The role of ultraviolet radiation in litter decomposition in arid ecosystems

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Received 18 April 2005; accepted 5 December 2005

Abstract

In arid ecosystems, as much as 75% of solar radiation that penetrates the atmosphere hits the surface of the soil. The combination of high irradiance, high temperature, and low moisture puts constraints on the activity and organization of microbial communities. To separate the direct effects of UV absorbance on litter decomposition from the indirect effects of microbial selection, we placed mixed cohorts of senescent piñon (Pinus edulis) and juniper (Juniperus monosperma) litter into triplicate microcosms assigned to four treatments: UV irradiated (0.6 mW/cm² UV-A and UV-B for 12 h/day), with and without water additions, and non-irradiated with and without water additions. After 26 weeks, mass loss rates did not differ significantly among treatments with 90% organic matter remaining for piñon litter and 60% for juniper. The distribution and abundance of functional groups as assessed by FTIR spectra did not reveal any differences in relation to treatment, but differences were observed in the quantity and quality of dissolved organic carbon (DOC) extracted from the samples. The amount of DOC extracted increased by 56% for piñon litter and decreased by 32% for juniper in the UV-only treatment compared to initial values. Litter treated with UV and water had the lowest concentration of DOC with a decrease of 69% for juniper litter and 28% for piñon. The largest concentration of reactive phenols was found in the UV-only treatment with a 309% increase for piñon litter and a 10% reduction for juniper when compared to initial values. The treatments receiving water in the presence or absence of UV showed a similar response for both litter types, a reduction of 20–30% in phenolic concentration. Five extracellular enzyme activities, used, as indicators of microbial activity, were higher in the treatments that received water, but activities did not show an interaction with UV irradiation. The results suggest that UV radiation alone, or in combination with microbial activity, was as effective at decomposing litter as microbial activity alone. Thus, solar radiation can be an important contributor to litter degradation in arid systems.

Keywords: Ultraviolet radiation; Litter chemistry; Dissolved organic matter; Extracellular enzyme activity

1. Introduction

The carbon cycle in terrestrial ecosystems is defined by the production of organic matter by plants and its subsequent decomposition. In arid ecosystems, decomposition rates are of similar magnitude to those of mesic systems but often are unrelated to measures of chemical composition such as C:N or lignin:N ratio. Such deviations are generally taken as evidence of the role of abiotic variables particularly, solar radiation and temperature in the degradation process (Murphy et al., 1998). These factors are not as relevant in mesic environments because closed canopies shield the soil surface from solar radiation. Although the importance of physicochemical degradation in arid ecosystems is recognized, there has been little empirical investigation of the relative contributions of biotic and abiotic processes.
Arid ecosystems consist of contiguous patches with varying vegetation that differ in carbon quality, nutrient availability, soil properties, and UV exposure, and thus are likely to select diverse microbial communities. Because of anthropogenic ozone depletion, ground level UV-B radiation is increasing by 2–3% per decade (Newsham et al., 2001) and is expected to peak within the next 50 years (Madronich et al., 1998). Most of the ecological research on UV effects has concentrated on plant responses (Caldwell et al., 2004). Although a variety of responses have been reported one consistent finding is an increase in the production of complex phenolics; UV-B stimulates the production of enzymes within the phenyl propanoid pathway (Rozema et al., 2002). These phenolic compounds not only serve as internal UV screens, but they also function in the plant as chemical defenses against herbivores and microbes.

UV-B exposure also affects rates of decomposition, both directly and indirectly (Caldwell and Flint, 1994; Duguay and Klironomos, 2000; Newsham et al., 2001). UV radiation indirectly effects decomposition by inducing plants to increase the production of protective compounds such as tannins and lignins that reduce the biodegradability of the litter (Johanson et al., 1995; Cybulski et al., 2000). However, if surface litter is exposed to UV radiation, photodegradation of aromatic secondary compounds may enhance decomposition rates. Studies in aquatic systems show that bacterial abundance and activity can increase as the result of photoreactions with dissolved organic matter (DOM). However, the magnitude of the effect varies with DOM source and may be negative if condensation reactions reduce the bioavailability of DOM (Denward et al., 1999; Hader et al., 1998; Osburn et al., 2001; Pérez et al., 2003).

