

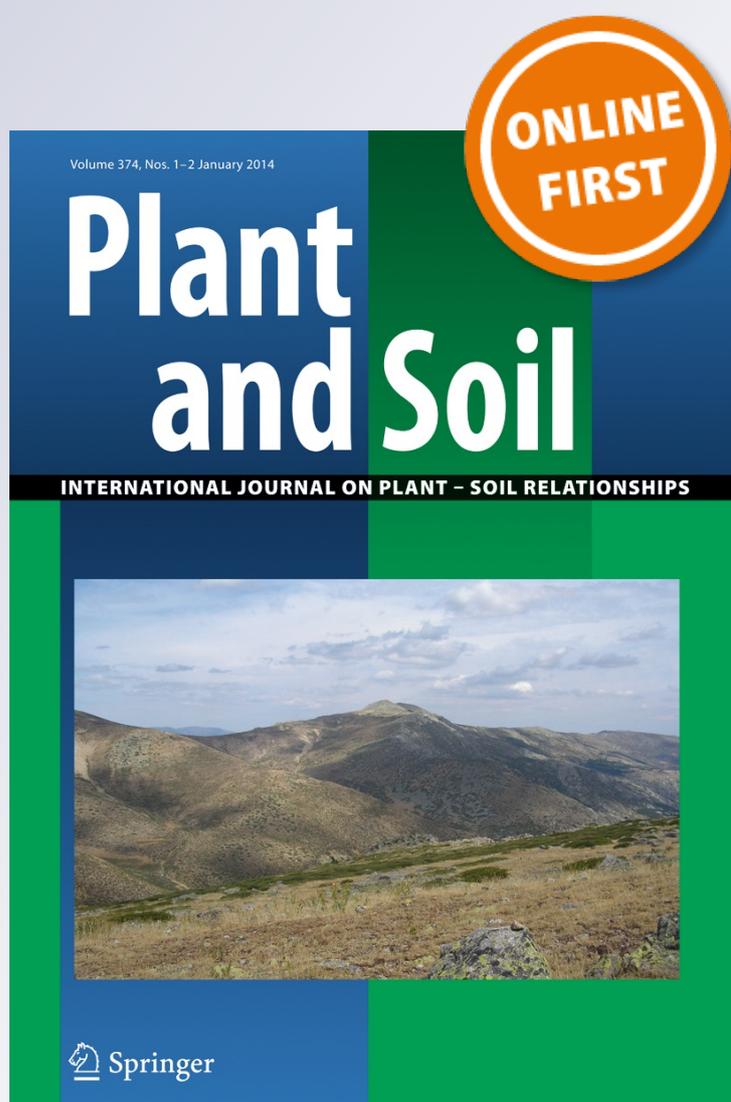
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Plant and Soil
An International Journal on Plant-Soil
Relationships

ISSN 0032-079X

Plant Soil
DOI 10.1007/s11104-013-2002-8



 Springer

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Effects of biocrusts and lichen-moss mats on plant productivity in a US sand dune ecosystem

Rachel K. Thiet · Alexis Doshas · Stephen M. Smith

Received: 6 March 2013 / Accepted: 6 December 2013
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Abstract

Background and aims Biocrusts are communities of cyanobacteria, algae, bryophytes, and lichens that influence plants and soils worldwide. In the Province Lands sand dunes of Cape Cod, algal biocrusts coexist with extensive bryophyte and lichen mats. The relationship between biocrusts, moss and lichen mats, and plants at this site has never been evaluated.

Methods We evaluated the effects of algal biocrusts and moss and lichen mats on soil moisture, plant productivity, and plant tissue water and nutrients of two dune plants, *Deschampsia flexuosa* and *Morella pensylvanica*.

Results Soil moisture was highest under lichen-moss mats and lowest under moss-only mats. Algae-only biocrusts and bryophyte and lichen mats significantly affected seedling survivorship, height, biomass, root growth, and tissue water and micronutrients. When compared to controls, algae-only biocrusts and moss-

only mats increased seedling survivorship and vigor, while lichen-moss mats decreased these plant responses. However, all biocrusts and mats tended to decrease plant productivity compared to controls.

Conclusions Biocrusts and mats play an important role in plant performance at this site, primarily via their effects on soil moisture, and possibly through their effects on plant tissue nutrients. Plants growing among biocrusts and mats at this site may experience a tradeoff between survivorship and productivity.

Keywords *Deschampsia flexuosa* · Green algae · *Morella pensylvanica* · Moss and lichen mats · Sand dune ecology · Temperate ecosystems

Responsible Editor: Hans Lambers.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-013-2002-8) contains supplementary material, which is available to authorized users.

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Introduction

Biological soil crusts (hereafter “biocrusts”) are communities of cyanobacteria, green algae, bryophytes, and lichens that are intimately entwined with surface soil particles, and which affect soil structure, soil moisture, nutrient cycling, and associated plant properties. In temperate biomes, soil crusts of green algae (Smith et al. 2004) and cyanobacteria (Thiet et al. 2005) colonize active sand dunes, where they often accompany early-successional vegetation (Belnap et al. 2001). In some sand dune systems, algal and cyanobacterial biocrusts coexist with extensive, well-developed mats of bryophytes and lichens in a mosaic on dune surfaces. While moss and lichen mats are not technically biocrusts because they do not bind soil particles, they

influence associated plants and soils via their effects on seed germination, seedling establishment, plant productivity, and soil properties (During and Tooren 1990; Zamfir 2000). In some systems, moss and lichen mats constitute a major component of the vegetation and strongly influence ecosystem productivity (Kytöviita and Crittenden 2007).

