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Few apparent short-term effects of elevated soil temperature and increased frequency of summer precipitation on the abundance and taxonomic diversity of desert soil micro- and meso-fauna

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ABSTRACT

Frequent hydration and drying of soils in arid systems can accelerate desert carbon and nitrogen mobilization due to respiration, microbial death, and release of intracellular solutes. Because desert microinvertebrates can mediate nutrient cycling, and the autotrophic components of crusts are known to be sensitive to rapid desiccation due to elevated temperatures after wetting events, we studied whether altered soil temperature and frequency of summer precipitation can also affect the composition of food web consumer functional groups. We conducted a two-year field study with experimentally-elevated temperature and frequency of summer precipitation in the Colorado Plateau desert, measuring the change in abundance of nematodes, protozoans, and microarthropods. We hypothesized that microfauna would be more adversely affected by the combination of elevated temperature and frequency of summer precipitation than either effect alone, as found previously for phototrophic crust biota. Microfauna experienced normal seasonal fluctuations in abundance, but the effect of elevated temperature and frequency of summer precipitation was statistically non-significant for most microfaunal groups, except amoebae. The seasonal increase in abundance of amoebae was reduced with combined elevated temperature and increased frequency of summer precipitation compared to either treatment alone, but comparable with control (untreated) plots. Based on our findings, we suggest that desert soil microfauna are relatively more tolerant to increases in ambient temperature and frequency of summer precipitation than the autotrophic components of biological soil crust at the surface.

1. Introduction

Desertification is the collective process of reduced productivity in arid and semi-arid lands that can result from long-term grazing, exotic shrub invasion, and extended drought (Schlesinger et al., 1990). The majority of global climate models used by the International Panel on Climate Change (IPCC) predict a transition to more arid conditions for much of the arid southwest US (Seager et al., 2007), in part due to projected increases of 2–4 °C by 2050 for Western North America. However, models differ in their predictions of drought through 1) reduced annual precipitation or 2) shifts toward precipitation in hot (summer) seasons. Biological soil crusts (comprised of cyanobacteria, lichens, green algae, and mosses) may slow desertification in many desert soils by increasing the physical stability of surfaces and improving soil fertility through dust entrapment, photosynthesis, nitrogen fixation, and mineral chelation (Belnap, 2003). However, rapid desiccation due to elevated temperatures after wetting events was found to adversely affect the autotrophic components of crusts because rapid wetting and drying cycles reduce quantum yield (an indication of radiation-induced damage to Photosystem II), chlorophyll content, and UV protective pigments of soil lichens (Belnap et al., 2004; Bowker et al., 2002), and high temperatures (>26 °C) inhibit nitrogen fixation (Belnap, 2002). Frequent small precipitation events in arid systems accelerate rates of carbon (C) and nitrogen (N) mineralization by increasing microbial respiration, death by membrane rupture, and release of intracellular solutes (Austin et al., 2004; Fierer and Schimel, 2003; Kieft et al., 1987; Miller et al., 2005). In the case of autotrophic components of desert biological soil crusts, rapid desiccation reduces their ability to conserve carbon by osmoregulation (Belnap et al., 2004). As a result, arid lands can

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experience significant losses of C and N by volatilization of gaseous compounds and leaching of aqueous compounds upon rewetting if nutrients are not immobilized by plant, microbial, or consumer uptake. To understand how changes in the climate of arid land regions affect the ability of soil food webs to mediate nutrient cycles, it is necessary to understand how the soil food web consumer groups themselves also respond to altered temperature and precipitation.

Previous studies have reported numerous impacts of altered temperature and precipitation on soil microfauna communities, but the changes documented appear to be idiosyncratic or without clear functional implications (Bakonyi and Nagy, 2000; Bakonyi et al., 2007; Sohlenius and Bostrom, 1999; Todd et al., 1999). Desert soil food webs are composed of multiple consumer groups that mobilize nutrients (Whitford, 1996), and various functional groups within these food webs contribute to different parts of the C and N cycle. For example, Santos et al. (1981) suggested that cephalobid nematodes in desert soils influence decomposition by regulating the population sizes and activity of their bacterial prey, while Santos and Whitford (1981) showed that microarthropods accelerated litter decomposition 200% in comparison to litter excluding microarthropods. Only 50% of nematodes in desert soils with similar texture and species composition were estimated to be metabolically active (Freckman and Mankau, 1986), with 30 °C representing an approximate threshold at which desert microfauna begin to die when hydrated and forced to be active (Darby et al., 2006).

