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Grassland Vegetation Changes and Nocturnal Global Warming

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Global minimum temperatures (T_{MIN}) are increasing faster than maximum temperatures, but the ecological consequences of this are largely unexplored. Long-term data sets from the shortgrass steppe were used to identify correlations between T_{MIN} and several vegetation variables. This ecosystem is potentially sensitive to increases in T_{MIN}. Most notably, increased spring T_{MIN} was correlated with decreased net primary production by the dominant C_4 grass (*Bouteloua gracilis*) and with increased abundance and production by exotic and native C_3 forbs. Reductions in *B. gracilis* may make this system more vulnerable to invasion by exotic species and less tolerant of drought and grazing.

There is general consensus that there is an anthropogenic warming signal in the long-term climate record (*1*). Over land, this is primarily due to average annual minimum temperatures (T_{MIN}) having increased at twice the rate of maximum temperatures (T_{MAX}) (*1*, *2*). At the global scale, these increases in T_{MIN} are related to increases in global cloudiness (*1*, *3*). Experiments with agricultural plants and insect pests suggest important roles for T_{MIN} in influencing plant and insect development (*4*, *5*). However, there has been little research on the consequences of elevated T_{MIN} for natural ecosystems (*6*, *7*). If elevated T_{MIN} leads to longer growing seasons, net primary production and carbon sequestration may increase as a consequence (*8*). However, the opposite may occur if elevated T_{MIN} leads to increased plant and microbial nocturnal respiration rates without a compensatory increase in photosynthesis. Additionally, elevated T_{MIN} could shift competitive interactions among C_3 (cool-season) and C_4 (warm-season) plants.

It is important to identify features of ecosystems that are sensitive to changes in T_{MIN}. To date, most modeling efforts and experimental manipulations investigating ecosystem responses to climate change have assumed that future warming will occur primarily during the day or uniformly over the diurnal cycle. This assumption clearly is not valid on a global level nor at most regional scales (*2*). Furthermore, there is no a priori reason to assume that ecosystems will respond similarly to changes in T_{MIN} and T_{MAX}. To investigate potential ecological consequences of elevated T_{MIN}, we examined a 23-year data set for correlations between temperature [T_{MIN}, T_{MAX}, and mean annual temperature (T_{AVE}) ($T_{\mathrm{AVE}} = (T_{\mathrm{MIN}} + T_{\mathrm{MAX}})/2$)] and both the abundance and aboveground net primary productivity (ANPP) of several key plant species and functional groups found at the Central Plains Experimental Range (*9*) in northeastern Colorado.

We identified seasonal and annual trends in T_{MIN} and T_{MAX} to determine whether asymmetric diurnal temperature increases held true for this site (*10*). The densities of most species were determined by counting all individuals within permanently marked quadrats (*11*). Harvests at time of peak standing crop were used as estimates of ANPP (*12*, *13*). Plants in the shortgrass steppe are commonly water-limited, and variation in precipitation could obscure plant responses to gradually changing temperatures (*9*, *14*). Therefore, we included annual and seasonal precipitation totals, in addition to annual and seasonal minimum and maximum temperatures, as variables for stepwise regression model selection (*15*). We constructed linear models to evaluate significant correlations between these variables and ANPP or plant species density (*16*).

Mean annual temperatures (T_{AVE}) have increased by an average of 0.12°C year^{-1} at this site since 1964 ($P = 0.0001$, $R^2 = 0.52$). During this period, T_{MAX} increased 0.085°C year^{-1} (Fig. 1A), whereas T_{MIN} increased 0.15°C year^{-1} (Fig. 1B). We limited further analyses of temperature to the period beginning in 1970, when standardized monitoring of vegetation density was initiated. Since 1970, T_{AVE} has risen over 1.3°C, largely due to a significant increase in T_{MIN} of 0.12°C year^{-1} ($P = 0.003$; $R^2 = 0.44$). However, there was no significant trend for T_{MAX} ($P = 0.49$). Averages of seasonal minimum temperatures since 1970 also exhibited significant warming, with similar trends in winter (0.17°C year^{-1}, $P = 0.0013$, $R^2 = 0.40$), spring (0.16°C year^{-1}, $P = 0.0007$, $R^2 = 0.43$), and summer T_{MIN} (0.12°C year^{-1}, $P = 0.004$, $R^2 = 0.33$). No significant trends were detected in fall T_{MIN} ($P = 0.64$, $R^2 = 0.01$). Annual precipitation (Fig. 1C) varied from 230 to 480 mm and has also exhibited a significant linear increase since 1970 (6 mm year^{-1}, $P = 0.007$, $R^2 = 0.30$). However, there were no significant correlations between annual or seasonal T_{MIN} and annual or seasonal precipitation ($P > 0.1$).

