Global Change Biology

Global Change Biology (2010) **16**, 484–495, doi: 10.1111/j.1365-2486.2009.01973.x

Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition

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Abstract

Altered surface ultraviolet-B (UV-B) radiation resulting from a combination of factors that include changes in stratospheric ozone concentrations, cloud cover, and aerosol conditions may affect litter decomposition and, thus, terrestrial nutrient cycling on a global scale. Although litter decomposition rates vary across biomes, patterns of decomposition suggest that UV-B radiation accelerates litter decay in xeric environments where precipitation is infrequent. However, under more frequent precipitation regimes where litter decay rates are characteristically high, the effect of UV-B radiation on litter decomposition has not been fully elucidated. To evaluate this association between moisture regime and UV-B exposure, a litter decomposition experiment was designed for aspen (*Populus tremuloides*) leaf litter, where conditions that influence both abiotic (photodegradation) and biotic (microbial) processes could be manipulated quantitatively. We found that experimentally increasing UV-B exposure (0, 7.4, and 11.2 kJ m^{-2} day^{-1}, respectively) did not consistently increase litter decomposition rates across simulated precipitation frequencies of 4, 12, and 24 days. Instead, a UV-B exposure of 11.2 kJ m^{-2} day^{-1} resulted in a 13% decrease in decomposition rates under the 4-day precipitation frequency, but an increase of 80% under the 24-day frequency. Furthermore, the same UV-B dose increased litter decomposition rates under the 24-day precipitation frequency by 78% even in conditions where microbial activity was suppressed. Therefore, under more xeric conditions, greater exposure to UV-B radiation increased decomposition rates, presumably through photodegradation. In contrast, when decomposition was not moisture-limited, greater UV-B exposure slowed decomposition rates, most likely from the resulting inhibition of microbial activity. Ultimately, these experimental results highlight UV-B radiation as a potential driver of decomposition, as well as indicate that both the direction and magnitude of the UV-B effect is dependent on moisture availability, a factor that may change according to future patterns in global precipitation.

Keywords: aspen litter, climate change, decomposition, photodegradation, ultraviolet-B, ultraviolet radiation, UV-B

Received 6 January 2009; revised version received 18 April 2009 and accepted 26 April 2009

Introduction

Litter decomposition rates in arid ecosystems are often underestimated by ecosystem models in which decomposition is a function of climate and litter quality alone (Meentemeyer, 1978; Whitford *et al.*, 1981). In most biomes, litter decomposition is driven primarily by biologically mediated enzyme activities (Meentemeyer, 1978; Swift *et al.*, 1979). However, in arid environments biological decomposition is often limited by low moisture availability. Yet, in these environments, litter decomposition persists even in the total absence of microbial activity (Austin & Vivanco, 2006), suggesting that abiotic mechanisms [e.g. ultraviolet-B (UV-B) radiation] may contribute significantly to decomposition rates.

While the importance of UV-B radiation is recognized for arid ecosystems, little is known about UV-B effects on decomposition in other ecosystems where litter is exposed to UV-B irradiance for at least part of the year.

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For example, aspen (*Populus tremuloides*) forests have a range that includes relatively high latitudes and high elevations, where total solar and UV-B radiation are elevated (Caldwell *et al*., 2007). Generally, UV-B radiation at the soil surface in forest environments is highly variable with relatively low annual cumulative exposure due to a closed-canopy during summer. However, aspen forests can remain snow-free for 1–2 months following autumn leaf abscission, and snowpack melt-out can occur 1–2 months before canopy closure in early summer, resulting in relatively high spring and fall sunlight exposure at the forest floor. In addition, the dose of UV-B radiation received by the forest floor can be increased by the reflection of UV-B radiation from adjacent areas where snow cover persists due to a deeper snowpack (Mckenzie *et al*., 1998). Therefore, in mountain aspen forests, altitude, a deciduous habitat, and extended periods of surrounding snow-cover may act in combination to periodically increase surface UV-B exposure throughout the year. Ultimately, this periodic UV-B exposure has the potential to significantly influence annual decomposition rates in these forest environments.

UV radiation accelerates litter decomposition via photodegradation, the physiochemical transformation of compounds into smaller compounds as a result of the absorption of high energy radiation (Vossbrinck *et al*., 1979). The UV region of the solar spectrum is divided into UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (100–280 nm). Of these, UV-B radiation is considered to have the largest impact on biosphere processes, including photodegradation, due to its high-energy wavelengths and capacity to penetrate the stratospheric ozone layer (Caldwell & Flint, 1994; Caldwell *et al*., 1998). Litter that is decomposed by photodegradation not only exhibits different kinetics than biologically decomposed litter, but likely results in decomposition by-products that differ in chemical composition from those that are metabolically derived (Anesio *et al*., 1999; Schade *et al*., 1999). Thus, UV-B radiation may alter both the rate at which litter decomposes and the rate at which it is incorporated into stable fractions of soil organic matter.

UV-B radiation can also affect decomposition indirectly by impacting microbial decomposer communities. Fungi appear to be especially sensitive to UV-B exposure (Gehrke *et al*., 1995; Duguay & Klironomos, 2000; Verhoef *et al*., 2000; Johnson, 2003) with documented UV-B induced effects including reductions in fungal mycelial extension rates, DNA repair, and spore germination (Moody *et al*., 1999; Booth *et al*., 2001; Gallo *et al*., 2006). Furthermore, Pancotto *et al*. (2003) documented a selective effect of UV-B radiation on pigmented bacteria during the early stages of decomposition, suggesting that bacterial community composition could also be sensitive to UV-B radiation. However, studies have also found that the effect of UV-B radiation on microbes is variable and often varies as a function of litter chemical composition (Gallo *et al*., 2006).

Owing to the potentially counteracting effects of UV-B radiation on decomposition, net effects on decomposition rates could be either positive or negative depending on environmental conditions. In the field, positive effects of UV-B radiation on decomposition rates have only been observed in arid environments, and results from moist environments are inconclusive. Studies conducted in these relatively moist environments have documented a variety of results, including negligible UV-B effects attributed to snow and canopy cover (Kochy & Wilson, 1997; Newsham *et al*., 1997; Pancotto *et al*., 2005) and negative UV-B effects attributed to microbial sensitivity to UV-B radiation (Moody *et al*., 2001; Pancotto *et al*., 2003). However, it is unclear in these studies how precipitation regime and thus moisture availability influenced the impact of UV-B radiation on decomposition.

