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Bromus tectorum litter alters photosynthetic characteristics of biological soil crusts from a semiarid shrubland

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ABSTRACT

Invasion by the exotic annual grass *Bromus tectorum* has increased the cover and connectivity of fine litter in the sagebrush steppes of western North America. This litter tends to cover biological soil crusts, which could affect their metabolism and growth. To investigate this possible phenomenon, biological soil crusts dominated by either the moss *Bryum argenteum* or the lichen *Diploschistes muscorum* were covered with *B. tectorum* litter (litter treatment) or left uncovered (control treatment) and exposed to natural field conditions. After periods of five and ten months, we removed the litter and compared the photosynthetic performance of biological soil crusts from the two treatments. Litter induced photosynthetic changes in our samples. In both *B. argenteum* and *D. muscorum*, biological soil crusts that had been covered with litter for ten months had lower rates of gross photosynthesis and lower chlorophyll content than control samples. Similarly in both biological soil crust types, litter reduced the rate of dark respiration. For *D. muscorum*, the reduction in dark respiration fully compensated for the decrease in gross photosynthesis, resulting in similar values of net photosynthesis in the two treatments. In contrast, for *B. argenteum*, net photosynthesis was four-times greater in the control than the litter treatment. Also under litter cover, *D. muscorum* showed three common adaptations to shade conditions: a decrease in the light compensation point, in the light intensity needed to achieve 95% of maximal net photosynthesis, and in the chlorophyll *a*/*b* ratio. None of these changes was apparent in *B. argenteum*. Overall, our results indicate that photosynthetic responses to the presence of litter varied among species of the crust biota and that the litter can reduce the photosynthetic capacity of biological soil crusts. These results help to explain field observations of decreases in biological soil crust cover and changes in biological soil crust composition with increases in litter cover, and suggest that the landscape-wide invasion by *B. tectorum* may have substantial effects on biological soil crust performance and therefore their capacity to function in semiarid shrublands.

1. Introduction

Biological soil crusts (henceforth referred to as 'biocrusts') are assemblages of mosses, lichens, liverworts, bacteria, fungi, and algae that form an intimate association with the soil surface (Belnap, 2003). These biocrusts are common in arid and semiarid lands, where they often dominate the less vegetated interspaces between vascular plants (Eldridge and Greene, 1994; Rosentreter and Belnap, 2003). Biocrusts play important ecological roles; they are a source of organic carbon, and free-living cyanobacteria and cyanolichens fix atmospheric nitrogen (West, 1990; Evans and Belnap, 1999; Elbert et al., 2012). Furthermore, biocrusts and their byproducts modify soil surfaces by altering surface roughness and physicochemical characteristics of the soil (Belnap, 2006; Chamizo et al., 2012). In arid lands, the effects of biocrusts on soil surface characteristics and on the organic content of the soil play a critical role in maintaining fertility, reducing erosion, and in affecting the distribution of limited resources such as water and nutrients (Eldridge et al., 2002; Bowker et al., 2010).

In the sagebrush steppes of western North America, including the cool deserts of the Great Basin, biocrusts are significant components of plant interspaces, often covering up to 70% of the soil surface (Rosentreter and Belnap, 2003; Hilty et al., 2004). However,

Abbreviations: biocrusts, Biological soil crusts; $\Delta F/F'_m$, photosystem II operating efficiency; F_v/F_m, maximum quantum efficiency of photosystem II photochemistry; LCP, light compensation point; *NPQ*, non-photochemical quenching; $PPFR_{95\%}$, light intensity necessary to achieve 95% of maximal net photosynthesis.

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disturbance by domestic grazers and invasion of exotic annual plants over the past century have reduced biocrust cover and transformed relatively stable, diverse sagebrush steppe communities into more homogenous grasslands dominated by exotic annuals (Brooks et al., 2004). While various non-native plants are responsible for changes in vegetation composition, perhaps the single most important factor causing replacement of native vegetation has been invasion by the annual grass *Bromus tectorum* L. (cheatgrass) (Brooks et al., 2004). In the Great Basin alone, more than 20,000 km^2 are now dominated by *B. tectorum*, which frequently forms extensive monocultures (Bradley and Mustard, 2005).

Invasion by *B. tectorum* can have various effects on biocrusts. The presence of this grass results in loss of biocrust habitat due to high density growth and gradual invasion of the less vegetated interspaces previously dominated by the biocrusts (Belnap, 2003). Furthermore, as *B. tectorum* plants dry out in early summer, their stems and inflorescences create large amounts of vegetation litter. This litter leads to the formation of a rather continuous and homogeneous layer of fine fuel that can drastically increase wild fire frequency to as often as once every five years and eliminate fire-sensitive vegetation including many biocrust components (Johansen, 2003; Bowker et al., 2004; Brooks et al., 2004). In addition, cover by litter is likely to alter the biocrust microenvironment, particularly in terms of light, temperature, and moisture (Belnap, 2003). These plausible changes in the biocrust microenvironment can ultimately lead to changes in biocrust composition and/or result in loss of biocrust organisms (Rosentreter and Belnap, 2003). For example, in the Colorado Plateau of North America, Belnap et al. (2006) found that soil surface litter cover (mainly *B. tectorum*) was negatively correlated with total lichen and moss cover. Similarly in the riverine plains of southeastern Australia, Briggs and Morgan (2008) observed a negative relationship between biocrust and litter cover, which was more pronounced for lichens than mosses. Thus, field surveys indicate that litter cover can affect biocrust composition and abundance, although sometimes it is difficult to separate the effect of litter cover from other environmental factors such as trampling history, fires, and soil and vegetation characteristics (Belnap et al., 2006; Martínez et al., 2006; Ochoa-Hueso et al., 2011).

At the physiological level, changes in the biocrust microenvironment brought about by litter cover are likely to affect the metabolism of biocrust organisms (Belnap, 2003; Belnap and Eldridge, 2003). The shading caused by the litter may reduce heat and drought stress, thus prolonging the period of photosynthetic activity. On the other hand, shading reduces the amount of light available for photosynthesis, and perhaps maintains the biocrust at temperatures below the optimal for photosynthesis, particularly during cool and moist periods when the biocrust organisms tend to be active (Lange, 2003). Based on these contrasting scenarios, the overall effect of litter on the functioning and growth of biocrusts is difficult to predict. Moreover, biocrust responses to litter cover will be influenced by differences in metabolic requirements among species. The environmental conditions that allow positive rates of net photosynthesis vary among autotrophic species of the biocrust (Lange, 2003; Marschall and Proctor, 2004). As the microenvironment changes with the presence of litter, some species may be able to fulfill their photosynthetic requirements better than others. Consequently, the carbon balance of different biocrust organisms will not be affected equally by the litter cover, which could lead to changes in biocrust composition (Belnap et al., 2006; Thompson et al., 2006). In addition, lichens and mosses adapt to changes in temperature and light intensity through various processes including adjustments in photosynthetic pigments, in the quantum efficiency for CO_2 assimilation, and in respiration (Lange, 2003; Marschall and Proctor, 2004; Lange and Green, 2005; Schroeter et al., 2012). The extent to which these and similar adjustments lessen negative effects on the biocrust carbon balance may largely determine the ability of the crust biota to cope with the new microenvironment created by the litter.