The effects of biocrusts and mats on plants may be facilitative or inhibitory depending upon biocrust and mat composition, distribution, microtopography, physiology, site characteristics, and the plant species in question (Hobbs 1985; During and Tooren 1990; Prasse and Bornkamm 2000; Sedia and Ehrenfeld 2003). Positive effects of lichen mats include higher light intensity at the mat surface, resistance to burning (Gibson 1993), and higher soil moisture beneath mats (Allen 1929; Bell and Bliss 1980; Zamfir 2000). Lichen mats may also have inhibitory effects on plants by secreting secondary allelopathic metabolites (Rundel 1978) or by uprooting seedlings during drying and rewetting cycles (e.g., *Cladonia*; Allen 1929). Moss mats may also increase soil water content (Bell and Bliss 1980) and plant productivity (Carlsson and Callaghan 1991; DeFalco et al. 2001) or, alternatively, create dry microhabitats that inhibit seedling establishment and productivity (Steijlen et al. 1995; Zamfir 2000).

Biocrusts and mats also affect plants via effects on tissue nutrient status. Plants growing in soils with biocrusts often have higher concentrations of various essential nutrients compared to plants growing in adjacent noncrusted soils (Belnap et al. 2001; Pendleton et al. 2003), as inorganic compounds (e.g., sulfides of copper, zinc, lead, zinc dust, magnesian oxide, and ferric hydroxide) may bind to crustal organisms and become available to vascular plants (Lange 1974; Gadd 1990; Geesey and Jang 1990; McLean and Beveridge 1990). In contrast, biocrusts may compete with plants for nutrients or reduce plant nutrient uptake; for example, DeFalco et al. (2001) observed that annuals growing in *Collema* and *Microcoleus* crusts had lower tissue N and P than plants growing in bare soils.

The objectives of this study were to evaluate the effects of algal biocrusts and moss and lichen-moss mats in the Province Lands sand dunes on Cape Cod, MA, USA, on soil moisture, plant productivity, and tissue water and nutrient content of *Deschampsia flexuosa* L. Trin (wavy hairgrass) and *Morella pensylvanica* Mirb. Kartesz (Northern bayberry). *Deschampsia flexuosa* (Gramineae) is one of two primary-successional dune

stabilizers (along with *Ammophila breviligulata*, American beachgrass) of Eastern coastal sand dunes. *Morella pensylvanica* (Myricaceae) is an early- to mid-successional shrub that is functionally important for its N-fixation activity in this highly nutrient-limited system.

Materials and methods

Site description

The Province Lands (42.058 N, 70.179 W) is a system of migrating parabolic dunes that spans approximately 1,800 ha at the northernmost tip of Cape Cod (Figure S1). The dunes formed ~6,000 years ago when long shore currents began transporting eroding sediments to the area from Atlantic-facing coastal bluffs south of the site. Clear-cutting of mature forests and animal grazing by early colonial settlers during the 1600s through 1800s eliminated the existing forest community and destabilized the soil surface (Smith et al. 2004). Presently the shifting dunes support a patchy matrix of primary successional herbaceous species and early- to mid-successional maritime forest assemblages (Gwilliam 2004; Miles 2008; Smith et al. 2008). The substrate is coarse-grained sand, and the climate is strongly influenced by its proximity to the Atlantic Ocean. Average temperatures range from 2.7 °C in February to 25 °C in August, and average annual precipitation is 110 cm with relatively little variation throughout the year (NOAA National Climatic Data Center 1981).

Biocrusts and mats in the Province Lands (Figure S2) exist by themselves or within a matrix of herbaceous and shrub vegetation dominated by *Ammophila breviligulata* (American beachgrass), *Deschampsia flexuosa*, *Morella pensylvanica*, and *Prunus maritima* (beach plum) (Smith 2006). In general, patchy mats of haircap moss (*Polytrichum juniperinum*) and Evans' reindeer lichen (*Cladina evansii*) occupy unshaded, low-lying open and forested areas (Figure S2) while green algal (mainly *Klebsormidium* sp.) crusts colonize the sides of dune slopes ($\leq 60^\circ$) and coexist with *A. breviligulata* and *D. flexuosa*. The latter are separate from the more morphologically complex lichen and bryophytic mats that colonize low-lying areas of the dunes (Smith et al. 2004; Miles 2008). Smith et al. (2004) documented that algal biocrusts in the Province

Lands enhance surface soil water retention and soil organic matter and nutrient levels. Since then, little work has been done on the Province Lands biocrusts, and no studies have evaluated the direct relationship between biocrusts, moss and lichen mats, and vascular plants at the site.

