope, if present, and UTMs (NAD27) were logged at the start of each transect. A list and collection of lichens and bryophytes was then made within an approximately 10m area around the transect. This was completed during a five to ten minute survey through the adjacent area until no new taxa were observed. Representative collections were placed in paper bags. Soil crust and environmental variables were then measured in twenty 20 X 20 cm plots at 1m intervals along each transect. If a plot was located on a spot that was not representative of the site, i.e., under a shrub (where the crust often has a different species composition and cover; McIntosh 2003), centered on a large grass tussock or rock, or in an area of atypical disturbance, the plot was moved either to the opposite side of the transect, or 0.5m along the transect if the opposite side was also not representative.

In each plot, surface cover of total biological crust, mineral soil, litter, vascular plant bases, stones or rock, and individual bryophyte and lichen species, or unknown taxa, were estimated using the cover estimation scale of Ponzetti and McCune (2001; Table 1), and cover data recorded on plot sheets. This sampling scale is useful when working with small species in small plots, and it reduces errors that would arise if actual percent were estimated. One observer was used for all plots in order to reduce estimation error. Ambiguous taxa, usually juvenile, sterile, or fragmented, were found in plots along all transects, and these were lumped into two categories: unidentified bryophytes or unidentified lichens. Collections were made of these taxa for identification later, if possible. All or the large majority of the species present along or near the transect were captured in the sampling plots. The principal author identified all of the bryophytes and most of the lichen taxa. A few of the lichen identifications were made by C. Bjork and T. Goward.

Sampling of the biological soil crust was completed in 47 of the 48 treatment sites; the crust in the NC treatment in the Black Rock research area was not measured as recent harvesting and vehicle use significantly altered the site.

Table 1. Sampling Cover Scale (from Ponzetti and McCune 2001)

Scale Value	Representative % Cover
1	< or = 1
2	> 1 - 4
3	> 4 – 10
4	> 10 – 25
5	> 25 – 50
6	> 50 – 75
7	> 75 – 95
8	> 95 - 100

Data Manipulation

Prior to data analysis, cover data of the environmental variables, lichens, and bryophytes were totaled for the 20 plots from each of the 47 treatment site and entered in to an EXCEL file. Unidentified lichen and moss records (<0.5% of the total) were not used in the data analysis, whereas other taxa that could not be confirmed to the species level were grouped into three broad-based genera before analysis. They are:

1. Species of *Cladonia*: species of *Cladonia* often are admixed in the field, with their squamules often overlapping somewhat, and most do not produce podetia (reproductive structures) in open habitats; podetia are usually critical for positive identification; however, some fertile collections were made in a few sheltered sites and the species that were identified and likely in the plots are listed in Table X (in similar habitats in British Columbia, the two most common species appear to be *Cladonia pyxidata* and *C. cariosa*).
2. Blackish lichen crust: most of this crust is probably comprised of species of *Collema*, but also of small *Leptogium* spp. or *Placynthiella uliginosa*; this group is one of the most difficult to identify, even with mature and fertile material.
3. *Syntrichia* (formerly *Tortula*): three species of *Syntrichia* were identified from the CRP fields, *S. caninervis*, S. *papillosissima*, and *S. ruralis*; the former two species were only observed once, and only *S. caninervis* was captured in a

plot, with a minimal cover value. The three species can be very difficult to separate in the field, but, because the former two taxa are probably rare in the soil crust, all records during sampling are treated as *S. ruralis*.

In an attempt to illustrate relationships or trends, treatment site and species data were assessed using Detrended Correspondence Analysis (using a free program called PAST; Hammer et al. 2001). The environmental and total crust cover attributes (see Table 3) were excluded from this analysis based on separate analyses using a variety of other programs including Canonical Correspondence (although a few patterns relating to the environmental data emerged from these analyses and are discussed below, these patterns were deemed inconclusive and possibly erroneous). Analysis of species and treatment site data were completed twice, the first time including all 33 species and species groups, and the second with a reduced set of species (N = 15; species were removed from the data set if they appeared in three or fewer of the 47 treatments; the removal of these species did not affect ordination results, but clarified the final illustrations considerably). The fifteen taxa used in the analyses are listed in Table 1 and in the caption for beneath Fig. 9. *Cladonia* spp. were grouped as CL, the blackish lichen group as CO, and the *Syntrichia* complex as SR.

