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UV Radiation Effects on Plant Growth and Forage Quality in a Shortgrass Steppe Ecosystem¶

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ABSTRACT

Levels of UV were manipulated in a native shortgrass steppe using open-sided structures with tops that either passed or blocked wavelengths shorter than ~370 nm. Precipitation was controlled to create a drought or a very wet year. Subplots were either nondefoliated or defoliated to simulate grazing by livestock, which is the primary land use. Plant community productivity and forage quality were assessed in response to the two climate change variables (UV, precipitation) and grazing stress. Productivity and seasonal standing biomass of the dominant grass species were negatively affected by passing *versus* blocking UV, but only in the dry year. Another species was negatively affected by passing UV in the wet year, indicating the potential for future shifts in species composition. Forage quality for ruminants increased when UV was passed compared with blocked, as determined by *in vitro* digestible dry matter, depending on species and precipitation. Nitrogen concentrations and soluble and fiber components of vegetation also displayed some UV effects, but they were generally small and depended on species, season or amount of precipitation (or all). Grazing treatment had large positive effects on current-year productivity only in the wet year and some small positive effects on quality in both wet and dry years. Interactions between UV and grazing treatment were not observed.

INTRODUCTION

Past and future climate change includes many variables such as CO_2 enrichment, increased temperatures, and altered precipitation and surface UV radiation levels. These changes in climate and abiotic conditions can interact with current uses of, and biotic stressors to, ecosystems. Alterations in surface UV radiation may result from ozone reduction or changes in atmospheric particulates and cloudiness (or both). Fewer than 5% of the studies of UV effects on plants have been conducted under field conditions and most of these used agricultural croplands (1). The shortgrass steppe of North America is native grassland situated at a relatively high altitude (1.65 km), where semiarid conditions result in a sparse canopy and high photosynthetically active radiation (PAR) intensities at ground level. Grazing by cattle is the primary land use of shortgrass steppe, and droughts are frequent (2). We studied potential interactions between UV, grazing and precipitation on productivity, decomposition and arthropod consumers of a native shortgrass steppe in Colorado. This report focuses on primary productivity of the community, and the quality of the material produced for ruminants during 2 years of study in which precipitation was manipulated to create a very wet and a drought year.

UV can affect ecosystems directly and indirectly. Direct effects can be physiological damage to plants, consumers and microorganisms, increased production of secondary compounds that screen UV and photodegradation effects on decomposition of plant litter (1,3). Indirect effects are feedbacks on ecosystem structure and function through many pathways, which include altered competitive relationships among species, biogeochemical cycles and carbon budgets. The direct effect of UV on plant production is generally negative and small (4). However, ecosystems are complex and positive production responses to UV have been reported. UV can in some cases reduce drought stress in plants and increase plant production through several potential water conservation and stress tolerance mechanisms (5–8), although the interactive effects of the two stresses have also been reported to be neutral (9–11) or negative (12,13). Drought-tolerant species may sometimes also be more tolerant of UV radiation (14,15).

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Abbreviations: ANPP, aboveground net primary production; ANOVA, analysis of variance; IVDDM, *in vitro* digestible dry matter; PAR, photosynthetically active radiation.

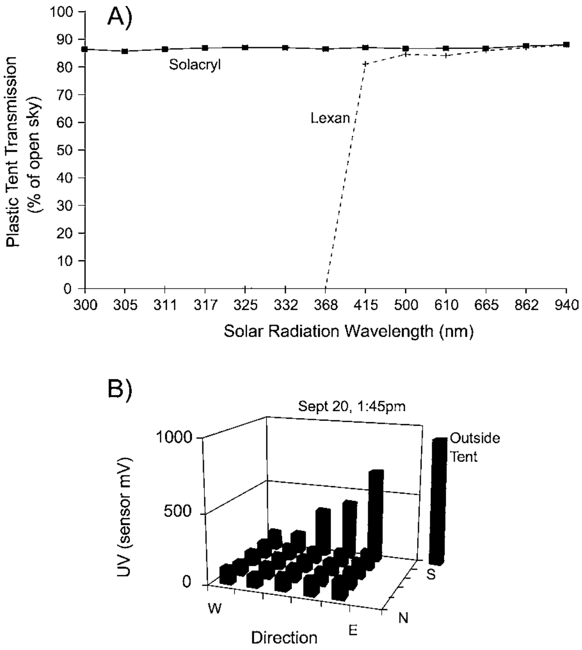

Figure 1. (A) Solar radiation wavelength transmission by the two types of plastic used over vegetation plots to pass or block UV in native shortgrass steppe ecosystem. (B) An example of UV edge effects under a test tent, where a sensor was moved throughout the plot at ground level. Area represented by the outside bars on all sides was not used for sampling. Part A of the figure is on the basis of measurements with sensors directly under the two plastic materials (UV block or UV pass) and represents transmission, whereas part B are measurements with sensors at ground level that allowed UV to enter through open sides of the structures with UV block material at roof level and represents the proportion not transmitted.

