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Dynamics of cover, UV-protective pigments, and quantum yield in biological soil crust communities of an undisturbed Mojave Desert shrubland

Jayne Belnap[a,*], Susan L. Phillips[a], Stanley D. Smith[b]

[a]*US Geological Survey, Southwest Biological Science Center, Canyonlands Research Station, 2290 S. West Resource Blvd., Moab, UT 84532, USA*

[b]*Department of Biological Sciences, University of Nevada, Las Vegas, 4505 Maryland Parkway, Las Vegas, NV 89154-4004, USA*

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Dedicated to Prof. Dr. Dr. h.c. mult. Otto Ludwig Lange on the occasion of his 80th birthday

Abstract

Biological soil crusts are an integral part of dryland ecosystems. We monitored the cover of lichens and mosses, cyanobacterial biomass, concentrations of UV-protective pigments in both free-living and lichenized cyanobacteria, and quantum yield in the soil lichen species *Collema* in an undisturbed Mojave Desert shrubland. During our sampling time, the site received historically high and low levels of precipitation, whereas temperatures were close to normal. Lichen cover, dominated by *Collema tenax* and *C. coccophorum*, and moss cover, dominated by *Syntrichia caninervis*, responded to both increases and decreases in precipitation. This finding for *Collema* spp. at a hot Mojave Desert site is in contrast to a similar study conducted at a cool desert site on the Colorado Plateau in SE Utah, USA, where *Collema* spp. cover dropped in response to elevated temperatures, but did not respond to changes in rainfall. The concentrations of UV-protective pigments in free-living cyanobacteria at the Mojave Desert site were also strongly and positively related to rainfall received between sampling times (R^2 values ranged from 0.78 to 0.99). However, pigment levels in the lichenized cyanobacteria showed little correlation with rainfall. Quantum yield in *Collema* spp. was closely correlated with rainfall. Climate models in this region predict a 3.5–4.0 °C rise in temperature and a 15–20% decline in winter precipitation by 2099. Based on our data, this rise in temperature is unlikely to have a strong effect on the dominant species of the soil crusts. However, the predicted drop in precipitation will likely lead to a decrease in soil lichen and moss cover, and high stress or mortality in soil cyanobacteria as levels of UV-protective pigments decline. In addition, surface-disturbing activities (e.g., recreation, military activities, fire) are rapidly increasing in the Mojave Desert, and these disturbances quickly remove soil lichens and mosses. These stresses combined are likely to lead to shifts in species composition and the local extirpation of some lichen or moss species. As these organisms are critical components of nutrient cycling, soil fertility, and soil stability, such changes are likely to reverberate throughout these ecosystems.

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*Corresponding author. Fax: +1 435 719 2350.
E-mail address: jayne_belnap@usgs.gov (J. Belnap).

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Introduction

Biological soil crusts (BSCs) are a critical component of most dryland ecosystems. The phototropic organisms in these soil surface communities are dominated by cyanobacteria, mosses, and lichens (Belnap and Lange, 2003) and, as they often completely cover the large soil interspaces between plants, can be the dominant living cover in these ecosystems. BSCs influence many aspects of dryland function. Cyanobacteria, lichens, and mosses all fix carbon (C) and can be an essential source of C for subsurface soil biota (Lange, 2003). Most cyanobacteria and cyanolichens that occur in these communities fix nitrogen (N) and can be the dominant source of this often-limiting nutrient for plant and soil communities (Evans and Ehleringer, 1993; Evans and Belnap, 1999). Crust organisms also contribute to keeping nutrients available to vascular plants by secreting powerful metal chelators (Lange, 1974; McLean and Beveridge, 1990; for more references see Belnap et al., 2003).

Biological crusts increase water infiltration (Barger et al., 2005) and the retention of 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 often higher in plants growing in soils covered by BSCs relative to those growing in adjacent uncrusted soils (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 (Anderson et al., 1984; Bolton et al., 1993; Darby et al., 2006; Rychert and Skujins, 1973). Biological crusts are also vital in reducing wind and water erosion, as most soil surfaces in drylands lack protection by rocks or plants and depend on BSCs for their stability (Warren, 2003).

Water is often a limiting factor for desert organisms, including BSCs. These organisms are metabolically active only when wet (Brostoff et al., 2005), and thus growth, maintenance, and repair activities are controlled by the amount and timing of precipitation events. As BSCs occur on the soil surface, they experience degradation of pigments and membranes during times when they are dry (Castenholz and Garcia-Pichel, 2000).

The deleterious effects of UV are diverse and well known. Effects include, but are not limited to, a reduction in photosynthesis, growth, cell differentiation, the protein matrix of PSII, and the synthesis of chlorophyll *a*, as well as an increase in lipid peroxidation, chlorophyll photobleaching, phycobilioprotein degradation, and direct damage to DNA (reviewed in Castenholz and Garcia-Pichel, 2000). Lichens and cyanobacteria manufacture pigments to protect their tissues from UV degradation. There are two basic types of pigments: one group stops incoming radiation (Garcia-Pichel and Castenholz, 1991; Garcia-Pichel and Belnap, 1996), and the second group captures free radicals generated by UV penetration within the cell (Adams et al., 1993). Scytonemin, in the first group, is a colored pigment that occurs in the extracellular polysaccharide sheaths of terrestrial cyanobacteria, absorbing UV before it enters the cell. The second group includes echinenone, canthaxanthin, β-carotene, lutein, zeaxanthin, and myxoxanthophylls. They occur intracellularly and protect cells from lethal singlet oxygen generated by UV (Karsten et al., 1998). These compounds are considered a second-tier defense against photooxidative damage, as they must be replaced after exposure to intracellular UV (Castenholz and Garcia-Pichel, 2000; Nienow et al., 1988).