The primary objective of this study was to determine if the magnitude and potentially the direction of the UV-B effect on aspen leaf litter decomposition is dependent on the frequency of precipitation. A litter decomposition experiment was set up under controlled conditions with three levels of precipitation frequency, three levels of exposure to UV-B radiation, and two levels of soil biological activity to distinguish abiotic vs. biotic decomposition. We hypothesized that photodegradation rates would increase with increasing levels of UV-B radiation, and that the proportion of biologically driven decomposition would decrease. We also expected that with increasing precipitation frequency, photodegradative decomposition would decrease relative to biologically driven decomposition.

Materials and methods

Site and sample collection

Leaf litter, soil, and soil biota were collected in a forest of deciduous broadleaf *P. tremuloides* Michx. (quaking aspen) in the San Juan National Forest (CO, USA; 40.58°N, 105.15°W; $\sim$ 2700 m elevation). Aspen litter was collected in autumn 2006 and an initial determination of litter chemistry was completed using three replicate samples. The litter chemistry characterization included determination of initial concentrations of carbon ($49.0 \pm 0.2\%$), nitrogen ($0.69 \pm 0.03\%$), cellulose ($21.0 \pm 1.1\%$), and lignin ($15.0 \pm 1.0\%$). In spring 2007, soil was collected in bulk to a depth of 12 cm and sieved (4 mm grate) to remove coarse materials and homogenize samples.

Experimental design

A litter decomposition experiment was initiated in Spring 2007, in a glasshouse at the USDA/ARS Crops Research Laboratory (Fort Collins, CO, USA). Temperature and humidity were measured continuously throughout the experiment and held steady at approximately 26 °C and 20% relative humidity. In addition, air within the glasshouse was recycled through fan-driven filters to supply continuous introduction of outside air without associated contaminants. Seventy-two containers ($27.9 \times 34.3 \times 7.6$ cm each) were washed thoroughly and then filled with approximately 2 kg of sieved soil. Twenty-four containers were assigned to each of the three precipitation treatments (low, intermediate, and high). Within each of the precipitation treatments, soil microcosms were further partitioned into three UV-B treatments (no UV-B, ambient UV-B, and elevated UV-B) and two soil treatments (reduced-microbial and control) resulting in a three-way factorial design with four replicates of each treatment.

Four open-top litter bags (10 cm × 10 cm, 1 mm stainless-steel mesh), were filled with 3 g air-dried leaf litter, which included leaf petioles, and placed within each soil microcosm resulting in a total of 288 open-top litter bags (four open-top litter bags × 96 microcosms). The open-top litter bag design was utilized to prevent filtering of UV-B radiation that may have occurred with the use of a traditional litter bag. In addition, the litter sample (3 g) and the total surface area of the litter bag ($100\,cm^2$) were selected as representative of a natural litter layer with an approximate depth of 2 cm, where only the surface litter receives full solar radiation.

Additional subsamples (3 g) of air-dried leaf litter were used to determine the initial ash-free dry weights for each litter bag. A single litter bag was randomly selected from each treatment and removed for analysis after 2, 4, 6, and 8 24-day precipitation cycles, resulting in a 192 day experiment. Final weights were calculated by oven-drying and then weighing each of the collected litter bags. Subsamples from each litter bag were used to determine final ash-free dry weights. Percent organic matter remaining over time was determined for each litter bag by dividing the final ash-free dry weight by the initial ash-free dry weight.

Determination of litter C and N content were also made prior to the start of the experiment using a LECO CHN-1000 C/N analyzer (LECO Corp., Saint Joseph, MI, USa). During each of the four collection periods, a subsample of air-dried litter was removed from each litter bag for measurement of C and N content. Percent N remaining over time was determined for each litter bag by multiplying the litter mass remaining by litter N content and expressing this as a percentage of the initial mass of N in the litter.

UV-B supplementation

The supplemental UV radiation methodology employed during this study was based on the hardware and techniques employed by Reddy *et al*. (1992, 2001). The glasshouse experienced ambient lighting, however, all ambient UV radiation was filtered by the glasshouse material (tempered glass and double wall acrylic) (Fig. 1a). Therefore, UV-B exposure was regulated using artificial irradiance, supplied by fluorescent UV-B lamps (UVB-313EL, Q-Panel Lab Products, Cleveland, OH, USA). Because these lamps emitted a radiation spike at 254 nm, a very biologically damaging UV-C wavelength, lamps were wrapped with pre-solarized cellulose acetate film (0.07 mm) to remove all UV-C radiation. Additionally, cellulose acetate film was replaced weekly to maintain acceptable limits of light transmission.

To compare solar UV radiation to the artificial UV radiation produced by the glasshouse UV-B lamps, a biological spectral weighting function (BSWF) was utilized (Caldwell, 1971). Although the Caldwell BSWF weights UV-B radiation heavily due to its relatively high-energy wavelengths, it does not weight UV-A radiation. As a result, UV-A exposure was not controlled for in this experiment, even though these lamps produced significant UV-A radiation (Fig. 1a). The use of UV-A controls in combination with a BSWF with more appropriate UV-A weighting would improve the accuracy of this approach.

Exposure levels for the glasshouse UV-B treatments were determined from field measurements collected from the USDA UV-B Monitoring Network station located at the University of Nevada Reno's Storm Peak Laboratory. Glasshouse treatments included control (No UV-B radiation, $0\,kJ\,m^{-2}\,day^{-1}$), ambient ($7.4 \pm 0.4\,kJ\,m^{-2}\,day^{-1}$), and elevated (~15% ozone reduction or $11.2 \pm 0.6\,kJ\,m^{-2}\,day^{-1}$) UV-B exposure (Fig. 1b). A value of $11.2 \pm 0.6\,kJ\,m^{-2}$, used to simulate elevated UV-B radiation, represented a 15% reduction in stratospheric ozone and was the approximate peak UV-B radiation level observed in the field for the summer of 2007 (Fig. 1c). Spectral output was measured using an EPP-2000 UV spectrometer (Stellarnet Inc., Tampa, FL, USA). Following the initial measurement, UV-B energy was measured daily at 0900 h with a UVX digital radiometer (UVP Inc., San Gabriel, CA, USA) which was calibrated using the Stellarnet spectrometer.

