Initial impacts of altered UVB radiation on plant growth and decomposition in shortgrass steppe

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ABSTRACT

We initiated a study in winter 2000 in a Colorado shortgrass steppe to investigate effects of altered ultraviolet-B (UVB) radiation and altered precipitation on plant growth, plant tissue decomposition, and litter faunal activity. In the field, open-air structures were constructed of solid plastic sheet material that either passed all wavelengths of solar radiation or passed only wavelengths greater than 400 nm (UVB =280-315 nm). Preliminary results indicate decreases in warm-season grass production under UVB radiation and drought conditions. Analysis of fiber constituents shows some significant seasonal and UVB treatment effects. The results of *in vitro* digestible dry matter analyses show significantly higher digestibility with UVB. Simulated grazing increased plant production, but there were no UVB by grazing interactions. Litter decomposition was affected by UVB exposure, the CO_2 growing conditions, and precipitation level. Under dry conditions, UVB radiation tended to increase litter decomposition, as measured by mass loss. There were no clear initial effects of UVB treatment on soluble and fiber constituents of litter. Exclusion of UVB resulted in reduced fungal hyphae counts in ambient CO_2-grown litter collected in fall 2002. Preliminary results indicate that litter arthropod density was lower with exposure to UVB and also lower under drought conditions.

Keywords: UVB radiation, ecosystem impacts, elevated CO_2, precipitation, NPP, litterbag decomposition, soil biology, tissue quality, species composition, grassland

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1. INTRODUCTION

Changes in stratospheric ozone and increasing air pollution modify atmospheric radiation and have important direct and indirect impacts on surface processes. Without an understanding of how changes in ultraviolet B (UVB) radiation may affect ecosystem processes, we cannot begin to predict how ecosystems will respond to these long-term changes. Changes in plant growth and decomposition affect rates of biogeochemical cycling and may alter the productivity and sustainability of an ecosystem. Measurements have shown that altered UVB radiation can affect plant productivity, tissue chemistry, and decomposition[1,2]. Previous studies have concentrated on examining changes in response to altered UVB at high latitudes because the largest changes in stratospheric ozone have occurred there[3,4]. The focus of our work is mid-latitude grasslands where intensity of UVB radiation is high and changes in plant tissue quality in particular have important implications for grazers. Here we describe the initial results from our study in a Colorado shortgrass steppe. The objectives of this work are to examine the impacts of changes in UVB on plant productivity and decomposition and to investigate the impacts of multiple environmental factors (UVB, atmospheric CO_2, and precipitation) on plant decomposition and soil biology. We hypothesize that UVB will negatively impact plant growth and decrease tissue digestibility. We expect decomposition rates to increase under UVB due to the contribution of photodegradative effects. We hypothesize that soil organisms will respond negatively to UVB due to the adverse effects of UVB on the organisms and decrease in plant tissue palatability.

2. METHODOLOGY

2.1 Site description

The study site is at the Central Plains Experimental Range (CPER) (40°49'N, 104°46'W) in north central Colorado, in the drier northwestern part of the shortgrass steppe of the North American Great Plains. Mean annual precipitation is 321 mm, with a standard deviation of 98 mm[5]. Approximately 71% of the precipitation occurs during the May through September growing season. Mean monthly air temperatures range from 22°C in July to below 0°C in January. Total vegetative basal cover at the CPER is typically 25-35%[6]. Soil at the site is a Remmit fine sandy loam (Ustollic camborthids). Cattle grazing is the dominant land-use of native shortgrass steppe, with intensities generally ranging from 50 to 65% removal of aboveground plant biomass.

2.2 Experimental design and sampling

UV-treatment plots were constructed of 1.5 m² square Lexan** (UV block) and Solacryl** (UV pass) solid plastic sheets in a gently sloping A-frame design supported by 1.9 cm square metal tubing, with sides open to air flow below 40 cm. Additional UV block and pass structures were constructed for monitoring UV and precipitation edge effects and any inside/outside temperature differentials. Wet and drought year precipitation scenarios were derived choosing the 1/8 most dry and 1/8 most wet years on record for the period when precipitation rather than snow is received (April thru Oct.). Precipitation was applied weekly by metered, hand-held hose spray wand from a water-tanker truck. Amounts applied for that period for wet and dry treatments were 340 mm and 165 mm, respectively, compared to approximately 260 mm for an average year. Snow was not controlled under the plots, but is only a small amount of annual precipitation.