Despite the importance of BSCs and the critical role of their protective pigments in their survival, there have been very few efforts to document the dynamics of lichens and mosses and their pigments in dryland ecosystems. The few studies that exist were conducted in Australia, Idaho (cool Great Basin desert), and Utah (cool Colorado Plateau desert; Belnap et al., 2006; Bowker et al., 2002; Eldridge et al., 2000; Rosentreter et al., 2003). This study contributes data on how the cover of lichens and mosses, fluorescence of the lichen species *Collema*, cyanobacterial biomass, and the concentrations of UV-protective pigments in cyanobacteria and the lichen species *Collema* change through time in an undisturbed, hot Mojave Desert ecosystem.

Materials and methods

This study was conducted at the Mojave Global Change Facility within the boundaries of the Nevada Test Site near Mercury, Nevada, USA. Vegetation at this site is typical of the northern Mojave Desert community, being dominated by the xerophytic shrubs *Larrea tridentata*, *Ambrosia dumosa*, *Lycium pallium*, *L. andersonii*, *Krascheninnikovia lanata*, and *Pleurophis rigida*. This remote area represents an essentially undisturbed desert ecosystem. Elevation is approximately 960 m, with the study plots occupying a broad alluvial fan sloping at 2–2.5% and comprising loamy to coarse sands derived from calcareous alluvium with a high component of gravel and stones (Jordan et al., 1999). Annual average rainfall in this area is 125 mm and occurs mostly in the winter. The maximum annual average high temperature is 24.8 °C, with the hottest month being July with a maximum average temperature of 35.6 °C. The annual minimum average low temperature is 10.1 °C.

Permanent plots, 14×14 m each and replicated four times in each of eight blocks, were established. Each plot was accessed by two perpendicular walkways, with

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stepping stones strategically placed for access to the BSCs without disturbing the soil surface. A meteorological station was onsite. Within each plot, we established 5 permanent subplots by tacking a 15×15 cm screen with 3 cm cells to the soil surface in the interspace between plants. The same five cells were divided into four quadrants for cover estimates (resulting in 100 cover estimates per plot), with observations done each spring and fall, from fall 2004 to spring 2007. We had 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. Cover classes were used to estimate cover within each of the small cells. Lichens and mosses were sampled when dry, as moistening the surface obscured differences among the dark-colored species. There are two species of *Collema* at this site: *C. tenax*, which represented about 40% of the total *Collema* cover, and *C. coccophorum*, which represented about 60% of the total *Collema* cover. As these species were very difficult to tell apart at this site due to the presence of many intermediate-appearing forms, we combined the two species for our measures and hereafter refer to them collectively as *Collema* spp. Other lichens (*Placidium squamulosum*, *P. lachneum*, *Peltula patellata*, *Heppia lutosa*, *Aspicilia desertorum* ssp. *terrestrialis*, and *Psora decipiens*) were present, but so rare that their cover was combined into an ''other lichen'' category. The dominant moss was *Syntrichia caninervis*. The mosses *S. ruralis* and *Pterygoneurum ovatum* were present, but cover was extremely low ($<0.02\%$) and so is not reported separately. The cover of all moss and lichen species present were combined for the ''moss plus lichen'' category.

At each sample time, effective quantum yield (hereafter referred to as ''quantum yield'') was measured on 30–40 permanently marked *Collema* spp. individuals within each plot. This was assessed with a PAM-2000 pulse amplitude fluorometer (Walz Inc., Germany), using the saturation pulse method (Bilger et al., 1995) during mid-daylight hours. Samples were wetted for 30 min before sampling. Samples were sprayed again with water just before the measurements were taken and shaded during measurements. Three measurements were taken per discrete *Collema* clump.

Five samples each of cyanobacteria-dominated and *Collema* spp.-dominated soils were collected from each plot each fall for laboratory analyses. Nitrogenase activity was determined on the *Collema* spp. samples. Samples were preconditioned before analysis by being left wet for 3 h under lights at 25 °C for 4 consecutive days. On the day of measurement, they were wetted and left under lights at 25 °C for 2 h. Air was then extracted and acetylene added to create a 10% acetylene atmosphere in the headspace of the sample tubes (Belnap, 2002). Samples were incubated for 4 h under lamps at 26 °C and analyzed with a Shimadzu FID gas chromatograph equipped with a 2.4 m, 8% NaCl on alumina column, using helium as the carrier gas ($30\,mL\,min^{-1}$). Simultaneous calibrations with ethylene standards were done.

Pigment concentrations were determined for both the cyanobacteria-dominated and *Collema* spp.-dominated soils, using HPLC analysis on acetone-extracted samples (Karsten and Garcia-Pichel, 1996). Concentrations for all pigments were quantified using peak areas integrated from photodiode array data at 436 nm and compared to commercially obtained standards. Because a scytonemin standard was not commercially available, scytonemin was quantified using its peak area at 436 nm and a modification of its extinction coefficient of $112.6\,L\,g^{-1}\,cm^{-1}$ at 384 nm (Garcia-Pichel et al., 1992). We used an extinction coefficient of $60.8\,L\,g^{-1}\,cm^{-1}$ at 436 nm. Data were analyzed using Millenium^{32} software (Waters, USA). The xanthophylls zeaxanthin, lutein, and myxoxanthophyll were grouped (hereafter referred to as xanthophylls or the xanthophyll group) on the basis of similar function, absorbance spectra, retention times, and/or the difficulty of distinguishing between these compounds.

Data normality was tested using the Shapiro–Wilk test. Most data were normal, and if not, were transformed. Differences between these values were then tested for significance using ANOVA, or Welch ANOVA if the assumption of equality of variance, as tested with a Levene test, did not hold. The Tukey HSD test was employed to determine which means differed. Repeated measures general linear model (GLM), with a Greenhouse–Geisser epsilon adjustment applied to the calculation of the *F*-test statistic, was used for analysis of variance in crust species cover across the different sampling dates. To test for differences among different repeated measures of a factor, we used the difference test of within-subject contrasts. All analyses were done using SPSS v.15. Significant results are reported at $P<0.05$.

