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Ultraviolet photodegradation facilitates microbial litter decomposition in a Mediterranean climate

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Abstract. Rates of litter decomposition in dryland ecosystems are consistently underestimated by decomposition models driven by temperature, moisture, and litter chemistry. The most common explanation for this pattern is that ultraviolet radiation (UV) increases decomposition through photodegradation of the litter lignin fraction. Alternatively, UV could increase decomposition through effects on microbial activity. To assess the mechanisms underlying UV photodegradation in a semiarid climate, we exposed high- and low-lignin litter to ambient and blocked UV over 15 months in a Mediterranean ecosystem. We hypothesized that UV would increase litter mass loss, that UV would preferentially increase mass loss of the lignin fraction, and that UV would have a negative effect on microbial activity. Consistent with our first hypothesis, we found that UV-blocking reduced litter mass loss from 16% to 1% in high-lignin litter and from 29% to 17% in low-lignin litter. Contrary to our second hypothesis, UV treatment did not have a significant effect on lignin content in either litter type. Instead, UV-blocking significantly reduced cellulose and hemicellulose mass loss in both litter types. Contrary to our third hypothesis, we observed a positive effect of UV on both fungal abundance and the potential activities of several assayed extracellular enzymes. Additionally, under ambient UV only, we found significant correlations between potential activities of cellulase and oxidase enzymes and both the concentrations and degradation rates of their target compounds. Our results indicate that UV is a significant driver of litter mass loss in Mediterranean ecosystems, but not solely because UV directly degrades carbon compounds such as lignin. Rather, UV facilitates microbial degradation of litter compounds, such as cellulose and hemicellulose. Thus, unexpectedly high rates of litter decomposition previously attributed directly to UV in dryland ecosystems may actually derive from a synergistic interaction between UV and microbes.

Key words: decomposition; extracellular enzymes; lignin; microbes; photodegradation; ultraviolet radiation.

INTRODUCTION

Litter decomposition is a key contributor to the global annual flux of ~68 Pg carbon (C) that enters the atmosphere from heterotrophic respiration (Raich and Schlesinger 2002). Much early work on litter decomposition was performed in mesic ecosystems, where temperature, moisture, and litter chemistry are primary drivers of decomposition rates (Meentemeyer 1978, Parton et al. 1987). However, models built around these three drivers consistently underestimate rates of decomposition in more xeric dryland ecosystems, such as semiarid Mediterranean grasslands and arid deserts (Whitford et al. 1981). Multiple hypotheses have been proposed for the unexplained mechanisms contributing to this discrepancy: foraging by subterranean microarthropods (Johnson and Whitford 1975), persistence of microbe-sustaining microclimates as a result of high overnight humidity (Whitford et al. 1981, Nagy and Macauley 1982, Dirks et al. 2010), and photodegradation by solar radiation (Pauli 1964, Moorhead and Reynolds 1989). Photodegradation in terrestrial ecosystems as a result of ultraviolet radiation (UV), in particular, has become the focus of a growing body of literature in the last decade (reviewed in King et al. 2012 and Song et al. 2013).

Photodegradation is thought to take on added importance in dryland ecosystems through a variety of mechanisms. First, litter in dryland ecosystems is subject to a greater intensity of solar radiation because there are fewer days of cloud cover and lower levels of shade than in more productive ecosystems (Pauli 1964). Second, in grassland ecosystems, litter is formed through the senescence of standing grass. This standing litter may be subject to photodegradation before it comes in contact with the soil microbial community (Austin and Vivanco 2006). Third, the presumed inhibition of microbial activity by dry climates should reduce the importance of microbial decomposition and increase the importance of abiotic drivers, such as photodegradation...
mass loss while inhibiting microbial activity. These months, UV might alter litter chemistry and stimulate terrestrial microbes (Hughes et al. 2003). On the other hand, UV facilitation of microbial communities could be important in semiarid Mediterranean ecosystems, as it is known to damage microbial DNA (Rohwer and Azam 2000), and suppress growth of terrestrial microbes (Hughes et al. 2003). On the other hand, UV facilitation of microbial communities could be especially important in semiarid Mediterranean ecosystems with marked seasonality. In the dry summer months, UV might alter litter chemistry and stimulate mass loss while inhibiting microbial activity. These changes in litter chemistry could then facilitate microbial decomposition during the wet winter months with lower UV radiation. Microbial communities in dryland ecosystems might also be adapted to UV radiation, and there is some evidence that UV exposure alters microbial community composition (Caldwell et al. 2007). Long-term exposure could select for microbes that are more capable of withstanding UV radiation or better able to use photodegraded litter compounds.

