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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

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Abstract

Biological soil crusts are an essential part of desert ecosystems throughout the world, as they are important in soil stabilization and soil fertility. Despite their importance, there have been few efforts to examine the population dynamics of the dominant species comprising these crusts or the effect of exotic plant invasions on these dynamics. In this study, we followed changes in lichen and moss cover for 8 years in plots dominated by native grasses or invaded by the exotic annual grass *Bromus tectorum* and across sites representing a range of land use histories. Our data showed that cover of both lichens and mosses can increase dramatically over short time periods, often going from just above 0% cover to as high as 9% cover in only 6 months. Cover of the nitrogen-fixing lichen *Collema* declined throughout the study, going from 19% in 1996 to as low as 2% in 2003, likely in response to an increase in monthly maximum temperatures during the study period. Changes in chlorolichen cover (lichens with green algal phycobionts), on the other hand, appeared related to precipitation patterns. Past grazing may be responsible for declines in species richness for both mosses and lichens and decline in cover for lichens. A recent *Bromus* invasion did not affect species richness in never-grazed plots, but a 50-year-old invasion appeared to be related to lower species richness in the previously intermittently grazed plots. *Bromus* invasion was related to lower cover of *Aspicilia*, *Collema*, *Placidium*, yellow lichens combined (*Caloplaca tominii*, *Candelariella terigena*, *Fulgensia bracteata*, and *Fulgensia desertorum*), total lichens, and total mosses in some plots in some years. Extended drought was likely responsible for a large decline of all species in 2003. Loss of lichen and moss cover is expected to affect many aspects of this ecosystem. Of special concern is the loss of *Collema*, as it is the dominant source of nitrogen for this region.
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Keywords: Arid lands; Biological soil crusts; *Bromus tectorum*; *Collema*; Deserts; Nitrogen cycles; Population dynamics

1. Introduction

Biological soil crusts are autotrophic communities consisting of cyanobacteria, mosses, and lichens that occur on soil surfaces throughout the world (Belnap and Lange, 2003). In deserts, they can completely cover the large soil interspaces found between plants, and thus are often the dominant living cover found in these regions. Biological soil crusts are a critical aspect of desert ecosystems, as they heavily influence soil fertility, soil stability, and local hydrology. They are often the dominant source of nitrogen (N) for desert plant and soil

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communities (Evans and Ehleringer, 1993; Evans and Belnap, 1999) and they fix carbon (C) at a rate equivalent to vascular plant leaves (Lange, 2003). Crust organisms secrete powerful metal chelators to help maintain nutrients in plant-available forms, important in high pH desert soils (Lange, 1974; McLean and Beveridge, 1990; for more references, see Belnap et al., 2003). Crusts reduce wind and water erosion (Warren, 2003) and increase soil temperature (Belnap, 1995), moisture (George et al., 2003), aeration, and porosity (Harper and Marble, 1988). In areas where soils freeze, crusts create a greatly roughened soil surface that increases capture and retention of water (Barger, 2003), nutrient-rich dust (Reynolds et al., 2001), seeds, and organic matter (Rao and Burns, 1990; Rogers and Burns, 1994). Plant productivity and concentrations of most plant-essential nutrients are higher in plants growing in crusted soils compared to adjacent uncrusted soils and plants often have increased survivorship (Harper and Belnap, 2001; for more references, see Belnap et al., 2003). Soil food webs are more complex and organisms more abundant under well-developed soil crusts compared to less-developed crusts (Rychert and Skujins, 1973; Yeates, 1979; Anderson et al., 1984; Bolton et al., 1993; for more references, see Belnap et al., 2003).

Soil surface disturbance, such as trampling by livestock, has repeatedly been shown to reduce or eliminate lichens and mosses from soil surfaces (Warren and Eldridge, 2003). It has been reported that other disturbances also decrease lichen and moss cover and diversity, including fire and the invasion of exotic annual grasses, such as *Bromus tectorum* (hereafter referred to as *Bromus*; Rickard and Vaughan, 1988; Rosentreter, 1992; Kaltenecker, 1997; Kaltenecker et al., 1999; Johansen, 2003). Because the degree to which biological soil crusts contribute to a particular ecosystem process depends on the type and abundance of crust organisms present, soil disturbance, or plant invasion can have a profound effect on ecosystem function. However, despite the importance of biological soil crusts in general and the importance of their specific floral composition in particular, there have been very few studies of their annual dynamics and the factors that control their species composition and cover at specific localities. To help address this problem, we monitored lichen and moss dynamics in three semiarid grasslands in SE Utah, USA with similar soils but different histories of grazing intensity and invasion by the annual grass *Bromus*.

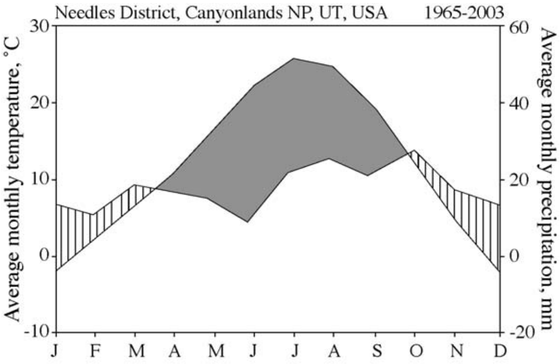

Fig. 1. A Walter diagram for the study site area. Note that April–September (6 months) are likely times of high water stress for soil surface organisms.

2. Methods

This study was conducted in Canyonlands National Park, 70 km south of Moab, Utah, at three grassland sites. Sites are at approximately 1700 m elevation. Climate data, obtained from the Western Region Climate Center, show annual average rainfall is 215 mm, with 35% occurring as summer monsoons (late July–August). Maximum annual average high temperatures are 20.2 °C, while annual minimum average lows are 3.6 °C, with evaporation exceeding precipitation most of the growing season (Fig. 1). Soils at all three sites are immature (little or no horizonation), alkaline, well-drained, fine sandy loams derived from calcareous sandstone (Table 1).

