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## Rapid plant community responses during the summer monsoon to nighttime warming in a northern Chihuahuan Desert grassland

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### ABSTRACT

Global environmental change is altering temperature, precipitation patterns, and resource availability in aridland ecosystems. In 2006, we established a multifactor global change experiment to determine the interactive effects of nighttime warming, increased atmospheric N deposition, and more frequent occurrence of El Niño years on plant community dynamics in a northern Chihuahuan Desert grassland. Here we only report the results of warming and N addition from the first monsoon growing season prior to the imposition of the precipitation treatments. Our passive nighttime warming treatment increased daily minimum temperatures by 1.4–3.0 °C. Fertilization increased NO<sub>3</sub>–N supply, as measured with Root Simulator Probes, by 28% and NO<sub>3</sub>–N supply in warmed plots was 12% higher than in control plots. After one monsoon season we found that warming significantly increased total plant cover. Responses among dominant species varied, however. Warming significantly increased cover of *Bouteloua eriopoda* ( $P < 0.05$ ) and tended to increase cover of the shrub *Gutierrezia sarothrae* ( $P = 0.064$ ), whereas N addition significantly increased the cover of *Bouteloua gracilis* ( $P < 0.05$ ). Our results demonstrate that rapid soil and plant community responses can occur in response to nighttime warming and N fertilization during one monsoon season in this semi-arid desert grassland. The sensitivity of this desert system to key drivers of global environmental change suggests that further increases in temperature and atmospheric deposition will likely alter community structure and ecosystem functioning in this and other aridland ecosystems.

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### 1. Introduction

Increasing temperatures, precipitation variability, and nitrogen (N) deposition are three global environmental changes influenced by human activities. Globally, average temperatures have increased by 0.6 °C and industrial N fixation has more than doubled reactive N since pre-industrial times (Gruber and Galloway, 2008; IPCC, 2007). Moreover, there is evidence that regional climate is becoming more variable, including the possibility of more intense, longer lasting heat waves and changes in the seasonal distribution of precipitation (IPCC, 2007; Karl and Trenbath, 2003; Meehl and Tebaldi, 2004; Pryor and Schoof, 2008; Seager et al., 2007 and Sheppard et al., 2002). While these changes are widely accepted, the effects of interactions among such global change drivers are the

largest source of uncertainty in global change research (Sala et al., 2000). Indeed, evidence suggests that warming and N deposition have already impacted plant communities by decreasing diversity and altering species phenology and range distributions (Kochy and Wilson, 2001; Parmesan and Yohe, 2003; Peñuelas and Filella, 2001; Stevens et al., 2004; Walther et al., 2002). As N deposition, warming, and climate variability continue to increase they are expected to have a dramatic impact on plant community structure and function over the course of the next century (Sala et al., 2000).

Globally, anthropogenic N fixation has more than doubled “natural” levels of reactive nitrogen (Galloway et al., 2008; Vitousek et al., 1997). Like in other regions, N deposition is increasing in arid and semi-arid areas of the world, driven by increasing population and industrialized agriculture (Fenn et al., 2003; Holland et al., 1999). In the arid southwestern USA, shrub- and grass-dominated areas have average rates of total inorganic N deposition of 0.3 and 0.5 g m<sup>-2</sup> y<sup>-1</sup> respectively, with some areas experiencing up to 1.3 g m<sup>-2</sup> y<sup>-1</sup> (Holland et al., 1999). These rates represent 6- and 9-fold increases over pre-industrial levels of N deposition in C<sub>3</sub> shrublands and C<sub>4</sub> grasslands, respectively. Although few studies

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predict future rates of N deposition, Sala et al., (2000) expected an increase of  $4.0 \text{ g m}^{-2} \text{ y}^{-1}$  in deserts and savannas and  $6.0 \text{ g m}^{-2} \text{ y}^{-1}$  in grasslands. However, as population growth and industrial agriculture increase regionally, N deposition may increase more quickly in aridland ecosystems than it has to date.

Although arid and semi-arid lands cover approximately one third of the earth's surface (Dregne, 1970), few studies have examined the interactive effects of climate change and N deposition in arid and semi-arid ecosystems. These pulse-driven nutrient poor ecosystems (Collins et al., 2008; Noy-Meir, 1973; Reynolds et al., 2004), which are already hot and dry, may be particularly susceptible to multiple climate change drivers. Arid systems may be particularly sensitive to warming for several reasons. First, many species are already stressed by high temperatures and low moisture availability, leading to possible threshold effects that could favor desertification. Second, the dominant species in many aridland systems are  $C_4$  grasses that can take advantage of summer monsoon rains, but make less use of winter/spring rainfall. A small increase in temperature, especially nighttime minimums, could lengthen the spring growing season for some subdominant species by weeks or months. This could result in dramatic shifts in community composition by favoring species adapted to winter/spring growth, particularly  $C_3$  shrubs and forbs.