Experimental design

In 2011, we conducted a mesocosm experiment in Wellfleet, MA, USA to evaluate the effects of three different Province Lands crust and mat communities (green algae only, moss only, and lichen-moss) on soil moisture, plant productivity, and tissue water and nutrient levels of *D. flexuosa* and *M. pensylvanica*. We chose *D. flexuosa* and *M. pensylvanica* because both are common species in the dune landscape that play a key role in successional processes that increasingly stabilize the dunes.

Mesocosms were established by filling round plastic pots (25.4 cm d×20 cm deep) with beach sand, then topping them with eight replicates (pots) of each of four treatments (total 32 pots): algae only, moss only, lichen-moss, and bare soil (controls). Moss-only and lichen-moss mats were harvested from existing communities in the Province Lands by cutting a 25.4-cm d circular sample using a garden edger and placing a metal baking sheet underneath to acquire an intact mat sample (Figure S3a). Samples were then transported to our study site in Wellfleet and transplanted into pot mesocosms so they were level with the pot edge (Figure S3b). Care was taken to prevent cracking the mat microstructure. Green algal biocrusts were too brittle to collect directly from the field without breaking. Thus, to establish algal biocrusts we harvested biocrusts from nearby dunes and grew the algae in 7.6 L glass jars filled with water (ratio algal crust:water=50:50) in a sunny location for 2 weeks in May 2011. The resulting algal slurry was then transported to the study site and poured onto the soil surface in each pot, allowing for full saturation (naturally occurring at 3–5 mm deep) of the bare soil. Algal biocrusts were evaluated prior to the onset of the study to ensure uniform thickness and inoculation. Mesocosm pots were arranged randomly with 10 cm between each pot, and percent cover of each crust or mat type (algae, moss, lichen-moss) was quantified prior to the onset of the study to ensure dominance by each designated type.

In May 2011 each mesocosm was planted with one established seedling (20–25 cm tall) each of *D. flexuosa* and *M. pensylvanica* (Figure S3b), as these species co-occur in the Province Lands. Seedlings were supplied by North Creek Nurseries (Landenberg, PA) and planted to a depth of 10–15 cm. Following planting, soil moisture and seedling survivorship, height, and vigor were recorded weekly for 14 consecutive weeks from May–August 2011. We quantified seedling survivorship weekly in each treatment by counting the number of living and dead seedlings, and seedling height was measured (cm) from the soil surface. *M. pensylvanica* seedling survival was high, so we measured seedling height weekly for 14 weeks; however, *D. flexuosa* mortality was high starting in week six, so we measured seedling height of *D. flexuosa* individuals for only 5 weeks. Seedling vigor was recorded by assessing approximately 90 % of foliage using a numerical system: 3=plant characteristically healthy with foliage of normal color, 2=foliage chlorotic or yellow, 1=foliage chlorotic and wilted, and 0=all foliage dried and brittle (Ganskopp 1986).

In late August 2011 we harvested all surviving seedlings and measured biomass, root length, and tissue water, N, P, K, and micronutrient (Al, B, Ca, Fe, Mg, Mn, S, and Zn) content. Total biomass (g) was measured on dried seedlings, and root length (cm) was quantified by harvesting plants, cleaning roots with distilled water, drying, and measuring. Plant tissue water content was quantified by weighing before and after drying (60 °C) for 24 h. Tissue N was analyzed by standard combustion analysis on a Carlo Erba 1500 series analyzer, and other tissue nutrients were quantified using standard digestions in a CEM MARS microwave and analyzed on a 6500 duo ICP Spectrometer (Thermo Fisher Scientific, Hudson, NH). All assays were conducted at the Atlantic Research Center at CCNS (Truro, MA) except tissue nutrients, which were analyzed by Brookside Laboratories (New Bremen, Ohio). We measured soil moisture ($\text{m}^3 \text{m}^{-3}$) once a week in each pot using a digital ECH₂O soil moisture sensor (model EC-5, Decagon Devices, Pullman, WA) inserted into soil to 7–8 cm depth, and all readings were taken between 10:00 AM and 12:00 PM.

Data analysis

Because many of our response variables may be correlated (e.g., plant height and biomass), we first tested for

correlations among all response variables using non-parametric Spearman's rank correlations to determine whether we could limit the number of statistical tests we performed and report. Very few correlations were statistically significant (data not shown); thus, we analyzed and report on each of our response variables.

Seedling vigor, height, biomass, root length, and tissue water and nutrient content data were non-normally distributed and did not normalize with data transformation. Thus, we used non-parametric Spearman's rank correlations to evaluate the relationship between soil moisture and these variables, as well as seedling survivorship data, within each treatment group. Correlations were run using data averaged over five (*D. flexuosa*) and 14 (*M. pensylvanica*) weeks, using pots as our experimental replicates ($n=8$).

To compare the effects of our crust and mat treatments on all plant response variables, we performed non-parametric distance-based analyses of variance using the software program DISTLMv.5 developed by Anderson (2001). DISTLM partitions the variances among treatment groups by computing the distance matrices of raw data, and the resulting F-statistic is not bound by the assumptions of the F distribution of traditional parametric techniques (Anderson 2001, 2004, 2005; McArdle and Anderson 2001). To evaluate the effects of treatments on plant vigor and seedling height, we used replicated data ($n=8$ pots for each treatment) at week 5 for *D. flexuosa* and week 14 for *M. pensylvanica*, when the majority of plants of each species were still alive. Since nearly all *D. flexuosa* seedlings died in week 6 of our experiment, we evaluated the effects of our four treatments on plant biomass, root length, and tissue water and nutrient content of *M. pensylvanica* only ($n=29$ of 32 seedlings survived all 14 weeks of the experiment).