Livestock grazing began in this area in the late 1800s. Prehistorically, this area was only lightly grazed in winter months by small family groups of pronghorn, if at all. Thus, the introduction of livestock to these grasslands represented a dramatic change in use inten-

Table 1
Means and standard errors of soil texture classes at the different vegetation types and sites

Site	Plot	Sand (%)	Clay (%)	Silt (%)	*N*
NG	H	64.3 ± 1.3	13.7 ± 0.3	22.1 ± 1.5	3
NG	HB	59.0 ± 0.9	14.7 ± 0.7	26.3 ± 0.5	3
NG	S	67.7 ± 1.5	13.8 ± 0.4	18.5 ± 1.7	3
NG	SB	60.0 ± 1.6	14.3 ± 0.3	25.6 ± 1.4	3
PIG	HB	71.3	11.8	16.9	1
PIG	S	71.9 ± 1.6	11.2 ± 0.6	17.0 ± 1.8	3
PIG	SB	71.7 ± 4.6	12.0 ± 1.5	16.3 ± 3.2	3
PCG	HB	68.1 ± 6.1	15.4 ± 2.8	16.5 ± 3.4	3

N, number of plots at a site. Note that there is only one HB plot in The PIG site, and therefore no standard error is reported. H, native *Hilaria* plots; HB, native *Hilaria* and exotic *Bromus* plots; S, native *Stipa* plots; SB, native *Stipa* with exotic *Bromus*. Sites are NG, never grazed; PIG, previously intermittently grazed; PCG, previously continuously grazed.

sity. Grazing was removed from this area when Canyonlands National Park was established in 1964. The three grassland sites used in this study have different grazing histories. Virginia Park was never grazed, and is hereafter referred to as the never-grazed (NG) site. Chesler Park was intermittently grazed only in winters when there was snow on the ground, which occurs every 2–4 years in this area, and is hereafter referred to as the previously intermittently grazed (PIG) site. Squaw Flat was grazed every spring and fall and is hereafter referred to as previously continuously grazed (PCG). The NG and PIG sites are directly adjacent to each other and separated by a 100 m tall, 50 m wide rock wall; the PCG site is approximately 5 km away.

Grasslands in this region contain two distinct perennial grassland associations: one dominated by the predominantly spring-active C_3 grasses *Stipa comata* and *Stipa* (*Oryzopsis*) *hymenoides* (hereafter referred to collectively as *Stipa*) and one dominated by the predominantly fall-active C_4 grass *Hilaria jamesii* (hereafter referred to as *Hilaria*; Welsh et al., 1993). Sometime after 1900, the PIG and PCG sites were invaded by *Bromus*, which was well established by 1940 (R. Redd, personal communication). The NG site resisted invasion until fall 1994.

We established permanent 0.5 ha plots in native and *Bromus*-dominated grasslands in the three sites during 1996–1998. Three replicates of the four vegetation types were sampled at each site if possible: *Stipa* (S), *Stipa*/*Bromus* (SB), *Hilaria* (H), and *Hilaria*/*Bromus* (HB). Six transect lines 5 m apart were marked within each plot, and random points were selected along these lines for vegetation and soil sampling.

All sites were sampled yearly in spring, with additional fall sampling at the NG site. There were two core observers throughout the study and in each year one or both of them were present to assure continuity and accuracy of the measurements. In addition, double-sampling was frequently employed to verify that cover estimates were accurate between observers. Live and dead vascular vegetation is sparse in this area and did not obscure visual identifications. Regardless of plant, ground litter, rock, lichen, and moss cover, there was always at least 15%, and more often 50%, of the soil surface available for new colonization of lichens and mosses. Within each plot, 30 replicates of a 0.25 m^2 nested-frequency quadrat frame and Daubenmire cover classes were used to estimate cover of vascular vegetation and ground litter (thick enough to prevent colonization of soil lichens or mosses). We placed four dowels in the lower lefthand corner of each permanent vegetation plot and at each sample time, placed a 0.1 m^2 frame containing 20-point hits over the four dowels for estimating lichen and moss cover. Because lichens and mosses in this region are tiny (generally 1–2 mm) and highly discontinuous, we used the point-hit method, as these conditions make the more commonly used line-intercept techniques less precise (Rosentreter et al., 2003). Lichens and mosses were sampled when dry, as moistening the surface obscured differences among the dark-colored species and significantly changed cover of mosses and the lichens *Collema tenax* and *C. coccophorum* (hereafter referred to collectively as *Collema*). Within each plot, 30 samples of soils (0–10 cm) were randomly collected in the spring and then composited into one sample per plot. Soil analyses were done by the Brigham Young University Soil Laboratory. Temperature and precipitation data have been collected in this area since 1964.

Statistics were run using SPSS v.12 (SPSS, 2003). Data were first tested for normality using a Kolmogorov–Smirnov statistic, with a Lilliefors significance level for testing normality. Levene's test was used to examine the equality of variances and both pooled- and separate-variance *t*-tests were used to examine for equality of means. Non-normal data were transformed, or if that was not possible, equivalent non-parametric tests were used. Repeated measure analysis was used to determine significant differences in cover through time for the individual and grouped lichens and mosses. Stepwise multiple linear regression models were used to determine correlations among lichen and moss cover, vascular plant cover, and climate variables. The *t*-tests were used to compare plots with and without *Bromus* in the same year for the same species. Differences discussed in the text are statistically significant at $P < 0.05$ unless otherwise noted.

3. Results

3.1. Soils, climate, and vascular vegetation

Soils were dominated by sand, and the texture classes did not differ significantly among plots or sites (Table 1). The relationship between the average temperature and precipitation in this region is presented in Fig. 1. The study period contained years with below-average, above-average, and average precipitation (Fig. 2), with total annual precipitation from 2000 to 2003 below the 40-year average. However, even during these drought years, a given month was often above average.

The cover of *Bromus*, total vascular plants, and ground litter was highly variable during the study period as well (Fig. 3). As would be expected, wetter years

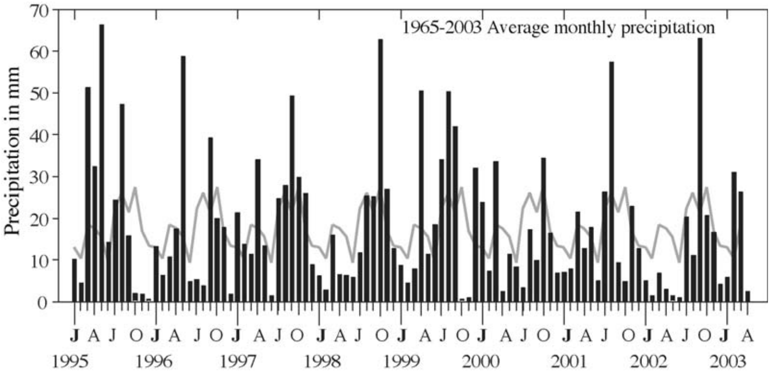

Fig. 2. Total monthly precipitation for the study period compared to the 40-year average precipitation (solid line).

(1997–1999, 2001) generally supported more cover of all three variables than the drier years.