Results

Climate

Fig. 1 shows the precipitation and temperatures at the site during our study (top panel) and the deviation of our monthly precipitation average from the long-term average precipitation (bottom panel; obtained from a station run by NOAA's Air Resources Laboratory, Special Operations and Research Division, located 5 km away). The period from fall 2004 through spring 2005 was extremely wet, setting historic records for this region. Summer 2005 though spring 2006 were fairly normal, but were followed by a severe drought that

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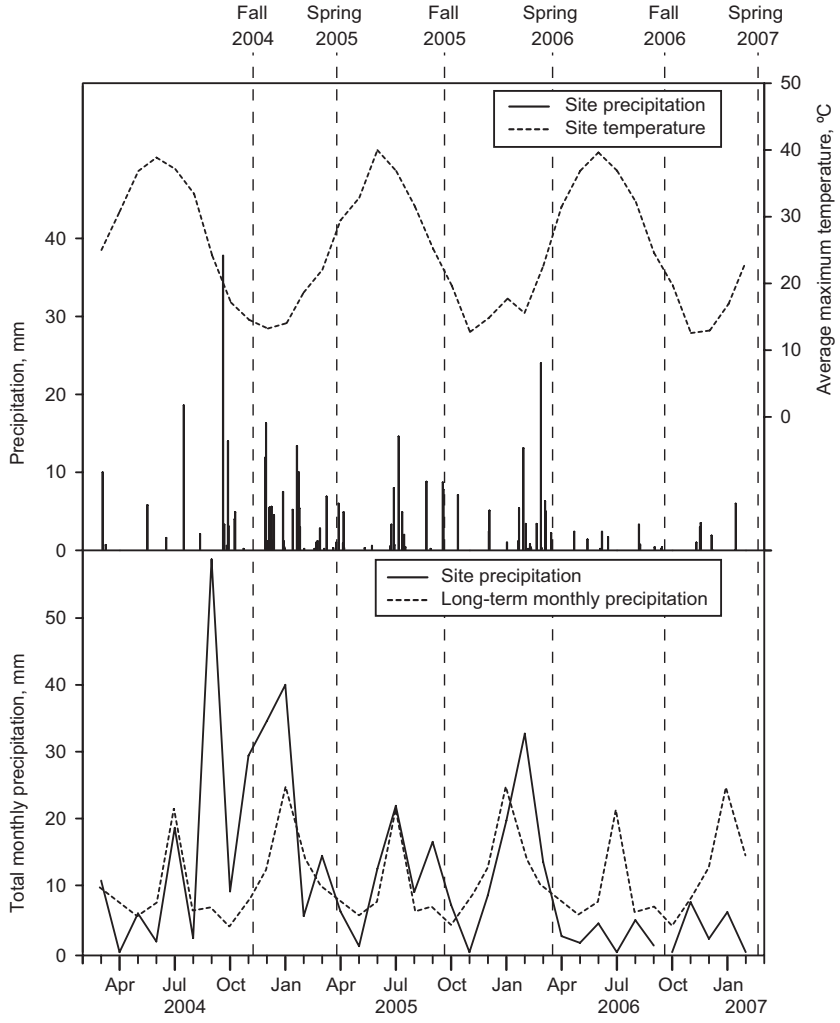

Fig. 1. Top panel: on-site precipitation and temperatures during the sample time. Bottom panel: on-site monthly average precipitation compared to the long-term average precipitation (data is from a station 5 km away).

continued through our last sampling time in April 2007. Temperatures during our sampling time were similar to long term averages in the different years.

Cover of lichens and mosses

The pattern in cover changes was similar for *Collema* spp., *S. caninervis*, and lichen plus moss measures, with an increase in cover occurring from spring 2005 until spring 2006, the time at which the highest cover found during our study was observed for these three groups (Fig. 2; Table 1). Cover then began dropping and by fall 2006 it was similar to that of fall 2004. It continued dropping until the lowest value observed in the study was obtained in spring 2007 (Fig. 2, left panels; $P<0.001$ for all groups). Thus, during our sampling time, *Collema* spp. cover increased 19% from spring 2005 (14.5% cover) to spring 2006 (17.2% cover) and dropped 30% between spring 2006 and spring 2007 (12.1% cover). The "other lichen" category, which represented less than 0.5% cover at its peak, showed no change in cover from spring 2005 to fall 2006, after which cover of these species dropped 82%, disappearing almost entirely. The dominant moss, *S. caninervis*, increased 46% from spring 2005 (1.3% cover) to spring 2006 (1.9% cover) and then dropped 58% by spring 2007 (0.8% cover; this low cover was not reflective of total moss cover at this site, as our plots were in the plant interspaces and most mosses occurred under the canopies of shrubs). Because *Collema* spp. and *S. caninervis* comprised the majority of the lichen and moss cover, respectively, total lichen plus moss cover reflected the cover patterns seen in the dominant species. Total lichen plus moss cover increased 17% from spring 2005 (16.7% cover) to spring 2006 (19.5% cover), dropping 33% by spring 2007 (13.1% cover).