While various effects of litter cover on biocrusts are plausible, direct experimental evidence to ascertain their impact on the physiological functioning of biocrust organisms is still lacking (Belnap and Eldridge, 2003; Belnap et al., 2006). The main aim of the present study was to gain information in this area. For this purpose, we analyzed the effect of *B. tectorum* litter on photosynthetic characteristics of two cosmopolitan biocrust species the moss *Bryum argenteum* Hedw. and the crustose lichen *Diploschistes muscorum* (Scop.) R. Sant. Both species are common components of biocrusts in sagebrush habitats of the northern portion of the Great Basin, where they are usually found in the interspaces between vascular plants (Rosentreter and Belnap, 2003). In addition, in areas invaded by *B. tectorum*, biocrusts can be found under various amounts of litter, where biocrusts are often visually undistinguishable from non-covered biocrusts. Nevertheless, changes may occur at the physiological level that ultimately may determine biocrust subsistence and its ability to adjust to the new environment. To investigate this possibility, we conducted an experiment in which samples of biocrusts dominated by *B. argenteum* and *D. muscorum* were covered with *B. tectorum* litter or were left uncovered for periods of 5 and 10 months. At the end of these periods, we removed the litter and compared photosynthetic characteristics of the biocrusts. Through this experiment, we were interested in answering the following four questions. Do the samples under the litter show adaptations that may help them to cope with a low light environment? Does exposure to litter reduce the photosynthetic capacity of the biocrusts? Do *B. argenteum* and *D. muscorum* differ in their response to the presence of litter? Does exposure to litter over a longer period worsen the conditions of the biocrust? Answering these questions can improve our understanding of the effects of litter on the functioning of biocrusts and may help to explain common observations of changes in biocrust cover and composition with increases in litter cover.

2. Materials and methods

2.1. Biological soil crusts and vegetation litter

Samples of biocrusts, dominated by either the moss *B. argenteum* or the lichen *D. muscorum*, were collected in June of 2011 from a sagebrush steppe community in the northern portion of the Great Basin at about 42 km southeast of Boise, Idaho (43° 20′ N, 115° 55′ W). *B. argenteum* forms short mats of about 1 mm in height and *D. muscorum* develops a hard and continuous thallus up to several cm in diameter (McCune and Rosentreter, 2007). Patches of biocrusts dominated by these species vary in size, but commonly range between 20 and 500 cm^2. Both biocrust types were collected in exposed, litter-free microsites in the plant interspaces. For *B. argenteum*, about 120 cores were taken with a bulb transplanter; each core was 5.5 cm in diameter and 4–6 cm in depth. Similarly, for *D. muscorum*, 100 thalli were carefully removed from the soil using spatulas; each thallus was between 20 and 30 cm^2 in area. After removal from the site, biocrust samples were kept dry under dark/cool conditions until the start of the experiment. Samples of *D. muscorum* were free of other photosynthetic organisms, while those with *B. argenteum* had minor levels of the moss *Syntrichia ruralis* Hedw. *B. tectorum* litter, comprising mainly dry stems and post seed fall inflorescences, was harvested from a heavily-invaded sagebrush community close to the biocrust collection site (43° 21′ N, 115° 57′ W).

2.2. Initial effect of litter-cover on photosynthesis and the hydration period of biocrusts

In a particular site invaded by *B. tectorum*, the distribution of litter is not uniform; patches of biocrusts can be found with no litter to nearly complete litter cover (Fig. 1A–D). The possibility of finding a patch with a particular cover depends on the degree of invasion of a site and the patch area considered. For example, finding large patches with dense cover is rare. This is in part because invasion begins to fragment the biocrust. On the other hand, patches of up to 30 cm^2 with dense cover are not uncommon. Although these individual patches are small, their sum can represent a significant area, which could contribute to determine the overall conditions of biocrusts at the landscape level. To begin investigating the effect of litter on physiological characteristics of biocrust organisms, we compared two markedly distinct scenarios found in natural habitats, no litter and sufficient litter to result in more than 80% cover. We reasoned that if we could not detect differences between these two treatments, smaller variances in litter cover will also be unnoticeable. Although analysis of the effect of various amounts of litter would have been preferable, the contribution of the non-covered areas to photosynthetic characteristics would have made more difficult to detect changes occurring directly under the litter. Also, preliminary experiments showed considerable variations in the photosynthetic rates of control biocrust samples. Based on these results, we decided to reduce the number of litter treatments and increase the number of replications while still being able to complete the photosynthetic measurements within a two to three week period. To achieve the desired amount of litter cover, samples were covered with approximately 23.5 mg of litter per cm^2 of biocrust surface. This addition provided a cover where the biocrust was barely visible (Fig. 1E and F). The amount of litter used is less than that found in monotypic stands of *B. tectorum*, but similar amounts can often be found in steppe communities with a lesser degree of invasion (Evans et al., 2001).

To estimate the immediate effect of the litter cover on photosynthesis, gas exchange measurements were made on the same biocrust samples, with and without litter. Prior to these measurements, cores of *B. argenteum* and *D. muscorum* were trimmed in thickness by detaching some of the soil under the biocrust samples. This resulted in a layer of soil of about 1.0 and 0.3 cm beneath *B. argenteum* and *D. muscorum*, respectively. Attempts to remove more soil resulted in substantial damage to the biocrusts and therefore such attempts were not pursued during routine measurements. In biocrusts with and without litter, photosynthesis was measured at light intensities of 0, 187, 375, 562, 750, 1125, and 1500 $\mu mol\ m^{-2}\ s^{-1}$, as described below under CO_2 gas exchange measurements. For each species, light curves were recorded in ten biocrust cores.

Following a wetting event, the presence of litter may help to maintain moisture in biocrust organisms, prolonging periods of hydration. To determine whether the litter had a significant effect on the hydration period, control and litter-covered biocrusts were initially mist irrigated to full saturation and then incubated in a greenhouse under a 14 h photoperiod and day/night conditions of $25/18 \pm 3\ ^{\circ}C$ without additional watering. In most poikilohydric organisms including *B. argenteum* and *D. muscorum*, water loss is accompanied by the loss of variable chlorophyll *a* fluorescence (Lange et al., 1989; Hájek and Beckett, 2008). This characteristic was used to estimate the hydration status of the biocrust organisms during the greenhouse incubation. For this purpose, chlorophyll *a* fluorescence was monitored at hourly intervals with a pulse amplitude modulated fluorometer (OS5p, Opti-Sciences, Inc, NH, USA) until the fluorescence signal was below the threshold detected by this instrument. The period between the initial rewetting and the time at which chlorophyll *a* fluorescence was no longer

Fig. 1. Illustrations of dense litter cover under natural conditions (A–D): A, Litter cover over a moss dominated biological soil crust; B, same area as in A after litter removal; C, litter cover over *Diploschistes muscorum* thalli; D, same area as in C after litter removal. Experimental setup to investigate the effect of litter on biological soil crusts (E, F): E, Samples in the control and litter-covered treatment; F, close view of litter cover. For the litter treatment, samples were covered with 3 g of litter per pot or approximately 23.5 mg of dry litter per cm^2.

detectable was taken as an estimate of the hydration period. Five replicates of each species and treatment were measured.