There were no significant differences in cover of *Bromus*, total plants, or ground litter between the SB plots at the NG and PIG sites in any years. However, cover of total vascular plants was higher in the S plots at the NG site compared to the PIG site in 1998–2001 ($P = 0.03$, 0.006, 0.008, respectively). There was a

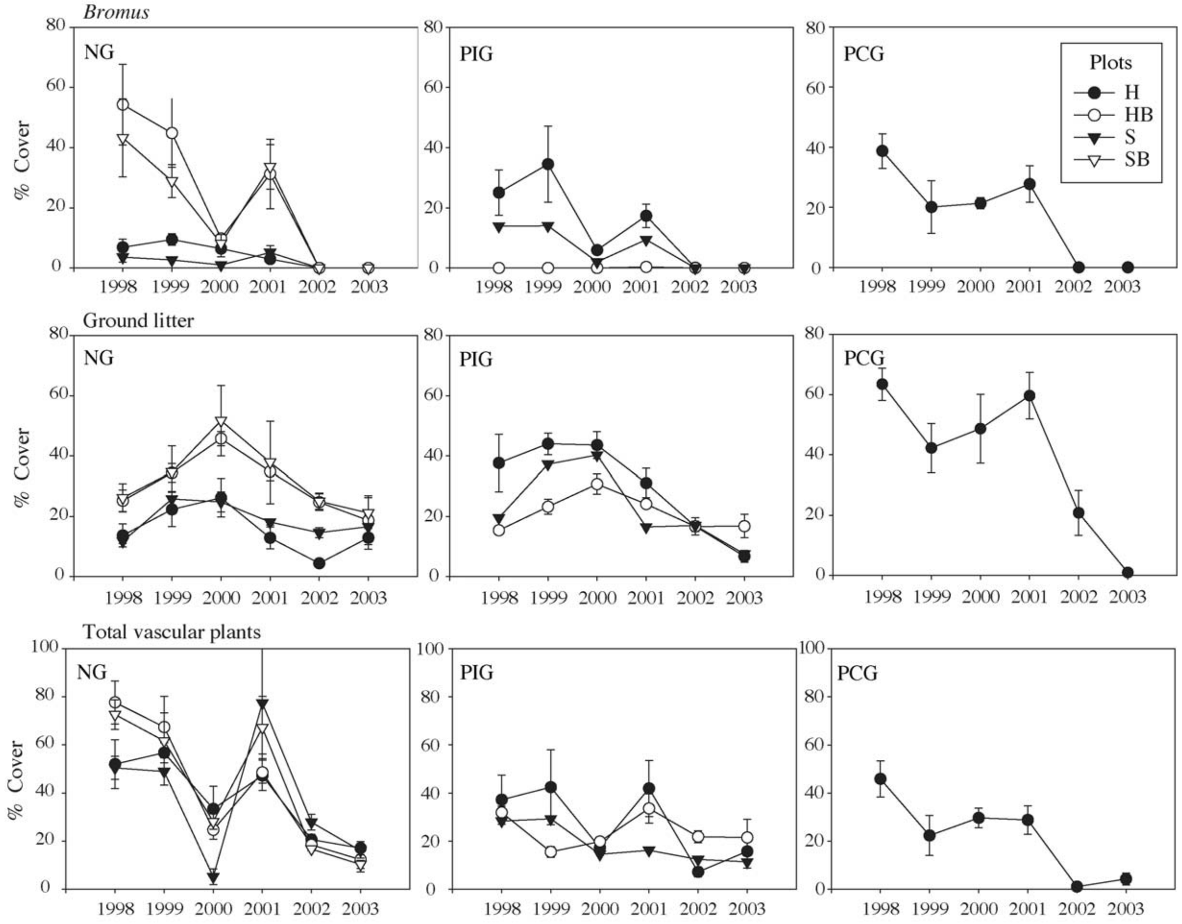

Fig. 3. Percent cover values for *Bromus*, total vascular plants, and ground litter in four vegetation types. Error bars represent 1S.E. (H, native *Hilaria* plots; HB, native *Hilaria* and exotic *Bromus* plots; S, native *Stipa* plots; SB, native *Stipa* with exotic *Bromus*) at the three study sites (NG, never grazed; PIG, previously intermittently grazed; PCG, previously continuously grazed). Note that there is only one HB plot in the PIG site, and therefore no standard error is reported.

slight difference in *Bromus* cover in the S plots at the two sites in 1999 and 2000, although the cover of *Bromus* was extremely low at both sites.

In the HB plots (the only type that could be compared across the three sites), there were no significant differences in cover of *Bromus* with one exception: in 2000 *Bromus* cover was higher at the PCG site than the NG or PIG site. Ground litter and total vascular plant cover were significantly higher in the NG than PCG site in 1998 ($P = 0.02$ and 0.04, respectively) and was higher at both the NG and PIG sites than the PCG site in 2001 ($P = 0.001$ and 0.02, respectively).

3.2. Lichen and moss species richness

The species richness of lichens (Table 2) was highest at the NG site (12–13 species) and lower at the PIG (4–6 species) and PCG plots (3 species). In contrast, the species richness of mosses was more equal between NG and PIG plots, with PCG plots lower than either NG or PIG plots. (The exception was the invaded SB plots at the PIG site, which had an equal number of species as the PCG plots.) Despite the many species recorded at these sites, the majority of cover was contributed by the lichen *C. tenax* and the moss *Syntrichia caninervis*, each of which had higher cover than all other species of lichens and mosses combined.

There was no difference in lichen species richness between invaded and uninvaded plots at the NG site (SB versus S and HB versus H). In contrast, invaded SB plots at the PIG site had two less lichen species (four versus six species) than the uninvaded S plots. Invaded HB plots at the NG site had one more moss species than the uninvaded H plots, with no difference between S and SB plots. Differences in moss and lichen species richness in the invaded SB plots, relative to the uninvaded S plots, at the PIG site were similar: the SB plots had two less species (two versus four species) than the uninvaded S plots. As we did not measure any uninvaded plots in the PCG site, we cannot determine the effects of *Bromus* at this site.

Table 2
List of lichens and mosses found in the different vegetation types at our three study sites

	Presence and absence of lichen and moss species							
	NG				PIG			PCG
	H	HB	S	SB	HB	S	SB	HB
Cyanolichens								
Collema coccophorum	x	x	x	x	x	x	x	x
Collema tenax	x	x	x	x	x	x	x	x
Heppia lutosa	x	x	o	o	o	o	o	o
Peltula patellata	x	x	x	x	x	x	o	o
Chlorolichens								
Aspicilia hispida	x	x	x	x	x	x	x	o
Caloplaca tominii	x	x	x	x	o	o	o	o
Candelariella terrigena	x	x	x	x	o	o	o	o
Placidium lachneum	x	x	x	x	x	x	x	o
Placidium squamulosum	x	x	x	x	o	o	o	o
Fulgensia bracteata	x	x	x	x	o	o	o	o
Fulgensia desertorum	x	x	x	x	o	o	o	o
Psora decipiens	x	x	x	x	o	x	o	x
Toninia sedifolia	x	x	x	x	o	o	o	o
Number of lichen species	13	13	12	12	5	6	4	3
Mosses								
Bryum argenteum	x	x	x	x	x	x	x	x
Didymodon vinealis	o	x	x	x	o	o	o	o
Pteryogoneurum ovatum	x	x	x	x	x	x	o	o
Syntrichia caninervis	x	x	x	x	x	x	x	x
Syntrichia ruralis	x	x	x	x	x	x	o	o
Number of moss species	4	5	5	5	4	4	2	2

"x", present; "o", absent; "–", species not sampled separately that year. H, native *Hilaria* plots; HB, native *Hilaria* and exotic *Bromus* plots; S, native *Stipa* plots; SB, native *Stipa* with exotic *Bromus* plots. Sites are NG, never grazed; PIG, previously intermittently grazed; PCG, previously continuously grazed.