Soil biota treatment

Experimental soil biota treatments included control and reduced-microbial treatments, designed to determine if the effect of UV-B radiation on decomposition is dependent on the level of biological activity. In control

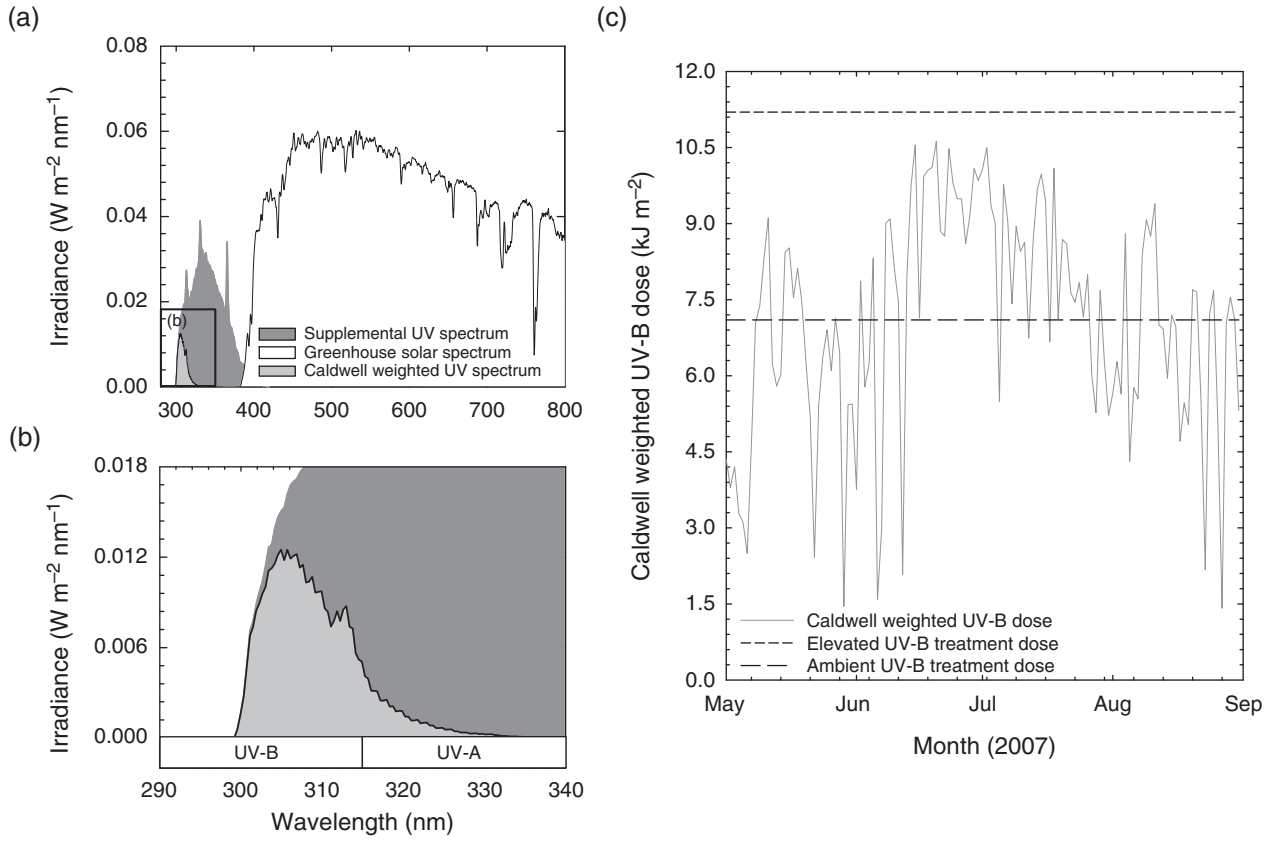

Fig. 1 (a) Spectra of irradiance incident at the litter surface specific to the ambient UV-B radiation treatment. The supplemental UV spectrum was supplied by fluorescent UVB-313EL lamps. The Caldwell weighted spectrum was calculated by multiplying the supplemental UV spectrum by the Caldwell weighting function (Caldwell, 1971). (b) A focused look at the Caldwell weighted spectrum incident at the litter surface [enlarged from (a)]. (c) Caldwell weighted UV-B daily dose for summer 2007. The solid line represents daily doses of UV-B radiation for summer 2007 collected at the USDA UV-B Monitoring Network station located at Storm Peak Laboratory. Represented by the long-dashed line is the average daily Caldwell weighted UV-B dose used for the ambient UV-B radiation treatment (7.1 kJ m^{-2}). The short dotted-line indicates the dose, used for the elevated UV-B treatment (11.2 kJ m^{-2}), and determined to correspond to a 15% reduction in ozone.

treatments, the homogenized, sieved soil collected from the field was used without treatment so that the ambient soil biota would be intact. For reduced microbial treatments, soil was initially autoclaved three consecutive times at 121 °C and 1.1 atm (~11 MPa) to reduce the abundance and diversity of naturally occurring biota. Although the initial sterilization treatment killed the majority of microbes, we recognized it would not be possible to maintain sterile conditions in the glasshouse environment without further intervention. Thus, soils were exposed to microwave radiation (625 watts, 2450 MHz) at an energy application of 248 J g^{-1} every 24 days to maintain minimal microbial activity (Trevors, 1996; Islam & Weil, 1998; Wang *et al*., 2001). A frequency of 24-day microwave treatment allowed application immediately before the precipitation treatment to prevent impacts of microwave heating and drying on moisture availability. It is important to note that this method of soil sterilization did not include sterilization of the litter, nor did we monitor litter microbial biomass. Instead, the initial and subsequent reductions in the soil biota were used to decrease litter colonization rates. This approach was adopted since sterilization of litter by autoclaving and repeated microwave treatment would have altered litter chemistry.