In addition to modifying substrate availability, UV also has direct effects on microorganisms. In areas of high UV exposure, selection pressures favor populations that can repair DNA efficiently and synthesize photoprotective pigments (Rohwer and Azam, 2000; Bowker et al., 2002; Hughes et al., 2003). It is also possible that UV exposure may indirectly affect decomposition rates and microbial metabolism by photodegrading the enzymes they release into the environment, even under dry conditions when microbial metabolism is nil.

To better understand the role of UV radiation in litter decomposition in arid ecosystems, we conducted a microcosm experiment to test two hypotheses. The first was that UV exposure would negatively affect microbial decomposition to a similar extent across litter types. The second was that direct photoreactions with litter would differentially affect mass loss rates as a function of chemical composition, and therefore mass loss rates in UV-treated piñon litter would change by a larger magnitude than UV-treated juniper litter.

2. Methods

Senescent piñon (Pinus edulis) and juniper (Juniperus monosperma) leaf litter was collected from the Sevilleta National Wildlife Refuge (latitude 34°22′6.3″N, longitude 106°32′5.7″W) and 5 g was placed into each open top mesh basket. Six baskets of each litter type were placed in terraria atop 5 cm of soil collected from the same area as the litter. There were three treatments with three microcosms per treatment. Six of the microcosms were placed beneath fluorescent lamps containing UV-A and UV-B tubes. There was a 12-h light:12-h dark cycle. Ambient UV-A and UV-B intensities were a constant 0.6 and 0.8 mW/cm², respectively, during the 12-h light period, which is roughly 1/3 of the outdoor, mid-day, mid-year intensities. The terraria were rotated twice a week to ensure uniform radiation of the litter baskets. The other three microcosms were not irradiated. The dark microcosms and three of the UV-radiated microcosms were sprinkled with water every 2–3 days to promote microbial activity. The remaining three UV irradiated microcosms received no moisture. All microcosms were kept at 21 °C. Litter initially collected was also analyzed for comparison; this litter was kept in the dark and not watered, and was not placed into litter baskets for mass loss measurements. The treatment regime was established 2 April 2003 with samples collected on 2 June, 30 June, 28 July, 1 September, 1 October, and 2 December 2003. At every sampling date mass loss measurements were taken and extracellular enzyme activities (EEA) were assayed. Organic matter was determined by combustion at 500 °C. Fourier transform infrared (FTIR) spectra, C and N analyses, and DOM characterizations were conducted on initial samples as well as litter sampled at the end of the experiment.

2.1. Extracellular enzyme assays (EEA)

Litter samples were assayed for acid phosphatase, β-1,4-glucosidase, cellobiohydrolase, leucine aminopeptidase, β-N-acetylglucosaminidase, phenol oxidase, and peroxidase using 4-methylumbelliferyl (MUF) phosphate, MUF-β-glucoside, MUF-cellobioside, L-leucine 7-amido-4 methyl coumarin, MUF-β-N-acetylglucosamine and L-3,4-dihydroxyphenylalanine (DOPA) as...
substrates, respectively, following published protocols (Saiya-Cork et al., 2002; Sinsabaugh et al., 2002). Sample suspensions were prepared by placing 0.5 g litter in a 125 ml Nalgene bottle. Acetate buffer (50 mM, pH 5) was added to the bottle and the resulting suspension was homogenized using a Brinkmann Polytron. Additional buffer was added to the bottle to bring the final suspension volume to 125 ml.

The phenol oxidase and peroxidase assays were conducted in clear 96-well microplates. Sixteen replicate wells were used for each assay; eight additional wells were used as negative substrate controls and another eight wells served as negative sample controls. The assay wells received 200 μL aliquots of sample suspension and 25 mM DOPA substrate. The negative sample control wells contained 200 μL aliquots of sample suspension and 50 μL of acetate buffer. The negative substrate control wells received 200 μL aliquots of acetate buffer and 50 μL substrate. For peroxidase assays, each well also received 10 μL of H2O2 (0.3%). The plates were placed in an Echotherm incubator at 20 °C. Activity was measured spectrophotometrically at 460 nm using a Molecular Devices VERSAmax plate reader. Activity was expressed as μmol/g OM/h.