2.3. Effects of 5 and 10 months litter cover on photosynthetic characteristics

The effect of prolonged litter cover on photosynthetic characteristics of biocrusts was investigated on two parallel experiments, one with *B. argenteum* and the other with *D. muscorum*. Each experiment consisted of a completely randomized factorial combination of two levels of litter application (0 and 23.5 mg cm^{-2}) and two periods of exposure to natural conditions (July to December and July to May). For each treatment combination, nine pots (experimental units) were prepared for *B. argenteum* and seven for *D. muscorum* for a total of 36 and 28 experimental units, respectively. Cores with *B. argenteum* or *D. muscorum* were trimmed as described above, and placed in pots (12.7 cm in diameter and 12.1 cm in height) previously filled with soil to within 3 cm from the top. Three cores of *B. argenteum* or *D. muscorum* thalli were placed in each pot. Pots assigned to the litter treatment received 3 g of *B. tectorum* litter per pot to provide an even cover over the biocrust surface (Fig. 1E). Garden mesh (1 cm × 1 cm grid size) was placed on top of each pot to prevent loss of *B. tectorum* litter during the experiment. These pots were placed outdoors in an experimental plot at the Idaho Botanical Garden (Boise, Idaho, USA, 43° 36′ N, 116° 13′ W) on July 1, 2011. A weather station at this site recorded temperature, relative humidity, and precipitation. For each species and litter treatment, half of the pots were in the field until December 2011 and the other half until May 2012. In both December and May, the samples were brought from the field to the laboratory over a two to three week period, as this was the time required to complete the photosynthetic measurements of all samples. A random approach was used to select the samples measured in the laboratory in a particular day. Furthermore, during the 48 h preceding their transport to the laboratory, the biocrusts were maintained at high water content by mist irrigation or precipitation. Attainment of high water content was inferred from the presence of external capillary water (Proctor et al., 1998). Subsequently, the samples were brought to the laboratory for photosynthetic measurements, and the litter removed immediately prior to these measurements. Prior to the photosynthetic measurements, external water was removed from the biocrusts by gently blotting the samples with absorbent paper.

2.4. Chlorophyll a fluorescence measurements

Cores of *B. argenteum* and *D. muscorum* thalli were dark-adapted for at least 2 h prior to measurements of chlorophyll *a* fluorescence with a pulse amplitude modulated fluorometer (OS5p, Opti-Sciences, Inc, NH, USA). After dark adaptation, minimal fluorescence (F_o) was determined with a red light of 0.1 μmol m^{-2} s^{-1} and maximal fluorescence (F_m) following a pulse of saturating light of 8000 μmol m^{-2} s^{-1} and 0.8 s duration. Subsequently, the samples were exposed for 20 min to actinic light of about 600 μmol m^{-2} s^{-1} provided by the halogen lamp of the OS5p. During this period, and at 2 min intervals, the samples were exposed to saturating light flashes to estimate the maximal fluorescence (F'_m) and steady fluorescence (F'_s) of light-adapted leaves. For both species, 20 min were adequate to reach stable values of F'_m and F'_s. From F_o, F_m, F'_m and F'_s, three photosynthetic parameters were estimated: the maximum quantum efficiency of photosystem II (PSII) photochemistry, $F_v/F_m = (F_m - F_o)/F_m$; the PSII operating efficiency, $\Delta F/F'_m = (F'_m - F')/F'_m$; and the non-photochemical quenching, $NPQ = F_m/F'_m - 1$ (Baker, 2008). The F_v/F_m ratio represents the maximum proportion of light absorbed by photosystem II that can be used to drive photosynthesis (photochemistry) rather than being dissipated as heat or fluorescence. Values of F_v/F_m are measured in dark-adapted leaves and various stresses tend to reduce these values (Cavender-Bares and Bazzaz, 2004). For an illuminated leaf, $\Delta F/F'_m$ measures the proportion of light absorbed by photosystem II that is used for photochemistry. For a particular sample, the value of $\Delta F/F'_m$ is smaller than F_v/F_m because under illumination there is an increase in heat dissipation (*NPQ*), which helps to prevent photodamage caused by excess light. The $\Delta F/F'_m$ and *NPQ* values are affected by characteristics of the growing environment including light intensity and temperature (Cavender-Bares and Bazzaz, 2004). Per experimental unit (each pot), we made three estimates of F_v/F_m, $\Delta F/F'_m$, and *NPQ*, one for each core. These estimates were then averaged to obtain one value of F_v/F_m, $\Delta F/F'_m$, and *NPQ* per pot.

2.5. CO_2 gas exchange measurements

CO_2 assimilation of biocrust samples was measured using a LI 6400-17L chamber connected to a LI-6400XT portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA). The LI 6400-17L chamber is normally used to measure photosynthesis of entire plant rosettes in 65 mm diameter pots. For the biocrust measurements, a similar pot was used, but the drainage holes were covered to prevent air leaks and the pot was filled with pebbles to 3/4 of its height. In the upper portion of the pot, the lower half of a 60 mm Petri dish was used to support the biocrust samples. Each sample consisted of one of the *D. muscorum* thalli or *B. argenteum* cores described above. Light was provided by the RGB light source of the LI 6400-17L chamber. For each sample, we recorded net photosynthetic carbon assimilation (net photosynthesis) and the rate of dark respiration. Unless otherwise indicated, net photosynthesis was measured at an incoming air CO_2 concentration of 400 μmol mol^{-1}, 23 (±1) °C air temperature, 75 (±4)% relative humidity, and a light intensity of about 1125 μmol m^{-2} s^{-1} at the biocrust surface. This intensity was estimated based on the output from the RGB light source and the distance between the light and the sample, as indicated by the manufacturer. Respiration was determined after turning off the light source of the LI 6400-17L. The net photosynthesis and dark respiration rates were recorded after the CO_2 assimilation rates stabilized and the infrared gas analyzer was matched prior to each measurement. Following CO_2 gas exchange measurements, each sample was photographed and its area estimated on the digital image using ImageJ 1.44p software. This area was then used to calculate the CO_2 assimilation rate per unit area of each sample. The values of net photosynthesis plus dark respiration were also used to calculate gross photosynthesis. We made three measurements of net photosynthesis, dark respiration, and gross photosynthesis per pot, one for each core. These estimates were then averaged to obtain one value for each of these parameters per pot.

The cores of *B. argenteum* and *D. muscorum* used in this study included a layer of soil that can increase dark respiration and reduce net photosynthesis, through microbial respiration. Attempts to estimate soil respiration were made using two approaches. The first approach consisted of measuring respiration in biocrust cores before and after removing soil from beneath the biocrust. Unexpectedly, removal of soil increased dark respiration; which perhaps was the result of an increase in metabolic activity associated with repairing the damage caused to organisms by soil removal. The second approach involved measuring the respiration from the soil that was removed from beneath the biocrusts. This approach gave values of dark respiration between −0.4 and −0.7 μmol m^{-2} s^{-1}, and no differences were observed between soils collected from the

control and the litter treatment. The reasons for the contrasting results obtained by the two methods are unclear, but may reflect artifacts caused by soil disturbances (Davidson et al., 2002). Given the uncertainties in estimating soil microbial respiration and the difficulties in completely separating *B. argenteum* and *D. muscorum* from the soil beneath, the measurements of net photosynthesis and dark respiration were not corrected for soil microbial respiration. Consequently, these measurements represent values for the entire soil biocrust cores.

After the final collection in May, we also measured light curves to characterize possible effects of long-term litter cover on the light intensity necessary to achieve 95% of maximal net photosynthesis ($PPFR_{95\%}$) and the light compensation point (LCP). In this case, light curves were constructed after litter removal and a minimum of 10 curves was measured for each species and treatment. The parameters $PPFR_{95\%}$ and LCP were obtained from light curves fitted to the modified Mitscherlich equation described by Marino et al. (2010). The equation used was:

$A_{(I)} = A_{\max}(1 - e^{[(-q(I)-\mathrm{LCP})/A_{\max}]})$; where $A_{\max}$ is the maximal rate of net photosynthesis, I is the light intensity, and q is the quantum yield at the light compensation point. After estimation of $A_{\max}$, q, and LCP, $PPFR_{95\%}$ was calculated as the light intensity that causes 95% of $A_{\max}$.