Here, we report on the first year treatment effects of an ongoing long-term experiment designed to determine the individual and combined effects of nighttime warming, elevated N deposition, and increased winter precipitation on community structure and ecosystem processes in a northern Chihuahuan Desert grassland. Results reported here occurred prior to the start of the winter rainfall treatments, thus we only focus on warming and N addition. We are particularly interested in nighttime warming because winter low temperatures are known to limit the northern distribution of many desert species (Nobel, 1980), including creosotebush (Martinez-Vilalta and Pockman, 2002), and because increases in nighttime temperatures are a strong indication of climate change. Significant increases in the frequency of warm nights, and decreases in the frequency of cold nights, occurred over 73–74% of the world, whereas significant changes in the frequency of cold and warm days were observed less frequently (IPCC, 2007). Our study site at the Sevilleta LTER in central New Mexico occurs at a vegetation transition zone dominated by two  $C_4$  perennial grasses, *Bouteloua gracilis* a dominant species in Central Plains shortgrass steppe to the north, and *Bouteloua eriopoda* a dominant species in Chihuahuan Desert grassland to the south. In addition numerous  $C_3$  shrubs, such as *Gutierrezia sarothrae*, occur as well. Our treatments were designed to mimic expected conditions in this region in the latter half of the 21st Century. We hypothesized that warming would favor the Chihuahuan Desert grassland species, *B. eriopoda*, over the Great Plains species, *B. gracilis*, but that N deposition would favor *G. sarothrae* and *B. gracilis* over *B. eriopoda* (Fig. 1)

## 2. Methods

### 2.1. Study site

The Sevilleta National Wildlife Refuge (SNWR) contains extensive semi-arid grassland dominated by  $C_4$  perennial grasses (*B. gracilis*, *B. eriopoda*, *Sporobolus* spp., *Hilaria jamesii*, *Muhlenbergia* spp.) located on relatively level topography along the western edge of the Los Pinos Mountains, central New Mexico, USA. Common shrubs include *Atriplex canescens*, *Larrea tridentata* and *G. sarothrae*. Total vegetation cover in these grasslands (live plus litter) averages 60%.

Our study system is characterized by two relatively distinct growth periods in most years. A flush of annuals and  $C_3$  species occurs in March and April in response to winter rainfall and spring soil moisture. May and June are hot and dry, and followed by the summer monsoon (July–September). Winter rains have little impact on summer production because that soil moisture is depleted by the time the summer monsoon begins. Seasonal production is most strongly correlation with seasonal soil moisture rather than precipitation (Muldavin et al., 2008; Xia et al., 2009) because precipitation, especially during the monsoon, is often lost through evaporation and surface flow. Mean annual temperature from 1989 to 2007 at the Deep Well meteorological station located adjacent to our experimental site was  $13.2^\circ \text{C}$ , with a mean monthly temperature of  $1.6^\circ \text{C}$  in January and  $25.1^\circ \text{C}$  in July. This site receives approximately 250 mm of precipitation annually, about 60% of which is delivered in isolated, short duration storm events during the summer monsoon; the remainder arrives with winter frontal systems. However, the relative contribution of summer monsoon and winter rains varies considerably from year to year (Pennington and Collins, 2007).

Total soil N and C pools in these grasslands are small ( $20$  and  $200 \text{ g m}^{-2}$ , respectively) and N mineralization rates are low relative to mesic systems (Crenshaw et al., 2008; Kieft et al., 1998; Stursova et al., 2006; Zak et al., 1994). Total potential mineralizable N ranges from  $1.6$  to  $4.0 \text{ g m}^{-2} \text{ y}^{-1}$  (White et al., 2004). Atmospheric N deposition averages  $0.2 \text{ g m}^{-2} \text{ y}^{-1}$  but is increasing (Báez et al., 2007). From 1999 to 2004 aboveground net primary production (ANPP) in these grasslands averaged  $52 \text{ g m}^{-2} \text{ y}^{-1}$  (Muldavin et al., 2008), but ANPP increased to  $147.0 \text{ g m}^{-2} \text{ y}^{-1}$  during 2006 in response to unusually high monsoon rainfall (Xia et al., 2009).