The hydrolase assays were conducted on black 96-well microplates. The assay design was similar to that described above except that reference standards (eight wells) and quench controls (eight wells per sample) were added to each plate. The reference standard for the acid phosphatase, β-1,4-glucosidase, and celllobiohydrolase assays was 10 mM 4-methylumbelliferone; for the leucine aminopeptidase assay 10 mM 7-amino-4-methylcoumarin was used. Quench control wells contained 200 μL of sample suspension and 50 μL of acetate buffer. The negative substrate control wells received 200 μL aliquots of acetate buffer and 50 μL substrate. For peroxidase assays, each well also received 10 μL of H2O2 (0.3%). The plates were placed in an Echotherm incubator at 20 °C. Activity was measured spectrophotometrically at 460 nm using a Molecular Devices VERSAmax plate reader. Activity was expressed as μmol/g OM/h.

2.2. Fourier transform infrared analysis of litter samples

Litter samples from the initial collection and samples collected on 2 December 2003 were milled (Wiley Mill fitted with a #20 mesh collection vessel) then dried for 48 h at 60 °C immediately prior to analysis. Spectra were collected using a Bruker Tensor 27 FTIR equipped with DLaTGS detector and a Pike Technologies diamond MIRacle single-bounce attenuated total reflectance sampling device. Subsamples of the litter were pressed onto the diamond surface of the MIRacle accessory using a pressure clamp. Spectra were collected at 4 cm⁻¹ resolution, averaging 30 scans per spectrum. Three subsample spectra were acquired and averaged to generate a single mean spectrum per sample.

2.3. DOM characterization

Dissolved organic matter (DOM) was extracted from litter samples collected on 2 December 2003, by placing 0.5 g soil in a 50 ml centrifuge tube with 20 ml of 50 mM sodium bicarbonate buffer, pH 8.2. The tubes were vortexed for 1 min at maximum speed. The resulting slurry was centrifuged for 10 min at 5000 × g. The supernatant was passed through glass fiber and 0.22 μm membrane filters. Three replicate subsamples were extracted for each sample.

To assess the aromaticity of each DOM extract, absorbance was measured from 200 to 500 nm (quartz cuvette, 1 cm path) using a Shimadzu 1601 UV–vis spectrophotometer; 50 mM sodium bicarbonate buffer, pH 8.2, was used as a baseline reference. Litter extracts were diluted 10⁻¹ in bicarbonate buffer, prior to scanning to ensure absorbance values did not exceed the range of the instrument. Mean absorbances, at 10 nm increments, were calculated from the replicate subsamples. Linear regression (LN (ABS) versus wavelength) was used to calculate a first order decay constant (S) for each sample ($A_1 = A_0 e^{-S}$). The regression analysis was performed on absorbances measured from 220 to 500 nm. The value of this decay constant declines as the relative abundance of aromatic molecules increases (Vodacek et al., 1997).

The concentration of reactive phenols in the DOM was quantified using the Folin assay. The assay was performed on DOM extracted by the method above except that deionized water was used instead of sodium bicarbonate buffer. The assay was conducted on clear 96-well microplates. Eight replicate wells were used for each sample. Wells contained 200 μL aliquots of DOM, 10 μL of Folin Ciocalteau reagent, and 10 μL of sodium phosphate. Eight blank wells were prepared using deionized water. Standard wells were prepared using tannic acid. The plates were incubated for an hour and read at 760 nm using a Molecular Devices VERSAmax plate reader. Results are expressed as mg/ml tannic acid equivalents.

Dissolved organic carbon (DOC) was quantified from the water-extracted sample collected on 1 October 2003. DOC concentrations of the filtrates, as well as
negative controls and internal standards, were measured using a Shimadzu TOC-5000A analyzer.

2.4. Elemental analysis

Elemental analyses (carbon and nitrogen) of litter were performed using a CE Instruments Thermoquest NC 2100 CN analyzer. Analyses were performed on initial samples as well as samples collected on 2 December 2003.