Two experimental designs were used: one for the plant productivity, grazing, and forage quality studies and one for the litter-decomposition and litter-fauna studies. The experimental design for the aboveground primary production/tissue quality/plant community composition part of the research consisted of 10 blocks of the two UV treatments. The effects of wet and dry years were assessed over time, by applying the wet-year precipitation scenario the first year and the dry during the second. Grazing treatments were nested within plot. Each plot (60 X 70 cm) was divided into an east and a west half (quadrat), and one side randomly appointed a defoliation treatment and the other left ungrazed. Defoliated sides of the plots were clipped during early July, and both sides harvested in September at peak standing crop. This provides live (July clip) and senescent (Sept. clip) material for chemical analyses, but also allows us to assess compensatory regrowth following grazing and the ANPP of grazed and ungrazed treatments. Biomass is sorted by species, whereby changes in species composition in response to a potential UV by grazing treatment interaction can

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be assessed under both wet and dry year conditions.

Plant material was dried at 55 °C, weighed, ground in a Wiley mill, and a subsample ashed at 550 °C for correction of weights and chemical analyses to an organic matter basis. Additional subsamples were analyzed for total carbon (C) and nitrogen (N) using an elemental analyzer, and for cell solubles, hemicellulose, cellulose, and lignin by the NDF, ADF, and sulfuric acid lignin fractionation method[7,8] modified for block refluxing and without sodium sulfite. All analyses were on the three most abundant species in the wet year, and on the dominant species and 'all others combined' in the drought year due to small sample sizes. In addition, *in vitro* digestible dry matter (IVDDM) analyses were performed. Inoculum for IVDDM was collected from a fistulated cow maintained on an exclusively grass-hay diet for one week prior to collection, with feed removed 12 hrs and water removed 3 hrs prior to rumen-pumping. Precautions in handling rumen fluid necessary to maintain microbial activity, and methods of preparing and delivering the inoculum, follow those described in Milchunas and Baker[9] (strain-layer method). IVDDM was run according to the two-stage, 96 hr method[10] (48 hr microbial digestion, followed by 48 hr acid pepsin stage that simulates lower gut digestion) with modifications and quality controls [9].

The litter studies included drought and wet year treatment, ambient and elevated CO_2-grown litter material of different tissue quality, and UV block and pass treatment, with seven replicate blocks. Each block consisted of a block of four wet and four dry treatment plots, and each of these four had two of each UV and two of each CO_2 treatments (7 blocks x 2 UV x 2 water x 2 CO_2 = 56 plots). Plant material for litter and fauna bags was obtained from a large open-top chamber CO_2 field experiment that had been operation for four years at ambient and elevated (~2 times ambient) atmospheric CO_2 concentrations[11]. Six litter decomposition bags and six arthropod/microorganism bags were placed on ground surface under each tent within a 70 X 70 cm area determined to minimize edge effects. The bags were 10 X 10 cm (usable inside area) fiberglass window screen mesh, soldered closed, with 3 g of one of the CO_2-treatment-grown plant materials in each. A total of 672 bags were constructed and placed in the field in December 2000. Sampling to date included one litterbag from each of the 56 plots in early September 2001, early April 2002, and Sept. 2002. Litterbags were processed and analyzed chemically as described above for plant material. Two fauna litterbags from each of the 56 plots were collected each autumn, one for arthropod and one for microorganism and fungi counts.

The density and biomass of fungi were estimated using materials from the litterbags collected in October 2001 and September 2002. Densities of fungi were estimated via direct counts[12] from a 10^{-2} serial dilution initiated with one gram of litter to 99 ml saline solution. Two $50 \mu l$ aliquots of the 10^{-2} dilution were placed in separate wells of 6 mm microscope slides. Each well was treated with DTAF (IB excitation 490 nm) and Calcifour White (UV excitation 334-365 nm) to stain the outer cells of the fungal hyphae. The wells were examined for fungal hyphae using epi-fluorescence microscopy, with the density of fungal hyphae (m g^{-1} dry soil) determined using the line intercept method[12]. Fungal biomass was determined using a morphometric conversion of 2.3×10^{-6} m g^{-1} hyphae[13]. Soil microarthropods were extracted from individual litterbags over a five-day period using modified Tullgren funnels. Arthropods were preserved in 70% ethanol, sorted under a dissecting microscope, and identified to genus using DIC compound microscopy. We divided the microarthropods into the following categories: total arthropods, mites, Prostigmata, Mesostigmata, Cryptostigmata, Collembola, and root feeding insects.

Statistical analysis for production studies was a split plot design with block as the whole plot and UV treatment the subplot, and grazing crossed with UV treatment. 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 Sept. weights for the grazed treatment. A second design, as above except without grazing but including 'season' as a factor, assessed July standing crop and Sept. regrowth for the grazed treatment. Analyses for production plots had to be done separately for each year because of the large difference in biomass/production values for the very wet and drought year and separately for chemical constituents because species grouping had to change from the three abundant ones to the dominant and 'all others'. Statistical analysis of the soil organisms included analysis of variance (ANOVA) along with post-hoc least of square means tests for UVB radiation effects, moisture effects, and litterbag data[14]. The data were transformed using a 1n(x+1). All p-values of $p \leq 0.1$ are reported in the text, with p-values of $p > 0.1$ reported as not significant (NS).