### 2.2. Treatments

Our experimental design eventually will consist of three fully crossed factors (warming, increased winter precipitation, and N addition) in a completely randomized design, for a total of eight treatment combinations, with five replicates of each treatment combination, for a total of 40 plots. Each plot is  $3 \times 3.5 \text{ m}$ . All plots contain *B. eriopoda*, *B. gracilis* and *G. sarothrae*. Our nighttime

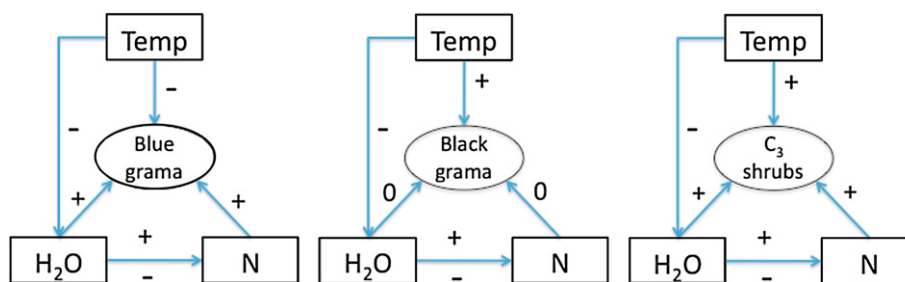


Fig. 1. Hypothesized effects of increased temperature, increased winter rainfall and increased N deposition on biomass of the Great Plains  $C_4$  dominant, *B. gracilis*, the Chihuahuan Desert  $C_4$  dominant, *B. eriopoda*, and  $C_3$  shrubs, such as *G. sarothrae*.

warming treatment, started in June 2006, is imposed using light-weight aluminum fabric shelters (mounted on rollers similar to a window shade) that are drawn across the warming plots each night to trap outgoing longwave radiation (Beier et al., 2004). The dataloggers controlling shelter movements are programmed to retract the shelters on nights when wind speeds exceed a threshold value (to prevent damage to shelters) and when rain is detected by a rain gauge or snow is detected by a leaf wetness sensor (to prevent an unintended rainout effect).

Based on long-term climate records, El Niño rains increase winter precipitation in our area by an average of 50%. In the future we will impose an El Niño-like rainfall regime each winter using an irrigation system and reverse osmosis water. El Niño rains will be added in 6 experimental storm events each winter that mimic actual El Niño winter-storm event size (four small, one intermediate and one large event each winter) and amount (50 mm). During El Niño years, as in the winter of 2006–2007, we use ambient rainfall and do not impose experimental rainfall events. Thus, our results for the first growing season are only analyzed for treatment effects of warming and N, since the rainfall treatment was not yet implemented. For N deposition, we added 2.0 g m<sup>-2</sup> y<sup>-1</sup> of N in the form of NH<sub>4</sub>NO<sub>3</sub> because NH<sub>4</sub> and NO<sub>3</sub> contribute approximately equally to N deposition at SNWR (57% NH<sub>4</sub> and 43% NO<sub>3</sub>; Báez et al., 2007). The NH<sub>4</sub>NO<sub>3</sub> was dissolved in 12 L of deionized water, equivalent to a 1 mm rainfall event, and applied with a backpack sprayer prior to the summer monsoon. Control plots received the same amount of deionized water.

### 2.3. Field measurements

Air and soil temperature were measured in each plot with copper constantan thermocouples positioned 20 cm above ground, and 2 and 10 cm below the soil surface in both grass-covered and soil/crust areas. Soil moisture in each plot was measured at 5 and 15 cm

beneath grass and soil interspace patches using 10 cm ECH<sub>2</sub>O probes buried horizontal to the surface. Soil N availability was measured from July through September using ion exchange membrane PRS<sup>sm</sup>-probes (WesternAg Industries, Calgary, Canada; Drohan et al., 2005) placed under grass and in interspace patches in each plot. Cover of all individual plants was recorded in two 1-m<sup>2</sup> permanent subplots in each treatment plot prior to the start of experimental treatments in February and May, and again in September 2006.

### 2.4. Analyses

We used one-way analysis of variance to determine if the warming treatment significantly affected air and soil temperature, and mean monthly soil moisture. We used two-way analysis of variance to determine the main effects and interactions of N addition and warming on soil N availability. Finally, following Fargione et al. (2007) we used repeated measures ANOVA with the Geisser and Greenhouse (1958) adjustment to quantify differences in pre-treatment cover and post-treatment cover increments for *B. eriopoda*, *B. gracilis* and *G. sarothrae* during the 2006 summer monsoon. All analyses were performed using JMP v.7.0.1 (SAS Institute, Inc., 2006).