2.5. Data analysis

Concentration of extractable DOC, aromaticity of DOM (S-values), mass loss decay constants (k-values), C:N, and concentration of reactive DOM phenols were compared within each litter type in relation to treatment using one-way analysis of variance (ANOVA). Enzyme activities were LN transformed prior to analysis. Enzyme activities within each litter type were compared using a two-way ANOVA, with treatment and date as fixed effects. For FTIR data, multivariate analysis of variance (MANOVA) was used to assess treatment effects, by comparing total peak areas for selected functional groups. Principal component analysis with varimax rotation was used to integrate extracellular enzyme activity changes with treatment.

3. Results

After six months mass loss rates were not significantly different between treatments for either litter type. Approximately 40% of the initial organic matter was lost during the course of the experiment for juniper litter ($k = -0.0014 \text{ day}^{-1}$), but only 10% for piñon litter ($k = -0.0005 \text{ day}^{-1}$) (Fig. 1; Table 1). FTIR spectra did not reveal a significant difference in the abundance or distribution of functional groups between treatments for either litter type (data not shown). DOM extracts from the juniper litter did not show any significant differences in aromaticity or in the concentration of reactive phenols (Table 1). Despite the lack of treatment response in mass loss and functional group composition, significant treatment effects were observed for juniper in the quantity of DOC extracted, in C:N ratio, and in the extracellular enzymes produced. Piñon litter showed significant treatment effects in the quality and quantity of DOM extracted and the extracellular enzyme activity, but did not reveal a difference in C:N. Hydrolytic enzyme activity per unit mass of piñon litter was twice that of juniper litter.

Extracellular enzyme analyses were performed to assess shifts in microbial function in relation to water and UV. Average changes in activity due to treatment were calculated in relation to activities measured on initial litter. No oxidative activity was detected over the course of the experiment. For juniper litter significant treatment effects were observed for all hydrolytic enzymes except acid phosphatase (AP) (Fig. 2A). Relative to initial values, cellubiohydrolase (CBH) and β-glucosidase (BG) activities increased by an average of 38% and 34%, respectively, in the wet–dark treatment; by 58% and 41% in the wet–UV treatment and declined by 2% and 5% in the dry–UV treatment. Leucine aminopeptidase activity (LAP) followed the same trend; in the wet–dark treatment activity increased by an average of 14%, in the wet–UV treatment activity increased 12% and in the dry–UV treatment activity declined 8%. AP and N-acetylglucosaminidase (NAG) activities declined by 12% and 30%, respectively, in the wet–dark treatment, and by 11% and 41% in the wet–UV treatment. Activities in the dry–UV treatment were unchanged for both enzymes.

For piñon litter (Fig. 2B), cellulase activity followed the same trend observed for juniper: CBH and BG increased by an average of 63% and 48% in the wet–dark treatment, by 54% and 44% in the wet–UV treatment and declined by 23% and 12% in the dry–UV treatment. LAP also showed a similar pattern of increased activity with water and a decline in activity in the dry–UV treatment that was consistent with juniper; in the wet–dark treatment LAP increased 22%, in the wet–UV treatment activity increased 10% and in the dry–UV treatment decreased by 47%. The responses of NAG and AP in the piñon litter differed from those observed for juniper (a decline in activity or no change): NAG increased by 73% in the wet–dark treatment, increased 74% in the wet–UV treatment and decreased 12% in the dry–UV treatment. AP activity increased by 49% in the wet–dark treatment, by 48% in the wet–UV treatment, and by 21% in the dry–UV treatment.

Juniper litter showed a decline in C:N with treatment; the C:N ratio ranged from 35.6 in the initial litter to 35.6 in the wet–dark treatment ($p = 0.003$, Table 1). There were significant differences between the initial litter and the treatments receiving water, but the dry–UV treatment was similar in C:N content. The changes in C:N ratios were mainly due to changes in %N, with an increase observed in all treatments.

There was a higher percentage of both C and N in piñon litter versus juniper litter. The C:N ratio of piñon litter increased with treatment and ranged from
Fig. 1. Mass loss for juniper (A) and piñon (B) litter by treatment. The natural log of the data was taken to calculate mass loss rates, which are expressed as first order rate constants \( k \) (values in Table 1). The error bars represent standard error. Each point has an \( n = 3 \). The wet–dark treatment represents a microbial control treatment. UV irradiation was approximately \( 1/3 \) of outdoor, mid-day, mid-year intensities. Mass loss rates within each litter type were not significantly different, but rates between litter types were significant, \( \alpha < 0.05 \).