RESULTS AND DISCUSSION

Species Diversity and Richness

Table 2 lists the taxa that were recorded or observed growing in biological soil crusts during this study. Included are twenty-six species of lichens, two of which remain unidentified (*Leptogium* sp. and *Collema* sp.), and twenty-one species of bryophytes, including three liverworts. One moss species, *Grimmia* cf. *alpestris*, and one liverwort, *Riccia* cf. *sorocarpa*, are only tentatively identified. In all cases, identifications have not been completed because of scant and sterile material. Of these taxa, the large majority were encountered during plot sampling. The nine taxa that were not captured are rare in all of the open soil crusts where we sampled, although of them are more common in other habitats: *Grimmia* cf. *alpestris* on rock or large stones, and *Syntrichia papillosissima* under larger shrubs, in particular big sage.

Table 2. Lichens and bryophytes recorded along or adjacent to CRP transects (taxa observed near the transects but not captured in the plots are denoted with a *)

Lichens	**Code**	**Taxon Cover Values** (numbers below indicate the total cover value for each treatment type across 8 research areas)		
		N	**O**	**S**
Acarospora schleicheri	AS	0	0	10
Arthonia glebosa		0	5	0
Aspicilia reptans	AR	0	1	64

*Caloplaca jungermanniae**				
*Caloplaca tominii**				
Candelariella terrigena		0	0	1
Cladonia cariosa	CL			
Cladonia chorophaea	CL			
Cladonia pocillum	CL			
Cladonia pyxidata	CL			
	Total CL	0	142	792
Collema tenax	CO			
Collema sp.	CO			
	Total CO	0	231	378
Diploschistes muscorum	DM	0	2	81
*Endocarpon pusillum**				
Lecanora muralis		0	0	1
*Lecidiella stigmatea**				
Leptochidium albociliatum		0	0	1
*Leptogium lichenoides**				
Leptogium sp.		0	0	9
*Peltigera lepidophora**				
Peltigera rufescens		0	0	3
Phaeorrhiza sareptana		0	0	6
Placynthiella uliginosa	Co			
Psora globifera	PG	0	0	42
Trapeliopsis steppica	TS	0	13	47
*Xanthoparmelia wyomingica**				
Bryophytes				
Mosses				
Brachythecium albicans		0	1	0
Bryoerythrophyllum columbianum		0	0	98
Bryum argenteum	BA	54	66	44
Bryum caespiticium	BC	555	261	69
Ceratodon purpureus	CP	680	1017	770
Didymodon australasiae (= *Trichostomopsis australasiae*)		0	6	3
Didymodon brachyphyllus	DB	57	91	50
*Didymodon nevadensis**	DB			

Funaria hygrometrica		24	0	0
Grimmia cf. *alpestris**				
Polytrichum piliferum		0	0	5
Pterygoneurum ovatum	PO	63	33	1
Pterygoneurum subsessile		7	0	0
Syntrichia caninervis (syn. *Tortula caninervis*)	SR	0	0	4
Syntrichia ruralis (syn. *Tortula ruralis*)	SR	12	30	315
Syntrichia papillosissima (syn. *Tortula papillosissima*)*	SR			
Tortula acaulon (formerly *Phascum cuspidatum*)		0	1	0
Tortula brevipes	TB	26	5	3
Liverworts				
Cephaloziella divaricata	CD	0	1	32
Mannia fragrans		0	0	2
Riccia cf. *sorocarpa*		0	1	1

Although the richness of the lichen taxa reported from the CRP sites is more or less consistent with biological crust surveys in similar shrub-steppe habitats elsewhere, the number of bryophyte taxa reported here is much higher than in most soil crust studies; Ponzetti and McCune (2001) is an exception. This discrepancy can be accounted for, possibly because the CRP study area is richer in bryophytes than other regions, but more likely because of the lack of training in bryophytes that most other soil crust research teams possess. Although lichens are often the prominent feature in many soil crusts, mosses are often present in high numbers yet may be missed and/or misidentified by untrained field crews. In contrast, the diversity of lichens that was reported from the CRP sites during the present research, particularly adjacent to the transects, but also, in some cases, from within the plots, is probably incomplete to some degree. The primary author of this article, although well trained in arid land bryophytes, is not as proficient at lichens in the field as researchers who focus primarily on lichens. Even though a number of unknowns were identified by experts, some remain unidentified and may alter the results slightly. Also, some taxa, in particular the 'black' lichen' group and species of *Lecanora*, may have been better defined in the field with more experience, although the 'blackish' lichen group often requires laboratory work in order to confirm the species, and are very often immature and identification is unlikely anyway.