Active microbial biomass estimates were determined for the control and reduced-microbial treatment soils (before and after microwave radiation) by following the methodology for substrate-induced respiration described in Anderson & Domsch (1978). All estimates were determined by averaging four randomly selected, microcosm soil subsamples. Subsamples were amended with a glucose concentration (10 mg g^{-1} soil) and then incubated at 25 °C. CO_2 evolution was determined for each subsample over a 4.5 h period following glucose addition, with headspace measurements occurring at

0.5, 2, and 4 h. All measurements were provided by a LiCor Li-6252 infrared CO_2 gas analyzer (LiCor Inc., Lincoln, NE, USA).

Precipitation simulation

Precipitation regime was simulated experimentally by gravimetrically returning soil to 60% water holding capacity (WHC) at 4-, 12-, and 24-day frequencies representing high, intermediate, and low precipitation treatments, respectively. These frequencies were selected to encompass a broad range of naturally occurring precipitation patterns by varying concurrently the total moisture addition, as well as the frequency of moisture addition, within each treatment. During each rewetting, a precise amount of sterile water was applied to return soil to 60% WHC similar to previous dry/rewetting experiments (Miller *et al*., 2005). Following each rewetting, soil moisture levels were estimated daily to quantify the rate at which individual treatments were drying. Water additions were applied equally to each litter bag and allowed to drain into the microcosm soil as would occur naturally in the field.

Modeling and statistical analysis

A set of *a priori* candidate models were developed based on the negative exponential decomposition equation (Olson, 1963) to determine the support in the data for treatment effects on decomposition:

$$M_t = m_0 e^{(-kt)}, \quad (1)$$

$$M_t = m_0 e^{(-(s_1 UV + k_0)t)}, \quad (2)$$

$$M_t = m_0 e^{(-(s_2 P + k_0)t)}, \quad (3)$$

$$M_t = m_0 e^{(-(s_1 UV + s_2 P + k_0)t)}, \quad (4)$$

$$M_t = m_0 e^{(-(s_1 UV + s_2 P + s_3 UVP + k_0)t)}, \quad (5)$$

where M_t is the fraction of mass remaining at time, t (year), m_0 is the percent initial litter mass, and k is the decomposition rate. In models that incorporated treatment effects, the decomposition rate, k, was modified to include the UV-B treatment effect, ($k = s_1 UV + k_0$), the precipitation (rewetting) treatment effect, ($k = s_2 P + k_0$), and their combined effect, ($k = s_1 UV + s_2 P + k_0$); where UV represents the three levels of UV-B treatment, P represents the three levels of precipitation treatment, s_1 and s_2 are the slopes associated with the UV-B and precipitation treatments, respectively, and k_0 represents the general decomposition rate. Finally, Eqn (5) incorporated an interactive term, *UVP*, and an associated slope, *s*3. Application of the precipitation treatment in the models was done categorically resulting in weights of 0, 1, and 2 applied to the 4-, 12-, and 24-day precipitation frequencies, respectively. Application of the UV-B treatment was applied quantitatively with weights determined relative to the UV-B radiation levels resulting in normalized weights of 0, 0.67, and 1 applied to the control, ambient, and elevated UV-B treatments, respectively. These candidate models were evaluated independently within each of the biota treatments, (control soil and reduced-microbial soil), to determine how UV-B radiation interacts with soil biota.

Akaike's Information Criterion modified for small sample sizes (AIC_c) was used to choose among models in the candidate set. The model with the most support in the data had the lowest corresponding AIC_c value and a ΔR ($\Delta R = AIC_c$ of each model – AIC_c best model) of zero. Also, models within 2 AIC_c points of the best model ($\Delta R \leq 2$) were considered to have substantial support in the data. Information on model selection uncertainty was also calculated using Akaike weights (w_r) which are the probability that the best model would be selected again, given the same set of models and a new set of similar, but independent, data (Burnham & Anderson, 2002). Models were fitted to the data and AIC_c was calculated using PROC NLMIXED in the software package SAS (SAS Institute, Cary, NC, USA). Data collected during the final collection period ($t = 0.53$ years) were also analyzed using a two-factor analysis of variance (ANOVA) to compare mean values and determine treatment effects on litter mass and final percent *N*. ANOVA was conducted using proc GLM and Tukey's method in the software package SAS (SAS Institute).

Results

Effectiveness of treatments

Microcosm rewetting frequencies of 4, 12, and 24 days resulted in a broad range of soil moisture levels. Soils treated under a 4-day frequency never fully dried before the reapplication of moisture, while soils treated with a 12-day precipitation frequency dried to approximately 23% WHC and soils treated with a 24-day frequency dried to 23% WHC and remained at that level for a 12-day period before reapplication of moisture (Fig. 2). Microbial biomass in the control soils (biologically active) was positively correlated with the corresponding precipitation treatment and was increased with increasing rewetting frequency (Fig. 3).

Autoclaving and repeated microwave sterilization treatments appeared successful in reducing soil biotic

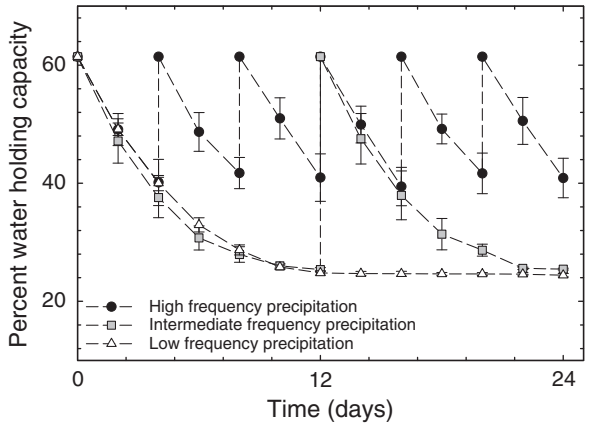

Fig. 2 Frequency of simulated precipitation for the three different precipitation treatments applied during the litter decomposition experiment. The low precipitation treatment occurred every 24 days, the intermediate precipitation treatment occurred every 12 days, and high precipitation treatment occurred every 4 days. Error bars, ± SEM.