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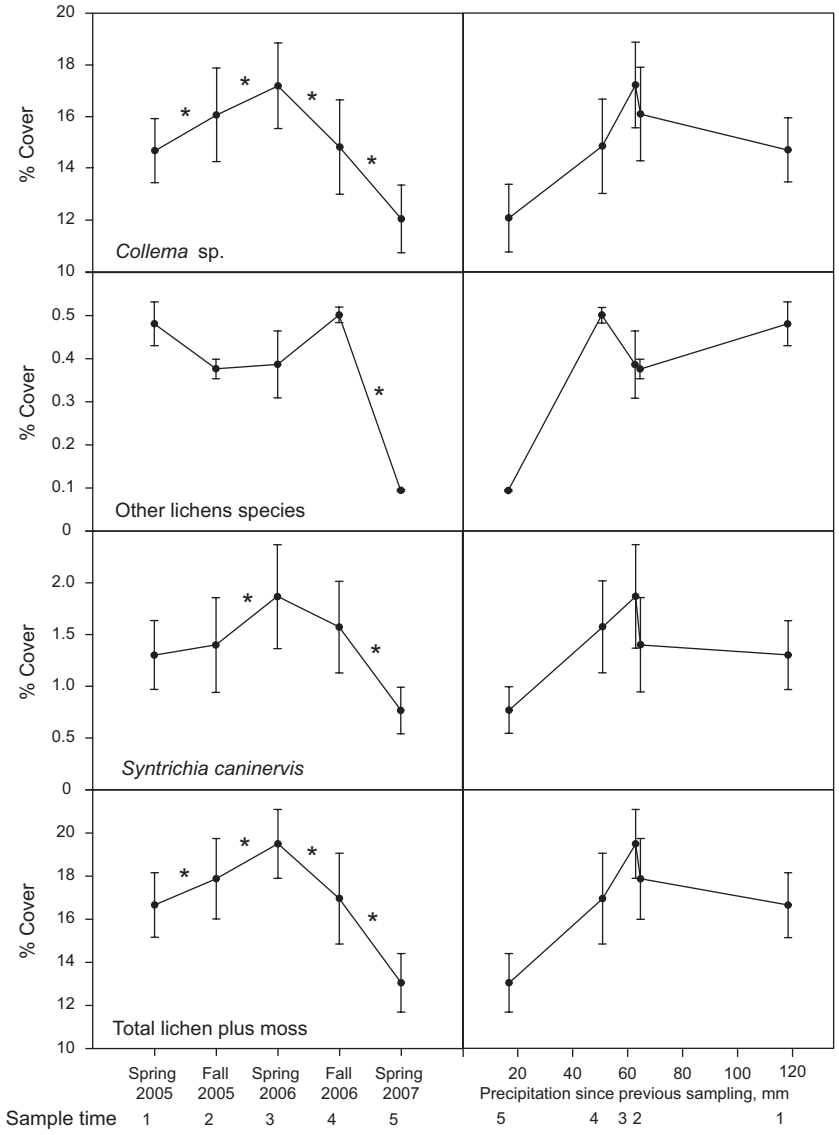

Fig. 2. Percent cover of the lichen *Collema* spp., other lichens combined, the moss *Syntrichia caninervis*, and total lichen plus moss cover. The * indicate a statistical difference between the latter sample time and all those preceding it (see Table 1 for statistical values). Using "other lichens" as an example, the * between sample times 4 and 5 indicates that the values obtained during sample time 5 are significantly different from all previous sample times.

As lichen and moss cover has previously been documented to increase during winter (a season when soils are usually wet the most and thus BSCs most active; Belnap et al., 2006), and yet our lowest cover was recorded after the winter of 2006–2007, we plotted the cover of the different groups against the amount of rainfall received since the last sampling time (Fig. 2, right panels). There was no large difference in cover among the measured organisms, despite a large range in rainfall, until the severe drought during the latter part of 2006 and spring 2007. After receiving only 17 mm of rain from the fall 2006 to the spring 2007 sampling time, lichen and moss cover was significantly reduced. In addition, there were only five rain events between our fall 2006 and spring 2007 sampling times, whereas there were 14 rain events between our fall 2005 and spring 2006 sampling times.

Cyanobacterial biomass

Chlorophyll *a* concentrations in soil are commonly used as indicators of cyanobacterial biomass (Bowker et al., 2002). Similar to the cover values for lichens and mosses, chlorophyll *a* concentrations showed no difference between fall 2004 and spring 2005 (Fig. 3, top left panel). It then dropped precipitously by fall of 2005 and stayed low throughout spring and fall 2006 (in contrast

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Table 1. Results of the repeated measures statistical analyses, comparing cover values among the sample times

Measure	Sampling	*F*	*P*-value
Collema	Fall 05 vs. Spring 05	10.999	0.001
	Spring 06 vs. all previous	20.099	0.000
	Fall 06 vs. all previous	11.582	0.001
	Spring 07 vs. all previous	94.884	0.000
Other lichens	Fall 05 vs. Spring 05	1.268	0.257
	Spring 06 vs. all previous	0.240	0.624
	Fall 06 vs. all previous	1.479	0.224
	Spring 07 vs. all previous	36.514	0.000
Syntrichia caninervis	Fall 05 vs. Spring 05	0.451	0.502
	Spring 06 vs. all previous	8.780	0.003
	Fall 06 vs. all previous	0.143	0.706
	Spring 07 vs. all previous	31.162	0.000
Total lichen plus moss	Fall 05 vs. Spring 05	7.698	0.006
	Spring 06 vs. all previous	27.415	0.000
	Fall 06 vs. all previous	8.526	0.004
	Spring 07 vs. all previous	137.124	0.000

to lichen and moss cover, which did not change during this time). In spring 2007, chlorophyll *a* concentrations decreased again, following the same pattern as seen in different measures of lichen and moss cover.

Similar to the cover of lichens and mosses, cyanobacterial biomass was also sensitive to the amount of rainfall received in the 6 months previous to sampling ($R^2 = 0.93$). However, whereas measures of lichen and moss cover did not decrease until the 6-month time period when precipitation dropped below 51 mm, cyanobacterial chlorophyll *a* levels did not drop until the time period when previous precipitation dropped below 98 mm. When precipitation between sample times increased from 65 to 98 mm, there was a large increase in cyanobacterial chlorophyll *a* concentrations. However, further increases above 98 mm did not result in any additional increases in chlorophyll *a* concentrations. There was no significant pattern when fall sampling times were compared to spring sampling times.

Free-living cyanobacterial UV-protective pigments

The patterns seen in the different UV-protective pigments were similar over time (Fig. 3, left panels). Although some pigments were higher than others at the fall 2004 sampling time, all pigments were at a high value in spring 2005, after a winter of extremely high rainfall. By the fall 2006 sampling time, all had dropped significantly. Values stayed the same through the fall 2006 sampling time, after which all pigments dropped to their lowest value. The exception was β-carotene, which dropped steadily from our fall 2004 sampling time until our spring 2007 sampling time, except for a short increase in fall 2006.