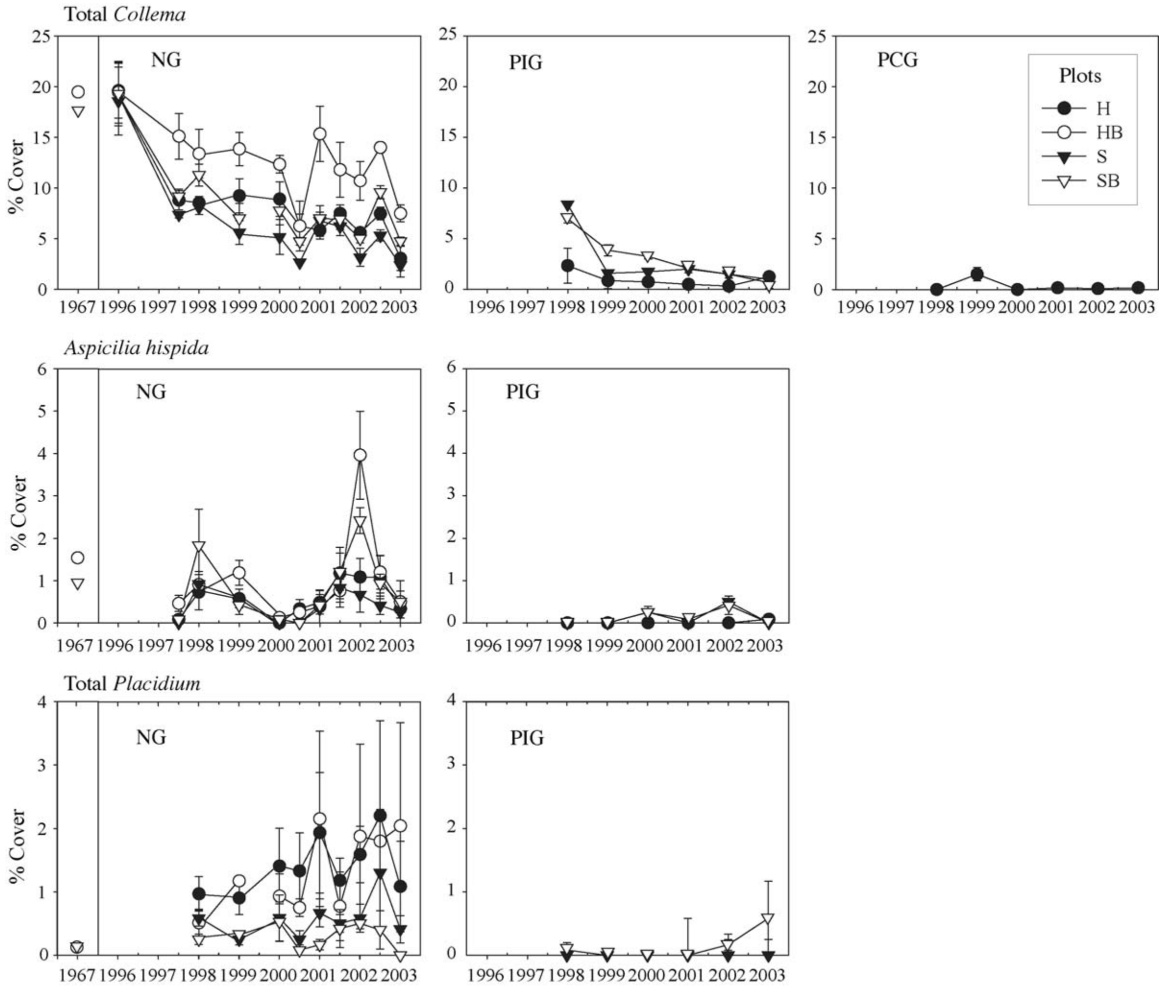

Fig. 4. Cover of *Collema* at the NG, PIG, and PCG sites (1967, 1996–2003) and cover of *Aspicilia* and *Placidium* at the NG and PIG sites (1967, 1996–2003). Error bars represent 1S.E. (H, native *Hilaria* plots; HB, native *Hilaria* and exotic *Bromus* plots; S, native *Stipa* plots; SB, native *Stipa* with exotic *Bromus*) at the three study sites (NG, never grazed; PIG, previously intermittently grazed; PCG, previously continuously grazed). Note that there is only one HB plot in the PIG site, and therefore no standard error is reported.

3.3. Lichen and moss cover

During most of the study, cover of individual lichen species and total lichen cover followed the same pattern as lichen species richness: cover was highest at the NG site, medium at the PIG site, and very low at the PCG site (Figs. 4–6). Patterns in total moss cover were also similar to those of total moss species richness: cover was similar at the NG and PIG sites, and much lower at the PCG site. However, the patterns in lichen and moss cover were disrupted at most sites in 2003, as cover for all species dropped to very low levels. Interestingly, *Collema* and total moss values recorded at the NG site in 1967 (Kleiner and Harper, 1977) were almost identical to the cover observed in 1996. In contrast, total chlorolichen cover at this site was much lower in 1967 than in 1996.

A surprising result from this study was the high seasonal and annual variability in cover for both lichens and mosses. Several patterns of change in cover emerged from our analyses. Total lichen and *Collema* cover typify the first pattern, where repeated measures analysis showed the total lichen and *Collema* cover declined significantly among years at the NG site (from 26.1% to 3.1% and 19% to 2–8%, respectively) and the PIG site (from 8.6 to 0.7% and from 8.4 to 0.7%, respectively, Figs. 4 and 6; Table 3). There were also significant interactions between community type and year at both sites for both lichen categories (Table 3). This was despite precipitation being highly variable