Of particular economic and ecological significance for grazing systems is the potential for indirect negative effects of UV through reduced plant tissue quality for consumers due to enhanced production of plant secondary compounds. An increased production of secondary compounds with UV can be common and relatively large compared with general production responses (4), and reductions in soluble protein content have also been reported (16,17). Again, however, positive responses to UV in tissue quality parameters may also occur (18,19). Most studies on the effects of UV on herbivores have been directed at arthropods (20–23), with relatively little focus on large ruminant herbivores. Ruminants differ from invertebrate and other mammalian herbivores because of microbial processing of forage in the rumen. Ruminants cannot always increase intake in response to poor quality forage but may become bulk-limited when fiber components are high and nutrients such as nitrogen are low. Rate and extent of digestion and physical breakdown can restrict passage from the rumen, reducing further intake. Soluble and fiber components and nitrogen concentrations of forages are important factors in the capacity of a rangeland to sustain domestic and wild ruminant species. Hemicellulose and cellulose of the fibrous fraction are potentially digestible but rate limiting, the degree of which depends on encrustation by lignin, the availability of nitrogen and the rate of particle-size breakdown (24). Lignin is virtually indigestible by the ruminant. Rate of passage in the ruminant is complex, but in general and in most cases, the higher the digestibility and the lower the lignin, the higher the rate of passage. The digestibility of a forage or diet integrates over other mineral nutrient compositions or limitations as well as over concentrations, ratios and structure of carbon and nitrogen in an index of the potential for microbial breakdown but does not account for physical breakdown processes such as mastication. In this study, we assess forage production and quality responses to UV, grazing and precipitation treatments through analyses of soluble and fiber fractions, nitrogen concentrations and *in vitro* digestibility of plant species growing in a native shortgrass steppe ecosystem.

MATERIALS AND METHODS

Experimental site and design. The study site is a 50 m by 85 m fenced area previously grazed by cattle at the Central Plains Experimental Range (40°49′N, 104°46′W) in north central Colorado. Mean annual precipitation is 321 mm (standard deviation 98 mm), of which 71% occurs during the May through September growing season (2). Soil at the site is a Remmit fine sandy loam classified as Ustollic camborthids. Total vegetative basal cover is typically 25–35% (25). Grazing by cattle is the dominant land use of native shortgrass steppe (40% of region), with intensities generally ranging from 50% to 65% annual removal of aboveground plant production.

A split-plot experimental design comprised 10 replicate blocks, each with a separate pass and a block UV treatment plot. Each square 1.4 m^2 plot was divided into a western and an eastern half that was randomly assigned as defoliated or nondefoliated (grazing) treatments. A precipitation treatment simulating a drought year was applied to all plots the first year (2001), and very wet year was simulated the second year (2002). Details of each of the three treatments follow.

Frames of 40 cm height were constructed with 1.9 cm square metal tubing over each plot, covered only on top with either Lexan (UV block treatment) (GE Plastics, Detroit, MI) or Solacryl (UV pass treatment) (Polycast, Stamford, CT) solid transparent sheets and elevated slightly in the middle in the north–south direction to shed water. The UV block material blocked all radiation from 290 to 368 nm and had an average 85% transmission of radiation from 415 to 940 nm, which spans PAR (Fig. 1A). The UV pass material passed an average of 87% of radiation for all wavelengths from 300 to 940 nm, uniformly across all wavelengths.