3. DATA

3.1 Plant community

Plant community/productivity plots received the wet-year precipitation regime in 2001 and the dry-year precipitation regime in 2002. Plant community responses to the UV, grazing, and wet/dry treatments were analyzed as standing biomass and as aboveground net primary production (ANPP) at species, functional group, and total vegetation levels. Standing biomass data represents mid-season standing current-year growth and the regrowth from the same clipped quadrat that occurs from mid-season until the final clip in September at peak-standing crop. This provides an

assessment of the effects of the treatments on regrowth following a defoliation stress and provides mid-season green tissue for chemical analyses and end-of season regrowth tissue for chemical analyses. The sum of the two season's biomasses yields an estimate of grazed ANPP. A quadrat in the second half of each tent is clipped only at end of season peak-standing crop. This sample represents ungrazed ANPP and provides a sample of ungrazed tissue for chemical analyses that can be compared with the regrowth, grazed end-of-season tissue.

Four species, all grasses, were sufficiently abundant on the plots for statistical analyses of seasonal standing biomass and annual production. Aboveground plant standing biomass of all species was greatly reduced by drought imposed under the tents during 2002 compared to the very wet year imposed during 2001, and regrowth biomass in September following defoliation in July was always less than July standing crop (Figure 1). Several significant effects of UV treatment were observed. The dominant species of the shortgrass steppe, the C_4 grass *Bouteloua gracilis*, showed a significant decrease in standing biomass with UV radiation, but this occurred only during the dry year and not during the wet year, and in July but not in September. The same relationships were observed for the C_3 grass *Stipa comata*. The biomass of the C_3 grass *Sitanion hystrix* was also negatively affected by UV radiation, but this occurred in the wet year, with insufficient biomass produced during the drought year to statistically test. *Aristida longiseta* did not respond to the UV treatments.

Significant UV radiation effects were also observed for standing biomass of some functional groups and for total plant biomass. UV radiation reduced C_4 grass biomass in the drought year, but not in the wet year (not shown). C_3 grass biomass was also reduced in the drought year, but only in July. UV radiation reduced forb standing biomass in the wet year in September, but there was insufficient forb biomass in the drought year to statistically analyze. No significant UV treatment effects were observed for species 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 radiation only in the drought year at the July, mid-season sampling.

Grazing significantly stimulated an increase in aboveground net primary production in the wet, but not the drought year, in all four species examined (Figure 2). UV radiation decreased production in *B. gracilis* and *S. hystrix*. 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 statistically analyze for the drought year. The effects of UV radiation on production of the dominant grass, *B gracilis*, resulted in a significant UV effect on C_4 grasses as well, but no other functional groups displayed significant responses. Total ANPP was significantly reduced by UV exposure only during the drought year, when a 24% reduction was observed.

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 radiation treatment effects. In the wet year, *S. comata* was the species most affected by UV treatment. Cell solubles (the labile fraction) for the mid-summer July sampling were higher under ambient UV levels than reduced UV, but no UV effect was observed in early autumn September sampling (Figure 3). The same was observed for the recalcitrant lignin component, but the significant UV effect was in September. While these components increased, cellulose decreased with UV exposure 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 (data not shown). No UV treatment effects on fiber fractions were observed in the drought year for either *B. gracilis* or other species combined. UV treatment effects were most prevalent in *A. longiseta* tissue. UV radiation increased the soluble component of aboveground plant tissue, and decreased hemicellulose in the wet year (not shown). 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.

The digestibility of vegetation for ruminants was generally lower in September than in July, but no UV treatment effects were observed for either year in the analyses of the seasonal data. UV treatment main effects were observed in analyses of the September samples for the grazed and ungrazed treatments (Figure 4). Grazing increased digestibility of all plant tissues except for *S. comata* in the wet year and other species combined in the dry year. UV radiation significantly increased digestibility in *B. gracilis* and *A. longiseta* in the wet year, but treatment differences were less than three percentage units of digestibility. No UV treatment effects were observed in the dry year.

3.2 Plant decomposition

Litter decomposition, measured as percent mass loss, was affected by UV conditions, CO_2 conditions under which the litter was grown, and precipitation level (Figure 5). Mass loss was greatest under wet conditions for plant material grown under ambient versus elevated CO_2. Overall, plant material grown under elevated CO_2 decomposed more slowly than that grown under ambient CO_2. Under dry conditions, exposure to UV radiation resulted in higher mass loss while under

wet conditions UV treatment had little effect. UV treatment had no significant effect on litter fiber quality (not shown). The largest differences in litter quality occur between litter grown under ambient versus elevated CO_2 conditions. Litter grown under elevated CO_2 tended to have lower solubles and lignin content and higher hemicellulose and cellulose content. These relative proportions are consistent with the initial quality of the litter at the start of the decomposition study. Precipitation levels had little effect on fiber fractions. Plant litter decomposed under wet conditions tended to have higher lignin and solubles content and lower cellulose.