All cyanobacterial pigments showed a significant and strong relationship between the amount in the soil and the amount of precipitation since the last sampling event (R^2 = chlorophyll *a*, 0.93; scytonemin, 0.85; echinenone, 0.94; canthoxanthin, 0.99; β-carotene, 0.78; Fig. 3, right panels). All pigments also decreased when the precipitation received in the previous 6 months dropped below 51 mm. Echinenone was the pigment that most closely tracked chlorophyll *a*. Concentrations of echinenone, chlorophyll *a*, and β-carotene increased when precipitation was between 65 and 98 mm. Scytonemin and canthoxanthin concentrations did not increase until the precipitation rose to 119 mm. As with chlorophyll *a* concentrations, there was no significant pattern in pigment concentrations when fall sampling times were compared to spring sampling times. Interestingly, we found extremely low levels of the xanthophyll group of pigments in the cyanobacterial samples (only lutein was present, and in very small amounts) at all sample times.

Collema spp. pigment concentrations

Pigment concentrations in *Collema* spp. were measured only in fall 2004, 2005, 2006, and spring 2007. Similar to concentrations in the free-living cyanobacteria, pigments were lower in fall 2006 and lowest in spring 2007 (Fig. 4). However, the patterns in the lichenized cyanobacteria were otherwise different than in the free-living cyanobacteria. Concentrations of chlorophyll *a*, scytonemin β-carotene, and the xanthophyll group were all lower in fall 2004 and fall 2006 than in fall 2005.

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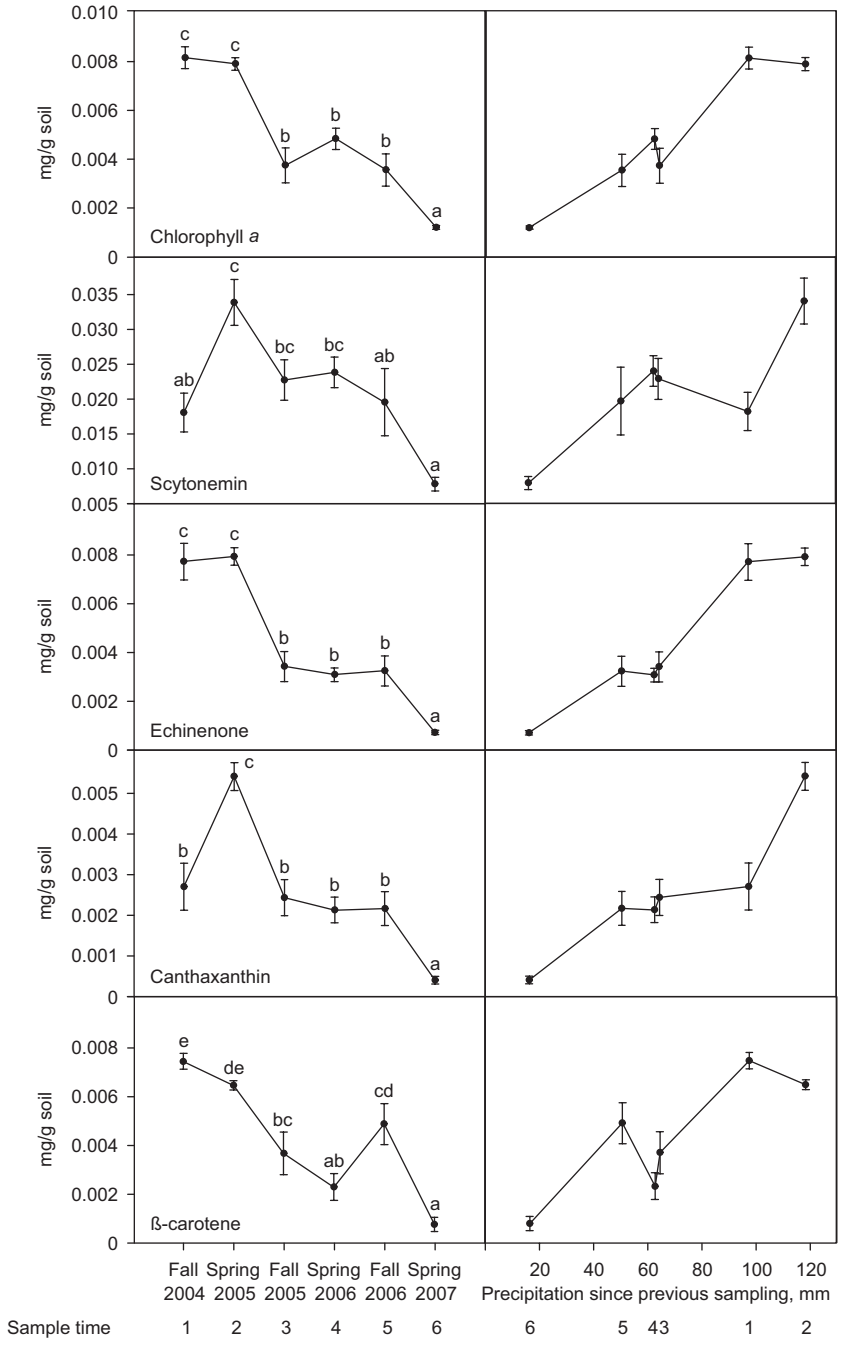

Fig. 3. Pigment concentrations in the free-living cyanobacteria by both sampling date (left side) and by the amount of precipitation that fell between sampling times (right side). Values with the same letter above them are not statistically different.

In contrast, echinenone and canthoxanthin were similar in fall 2004 and fall 2005, dropping in fall 2006. The correlation between a specific pigment concentration and the amount of rainfall received since the last sample time was not statistically distinct for any pigment except echinenone ($R = 0.44$). In addition, only echinenone and canthoxanthin showed any evidence of a precipitation threshold that influenced pigment values, with values dropping when the precipitation received during the previous 6 months was less than 65 mm. The other pigment concentrations actually dropped when higher precipitation amounts were received.