2.6. Extraction and analysis of photosynthetic pigments

Samples of *B. argenteum* were extracted five times with DMSO. The extracts were combined and their absorbances at 649, 665, and 750 nm measured with a Cary 100 spectrophotometer. Extraction of photosynthetic pigments from lichens can result in the conversion of chlorophylls to pheophytin due to the presence of lichen acids. To minimize this problem, chlorophylls were extracted as recommended by Barnes et al. (1992). Acids were removed by rinsing dry thalli in saturated $CaCO_3$ in 100% acetone. Subsequently, samples were incubated for 40 min in 2.5 mg ml^{-1} polyvinylpolypyrrolidone in DMSO; incubations were conducted in the dark at 65 °C. Two of these extractions were made per sample, the extracts were combined, and their absorbances measured as described above. For both *B. argenteum* and *D. muscorum*, chlorophyll *a* and chlorophyll *b* concentrations were calculated using Wellburn's equations (Wellburn, 1994).

2.7. Data analyses

For each biocrust type, the effects of litter amount and period of exposure on chlorophyll fluorescence parameters and CO_2 assimilation were tested using the MIXED procedure model in SAS 9.3 (SAS Institute Inc., Cary, NC, USA) for a completely randomized design. Fixed factors in the analysis were litter amount, exposure period, and their interaction. The data were not transformed prior to statistical analysis because the Shapiro–Wilk test confirmed the normality of residuals. When necessary, different variances were modeled in the MIXED procedure to allow for unequal variance among treatments (Littell et al., 2002). Significant differences among treatments were determined using Tukey–Kramer least square means test at $p < 0.05$. For two level analyses such as the comparison of pigment concentration, $PPF_{95\%}$, and LCP between the control and litter treatment, the data were analyzed using an independent *t*-test or a Welch *t*-test if variances were equal and unequal, respectively. Light curves were fitted to the Mitscherlich equation separately for each sample using the nonlinear least square regression function in R (R-Development-Core-Team, 2011). All estimates of treatment variability are reported as standard errors.

3. Results

3.1. Initial effect of litter-cover on photosynthesis and the hydration period of biocrusts

The amount of litter applied substantially reduced net photosynthesis in both species (Fig. 2A and B). In *B. argenteum*, the magnitude of this decrease was negatively correlated with light intensity ($p = <0.0001$). At 187 and 1500 μmol photons m^{-2} s^{-1}, the litter decreased net photosynthesis by 2.6 (±0.2) and 1.1 (±0.3) μmol CO_2 m^{-2} s^{-1}, respectively. For *D. muscorum*, the decrease in net photosynthesis caused by the litter was between 1.0 and 2.0 μmol CO_2 m^{-2} s^{-1}, but this decrease was not correlated with light intensity ($p = 0.30$). Under litter cover, *B. argenteum* and *D. muscorum* showed positive values of net photosynthesis at irradiances above 400 and 750 μmol m^{-2} s^{-1}, respectively; while control cores of *B. argenteum* and *D. muscorum* showed positive rates at about 120 and 250 μmol m^{-2} s^{-1}, respectively (Fig. 2).

From the values of net photosynthesis and dark respiration (zero irradiance) used to make Fig. 2, we also estimated gross photosynthesis. In *B. argenteum*, gross photosynthesis of biocrusts with litter was between 29 and 75% of that of the same samples without litter. Similarly for *D. muscorum*, gross photosynthesis of biocrusts with litter was between 46 and 62% of that of the same samples without litter. In both biocrusts, the higher percentages tended to occur at higher light intensities. For biocrusts with litter, the percent of uncovered areas was less than 20%. Consequently, in biocrusts with litter photosynthesis did not appear to have been limited to areas lacking litter cover. If only the 20% surface area not covered by litter were responsible for gross photosynthesis, we would expect gross photosynthesis to have been less than 20% of that of samples without litter.

As measured by the decrease in chlorophyll *a* fluorescence, the presence of litter significantly increased the biocrust hydration period ($p = 0.0007$). Under greenhouse conditions, control and litter covered samples of *B. argenteum* remained hydrated for 29.6

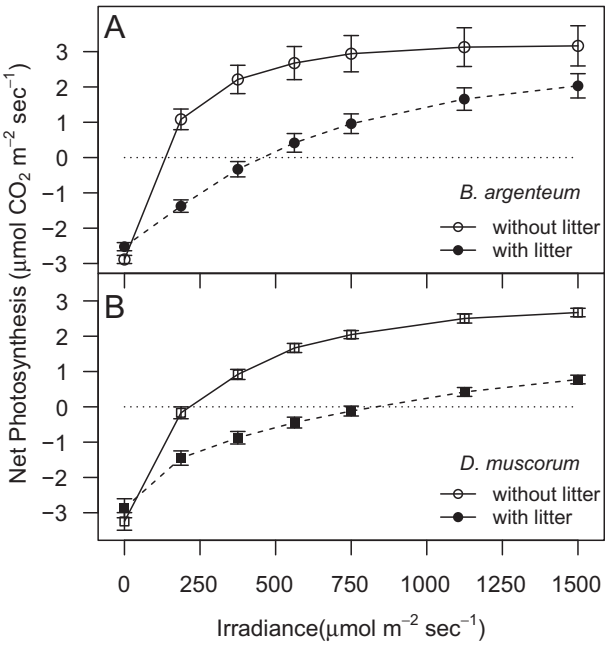

Fig. 2. Initial effect of litter on net photosynthesis of the moss *Bryum argenteum* (A) and the lichen *Diploschistes muscorum* (B). The same biological soil crust samples were measured in the absence and presence of litter. Each point represents the mean (±SE) of ten biocrust samples.

(±0.4) and 54.6 (±0.2) h, respectively. The hydration period was much shorter in *D. muscorum*, but clear differences were observed between the control and litter treatment which remained hydrated for 4.7 (±0.1) and 9.2 (±0.5) h, respectively.

3.2. Climatic conditions

Control and litter-covered samples were exposed to natural climatic conditions from July to December 2011 or from July 2011 to May 2012 (Fig. 3). From July to September, total precipitation was less than 4 mm and temperatures were always above the dew point (data not shown), indicating that biocrusts remained dry through most of the summer. In October and to a lesser extent in November, moisture and temperature were more favorable for biocrust photosynthesis, with a total of 50 mm of precipitation. The highest intensity of precipitation in the form of snow and rain occurred in the second half of January, with 81 mm of precipitation. At this time, photosynthesis may have been limited by low temperatures, which were often below freezing. From the middle of February to the middle of May, total precipitation was 122 mm and average temperatures gradually increased from about 3 °C in February to 15 °C in May. When compared with average values for Boise (National weather service forecast office), precipitation during the first five months of the experiment was lower than normal, 61 and 103 mm, respectively. In contrast for the second half of the experiment, precipitation was higher than normally, 204 and 160 mm, respectively.

3.3. Effects of 5 and 10 months litter cover on chlorophyll a fluorescence parameters

Continued exposure to litter had an effect on the three fluorescence parameters measured in *B. argenteum* (Table 1). For F_v/F_m, the litter treatment had higher values than the control, although this difference was only significant for biocrusts collected at the end of the fall (Fig. 4A). Even when the litter had a positive effect on F_v/F_m, this did not result in an increase in the PSII operating efficiency ($\Delta F/F'_m$). Cover with litter led to a decrease in $\Delta F/F'_m$ values, but there was a significant interaction between the two experimental factors, litter amount and exposure period (Table 1). During the fall, $\Delta F/F'_m$ was higher in the control than the litter treatment, while no differences were apparent in the spring (Fig. 4B). The contrasting effects of litter on F_v/F_m and $\Delta F/F'_m$ were largely attributed to differences in non-photochemical quenching (*NPQ*). The litter treatment had higher *NPQ* values than the control for both fall and spring samples (Fig. 4C, Table 1).