3.3 Soil biology

In 2001 the density of fungi (m g^{-1} dry soil) did not differ under any treatment combination. However, in 2002 there was a significant interaction between ambient CO_2 levels and reduced UVB where lower counts ($p=0.0172$) of fungal hyphae (m g^{-1} dry soil) were recorded in ambient CO_2 litter under reduced UVB combinations (Figure 6). The UVB and precipitation treatments significantly affected arthropod numbers (Figure 7). From 2001 it is evident that UV treatment had as large an effect on arthropod numbers as did dry versus wet year conditions. Exclusion of UVB resulted in nearly twice as many total arthropods as the ambient UV treatment ($p=0.0021$), while wet-year conditions compared to drought conditions also resulted in nearly twice as many total arthropods ($p=0.0035$). The response of different groups of arthropods to UVB exclusion compared to ambient treatment mirrored the response to wet-year compared to dry-year conditions, with the exception of Cryptostigmata. Prostigmata and root feeding insects were significantly affected by UVB whereas detritivorous Cryptostigmata and predaceous Mesostigmata were unaffected. After two years of data, there were a total of two Collembola collected; we therefore cannot deduce anything for this category of microarthropod.

4. RESULTS

4.1 Plant production

Although UV radiation most often causes only small reductions in plant biomass under high levels of UV enhancement[15], results from this semiarid ecosystem indicate reductions in standing plant biomass and net primary production occur in some plant species under different levels of precipitation even for ambient compared to reduced levels of UV radiation. Light is seldom limiting in the shortgrass steppe due to the short, sparse canopy development[16], and the study site is at a relatively high elevation (1646 m) for a semiarid grassland. Light exposure levels are, therefore, very high, and plants often close stomates mid-day to conserve water loss. Another characteristic of the response to UV in this ecosystem is also counter to generalities that have been reported. Grasses are generally less sensitive to UV damage than dicots[17,18], but we observed reductions in biomass for both grasses and forbs and reductions in production of grasses with UV radiation. Reductions in biomass occurred in both 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 abundances and composition[19] in this native grassland community, and this will be assessed in subsequent treatment years. However, Phoenix et al.[20] found no change in dwarf shrub abundances after five years even though one of four species examined decreased growth and increased seed production with enhanced UV radiation.

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 responses, and various biochemical and water relation mechanisms have been implicated[21,22,23,24,25,26]. All UV effects on species 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 radiation on ANPP was observed for *B. gracilis* in the dry year but not the wet year, and a significant negative effect of UV on production was observed for *S. hystrix* in the wet year but not 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 effect only during the drought is an unusual response pattern. Tevini et al.[22] found that a more sensitive species to drought was also more sensitive to UV, producing the synergistic effect of the two combined. Drought resistant wheat has been found to respond positively to UV compared to a sensitive broad bean species[27]. Teramura et al.[21] hypothesized that UVB may inhibit stomatal closure, producing localized water stress in some species. In this case however, *B. gracilis* is the drought resistant species. 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 UV during the wet year, but so affected by the drought as to 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 potentially interact with UV stress, 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. While current-year defoliation has previously been shown to increase plant productivity[28], the longer-term effects are negative[29].

In addition to productivity, UV treatment can affect a number of plant constituents that impact the quality of forage for grazing animals. Nitrogen is often limiting to ruminant microbial populations, as is protein to monogastrics (N x 6.25 = crude protein). Fiber components are a major determinant of the energy available to an herbivore. Cell solubles are readily digestible, lignin is practically indigestible, and hemicellulose and cellulose digestibility vary depending on N and mineral availability and on encrustation by lignin. High lignin, low N and high cellulose content can limit rate of passage, and the capacity for further intake if quality is very low. UV radiation is known under some conditions to increase synthesis of plant secondary compounds that act as UV filters, or 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[23,30,1]. Some secondary compounds that are produced (phenolics, terpenoids, tannins) can also affect digestibility of forages[31,18]. We observed only a few significant effects of UV treatment on soluble-fiber fractions of plants, and these responses were small in magnitude. The UV response 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 UV were also positive for N content of *B. gracilis* in the drought year, similar to findings of Tevini et al.[22] for protein in cucumber under drought plus UV. Rousseaux et al.[32] also found slightly higher N contents in a natural community exposed to UV compared to 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[33]. However, Rousseaux et al.[34] found that caterpillars tended to eat more of leaves grown without UV compared to ambient, suggesting a higher quality of ambient UV forage that reduced the necessity for greater intake. Plant-ruminant compared to 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 while ruminants can become rate-of-passage, bulk limited when quality becomes very low.