Collema spp. quantum yield

Quantum yield in *Collema* spp. showed a pattern similar to *Collema* spp. chlorophyll *a* and pigment

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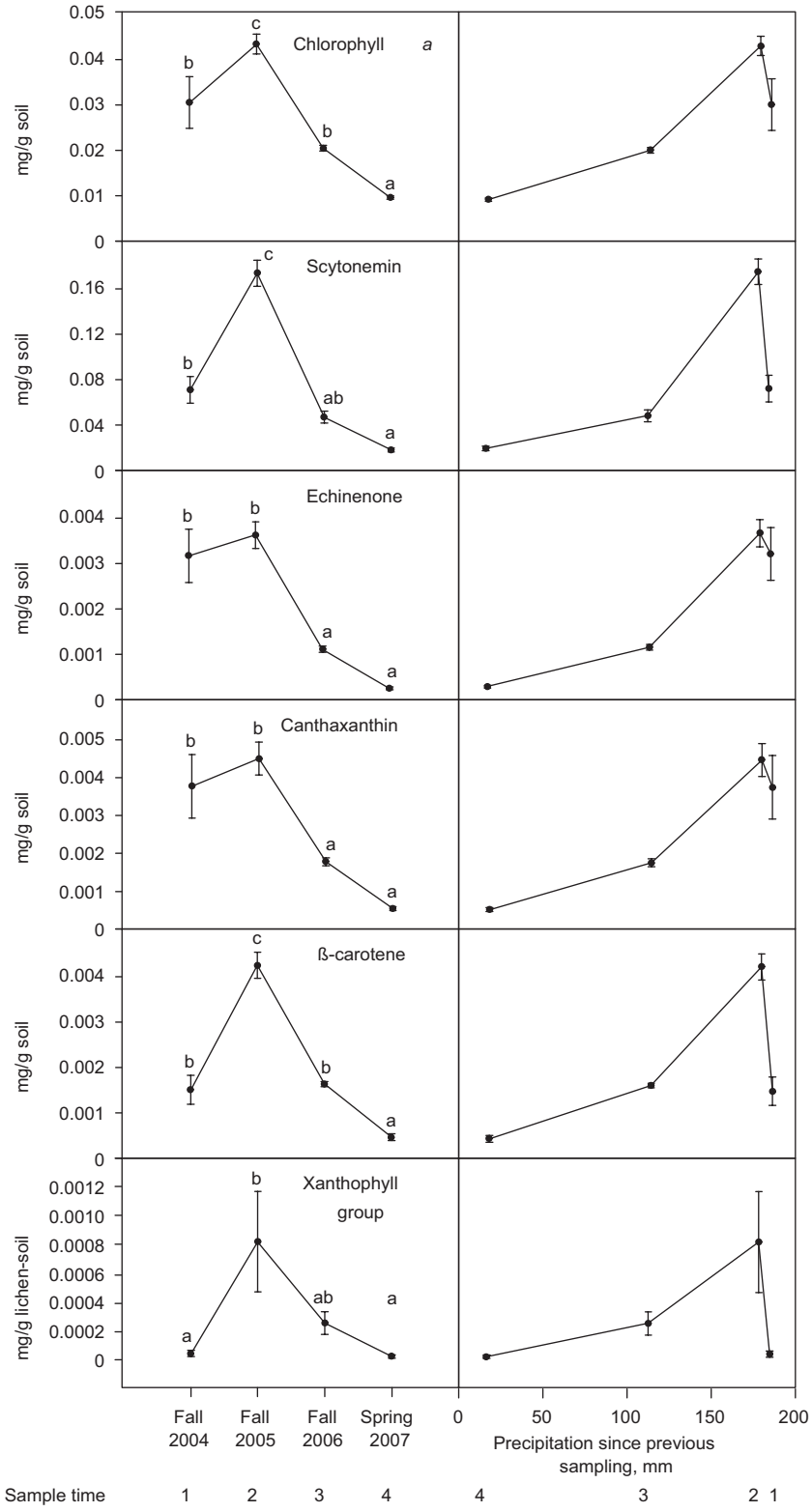

Fig. 4. Pigment concentrations in the lichen *Collema* spp. by both sampling date (left side) and by the amount of precipitation that fell between sampling times (right side). Values with the same letter above them are not statistically different.

concentrations: values were high in fall 2005 and lowest in spring 2007 (Fig. 5). Quantum yield increased when precipitation received during the previous 6 months exceeded 51 mm, but additional precipitation beyond that did not affect quantum yield values.

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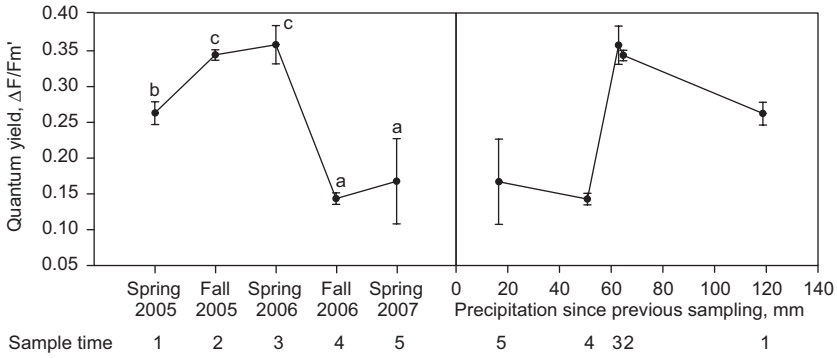

Fig. 5. Quantum yield in *Collema* spp. by both sampling date (left side) and by the amount of precipitation that fell between sampling times (right side). Values with the same letter above them are not statistically different.