Soil moisture and seedling survivorship data were also non-normally distributed and transformation did not improve the data distribution. Therefore, we used Marti Anderson's PERMANOVA software program (Anderson 2001, 2005; McArdle and Anderson 2001) to evaluate the effects of our treatments on those response variables. PERMANOVA functions similarly to DISTLM; in this case, we chose PERMANOVA because our design for these variables was balanced, and because PERMANOVA has the advantage of performing post-hoc pairwise comparisons directly in the original analysis. Statistical significance for all analyses was determined at $\alpha=0.05$ unless otherwise noted.

When DISTLM and PERMANOVA detected significant differences among our four treatment groups, we performed separate post-hoc pairwise comparisons of each treatment group (six pairwise comparisons). In both programs, post-hoc pairwise comparisons are not adjusted for the experimental error rate; thus, with an a-priori significance level of $\alpha=0.05$ and an unadjusted experimental error rate, we might encounter a significant result by chance alone (i.e., Type I error) in one out of every 20 independent comparisons (Anderson 2001). While Bonferroni adjustment reduces the risk of committing Type I errors, it also increases the risk of obtaining false negatives (i.e., Type II errors). Thus, to mitigate the risk of reporting false positives and false negatives, we report significance of all pairwise comparisons at the Bonferroni adjusted $\alpha=0.008$ as well as pairwise comparisons that were significant at the unadjusted $\alpha=0.05$.

Results

Soil moisture

Soil moisture in mesocosms ($n=32$) was consistently highest under lichen-moss mats ($\bar{x} \pm \text{SE}$: $0.048 \pm 0.01 \text{ m}^3 \text{ m}^{-3}$) and lowest under moss-only

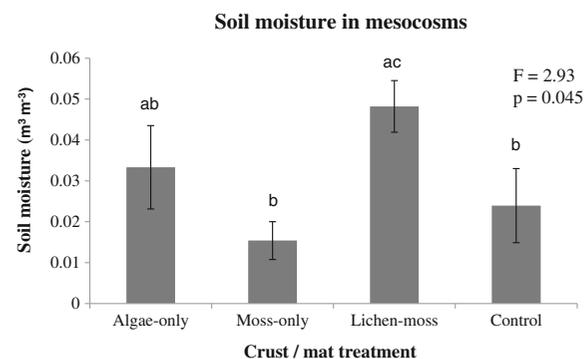


Fig. 1 Mean soil moisture ($\text{m}^3 \text{ m}^{-3}$) ($\pm \text{SE}$) in soil beneath each of four biocrust/mat treatments ($n=8$ mesocosms per treatment) at five (*D. flexuosa*) and 14 (*M. pensylvanica*) weeks in Wellfleet, MA, May–August 2011. Soil moisture measurements were not separated by plant species (e.g., *D. flexuosa* and *M. pensylvanica*). We averaged moisture in each pot over the 14-week study, and then averaged moisture across the eight replicate pots in each treatment. Different letters above bars within each species denote significant differences among treatments at Bonferroni-adjusted $\alpha \leq 0.008$ as well as at unadjusted $\alpha \leq 0.05$ (see Table S1 for specific α values)

mats ($\bar{x} \pm SE$: 0.015±0.00), and differences among our four treatments were significant (Fig. 1; Table S1).

Soil moisture was not correlated with *D. flexuosa* survivorship or vigor, but moisture was positively correlated with *D. flexuosa* height in lichen-moss mats (Table 1). Moisture was not correlated with *M. pensylvanica* survivorship, height, or vigor in any of our four treatment groups (Table 1). However, *M. pensylvanica* root length and tissue water content were significantly negatively correlated with soil moisture in algae-only biocrusts and positively correlated with soil moisture in bare soils. Biomass of this species was significantly negatively correlated with soil moisture in bare soils (Table 1).

Plant survivorship, height, and vigor

For *D. flexuosa*, survivorship and vigor were highest in algae-only biocrusts ($\bar{x} \pm SE$: 5.29±0.45 and 11.36±1.75, respectively) and lowest in lichen-moss mats ($\bar{x} \pm SE$: 2.64±0.79 and 5.21±1.95, respectively), and although vigor differences among treatments were not significant ($F=0.85$, $p=0.37$; Fig. 2a), survivorship of this species was significantly different among treatments at $\alpha \leq 0.10$ ($F=2.36$, $p=0.09$; Fig. 2b). *D. flexuosa* seedlings gained the most height in controls ($\bar{x} \pm SE$: 28.95±1.09 cm) and the least in moss-only mats ($\bar{x} \pm SE$: 25.69±1.17 cm), but differences among treatments were not significant ($F=0.58$, $p=0.51$; Fig. 2c).