### 3. Results

The warming treatment significantly elevated average nighttime temperature by 1.6, 4.3, and 1.7 °C during June, July and September 2006 (Table 1). Data for August 2006 were not available because of a datalogger failure. Warming also resulted in slightly elevated daytime temperatures in June and July, as well. Daytime warming was likely a function of heat transferred from the soil because soil temperatures at 2 cm were also elevated during the nighttime and morning throughout the growing season in both interspace patches and under grass patches. There was no effect of warming on soil temperature at 10 cm. Thus, the passive warming

**Table 1**

Effects of passive nighttime warming on air and soil temperature in a native northern Chihuahuan Desert grassland. Temperature was measured with copper constantan thermocouples at 20 cm above the soil surface and at 2 cm below the soil surface under patches of black grama (*Bouteloua eriopoda*) or under interspace patches. Morning = 08:00–12:00 h, Day = 13:00–16:00 h, Night = 01:00–04:00 h.

	Month	Period	Control				Warmed			
			Mean	Max	Min	Range	Mean	Max	Min	Range
Air temp	June	Day	38.4	52.0	22.5	29.5	39.2	59.2	22.7	36.5
	June	Morning	34.4	51.1	18.2	32.9	35.0	58.9	18.4	40.5
	June	Night	17.3	26.4	7.0	19.4	18.9	28.9	8.9	20.0
	July	Day	37.6	51.9	18.9	33.0	38.2	57.7	18.8	38.9
	July	Morning	34.1	50.8	18.4	32.4	34.2	57.2	18.6	38.6
	July	Night	20.0	27.3	12.9	14.5	24.3	22.0	13.7	10.7
	Sept	Day	28.9	35.8	19.0	16.9	29.0	36.6	18.8	17.9
	Sept	Morning	25.1	35.1	15.5	19.6	25.5	36.2	15.6	20.6
	Sept	Night	11.3	16.4	4.1	12.3	13.0	18.5	7.0	11.5
Bare soil 2 cm	June	Morning	37.5	61.2	19.4	41.7	38.8	65.0	19.9	45.1
	June	Night	22.2	31.6	13.7	17.9	25.3	34.3	16.0	18.3
	June	Day	44.1	62.5	26.8	35.7	44.9	65.4	26.3	39.2
	July	Morning	36.7	61.2	21.3	39.9	37.0	64.1	21.6	42.5
	July	Night	24.3	31.0	17.5	13.5	25.5	33.3	17.6	15.7
	July	Day	32.0	42.2	21.1	21.1	34.5	46.5	21.4	25.2
	Sept	Morning	25.5	43.3	14.7	28.7	26.9	45.4	15.9	29.6
	Sept	Night	16.8	24.9	11.0	13.9	19.3	26.3	15.4	10.9
Grass 2 cm	June	Day	42.9	59.4	28.0	31.4	42.7	64.0	25.6	38.4
	June	Morning	35.5	58.7	19.3	39.4	36.5	59.3	19.0	40.3
	June	Night	22.6	31.2	15.2	16.1	25.1	33.9	11.9	21.9
	July	Day	40.9	58.9	26.5	32.3	40.2	62.2	22.8	39.4
	July	Morning	34.6	57.4	21.4	36.0	35.0	58.8	19.9	39.0
	July	Night	24.5	30.8	18.3	12.5	25.6	33.1	15.4	17.7
	Sept	Day	29.5	44.0	20.5	23.5	30.4	46.2	20.2	26.0
	Sept	Morning	23.2	44.9	15.2	29.7	24.0	42.7	16.3	26.5
	Sept	Night	16.6	23.0	11.7	11.2	19.3	25.5	14.8	10.7