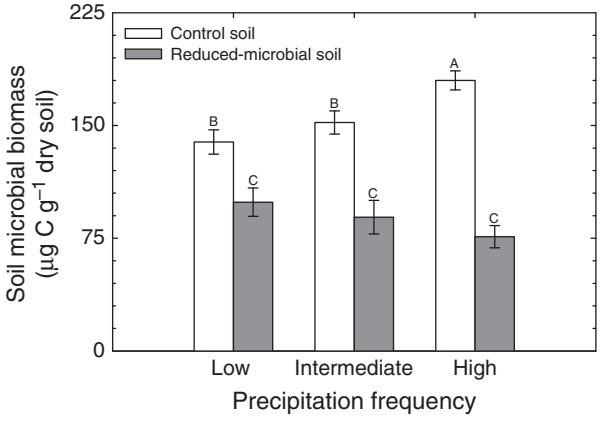

Fig. 3 Soil microbial biomass as a function of precipitation frequency observed over the course of the litter decomposition experiment. Total microbial biomass was estimated according to the methodology described in Anderson & Domsch (1978). Letters indicate significant pair-wise differences (Tukey's HSD; $F = 34.8$, $P < 0.0001$). Error bars, ± SEM.

activity. Soil microbial biomass was significantly reduced in the reduced-microbial treatment by approximately 58%, 41%, and 29% for the 4-, 12-, and 24-day rewet frequencies respectively, and this reduction was maintained successfully throughout the investigation (Fig. 3).

Although we did not directly measure microbial biomass on leaf litter, our data suggests that the colonization of litter by decomposing microbes was decreased by the reduction of soil microbial biomass. Decomposition rates in control soil treatments were 30% higher than decomposition rates observed in reduced-microbial soil treatments (Table 1), consistent with an overall reduction in litter microbial activity.

Litter mass loss

The effect of UV-B radiation on decomposition rates was strongly dependent on precipitation frequency (Fig. 4). In the control soil treatment (biologically active), precipitation frequency was the dominant driver of decomposition and alone accounted for approximately 78% of the observed variance in the data (Table 1). Decomposition rates increased with increasing precipitation frequency resulting in decay rates of 0.06, 0.16, and 0.26 years^{-1} for 24-, 12-, and 4-day precipitation frequencies, respectively.

Precipitation frequency had a strong negative correlation on the effects of UV-B radiation on decomposition rates (Fig. 4). When precipitation was limited to a frequency of 24 days, UV-B radiation accelerated decomposition in the control (biologically active) soils resulting in decay rates of 0.02, 0.07, and 0.10 years^{-1} for the no, ambient, and elevated UV-B exposure treatments, respectively (Fig. 4). When precipitation was increased to every 12 days, the positive effect of UV-B radiation on decomposition was weaker, with decay rates of 0.15, 0.16, and 0.17 years^{-1} for the no, ambient, and elevated UV-B radiation treatments, respectively (Fig. 4). In contrast, when rewetting occurred every 4 days, the effect of UV-B radiation was negative with decay rates of 0.30, 0.27, and 0.26 years^{-1} observed for the three UV-B treatments, respectively (Fig. 4).

Reducing biological activity in the microcosms by periodically sterilizing the soils decreased litter decay rates and led to a 29% decrease in the magnitude of the effect of precipitation frequency on litter mass loss (Table 1). The effect of UV-B radiation on decomposition rates in reduced microbial soil treatments, however, was similar in magnitude and direction to the effects observed in the biologically active microcosms (Table 1).

The strong interaction between simulated precipitation frequency (rewetting) and UV-B radiation exposure was verified by strong statistical support for the interaction model ($w_r \geq 0.999$), and very little support for any of the alternative models ($w_r \leq 0.001$) for both the control and reduced-microbial soil treatments (Table 1). Similarly, in the analysis of litter mass remaining at the end of the experiment, the interaction of UV-B radiation and precipitation was significant (Table 2). In slightly over 6 months (0.53 years), both precipitation frequency and UV-B radiation had significant effects on percent organic matter remaining with the effect of UV-B radiation varying in direction in relation to precipitation frequency (Fig. 5).

In the control soil treatment, increasing precipitation frequency resulted in significantly less organic matter

Table 1 Strength of evidence and parameter estimates for competing models of litter decomposition

Soil treatment	Model	AIC_c	ΔR	K	w_r	R^2	m_0	k	k_0	s_1	s_2	S_3
Control soil												
Interaction Model	$M_t = m_0 e^{(-(s_1 UV + s_2 P + s_3 UVP + k_0)t)}$	741.2	0.0	6	0.999	0.80	93.6	—	0.02	0.08*	0.14*	−0.06*
Combined Model	$M_t = m_0 e^{(-(s_1 UV + s_2 P + k_0)t)}$	756.6	15.4	5	0.001	0.78	93.6	—	0.05*	0.02	0.10*	—
Precipitation Model	$M_t = m_0 e^{(-(s_2 P + k_0)t)}$	757.8	16.6	4	0.000	0.78	93.6	—	0.06*	—	0.10*	—
No Effect Model	$M_t = m_0 e^{(-kt)}$	922.1	180.9	3	0.000	0.43	93.6	0.16*	—	—	—	—
UV-B Model	$M_t = m_0 e^{(-(s_1 UV + k_0)t)}$	923.1	181.9	4	0.000	0.44	93.6	—	0.15*	0.02	—	—
Reduced-microbial soil												
Interaction Model	$M_t = m_0 e^{(-(s_1 UV + s_2 P + s_3 UVP + k_0)t)}$	763.9	0.0	6	0.993	0.67	93.1	—	0.02	0.07*	0.10*	−0.06*
Precipitation Model	$M_t = m_0 e^{(-(s_2 P + k_0)t)}$	775.0	11.1	5	0.004	0.64	93.1	—	0.06*	—	0.07*	—
Combined Model	$M_t = m_0 e^{(-(s_1 UV + s_2 P + k_0)t)}$	775.6	11.7	4	0.003	0.64	93.1	—	0.05*	0.02	0.07*	—
No Effect Model	$M_t = m_0 e^{(-kt)}$	860.8	96.9	3	0.000	0.41	93.1	0.13*	—	—	—	—
UV-B Model	$M_t = m_0 e^{(-(s_1 UV + k_0)t)}$	862.1	98.2	4	0.000	0.41	93.1	—	0.12*	0.01	—	—

Models are variations of the negative exponential decomposition function. Akaike's Information Criterion values, ΔAIC_c values, and number of model parameters are represented by AIC_c, ΔR, and K, respectively. Initial percent organic matter remaining and decomposition rates are represented by m_0 and k or k_0, respectively. Slope of the UV-B effect (*UV*), precipitation effect (*P*), and interactive effect are represented by s_1, s_2, and s_3, respectively. All parameters estimated using AIC_c analysis to be significantly different from zero at an $\alpha = 0.05$ significance level are indicated with an *.