Discussion

Environmental controls on lichen and moss cover and cyanobacterial biomass

It has long been believed that desert lichens and mosses are slow-growing organisms with little capacity for short-term growth response to environmental conditions. A recent study, however, showed that cover of lichens and mosses can fluctuate widely in response to seasonal changes in temperature and moisture (Belnap et al., 2006). In this current study, there were no apparent seasonal effects on cover, as we did not observe any consistent direction in the cover change for lichen (mostly *Collema* spp.) or moss (mostly *S. caninervis*) cover when values from the spring sampling times were compared to values from the fall sampling times. However, we did record a large drop in cover of all lichens and mosses from the spring 2006 to the spring 2007 sampling time. This drop in cover is not explained by temperature, as summer temperatures during 2006 were slightly lower than those during summer 2004 and 2005. In addition, there was nothing exceptional in the fall or winter temperatures that preceded the drop in 2007 cover when compared with the temperatures during the fall and winters that preceded the 2005 and 2006 measures (where there was no significant change in cover).

The large amounts of precipitation recorded at this site in 2005 resulted in an increase in cover for both *Collema* spp. and *S. caninervis*. However, an extended drought began in May 2006. Sufficient precipitation (51 mm) fell between spring 2006 and the fall 2006 sampling time to keep moss and lichen cover relatively close to spring 2006 levels. However, only 17 mm fell between fall 2006 and spring 2007. This extremely low amount of rainfall likely explains the decline in lichen and moss cover seen in 2007. This suggests that there may be a threshold of rainfall required to maintain cover of these organisms that is somewhere between 17 and 51 mm (falling within a 6-month period). Below this amount, these lichens and mosses appear unable to sustain themselves.

A similar study of the same two *Collema* species (*C. tenax* and *C. coccophorum*) and the same moss, *S. caninervis*, was done at a cool desert site on the Colorado Plateau in SE Utah, USA, from 1996 to 2003 (Belnap et al., 2006). Relative to the Mojave site, the Colorado Plateau site is cooler, with an annual average maximum temperature of 20.2 °C compared to 24.8 °C at the Mojave site. In addition, the average maximum May through September temperature at the Colorado Plateau site is 30.9 °C, whereas at the Mojave site it is 34.3 °C. At the Colorado Plateau site, *Collema* spp. cover dropped from approximately 19% in 1999 to 2% by 2003. Regression analyses showed very low or no relationship between *Collema* spp. cover and precipitation during any single month, combination of months, or during the entire sample period, although the sample period spanned years of both above average precipitation and historically low precipitation. There was also no relationship with the amount of precipitation between sampling times. Instead, there was a very strong and significant relationship with the maximum June temperature of the preceding year for each year of decline ($R^2 = 0.97$).

Comparing the results from these two studies, it appears that the *Collema* spp. from the hot Mojave Desert site, where temperatures are high and remain high over an extended period of time, are less sensitive to high temperatures than *Collema* spp. growing at the cool Colorado Plateau desert site, where temperatures are generally lower and high temperatures last for a shorter period of time. *Collema* spp. growing in either desert seem fairly unresponsive during times when precipitation amounts are above 51 mm, as comparable cover is maintained despite wide fluctuations in rainfall amount (Belnap et al., 2006; this study). There was also no drop in *Collema* spp. cover at the Colorado Plateau site when rainfall received between two sampling times

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(spring 2004 to fall 2004) was only 35 mm, the lowest we have recorded at this site. Therefore, if there is a threshold for *Collema* spp. cover at this site, it is lower than 35 mm. As this low of 35 mm occurred during summer, the threshold may be lower during times of cooler temperatures, as was the case for the Mojave site (the 17 mm occurred during winter).

The differences in the *Collema* spp. response between these two sites may be influenced by the different proportion of the two *Collema* species found in these regions: whereas our Colorado Plateau site is almost exclusively *C. tenax* (98% of the total *Collema* spp.), *C. tenax* is only about 40% of the total *Collema* spp. at the Mojave site, with the other 60% being *C. coccophorum*. Therefore, it may be that while *C. tenax* is sensitive to high temperatures and relatively insensitive to precipitation above a minimum amount, *C. coccophorum* is fairly insensitive to high temperatures, but very sensitive to the amount of precipitation it receives.

Our observations of changes in cover are not necessarily a response to actual air temperatures. In the Mojave Desert, summer precipitation events are rare, and thus lichens are seldom wet when air temperatures are high. In contrast, the Colorado Plateau receives substantial summer rain. If lichens are wet when air temperatures are higher, they dry quickly. This can easily result in a carbon deficit if they dry before they reach their net compensation point (Jeffries et al., 1993; Belnap et al., 2004, 2006). Thus, an indirect effect of higher temperatures may be that summer precipitation events can be deleterious.

Cyanobacterial biomass has been shown to decline over summer periods and to increase during late fall to early spring at a nearby Colorado Plateau site (Bowker et al., 2002). Summer is a time of high UV and of high soil temperatures, resulting in only a short amount of time when soils are sufficiently wet for BSC organisms to maintain or replace damaged chlorophyll. Late fall through early spring, in contrast, is a time of low UV (and thus low chlorophyll degradation) and low air temperatures that allow increased activity time in BSCs during which chlorophyll can be synthesized. However, we saw no seasonal pattern in chlorophyll *a* concentrations at the Mojave site: as expected, fall 2005 and 2006 had relatively low chlorophyll *a* concentrations relative to spring, but fall 2004 had quite high chlorophyll *a* concentrations relative to the prior or following spring. Spring also lacked consistent increases in chlorophyll *a* concentrations: spring 2005 showed high concentrations, as would be expected, but spring 2006 had very low concentrations relative to some fall periods, contrary to expectations.

When chlorophyll *a* concentrations were examined in light of precipitation amounts received prior to the sampling time, a pattern was observed similar to that seen in lichen and moss cover: low amounts of precipitation resulted in low concentrations of chlorophyll *a*. However, surprisingly, it appears that more precipitation was required to prevent a drop in chlorophyll *a* concentrations than required to prevent a drop in lichen or moss cover. Whereas a relatively high cover of lichens and mosses was maintained with 51 mm of precipitation falling during the 6 months previous to our sampling time, chlorophyll *a* concentrations declined with this amount of rainfall. Instead, chlorophyll *a* concentrations stayed low until rainfall amounts between 51 and 98 mm were received. This was unexpected and puzzling, as cyanobacteria are able to grow in deserts where insufficient rainfall prevents the growth of lichens and mosses, indicating they need less water for growth and survival than lichens and mosses. In addition, as cyanobacteria are embedded in the soil, and thus dry more slowly than lichen or moss tissue, which grows above the soil surface, the same amount of rain would last longer for the cyanobacteria than the lichens or mosses. Analyses of patterns in chlorophyll *a* concentrations from a Colorado Plateau site (spring and fall samples collected between April 2003 and September 2005) show no correlation between rainfall received and chlorophyll *a* concentrations (Belnap, unpub. data).