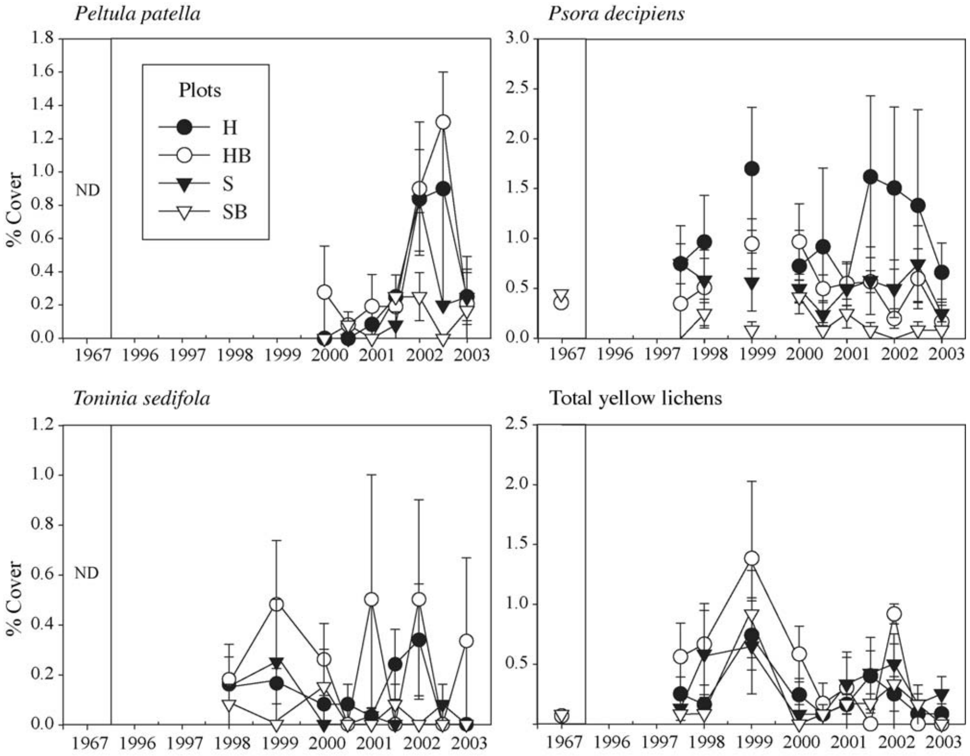

Fig. 5. Cover of individual chlorolichens at the NG site from 1996–2003. Error bars represent 1S.E.

during the study period (Fig. 2). In 1997 and 2001–2002, the presence of *Bromus* either tended to, or significantly did, reduce total lichen and *Collema* cover in *Hilaria* versus *Hilaria*/*Bromus* plots (Table 4). In addition, total lichen cover tended to be lower in 1999 and *Collema* cover tended to be lower in 2003 in the invaded sites. In contrast, there was no reduction of total lichen or *Collema* cover in the *Stipa* versus *Stipa*/*Bromus* plots (Figs. 4 and 6). Although *Collema* cover was variable between the spring and fall surveys, no consistent pattern could be seen (in contrast to the individual chlorolichens discussed below). Multiple regression analysis showed that changes in *Collema* cover were mostly associated with a negative response to the average maximum temperatures of the previous summer (May–October, Table 5). The strongest relationship was with previous June temperatures ($R^2 = 0.97$; Fig. 7). In addition, there was also a weaker relationship with average minimum and maximum previous spring temperatures and ground litter (primarily *Bromus*, Table 5).

Two other cyanolichens (lichens with cyanobacteria phycobionts) appeared in our plots, although both had very low cover. *Heppia* cover was so low and sporadic we do not discuss it further. *Peltula* cover showed significant changes in the HB and SB plots but not in the H or S plots through time (Table 3). No effect of *Bromus* was observed in any year for *Peltula*. Multiple regression showed a relationship between *Peltula* and precipitation timing in the H, S, and SB plots (Table 5). Cover in the HB plot was highly, and negatively, related to minimum March temperatures.

Unlike *Collema* and total lichen cover, individual and total chlorolichen cover did not show a more or less steady decline throughout the study period; instead, these species showed marked increases and decreases through time (Figs. 4 and 5; Table 3). Individual and total chlorolichens generally had larger cover values in spring compared to the preceding fall, increasing from almost 0% to up to 9% (Figs. 4 and 5).

Looking at the individual chlorolichen species (Tables 3–5; Figs. 4 and 5), repeated measures showed *Aspicilia* cover significantly varied in all NG plot types over time as well as in the combined plot analysis. Changes at the PIG site were not significant. Multiple regression analysis showed *Aspicilia* cover was negatively related to late winter precipitation and average minimum temperatures, *Bromus* cover, and ground litter (composed mostly of dead *Bromus*) in the different plots. Repeated measures showed that cover of the yellow lichen group (*Fulgensia*, *Caloplaca*, and

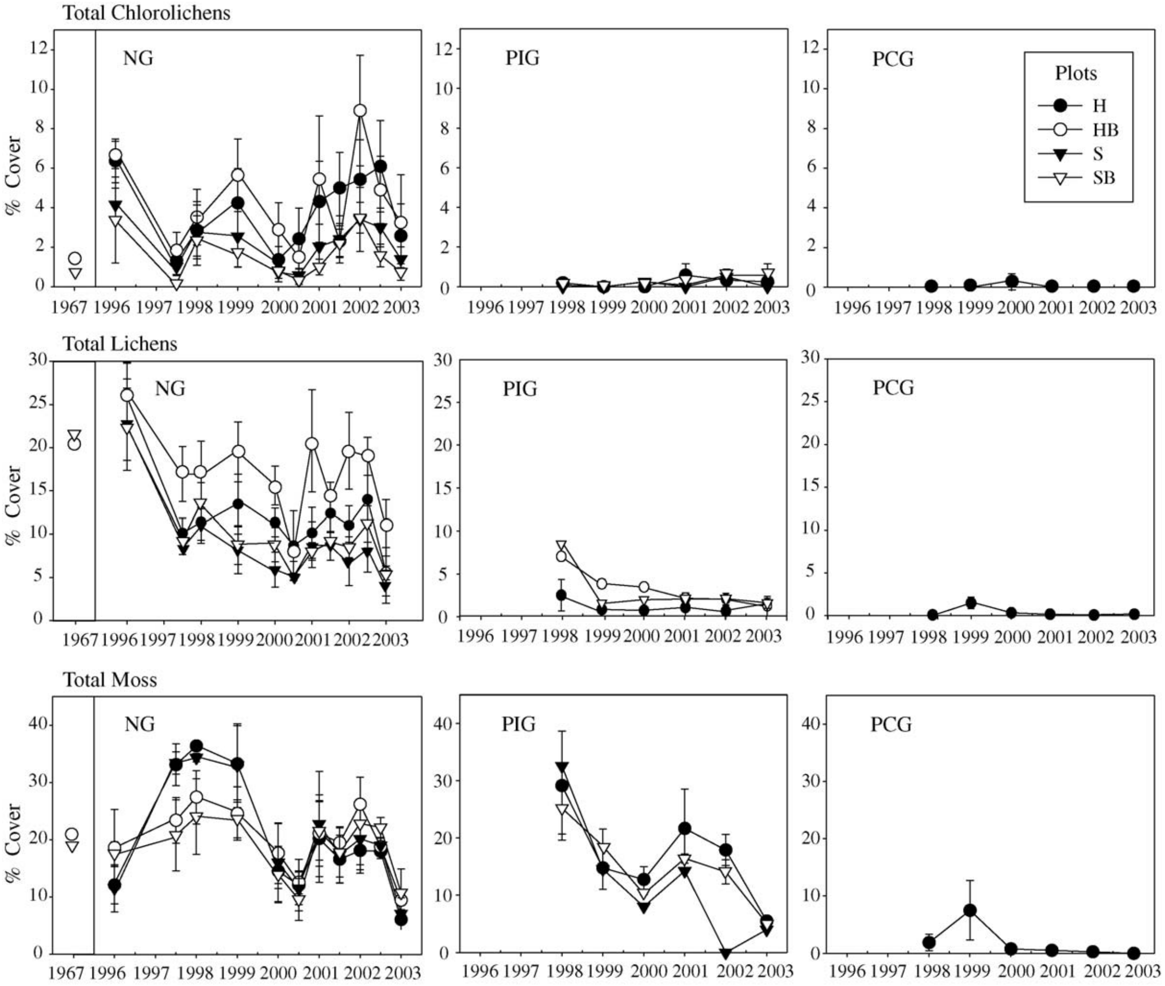

Fig. 6. Cover of total chlorolichens, total lichens, and total mosses for 1967 and 1996–2003. Error bars represent 1S.E. Statistical analyses of trends in cover over time are presented in Table 3.