Table 1 Results of Spearman's rank correlation (R_s) analyses between mean soil moisture and *D. flexuosa* and *M. pensylvanica* plant response variables. Bolded values are statistically significant at $\alpha \leq 0.05$. "N/A" denotes "not applicable,"

because we had 100 % survivorship of *M. pensylvanica* in algae-only biocrusts and moss-only mats, and because we had zero moisture in moss-only mats at week 14 when biomass, root length, and tissue H₂O and nutrient content were measured

<i>D. flexuosa</i>	Algae-only	Moss-only	Lichen-moss	Control
Soil moisture/survivorship	$R_s=0.20$ $p=0.54$	$R_s=0.11$ $p=0.73$	$R_s=0.13$ $p=0.69$	$R_s=0.45$ $p=0.14$
Soil moisture/height	$R_s=0.67$ $p>0.10$	$R_s=0.45$ $p>0.10$	$R_s=0.90$ $0.05>p>0.025$	$R_s=0.70$ $p>0.10$
Soil moisture/vigor	$R_s=-0.03$ $p>0.10$	$R_s=0.46$ $p>0.10$	$R_s=0.20$ $p>0.10$	$R_s=0.41$ $p>0.10$
<i>M. pensylvanica</i>	Algae-only	Moss-only	Lichen-moss	Control
Soil moisture/survivorship	N/A	N/A	$R_s=0.25$ $p=0.44$	$R_s=0.44$ $p=0.15$
Soil moisture/height	$R_s=-0.11$ $p=0.74$	$R_s=0.37$ $p=0.24$	$R_s=-0.19$ $p=0.56$	$R_s=-0.21$ $p=0.51$
Soil moisture/vigor	$R_s=-0.19$ $p=0.56$	$R_s=-0.47$ $p=0.13$	$R_s=0.14$ $p=0.67$	$R_s=0.16$ $p=0.62$
Soil moisture/biomass	$R_s=-0.40$ $p>0.10$	N/A	$R_s=-0.26$ $p>0.10$	$R_s=-0.70$ $0.05>p>0.025$
Soil moisture/tissue H ₂ O content	$R_s=-0.70$ $0.05>p>0.025$	N/A	$R_s=-0.14$ $p>0.10$	$R_s=0.70$ $0.05>p>0.025$
Soil moisture/root length	$R_s=-0.83$ $0.025>p>0.01$	N/A	$R_s=0.33$ $p>0.10$	$R_s=0.92$ $0.01>p>0.005$
Soil moisture/tissue S	$R_s=-0.19$ $p>0.10$	N/A	$R_s=0.43$ $p>0.10$	$R_s=0.87$ $p=0.025>p>0.01$
Soil moisture/tissue Mn	$R_s=0.80$ $p=0.025>p>0.01$	N/A	$R_s=0.99$ $0.005>p>0.001$	$R_s=-0.28$ $p>0.10$
Soil moisture/tissue Zn	$R_s=-0.33$ $p>0.10$	N/A	$R_s=0.13$ $p>0.10$	$R_s=-0.95$ $0.005>p>0.001$

M. pensylvanica survivorship was highest in algae-only biocrusts and moss-only mats ($\bar{x} \pm \text{SE}$: 8.0 ± 0 each) and lowest in lichen-moss mats ($\bar{x} \pm \text{SE}$: 6.5 ± 0.23) (Fig. 2b), and differences among treatments were significant ($F=31.95$, $p=0.001$). Significantly fewer *M. pensylvanica* survived in lichen-moss mats than in all other treatments (Table S2). Seedlings of this species gained the most height in controls ($\bar{x} \pm \text{SE}$: 22.61 ± 0.85 cm) and the least in moss-only mats ($\bar{x} \pm \text{SE}$: 17.19 ± 0.61 cm), and differences among treatments were significant ($F=4.27$, $p=0.002$; Fig. 2c, Table S2). Vigor of this species was highest in algae-only biocrusts ($\bar{x} \pm \text{SE}$: 18.36 ± 0.41) and lowest in lichen-moss mats ($\bar{x} \pm \text{SE}$: 14.08 ± 0.73), but vigor differences among treatments were not significant ($F=0.46$, $p=0.80$; Fig. 2a).

M. pensylvanica seedling biomass, root length, and tissue water and nutrient content

M. pensylvanica seedling biomass was highest in controls ($\bar{x} \pm \text{SE}$: 12.48 ± 0.67 g) and lowest in moss-only mats ($\bar{x} \pm \text{SE}$: 6.96 ± 0.92 g) (Fig. 3, Table S2). Root length of this species was highest in controls ($\bar{x} \pm \text{SE}$: 38.31 ± 3.3 cm) and lowest in algae-only biocrusts ($\bar{x} \pm \text{SE}$: 28.01 ± 2.14 cm) and moss-only mats ($\bar{x} \pm \text{SE}$: 28.08 ± 2.17 cm) (Fig. 4, Table S2). *M. pensylvanica* tissue water content was highest in controls ($\bar{x} \pm \text{SE}$: 6.9 ± 0.73 g) and lowest in moss-only mats ($\bar{x} \pm \text{SE}$: 4.31 ± 0.58 g), and differences among mat treatments were significant (Fig. 3, Table S2).