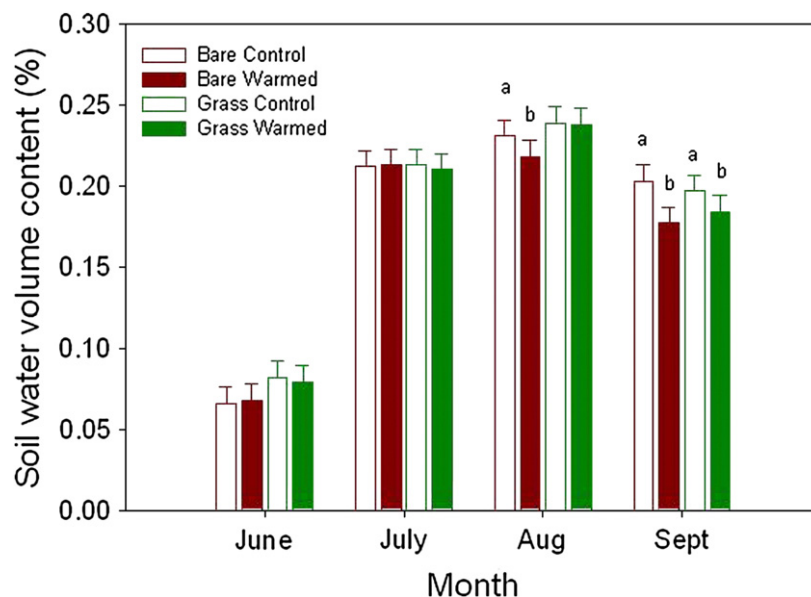


Fig. 2. Effect of nighttime warming on soil moisture 5 cm below the soil surface under grass canopies and interspace patches. Error bars are +2 s.e. Letters indicate significantly different values for each pairwise warmed vs. control comparison based on one-way ANOVA (Aug interspace warmed vs interspace control  $F_{1,32,020} = 501.0, P < 0.0001$ ; September interspace warmed vs. interspace control  $F_{1,7362} = 481.4, P < 0.0001$ ; September grass warmed vs. grass control  $F_{1,7398} = 254.0, P < 0.0001$ ).

mechanism provides an effective means of increasing both nighttime air and shallow soil temperatures during the growing season.

Rainfall during summer 2006 was 100% above the long-term average resulting in the largest seasonal monsoon since the Sevilleta LTER program started in 1989. In June, prior to the start of the 2006 monsoon season, all the sites were dry with a soil volumetric water content (VWC) below 10% while interspace patches were drier than soils under patches of grass with no apparent warming treatment effect (Fig. 2). In July, VWC increased to over 20% and was uniform across both location (interspace patch or grass canopy) and treatment (warmed or not). However, as the season progressed, warming had a significant drying effect on soil moisture first under interspace patches in August and then beneath both interspace patches and grass canopies in September.

Plant available soil nitrogen was significantly higher ( $P = 0.001$ ) beneath the grass canopy relative to interspace patches (Fig. 3). Fertilization significantly increased ( $P = 0.01$ ) total soil nitrogen availability beneath grass patches during the growing season. This was true for both  $\text{NH}_4$  (15% increase) and  $\text{NO}_3$  (28% increase). There was also a slight but not significant ( $P = 0.29$ ) tendency for higher total soil nitrogen in warmed plots compared to controls. This mostly reflected a 12% increase in soil  $\text{NO}_3$  availability.

At the end of the growing season, total live plant cover was 32% in control plots, 39% in N addition plots, 40% in warmed plots, and 41% in plots that were both warmed and fertilized. Total live plant cover increased significantly in response to nighttime warming ( $F = 5.35, P = 0.015$ ) (Fig. 4), but we did not find any significant effect of N on total cover, nor a warming by N interaction. Key species, however, responded differently to these environmental drivers (Fig. 5). Warming significantly increased the cover of *B. eriopoda* ( $F = 7.0, P = 0.003$ ) and cover of *G. sarothrae* tended to increase with warming, as well ( $F = 3.26, P = 0.064$ ), whereas cover of *B. gracilis* significantly increased ( $F = 5.29, P = 0.016$ ) in response to N addition, but not warming.

#### 4. Discussion

We are conducting a multi-factorial field experiment to determine the direct and interactive effects of increased nighttime

temperatures, N deposition, and eventually winter precipitation, on grassland community structure and ecosystem functioning. Our treatments are relatively subtle, (e.g.,  $2.0 \text{ g Nm}^{-2} \text{ y}^{-1}$ ,  $1.0\text{--}2.0 \text{ }^\circ\text{C}$  seasonal nighttime warming), yet they fall within the range of conditions predicted to occur in our region by the latter half of this century (Báez et al., 2007; IPCC, 2007; Pryor and Schoof, 2008). Because the passive warming treatment works by trapping heat radiating from the soil, our site, which experiences large temperature fluctuations, low cloud cover, and low humidity, is particularly amenable to this type of warming treatment. In addition, aridland soils are frequently N limited (Austin et al., 2004), yet N deposition is increasing regionally and locally (Báez et al., 2007; Fenn et al., 2003). Although warming is expected to favor southern species, such as *B.*

