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Temporal Variation in Community Composition, Pigmentation, and F_v/F_m of Desert Cyanobacterial Soil Crusts

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ABSTRACT

Summers on the Colorado Plateau (USA) are typified by harsh conditions such as high temperatures, brief soil hydration periods, and high UV and visible radiation. We investigated whether community composition, physiological status, and pigmentation might vary in biological soil crusts as a result of such conditions. Representative surface cores were sampled at the ENE, WSW, and top microaspects of 20 individual soil crust pedicels at a single site in Canyonlands National Park, Utah, in spring and fall of 1999. Frequency of cyanobacterial taxa, pigment concentrations, and dark adapted quantum yield (F_v/F_m) were measured for each core. The frequency of major cyanobacterial taxa was lower in the fall compared to spring. The less-pigmented cyanobacterium *Microcoleus vaginatus* showed significant mortality when not in the presence of *Nostoc* spp. and *Scytonema myochrous* (Dillw.) Agardh. (both synthesizers of UV radiation-linked pigments) but had little or no mortality when these species were abundant. We hypothesize that the sunscreen pigments produced by *Nostoc* and *Scytonema* in the surface of crusts protect other, less-pigmented taxa. When fall and spring samples were compared, overall cyanobacterial frequency was lower in fall, while sunscreen pigment concentrations, chlorophyll *a* concentration, and F_v/F_m were higher in fall. The ratio of cyanobacterial frequency/chlorophyll *a* concentrations was 2–3 times lower in fall than spring. Because chlorophyll *a* is commonly used as a surrogate measure of soil cyanobacterial biomass, these results indicate that seasonality needs to be taken into consideration. In the fall sample, most pigments associated with UV radiation protection or repair were at their highest concentrations on pedicel tops and WSW microaspects, and at their lowest concentrations on ENE microaspects. We suggest that differential pigment concentrations between microaspects are induced by varying UV radiation dosage at the soil surface on these different microaspects.

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Introduction

Biological soil crusts (also referred to as microbiotic crusts, cryptobiotic crusts, and cryptogamic crusts) are a common feature of arid ecosystems worldwide and are important for soil stability and nutrient cycles in these ecosystems [8, 48, 72]. Generally, these crusts are a soil surface feature consisting of a matrix of soil particles, cyanobacterial filaments and exudates [8, 47], and heterotrophic bacteria [67, 73]. Well-developed crusts may also contain such diverse organisms as mosses, liverworts [17, 20], microfungi [66], chlorophytes, diatoms, flagellates [10, 30, 31], and lichens [61, 65]. Seasonality and lack of summer growth, based upon repeated cell counts, was demonstrated in crust species composition and abundance of the various taxa by workers on the Great Basin [31] and the Columbia Basin [30].

On the Colorado Plateau, biological soil crusts typically have an upheaved, pedicelled structure caused by frost heaving [8]. Pedicels tend to be oriented according to a NNW–SSE axis (Fig. 1), giving rise to distinct micro-aspects on the pedicel surfaces [26]. The reason for the constant orientation likely involves differential performance of crust species on different aspects, differential scouring by aeolian sediment, or both [26]. These various aspects are subjected to very different microclimates (Belnap et al., in prep.), and indeed display variations in the composition of the lichen and moss component [26] (Belnap et al., in prep.).

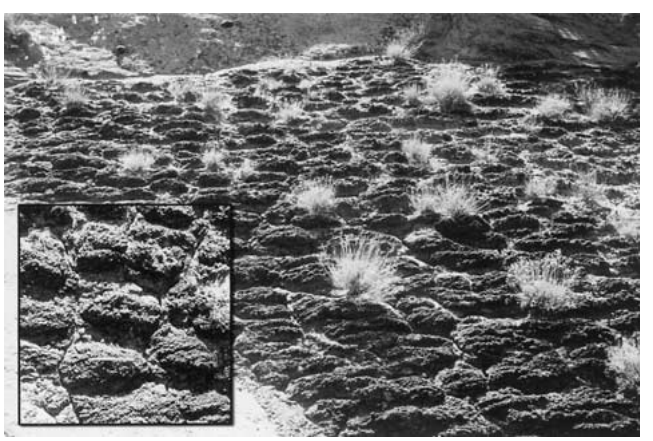

Fig. 1. On the Colorado Plateau, biological soil crusts tend to have a parallel linear ridged morphology which corresponds to a NNW–SSE axis. The inset shows a top view of soil crust pedicels.

Studies of microbes, including cyanobacteria, have shown that UV radiation can have a wide variety of negative effects on these organisms. Some of the responses to UV radiation include damage to the D1/D2 protein complex in PSII, damage to the reaction center of PSII, damage to other cell proteins, damage to DNA, inhibition of heterocyst formation, decreased motility, and the need for organisms to expend resources on repair and defense [16, 21, 27, 42, 63]. Most researchers consider damage to one or more component processes of photosynthesis detrimental to carbon fixation capabilities, although some workers disagree [2]. Deleterious impacts of UV radiation are becoming increasingly important to understand as ozone depletion allows a greater dosage of UV radiation to reach the earth's surface [45].

Among crust organisms, cyanobacteria are good candidates for study of UV impacts because they are widespread, abundant (in terms of biomass), and live in the uppermost surface layers of the soil. There are three general strategies cyanobacteria can use to decrease mortality from increased UV radiation: avoidance, repair, and protection [12]. The avoidance strategy is exemplified by a vertical migration of the organism into the soil substratum [4, 58]. The repair strategy consists of restoring photosynthetic capability compromised by damage to PSII, repairing DNA damage, or expression of genes which encode for replacement of bleached chlorophylls and antenna pigments [11]. The protection strategy involves the synthesis of pigments which either screen incoming UV radiation [23, 24] or function in the quenching of free radicals generated by UV radiation [1]. The UV radiation-protection pigments can be split into three groups: scytonemins, mycosporin-like amino acids (MAAs), and carotenoids. Scytonemin is found in the polysaccharide sheaths of terrestrial cyanobacteria and has absorbance peaks in the UV-A (320–400 nm) and UV-C (190–280 nm) wavelengths [23]. Scytonemin synthesis is well documented to increase in response to UV radiation and can protect cells even when the organism is desiccated [15, 25]. MAAs are located intercellularly in the cytoplasm in most cases [24], but there is a unique MAA that has been isolated from *Nostoc commune* Vaucher that is associated with extracellular polysaccharide exudates [19]. MAAs absorb at a wide range of wavelengths because of the variation of their molecular substituents, which are incorporated onto the basic cyclohexenone or cylcohexenimine chromophore [11]. MAAs are also shown to provide significant UV screening to DNA [12]. Carotenoids were

first observed and recorded in the early 19th century. These pigments have since been shown to protect cells from the lethal effect of photooxidation by singlet oxygen [36] and are concentrated mainly in thylakoid membranes, cell membranes, and cell walls of cyanobacteria [28]. Many carotenoids increase significantly with an increase in UV radiation, suggesting a possible passive protective role in cyanobacterial crust species [18, 41, 54].