For *D. muscorum*, the effect of litter on F_v/F_m was similar to that observed for *B. argenteum*; during the fall, the litter treatment increased F_v/F_m values (Fig. 4D). However for $\Delta F/F'_m$ and *NPQ*, the response of *D. muscorum* to the presence of litter differed from that observed in *B. argenteum* (Fig. 4). In *D. muscorum*, there was a significant interaction between litter amount and exposure period on $\Delta F/F'_m$ and only during the spring was $\Delta F/F'_m$ higher in the control than the litter treatment (Table 1, Fig. 4E). Further, the litter treatment did not have an effect on *NPQ* of *D. muscorum* (Fig. 4F, Table 1), which contrast with the results obtained in *B. argenteum*.

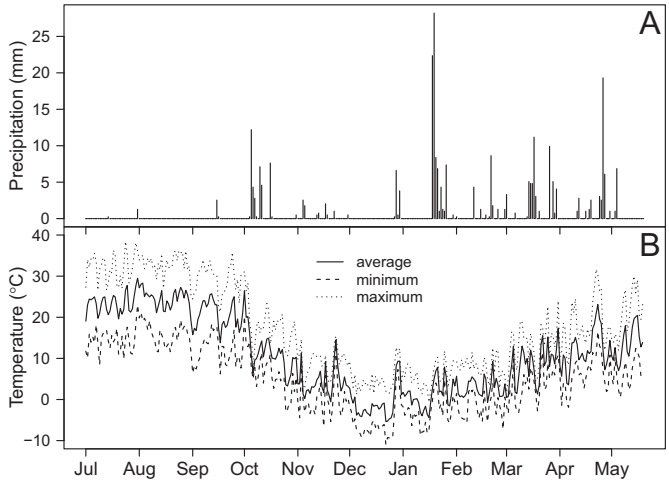

Fig. 3. Precipitation events and temperatures that the biological soil crusts experienced under field conditions from July 1, 2011 to May 15, 2012.

3.4. Effects of 5 and 10 months litter cover on photosynthesis and dark respiration

For *B. argenteum*, net photosynthesis showed a significant interaction between litter amount and exposure period (Table 1). After removal of the litter, *B. argenteum* cores that had been covered with litter from July to December had rates of net photosynthesis that although higher were not significantly different from the controls (Fig. 5A). In contrast, after ten months of litter cover, the control cores had significantly higher rates of net photosynthesis than those treated with litter, 2.7 (±0.5) and 0.60 (±0.20) μmol CO_2 m^{-2} s^{-1}, respectively. Dark respiration was also affected by the litter; while no significant interaction was detected between litter amount and exposure period (Table 1). After both 5 and 10 months, the controls had more negative rates of dark respiration (higher CO_2 losses) than the litter treated cores (Fig. 5B). Litter cover led to a decrease in CO_2 losses by dark respiration of about 26 and 28% for the 5 and 10 month samples, respectively. In addition, there were marked seasonal differences in dark respiration. Independent of the litter treatment, dark respiration was more negative in samples collected during the fall than those collected during the spring (Fig. 5B). As judged by the values of gross photosynthesis, litter cover from July to December did not affect the ability of *B. argenteum* to fix CO_2 via photosynthesis (Fig. 5C). However, litter cover for an additional five months was associated with a marked reduction in the photosynthetic capacity of the *B. argenteum* biocrust (Fig. 5C). For cores collected in the spring, the less negative dark respiration rates in the litter treatment were not sufficient to compensate for the decline in gross photosynthesis, resulting in lower net photosynthesis in litter treated than control cores.

In *D. muscorum*, cover by litter did not have an effect on net photosynthesis, but it affected both dark respiration and gross photosynthesis (Fig. 5D–F, Table 1). After 5 and 10 months, dark respiration averages in the controls were respectively 1.2 and 0.9 μmol CO_2 m^{-2} s^{-1} more negative than those of the litter treatment. These differences were compensated by differences in gross photosynthesis, which was higher in the control than the litter treatment (Fig. 5F). In addition to the effect of litter on gas exchange characteristics, the results revealed an effect of sampling period on net photosynthesis, dark respiration, and gross photosynthesis (Table 1). Combining both control and litter treated thalli, net photosynthesis was 1.15 (±0.16) μmol CO_2 m^{-2} s^{-1} higher in the spring than in the fall, while the differences in dark respiration and gross photosynthesis were 0.59 (±0.18) and 0.56 (±0.20) μmol CO_2 m^{-2} s^{-1}, respectively. Thus, the observed increase in net photosynthesis from fall to spring appears to be attributed in roughly equal amounts to a reduction in respiration (less negative values) and an increase in photosynthetic capacity.

To further analyze the effect of litter on photosynthetic characteristics, we measured light response curves in a subsample of

Table 1
Test for significance of fixed factors (litter amount, exposure period, and litter amount × exposure period) on photosynthetic characteristics of *Bryum argenteum* and *Diploschistes muscorum*. F_v/F_m, maximum quantum efficiency of photosystem II photochemistry; $\Delta F/F'_m$, PSII operating efficiency; *NPQ*, non-photochemical quenching.

Species	Parameter	DF num	DF den	Litter amount	Exposure period	Litter × exposure
				p value	*p* value	*p* value
Bryum argenteum	F_v/F_m	1	30	0.0012	0.0083	0.068
	$\Delta F/F'_m$	1	30	0.0001	0.019	0.0177
	NPQ	1	30	<0.0001	0.2339	0.0572
	Net photosynthesis	1	21.4	0.2479	0.1128	0.0006
	Dark respiration	1	30	<0.0001	<0.0001	0.6895
	Gross photosynthesis	1	18.9	0.0005	0.0206	0.0018
Diploschistes muscorum	F_v/F_m	1	16.9	0.3246	0.0073	0.0005
	$\Delta F/F'_m$	1	19.1	0.0273	0.2826	0.0251
	NPQ	1	15.5	0.3251	0.0583	0.3669
	Net photosynthesis	1	22	0.2275	<0.0001	0.6895
	Dark respiration	1	14.7	<0.0001	0.0046	0.404
	Gross photosynthesis	1	22	<0.0001	0.0122	0.3042

the biocrust cores collected in spring. Cores of both *B. argenteum* and *D. muscorum* showed typical CO_2 assimilation responses to increases in light intensities that were accurately described by the Mitscherlich equation. However, the effect of the litter on parameters that characterize the light curves was different between species. For *B. argenteum*, samples that have been exposed to litter had a higher LCP than those of the control and no differences were observed in $PPFR_{95\%}$ (Table 2). In contrast, *D. muscorum* thalli that had been covered with litter had lower values of LCP and $PPFR_{95\%}$ than those of the controls (Table 2).