Environmental controls on UV-protective pigments

In contrast to chlorophyll *a* concentrations, the concentration of UV-protective pigments was expected to be higher in fall than spring in both free-living cyanobacteria and the lichen species *Collema*, as these pigments are believed to be manufactured in response to high levels of UV radiation that occur during summer (Bowker et al., 2002). However, this was not true for cyanobacterial pigments in this study, as there were no consistent peaks in fall concentrations when compared to spring values. Instead, pigment concentrations in the free-living cyanobacteria were likely responding almost exclusively to the amount of precipitation received, given the highly robust relationships we found between these two factors. However, higher concentrations of echinenone and β-carotene appeared to be maintained only when the precipitation received was at least 98 mm. Scytonemin and canthoxanthin concentrations dropped during times when the rainfall received decreased below 119 mm. As this site seldom receives this level of rainfall, this presents the possibility that these organisms either (a) operate at sub-optimal levels of pigments in most years or, more likely, (b) make as many pigments as possible with the available resources, as at least scytonemin is stable through time and the others are only inactivated with UV exposure.

The UV-protective pigment concentrations may also be responding to chlorophyll *a* concentrations and/or

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photosynthetic capacity. This is supported by the results obtained for *Collema* spp. Quantum yield, and chlorophyll *a* concentrations were similar to patterns in scytonemin, β-carotene, and the xanthophyll group during all sampling times. Patterns were also similar for echinenone and canthoxanthin values in 2005 and 2006, but not 2004. As quantum yield and chlorophyll *a* levels are indicators of BSCs' capacity to fix carbon, and the manufacture of pigments requires carbon, it is not surprising they are related. There was also a strong relationship between the patterns seen in chlorophyll *a* and the UV-protective pigments in free-living cyanobacteria. As there was also a strong relationship with precipitation, this data cannot be used to examine this hypothesis. However, if pigment concentrations are related to chlorophyll *a* concentrations, our data would suggest that echinenone and β-carotene are manufactured first, as they closely tracked chlorophyll *a* concentrations, whereas there appears to be a time lag between high chlorophyll *a* concentrations and increases in scytonemin and canthoxanthin concentrations. That said, the cyanobacteria in *Collema* spp. are surrounded by dark-colored fungal tissue, which protects them from UV, and so mechanisms that control or trigger pigment production in the lichenized cyanobacteria may be very different from those creating a response in free-living cyanobacteria.

Unfortunately, little is known about the factors that control the synthesis of UV pigments in BSCs. Scytonemin production is known to be initiated by a species-specific photon fluence rate threshold; thus UV exposure must occur before the manufacture of this pigment (Garcia-Pichel and Belnap, 1996). We know less about factors controlling the synthesis of the other pigments. Studies have shown that β-carotene, echinenone, and pigments in our xanthophyll group can increase after UV radiation exposure (Ehling-Schulz et al., 1997; Oren 1997), but these results are not consistent among studies (Cameron, 1960; Downing and Selkirk, 1993; Leavitt et al., 1997). Canthaxanthin, echininone, and pigments in our xanthophyll group may be synthesized from β-carotene by the addition of oxygen-containing side groups (Häder, 1997). While pigment concentrations may respond to environmental variables, the making of optimal levels of these compounds can be very slow (Donkor et al., 1993; Garcia-Pichel and Castenholz, 1991). As BSC organisms are active only when hydrated, and hydration periods are infrequent and short in deserts, especially hot deserts, there may be a substantial delay between the time UV thresholds are experienced and when peak pigment concentrations are reached.

Another complicating factor is that small rain events in the summer can strongly and negatively impact pigment production in cyanobacteria (Belnap et al., 2004). In this study, there was a large drop in pigment concentrations between our spring 2005 and fall 2005 sampling dates, despite a relatively large amount of rainfall during that time period. However, this rain occurred in 19 events that averaged 3.4 mm. The number and size of events are likely sufficient to highly stress the cyanobacteria and reduce their pigment production (Belnap et al., 2004). In contrast, between the spring 2006 and fall 2006 sampling times, when pigments mostly did not change from their previous levels, there were only 12 events, which averaged 4.2 mm. Overall, there is likely a complicated relationship between specific pigment concentrations and UV, water availability, chlorophyll *a* concentrations, and perhaps other factors (as suggested by Pentecost, 1993), especially in environments where air temperatures are high.

Global change and Biological Soil Crusts

Mojave Desert BSCs will likely be impacted by future climate change. An average of 21 models, presented by Christensen et al. (2007), predicts that summer temperatures in the Mojave Desert will increase 3.5–4.0 °C by 2099. Based on results from this study, a rise in temperature is unlikely to impact the BSCs at this Mojave Desert site. However, the predicted 15–20% decline in winter precipitation will likely have highly negative impacts on the cover of lichens and mosses, cyanobacterial biomass, and the manufacture of UV-protective pigments in both cyanobacteria and the lichen species *Collema*, especially *C. coccophorum*. There will likely be other impacts to BSCs not yet recognized.

These landscapes are also being subjected to ever-increasing soil-surface disturbances (recreation, military activities, fire), and BSCs, especially mosses and lichens, are highly vulnerable to such disturbances. When threats from climate change are combined with threats from increasing soil surface disturbance, BSCs in the Mojave Desert are at high risk of dramatic community changes or local extirpation of some lichen or moss species in the future. As these communities are critical to many aspects of dryland function, their loss will reverberate throughout these ecosystems, affecting nutrient cycling, soil fertility, soil stability, and vascular plants.

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