Additional UV block and UV pass structures were constructed for monitoring UV and natural precipitation edge effects to determine a quadrat size in the middle of the plots for subsequent sampling and to quantify inside and outside temperature differentials. Within-plot variation in precipitation and UV radiation was assessed by rainfall gauges sunk to ground level and by soil moisture time domain reflectometer probes located at different positions along grids or by moving a UV-B-1 broadband meter with 280–360 nm spectral response (26) throughout grid positions *versus* open sky. We determined that a 0.42 m^2 usable plot area under a total covered plot area of 1.4 m^2 allowed a liberal amount of edge to minimize incoming natural precipitation. A nonwatered test tent clearly confirmed this because edges remained green whereas the central area eventually turned brown. UV edge effect measurements were taken on clear-sky days, during different months of the year and different times of the day (Fig. 1B). For eight periods sampled, the UV block treatment blocked an average of 86% of UV levels outside the structures within the area used for sampling, with a range for sampling periods from 73% to 93%. The inside–outside air-temperature differential was low at an average of 0.3°C, as measured in the center of plots.

Wet and drought year precipitation scenarios were derived for the period when rain rather than snow is received (sum of April through October) by ordering (sorting) precipitation data of all years from 1939 through 2000 from lowest to highest and choosing the 14th driest and 15th wettest year (*i.e.* one-eighth in on the tails of the distribution). The dry year simulation was on the basis of the 1970 precipitation data, and the wet year was of 1961. Weekly sums of precipitation for each of the 2 years were calculated and applied weekly by metered, hand-held hose spray wand from a mobile water tanker. The dry treatment was simulated the first year and the wet the second year. Conditions other than precipitation that may vary between years may also be a factor in what we will term the wet and dry year treatments, but in this semiarid environment, the overwhelming control on otherwise similarly disturbed communities is precipitation (2). Amounts applied for the April–October period for wet and dry treatments were 340 mm and 165 mm, respectively, compared with approximately 260 mm for an average year. Snow was not controlled under the plots but blows freely under the structures in this windy environment and is only a small amount

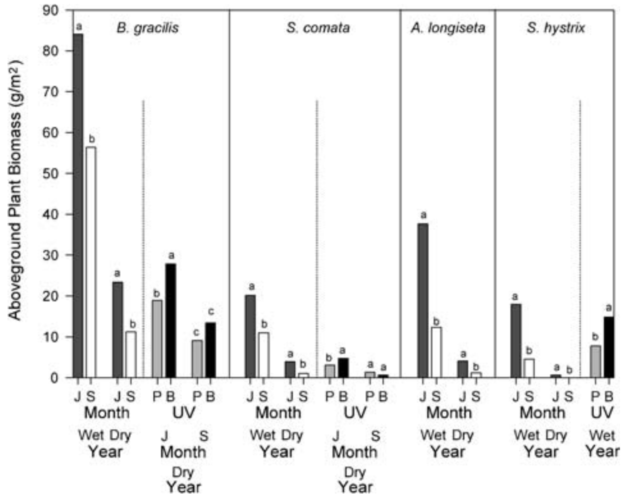

Figure 2. Aboveground plant biomass of *B. gracilis*, *S. comata*, *A. longiseta*, and *S. hystrix* in July (J) and September (S) of the wet year (2001) and dry year (2002) for UV pass (P) and UV block (B) treatments. Different letters above the bars indicate significant differences at the $P = 0.05$ level.

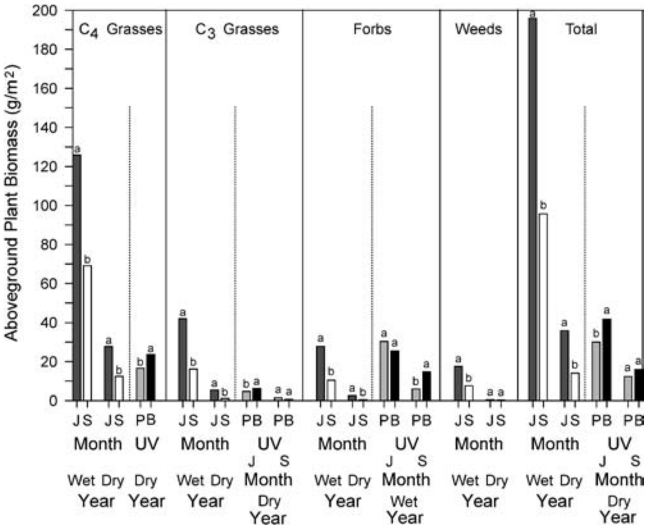

Figure 3. Aboveground plant biomass of C_4 and C_3 grasses, forbs, weeds and total vegetation in July (J) and September (S) of the wet year (2001) and dry year (2002) for UV pass (P) and UV block (B) treatments. Different letters above the bars indicate significant differences at the $P = 0.05$ level.

of annual precipitation, much of which sublimes and is not effective in soil water recharge.