The incoming UV radiation dosage reaching the soil surface is dependent upon latitude, season, and altitude [11]. The degree of seasonality of incoming UV radiation is compounded by latitude, and in the temperate zone of the northern hemisphere the UV radiation dosage peaks in late June (Fig. 2). Directional aspects of landform features at both a macro and micro scale also strongly influence incident radiation. In the northern hemisphere, more solar radiation is received on the southerly exposures than other aspects during winter, whereas in the summer the tops of features receive the largest dosage and the difference between aspects is at its minimum. This creates an opportunity to study seasonal effects as well as effects of varying UV radiation levels, as influenced by microaspect, within those seasons. In the present work, we ask the following questions: (1) Is there a change in pigmentation that can be seen by sampling before and after peak incoming visible and UV radiation? (2) Does community composition and photosynthetic capability (as measured by F_v/F_m) of soil crusts vary at different times of the year? (3) Are these results the same in both light crusts (averaging >65% *Microcoleus vaginatus*) and dark crusts (averaging >50% *Nostoc* spp. + *Scytonema myochrous*)? (4) Is there a significant difference in pigmentation, community composition, and photosynthetic capability of cyanobacterial crusts on the various pedicel microaspects? Ozone depletion and the subsequent increase in UV radiation are trends that are likely to continue. Thus, it is important that scientists understand possible repercussions with regards to species composition, photosynthetic rate, and abundance in primary producers such as soil crust cyanobacteria.

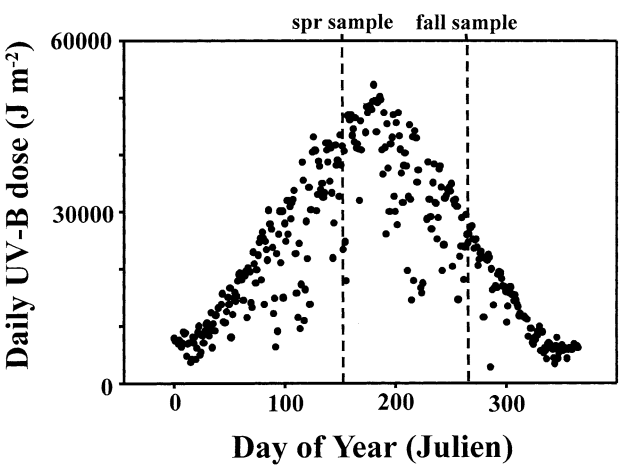

Fig. 2. Daily UV-B radiation (<315 nm) dosage for Canyonlands National Park, 1999. Data provided by J. Schreffler (EPA UV Monitoring Program/NPS Prime-Net). Peak is shortly after summer solstice. Sampling times are indicated by dashed lines.

Materials and Methods

Study Site

A single site with minimal vascular plant cover and well-developed cyanobacterial crusts was sampled near Wooden Shoe Arch, Needles District, Canyonlands National Park (109°47′E, 38°07′N, 1,545 m). Soils were similar throughout the study area, and soil crusts represented a gradient from very light (exclusively *Microcoleus vaginatus*) to very dark (dominated by *Nostoc* spp. + *Scytonema myochrous*). In contrast to *Microcoleus,* which does not produce sunscreens, *Nostoc* and *Scytonema* contain extracellular, dark-colored pigments that give the soils the dark color (depending on their density). Climate data was collected at the Needles District by the National Park Service staff, and incoming UV radiation measurements were collected approximately 30 km N of the sample site by the EPA (Schreffler and Collins, EPA UV Monitoring Program).

Sampling Methods

Five sampling areas were nonrandomly selected to represent a gradient of crust darkness, and therefore species composition. Four individual crust pedicels were selected in each sampling area for the following characteristics: (1) well-developed pedicellation, with distinguishable ENE, WSW, and top aspects; (2) minimal lichen and moss cover; and (3) a degree of darkness representative of the sampling area. Each pedicel was surface cored with a plastic vial cap 25 mm in diameter and 5 mm deep on ENE, WSW, and top aspects (n = 60 total cores, 20 per aspect). Pedicels were moistened with deionized water prior to coring to keep the cores intact. Sampling was done on 4 June 1999 (spring), and repeated on 4 October 1999 (fall).

Dark-Adapted Fluorescence Measurement

Cores were transported to the laboratory, where a digital image was taken of the core using a digital camera (see below). Cores were then dark-adapted by keeping them dark indoors for at least 10 h, then hydrated with 0.7 mL deionized (DI) water. After being hydrated for at least 2 h, F_v/F_m was measured with a portable pulse amplitude flourometer (PAM-2000, Walz Inc., Germany)

using the saturation pulse method [9]. Dark adapted F_v/F_m is equivalent to the quantum efficiency of PSII, and decreases in F_v/F_m are most often a result of photoinhibition caused by excess light [44]. Three measurements were obtained and averaged for each core.

Microscopic Species Frequency Quantification

The active cyanobacterial layer (top 2–3 mm) of each core was removed by hand with a razor blade, after moistening with 1 mL DI water. This active layer material was air-dried and homogenized using a mortar and pestle. A subsample weighing 0.87 g was taken from each sample and made into a slurry with 3 mL DI water. A 1 mL subsample was drawn off from the slurry using a disposable plastic pipette and transferred to a slide to make a wet mount. Twenty randomly selected microscope fields were viewed for each sample using a compound microscope at 400× power. Notations were made for each cyanobacterial taxon that was present anywhere in the field being viewed. Taxon frequency was calculated as the percentage of total fields viewed per sample in which a given taxon was present. The remainder of the slurry from each sample was allowed to air dry in the dark and refrigerated for pigment analysis.