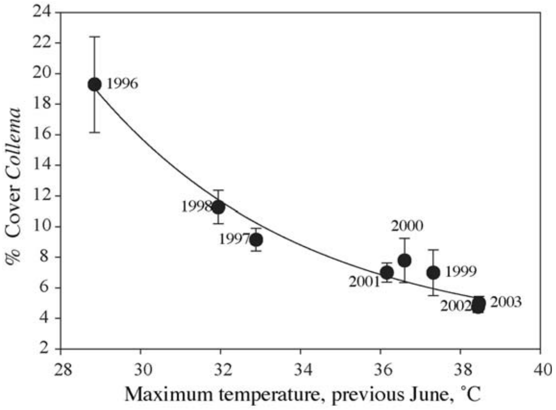

Fig. 7. Decline of *Collema* cover with increasing previous June's average maximum temperature ($R^2 = 0.97$; $P < 0.0001$).

Candelariella) varied among years in the S and HB plots and when all plots were combined at the NG site. Regression analysis showed cover in this lichen group in the different plots was positively related to fall and spring precipitation and maximum average June temperatures (these are the only lichens positively related to maximum temperature). Multiple regression analysis showed cover of this lichen group was negatively associated with *Bromus* cover over time, although *t*-tests showed this only for 2002.

Total *Placidium* (*Placidium lachneum* plus *P. squamulosum*) cover changed through time only in the HB and combined plots at the NG site, while change was not significant at the PIG site ($P = 0.15$). The *t*-tests showed a response to *Bromus* only in 2002 in the HB plots at the NG site. Using multiple regression analyses, we found that *Placidium* cover in the HB plots was

Table 3
Results from a repeated measures analysis of lichen and moss species, both in separate plots and all plots combined

Site	Community	Effect of year		Effect of community		Year × community	
		F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Aspicilia							
NG	H	5.232	0.007				
NG	HB	4.073	0.004				
NG	S	7.900	<0.0001				
NG	SB	2.702	0.038				
NG	All	18.599	<0.0001	3.628	0.014	2.637	0.004
Collema							
NG	H	3.475	0.003				
NG	HB	15.126	<0.0001				
NG	S	8.191	<0.0001				
NG	SB	14.194	<0.0001				
NG	All	25.345	<0.0001	5.011	0.003	2.070	0.016
PIG	HB	4.725	0.012				
PIG	S	11.910	<0.0001				
PIG	SB	7.293	0.003				
PIG	All	22.317	<0.0001	13.264	<0.0001	4.074	0.001
Peltula							
NG	HB	5.235	0.01				
NG	SB	6.016	0.006				
NG	All	9.657	<0.0001	0.986	0.428	1.621	0.186
Placidium							
NG	HB	2.999	0.019				
NG	All	5.008	<0.0001	1.937	0.024	11.846	<0.0001
Yellow lichen group							
NG	HB	2.840	0.032				
NG	S	5.454	0.004				
NG	All	7.769	<0.0001	0.973	0.47	1.077	0.36
Total chlorolichens							
NG	HB	3.849	0.011				
NG	S	2.131	0.098				
NG	SB	2.945	0.022				
NG	All	9.165	<0.0001	4.175	0.008	0.630	0.814
Total lichens							
NG	H	4.803	0.003				
NG	HB	6.202	<0.0001				
NG	S	6.373	<0.0001				
NG	SB	2.749	0.027				
NG	All	17.366	<0.0001	6.770	<0.0001	2.028	0.15
PIG	HB	3.582	0.017				
PIG	S	10.794	<0.0001				
PIG	SB	5.794	0.005				
PIG	All	18.05	<0.0001	9.303	<0.0001	3.663	0.001
Total moss							
NG	H	7.001	<0.0001				
NG	HB	35.881	<0.0001				
NG	S	3.106	0.024				
NG	SB	20.993	<0.0001				
NG	All	38.029	<0.0001	2.558	0.06	4.148	<0.0001
PIG	HB	20.712	<.0001				
PIG	S	20.264	<0.0001				
PIG	SB	16.538	<0.0001				
PIG	All	41.085	<0.0001	0.635	0.53	2.133	0.05

All species and sites listed in Table 2 were analyzed; this table lists only species that showed statistically significant changes ($P < 0.05$). H, native *Hilaria* plots; HB, native *Hilaria* and exotic *Bromus* plots; S, native *Stipa* plots; SB, native *Stipa* with exotic *Bromus* plots. Sites are NG, never grazed and PIG, previously intermittently grazed.

Table 4
Results of a *t*-test analysis for all species, comparing invaded and uninvaded plots within the same native grass type

Plot	Species	1996	1997	1998	1999	2000	2001	2002	2003
H vs. HB	*Aspicilia*	–	ns	ns	ns	ns	ns	0.08	ns
	Collema	ns	0.06	ns	ns	ns	0.03	0.02	0.08
	Placidium	–	0.08	ns	ns	ns	ns	ns	ns
	Yellow lichen group	–	ns	ns	ns	ns	ns	0.08	ns
	Total lichens	ns	0.05	ns	0.07	ns	0.01	0.06	ns
	Total moss	ns	ns	0.10	ns	ns	ns	0.09	ns
S vs. SB	*Aspicilia*	–	ns	ns	ns	ns	ns	0.05	ns
	Total chlorolichens	ns	0.08	ns	ns	ns	ns	ns	ns
	Total moss	ns	ns	0.10	ns	ns	ns	ns	ns

All species and sites listed in Table 2 were analyzed; this table contains only those comparisons that were statistically significant differences ($P < 0.10$). H, native *Hilaria* plots; HB, native *Hilaria* and exotic *Bromus* plots; S, native *Stipa* plots; SB, native *Stipa* with exotic *Bromus* plots.