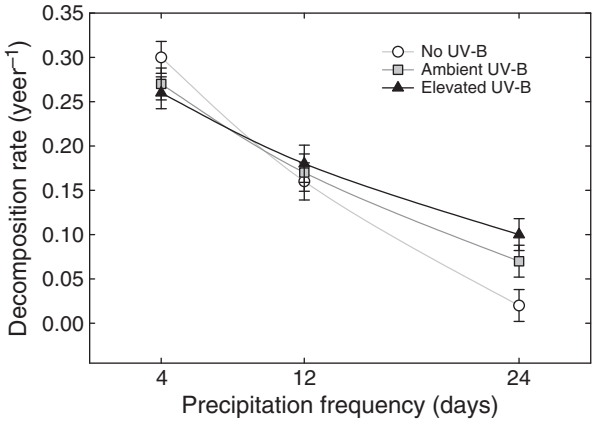

Fig. 4 Constants of decomposition or decay rates ($years^{-1}$) observed within the control soil treatment during the litter decomposition experiment. Decomposition rates were calculated from parameter estimates made by the interaction model. Error bars, ± SEM.

Table 2 Percent organic matter remaining 2-way ANOVA results for control and reduced-microbial soil determine at the final collection period ($t = 0.53$ yr.)

Percent organic matter remaining	N	MS	F	P
Control soil				
UV	12	0.66 (16.21)	0.04	0.96
P	12	196.71 (4.33)	45.41	<0.0001
UVxP	4	58.29 (2.60)	22.46	<0.0001
Reduced-microbial soil				
UV	12	4.65 (10.06)	0.46	0.63
P	12	76.28 (5.72)	13.33	<0.0001
UVxP	4	27.54 (4.48)	6.14	0.0002

Sample size, mean square (mean square error), *F*-value, and the *P* statistic are represented in the table by *N*, MS, *F*, and *P*, respectively. The UV-B and precipitation treatments are represented by UV and P, respectively.

remaining with 89.8%, 86.7%, and 81.8% organic matter remaining in the 24-, 12-, and 4-day precipitation frequency treatments, respectively ($F = 45.4$, $P < 0.0001$) (Table 2). Moreover, UV-B radiation significantly altered percent organic matter remaining as a function of precipitation frequency in the control soil treatment by accelerating mass loss in the 24-day rewetting treatment ($F = 7.44$, 0.012) and decelerating mass loss in the 4-day treatment ($F = 6.92$, $P = 0.015$) (Fig. 5). However, UV-B radiation did not lead to significant differences in litter mass remaining in the 12-day rewetting treatment ($F = 0.28$, 0.76) (Fig. 5).

In the reduced-microbial soil treatment, results were comparable to the control soil treatment, with the exception again being the magnitude of the effect of precipitation on mass loss. In the reduced-microbial soil treatment, the effect of precipitation on decomposition was reduced, resulting in 89.9%, 86.8%, and 84.4% litter mass remaining for the 24-, 12-, and 4-day precipitation frequency treatments, respectively ($F = 13.33$, $P < 0.0001$) (Table 2). As a result of the reduced precipitation effect, the only effect of UV-B exposure was to accelerate mass loss only within the 24-day precipitation treatment ($F = 16.28$, $P = 0.001$) (Fig. 5).

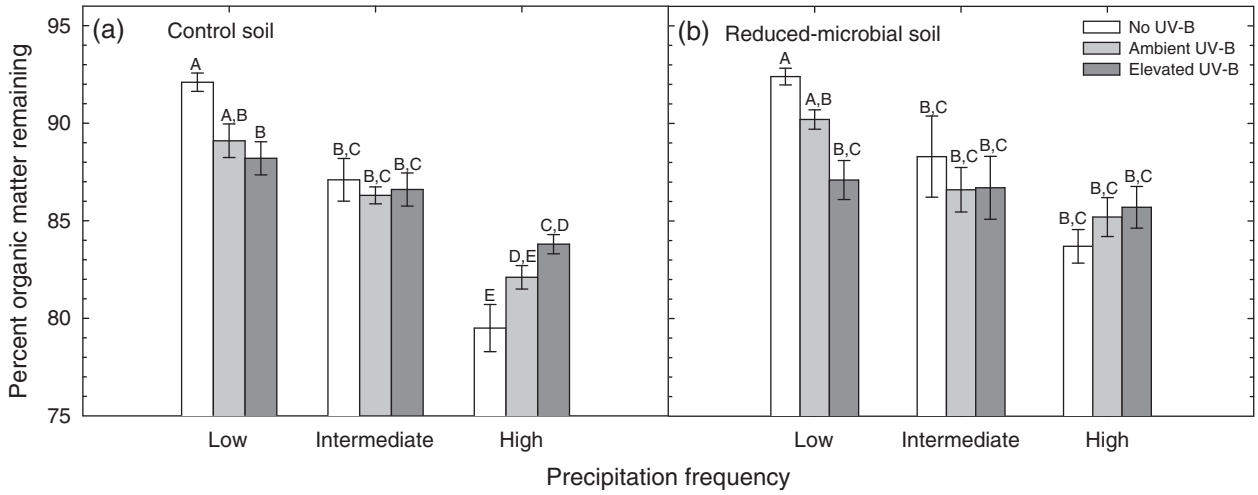

Fig. 5 (a) Percent organic matter remaining observed at the final collection period ($t = 0.53$ years) for the control soil treatment. Letters indicate significant pair-wise differences (Tukey's HSD; $F = 22.5$, $P < 0.0001$). Error bars, ± SEM. (b) Percent organic matter remaining observed at the final collection period ($t = 0.53$ years) for the reduced-microbial soil treatment. Letters indicate significant pair-wise differences (Tukey's HSD; $F = 6.14$, $P = 0.0002$). Error bars, ± SEM.