Table 1

<table>
<thead>
<tr>
<th>Litter</th>
<th>Treatment</th>
<th>( k )</th>
<th>DOC (%)</th>
<th>Phenols (mg/ml)</th>
<th>( S )</th>
<th>C (%)</th>
<th>N (%)</th>
<th>C:N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juniper</td>
<td>Initial</td>
<td>N/A</td>
<td>3.88 (0.78)(^a)</td>
<td>0.528 (0.05)</td>
<td>-0.0133 (0.000)</td>
<td>24.5 (2.39)</td>
<td>0.6 (0.04)(^a)</td>
<td>44.5 (3.45)(^a)</td>
</tr>
<tr>
<td></td>
<td>Wet–dark</td>
<td>-0.0011 (0.0002)</td>
<td>1.60 (0.41)(^a)</td>
<td>0.395 (0.19)</td>
<td>-0.0126 (0.001)</td>
<td>29.4 (7.71)</td>
<td>0.8 (0.16)(^a)</td>
<td>35.6 (2.33)(^a)</td>
</tr>
<tr>
<td></td>
<td>Wet–UV</td>
<td>-0.0018 (0.0009)</td>
<td>1.21 (0.43)(^a)</td>
<td>0.381 (0.23)</td>
<td>-0.0134 (0.0009)</td>
<td>28.7 (5.06)</td>
<td>0.8 (0.17)(^a)</td>
<td>37.2 (1.93)(^a)</td>
</tr>
<tr>
<td></td>
<td>Dry–UV</td>
<td>-0.0013 (0.0005)</td>
<td>2.64 (0.29)(^a)</td>
<td>0.478 (0.19)</td>
<td>-0.0134 (0.0001)</td>
<td>32.4 (2.81)</td>
<td>0.7 (0.08)(^a)</td>
<td>44.0 (1.31)(^a)</td>
</tr>
<tr>
<td>Piñon</td>
<td>Initial</td>
<td>N/A</td>
<td>2.07 (0.58)(^a)</td>
<td>0.195 (0.19)(^a)</td>
<td>-0.0134(^a) (0.000)</td>
<td>40.0 (3.30)</td>
<td>1.2 (0.17)</td>
<td>32.4 (1.98)</td>
</tr>
<tr>
<td></td>
<td>Wet–dark</td>
<td>-0.0006 (0.0002)</td>
<td>1.83 (0.33)(^a)</td>
<td>0.230 (0.10)(^a)</td>
<td>-0.0142(^a) (0.0002)</td>
<td>44.1 (3.15)</td>
<td>1.2 (0.05)</td>
<td>37.4 (4.01)</td>
</tr>
<tr>
<td></td>
<td>Wet–UV</td>
<td>-0.0005 (0.0003)</td>
<td>1.50 (0.36)(^a)</td>
<td>0.147 (0.04)(^a)</td>
<td>-0.0141(^a) (0.0006)</td>
<td>44.9 (0.64)</td>
<td>1.3 (0.06)</td>
<td>35.3 (2.27)</td>
</tr>
<tr>
<td></td>
<td>Dry–UV</td>
<td>-0.0004 (0.0000)</td>
<td>3.22 (0.60)(^a)</td>
<td>0.798 (0.19)(^a)</td>
<td>-0.0137(^a) (0.0002)</td>
<td>45.1 (1.13)</td>
<td>1.2 (0.01)</td>
<td>36.2 (0.59)</td>
</tr>
</tbody>
</table>

The values are the mean of three replicates; values in parentheses are standard deviations; \( k \) = decay rate. Rates are first order constants determined from the natural log of percent organic matter remaining. The rates are expressed as %OM lost/day. Concentration of phenols was determined using a tannic acid standard. \( S \) is the slope of the line determined from the natural log of absorbance measured in 10 nm intervals from 220–500 nm.

\(^a\) Significant treatment effect, \( \alpha < 0.05 \).
32.4 in the initial litter to 37.4 in the wet–dark treatment \( (p = 0.17, \text{ Table 1}) \). The changes in C:N were due to slight alterations in the %C present in the samples.