4.2 Plant decomposition

Decomposition of plant material can be strongly influenced by both biotic and abiotic factors. Our results to date suggest that under conditions that favor biotic processes, wet conditions in the shortgrass steppe, UV treatment has little effect on rates of mass loss. However, under conditions that limit biotic activity, i.e. drought conditions, mass loss is greater under ambient UV radiation compared to reduced UV radiation. The results under drought conditions are in agreement with Rozema et al.[35] who found that mass loss tended to be higher under enhanced UVB radiation. However, a similar study on subarctic plants found no effects of UV on decomposition[3]. The effects of UV radiation on decomposition vary between species[36] and also by environment[37], and the mechanisms that control response to UV are not well understood. Overall, we observed greater mass loss of litter grown under ambient CO_2 versus elevated CO_2 conditions. This is as expected due to the higher N content of plant material grown under ambient CO_2 compared to elevated CO_2.

4.3 Soil biology

In 2001 there was no significant difference found in observed counts of fungal hyphae. However, in 2002 there was a significant interaction between source of litter (ambient versus elevated CO_2) and UVB conditions. The significant reduction in fungal hyphae counts in ambient CO_2 litter under reduced UVB in 2002 is not well understood. However, it does confirm that litter quality and UVB interact to affect microbial abundance. We observed a decrease in arthropod abundance from 2001 to 2002. This year-to-year variation is not uncommon and may reflect the overall warmer temperatures in 2002 compared to 2001. With the exception of the predatory Mesostigmata, all groups of microarthropods were affected by precipitation. The exclusion of UVB resulted in an increase in numbers for all groups, with the exceptions of Cryptostigmata and Mesostigmata. This result could be due to the heavily sclerotized bodies of both Cryptostigmata and Mesostigmata, as well as the increased levels of pigmentation typically found in Cryptostigmata. For Cryptostigmata, UVB may be muted by the heavy pigmentation thereby increasing desiccation levels. Mesostigmata are surface-active predators, and this behavior may explain a pre-adaptation to drier soil surface conditions and hence the lack of significant effect from precipitation changes. Interestingly there was no effect of litter

source on arthropod abundance in 2001 and 2002 despite differences in N content and fiber constituents in the original litter. *In both 2001 and 2002 there was a negative effect of UV on root feeding insects, suggesting the potential for belowground mediated effects of UVB on plants as well as the effects through litter decomposition.*

5. CONCLUSIONS

Our initial results show that plant biomass production is reduced under UVB exposure and that plant production responses to UVB treatment vary by species and by precipitation levels. Plant tissue decomposition was enhanced by UVB exposure under dry conditions, suggesting that photodegradation plays an important role in drought conditions. This result is in agreement with our observations that soil organisms respond negatively to UVB radiation and negatively to drought conditions. Our results suggest overall negative impacts on ecosystem productivity under higher UVB radiation. Furthermore, impacts on root-feeding insects indicate that changes at the surface may have important effects on belowground processes. In order to understand whole ecosystem biogeochemical cycling under altered UVB, longer term studies are need with particular attention to belowground responses.