Comparison of the three major treatment types shows that numbers of species that are present increase from N sites through to steppe sites: N sites had 64 total species hits. O sites had 109 species hits, and S sites had 155 species hits (although the N sites had one less treatment site available for this count, it would have increased the N number only slightly). This difference in species richness occurs within all research areas except between a few O and S sites in a few of the areas (at all research areas, the species richness is lowest in the N sites). In the Black Rock research area, the O sites have higher numbers of taxa than the S sites (16 vs. 14) and in the Tracy Rock area the numbers between O and S treatments is the same. Although the lower number of species in the Black Rock area cannot be accounted for, the number of taxa in the Tracy Rock area is reduced because, probably, of the highly stony soils of the SC treatment site.

Treatment Site and Species Relationships

The results of this research show a number of trends and provides insight related to the recovery and successional patterns of biological soil crusts in former shrub-steppe habitats in central Washington State. Figure 5 shows an ordination of the 47 CRP treatment sites as well as the 15 species variables (in blue).

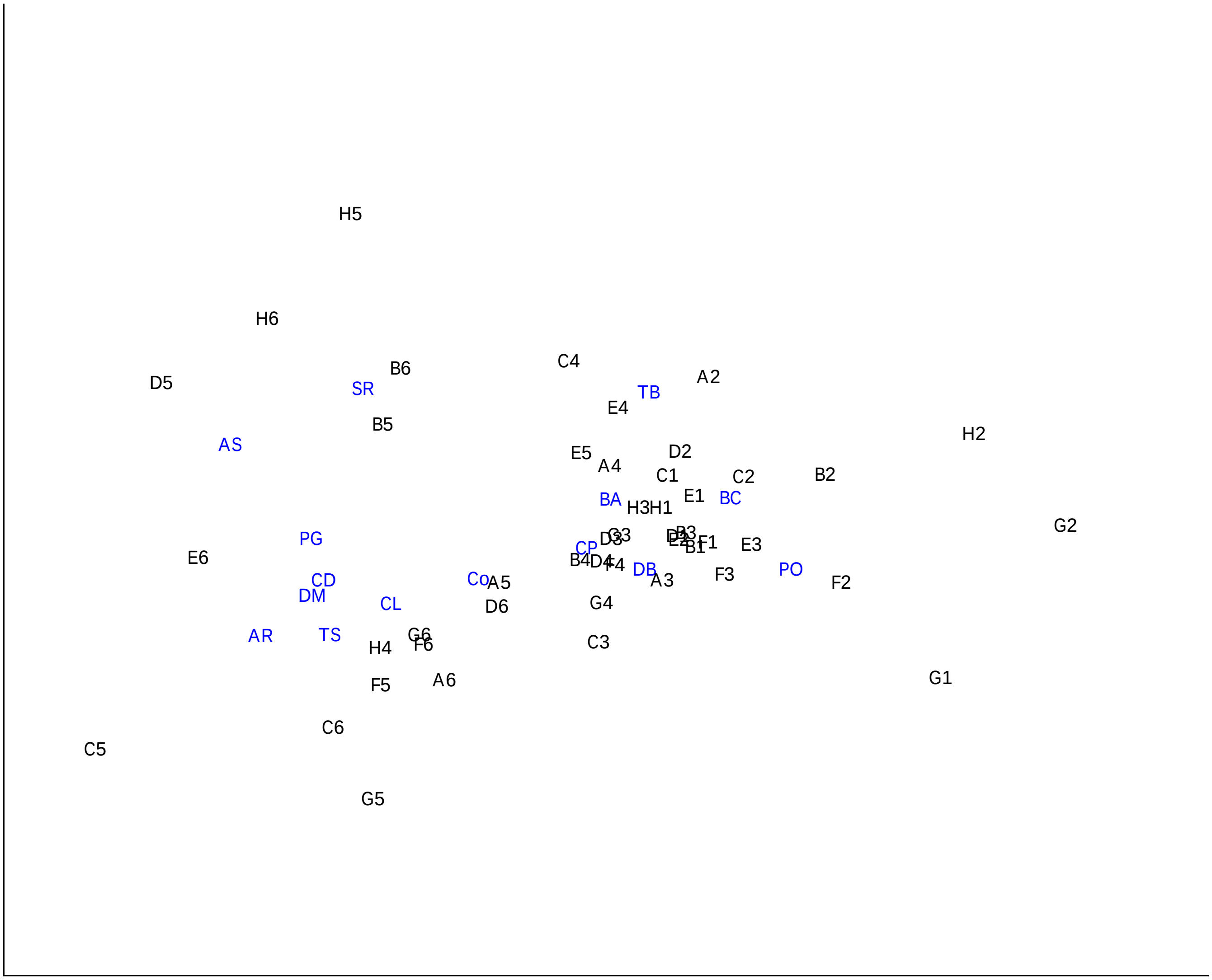

Figure 9. Detrended Correspondence Analysis ordination of 47 CRP treatment sites (in black, showing the variables, species, in blue); research areas are identified as follows: A = Black Rock, B = Chester Butte, C = Coyote Canyon, D = Jameson Lake, E = Pine Canyon, and F = Pacific lake; numbers refer the treatment type as follows as described in the Study Design Section: 1 = NC, 2 = NS, 3 = OC, 4 = OS, 5 = SC, and 6 = SS; the 15 species and species group variables are the lichens *Aspicilia reptans* (AR), *Acarospora schleicheri* (AS), *Cladonia* spp. (CL), blackish lichen crust spp. (Co), *Diploschistes muscorum* (DM), *Psora globifera* (PG), and *Trapeliopsis steppica*. (TS), the mosses *Bryum argenteum* (BA), *B. caespiticium* (BC), *Ceratodon purpureus* (CP), *Didymodon brachyphyllus* (DB), *Pterygoneurum ovatum* (PO), *Syntrichia ruralis* (SR), and *Tortula brevipes* (TB), and the leafy liverwort *Cephaloziella divaricata* (CD).

The most obvious trend shown by the ordination is soil crust succession of the various treatments, from early seral (recently planted fields; e.g., Fig. 6) through mid-seral (fields planted between 1986 and 1988; e.g., Fig. 7) to late seral (shrub-steppe habitats; e.g., Fig. 8 and 9). Newly planted sites, where soil has been available for colonization for a shorter period of time than in the other treatments, are located to the right side of the ordination, fields that were planted earlier are in the central sector, and most shrub-steppe sites are situated to the left. The treatment sites that do not follow this pattern can always be accounted for by site