Defoliated sides of the inner, usable plot areas were clipped during each early July, and both sides were harvested in each September at peak standing crop. This provides green (July clip) and senescent (September clip) material for chemical analyses, a comparison of grazed and ungrazed tissue quality in September and also allows assessment of the capacity for compensatory regrowth after grazing and the aboveground net primary production (ANPP) of grazed and ungrazed treatments. The sum of the two seasons' biomasses yields an estimate of grazed ANPP, and peak-standing current-year growth yields an estimate of ANPP of ungrazed treatment. All clipped biomass was sorted by species and for ANPP purposes is live plus recent dead without old-standing dead material.

Sample processing. Plant material was dried at 55°C in a forced-draft oven, weighed and ground in a Wiley mill. Subsamples were analyzed for total carbon and nitrogen using a C/N combustion analyzer (PDZ Europa Ltd., Cheshire, England) and for cell solubles, hemicellulose, cellulose and lignin by the neutral detergent fiber, acid detergent fiber and sulfuric-acid lignin fractionation method modified for block refluxing and without sodium sulfite (27,28). All analyses were performed on the three most abundant species in the wet year (*B. gracilis*, *S. comata*, and *A. longiseta*) and on the dominant species (*B. gracilis*) and a combined sample of all other species in the dry year because drought resulted in low growth and insufficient sample size. Additional subsamples were ashed (minteralized) at 550°C for correction of weights and chemical analyses to an organic matter basis.

Inoculum for *in vitro* digestible dry matter (IVDDM) analyses was collected from a fistulated cow maintained on an exclusively grass–hay diet for 1 week before collection, with feed removed 12 h and water removed 3 h before rumen pumping. Precautions in handling rumen fluid necessary to maintain microbial activity in transit to the lab and methods of preparing and delivering the inoculum were according to those described in Milchunas and Baker (29; strain-layer method). IVDDM was run according to the two-stage, 96 h method (30) (a 48 h microbial digestion that simulates breakdown of forage in the rumen, followed by 48 h acid pepsin stage that simulates lower gut digestion). Test tubes were maintained in large water baths at 39°C and kept anaerobic by flushing with CO_2 before closing with one-way valves that allow microbial gases to escape. There is a good relationship between IVDDM and *in vivo* digestible dry matter and a close 1:1 relationship between digestible dry matter and digestible energy for a variety of domestic and wild ruminants (29).

Statistical analyses. Statistical analysis was a split-plot design with UV as the whole plot and grazing treatment as the subplot and grazing crossed with UV treatment. Year was not a factor in the design because each year was analyzed separately because of differences in variances of means in the very wet compared with the very dry year. This design was for September samples on both grazing treatments, and for ANPP data that was for September ungrazed treatment *versus* July weights added to September weights for the grazed treatment. A second design, as above except without grazing, but including ''season'' as a factor, assessed July standing crop *versus* September regrowth for the grazed treatment. SAS Proc-Mixed was used for analysis of variance (ANOVA), and Tukey's honestly significant differences were calculated as the means separation test at the $P < 0.05$ or $P < 0.01$ levels of significance, depending on the ANOVA results.

RESULTS

Grasses are the dominant plant life form of the shortgrass steppe, and four species were sufficiently abundant on the plots for statistical analyses of seasonal standing biomass and annual production. Significant effects of UV pass *versus* UV block treatments were observed for three of four species, but effects were not consistent for all sampling times or all species (Fig. 2). *Bouteloua gracilis* (a C_4 grass and the dominant species) and *Stipa comata* (C_3 grass) showed a significant decrease in standing biomass with UV pass compared with UV block treatment, but this occurred only during the dry year and not during the wet year and in July but not in September. The biomass of *Sitanion hystrix* (C_3 grass) was also negatively affected by passing UV, but this occurred in the wet year, with insufficient biomass produced during the drought year to test statistically. *Aristida longiseta* (C_4 grass) did not respond to the UV treatments. Drought greatly reduced aboveground plant standing biomass of all species compared with the very wet year. Regrowth relative to July biomass, an indicator of ability to tolerate grazing, was greatest for *B. gracilis*, followed by *S. comata*, *A. longiseta* and *S. hystrix*.