Crust and mat treatments had no significant effects on *M. pensylvanica* tissue N, P, K, Al, B, Ca, Cu, Fe, and Mg; however, tissue Mn, S, and Zn differed significantly among treatments (Table 2). *M. pensylvanica* tissue Mn was significantly higher (nearly double) in moss-only mats than algae-only biocrusts and controls (Table 2). *M. pensylvanica* growing in controls had the highest tissue S levels (Table 2), and seedlings in lichen-moss mats had significantly lower S than moss-only and algae-only treatments (Table S2). *M. pensylvanica* tissue Zn was highest in moss-only mats (Table 2), and was significantly higher in moss-only treatments than control treatments (Table S2). Seedlings in moss-only mats had higher Zn than those in algae-only and lichen-moss treatments at the unadjusted $\alpha=0.05$ (Table S2).

Discussion

Algal biocrusts and moss and lichen-moss mats significantly influenced nearly all of our plant response variables. When compared to controls, algal biocrusts and moss mats tended to increase seedling survivorship and vigor while lichen-moss mats decreased survivorship and vigor. However, biocrusts and mats reduced plant biomass, tissue water content, shoot height, and root

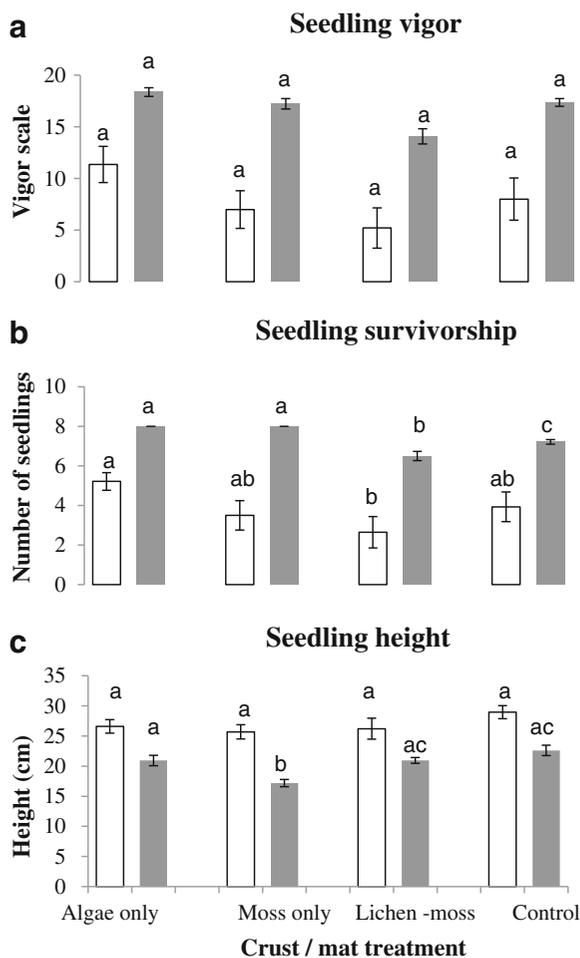


Fig. 2 Mean (\pm SE) vigor (a), survivorship (b), and height (cm) (c) of *D. flexuosa* and *M. pensylvanica* seedlings (total $n=32$ planted of each species) at five (*D. flexuosa*) and 14 (*M. pensylvanica*) weeks in Wellfleet, MA, May-August 2011. Open bars are *D. flexuosa* and solid bars are *M. pensylvanica*. *D. flexuosa* seedling heights were only measured for the first 5 weeks of the experiment due to seedling die-off in moss-only and lichen-moss mats during week 6. Different letters above bars within each species denote significant differences among treatments at Bonferroni-adjusted $\alpha \leq 0.008$ as well as at unadjusted $\alpha \leq 0.05$ (see Table S2 for specific α values)

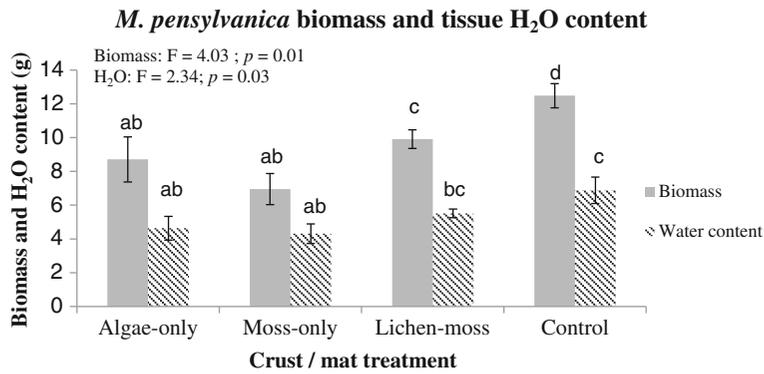


Fig. 3 Mean biomass (g) and tissue H₂O content (g) (\pm SE) of *M. pensylvanica* seedlings at the end of the 14-week study in Wellfleet, MA, May-August 2011 ($n=29$ surviving seedlings). Different letters above bars within each response variable denote

significant differences among treatments at Bonferroni-adjusted $\alpha \leq 0.008$ as well as at unadjusted $\alpha \leq 0.05$ (see Table S2 for specific α values)