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FIGURES
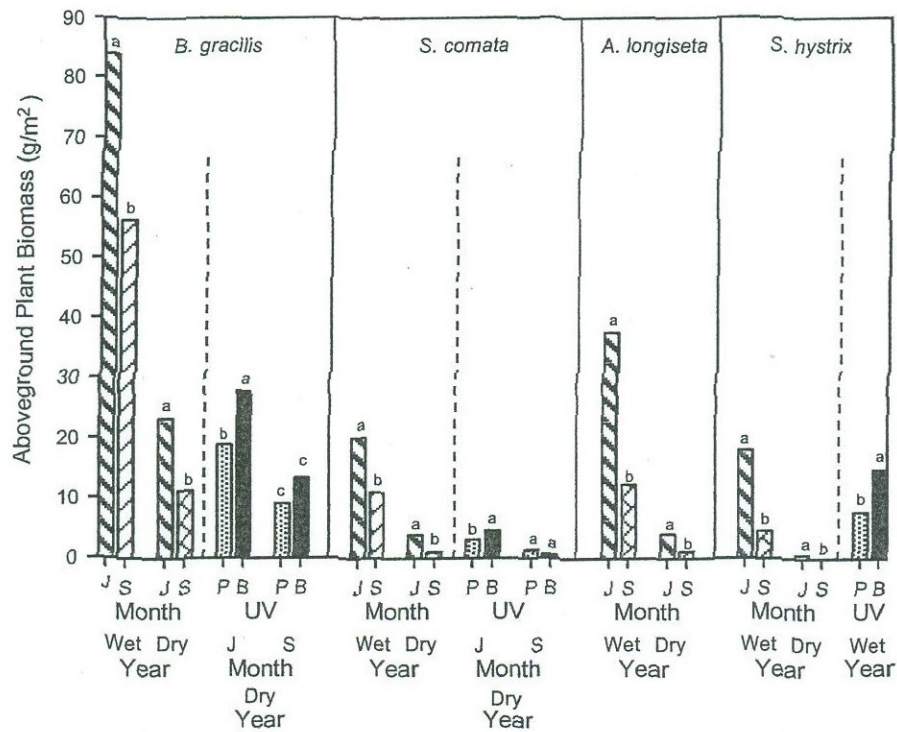
Figure 1. Aboveground plant biomass of *B. gracilis*, *S. comata*, *A. longiseta*, and *S. hystrix* in July (J) and September (S) of the wet year (2001) and dry year (2002) for UV pass (P) and block (B) treatments. Different letters above the bars indicate significant differences at the p≤0.05 level.
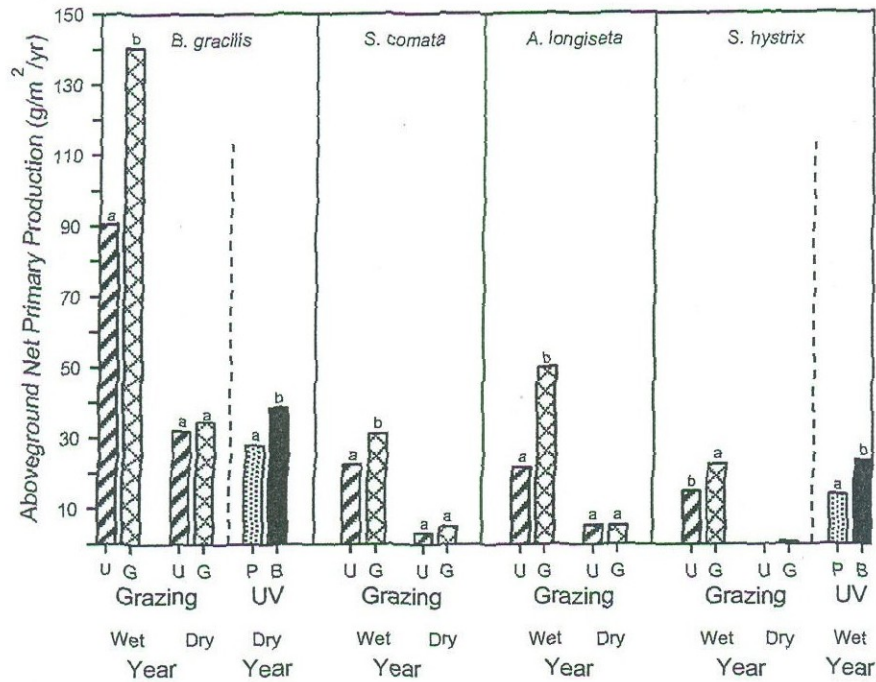
Figure 2. Aboveground net primary production (ANPP) of *B. gracilis*, *S. comata*, *A. longiseta*, and *S. hystrix* in wet (2001) and dry (2002) years for UV pass (P) and UV block (B) treatments and grazed (G) and ungrazed (U) treatments. Different letters above the bars indicate significant differences at the $p \leq 0.05$ level.
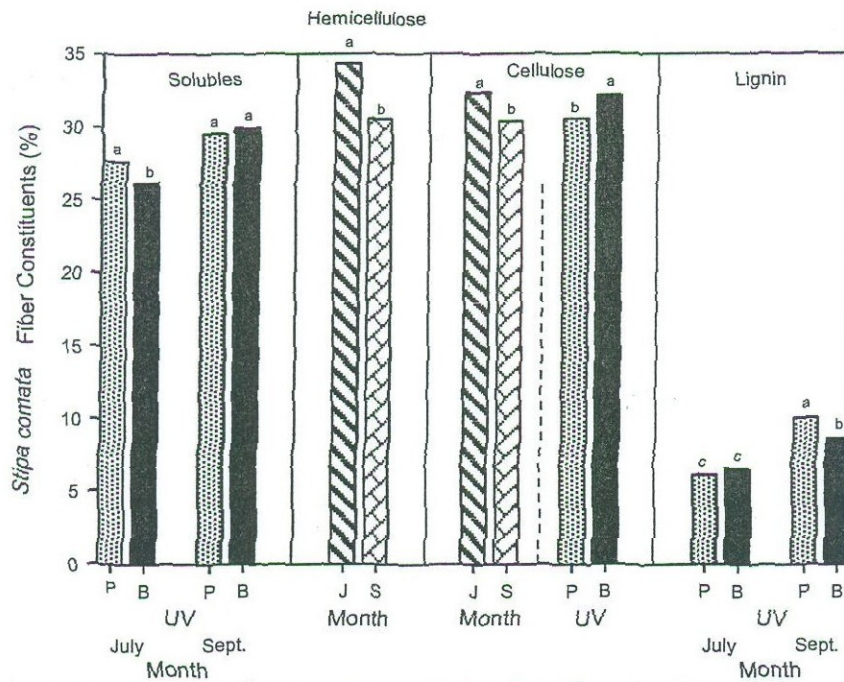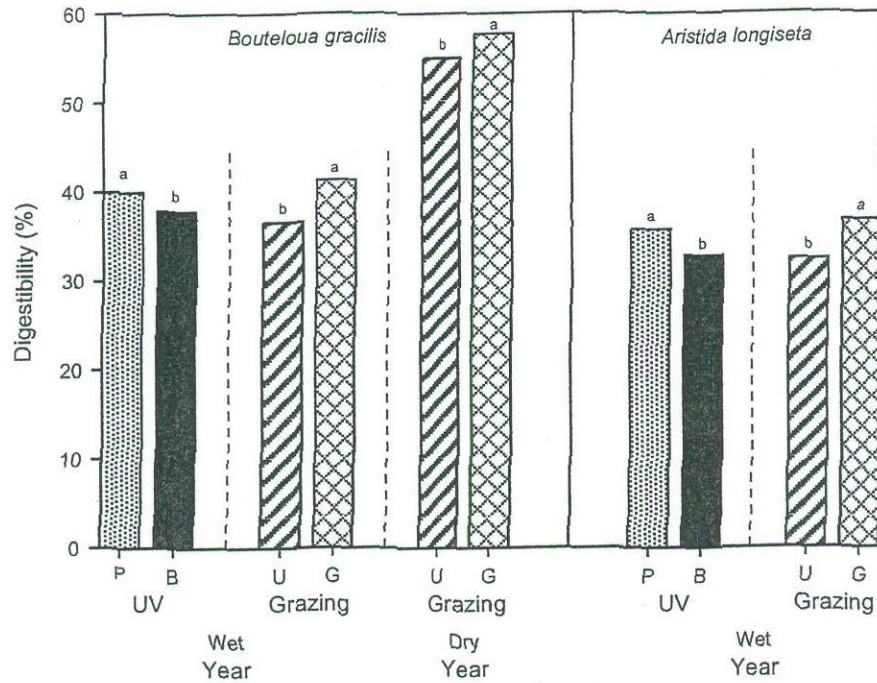