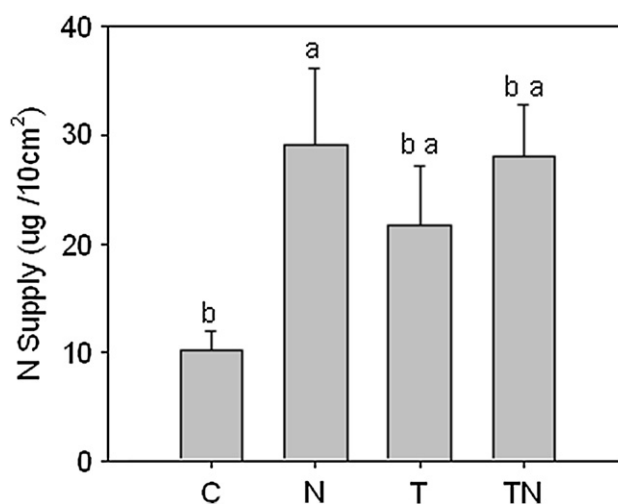
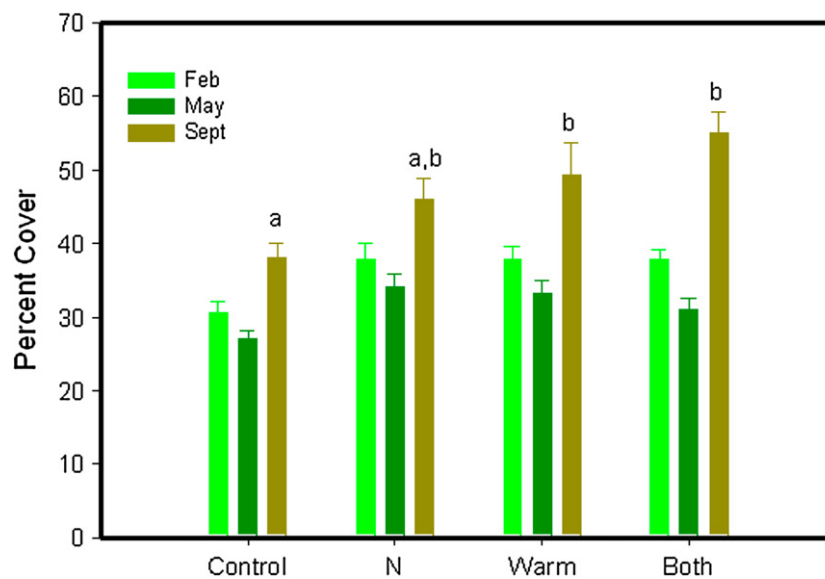


Fig. 3. Seasonal soil nitrogen supply as measured by Root Simulator Probes (Drohan et al., 2005). Nitrogen addition rates were  $2.0 \text{ g Nm}^{-2} \text{ y}^{-1}$  and nighttime temperatures were increased by  $1\text{--}2 \text{ }^\circ\text{C}$  during the growing season. Values are expressed as units of N per  $10\text{-cm}^2$  surface area of ion exchange membrane. C = Control, N = nitrogen addition, T = elevated nighttime temperature, TN = elevated nighttime temperature and nitrogen addition. Different letters indicate significantly different values among treatments based on ANOVA.



**Fig. 4.** Effect of nighttime warming and nitrogen (N) fertilization ( $2.0 \text{ g Nm}^{-2} \text{ yr}^{-1}$ ) on changes in total vegetation cover during the 2006 growing season based on cover estimates in February, May and September. Warming significantly increased total cover (warming\*time  $F = 5.35$ ,  $P = 0.015$ ) relative to ambient and N treatments based on repeated measures ANOVA.

*eriopoda* and eventually  $C_3$  shrubs such as *G. sarothrae* and especially *L. tridentata*, N deposition may favor northern species, such as *B. gracilis*, and potentially invasive species, as well (e.g., Brooks, 2003). How these contrary forces will interact over the long term to determine community composition is unknown. With continuing treatment, our experiment will provide the long-term data necessary to understand whether interactions among treatments ameliorate or amplify the short-term responses reported here.