Pigment Extraction and Chromatographic Analysis

For pigment extraction, the soil samples were further pulverized by forceful stirring and crushing employing a mortar and pestle. Each sample, after stirring, was weighed so that pigment concentrations could be calculated on a per mass basis, and the samples were then returned to the mortar and ground with about 0.5 mL of DI water. Grinding was continued until all components were completely mixed, at which point about 4 mL of HPLC-grade acetone was added and the grinding was repeated. The samples were transferred, using acetone, to a 7 mL Kontes tissue grinder and ground until all pigment-bearing components were pulverized. The samples were transferred to test tubes, each sample having an end volume of about 10 mL and a final extraction concentration of about 95% acetone. The head space of each test tube was filled with N_2 gas, sealed with Parafilm, and refrigerated in the dark at 8°C overnight. The following day the samples were filtered under vacuum on Whatman GF/F filter paper. Filtrates were repeatedly rinsed with acetone to remove all pigments. The samples were condensed, using N_2, to a 3 mL volume.

Quantitative and qualitative HPLC analysis was performed according to the method of Karsten and Garcia-Pichel [33], modified as follows. Pigments were separated on a Symmetry C_{18} column (5 μm, 3.9 × 150 mm, Waters Corporation, Milford, MA) with a Symmetry guard column of the same composition (5 μm, 3.9 × 20 mm, Waters Corporation, Milford, MA). The Waters HPLC system consisted of a degasser, a high-pressure gradient pump, an autosampler, a column oven, a dark refrigerated autosampler chamber, a photodiode array detector (Waters 996), and a fluorescence detector (Waters 474). One hundred μL of the acetone–pigment solution was injected by the autosampler into the system. At 16 min, the mobile phase rate increased to 2.0 mL min^{-1}, and the elution lasted 23 min. Pigments were identified by comparative retention times and characteristic absorption maxima obtained from the photodiode array and fluorescence detectors. Concentrations for all pigments except scytonemin were quantified using peak areas integrated from photodiode array data at 436 nm and external standards (Fig. 3). A standard curve was generated by injection of a concentration series of the pigment into the HPLC system employing the modified Karsten and Garcia-Pichel method described above [33]. Commercial standards of chlorophyll *a*, chlorophyll *b*, and β-carotene were obtained from Sigma Chemical Co., USA. Alloxanthin, canthaxanthin, chlorophyll *c*2, echinenone, fucoxanthin, lutein, myxoxanthophyll, pheophytin *a*, violaxanthin, and zeaxanthin were purchased from DHI Water and Environment, Denmark. 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 [25]. An extinction coefficient of 60.8 L g^{-1} cm^{-1} for 436 nm was used. Data were analyzed using Millennium^{32} software (Waters, USA). To enable statistical analysis, the xanthophylls zeaxanthin, lutein, and myxoxanthophyll were grouped (referred to as the xanthophyll subgroup) on the basis of similar function, similar absorbance spectra, similar retention times, and difficulty of distinguishing between two of the pigments (lutein and zeaxanthin).

Digital Image Analysis

To obtain a darkness index, each core was photographed using a Nikon Coolpix 950 digital camera at constant lighting conditions for each season. Using Scan Pro 4.01 (1987–1997, SPSS Inc.) the images were defined by a user-set color intensity. This value was

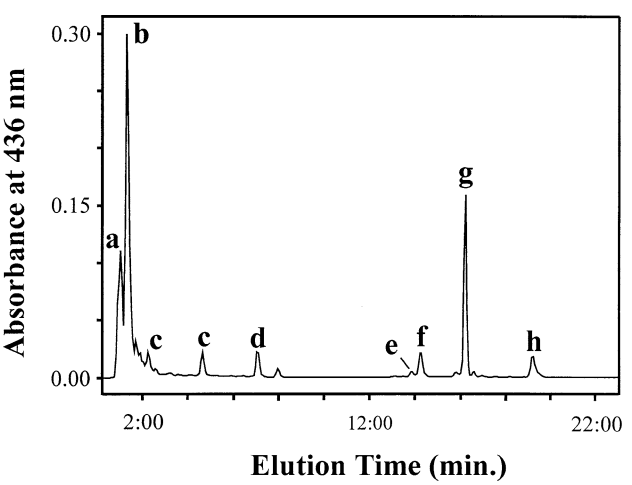

Fig. 3. HPLC photodiode array chromatogram showing discrete absorbance peaks for a system peak (a), scytonemin (b), myxoxanthophylls (c), canthaxanthin (d), chlorophyll *b* (e), echinenone (f), chlorophyll *a* (g), and β-carotene (h). Area of the absorbance peaks is used to quantify pigment concentrations.

selected to represent what appeared to be dark cyanobacterial cover (consisting of *Scytonema* + *Nostoc* and their dark pigmented exudates) in the images. The area of the image that had an intensity value greater or equal to the selected intensity value was calculated using Scan Pro 4.01 and used as a darkness index. To define "dark" and "light" crusts for analysis in each season, plugs lighter than the median darkness index value were classified as "light" and those that were darker were classified as "dark."

Statistical Analysis

The normality of the distribution of the data was tested using the Shapiro–Wilk test. When necessary, datasets were $\log_{10}$ transformed or $\log_{10} + 1$ transformed to create a normal distribution. If the distribution was normal, the data were analyzed using an independent *t*-test (for two level analyses) or one-way ANOVA (for multilevel analyses) if variances were equal (determined by Levene's test), or a Welch ANOVA if variances were not equal. If three or more means were being compared, a Tukey–Kramer test was employed to determine significant differences. When datasets were not normally distributed and could not be transformed, nonparametric tests were used: Mann–Whitney *U* test for comparisons of two datasets, and the Kruskal–Wallis test for comparison of three or more datasets. Kruskal–Wallis tests were also followed with Tukey–Kramer tests to test for significant differences. The above statistics were done using JMP IN 3.2.1 (1998 SAS Institute). Mean values for the seven pigments were computed for the three aspects in both the June and October datasets. A Friedman mean rank test was performed using these means in SPSS 10.0 (1999, SPSS Inc.).