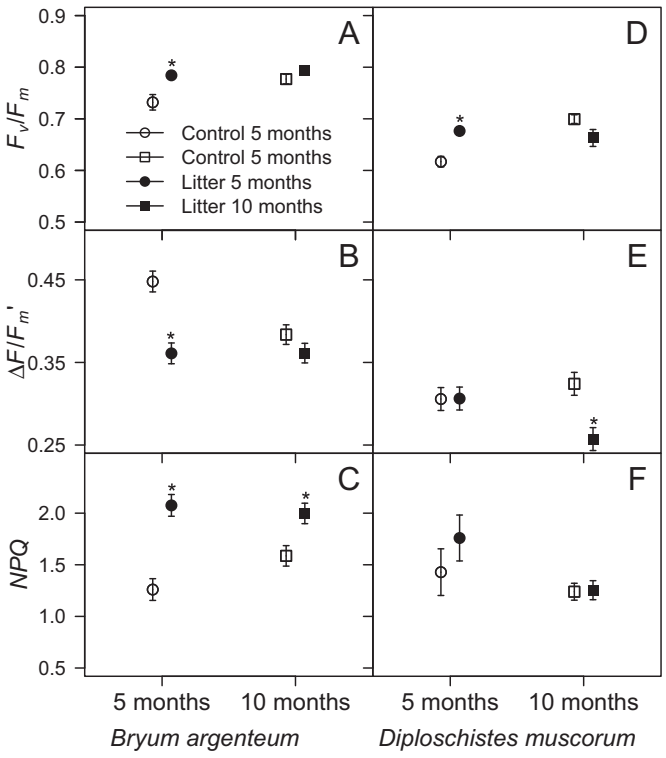

Fig. 4. Chlorophyll fluorescence parameters of *Bryum argenteum* (A–C) and *Diploschistes muscorum* (D–F) after exposure to litter for five (from July 1 to December 2011) or ten months (from July 1, 2011 to May 12). The litter was removed prior to the measurements of chlorophyll fluorescence. F_v/F_m, maximum quantum efficiency of photosystem II (A, D); $\Delta F/F'_m$, photosystem II operating efficiency (B, E); *NPQ*, non-photochemical quenching (C, F). Each symbol represents the mean (±SE) of six to nine experimental units; the values for each unit were the average of three measurements made in different biocrust cores. For each species and collection period, symbols marked by asterisk are significantly different from the control treatment ($p < 0.05$).

3.5. Comparison of chlorophyll content in control and litter covered biocrusts

For *B. argenteum* cores collected after 5 months in the field, we detected no difference in chlorophyll content between the litter and control treatment (Table 3). In contrast, after 10 months the average chlorophyll content for the litter treatment was 34% lower than that of the control. This decrease occurred in similar proportions for chlorophyll *a* and *b*, and consequently, no significant changes were observed in the chlorophyll *a*/*b* ratio (Table 3). The effect of litter on chlorophyll was somewhat different on *D. muscorum*. In this species, both the chlorophyll content and the

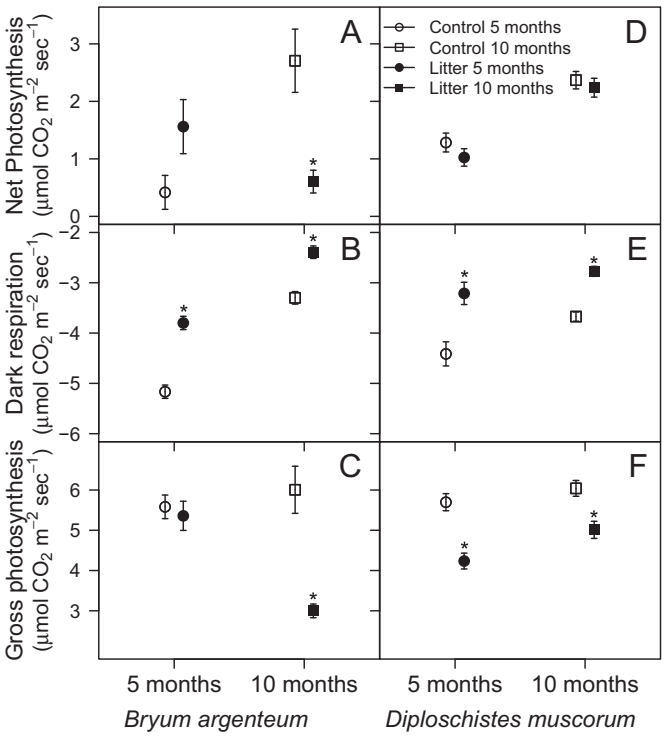

Fig. 5. Net photosynthesis (A–D), dark respiration (B–E), and gross photosynthesis (C–F) of *Bryum argenteum* (A–C) and *D. muscorum* (D–E) after exposure to litter cover for five (from July 1 to December 2011) or ten months (from July 1, 2011 to May 12). The litter was removed prior to the measurements of photosynthesis and respiration. Each symbol represents the mean (±SE) of six to nine experimental units; the values for each unit were the average of three measurements made in different biocrust cores. For each species and collection period, symbols marked by asterisk are significantly different from the control treatment ($p < 0.05$).

Table 2
Light compensation point (LCP), light intensity necessary to achieve 95% of maximal net photosynthesis ($PPFR_{95\%}$), and quantum yield at the light compensation point (q) of biological soil crusts after 10 months of exposure to field conditions without (controls) and with litter (litter covered). LCP, $PPFR_{95\%}$, and q were estimated from fitted light response curves; the litter was removed prior to the light responses measurements. Mean (±SE) of ten light curves.

Sample	Parameter	Control	Litter covered	p^*
B. argenteum	LCP ($\mu mol\ m^{-2}\ s^{-1}$)	119 (±12)	203 (±18)	0.0044
	$PPFR_{95\%}$ ($\mu mol\ m^{-2}\ s^{-1}$)	652 (±37)	606 (±35)	0.3892
	q (mmol/mol)	17 (±3)	5 (±1)	<0.001
D. muscorum	LCP ($\mu mol\ m^{-2}\ s^{-1}$)	257 (±14)	183 (±19)	0.0059
	$PPFR_{95\%}$ ($\mu mol\ m^{-2}\ s^{-1}$)	1168 (±48)	867 (±122)	0.0413
	q (mmol/mol)	9.0 (±0.6)	8.3 (±0.8)	0.5411

*p Values based on independent t-test.

chlorophyll a/b ratio were affected by the litter. The average chlorophyll content for the litter treatment was 39% lower than that of the control. In the control and litter treatment, the chlorophyll a content was 293 (±15) and 163 (±15) mg m^{-2}, respectively, while that of chlorophyll b was 100 (±8.4) and 77 (±8.6), respectively. These unequal changes in chlorophyll a and b resulted in differences in the chlorophyll a/b ratio, which was higher in the control than the litter treatment (Table 3).

4. Discussion

Our laboratory measurements indicated that, under litter, biocrusts had lower rates of photosynthesis and longer hydration periods than those without litter. Albeit to varying degrees, similar responses would be expected under field conditions. A decrease in photosynthesis due to the litter would have a negative effect on the biocrust carbon balance, while an increase in the hydration period can have different effects depending on light intensity and the light compensation point of the biocrust. For example, the reduction in light intensity caused by the litter may prevent the biocrust organisms from reaching positive values of net photosynthesis. Under these conditions, hydration would have a negative effect on biocrusts due to higher carbon losses via respiration than in the dry state. Alternatively, if the increase in the hydration period is accompanied by an increase in the duration of periods with positive net photosynthesis, this would tend to compensate for the reduced rates of photosynthesis under the litter.

At 23 °C and under the litter, *B. argenteum* and *D. muscorum* reached positive net photosynthesis values (operative LCP) at irradiances of 400 and 750 μmol $m^{-2}\ s^{-1}$, respectively (*cf.* Fig. 2). During periods with adequate moisture, temperatures in the field were cooler than 23 °C, which would decrease the LCP values (Green et al., 1998; Pintado et al., 2005). Thus on cool days with moderate light intensity, moist biocrusts under litter probably reached positive net photosynthesis values. Whether the carbon gain during these periods was sufficient to compensate for the overall reduction in carbon assimilation caused by the litter is unclear. However, some of our results suggest the contrary. In the laboratory, rates of net photosynthesis under the litter were less than half of those without litter (*cf.* Fig. 2), while the hydration period was somewhat less than double. Furthermore, the reduction in light intensity caused by the litter tends to decrease the periods with positive net photosynthesis. Thus, the increase in periods with positive net photosynthesis, if any, would be insufficient to compensate for the reduction in the rates of photosynthesis. Also, the decrease in chlorophyll content and gross photosynthesis observed in both biocrust types after 10 months exposure to litter is consistent with the notion that this treatment caused a reduction in the carbon available to maintain the photosynthetic machinery. Independent of the exact effect of the litter on the biocrust carbon balance, several months of litter cover caused various alterations in photosynthetic characteristics including changes in chlorophyll a fluorescence parameters, gas exchange, and chlorophyll content.