Results of our treatments during the first monsoon season demonstrate that this arid grassland can respond rapidly to these subtle environmental changes. We found that our passive warming treatment elevated minimum nighttime temperatures by a seasonal average of  $2.5^\circ\text{C}$  and that the warmer nighttime air translated into warmer morning (from 08:00 to 12:00 hrs) soil temperatures at 2 cm depth by a seasonal average of  $0.7^\circ\text{C}$ , a time period when moisture stress should be minimal (Table 1). Passive nighttime warming at four study sites across Europe caused an increase in mean daily minimum temperatures of  $0.5\text{--}1.2^\circ\text{C}$  (Beier et al., 2004). Thus, our results are consistent with other studies showing that passive warming effectively increases both nighttime and morning minimum air temperatures.

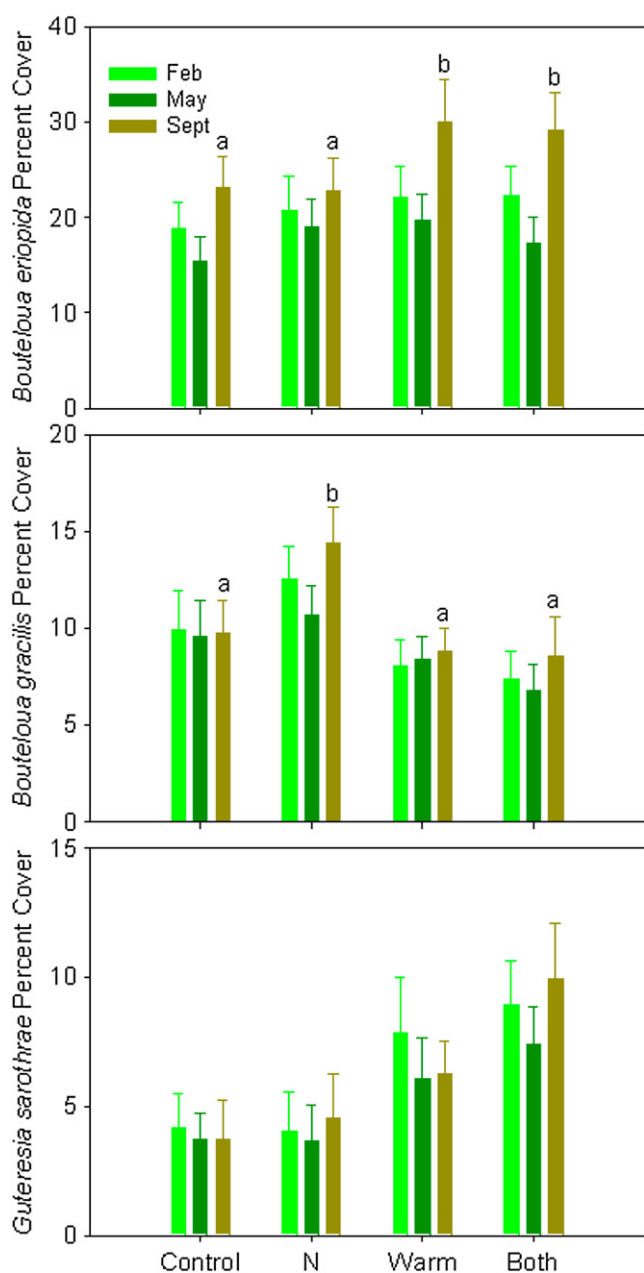
Elevated nighttime temperatures at our site resulted in a significant decrease in shallow soil volume water content (Fig. 2) later in the monsoon season when most annual aboveground net primary production occurs at our site (Muldavin et al., 2008; Pennington and Collins, 2007). In the European studies the differences in soil temperature between treatment and control plots were also maintained throughout the day, and the differences in air temperatures were partially maintained throughout the day (Beier et al., 2004), similar to our findings. Thus, although the increase in air temperatures was greatest at night, the heat retained in soils was found to affect daytime temperatures as well. These generally warmer environmental conditions may favor Chihuahuan Desert species over those commonly occurring in Great Plains grasslands.

Nitrogen fertilization significantly increased plant available N in our experiment (Fig. 3) as well as aboveground net primary production (Fig. 4). Nitrogen deposition has been shown to increase aboveground net primary production and decrease plant species richness in many herbaceous communities (Clark and Tilman, 2008; Stevens et al., 2004; Suding et al., 2005). Responses are contingent

upon species composition (Pennings et al., 2005) as well as abiotic constraints, particularly soil cation exchange capacity (Clark et al., 2007) and soil moisture availability in xeric systems (Collins et al., 2008; Lauenroth et al., 1978). Chalcraft et al., (2008) found that N-enrichment increased beta diversity in xeric systems but decreased beta diversity in mesic systems. During wet years, N-fertilization increased forb richness and ANPP on plots in the shortgrass steppe of Colorado (Lauenroth et al., 1978) and the northern Chihuahuan Desert of New Mexico (Collins, unpublished). In addition, production of *B. gracilis* nearly doubled whereas *B. eriopoda* showed no response to small additions of N ( $2.0 \text{ g m}^{-2} \text{ yr}^{-1}$ ) at the Sevilleta (Báez et al., 2007). Thus, the effects of N addition at the Sevilleta are contingent upon both biotic and abiotic factors.

