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Effects of increased summer precipitation and N deposition on Mojave Desert populations of the biological crust moss *Syntrichia caninervis*

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ABSTRACT

Climate change in the Mojave Desert (USA) may result in a greater intensity of summer (monsoon) rain events and greater atmospheric N deposition. Patches of the dominant biological crust moss *Syntrichia caninervis* were exposed to field treatments of low and high nitrogen supplementation, added summer rain, and combinations thereof, for a period of five years. In the lab, shoots were subjected to a moderate (single rapid-dry treatment) and a severe (double rapid-dry treatment) desiccation stress. Shoots were then hydrated and allowed to regenerate for 6 weeks on sterile sand. Shoots exhibited lower above-ground biomass from the +monsoon treatment, indicating carbon balance deficits under conditions of recurring summer rainfall. The low N treatment and the severe desiccation stress promoted shoot burning (chlorosis) and negatively affected regeneration responses. High N treatment, however, only adversely affected the resumption of apical meristematic growth. Summer irrigation and N application interacted to mitigate the effects of later protonemal emergence time, lower protonemal cover, and lower shoot numbers. Increased monsoonal frequency and higher N deposition as forecast for the northern Mojave Desert may result in declines in shoot biomass and reduced regenerational vigor in *S. caninervis*.

1. Introduction

Biological soil crusts (BSCs) are autotrophic communities consisting of cyanobacteria, mosses, lichens, algae, and fungi that can be the dominant cover of soil in desert and steppe habitats in the western USA. These soil surface communities positively influence soil fertility, soil stability, soil hydrology, and the establishment and growth of associated seed plant species (Belnap and Lange, 2003; Pendleton et al., 2003). In addition, the BSC contribution to the cycling of trace gases can be significant in regard to global budgets (Zaady et al., 2000). Soil restoration of BSCs can be accomplished by raising mosses in the lab and transplanting them into the field (Xu et al., 2008).

Experimental N addition to *Sphagnum*, *Racomitrium*, *Calliergonella*, and *Hylocomium*-dominated communities often causes rapid negative and sometimes toxic effects on growth, survival, regeneration, or cover (Berendse et al., 2001; Bragazza et al., 2004; Jägerbrand et al., 2003; Jauhiainen et al., 1998; Jones et al., 2002; Mitchell et al., 2002; Paulissen et al., 2005; Pearce et al., 2003) and can alter competitive species relationships (Limpens et al., 2003). This indicates that most bryophytes are probably adapted to low N levels (Li and Glime, 1990) and absorb N preferentially in upper shoot segments (Soares and Pearson, 1997), although mesophile and nitrophilic species exist. The deleterious effects of fertilizing moss populations are attributable to (i) shading and litter deposition by herbs and grasses (Berendse et al., 2001; Press et al., 1998), and (ii) direct toxicity effects (e.g., Pearce et al., 2003). However, changes in moss cover and abundance in response to N deposition can be independent of changes in vascular plant cover (Carroll et al., 2003) and in fact stimulate bryophyte biomass in some communities (Plassmann et al., 2009). Experimentally changing the timing and size of rain events on the BSC of the Colorado Plateau (USA) resulted in declines in photosynthetic efficiency, chlorophyll *a*, and protective pigments in the lichen *Collema*. Such observations indicate that soil lichen cover and richness (and most likely bryophyte parameters) decline as the frequency of monsoon events increases, with C deficits produced in response to summer precipitation events (Belnap et al., 2004). In the laboratory, intermittent desiccation of the mesic mosses *Brachythecium* and *Pseudoscleropodium* reduced productivity compared to continuously hydrated controls, but reabsorption of leaked solutes during rehydration was implicated in higher N contents of desiccated plants (Bates, 1997). Interactions of N addition and desiccation can stimulate growth of mosses in the permafrost (*Sphagnum* and *Dicranum*

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species; Sonesson et al., 2002), but desiccation has also been shown to impede N uptake in *Calliergonella* and *Dicranum* (Bakken, 1994; Van Tooren et al., 1990). In *Racomitrium*, N deposition may initially stimulate growth but later cause adverse effects on shoot elongation and survival (Jones et al., 2002).

The western USA experienced a multiyear drought up through 2003 that has not entirely abated. As warming trends continue, a serious consequence across the arid portions of western N. America is increased aridity (Cook et al., 2004). The widespread chlorosis observed in Mojave Desert (USA) populations of *Syntrichia caninervis* was linked to ongoing drought conditions characterized by rain events smaller than normal (<3.5 mm), with the chlorotic condition likely resulting from a negative carbon balance brought about by the desiccation stress of rapid-drying (Barker et al., 2005). Thus while bryophytes can tolerate long-term drought conditions by remaining essentially dormant in the dried state for years, chlorosis of tissues results from a drought punctuated by short hydration events in which plant desiccation is rapid (Proctor et al., 2007). In addition to constitutive desiccation protection, bryophytes employ a rehydration-induced repair system to physiologically recover from loss of water (Oliver et al., 2000), with gene expression altered upon rehydration through translational control (Oliver, 1991). During slow desiccation (over a 6 h period), transcripts encoding rehydrin repair proteins are sequestered in messenger ribonucleoprotein particles (mRNPs) for storage in the desiccated state (Wood and Oliver, 1999). However, if mosses are rapidly dried (dried in <2 h), such transcript sequestration is compromised, and this is the reason why rapid-drying presents a severe stress even in desiccation tolerant species of bryophytes (Bewley, 1979; Stark et al., 2007).