The primary objective of this study was to determine the response of microfaunal groups of desert soil food webs to an annual scale elevated temperature and increase in frequency of summer precipitation. We conducted a two-year field experiment with treatments in a complete factorial combination with sampling in both spring and early fall to capture seasonal dynamics over a winter and summer period, respectively. It has been previously shown that the autotrophic components of crusts are sensitive to rapid desiccation due to elevated temperatures after wetting events (Belnap et al., 2004; Bowker et al., 2002), and that high temperatures (>26 °C) inhibit nitrogen fixation (Belnap, 2002). Consequently, we asked whether the microfaunal consumers of the desert soil food web (e.g., protozoa, nematodes, and microarthropods) are similarly sensitive to elevated temperature and increased frequency of summer precipitation. Desert microfauna are capable of tolerating considerable drought and temperature extremes by entering and exiting from the dormant state. However, such stress tolerance is metabolically costly (Crowe et al., 1977), so we hypothesized that microfauna would be affected adversely by the combination of elevated temperature and frequency of summer precipitation more than either factor alone. An additional objective of this study is to simply characterize the abundance of nematodes, protozoa, and microarthropods together from this cool-desert location in southeastern Utah, USA, as well as the composition of nematode and microarthropod taxa. For this reason, we report the major taxa found from each group, and suggest characteristics of the consumer portion of this desert food web that differ from temperate food webs and may be of functional significance.

2. Methods

2.1. Field experiment design

A study site (60 m by 60 m) was selected in fall of 2005 near Moab, Utah (38.67485 N, –109.4163 W, 1310 m.a.s.l.), representative of the Colorado Plateau, where about 65% of the precipitation occurs in winter. The soil at this site is classified as loamy, mixed (calcareous), mesic Lithic Ustic Torriorthent. Vascular plant vegetation at this site, comprising 5–20% of the total cover, is dominated by the grasses *Pleuraphis jamesii* (Torr.) (syn. *Hilaria jamesii*), *Achnatherum hymenoides* (Roem. & Schult.) (syn. *Stipa hymenoides*), and *Bromus tectorum* (L.) (Rosentreter and Belnap, 2001). Biological soil crusts at this site, comprising 70–90% of total cover, are dominated by the lichen *Collema tenax* (Sw.) Ach., the cyanobacterium *Microcoleus vaginatus* (Vauch.) Gomont, and the moss *Syntrichia caninervis* Mitt. Experimental field units were arranged in a randomized block design with five replicate blocks arranged perpendicular to a gradual slope. Each block contained five, 2-m by 2-m plots containing representative vegetative cover and composition. One of five treatments was applied randomly to each experimental unit within a block: 1) control, 2) lamp control, 3) elevated temperature, 4) elevated frequency of summer precipitation, and 5) both elevated temperature and frequency of summer precipitation. Control plots (1) had no lamp shell, while all other plots (2, 3, 4, 5) had a lamp shell 1.5 m above the soil; the plots without elevated temperature treatments (2, 4) included the lamp shell with no heating filament, whereas the plots with elevated temperature treatments (3, 5) included a working infrared heating filament (Model MRM-1208, 120 V, 800 W, 6.7 A, 35 in., Kalglo Electronics Co. Inc, Bethlehem, PA). The lamps add no photosynthetically active radiation and have been used successfully to warm soils in previous climate change experiments (Harte et al., 1995; Bridgham et al., 1999; Zavaleta et al., 2003). The heating lamps (active throughout the entire two-year experiment) provide greater warming at night than during the day, and greater warming in the winter than the summer which better mimics empirical climate change data than other warming technologies. The frequency of summer precipitation was increased to approximately twice the 40-year summer median with 2-mm artificial rainfall events (6 L of water per plot, or approximately the 40-year median event size) applied five times per two-week interval through summer (June, July, August, and September). Thus, both frequency of total summer precipitation was increased, but no individual rainfall event size was increased beyond ambient. Simulated rainfall was provided with a watering nozzle calibrated to supply raindrop sizes appropriate for this region. Thermopiles were constructed from 24 ga Type-T thermocouple wire (Omega Engineering, Inc., Stamford, CT) and installed in every plot of every treatment to record half-hourly temperature data at 1-, 5-, and 15-cm to confirm elevated temperature treatments. Campbell CS616 water content reflectometer probes (Campbell Scientific, Inc., Logan, UT) were installed in every plot of every treatment to measure volumetric water content at 5-cm depths every 30 min. In general, the field site experienced comparable climatic conditions for the region (Fig. 1) and experimental treatments elevated temperatures 2–3° for most of the year relative to control plots (Fig. S1). To assess vegetative cover for comparison with nematode and mite communities, we estimated percent cover at the final sampling date (September 2007) by visual inspection of each plot's sampling area for seven major cover-type groups: bare/rock, lichen, cyanobacteria, moss, *P. jamesii*, *A. hymenoides*, and *B. tectorum*.

2.2. Sampling

Sampling of all 25 plots for nematodes and protozoa occurred on rain-free days in March 2006, September 2006, May 2007, and September 2007. The spring and fall sampling dates were selected to be able to assess the population dynamics that occur between the two most contrasting seasons at this site, winter and summer respectively. Surface (0–10 cm depth) soil was collected with approximately 8–10 cores (2.5 cm diameter) to obtain at least 250 g soil for the nematode and protozoa assay. On each sampling date, cores were collected from within an 8-cm wide segment adjacent