Table 3
Comparison of chlorophyll content (mg Chl $a + b$ m^{-2}) and chlorophyll a/b ratio of control and litter covered biological soil crusts. *Bryum argenteum* samples were analyzed after five and ten months in the field. *Diploschistes muscorum* was only analyzed after ten months. Mean (±SE) of 7–9 replicates.

Sample	Parameter	Control	Litter covered	p^*
B. argenteum	Chl $a + b$	492 (±46)	524 (±46)	0.63
5 months	Chl a/b ratio	2.58 (±0.09)	2.61 (±0.07)	0.78
B. argenteum	Chl $a + b$	508 (±39)	337 (±20)	0.001
10 months	Chl a/b ratio	3.23 (±0.14)	2.84 (±0.30)	0.26
D. muscorum	Chl $a + b$	392 (±21)	240 (±22)	<0.0001
10 months	Chl a/b ratio	3.02 (±0.22)	2.16 (±0.20)	0.016

*p Values based on independent t-test.

4.1. Effects of litter cover on chlorophyll a fluorescence parameters

In mosses and lichens, light can affect the F_v/F_m ratio. Low light intensities due to topography, seasonal changes, or shade by adjacent vegetation tend to increase F_v/F_m values (Hamerlynck et al., 2002; Backor et al., 2006; Vráblíková et al., 2006). In *B. argenteum* and *D. muscorum*, litter cover had a similar effect, but only for the samples collected in December. At this time, F_v/F_m was higher in the litter than the control treatment, while no differences were detected in May. A decline in F_v/F_m may be an indication of light stress, which occurs more frequently under a combination of high light intensity and cold conditions (Cavender-Bares and Bazzaz, 2004). In our experiments, these conditions were common during late fall and early winter. During this period, shading by the litter may have protected the biocrusts from excessive light reducing photodamage.

Notwithstanding the potentially beneficial effect of the litter in reducing photodamage, $\Delta F/F'_m$, which is proportional to the electron transport rate, did not increase with this treatment. This was largely attributed to differences in the dissipation of the absorbed light by non-photochemical processes. In particular for *B. argenteum*, *NPQ* was higher in the litter than the control treatment. In general, plants growing under high light intensity have higher rates of *NPQ* than those growing at low light intensity (Demmig-Adams, 1998; Marschall and Proctor, 2004). However, exceptions to this pattern have been reported for *S. ruralis* and *B. argenteum* growing in central Europe and Antarctica, respectively (Hamerlynck et al., 2002; Schroeter et al., 2012). In both of these studies, mosses exposed to full sunlight had lower *NPQ* values than those growing at lower light intensities, which is similar to the results observed in the present study. The advantage for the mosses to maintain high *NPQ* under shaded conditions is not clear, but one possibility would be to protect them from photodamage if light conditions change (Hamerlynck et al., 2002). Such changes could occur, for example, due to litter movement by wind or animals. Protection against photodamage would be particularly important if the litter reduces the carboxylation capacity of the mosses. Without high *NPQ*, electron flow in the new and high light environment would exceed the needs for carbon fixation and other metabolic processes leading to the formation of reactive oxygen species and cellular damage (Müller et al., 2001).

4.2. Changes in CO_2 assimilation and chlorophyll content

Prolonged litter cover resulted in decreases in gross and net photosynthesis that varied in timing and magnitude among the two biocrust types. Some of these differences may be attributed to

differences in the hydration period. Based on the greenhouse measurements, *B. argenteum* has a longer hydration period than *D. muscorum*. Beneath the litter, the carbon balance of moist biocrusts may be negative. Under this scenario, *B. argenteum* would be more negatively affected by the litter than *D. muscorum* due to carbon losses occurring over a longer period. This notion requires further investigation, but *B. argenteum* was more negatively affected by the litter than *D. muscorum*. For *B. argenteum*, negative carbon balances during hydration periods could also account for the differences in photosynthesis between fall and spring collected samples. Based on the precipitation data, the overall duration of hydration periods was probably much shorter during the first five months in the field than during the second five months. In late winter and spring, long hydration periods under the litter may have caused enough carbon losses to reduce the photosynthetic capacity of the moss.

Disparities in the response to litter cover may also reflect different mechanisms of coping with the presence of litter. Some support for this notion comes from the analysis of changes in chlorophyll content, LCP, and $PPFR_{95\%}$. Although the litter caused a decrease in chlorophyll content in both biocrusts, a decrease in the chlorophyll *a*/*b* ratio was only observed in *D. muscorum*. Similarly, the presence of litter resulted in a decrease in LCP and $PPFR_{95\%}$ in *D. muscorum*, but not in *B. argenteum*. Decreases in the chlorophyll *a*/*b* ratio, LCP and $PPFR_{95\%}$ are typical responses to low irradiance (Lambers et al., 2008), which under the litter were only apparent in *D. muscorum*. Perhaps, decreases in LCP and $PPFR_{95\%}$ initially occurred in *B. argenteum*, but after ten months of litter cover were no longer evident due to deterioration of the biocrust (Schroeter et al., 2012).

For both *B. argenteum* and *D. muscorum*, control samples were exposed to higher irradiance and had higher chlorophyll content than biocrusts under the litter. Thus, our results indicate a positive relationship between irradiance and chlorophyll content. Such a relationship is not common in vascular plants, where adaptations to shade conditions usually involve an increase in chlorophyll content to maximize capture of the limited light available (Lambers et al., 2008). For mosses and lichens, the relationship between irradiance and chlorophyll content show less clear patterns (Marschall and Proctor, 2004; Piccotto and Tretiach, 2010). While some results are consistent with those observed in vascular plants (Tretiach and Brown, 1995; Green et al., 1997), others show higher chlorophyll content in habitats with higher irradiance (Pintado et al., 1997; Piccotto and Tretiach, 2010; Schroeter et al., 2012). The latter pattern suggests that in some poikilohydrous organisms other factors are more important than light in controlling adjustments of photosynthetic components (Pintado et al., 1997; Piccotto and Tretiach, 2010). One of these factors may be the duration of hydration periods (Pintado et al., 1997). Pintado et al. (1997, 2005) suggested that short hydration periods may increase the necessity to maximize photosynthesis during the brief moments of metabolic activity. This can be accompanied by the maintenance of a high content of chlorophyll and other photosynthetic components (Pintado et al., 1997). Our results seem consistent with these notions; within a species, the treatment that presumably experienced shorter hydration periods had the higher chlorophyll content and rates of CO_2 assimilation.