disturbance factors. The main exception in shrub-steppe sites (E5; PCSC; near the center of the ordination) has been heavily disturbed by a fire that damaged many of the biological crust taxa and reduced their cover markedly; also, the soil crust at this site is highly patchy, and these patches often fragmented. Even though the late successional taxa discussed below are present throughout the area surrounding the transect, they were rarely captured during plot sampling. Thus, its biological crust could be considered mid-seral. Another disturbance that plays a role in the location of a site in the ordination is livestock grazing and subsequent trampling of the soil crust. Livestock disturbance has occurred at A5 (BRCS; there also appears to have been a fairly recent low intensity fire here) and D6 (JLSS). However, severe climatic conditions, including high winds, possible frost heave, and uneven surface runoff appear to continually disturb the soil crust at E6 (PCSS), yet these factors do not appear to have affected its late successional status.

Figure 6. Bare soil and colonizing moss layer in new CRP site (center of photo; SLNS).

Figure 7. Colonizing, principally moss crust in old CRP site (CCOC).

Figure 8. Biological soil crust in shrub-steppe (BRSC).

Figure 9. Biological soil crust in shrub-steppe (CCSS).

Inferences can also be made from Fig. 5 regarding the succession of individual species, as well as from the treatment site total cover values presented in Table 1. Species and species group relationships in the ordination reflect ecological tendencies of most of the species. For example, characteristic colonizing mosses dominate early seral habitats and are clustered near the center of the ordination mainly within the new and old CRP sites. They include *Ceratodon purpureus* (CP), *Bryum caespiticium* (BC), *B. argenteum* (BA), *Didymodon brachyphyllus* (DB), *Pterygoneurum ovatum* (PO) and *Tortula brevipes* (TB). However, and not often recognized, some of these mosses are also important components of more mature biological crusts in shrub-steppe sites, in particular *Ceratodon purpureus* and *B. argenteum* (also observed by Hilty *et al.* 2004), but also, to a lesser degree, *Didymodon brachyphyllus* and *Bryum caespiticium*. The presence of these colonizing taxa in late successional crusts may indicate that they are taking advantage of natural micro-disturbance that occurs in all shrub-steppe habitats at the ground level such as through animal disturbance, including ground squirrels or hoof marks, or micro-climatic alterations of the crust. The soil surface at all late seral sites, including ungrazed shrub-steppe sites that have no livestock damage, exhibited a mosaic of patterning from patches of open soil, including soil cracks, to patches of crust, mainly as a result of past or ongoing natural disturbance of some kind. This is a common observation in biological crusts throughout the Columbia Basin.