Since 1983 (*12*), ANPP of *Bouteloua gracilis*, the dominant C_4 grass of the shortgrass steppe, declined over time (–12.2 g m^{-2} year^{-1}; $P = 0.002$; $R^2 = 0.78$), and was negatively correlated with average spring T_{MIN} (Fig. 2A). ANPP of the most abundant C_3 forb, *Sphaeralcea coccinea*, was negatively correlated with winter T_{MIN} (Fig. 2B). In contrast, ANPP of

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both the C_3 sedge *Carex eleocharis* (Fig. 2C) and of all C_3 forbs combined (Fig. 2D) was positively correlated with fall and summer T_{MIN}, respectively. Plant density was also correlated with T_{MIN}. Exotic forb density was positively correlated with spring T_{MIN} (Fig. 2E), whereas the density of the C_3 grass *Sitanion hystrix* was positively correlated with winter T_{MIN} (Fig. 2F).

The relationships between T_{MIN} and vegetation revealed by these analyses highlight potential effects of climate change on natural ecosystems. This shortgrass steppe site has experienced increases in T_{MIN} over the past few decades that are similar to trends found by others at larger spatial and temporal scales (*2*). For each 1°C increase in average spring T_{MIN}, ANPP of the dominant grass decreased by nearly one-third (Fig. 2A). Because this one species (*B. gracilis*) represents an average of 66% of total ANPP and nearly 90% of the total basal cover (*9*), this result has serious implications for both the structure and function of the shortgrass steppe, if its productivity is causally related to T_{MIN}. *Bouteloua gracilis* is a drought- and grazing-tolerant species that makes up as much as 40% of the diet of cattle on the shortgrass steppe (*17*). A major reduction in this species could have substantial consequences for livestock production if it were not replaced by other palatable species. Also of concern is the increase in exotic forb density, because invasive exotic plants are already recognized as a threat to the structure and function of numerous natural ecosystems (*18*); increasing T_{MIN} may exacerbate this threat.

Elevated T_{MIN} may have direct, but counterbalancing, effects on ANPP and the abundance of plants through mechanisms such as increased rates of carbon assimilation due to warmer mornings, accelerated carbon loss through increased rates of respiration due to warmer nights, and differential effects on C_3- versus C_4-photosynthesizing plants. Positive correlations between T_{MIN} and both forb ANPP and exotic plant densities (Fig. 2, D and E) support the hypothesis that increased production will be observed in some plants, and the negative correlation between T_{MIN} and *B. gracilis* ANPP (Fig. 2A) is consistent with the increased respiration hypothesis. In addition to direct effects on rates of plant physiological processes, increases in T_{MIN} could affect plant growth indirectly through changes in the length of growing seasons through increased duration of the frost-free period or changes in the availability of soil water. An increase in season duration would be expected to primarily benefit cool-season plants that are growing most rapidly, and preemptively consuming resources, early and late in the growing season. The positive correlation between spring T_{MIN} and exotic C_3 forbs (Fig. 2E) and between fall T_{MIN} and *C. eleocharis* (Fig. 2C) is consistent with this hypothesis.

Some of the correlations could be the result of effects of elevated T_{MIN} on biotic interactions. Some plants may be increasing (Fig. 2, C through F) in response to the decrease in *B. gracilis* ANPP and the consequent increase in availability of space, nutrients, or water, rather than because of any direct effects of elevated T_{MIN} on these plants. Alternatively, if increased T_{MIN} benefits the growth of C_3 plants (Fig. 2, C through F), this could subsequently result in negative effects on the C_4 *B. gracilis* (Fig. 2A). Such a scenario might occur if cool-season plants were able to reduce available soil moisture before the period of rapid growth of warm-season plants. Intertrophic interactions might also be affected. If increased developmental and consumption rates by insects in response to elevated T_{MIN} (*4*) are common, increased herbivory could alter plant responses to climate change.

Without a clear causal link, there is no compelling evidence to eliminate factors other than increased T_{MIN} as causes of observed changes in ANPP and plant densities. Unfortunately, most experiments and models designed to investigate climate change effects have focused on manipulating T_{MAX} or have assumed equal contributions by T_{MIN} and T_{MAX} toward achieving an increase in T_{AVE}. The outcomes of such experiments may not realistically predict the future structure and