Data for all species sampled were compiled into functional groups and total biomass and some significant UV treatment effects were observed. UV pass compared with block UV treatment reduced C_4 grass biomass in the drought year but not in the wet year (Fig. 3). C_3 grass biomass was also reduced in the drought year but only in July. UV pass treatment reduced standing biomass of forbs in the wet year in September, but there was insufficient forb biomass in the drought year to analyze statistically. No significant UV treatment effects were observed for species

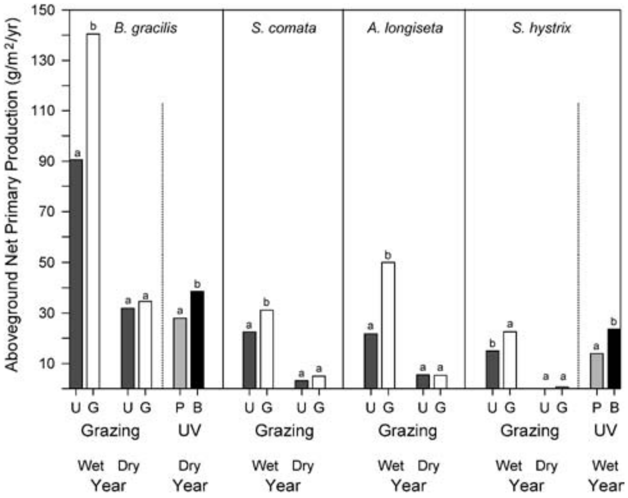

Figure 4. ANPP of *B. gracilis*, *S. comata*, *A. longiseta* and *S. hystrix* in wet (2001) and dry (2002) years for UV pass (P) and UV block (B) treatments and grazed (G) and ungrazed (U) treatments. Different letters above the bars indicate significant differences at the $P = 0.05$ level.

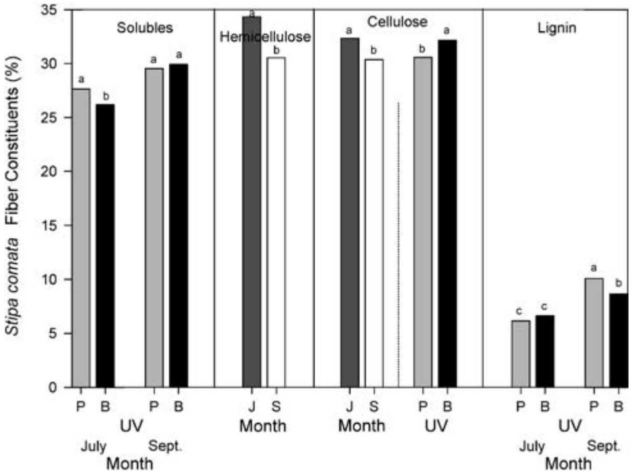

Figure 6. Fiber constituents of *S. comata* plant biomass collected in July (J) and September (S) in the wet year (2002) from UV pass (P) and UV block (B) treatments. Different letters above the bars indicate significant differences at the $P = 0.05$ level.

classified as weeds. The significant species and functional group responses to UV treatment translated into significant effects on total standing biomass. However, total standing biomass was reduced by UV pass compared with UV block treatment only in the drought year at the July, midseason sampling.

UV pass compared with UV block treatment decreased aboveground net primary production in *B. gracilis* and *S. hystrix* (Fig. 4). However, the decrease was only in the drought year for the former species and the wet year for the latter, although there was insufficient production of *S. hystrix* to analyze statistically for the drought year. Defoliation significantly stimulated an increase in aboveground net primary production in the wet but not the drought year, in all four species examined. The effects of UV treatment on production of the dominant grass, *B. gracilis*, resulted in a significant UV effect on C_4 grasses but no other functional groups displayed significant responses (Fig. 5). Total aboveground net primary production was significantly reduced by UV pass compared with UV block only during the drought year, when a 24% reduction was observed. Grazing stimulated production of all groups and of total production in the wet year but not in the dry year.

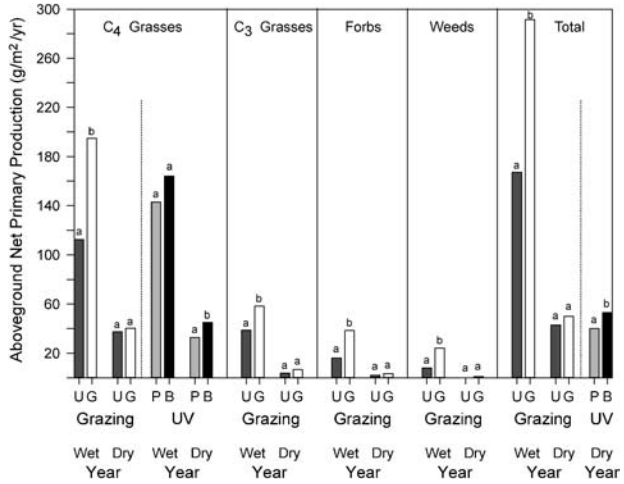

Figure 5. ANPP of C_4 and C_3 grasses, forbs, weeds and total vegetation in wet (2001) and dry (2002) years for UV pass (P) and UV block (B) treatments and grazed (G) and ungrazed (U) treatments. Different letters above the bars indicate significant differences at the $P = 0.05$ level.