Results

Climate and UV-Radiation Data

Based on a 35-year weather record, the site receives 216 mm mean annual precipitation, with about 35–40% of this occurring as summer thunderstorms (National Park Service, Climate Records). In 1999, monthly precipitation for the months June, July, August, and September were 18, 34, 50, and 42 mm, respectively (35-year averages for these months were 10, 24, 27, and 22 mm, respectively). Thirty-two individual measurable rain events were recorded for the time period between 4 June and 4 October, for an above-average total of 155 mm. Mean daily UV-B radiation dose for the months June, July, August, and September 1999 were 4213.8, 3969.9, 3231.8, and 2725.7 J m^{-2} (Schreffler, EPA UV Monitoring Program), respectively. Incoming UV-B radiation dose peaked shortly after the summer solstice (Fig. 2). Typical summer soil surface temperatures range from 40 to 50°C (sometimes higher) at midday (Belnap et al., unpublished data). Hydration periods at the soil surface are usually only a few to several hours following a summer rain event; thus, soils are typically dry (Belnap et al., in prep.). In 1999, June and July were typically hot, while August and September were cooler than normal.

Comparisons of Pigmentation as a Function of Season

The concentrations of six of the seven measured pigments were higher in fall compared to spring (Table 1). Mean F_v/F_m increased from 0.221 to 0.379 (p = <0.0001) and was accompanied by a corresponding rise in chlorophyll *a* (mg g $soil^{-1}$) from 0.013 to 0.020 (p = <0.0001). Significant increases were also detected in scytonemin, the xanthophyll subgroup, canthaxanthin, echinenone, and chlorophyll *b*. All of these increased by at least 32%. Especially notable were scytonemin, which almost doubled (p = 0.0002); chlorophyll *b*, which almost tripled (p = 0.008); and the xanthophyll subgroup, which increased by more than 400% (p = <0.0001). β-carotene concentration did not change significantly.

Comparisons of Communtity Composition as a Function of Season

Total cyanobacterial frequency decreased in fall samples relative to spring samples (Table 1). The ratio of darkly pigmented cyanobacteria (*Nostoc* + *Scytonema*) to *Microcoleus* occurrences did not differ significantly between the two seasons, because of a concomitant decrease in *Nostoc* spp. and *M. vaginatus* frequency. *Microcoleus* decreased by approximately 11% (p = 0.03), while *Nostoc* spp. decreased by about 37% (p = 0.04). *Scytonema* frequency showed a tendency to decrease when fall samples were compared to spring samples, but this difference was

Table 1. Frequency of cyanobacterial taxa, F_v/F_m, and pigment concentrations (mg g $soil^{-1} \times 10^{-4}$) in all cores, as a function of season[a]

Dependent Variable	Spring Mean ± SE	Fall Mean ± SE	*p*
M. vaginatus frequency	86.4 ± 2.1	77.6 ± 2.9	**0.03**
Nostoc spp. frequency	40.5 ± 4.5	25.7 ± 2.9	**0.04**
S. myochrous frequency	32.5 ± 3.6	25.6 ± 3.0	0.2
F_v/F_m	0.221 ± 0.011	0.379 ± 0.009	**<0.0001**
Chlorophyll *a*	130.9 ± 10.4	200.0 ± 98.0	**<0.0001**
Scytonemin	659.6 ± 73.0	1150.7 ± 104.3	**0.0002**
Xanthophyll subgroup	5.1 ± 1.2	21.7 ± 3.4	**0.0001**
Canthaxanthin	11.2 ± 1.5	15.2 ± 1.2	**0.004**
Echininone	12.1 ± 1.1	17.8 ± 1.3	**0.0004**
Chlorophyll *b*	1.3 ± 0.3	3.1 ± 0.5	**0.008**
β-Carotene	7.2 ± 0.8	7.3 ± 0.5	0.5

[a] Significant *p* values are indicated in bold text.

not statistically significant. Despite the overall decrease of cyanobacterial taxa density, dark-adapted F_v/F_m values were significantly higher in fall.

Comparisons between Light and Dark Crusts

In light crusts, *Microcoleus* frequency was 18% less in fall compared to spring (p = 0.01), while *Nostoc* and *Scytonema* frequency did not change significantly (Table 2). In contrast, F_v/F_m values for fall were nearly twice those observed in spring (p = <0.0001). Chlorophyll *a*, scytonemin, the xanthophyll subgroup, and chlorophyll *b* also increased dramatically from spring to fall, with the xanthophyll subgroup and chlrophyll *b* increasing 13- and 17-fold, respectively. Again, β-carotene did not change significantly; canthaxanthin showed a near-significant increase. No pigments decreased from spring to fall in the light crust.

Greater total cyanobacterial frequency and greater relative abundance of dark-pigmented taxa were observed in dark crust in both seasons (Table 3). Light crusts were *Microcoleus*-dominated: 81% *Microcoleus* frequency vs 34% *Nostoc* + *Scytonema* frequency in spring, and 66% *Microcoleus* frequency vs 33% *Nostoc* + *Scytonema* frequency in fall. Dark crusts were characterized by greater overall biomass, and much more *Nostoc* and *Scytonema* biomass than light crusts: 91% *Microcoleus* frequency vs 109% *Nostoc* + *Scytonema* frequency in spring, and 89% *Microcoleus* frequency vs 69% *Nostoc* + *Scytonema* frequency in fall. (Because frequency for taxa were computed separately, and all taxa in a microscopic field were noted, values can exceed 100%.) In contrast to light crusts, *Microcoleus* frequency in dark crusts did not decrease significantly when comparing spring to fall samples, while *Nostoc* frequency decreased by 40% (p = 0.005), and *Scytonema myochrous* frequency decreased by 32% (p = 0.02). F_v/F_m increased significantly from 0.222 to 0.382 (spring and fall, respectively), and most pigments, including chlorophyll *a*, scytonemin, the xanthophyll subgroup, canthaxanthin, and echinenone, increased significantly. The xanthophyll subgroup again showed a pronounced (nearly 3-fold) increase from spring to fall. No significant change in β-carotene was detected. All pigments were found in greater concentrations in dark crusts than light crusts, regardless of season (p = <0.0001).