There was no significant difference in the amount of DOC extracted between litter types. For juniper litter relative to initial values, extractable DOC decreased significantly in all treatments with the most dramatic differences observed in the wet treatments; the residual litter from the wet–dark treatment contained 59% less DOC per gram than the initial litter, the corresponding declines for the wet–UV treatment and the dry–UV treatment were 69% and 32% (Table 1, Fig. 3A). Comparable effects were observed in piñon litter, but the wet treatments and the dry–UV treatment responded differentially. The concentration of DOC extracted from the dry–UV treatment was 56% higher than that from the initial litter samples, the wet–dark treatment produced 12% less DOC than the initial litter and the wet–UV treatment was 28% lower (Table 1; Fig. 3A).

Juniper litter did not show differences in DOM quality, but the trend in phenol concentration was a decrease in all treatments in conjunction with the observed decrease in extractable DOC. Reactive phenols declined by 25% in the wet–dark treatment,
by 28% in the wet–UV treatment and by 10% in the dry–UV treatment (Table 1; Fig. 3B). Overall aromaticity, as indicated by UV–vis absorbance spectra, displayed slight shifts in relation to initial samples. Aromaticity decreased by 1% in UV–treated litter regardless of the addition of water, while the wet–dark treatment showed an increase in aromaticity of 5% compared to initial values (Table 1).

In contrast to the juniper litter, piñon litter showed a significant difference in the quality of DOM extracted. In general, the overall aromaticity of piñon DOM was similar to juniper, but the average concentration of reactive phenols was less. The amount of reactive phenols extracted from the wet–dark treatment increased 18% when compared to the initial litter collected. The wet–UV treatment decreased 25%, while the dry–UV treatment increased 309% (Table 1; Fig. 3B). UV–vis absorbance spectra also revealed treatment effects in the quality of DOM extracted. The DOM extracted from all of the treatments was less aromatic than the DOM extracted from the initial litter. The slope value for the wet–dark treatment showed a 6% decrease in aromaticity, the wet–UV treatment was 5% less aromatic and the dry–UV treatment was 2% less aromatic (Table 1).

Principal component analysis was performed on the enzyme activities to reduce the data to one integrated factor for use in explaining overall enzyme activity response to treatment. The principle component factor created explained 66% of the variance and was positively correlated with all enzymes, but the following enzymes were correlated to the factor at values higher than 0.80: AP, βG, NAG, and CBH. Factor scores from the component were plotted against %DOC and concentration of reactive phenols (Fig. 3B) to relate changes in biotic processes to changes in substrate chemistry. The addition of water regardless of the presence of UV increased overall enzyme activity for both litter types when compared to the initial litter. Piñon activity was affected to a greater extent than juniper activity by the addition of water, but the dry–UV treatments for both litter types were comparable to the values observed for the initial litter. The presence of water alone had a larger influence on %DOC in juniper litter than piñon. The combination of UV and water depressed %DOC to the greatest extent in both litters and the UV only treatment showed a differential response, an increase in DOC in piñon and a decrease in juniper. Fig. 3B revealed that juniper DOM quality was influenced the most by water, while UV affected piñon more. The combination of UV and water further depressed phenol concentration in piñon.
4. Discussion

No clear relationship exists between duration and frequency of moisture inputs and mass loss rates in desert systems as would be expected if mass loss rates were a function of biotic processes alone (Whitford, 1985). This observation highlights the potential importance of photodegradation in the carbon dynamics of arid ecosystems.

The direct effect of UV irradiation on litter chemistry and hence on litter decomposition has been demonstrated in several studies, including our own, with mixed results. Rozema et al. (1997) showed increased mass loss rates in conjunction with lower concentrations of lignin and hemicellulose in litter subjected to enhanced UV. Other studies have shown reduced mass loss rates in litter exposed to high irradiation despite lower concentrations of lignin (Duguay and Klironomos, 2000; Gehrke et al., 1995). Verhoef et al. (2000) examined changes in the mass loss rates of the dune grasses, Calamagrostis epigeios and Carex arenaria, and observed no difference under enhanced UV. The overall results of these studies indicate that photodegradation is important in reducing the lignin content of the substrate, but species responses to UV are variable.