The July and September season effects were often significant for fiber constituents of the three most abundant grasses in the wet year, and for *B. gracilis* and all other vegetation combined in the drought year. However, seasonal effects were small, as were UV treatment effects. In the wet year, *S. comata* was the species whose fiber constituents were most affected by UV treatment. Cell solubles (the labile fraction) for the midsummer July sampling were higher under UV pass treatment than when blocked, but no UV effect was observed in early autumn sampling in September (Fig. 6). The same was observed for the recalcitrant lignin component but the significant UV effect was in September. Although these components increased, cellulose decreased with UV pass compared with UV block treatment in both seasons. The only other species showing a significant UV treatment effect in the wet year was *A. longiseta*, where a slight increase in hemicellulose was observed in September in the UV pass treatment (data not shown). No UV treatment effects on fiber fractions were observed in the drought year for either *B. gracilis* or other species combined. Similar to season effects, grazing treatment often had effect on fiber fractions of the species examined and effects were similarly small (Fig. 7). Interactions between UV and grazing treatment were not observed. UV treatment effects were most prevalent in *A. longiseta* tissue constituents when analyzed among grazing treatments. UV pass compared with UV block treatment increased the soluble component of aboveground plant tissue and decreased hemicellulose in the wet year. No UV treatment effects were observed for lignin. No UV treatment effects on fiber components were observed in the dry year for either *B. gracilis* or other species combined.

UV treatment effects on plant nitrogen concentration were only found for *B. gracilis*, and grazing and season effects when significant on this species reflect the responses also observed for

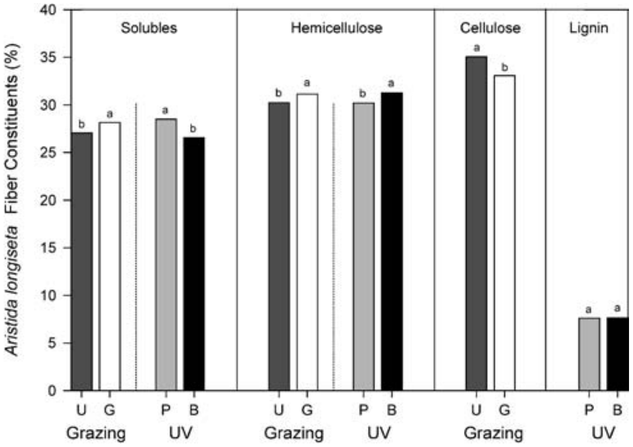

Figure 7. Fiber constituents of *A. longiseta* plant biomass in the wet year (2002) from UV pass (P) and UV block (B) treatments and grazed (G) and ungrazed (U) treatments. Different letters above the bars indicate significant differences at the $P = 0.05$ level.

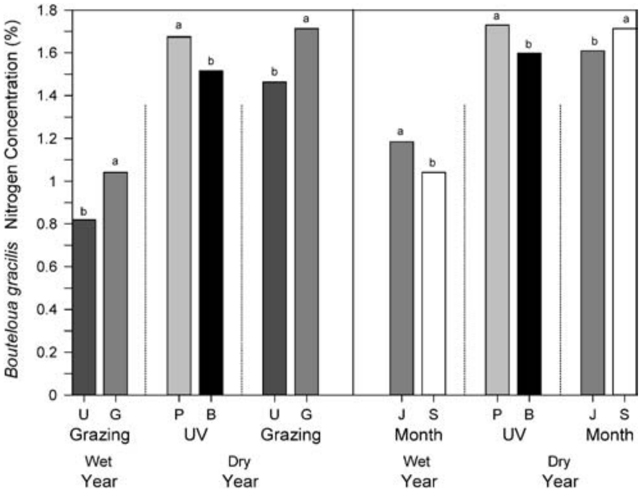

Figure 8. Nitrogen concentration of *B. gracilis* plant biomass collected in July (J) and September (S) in the wet year (2002) from UV pass (P) and UV block (B) treatments and grazed (G) and ungrazed (U) treatments. Different letters above the bars indicate significant differences at the $P = 0.05$ level.

other species (Fig. 8). Nitrogen concentrations of *B. gracilis* were greater with UV pass compared with UV block treatment in the dry year for both grazing treatments in September and when assessed during the July and September sampling periods in the grazed treatment. A UV by grazing treatment interaction or UV treatment by season interaction was not observed. Grazing treatment increased *B. gracilis* nitrogen concentration in both years, and higher nitrogen concentrations were observed in the dry than in the wet year.