Litter nitrogen dynamics

Litter percent N remaining in the control soil treatment was significantly greater when rewetting was more frequent ($F = 16.30$ $P < 0.0001$) (Table 3, Fig. 6). However, the magnitude of this trend was less in the reduced-microbial soil treatments ($F = 13.30$, $P < 0.0001$) (Table 3, Fig. 6). Additionally, UV-B radiation interacted with precipitation regime in both the control ($F = 6.56$, $P < 0.0001$) and reduced-microbial ($F = 4.19$, $P = 0.002$) soil treatments (Table 3, Fig. 6) resulting in decreased percent litter *N* remaining with increasing UV-B radiation. This trend was most notable in the control soil treatment, under the 4- and 24-day rewetting frequency (Fig. 6).

Table 3 Percent nitrogen remaining 2-way ANOVA results for control and reduced-microbial soil determine at the final collection period ($t = 0.53$ years)

Percent nitrogen Remaining	*N*	MS	*F*	*P*
Control soil				
UV	12	441.41 (169.33)	2.61	0.09
P	12	1607.69 (98.66)	16.30	<0.0001
UVxP	4	534.18 (81.39)	6.56	<0.0001
Reduced-microbial soil				
UV	12	86.42 (168.95)	0.51	0.60
P	12	1282.51 (96.46)	13.30	<0.0001
UVxP	4	397.99 (94.97)	4.19	0.002

Sample size, mean square (mean square error), *F*-value, and the p statistic are represented in the table by *N*, MS, *F*, and *P*, respectively. The UV-B and precipitation treatments are represented by UV and *P*, respectively.

Discussion

The results from our glasshouse experiment suggest that UV-B radiation has the potential to affect litter decay rates in aspen forests under a broad range of precipitation regimes. However, the effects of UV-B radiation vary with precipitation frequency, leading to differences in the magnitude and even direction of its net effect on litter decomposition (Fig. 4). When aspen leaf litter is moist (e.g. 4-day precipitation frequency), biotic processes are the primary drivers of decomposition, although the high rate of mass loss we observed could be partly due to higher rates of leaching. Under these conditions, UV-B exposure may have a negative effect on decomposition rates by decreasing microbial biomass and activity (Fig. 4). When aspen leaf litter is dry (e.g. 24-day precipitation frequency), biotic processes are slow, and UV-B exposure may have a net positive effect on decomposition rates through photodegradation (Fig. 4).

The positive effect of UV-B radiation on aspen leaf litter decomposition rates under dry conditions (24-day precipitation frequency) parallels field studies of UV-B effects on decomposition in arid and semi-arid environments (Rozema *et al*., 1997; Austin & Vivanco, 2006; Brandt *et al*., 2007; Day *et al*., 2007). In our study, decomposition rates within the 24-day rewetting treatment did not differ between control and reduced-microbial soil (Fig. 5), suggesting that biological activity was moisture-limited and that decomposition was

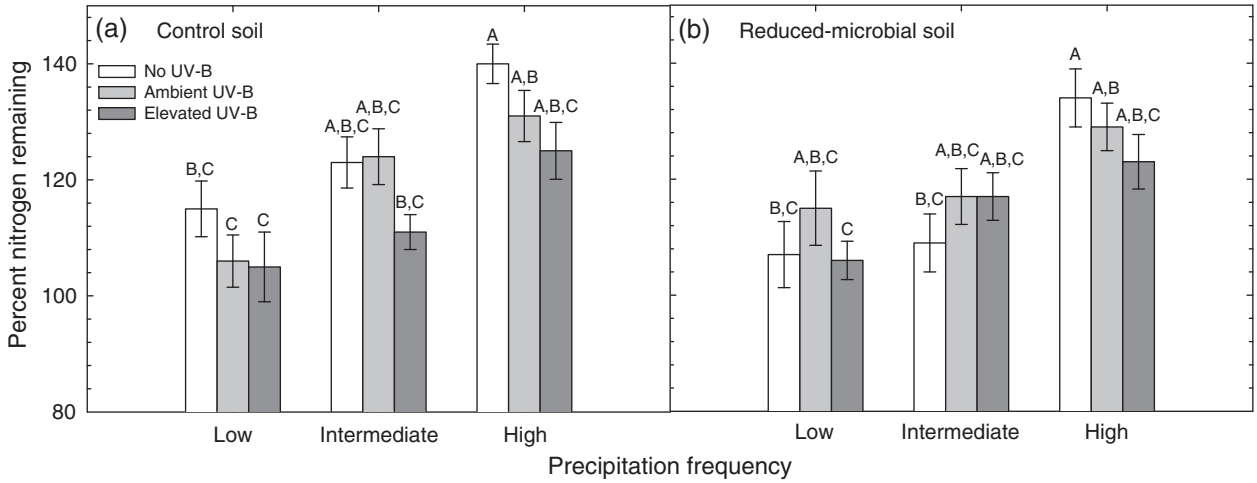

Fig. 6 (a) Litter percent nitrogen remaining observed at the final sample collection period ($t = 0.53$ years) for the control soil treatment. Letters indicate significant pair-wise differences (Tukey's HSD; $F = 6.56$, $P < 0.0001$). Error bars, ± SEM. (b) Litter percent nitrogen remaining observed at the final sample collection period ($t = 0.53$ yr.) for the reduced-microbial soil treatment. Letters indicate significant pair-wise differences (Tukey's HSD; $F = 4.19$, $P = 0.002$). Error bars, ± SEM.

primarily the result of photodegradation. This finding seems to be consistent with Austin & Vivanco (2006), who also observed photodegradation of litter in the Patagonia steppe in the absence of microbial activity and it appears to support our hypothesis that photodegradation would increase with increasing UV-B radiation while the proportion of biologically driven decomposition would decrease.

Under relatively wet conditions (4-day precipitation frequency), the experimental reduction of soil microbial biomass had a strong negative effect, while increased UV-B radiation had a moderately negative effect on decomposition rates (Fig. 5), suggesting that the dominant UV-B effect on decomposition shifted from photodegradation of litter under dry conditions to microbial inhibition resulting from UV-B exposure under moist conditions. Similar conclusions have been drawn from field studies that have detected microbial inhibition in response to UV-B radiation (Moody *et al*., 1999; Pancotto *et al*., 2003), although these data are in contrast to the findings of Brandt *et al*. (2007), in which a strong positive enhancement of decomposition with increased water addition was demonstrated but no negative effect of UV-B radiation was observed. Discrepancies in the literature could be attributed to the influence of additional factors, such as litter quality. However, our observations support our hypothesis that increasing precipitation frequency will lead to less abiotic photodegradation and greater biologically driven decomposition.