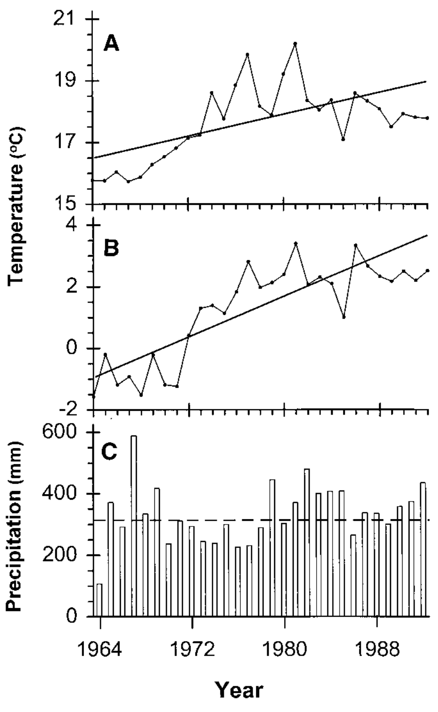

Fig. 1. Summary of climate data for the Central Plains Experimental Range site. (**A**) Average annual T_{MAX}. The heavy line is the significant linear trend in T_{MAX} [$T_{\mathrm{MAX}} = -150 + 0.085$ (year); $P = 0.001$; $R^2 = 0.36$]. (**B**) Average annual T_{MIN}. The heavy line is the significant linear trend in T_{MIN} [$T_{\mathrm{MIN}} = -299 + 0.15$ (year); $P = 3.3 \times 10^{-8}$; $R^2 = 0.68$]. (**C**) Total annual precipitation. The horizontal dashed line identifies the average annual precipitation (323 mm) at this site since 1939.

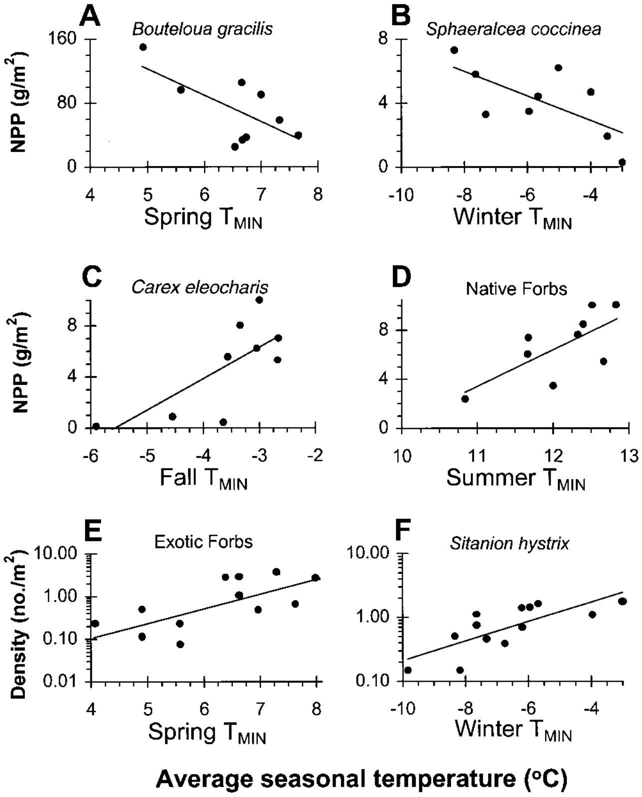

Fig. 2. Vegetation correlations with seasonal average T_{MIN}. (**A**) *Bouteloua gracilis* and spring T_{MIN} [ANPP = 288 – 33.1 (T_{MIN}); $P = 0.039$; $R^2 = 0.48$]. (**B**) *Sphaeralcea coccinea* and winter T_{MIN} [ANPP = 0.149 – 0.77 (T_{MIN}); $P = 0.038$; $R^2 = 0.48$]. (**C**) *Carex eleocharis* and fall T_{MIN} [ANPP = 13.6 + 2.44 (T_{MIN}); $P = 0.019$; $R^2 = 0.56$]. (**D**) Native forb (herbaceous dicots) and summer T_{MIN} [ANPP = –29.5 + 2.99 (T_{MIN}); $P = 0.028$; $R^2 = 0.52$]. (**E**) Exotic (nonnative) forb density and spring T_{MIN} [density = $0.008e^{0.71(T_{\mathrm{MIN}})}$; $P = 0.014$; $R^2 = 0.46$]. (**F**) *Sitanion hystrix* density and winter T_{MIN} [density = $6.4e^{0.33(T_{\mathrm{MIN}})}$; $P = 0.002$; $R^2 = 0.57$]. Methods for obtaining density and ANPP data are described in (*11*, *12*).

dynamics of ecosystems if climate change continues to be manifested primarily as increases in T_{MIN}. There is a need for experiments that define the relationship between T_{MIN}, plant abundance, and ANPP and that identify mechanisms behind the relationship.

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13. The following species and functional groups were represented in the analyses: *Artemesia frigida*, *Aristida longiseta*, *Bouteloua gracilis*, *Carex eleocharis*, *Kochia scoparia*, *Opuntia polyacantha*, *Sitanion hystrix*, and *Sphaeralcea coccinea*, warm-season grasses, cool-season grasses and sedges, annual grasses, all grasses and sedges combined, forbs (native herbaceous dicots), exotic (nonnative) forbs, dwarf shrubs, and total biomass from all species. Species richness was also analyzed.
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16. Significant correlations were identified with a stepwise model-building routine [SAS, version 6.11 (SAS Institute, Cary, NC, 1996); PROC REG with STEPWISE method; enter and exit $\alpha = 0.1$]. Plant density values were log-transformed. We report the single factor that explained the most variation in each species' responses.
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