Nighttime warming and atmospheric N deposition may interact to have important direct and indirect consequences for aridland plant communities. Overall, we found that warming slightly increased N availability and significantly increased aboveground net primary production. Yet, not all dominant species were affected equally (Fig. 5). Warming led to an increase in the Chihuahuan desert grass *B. eriopoda* and the  $C_3$  shrub *G. sarothrae*, whereas N fertilization led to an increase in cover of the Central Plains species *B. gracilis*. This is consistent with previous research showing that increased average annual nighttime temperature since 1970 in shortgrass prairie was correlated with a decrease in dominant grasses and an increase in invasive forbs (Alward et al., 1999). Warming plus N fertilization also had additive effects on ANPP and species richness in serpentine grassland (Shaw et al., 2002; Zavaleta et al., 2003). Together, these results suggest that forbs and shrubs are likely to increase at the expense of  $C_4$  grasses in the northern Chihuahuan Desert as temperature continues to rise and atmospheric N deposition increases.

Despite the decrease in shallow soil moisture, we found that warming increased aboveground net primary production at our site. This increase in ANPP may have occurred because the unusually large monsoon rainfall in 2006 counteracted the drying effect of higher air and soil temperatures. In the European cross-site nighttime warming study aboveground plant biomass increased 15% (Peñuelas et al., 2004), rate of litter decomposition increased 22% (Emmett et al., 2004), soil respiration increased 19% (Emmett et al., 2004), and N loss increased 74% (Schmidt et al., 2004),



**Fig. 5.** Effect of nighttime warming and nitrogen fertilization ( $2 \text{ g Nm}^{-2} \text{ yr}^{-1}$ ) on changes in cover of blue grama (*B. gracilis*), black grama (*B. eriopoda*) and  $\text{C}_3$  shrubs (e.g., *G. sarothrae*) during the 2006 growing season based on cover estimates in February, May and September. Warming significantly increased cover of *B. eriopoda* (warming\*time  $F = 7.00$ ,  $P = 0.003$ ) whereas N addition significantly increased cover of *B. gracilis* (time\*N  $F = 5.29$ ,  $P = 0.016$ ) and marginally significantly increased cover of *G. sarothrae* ( $F = 3.26$ ,  $P = 0.064$ ) based on repeated measures ANOVA.

demonstrating that this level of warming has important ecological effects that may not be directly related to soil volume water content. Moreover, higher N losses, particularly via ammonium volatilization in high pH soils like those at the SNWR, could potentially counteract the fertilization effects, leaving warming and its indirect effects on soil moisture as the key drivers of environmental change in this ecosystem. Together, our results highlight the complex responses to be expected from the interaction of multiple global change drivers in this aridland system.

By the end of this century, global mean temperatures are expected to increase by  $1.4\text{--}5.8^\circ\text{C}$ , inorganic N deposition is expected to increase by  $2.0\text{--}6.0 \text{ g m}^{-2} \text{ yr}^{-1}$ , and most models predict that El

Niño conditions will increase or stay at the current elevated level (Han and Roads, 2004; IPCC, 2007; Leung et al., 2004; Sala et al., 2000; S.R.A.G., 2000). Regional predictions for southwestern North America are for increases of  $1\text{--}4^\circ\text{C}$  warming,  $4.0 \text{ g m}^{-2} \text{ yr}^{-1}$  of N deposition and increased winter precipitation due to El Niño. Arid ecosystems, which cover approximately 33% of terrestrial land, are considered to be highly sensitive to increased interannual climate variability, atmospheric N deposition and precipitation intensity and amount (Diffenbaugh et al., 2008). However, the effects of these impacts on species interactions and changes in species composition are uncertain. Our long-term nighttime warming, winter precipitation, and N deposition experiment is designed to address the individual and interactive effects of these key global environmental drivers on an aridland ecosystem at the interface of grassland and shrubland community-types. Preliminary results show that these aridland ecosystems are highly and rapidly responsive to these subtle but pervasive drivers of global environmental change.

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