Eight, principally lichen taxa are more prominent and often only present in shrub-steppe and, to a lesser degree, older CRP field soil crusts, and are to the left of the ordination. They include the lichens *Acarospora schleicheri*, *Aspicilia reptans*, *Cladonia* spp., *Diploschistes muscorum*, *Psora globifera*, and *Trapeliopsis steppica*, but also include a moss, *Syntrichia ruralis*, and a leafy liverwort, *Cephaloziella divaricata*. Of these eight taxa, only *Syntrichia ruralis* was recorded during plot surveys in newly planted CRP fields and with a very low cover value. This species was slightly more common in older CRP fields, but was most prominent in shrub-steppe. Five of these taxa, *Aspicilia reptans*, *Cephaloziella divaricata*, *Cladonia* spp., *Diploschistes muscorum,* and *Trapeliopsis steppica*, were recorded in older CRP fields, but also had much higher cover values in shrub-steppe plots. However, in all of the older CRP fields where these five species were found, all of them, except for a few patches of *Cladonia*, were either in a juvenile growth stage or the patches were much smaller than noted in shrub-steppe sites. This indicates that these eight taxa can be considered late seral biological crust species, although not restricted to that condition.

The *Collema* complex is situated just to the left of the center of the ordination, and may represent the complexity of the taxa that are included in this artificial group. No 'blackish crust' was recorded in any of the recently planted CRP sites, having their highest cover in late seral (shrub-steppe) and, to a slightly lesser degree, in the older CRP fields.

Other species that were recorded from the CRP research sites that were not used in the ordination can also can be placed along the successional gradient, based on the results from this project as well as from observations in steppe habitats elsewhere in the region. They include late seral taxa, the lichens *Leptogium* sp., *Lecanora murali*s (in stony sites), *Leptochidium albociliatum*, *Peltigera rufescens*, *Phaeorrhiza sareptana*, the mosses *Bryoerythrophyllum columbianum*, *Polytrichum piliferum*, and *Syntrichia caninervis,* and the liverwort *Mannia fragrans*. Although *Xanthoparmelia wyomingica* was not captured in any plots, it should also be considered as a late successional species based on observations near the CRP plots and elsewhere. Taxa that might be considered as early to mid-successional taxa include *Arthonia glebosa*, *Funaria hygrometrica* (a well known moss species of bare soil in burned sites), *Pterygoneurum subsessile*, and *Tortula acaulon*.

Ponzetti and McCune (2001) and McIntosh (2003) provide data that support most of these observations regarding the characteristic seral stage of the taxa found in this study. Only two of the taxa in the Ponzetti and McCune (2001) study contrast somewhat to the results from the CRP study and McIntosh (2003). They show that *Arthonia glebosa* is more correlated with total crust and, by inference, to a later seral stage than the other studies, and show that *Syntrichia ruralis* (as *Tortula ruralis*) is somewhat more correlated to a mid to earlier seral stage.

Based on this project, as well as through inspections of shrub-steppe communities at other sites, the more mature biological soil crusts across the study area, for example at the CCSS site (Fig. 8), can be considered a northern and climatically cooler variant of the *Trapeliopsis steppica - Bryoerythrophyllum columbianum* Biological Crust Community described in McIntosh (2003) for the Hanford Reach National Monument in southern Washington State. At Hanford, this community is described as characteristic of sandy-loam to silt-loam soils, and is associated with big sage, blue-bunch wheatgrass, Sandberg’s bluegrass, characteristic species in CRP shrub-steppe treatment sites. Associated indicator mature crust species at Hanford that are present in the present study include the lichens *Acarospora schleicheri*, *Arthonia glebosa*, *Aspicilia* sp., *Cladonia* spp., *Diploschistes muscorum*, *Leptochidium albociliatum*, *Leptogium* cf. *lichenoides,* and *Trapeliopsis steppica*, and the mosses *Bryoerythrophyllum columbianum*, *Syntrichia ruralis,* and *Trichostomopsis australasiae*.