Table 2. Frequency of cyanobacterial taxa, F_v/F_m, and pigment concentrations (mg g soil$^{-1} \times 10^{-4}$) in "light" cores, as a function of season[a]

Dependent Variable	Spring Mean ± SE	Fall Mean ± SE	p
M. vaginatus frequency	80.7 ± 3.5	66.3 ± 4.3	**0.01**
Nostoc spp. frequency	20.0 ± 4.4	15.5 ± 2.9	0.6
S. myochrous frequency	14.1 ± 2.6	17.7 ± 3.9	0.9
F_v/F_m	0.225 ± 0.017	0.376 ± 0.012	**<0.0001**
Chlorophyll *a*	75.8 ± 43.0	155.4 ± 82.4	**0.0001**
Scytonemin	368.8 ± 65.0	1043.0 ± 154.4	**<0.0001**
Xanthophyll subgroup	0.5 ± 0.2	8.6 ± 2.9	**<0.0001**
Canthaxanthin	2.2 ± 0.5	3.1 ± 0.3	0.1
Echininone	2.9 ± 0.4	6.4 ± 0.8	**0.0007**
Chlorophyll *b*	1.7 ± 0.9	3.7 ± 2.0	**0.006**
β-Carotene	4.2 ± 0.5	5.4 ± 0.6	0.2

[a] Significant p values are indicated in bold text.

Table 3. Frequency of cyanobacterial taxa, F_v/F_m, and pigment concentrations (mg g soil$^{-1} \times 10^{-4}$) in "dark" cores, as a function of season[a]

Dependent Variable	Spring Mean ± SE	Fall Mean ± SE	p
M. vaginatus frequency	91.4 ± 2.1	88.6 ± 2.5	0.3
Nostoc spp. frequency	59.7 ± 6.0	35.5 ± 4.3	**0.005**
S. myochrous frequency	49.3 ± 4.7	33.5 ± 4.1	**0.02**
F_v/F_m	0.222 ± 0.016	0.382 ± 0.078	**<0.0001**
Chlorophyll *a*	182.4 ± 70.4	234.2 ± 96.4	**0.01**
Scytonemin	1625.8 ± 140.3	2146.3 ± 201.2	**0.02**
Xanthophyll subgroup	6.9 ± 1.5	21.8 ± 3.5	**<0.0001**
Canthaxanthin	5.2 ± 0.5	6.1 ± 0.4	**0.01**
Echininone	7.7 ± 0.7	9.5 ± 0.8	**0.005**
Chlorophyll *b*	13.2 ± 1.9	21.2 ± 1.5	**0.09**
β-Carotene	8.5 ± 0.7	7.3 ± 0.4	0.6

[a] Significant p values are indicated in bold text.

Comparisons by Aspect

Whether spring and fall data sets were analyzed separately or pooled, ANOVA and/or Kruskal–Wallis testing did not detect significant differences in species composition, F_v/F_m or individual pigment concentrations between pedicel aspects (Table 4). A Freidman mean rank test failed to detect a significant difference between mean concentrations of the seven pigments in the spring data, although pedicel tops tended to have higher pigment concentration. The same test was repeated for the fall data, wherein ENE pigment concentrations were significantly lower (p = 0.005) than both the top and WSW aspects.

Discussion

Variation in UV Radiation-Linked Pigment Concentrations

Concentrations per gram of soil of scytonemins, MAAs, xanthophylls, and carotenoids commonly increase after

Table 4. Frequency of cyanobacterial taxa, F_v/F_m, and pigment concentrations (mg g soil^{-1} × 10^{-4}) among pedicel aspects, as a function of season[a,b]

Dependent variable	Sample time (Spr/Fall)	ENE Mean ± SE	Top Mean ± SE	WSW Mean ± SE
M. vaginatus frequency	Spr	83.3 ± 3.9	88.2 ± 4.3	87.5 ± 2.5
	Fall	78.5 ± 4.7	73.9 ± 5.9	80.6 ± 4.1
Nostoc spp. frequency	Spr	44.2 ± 7.9*	38.4 ± 8.2	39.3 ± 7.9
	Fall	20.5 ± 4.6	28.9 ± 5.4	28.1 ± 5.2
S. myochrous frequency	Spr	35.6 ± 6.1	33.4 ± 7	28.8 ± 5.6
	Fall	28.5 ± 5.3	23.8 ± 5.5	23.1 ± 4.9
F_v/F_m	Spr	0.240 ± 0.021***	0.206 ± 0.019***	0.219 ± 0.089***
	Fall	0.373 ± 0.015	0.360 ± 0.016	0.405 ± 0.015
Chlorophyll *a*	Spr	102.8 ± 10.9**	156.7 ± 20.8	131.7 ± 18.8**
	Fall	176.9 ± 17.5	206.3 ± 26.9	221.3 ± 24.9
Scytonemin	Spr	859.6 ± 168.4*	1200.7 ± 180.2	983.9 ± 230.5**
	Fall	1426.2 ± 199.9	1610.5 ± 272.8	2045.2 ± 314.1
Xanthophyll subgroup	Spr	3.4 ± 1.6*	4.5 ± 1.7***	3.3 ± 1.4**
	Fall	11.9 ± 3.0	19.3 ± 5.4	17.2 ± 4.0
Canthoxanthin	Spr	2.9 ± 0.4	4.0 ± 0.7	4.2 ± 0.8
	Fall	4.1 ± 0.4	5.2 ± 0.6	5.3 ± 0.7
Echinenone	Spr	3.9 ± 0.5**	6.8 ± 1.2	5.4 ± 0.8
	Fall	7.6 ± 0.8	9.1 ± 1.3	7.7 ± 1.1
Chlorophyll *b*	Spr	7.7 ± 2.5	8.3 ± 2.4	6.5 ± 2.1
	Fall	10.3 ± 2.6	14.6 ± 3.0	16.5 ± 3.2
β-Carotene	Spr	5.7 ± 0.8	7.2 ± 0.9	6.4 ± 0.9
	Fall	6.1 ± 0.5	6.8 ± 0.8	6.5 ± 0.6