length when compared to controls. Despite that soil moisture was consistently highest under lichen-moss mats, *D. flexuosa* and *M. pensylvanica* seedling performance was consistently lowest in these mats. *D. flexuosa* seedlings performed best in algae-only biocrusts, and *M. pensylvanica* did best in algae-only and control treatments. Thus, the positive effects of lichen-moss mats on soil moisture (Deines 2006) at this site do not necessarily result in improved plant performance, perhaps because both *D. flexuosa* and *M. pensylvanica* are highly drought-tolerant or because lichens may be intercepting important plant micronutrients (e.g., S). Differences in plant responses were strongest for *M. pensylvanica*, but *D. flexuosa* showed similar trends in its responses to biocrust and mat treatments; the effects of our treatments on *D. flexuosa* may have been more evident if we had not had such high mortality of this species in week six of our experiment.

Both *D. flexuosa* and *M. pensylvanica* performed poorly in moss-only mats, suggesting that moss mats

in the Province Lands intercept more precipitation (and thus nutrients) than they contribute to soils beneath them. In fact, by week 14 of our experiment, soils beneath moss mats had no measurable moisture. Moss-dominated biocrusts can increase water infiltration rates to underlying soil when rhizoids direct water downward (Brotherson and Rushforth 1983; Ladyman and Muldavin 1996), but they may also limit water availability to plants due to their high water absorption capacity (During and Tooren 1990; Proctor et al. 1998; Deines 2006). This effect may be particularly pronounced at extremely xeric sites like the Province Lands, where mosses regularly experience desiccation but swell rapidly when they absorb water during heavy rain events. Since nutrient-stressed plants produce more root biomass than plants grown in more fertile soil (Chapin 1980; Kachi and Rorison 1989; Redente et al. 1992; Pendleton et al. 2003), if moss mats at the Province Lands were intercepting precipitation and nutrients as we suspect, then we would expect to see greater root growth in *M. pensylvanica* seedlings than

Fig. 4 Mean root length (cm) (\pm SE) of *M. pensylvanica* seedlings at the end of the 14-week study in Wellfleet, MA, May-August 2011 ($n=29$ surviving seedlings). Different letters above bars denote significant differences among treatments at Bonferroni-adjusted $\alpha \leq 0.008$ as well as at unadjusted $\alpha \leq 0.05$ (see Table S2 for specific α values)

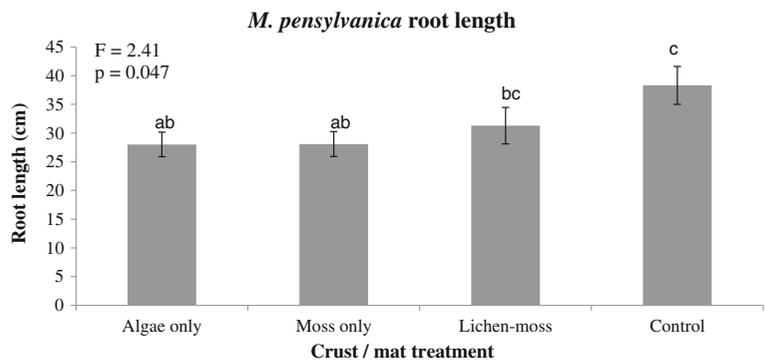


Table 2 Results from non-parametric ANOVA (Anderson 2001) of *M. pensylvanica* tissue nutrient content for algae-only biological soil crusts, moss-only and lichen-moss mats, and controls at the end of the 14-week study in Wellfleet, MA, May-August 2011 ($n=29$ surviving seedlings). Data are mean \pm SE. Bolded values are statistically significant at $\alpha \leq 0.05$, and different letters after means denote significant differences among treatments at Bonferroni-adjusted $\alpha \leq 0.008$ as well as at unadjusted $\alpha \leq 0.05$ (see Table S2 for specific α values)

	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	S (%)	B (ppm)	Fe (ppm)	Mn (ppm)	Cu (ppm)	Zn (ppm)	Al (ppm)			
Algae-only	1.55 \pm 0.11	0.13 \pm 0.02	0.66 \pm 0.02	0.53 \pm 0.03	0.21 \pm 0.01	0.12 \pm 0.00	ab	20.24 \pm 0.94	317.63 \pm 67.24	66.06 \pm 4.68	a	6.70 \pm 0.53	25.35 \pm 2.29	a	194.40 \pm 35.28
Moss-only	1.53 \pm 0.05	0.14 \pm 0.01	0.68 \pm 0.03	0.61 \pm 0.03	0.22 \pm 0.01	0.11 \pm 0.01	b	22.55 \pm 1.06	362.50 \pm 70.09	121.29 \pm 10.32	b	7.48 \pm 0.73	32.01 \pm 2.06	b	288.23 \pm 84.51
Lichen-moss	1.47 \pm 0.06	0.11 \pm 0.00	0.67 \pm 0.01	0.54 \pm 0.02	0.20 \pm 0.01	0.08 \pm 0.00	c	19.42 \pm 0.91	257.40 \pm 37.65	91.82 \pm 10.88	bc	5.86 \pm 0.26	22.74 \pm 0.64	ac	166.36 \pm 20.14
Control	1.58 \pm 0.07	0.12 \pm 0.01	0.70 \pm 0.04	0.57 \pm 0.03	0.21 \pm 0.01	0.12 \pm 0.00	abc	21.51 \pm 0.87	308.00 \pm 26.90	76.31 \pm 5.08	ac	5.97 \pm 0.20	22.80 \pm 1.04	ac	242.00 \pm 22.43
F-value	2.62	5.87	0.89	4.46	3.02	5.28		4.52	1.87	7.42		6.57	4.11		7.03
p-value	0.46	0.12	0.83	0.22	0.39	0.003		0.21	0.60	0.001		0.09	0.008		0.07