4.3. Differential dark respiration among treatments and seasons

The reduction in dark respiration (less losses of CO_2) observed in the litter treatment suggests an adaptation to cope with a low light environment. Fewer losses of carbon via respiration tend to compensate for the reduction in carbon assimilation caused by the litter; thus, helping to maintain positive or at least less negative overall carbon balances (Lange, 2003). For *B. argenteum*, the results are consistent with observations in mosses of positive correlations between the light intensity of the moss habitat and dark respiration (Gabriel and Bates, 2003; Waite and Sack, 2010). Acclimation responses to low irradiance through a decrease in dark respiration are common in plants and often develop gradually over a few days (Noguchi et al., 2001). In our experiment, acclimation may have occurred in October, when the biocrusts were first exposed to environmental conditions conducive to photosynthesis and high metabolic activity. Like *B. argenteum*, *D. muscorum* showed a decrease in dark respiration after exposure to litter. In lichens, it is assumed that dark respiration is mainly attributed to fungal respiration because the mycobiont makes up the majority of the thallus (Palmqvist, 2000; Lange and Green, 2005). Notwithstanding this view, a link has been observed between lichen respiration and photosynthetic capacity (Palmqvist et al., 2002). The mechanisms underlying this are unclear, but lichen species with low photosynthetic capacity tend to have low respiration rates and *vice versa* (Palmqvist, 2000; Palmqvist et al., 2002). Our results suggest that a similar phenomenon may occur within a species. *D. muscorum* thalli that had been covered with litter not only had lower dark respiration but also lower chlorophyll content and gross photosynthesis than the controls.

The above discussion assumes that changes in dark respiration mainly occurred in the moss or the lichen. Changes in dark respiration may also be attributed to changes in soil respiration. However, it seems unlikely that soil respiration was the main factor driving changes in dark respiration of the entire biocrust core. The magnitude of the decrease in dark respiration caused by the litter was similar in *B. argenteum* and *D. muscorum* even though the former had three times more soil than the latter one. If changes in soil respiration were the main drivers of changes in dark respiration, a larger decrease would be expected in the *B. argenteum* biocrust. Nevertheless, the possibility that soil respiration somewhat contributed to the decrease in dark respiration cannot be discarded. In this case, the decrease in dark respiration would tend to maintain the carbon balance of the whole biocrust core, but it would be less effective at maintaining the carbon balance of the photosynthetic organisms.

In addition to the difference in dark respiration caused by the litter treatment, differences in this parameter were noticeable between seasons; dark respiration was higher (more losses of CO_2) for the samples collected in December than those collected in May. These differences may be attributed to thermal acclimation (Atkin and Tjoelker, 2003). Average daily temperatures prior to the December collection were below 5 °C, while those prior to the May collection were between 15 and 20 °C. Thermal acclimation is the result of respiration adjustments in response to long term changes in temperature. These adjustments give heterothermic organisms a certain degree of respiration homeostasis such that at a given temperature respiration during the winter is higher than during the summer (Atkin and Tjoelker, 2003). Thermal acclimation is common in plants and its occurrence has also been demonstrated in lichens including *D. muscorum* (Atkin and Tjoelker, 2003; Lange and Green, 2005). The seasonal differences in dark respiration observed in *B. argenteum* and *D. muscorum* are consistent with the notion that these organisms undergo thermal acclimation.

4.4. Ecological considerations

In semiarid environments, the presence of plant litter often correlates with changes in biological soil crust cover and composition (Belnap et al., 2006; Martínez et al., 2006). It has been difficult to ascertain whether these changes are due to a direct effect of litter on biocrusts or to other environmental disturbances such as

grazing history or fires (Belnap et al., 2006). The results of the present study indicate that litter cover had a direct effect on biocrust function, independent of other disturbances. Moreover, some of the modifications caused by the litter could lead to structural changes in biocrusts. Ten months of litter cover was associated with a reduction in chlorophyll content of 34% and 39% for *B. argenteum* and *D. muscorum*, respectively. A continuation of this trend over a few years may be sufficient to cause irreversible damage to biocrusts leading to reduced cover. Given that the addition of litter had a more negative effect on *B. argenteum* than *D. muscorum*, this could also lead to changes in biocrust composition.

Our study only analyzed the effect of one amount of litter cover and two periods of exposure. In natural field settings, a range of litter amounts can be found. At early stages of invasion, the cover and biomass of *B. tectorum* litter is low, but both increase considerably with invasion (Evans et al., 2001). The consequences of different amounts of litter cover and longer periods of exposure on biocrust photosynthesis require further investigation. A linear response to litter cannot be inferred from our data. For example, a small amount of litter may be beneficial for biocrust performance because it may increase hydration times without significantly reducing photosynthesis. In contrast, as litter increases, degradation thresholds might begin to develop when the biocrust cannot longer maintain positive carbon balances. At least for *B. argenteum*, the amount of litter applied appears to have been above this threshold, resulting in a significant reduction in the biocrust's capacity for CO_2 assimilation. For *D. muscorum*, more work is needed to determine whether the changes observed represent a sustainable condition for this lichen or a step toward a further decline in photosynthetic capacity and functioning.

As noted earlier, biocrusts play essential roles in maintaining soil fertility, reducing erosion, and affecting the distribution of limited resources such as water and nutrients. Some of these processes may be affected by changes in biocrust photosynthesis and structural characteristics. For example, a reduction in photosynthesis in *B. argenteum* under the litter may lead to a less dense biocrust. Such change in biocrust density could have consequences on water infiltration and runoff (Bowker et al., 2008). In addition, various organisms, including bacteria, protists, fungi, and soil microarthropods, depend on biocrust byproducts for their nutrition (Bowker et al., 2010). Changes in the availability of these byproducts due to decreased photosynthesis may alter the abundance and activities of these organisms, which play important roles in decomposition and mineralization processes (West, 1990; Bowker et al., 2010). Thus, reduced carbon fixation by the biocrust could lead to changes in various physical and biogeochemical processes (Chamizo et al., 2012). These changes may represent early events leading to destabilization of shrubland habitats as result of *B. tectorum* invasion.

While the focus of this study was aimed at characterizing the impact of *B. tectorum* litter on biocrust physiological processes, other effects of litter are known to cause major disturbances on sagebrush steppe communities. The accumulation of litter decreases the amount of N available for microbial activity and the increased fire frequency augments N losses by volatilization (Evans et al., 2001). Moreover, an increased fire return period from about once per century to once every four to five years induces positive feedback processes on *B. tectorum* and ultimately destabilization of shrubland structure by removing shrubs and other native vegetation (Brooks et al., 2004). Similarly, fires damage the crust biota and frequent fires may prevent biocrust reestablishment to pre-disturbance levels (Greene et al., 1989; Johansen, 2003; Hilty et al., 2004). Given the negative effects of *B. tectorum* litter on sagebrush communities, the development of practices that prevent its accumulation seems crucial to the maintenance and restoration of these communities. This remains a major challenge, particularly if practices are aimed at controlling the litter without damaging biocrusts.

4.5. Conclusions

The results of this study showed that the litter cover induced various physiological changes in biological soil crusts. Samples covered for ten months had lower concentration of chlorophyll per unit surface area and lower values of gross photosynthesis than the controls indicating that the litter reduced biocrust photosynthetic capacity. Biological soil crusts partially adjusted to the presence of litter through various responses that may help them to cope with a low light environment. For both *B. argenteum* and *D. muscorum* biocrusts, the litter treatment had less negative rates of dark respiration than the controls. Such changes in dark respiration may help to maintain positive or at least less negative overall carbon balances. Furthermore, *D. muscorum* showed decreases in LCP and the chlorophyll *a*/*b* ratio that may have helped this lichen to make more efficient use of the limited light available. Notwithstanding these physiological adjustments, negative effects of the litter on the biocrusts were apparent, particularly for *B. argenteum* where major declines in gross and net photosynthesis rates were observed. Different effects of the litter on the two studied species may be partly attributed to differences in their hydration period. Beneath the litter, biocrusts might have experienced negative carbon balances due to a combination of lower rates of photosynthesis and carbon losses occurring over extended periods. Under these circumstances, the species with the longer hydration periods would be more negatively impacted by the litter.

Acknowledgments

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