[a] Significant differences between spring and fall values are indicated by *, **, *** for significance to 0.05, 0.001, and 0.0001 levels, respectively.
[b] A Freidman mean rank test detected significantly ($p = 0.005$) higher mean pigment concentrations on top and WSW aspects than ENE aspects in fall.

exposure to UV radiation in a wide variety of cyanobacterial taxa from varying habitat types [18, 23, 51]. This study shows that temporal variation of some of these pigments also occurs in desert biological soil crusts. Scytonemin, a proven photoprotective pigment, is synthesized in desert soil crusts by the genera *Scytonema* and *Nostoc*. Scytonemin was consistently higher in light crusts, dark crusts, and pooled crusts, regardless of microaspect, when fall samples were compared to spring samples. This pigment, in combination with MAAs, absorbs much incoming UV radiation before it reaches cyanobacterial cells. We did not measure MAA concentrations; therefore, their omission does not reflect their absence in these cyanobacteria. Carotenoids and xanthophylls are represented here by echinenone, canthaxanthin, β-carotene, and the xanthophyll subgroup (myxoxanthophyll, lutein, zeaxanthin). Echinenor and canthaxanthin were higher in fall than spring in dark crusts, and the xanthophyll subgroup was consistently many times higher in dark crusts, light crusts, and pooled crusts. By quenching free radicals, the presence of these compounds may provide a second-tier defense against excess visible and UV radiation-induced photooxidative damage.

The high levels found in fall relative to spring suggests that scytonemin was synthesized in response to the summer UV radiation peak (Fig. 2). Synthesis of scytonemin is initiated by a species specific photon fluence rate threshold; thus UV exposure must occur before this pigment is made [23]. Terrestrial cyanobacteria take 2–3 days (with constant hydration) after exposure to UV thresholds to obtain optimal levels of UV screening [17, 24]. Pigment synthesis can only take place when crust organisms are hydrated and active: in desert soil crusts, hydration periods are infrequent and short and therefore there may be a substantial delay between the time UV thresholds are experienced and when peak scytonemin concentrations are reached. In addition, scytonemin is chemically and photochemically stable [57], can persist in exopolysaccharides for some time after the period of maximal synthesis [22, 24], and has been recovered from ancient lake sediments [40]. Therefore, we would expect to see higher scytonemin concentrations in fall-collected soils, after a summer of excessive UV exposure, than in spring-collected soils.

Whether carotenoids exhibit a similar pattern warrants further investigation. β-carotene has been shown by Paerl [54] to increase after UV radiation exposure, but other workers have not observed this result [11, 18, 41]. β-carotene concentration did not change significantly in this study, while the other carotenoids and xanthophylls increased markedly. Xanthophyll biosynthesis in cyanobacteria is currently unresolved [28]. It is feasible that

xanthophylls are synthesized from β-carotene by the addition of oxygen-containing side groups [28]. Our observed lack of change in β-carotene may result from its immediate conversion to canthaxanthin, echininone, pigments of the xanthophyll subgroup, or other carotenoids.

Concentration of Chlorophylls Relative to Cyanobacterial Frequency

Chlorophyll *a* concentration was much higher in fall than spring, despite a significant decrease in cyanobacterial frequency. The ratio of cyanobacterial frequency to chlorophyll *a* concentration was 2–3 times lower in fall than spring in light, dark, and pooled crusts. Chlorophyll *a* concentration has traditionally been used as a surrogate measure for cyanobacterial abundance and/or biomass in marine, freshwater, and terrestrial habitats [6, 52, 55]. However, studies show cyanobacterial chlorophyll *a* concentrations respond to environmental conditions such as low light [70], high light [52], and Cu concentration [61] while cell counts remain constant. Thus, chlorophyll *a* concentration is probably not a good indicator of cyanobacterial abundance in soil crusts. We did not measure cyanobacterial biomass in this study. However, seasonally large variations in cell size have not been observed in desert soil cyanobacteria (Belnap, pers. obs.), suggesting that chlorophyll *a* is also unlikely to be a good surrogate for soil crust cyanobacterial biomass. When soil crust cyanobacterial enumeration is desired, we suggest that microscopic quantification may be preferable to the chlorophyll *a* assay.

In desert soil crusts, abundance or biomass estimates are often used as an indicator of ecosystem functions (e.g., soil stability, nutrient inputs). In cases where a measure of soil stability is needed, it may be best to measure stability directly or develop other potential surrogate indicators (e.g., polysaccharide assay). For carbon inputs, chlorophyll *a* may be the best assay, in that it directly relates to potential carbon fixation. A similar situation exists for nitrogen fixation, which depends on carbon fixation rates [7]. More research is needed in this arena.

Chlorophyll *b* was also higher in fall relative to spring. This pigment is synthesized in crusts by chlorophytes, but not by cyanobacteria. Prochlorophytes, which are believed to be cyanobacteria [29], also synthesize chlorophyll *b,* but they remain unreported in soil crusts. Chlorophytes were only rarely observed in the soils used in this study. The higher fall values could indicate a greater concentration of this pigment in crust chlorophytes, or greater abundance of chlorophytes in fall. Because the chlorophyll *b* values are higher than we would expect (based upon the rarity of chlorophytes), we cannot rule out that the pigment came from organisms other than chlorophytes.

Mortality in Biological Soil Crusts

Our cell frequency data suggest an apparent cyanobacterial die-off in soil crusts between our spring and fall samples. Although we cannot pinpoint precisely when the mortality occurred, we propose that the most likely explanation is a summer die-off event. Such changes in abundance of the taxa are consistent with the findings of Johansen and Rushforth in central Utah [31]. They found that high densities of *Microcoleus vaginatus* and *Nostoc* sp. in late spring are followed by a dramatic decrease in July, a significant rise in August (perhaps due to monsoonal rains), and a subsequent decline into early autumn. In the Columbia Basin, summer mortality of *M. vaginatus* was also observed, while *Nostoc* spp. did not display a clear trend [31]. Seasonality of microbial species composition and relative abundance of species is a widespread phenomenon in phytoplanktonic communities [14], epilithic communities [49], cryptoendolithic communities [5], and intertidal cyanobacterial mats [34].