UV treatment effects on forage digestibility for ruminants were not observed for either year in analyses of the seasonal data, but digestibility was generally lower in September than in July. UV treatment main effects were observed in analyses of the September samples for the grazed and ungrazed treatments (Fig. 9). UV pass compared with UV block treatment significantly increased digestibility in *B. gracilis* and *A. longiseta* in the wet year, but treatment differences were less than three percentage units of digestibility. UV treatment effects on digestibility were not observed in the dry year. Grazing increased digestibility of all plant tissues except for *S. comata* in the wet year and other species combined in the dry year.

DISCUSSION

UV radiation most often causes only small reductions in plant biomass under high levels of UV enhancement (4). Results from this semiarid ecosystem indicate that reductions in standing plant biomass and net primary production occur in some plant species under different levels of precipitation even for near-ambient compared with reduced levels of UV radiation. PAR is seldom limiting in the shortgrass steppe because of the short, sparse canopy development (31) and the high elevation (1.65 km) of this semiarid grassland. PAR exposure levels are, therefore, very high, and plants often close stomata at midday to conserve water. Another characteristic of the response of this ecosystem to UV is also counter to generalities that have been reported. Grasses are generally less sensitive to UV damage than dicots (32,33), but we observed reductions in seasonal standing biomass for both grasses and forbs, and reductions in production of grasses with UV pass compared with UV block treatment. Reductions in biomass occurred in both a C_3 and C_4 grass species but the reduction in ANPP translated to only C_4 grasses as a whole group, and this resulted in a reduction for total vegetation as well. The different species responses to UV treatment could potentially lead to changes in species abundance and composition (15) in this native grassland community. However, Phoenix *et al.* (34) found no change in dwarf shrub densities and only small changes in cover of species after 5 years even though one of four species examined showed decreased growth and increased seed production with enhanced UV radiation. These authors concluded that changes at the community level may occur but may take many years and are difficult to measure.

Drought is a common stress in the semiarid shortgrass steppe, and there is the potential for important interactions between UV radiation and drought. Both positive and negative interactions between UV and drought have been reported for plant growth

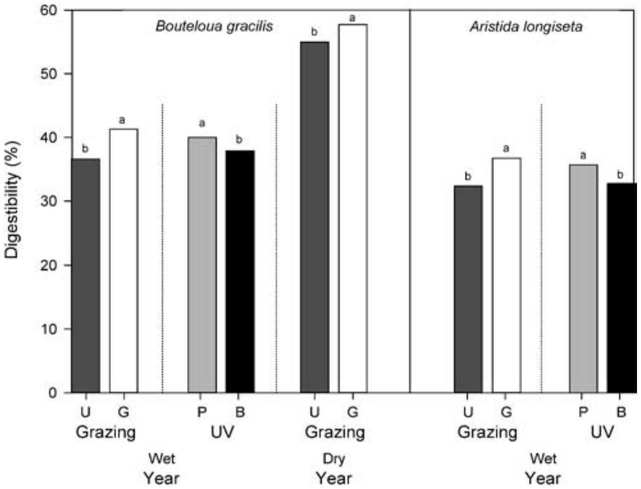

Figure 9. *In vitro* digestible dry matter (%) of *B. gracilis* and *A. longiseta* for ungrazed (U) and grazed (G) treatments and UV pass (P) and UV block (B) treatments in wet and dry years. Different letters above the bars indicate significant differences at the $P = 0.05$ level.