Total Soil Crust Cover and Environmental Attributes

Although some general trends in the total soil crust cover and environmental attributes data are supported by observations in steppe elsewhere, these need clarification and further investigation at some point. For example, as shown in Table 3, even though the total crust cover is increases from N to O sites, and usually represents an increasing crust development through time, crust cover is not a good indicator of successional trends at all of the sites. Either because of soil type, another unknown environmental variable (such as microclimate or slope), or stochastic events, such as a heavier spore-fall of early successional species or a better habitat for these taxa, a number of N and O treatment sites in some research areas have higher than or similar crust cover values as the S plots. However, their species composition is always quite different with the N and O sites being dominated by colonizing moss species, contrasting with steppe sites often more dominated by lichens.

Table 3. Summary of total cover values for biological soil crust and environmental attributes for CRP treatment areas combined (C = soil crust, M = mineral soil, L = litter, H = bases of grasses and forbs, R = stones and rock).

	C	M	L	H	R
N	940	1921	903	281	27
O	1164	1905	977	334	32
S	1457	1706	716	630	94

Mineral soil decreases slightly from N and O plots to S plots, but this does not appear significant, and varies widely among treatments, depending often on the degree of site disturbance, in particular the past use by livestock. We did not differentiate between surficial soil types (coarseness, for example), and this variable has been shown to be an important factor in crust composition (Belnap *et al.* 2001, McIntosh 2001, Ponzetti and McCune 2001) and may help to separate the treatments more satisfactorily. Surficial rock and stones are also variable between and within research areas. Often sites within some of the research areas that were chosen in the original WDFW study, although they may be appropriate for wildlife research, vary greatly with the amount of stones and rocks at the surface, particularly evident in the CCSS and TRSC treatment sites. Stoniness may play a role in the type of crust that develops in this region, but this is unknown at this time.

Litter varies with exposure to wind and other disturbances, such as livestock use, and with the type of grass that was planted at various times. However, a general trend is expressed and supported by observations across the whole study area that shows a decrease in litter from early to late seral condition.

The cover of grass and forb bases increases from N and O to S, and, although this appears significant, it may be a result of sampling error. Most of the grasses in O and N fields were planted in rows and this greatly contrasts with the variety of natural patterns that the vascular plants express in steppe communities.

SUMMARY

Studies of biological soil crusts have a sporadic but increasing role in the ecological understanding of arid land ecosystems, especially with respect to their management and conservation (e.g., Bowker *et al.* 2004, Rosentreter and Eldridge 2002). Although few range managers utilize this part of the habitat for their research, possibly because of the difficulty in identifying taxa but also because many managers or users haven't been made aware of the presence and importance of biological soil crusts, the rewards of studying crusts are high. Not only are soil crusts ecologically functioning components of shrub-steppe ecosystems, providing a series of important biological functions, they are also excellent indicators of ecosystem stress and recovery.

This study is a preliminary investigation on the recovery and succession of biological crusts in CRP sites in eastern Washington that were completely altered through crop production. Belnap and Eldridge (2001) and Hilty *et al.* (2004) consider that factors that influence biological soil crust recovery rates are the type of organisms comprising the crust, the size and severity of the disturbance, and the proximity of inoculant sources to the disturbed area. Their research was completed in areas recovering from livestock use or fire, and, in all cases, inoculant sources were close by. The present research differs in that inoculants, in our case lichen and bryophyte spores or propagula, originated from a much longer distance, from hundreds of meters to kilometers away.

The investigation and understanding of successional trends within biological soil crust communities is at an early stage (Belnap *et al.* 2001, McIntosh 2003). Communities of microbiotic organisms are often difficult to define, especially in disturbed environments, and very little is known about the community dynamics and rates of succession in soil crusts. Crust succession is related to soil composition and other factors. As has been observed in other areas, mosses and rarely lichens appear to be the principal early colonizers of shrub-steppe soil. Distinct successional patterns of lichen and bryophyte species occur, with lichens tending to dominate in mid to late succession on silt and clay rich soils, and mosses tending to dominate in mid to late succession on sandier soils (McIntosh 2003). Mature or 'climax' crusts rarely completely cover the soil surface; micro-perturbations frequently occur across the shrub-steppe that continually disturb the crust at a small scale. Although some species are prevalent in early successional crusts, and others mainly in late seral crusts, other species, for example the moss *Ceratodon purpureus*, are present across the successional cline reflecting either their wide range of tolerances and competitive ability, or the continual micro-disturbance of the crust itself.

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