we observed. Thus, the lower root growth under moss-only mats likely reflects the lower overall plant biomass in that treatment, rather than reallocation of plant resources to roots under conditions of relatively low resource availability. Further, the high drought tolerance of *M. pensylvanica* may preclude its reallocating resources belowground under water and nutrient stress (i.e., under moss-only mats).

Algal biocrusts and moss and lichen-moss mats significantly influenced soil moisture in our mesocosms. Soil moisture was negatively correlated with *M. pensylvanica* root length and tissue water content in algal biocrusts. Decreased rainwater infiltration through algal crusts is pronounced in very sandy soils where high porosity is blocked by the swelling of algal sheaths during rehydration (Verrecchia et al. 1995; Warren 2001). This results in water being held in the top few mm of the soil (Smith et al. 2004), which may limit the soil moisture-mediated effects of these crusts on deep-rooted species like *M. pensylvanica*, whose roots may extend as deep as 20 cm under field conditions (Hauser 2006). For *M. pensylvanica*, lower root:shoot ratios in algae-only biocrusts may result from nutrient enhancement beneath crusts (Smith et al. 2004), as root:shoot ratios decrease proportionally to crust coverage because plants produce less root tissue as nutrients from crusts become available (Pendleton and Warren 1995).

Moss-only mats had highly significant positive effects on seedling tissue Mn and Zn. Enhanced nutrient uptake by vascular plants growing among biocrusts has been well documented (Lange 1974; Geesey and Jang 1990; Harper and Belnap 2001; Langhans et al. 2009), but certain biocrust and mat types also prefer specific soil nutrient conditions; e.g., mosses and lichens are limited by Mn and Zn and thus are commonly found atop Mn- and Zn-enriched soils (Bowker et al. 2005). Thus, it is unclear whether moss mats in our study translocated Mn and Zn directly to *M. pensylvanica* seedlings, or whether our results reflect enriched soil Mn and Zn under moss-only mats collected from the field. The results for Zn suggest that mosses may actually be directly translocating micronutrients to vascular plants at this site, since we would expect to see similar tissue Zn levels in seedlings growing in moss-only and lichen-moss mats if our results were merely an artifact of sampling. Further, we collected exclusively mats from the field for transplantation into our mesocosms, i.e., we did not collect and transplant any soil from underneath field-collected mats.

Plant tissue S was significantly lower in lichen-moss mats than in all other treatments, suggesting that lichens compete with vascular plants for S at this site. Lichens and bryophytes are known to capture and immediately absorb S, and lichens in particular rapidly absorb S through their permeable cell walls (Berg and Steinnes 1997; Conti and Cecchetti 2001; Raymond et al. 2010). S is essential for the formation of plant proteins, lipids, intermediate metabolites, and other cellular compounds; thus, under conditions of S starvation, plants readily increase the production of key enzymes for S assimilation of both internal and external S sources (Grossman and Takahashi 2001). Therefore, if lichen-dominated mats are competing with *M. pensylvanica* for S, it is unclear why *M. pensylvanica* did not appear to respond to relatively lower S levels beneath lichen-moss mats by increasing S uptake; longer-term studies may be necessary to observe this response. Mass-balance analyses would shed light on whether lichens are competing with plants for S at this site.

Concluding remarks

Our study is the first to evaluate the effects of soil biocrusts and mats on plants in the temperate sand dunes of Cape Cod. Biocrusts and mats had a consistent influence on plant survivorship and productivity in our study system. Algal biocrusts and moss and lichen mats tended to increase plant survivorship but decrease plant productivity compared to controls, suggesting that early- and mid-successional plants growing among biocrusts and mats in this stressful system experience a tradeoff between survival and growth. Biocrusts and mats (particularly algal crusts and moss mats) may help plants establish and survive by providing safe microsites that buffer seedlings against drought and wind, but seedlings may then be forced to compete with crusts and mats for moisture and nutrients (e.g., in moss-only and lichen-moss mats). Therefore, plant ecologists and managers should consider the effects of biocrusts and mats on plant establishment and productivity to gain the fullest understanding of plant-soil dynamics at this site.

Acknowledgments The authors thank Mark Adams, Judith Oset, Megan Tyrrell, and Krista Lee of Cape Cod National Seashore for laboratory and project assistance, Mel Knorr and three anonymous reviewers for input into an earlier draft of this manuscript, and Gordon Peabody and Tony Leonard for support and

guidance. This study was funded by a Garden Club of America Ecological Restoration fellowship to Alexis Doshas.

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