Our results are consistent with those of Verhoef et al. (2000). We saw no difference in the mass loss rates of juniper or piñon litter exposed to UV irradiation in the presence or absence of water. We predicted that mass loss rates would change more dramatically with treatment in the piñon litter based on the litter quality analyses performed by Murphy et al. (1998), but this was not the case. The lack of significant differences in the Verhoef study and our study are most likely due to the short duration of the experiments (6 months) and/or the use of partially degraded litter in the treatments. But mass loss rates between litter types were significantly different (Fig. 1) with piñon losing 10% of its OM and juniper losing 40%. Overall aromaticity of juniper and piñon litter was similar, but the enzyme activity on piñon litter was double that observed on juniper. The C:N ratio of juniper varied with treatment, while piñon litter was similar across treatment. The higher enzymatic activity of piñon, lower degradation rates, and similar C:N lends support to the model proposed by Schimel and Weintraub (2003), in which saturation kinetics, i.e. the number of available binding sites, imposes control on decomposition rather than the overall recalcitrance of the substrate.

The difference in mass loss rates between juniper and piñon as well as the variability observed between studies suggests that initial litter chemistry strongly influences species response; the endemic microbial community may also influence species response to elevated UV. The similarity in mass loss rates observed across our treatments also suggest that UV and microbes are both effective at decomposition over a range of conditions. It appears that the potential negative effects of UV on microbial communities are offset by the positive effect of UV on secondary compound degradation.

In our study the lack of differences in mass loss rates and functional groups between treatments suggests that regardless of locale (high light or shaded area), decomposition will occur at approximately the same level, but examination of fine-scale changes, i.e. qualitative and quantitative differences in DOM indicate that UV has an important role. It is evident that the initial chemical composition of the litter regulates the degree of litter breakdown by UV and, in turn the accessibility of usable degradation products by the resident microbial community. The concentration of reactive phenols in the initial juniper litter was higher than that of piñon litter, but the direct effect of UV on the concentration of phenols was more dramatic in the piñon litter (Fig. 3). Degradation of the more aromatic piñon litter by UV resulted in a large release of reactive phenols and a corresponding increase in %DOC (Fig. 3). This result is consistent with Yue et al. (1998), who found that UV-B stimulated the release of organic carbon in spring wheat. The concentration of phenols in piñon was not altered by the sole addition of water as juniper was, suggesting that microbial degradation of piñon is controlled by accessibility to labile components. The interaction effect of moisture and UV decreased the concentrations of DOC and phenols in both litters more than water alone. This suggests a mechanism of photodegradation of polyphenols in the surface litter and utilization of the degradation products by the microbial community.

UV will indirectly impact litter decomposition by selecting for microbial populations that are more tolerant of UV irradiation. It has been shown that UV-B induces the production of photopigments, such as scytoneimin and carotenoids, in Nostoc (Ehling-Schulz et al., 1997). Hughes et al. (2003) found that the growth of fungal hyphae in five species was inhibited under elevated UV-B and Booth et al. (2001) found that the production of a protein involved in DNA repair, RecA, was induced under UV irradiation.

Our study did not directly measure shifts in microbial community composition, but alterations in composition were inferred from differences in
extracellular enzyme production. The organization of the treatments along the EEA factor (Fig. 3) showed that the presence of water increased enzyme activity in both litter types, while UV irradiation alone has minimal effect on enzyme activity. Similar levels of enzymatic activity between the initial litters and the treatments receiving UV only suggest the enzymes are stable under irradiation. Together these results indicate that the presence of water is the overriding factor in modulating microbial activity. The combination of UV and water increased activity for pinon while the interaction of water and UV on juniper decreased activity relative to the water only treatment. The differential response of the litters to the interaction of water and UV suggests that the microbial community organized on the juniper litter may be more susceptible to UV damage. If the water additions were applied in an amount and frequency that mimicked the natural system the observed differences between the wet–dark and wet–UV treatment may have been larger. Caldwell et al. (2004) found that UV-B effects were dampened if enough water was applied to drought stressed species.

The results of this study suggest that ultraviolet radiation is just as effective as microbial activity in degrading litter in arid ecosystems. This effect however is variable with litter composition and therefore our ability to predict ecosystem response necessitates the continued study of microbial communities in UV exposed litter.

Acknowledgement

This research was supported by the University of New Mexico, RAC, interdisciplinary grant no. 03-IG-06.

References