Table 5
Results of stepwise multiple regression analyses of lichen percent cover at the NG and PIG sites from 1997 to 2003

Species	H		HB		S		SB	
	Result	R^2	Result	R^2	Result	R^2	Result	R^2
Aspicilia-NG	T_{mn} Th March T_{mn} Th January	−0.59 −0.84	P Th January C *Bromus*	−0.38	C Ground litter P Th February C *Bromus*	−0.49 −0.65 −0.76	C Ground litter	−0.29
Collema-NG	T_{mx} Pr June	−0.28	T_{mx} Pr May T_{mx} Pr September P Th February	−0.60 −0.76 −0.81	T_{mx} Pr June T_{mn} Pr June	−0.70 +0.80	T_{mx} Pr June T_{mn} Pr May C Ground litter P Th January	−0.64 +0.77 +0.88 +0.94
Collema-PIG	N/A				T_{mx} Th March	+0.94		
Peltula-NG	P Th February	−0.79	T_{mn} Th March	−0.94	P Pr May	+0.50	P Pr May	+0.71
Placidium-NG	T_{mn} Th March	−0.46	P Pr March	+0.44	T_{mn} Th March T_{mn} Pr April	−0.63 −0.83	T_{mn} Th March C Ground litter	−0.43 −0.61
Psora-NG					P Th March	+0.41		
Toninia-NG					P Th January	+0.26		
Yellow lichen group-NG			P Th April C *Bromus* P Pr October	+0.24 −0.45 +0.61	P Pr October T_{mx} Pr June	+0.32 +0.48	C Ground litter	−0.34
Total chlorolichens-NG	P Pre September P Th February	−0.50 −0.64	P Pr September	−0.35	P Th February P Pr May	−0.26 +0.43	C Ground litter P Pr March P Pr July	−0.22 +0.47 +0.62
Total lichens-NG	P Pr March	+0.60	P Pr March T_{mx} Pr May T_{mn} Pr June	+0.53 −0.74 +0.80	T_{mx} Pr May P Pr March	−0.66 +0.82	T_{mx} Pr June T_{mn} Pr July C Ground litter P Th February	−0.54 −0.67 −0.81 −0.92
Total moss-NG	C Ground litter T_{mx} Pr March	−0.62 −0.69	P Pr June P Pr September	−0.43 −0.59			C Ground litter P Pr September T_{mx} Pr August	−0.43 −0.63 −0.76
Total moss-PIG	N/A				T_{mx} Pr December	+0.73		

All species listed in Table 2 were analyzed; here we report only those species and regression model variables with $R^2 > 0.10$ and $P < 0.05$. H, native *Hilaria* plots; HB, native *Hilaria* and exotic *Bromus* plots; S, native *Stipa* plots; SB, native *Stipa* with exotic *Bromus* plots. We analyzed for C, cover (*Bromus* or ground); P, monthly precipitation; T_{mx}, average monthly maximum temperature; T_{mn}, average monthly minimum temperature; Th, that year's monthly precipitation; Pr, the previous year's monthly precipitation or temperature; "−", negative correlation; "+", positive correlation. Total plant cover was included in the analysis but was not a significant predictor.

positively related to precipitation and in all plots was negatively associated with average minimum temperatures the previous spring. *Placidium* cover was also negatively related to ground litter cover. *Psora* and *Toninia* cover showed no change in time in any plot type when plots were analyzed separately, although changes in both species were almost significant when plots were combined ($P = 0.08$ and 0.06, respectively). Both species were weakly associated with spring precipitation in the S plots.

Total chlorolichen cover changed through time in all but the H plots. Regression analyses showed that cover of this lichen group was negatively related to late fall and winter precipitation and ground litter (mostly *Bromus*) cover. Positive associations were seen with previous spring–summer precipitation.

Total lichen cover changed in all plots through time at both the NG and PIG sites. The regression analysis clearly reflected the negative relationship between maximum temperatures and *Collema*, and the association between the chlorolichens and precipitation patterns. Total lichen cover showed a response to *Bromus* in HB plots in 1997, 1999, 2001, and 2002 ($p < 0.01$).

Total moss cover showed yet a different pattern than either total lichen, *Collema* or chlorolichen cover. Repeated measures analysis showed significant differences in cover through time within each plot individually and all plots combined at the NG and PIG sites. Plot type × year interactions were also significant. In general, total moss cover showed a bimodal response over the study period, with significantly lower values in 1996, 2000, and 2003 relative to the other years measured. We only collected data on individual moss species in 2002 and 2003. This limited data set showed that the 2003 decline of *Syntrichia caninervis* dominated the response seen in total moss cover (data not shown). Total moss cover showed an almost significant response to the presence of *Bromus* in 1998 (SB versus S, $P = 0.10$) and in 2002 (HB versus H, $P = 0.09$). Multiple regression showed total moss cover was negatively associated with ground litter (mostly *Bromus*), maximum spring-summer temperatures, and precipitation during the previous summer (June–September).

4. Discussion

4.1. Seasonal and annual cover changes in lichen and moss species

Large absolute and relative increases and decreases in cover were observed within and between years for both lichens and mosses in this study. These findings are in contrast to the general impression that these organisms have a limited ability to respond to environmental conditions due to assumed slow growth and high tolerance for extreme climatic conditions. The largest within-year changes in cover were shown by the chlorolichen group, which repeatedly increased from almost 0% cover in fall to up to 9% cover in spring. Most lichen species and lichen groups showed the ability to increase cover by more than 200% or more during the cool months between fall and spring. It may be possible that these lichens pull their surface thalli down into the soil after dry, hot summers, and then reappear on the surface in the spring. On the other hand, these observed increases after winter may represent new colonization events. However, the extremely low numbers of green algae generally found in the soil makes this unlikely. Total moss cover increased by up to 20% in 1 year, indicating they also can grow rapidly in response to changing conditions. The cover of the moss and lichen species plummeted in 2003, with the exception of *Placidium* in H and HB plots, presumably due to the effects of an extreme drought in this area.

We could find only one other published long-term study of lichen and moss cover dynamics (Rosentreter et al., 2003). Lichen and moss cover in different Australian vegetation communities showed a range of responses over time, with very little cover change in some communities and large cover increases in other communities. The authors attributed the increases to a reduction of vascular vegetation which made lichens and mosses easier to detect. However, this is an unlikely explanation for our study. Dead and live plant materials were sparse and did not obscure the soil surface. In addition, the years in which we documented increases in vascular vegetation were the same years in which the cover of many lichen and moss species increased as well.