Figure 3. Fiber constituents of *S. comata* plant biomass collected in July (J) and September (S) in the wet year (2002) from UV pass (P) and UV block (B) treatments. Different letters above the bars indicate significant differences at the $p \leq 0.05$ level.

Figure 4. *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. Different letters above the bars indicate significant differences at the $p \leq 0.05$ level.
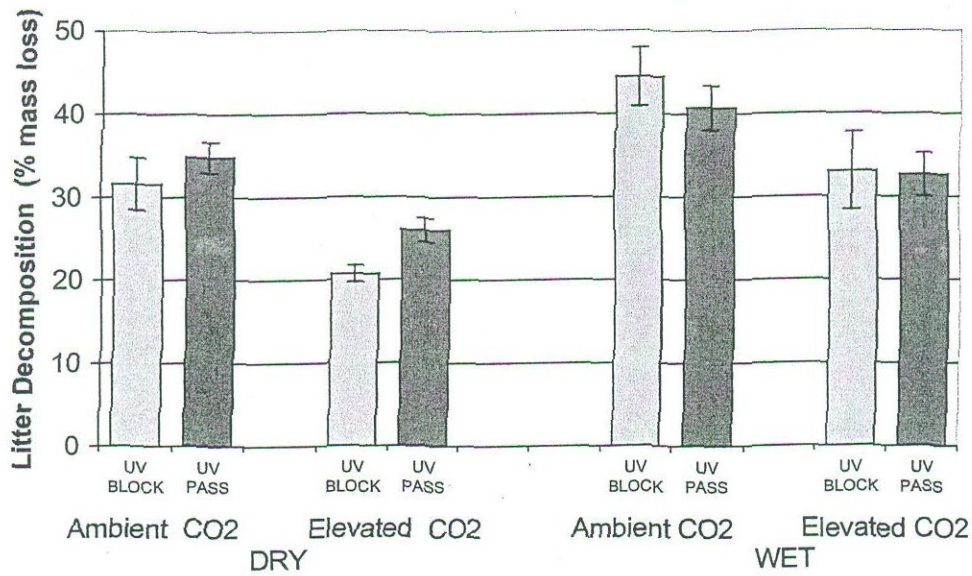