responses and various biochemical and water relation mechanisms have been implicated (5,6,12,13,16,35). All UV pass compared with UV block effects on primary production were negative in this study, and, depending on plant species, some occurred only in the wet year and some only in the dry year. A significant negative effect of UV pass compared with UV block treatment on ANPP was observed for *B. gracilis* in the dry year but not in the wet year, and a significant negative effect of UV on production was observed for *S. hystrix* in the wet year but not in the dry year. *B. gracilis* is known as a very drought-tolerant grass, and production in the drought *versus* wet year reflects this tolerance (*B. gracilis* 28.8%, *S. comata* 15.3%, *A. longiseta* 15.0%, *S. hystrix* 1.7% of wet year production). A lower reduction in productivity during the drought year and the negative UV-pass effect only during the drought is an unusual response pattern. Tevini *et al.* (13) found that a more sensitive species to drought was also more sensitive to UV, producing a synergistic effect of the two combined stresses. Drought-resistant wheat has been found to respond positively to UV compared with a sensitive broad bean species (14). Teramura *et al.* (12) hypothesized that UV may inhibit stomatal closure, producing localized water stress in some species. However, in this case, *B. gracilis* is the drought-resistant species. Passing UV may have interfered with the potential of *B. gracilis* to even better cope with drought, and the severity of the drought overrode any UV effect in the other species, but magnified the effect of the drought in the species that could maintain a minimal level of function during the severe stress. Thus, *S. hystrix* may be sensitive to both drought and UV, responding negatively to passing UV during the wet year, but so affected by the drought such that it did not appear in sufficient quantities to be sampled.

Approximately 40% of the shortgrass steppe of the North American Great Plains remains in native grassland, and the primary land use is grazing of domestic livestock. Pronghorn antelope and a variety of small herbivores are important native components of the ecosystem. Defoliation of plants by grazing animals may also interact potentially with UV levels and studies of interactions such as this are lacking. No interactions between UV and grazing treatment on primary productivity were observed in this study. Grazing stimulated primary production of all functional groups and species in the wet year but this was often not the case in the dry year. Although current-year defoliation has been shown previously to increase plant productivity in this particular system (36), the longer-term effects are negative (37).

In addition to productivity, UV radiation is known under some conditions to increase synthesis of plant secondary compounds that act as UV filters or to increase leaf thickness, and the UV influence on plant growth can also affect tissue chemistry. These biochemical, physiological and growth responses can influence fiber–soluble fractions (starch, carbohydrate, lignin) and N and protein contents of forage (1,16,38). Some secondary compounds that are produced (phenolics, terpenoids, tannins) can also affect digestibility of forages (39,40). We observed only a few significant effects of UV pass compared with UV block treatment on soluble-fiber fractions of plants, and these responses were small in magnitude. The response to passing UV compared with blocking UV was positive in terms of forage quality, except for an increase in lignin in *S. comata* in the autumn of the wet year. Responses to passing UV were also positive for N content of *B. gracilis* in the drought year, similar to findings of Tevini *et al.* (13) for protein in cucumber under drought plus UV. Rousseaux *et al.* (41) also found slightly higher N contents in a natural community exposed to UV compared with UV block treatment.

The digestibility of plant tissue indexes all factors combined that may influence forage quality for ruminants. Small increases in digestibility were observed only in the wet year in two species. This is in contrast to several plant–insect studies indicating a negative effect of UV on herbivores mediated through secondary compounds (22). However, Rousseaux *et al.* (42) found that caterpillars tended to eat more of leaves grown without UV compared with ambient, suggesting a higher quality of ambient UV forage that reduced the necessity for greater intake. Plant–ruminant compared with plant–insect interactions in response to changes in plant-tissue quality can be very different because insects can increase intake in response to lower quality whereas ruminants can become rate-of-passage, bulk limited when quality becomes very low.

In this particular system, the overall effect of UV pass compared with UV block treatment was to decrease forage quantity but increase quality. These effects are opposite to those observed for CO_2 enrichment at a study site just adjacent to this UV experiment site (43), indicating that these two climate change variables at least tend to dampen rather than exacerbate each other. All UV treatment effects observed in this experiment were small or occurred only under particular environmental conditions or seasons (or both). However, UV effects differed among plant species, and long-term consequences could result in changes in species composition of the plant community. The species most negatively affected by passing UV compared with blocking UV is a drought and grazing-tolerant species that is important in stabilizing the system with respect to these two common stresses to the plant community (43). Long-term effects may also manifest through altered carbon dynamics of the system because higher quality tissue can be decomposed faster by soil organisms just as it can be digested more readily by rumen microbes. The small but additive effects of decreased production, plus increased decomposition when passing UV compared with blocking UV, would result in lower carbon sequestration, lower soil organic matter and lower water and nutrient holding capacity. Longer-term study would be necessary to assess how these potential factors feedback on system level dynamics.

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