Several factors alone or in combination may be responsible for the proposed summer die-off. Soil surface temperatures greater than 40°C are typical of summer conditions and are supraoptimal for photosynthetic activity of cyanobacteria [39]. These cyanobacteria can survive long droughts in an inactive state [39]. Upon rewetting, poikylohydric organisms experience carbon loss via respiration before reaching a net carbon gain via photosynthesis [3, 68].

Successive hydration periods too short to allow net carbon gains could induce mortality [32]. During this study period, 28 individual rain events occurred, of which 36% occurred during the morning or midday, and 64% during the evening or at night. Thus, since hydration periods were short, as in Garcia-Pichel and Belnap [22], and mostly occurred when light was limiting, it is likely that significant carbon loss occurred during this time. Relatively frequent rain events which hydrate the soil to field capacity could also cause some microbial cells to burst, as in some California grassland soils [35].

Incoming solar radiation peaks in summer and is a factor in the success of photosynthetic organisms. Usually, longer day lengths result in more time in which photo-

synthetically active radiation (PAR) is sufficiently available to maintain a positive carbon budget: however, since incoming UV radiation and PAR peak around the summer solstice (Fig. 2), solar radiation-induced damage to PSII and bleaching of photosynthetic pigments could result in lower PS rates [69]. In addition, the large increases in pigment concentration after spring incur a metabolic cost. For example, an MAA found in *Nostoc commune* may represent up to 10% of the dry weight of the colony [62], indicating that allocation of photosynthates to the manufacturing of this pigment can be quite large. The high cost of these compounds is incurred when it is most difficult for cyanobacteria to achieve net PS due to short hydration periods and thermal limits to PS, thus potentially resulting in mortality. The fact that chlorophyll *a* and F_v/F_m were consistently higher in fall, relative to spring, samples suggests that although there were fewer organisms present in the soil, those that were present did not sustain major UV-B radiation induced damage to PSII, or damage was repaired by our fall sampling time. Higher chlorophyll *a* and F_v/F_m indicates that carbon assimilation rates were probably also higher in the fall, although there are examples of UV-B radiation suppression of carbon assimilation without corresponding suppression of F_v/F_m [2]. In fall, cyanobacteria may have been producing chlorophyll *a* at high rates unimpeded by high solar radiation, because of the large concentration of sunscreen pigments persistent in the soil crust matrix. Alternatively, decreased incoming PAR could increase the need for light harvesting pigments, thus stimulating biosynthesis of chlorophylls. Such hypotheses need to be tested with repeated sampling in multiple years.

Differential Mortality and Stratification of Cyanobacterial Taxa

Multi-specific biological soil crusts are often vertically stratified. In the Negev Desert [38] and on the Colorado Plateau [22] (Fig. 4), the heavily pigmented, nonmotile species occur at the soil surface where PAR is most available, and the more motile, less pigmented species extend down into the soil column a few millimeters. Such stratification is a recurring pattern in complex microbial communities including intertidal marine mats [34, 56], mats from hypersaline ponds [37], terrestrial fellfield mats [13] and endolithic communities [46, 50]. In one particularly good example, a microbial community at the bottom of a saltern pond was stratified from the top down into an orange-brown layer (unicellular cyanobacteria), a green layer (unicellular and filamentous cyanobacteria), a sometimes-present white

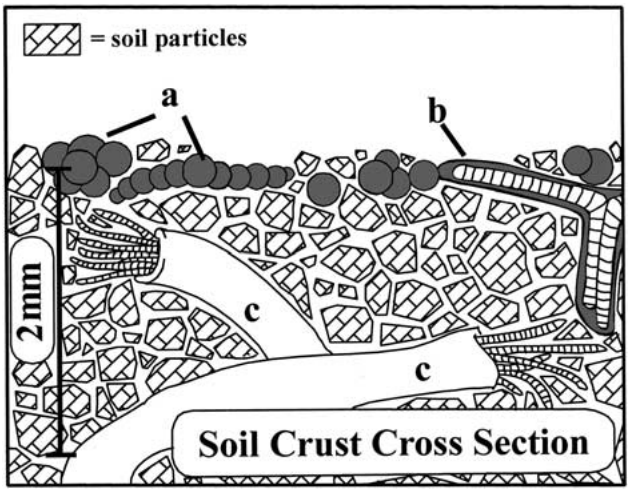

Fig. 4. Well developed biological soil crusts tend to display stratification with dark-pigmented *Nostoc* spp.(a) and *Scytonema myochrous* (b) restricted to the soil surface, and motile filamentous *Microcoleus vaginatus* (c) extending as deep as 5 mm below the soil surface.

layer (sulfur bacteria), and a purple layer (sulfur bacteria) [53]. Pigment concentrations also tend to be stratified in various microbial communities, with higher concentrations of MAAs, scytonemin, or carotenoids in the upper layers, and higher concentrations of chlorophyll *a* and phycobilisomes in the lower portions [33, 43, 53], but this is not always due to differences in species composition [59].

In this study, there was no significant die-off of *Microcoleus* in the dark crusts (where the heavily pigmented *Nostoc* and *Scytonema* were present), whereas there was *Microcoleus* mortality in the light crusts (Tables 2 and 3). When motile cyanobacteria such as *Microcoleus* are isolated from their physical habitats and exposed to laboratory-applied high visible and/or UV radiation, they experience greater deleterious effects when compared to more pigmented, nonmotile strains such as *Nostoc* or *Scytonema* [58, 64]. The results of the present study suggest that increased pigments, such as scytonemin or MAAs, synthesized by *Nostoc* and/or *Scytonema* (which form colonies in the uppermost layers) (Fig. 4), may benefit *Microcoleus* by screening incoming UV radiation and/or protecting pigments from bleaching. Analogous community dynamics are found in marine cyanobacterial mats, where *Microcoleus chthonoplastes* Thuret grows at peak incoming UV-B radiation levels when the scytonemin-producing *Lyngbya* cf. *aestuarii* Liebm. is present in a layer above it [34]. Kruschel and Castenholz [37] observed that a switch from green-filtered to UV-A/B light induces motile *Oscillatoria* to shift its position from the

surface of a microbial mat to a subsurface position underneath a nonmotite cyanobacterial and diatom layer containing carotenoids.