Figure 5. Litter decomposition measured as percent mass loss for litterbags collected in September 2002. Litterbags contained litter grown under either ambient or elevated CO_2 conditions and were decomposed under wet or dry conditions and UV pass or UV block conditions. Error bars represent standard errors (n=7).
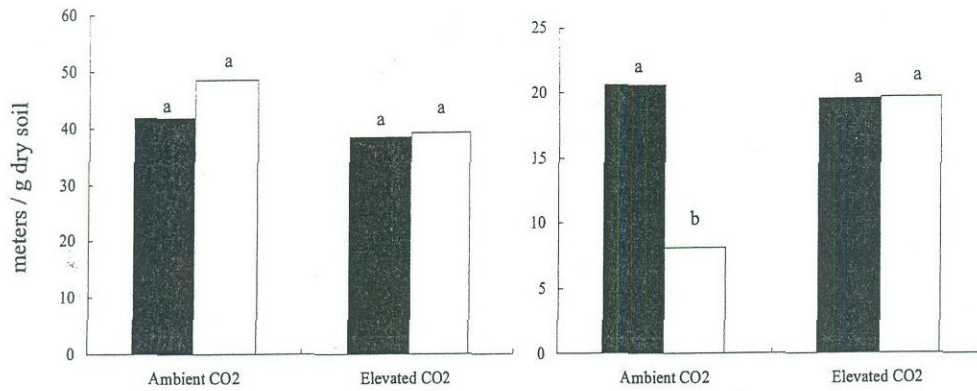
Figure 6. Fungal hyphae lengths from litter collected in 2001 (left) and 2002 (right) from UV pass (black) and UV block (white) treatments. Litter was grown under ambient or elevated CO_2 conditions. Different letters are significantly different at the $p \leq 0.05$ level.
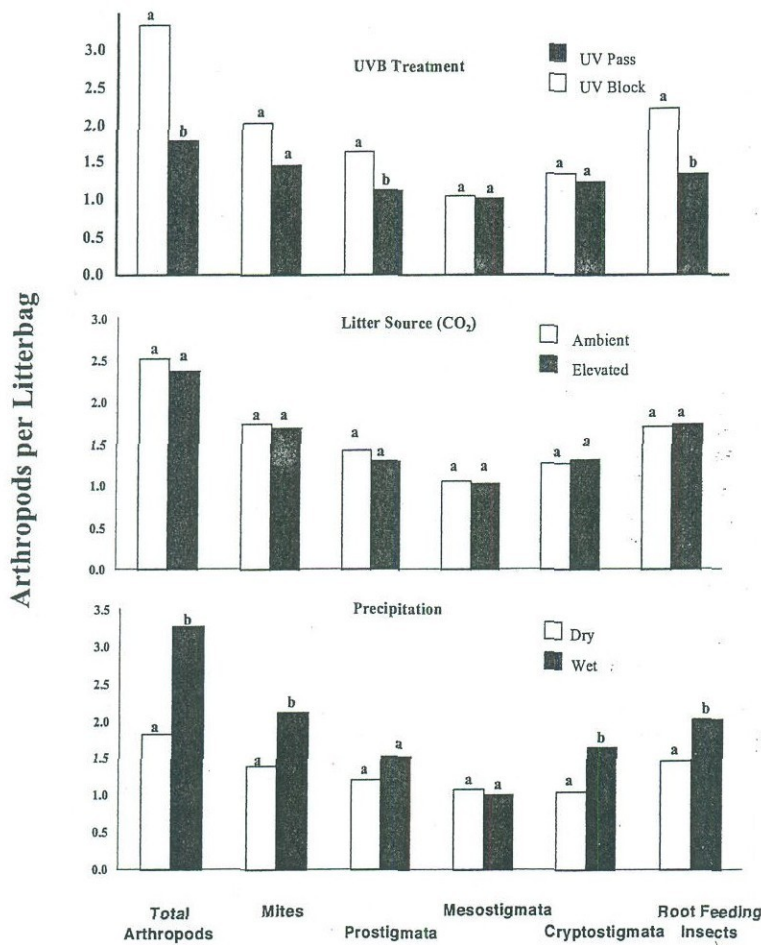

Figure 7. Total arthropod numbers and numbers of various groups of arthropods from litter bags with litter grown under ambient or elevated CO_2 treatments and exposed to UV pass or block conditions, and wet or dry levels of precipitation from December 2000 until collected in September 2001. Different letters above the bars indicate that the treatments are significantly different at the $p \leq 0.1$ level.