4.2. Factors influencing changes in lichen and moss cover

4.2.1. Invasion by Bromus and possible interactions with previous grazing regimes

The presence of *Bromus* appeared related to differences in the biological soil crusts at our sites. Lichen and moss species richness were reduced at the PIG *Hilaria*/*Bromus*, relative to *Hilaria*, sites by 33% and 50%, respectively, although we saw no differences at the NG site for species richness. (The PIG and NG plots had similar *Bromus* cover.) There were also differences in lichen and moss cover. At the NG site, cover of *Aspicilia*, *Collema*, *Placidium*, the yellow lichen group, total lichens, and total moss was lower in the invaded plots relative to the uninvaded plots during one or more of the study years, with *Collema* and total lichens being most often affected. Most reductions in cover occurred when *Hilaria* plots were compared to the *Hilaria*/*Bromus* plots, with only a few instances seen when *Stipa* plots were compared to *Stipa*/*Bromus* plots. At the PIG site, where we could only compare *Stipa* and *Stipa*/*Bromus* plots, *Collema* cover was also lower in some years in the invaded compared to the uninvaded plots. Lack of *Hilaria* plots precluded any comparisons between invaded and uninvaded plots at the PCG site. Ground litter (mostly *Bromus*) was also negatively related to cover of *Aspicilia*, the yellow lichen group, *Placidium*, total chlorolichens, total lichens, and total mosses in many plots. Interestingly, ground litter cover was positively associated with *Collema* in the SB plots at the NG site. It is also interesting to note that when comparing the multiple regression analyses for each species between uninvaded and invaded plots (H versus HB and S versus SB), invasion appeared to increase relationships to precipitation in the HB plots relative to the H plots, and the correlation with ground litter cover in the SB relative to the S plots.

Bromus invasion in this study appeared to have much less of an effect on lichen and moss communities compared to other studies where drastic reduction or extirpation of lichens and moss species are generally reported (Rickard and Vaughan, 1988; Rosentreter, 1992; Kaltenecker, 1997; Kaltenecker et al., 1999; Johansen, 2003). However, these previous studies were all complicated by the fact that study sites were burned and/or grazed before and/or after the *Bromus* invasion, and both fire and grazing are known to reduce lichen and moss species richness and cover (Warren, 2003; Johansen, 2003).

Teasing apart the relative impacts on soil crusts by grazing and *Bromus* and the interaction between these two factors is difficult. Although ranchers who have been in this area for generations report that before the invasion and dominance by *Bromus* the vascular plant communities at our three study sites were quite similar (H. Redd, personal communication), we have no information on the biological soil crust communities. However, we do have multiple relict grassland areas spread throughout SE Utah and northern Arizona that were never grazed, all of which have a similar vascular plant, lichen, and moss community as our NG site. If we can assume that our three sites once had similar lichen and moss cover, then either grazing, the *Bromus* invasion, or an interaction between the two has greatly impacted species richness and cover of lichens and mosses over time at the PIG and PCG sites.

The fact that lichen species richness and cover are much lower at the uninvaded PIG plots when compared to uninvaded NG plots supports the idea that grazing is likely responsible for at least some of the decline observed at the PIG sites. Although soil texture may also play a role, as the NG sites appear somewhat sandier than the PIG sites, we did not find statistically distinct differences in texture between the sites. In addition, the pattern of reduction in lichen and moss species richness and cover follows that of previous grazing intensity (NG > PIG > PCG). Many studies have found a similar effect of grazing on soil lichens and mosses (reviewed in Warren and Eldridge, 2003). However, there is also some evidence that an interaction between the effects of past grazing and the *Bromus* invasion is responsible. Lichen and moss species richness were lower in the invaded plots relative to the uninvaded plots at the previously grazed PIG site but not at the never-grazed NG site. Total moss cover was also lower in the invaded PIG plots but not in the invaded NG plots in 2002.

4.2.2. Climate

Different lichens showed various responses to the wide range of climatic conditions that occurred during this study. The large declines in the cover of the cyanolichen *Collema* occurred in both *Bromus*-invaded and -uninvaded plots, across wetter and drier years, at both the NG and PIG sites (there was no *Collema* at the PCG site), and in the absence of any soil surface disturbance. Therefore, it is likely that this decline was associated with the changes in temperature. This was corroborated by our regression analyses, where *Collema* was strongly and negatively ($R^2 = 0.97$) related to summer maximum temperatures and positively associated with late spring minimum temperatures. Because *Collema* is a gelatinous lichen that readily absorbs water, any size rainfall event will initiate respiratory carbon losses. This is in contrast to squamulose and crustose growth forms of the chlorolichens in this study, which are slightly hydrophobic and shed small rain events. In addition, it takes *Collema* up to 60 min in light to compensate for this respiratory loss with newly fixed carbon (Lange et al., 1998). As higher temperatures likely result in both quicker drying and higher respiration rates, the likelihood of carbon deficits in this lichen increases as temperatures increase. As *Collema* is the dominant source of N for these grasslands, the loss of this species is likely to have profound consequences for N cycles (Evans and Belnap, 1999).

In contrast to *Collema*, the chlorolichens showed times of decrease but also times of increase during our study. Our regression analyses suggested these lichens were correlated with changes in precipitation rather than the higher temperatures that were negatively correlated with *Collema* cover. Mosses showed an intermediate response, as changes in cover were associated with both temperature and precipitation.

It has long been believed that desert mosses and lichens are extremely tolerant of long-term drought. However, our results suggested that this may not be true. Chlorolichen cover appears to drop even with the short-term droughts encountered during summer. Although most of the lichens and mosses we monitored tolerated the drought years of 2001 and 2002, almost all succumbed to the lack of precipitation and/or higher temperatures by 2003. Interestingly, the C_3 grasses (*Stipa hymenoides* and *Stipa comata*) at this site also declined during this study. Thus, it may be that cover of both *Collema* and C_3 grasses decline when temperatures increase due to increased respiratory losses. However, most C_3 shrubs and C_4 perennial grasses and shrubs did not show heightened mortality during this drought, indicating they may be more tolerant of prolonged drought than most of the moss and lichen species observed in this study.

5. Conclusion

Given the importance of soil lichens and mosses to desert ecosystems around the world, it is unfortunate that we know so little about what factors affect their population dynamics. This is especially true in light of their apparent sensitivity to changes in multiple environmental variables, including plant invasions, increasing air temperatures, precipitation timing, and grazing, all of which are becoming increasingly important globally. The loss of lichen and moss cover, regardless of the cause, is likely to have a dramatic effect on ecosystem functioning at our sites. When compared to bare or cyanobacterially dominated soil crusts, lichen–moss soil crusts stabilize soils better and contribute to higher soil carbon and nitrogen, soil moisture, and plant-available nutrients (Reynolds et al., 2001; Barger, 2003; Belnap and Lange, 2003; Warren, 2003). The loss of *Collema* is of special concern, as it is the dominant source of N input to these ecosystems (Evans and Ehleringer, 1993; Evans and Belnap, 1999).

This study showed that mosses and lichens can respond rapidly to environmental changes through both decreases and increases in cover. However, it appears some of these organisms may have low resilience to *Bromus* invasion and climate changes (e.g., *Collema*), whereas others may show more resilience to these factors but less to soil surface disturbance (e.g., the chlorolichens). Surprisingly, it also appears that desert lichen and moss species may be less tolerant of drought than many desert vascular plant species, especially shrubs and C_4 grasses.

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