When simulated precipitation (rewetting) occurred every 12 days, there was no clear evidence that UV-B radiation influenced aspen leaf litter decomposition rates (Fig. 5). In ecosystems with relatively moderate moisture regimes, UV-B radiation generally has a negligible effect on decomposition rates (Newsham *et al*., 1997; Moody *et al*., 2001). However, this does not necessarily suggest that the likely mechanisms driving increased decomposition rates under dry conditions (photodegradation) and decreased decomposition rates under wet conditions (biological stress) are not operating under moderate moisture regimes. Rather, these counteracting effects may cancel each other out, resulting in no measurable net effect of UV-B radiation on decomposition. In our study, we expected that decomposition rates would increase with elevated UV-B in all reduced-microbial treatments, since the negative effects of UV-B should be negligible in the absence of biological decomposition. However, UV-B radiation did not significantly increase mass loss in reduced-microbial soil treatments under conditions of 4- or 12-day precipitation treatment. Since we did not sterilize the litter surface directly, biotic processes were likely still contributing to leaf litter decay under the reduced-microbial treatment, albeit at a reduced rate compared to microcosms where soils were not sterilized. Thus, the negative effects of UV-B radiation on biological activity likely contributed to the lack of a net effect of UV-B on litter decay rates under these simulated precipitation regimes, even in the reduced-microbial treatments.

Regardless of precipitation frequency, N immobilization declined with increasing UV-B radiation in treatments where soils were not sterilized (Fig. 6). This trend is consistent with a reduction in microbial activity due to UV-B exposure, since biotic processes are the most likely driver of N immobilization. In a 3-year field experiment in a short grass steppe ecosystem, UV

radiation also reduced N immobilization over the summer months (Brandt *et al*. (2007), suggesting that similar mechanisms were operating in our glasshouse experiment. Microbial inhibition by UV-B radiation may result from several different mechanisms including degradation of nucleic acids (Johnson, 2003), reductions in fungal mycelial extension rates and spore germination (Moody *et al*., 1999), and UV-B radiation stress-induced growth inhibition (Pancotto *et al*., 2003). We do not know of any studies that have examined the role of moisture in UV-B damage, but we speculate that microbes are more resilient to UV-B damage when they are not under moisture stress.

Percent litter N remaining was also significantly increased by precipitation frequency, independent of soil treatment. This trend may be due to either N immobilization or the leaching of compounds with higher C : N ratios (Parton *et al*., 2007). Nitrogen immobilization is commonly attributed to fungal transport of N from soils to litter during decomposition (Aber & Melillo, 1982; Parton *et al*., 2007), but increasing percent N remaining during decomposition can also result from the activity of N fixers on the leaf surface (Vitousek & Hobbie, 2000; Reed *et al*., 2007). The magnitude of the positive effect of precipitation frequency on litter N was, however, reduced in the reduced-microbial treatment (Fig. 6). Since only the soil was sterilized rather than the leaf surface, we speculate that reduced N transport by fungi was more affected than leaf surface N-fixation. We might have expected that patterns of N vs. mass remaining would differ depending on the relative contribution of photodegradation vs. biologically driven decomposition, however, we did not find any treatment effects on the slope of this relationship (results not shown).

The results of this glasshouse study cannot be quantitatively extrapolated to field conditions because of limited data of actual conditions at the litter surface in the field. Moreover, decay rates observed for this study are not comparable to average field decay rates recorded for aspen forests (Kochy & Wilson, 1997) due to differences between field and glasshouse conditions. For example, temperatures in the glasshouse were higher than average field conditions and did not simulate field variability. In addition, variables important in regulating surface UV-B radiation, such as canopy and cloud cover, were absent from the glasshouse experiment. Although we have frequently observed leaf litter exposed to sunlight at our field site, there is a need to collect actual UV-B radiation data and at the litter surface as well as litter moisture throughout the year.

UV-B exposure affects litter decomposition in different ways, likely through different mechanisms, depending on water availability. Recent studies have found that climate and litter quality alone predict roughly 80% of the variation in litter decomposition rates across all environments except arid and semi-arid habitats (Parton *et al*., 2007), suggesting that photodegradation of litter in relatively dry environments is the only significant effect of UV-B radiation on decomposition. However, our results suggest that UV-B exposure can affect decomposition in any environment where litter is exposed to UV radiation for even part of the year. Under moisture-limited conditions, photodegradation appears to be an important driver of decomposition when litter is exposed to UV-B (Rozema *et al*., 1997; Austin & Vivanco, 2006; Brandt *et al*., 2007; Day *et al*., 2007), which may result in the volatilization of a fraction of the CO_2 (Brandt *et al*., 2009) that would have been cycled through the soil C pool via microbes during typical biotic decomposition (Schade *et al*., 1999; Austin & Vivanco, 2006; Gallo *et al*., 2006). Thus, photodegradation could directly influence C sequestration, and could be magnified under the altered global precipitation, cloud regimes, and snow cover predicted for a changing climate. For example, one scenario of climate change predicts extended periods of drought coupled with extreme rain events (Carter *et al*., 2007). Under this scenario, photodegradation could become increasingly important because long-term drought will result in microbial inhibition, as well as potentially increased UV-B radiation resulting from reduced cloud cover. Ultimately, future research projects conducted under more natural field conditions and incorporating different combinations of stress factors are needed to gain a more integrated understanding of UV-B radiation effects on abiotic and biotic processes.

Acknowledgements

This study was funded by the USDA UV-B Monitoring and Research Program under a grant from USDA CSREES (Agreement 2006-06106). Laboratory analyses were funded by the National Science Foundation under grant number 0816720 awarded to Heidi Steltzer and Matthew Wallenstein. Glasshouse use and technical support was provided by Jack Morgan at the USDA/ARS Crops Research Laboratory (Fort Collins, CO, USA). Many individuals made important contributions to this research project, including William Parton, George Janson, John Davis, and Roger Reddy. Finally, valuable contributions were made to the writing of this manuscript by the anonymous referees at Global Change Biology.

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