Several global change models predict significant increases in summer precipitation (a monsoon effect) in the northern Mojave Desert, increased atmospheric N deposition, and continued increases in atmospheric CO_2 (e.g., Higgins and Shi, 2001; Taylor and Penner, 1994). Some projections call for larger and less frequent rain events in xeric regions (Knapp et al., 2008), and while this consequence may result in greater water availability at increased soil depths, for bryophytes this would result in decreased hydroperiods ultimately causing greater desiccation stress. Because BSCs are metabolically active only when wet, any alteration in the timing and duration of precipitation should markedly affect their physiology, carbon balance, and stress tolerance. Given that an increased monsoon effect adversely affected biomass, sex expression, and cyanosymbiont associations in *S. caninervis* (Stark et al., 2011), our goal here is to determine how these projected elements of climate change affect desiccation tolerance in this moss.

First, we hypothesize that N enrichment may promote desiccation tolerance (DT) given that DT in bryophytes requires the manufacture of a broad array of repair proteins (Oliver et al., 1997). Second, we hypothesize that summer rainfall treatments are expected to negatively impact the health (regenerative ability and DT) of *Syntrichia* plants, given that rapid-drying is promoted by summer precipitation and this should negatively affect the C balance of the plants.

2. Materials and methods

2.1. Experimental field site

The Mojave Global Change Facility (MGCF) was established in 2001 on the U.S. Department of Energy's Nevada Test Site in southern Nevada (36°49′N, 115°55′W, elev. 970 m), in order to study long-term effects of climate change on desert ecosystems. Mean annual precipitation at the MGCF is 138 ± 62 mm, falling mostly during winter months (Hunter, 1994), with highly episodic summer precipitation and a low relative frequency of large rainfall events (Huxman et al., 2004). This community is dominated by the xerophytic shrubs *Larrea tridentata*, *Ambrosia dumosa*, *Lycium pallidum*, *Lycium andersonii*, and the C_4 bunchgrass *Pleuraphis rigida* (Jordan et al., 1999). This remote area represents an essentially undisturbed desert ecosystem closed to the public and free of any livestock grazing for at least 60 years. The MGCF spans 36 ha, comprised of 96 plots each measuring 14×14 m. For each treatment, a 16×16 m area was subjected to the treatment (or treatment combination), which allows for a 2-m buffer area so that the entire 14×14 m plot could be used for measurements. Overall, the experiment involved three factors arranged in a factorial design (8 blocks, each with 12 plots) with two monsoon treatments (+ and 0), three N treatments (0, 10, and 40 kg N ha^{-1} yr^{-1}), and two biological soil disturbance regimes (+ and 0). In this paper, we focus on results from treatments having no soil disturbance, equating to 48 of the 96 plots. From 2001 forward, irrigation was applied in three 25 mm events once every three weeks from early July to mid-August through a sprinkler system tested for even coverage. Local ground water was delivered evenly during windless nights at rates below the infiltration rate of the soil. The total supplemental 75 mm H_2O represents a 3-fold increase in mean annual summer precipitation, but only a 50% increase in annual precipitation. Supplemental N was added in November of each year as $CaNO_3$ in solution via sprinklers, approximating the range of N deposition in the Las Vegas, NV, USA (10 kg N ha^{-1} yr^{-1}) and Los Angeles, CA, USA (40 kg N ha^{-1} yr^{-1}) areas. This resulted in a total application of no more than 5 mm of water, which was also added to all non-+N plots to ensure equal watering among treatments.

2.2. Patch sampling and shoot selection

In December of 2005, desiccated patches of the moss *S. caninervis* were sampled in each of the 48 plots. One patch per plot having at least one contiguous clump measuring $>10 \times 10$ cm and which was situated under a shrub or perennial grass canopy was targeted. Patches had been previously randomly assigned for the present study and for additional studies monitoring phenology and disturbance based on the minimum size requirements above. If more than one of these clumps existed in the patch, then the central most one in the patch was selected. Using fine forceps, ~40 ramets were removed from the clump, placed in a microenvelope and transported to the laboratory. If the patch did not contain a clump with 10×10 cm dimensions located in the understory, or if the plot did not contain a suitably sized patch (in 8 instances), then we selected an alternate patch in another plot of the same treatment. Shoots were stored in a herbarium cabinet in sealed microenvelopes from collection until experimental installation (3 mos). From each field plot collection, 9 shoots measuring from 2–3 mm in length above the ground level were randomly selected. Using sterilized utensils, each desiccated shoot was cut at the ground level using a straight edge, weighed to the nearest 0.01 mg (initial shoot biomass), and placed into individual wellholes in 48-hole tissue culture plates, handling the shoot by the hyaline awns whenever possible.

2.3. Experimental design

Nine shoots from each field treatment (control, low N, high N, monsoon, low N + monsoon, high N + monsoon) were allocated to three desiccation treatments (control, RD*x*1, RD*x*2; "RD" = rapid-dry). Thus, a given category (e.g., low N, RD*x*1) had 24 shoots, with a total experimental shoot number of 432, in a randomized block design of 3 shoots per Petri dish.