In a comparison between rock-dwelling and sediment-dwelling littoral microbial communities exposed to various UV radiation exposure treatments, rock-dwelling communities were inhibited following UV-A exposure, whereas abundance of several types of organisms (including filamentous cyanobacteria) increased in nearby sediment-dwelling communities [71]. This result is attributed to the sediment providing a physical refuge for the cyanobacteria [71]. In a marine sand-associated microbenthic community, experimentally enhanced UV-B radiation coincided with mortality of coccoid cyanobacteria, and an increase in filamentous cyanobacteria and motile diatoms [51]. However, because these same species composition changes also occurred in controls (albeit less pronounced), they cannot be attributed exclusively to the enhanced UV-B radiation treatment and may constitute a background successional pattern [51]. *Microcoleus* found in desert biological soil crusts has been observed to migrate to the soil surface after wetting in both the lab and the field, and to migrate downward as the surface dries (Belnap and Garcia-Pichel, pers. obs.). In addition, hydrated *Microcoleus* will leave the soil surface when exposed to UV lamps in the lab (Garcia-Pichel, unpublished data). The patterns in our results and other studies suggests that in desert biological soil crusts, movement into physical refugia may be a more effective strategy to avoid UV radiation-caused mortality than pigment production.

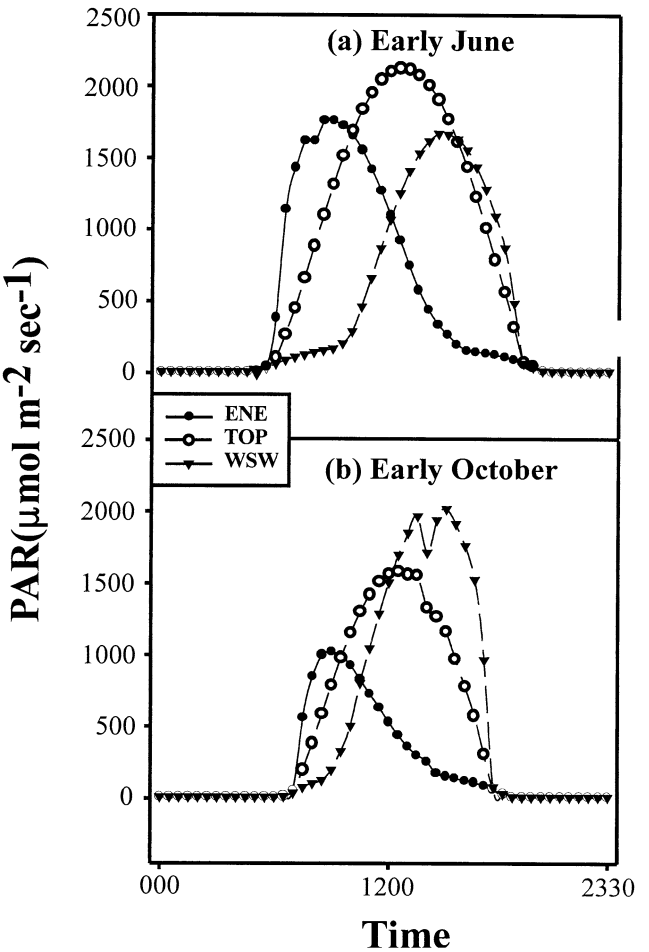

Fig. 5. Incoming photosynthetically active radiation (PAR) measured on three microaspects at the surfaces of soil crust pedicels (Belnap et al., in prep.). (a) All aspects receive a large dose of incoming radiation in early June, especially pedicel tops, which generally had more pigmentation. (b) Sun exposure has changed markedly by early October, with the ENE and tops receiving less radiation than June, and WSW receiving more.

Effects of Microaspect on Pigmentation and Community Composition

Among pedicel microaspects, patterns in pigmentation paralleled patterns in relative solar radiation exposure. In early June, the sun is nearly directly overhead at solar noon and incoming solar radiation is at its diurnal peak. The pedicel tops should receive the greatest dose of incoming UV radiation at this time, as UV radiation is positively correlated with PAR [21, 69] (Fig. 5a). This corresponds well with the tendency of pigment concentrations to be relatively high on pedicel tops in early June. In October, the diurnal arc of the sun is considerably lower on the horizon, enhancing the effect of microaspect (Fig. 5b). The WSW and top aspects should both receive relatively more UV radiation at this point than ENE aspects, and this was reflected in the significantly higher pigment concentrations in soils from the WSW and top aspects. The fact that species composition was not significantly different between aspects in either season supports the assertion that pigment concentration can change independently of species composition. Lichens and mosses have been found to prefer particular microaspects in this region [26] (Belnap et al. in prep.), and it is unclear why cyanobacterial community composition did not show a similar pattern. Perhaps this disparity reflects two different strategies for dealing with microclimate differences: (1) preferential growth on microaspects with a climate that favors growth (lichens and mosses), and (2) homogenous growth across differing microaspects with differential expenditures on local adaptations, such as pigment biosynthesis (cyanobacteria).

Conclusions

In this study, we have demonstrated that mortality of cyanobacteria in desert biological soil crusts occurred between late spring and early fall. Several sunscreen and antioxidant pigments were shown to be much higher after the time of peak incoming solar radiation, and this is primarily attributed to biosynthesis by surface-bound *Nostoc* and *Scytonema*. Despite increased pigmentation, *Nostoc* frequency significantly decreased, possibly as a result of UV radiation-induced damage or a carbon deficit. Frequency of the motile filamentous *Microcoleus* only decreased significantly when sunscreen-producing *Nostoc* and *Scytonema* were not present. We propose that in multispecies crusts, migration underneath the sunscreen-producing species decreases solar radiation-induced damage to *Microcoleus* and thus prevents significant mortality. This is currently being tested using a UV radiation-modification experiment. We are also beginning to examine how chlorophyll *a* varies in relation to cyanobacterial biomass on an annual cycle.

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