We tested three hypotheses in a litterbag experiment whereby UV exposure and litter chemistry were both manipulated at two levels. First, we hypothesized that UV photodegradation would enhance litter mass loss in a Mediterranean ecosystem, potentially as a result of direct or indirect photolysis of organic compounds in litter (King et al. 2012). Second, we hypothesized that UV would preferentially degrade the lignin fraction in litter, as its aromatic structure is known to absorb UV wavelengths (Austin and Ballaré 2010) and is thought to undergo chemical changes when exposed to solar radiation (Lanzalunga and Bietti 2000). Finally, we hypothesized that the net result of UV is inhibition of microbial activity, given previous observations that UV can damage microbial DNA (Rohwer and Azam 2000), slow the growth of microbial communities (Hughes et al. 2003), and result in altered microbial community composition (Caldwell et al. 2007).

**Materials and Methods**

**Site description and field manipulation**

To test our hypotheses, we used a litterbag study with a split-plot design. Twelve 1-m² plots were paired into six split-plots at the University of California, Irvine Arboretum in Irvine, California, USA (33°39′ N, 117°51′ W). The Arboretum is situated 30 m above sea level and has a mean annual temperature of 17°C and mean annual precipitation of 30 cm. Local vegetation consists of coastal sage scrub.

Each set of paired plots consisted of one ambient plot (hereafter referred to as the UV-pass treatment) and one plot covered with polyester UV-blocking film supported by a PVC frame (hereafter referred to as the UV-block treatment). This film blocked 68% of all UV while allowing 90% transmittance of visible light, as measured by a UV photometer on-site. PVC frames were 1 m on each side and set up 40 cm above the soil surface, with strips of UV-blocking film 20 cm wide used to cover the plot area under the frame. Gaps 1 cm wide between strips of film allowed precipitation to infiltrate to the plot area, and the distance between the frame and soil surface was chosen to limit the potentially strong greenhouse effects of film coverage found by Uselman et al. (2011). Ambient plots had no PVC frame or film covering.

Within each paired plot, two types of litterbags were deployed: four containing litter of *Avena* species (*A. barbata* and *A. fatua*) with 7.38% (±0.05%; mean ± SE) lignin by mass, and four containing litter of *Elymus*
condensatus (Giant wild rye), a grass species with 13.05% (±0.08%) lignin by mass. *Avena* litter contained 4.79% (±0.10%) crude protein and 4.08% (±0.03%) ethanol soluble carbohydrates, while *Elymus* litter contained 3.81% (±0.09) and 2.44% (±0.19), respectively. Both litter types were more similar in cellulose and hemicellulose content than they were in lignin content (Table 2). Hereafter, *Avena* litter is referred to as low lignin and *Elymus* litter is referred to as high lignin. Both litter types were collected in late June of 2012 as standing, senesced litter from Loma Ridge (33°44' N, 117°42' W, 365 m elevation), a Mediterranean grassland managed by the Irvine Ranch Conservancy 16 km northeast of the field site in Irvine. Litter of each type was collected by clipping standing litter at least 20 cm above the soil surface to minimize prior soil contact, then homogenized by clipping to <5 cm lengths and mixing. A subsample was weighed and oven-dried to determine moisture content. The equivalent of 1.9-g dry mass of litter (including ash content) was then added to litterbags for each litter type and deployed in the field on 18 July 2012. Each litterbag was made of two types of mesh: a 1.5-mm aluminum mesh used for the side exposed to the sun and a 0.5-mm nylon bridal mesh used for the side exposed to the soil surface.

Four litterbags of both litter types were deployed into each of the six paired plots, resulting in 96 total litterbags (4 × 2 × 6 × 2). One litterbag of each litter type was then collected randomly from each of the paired plots at the end of the first dry season (2 October 2012), the middle of the wet season (18 January 2013), the end of the wet season (4 June 2013), and the end of the second dry season (17 September 2013), for a total of five time points (including the initial deployment) over a period of 15 months. Collected litter was weighed to determine mass loss before being ground into fragments <0.5 cm in length and subsampled for extracellular enzyme assays, a bacterial cell count assay, and a fungal hyphae staining assay. The remainder of the litter was weighed and oven-dried to determine moisture content before being sent off for near-infrared (or near-IR) analysis of litter chemistry.

**Extracellular enzyme assays**

Litter was assayed for potential activity of eight enzyme classes using fluorescently labeled substrates (for hydrolytic enzymes) or colorimetric assays (for oxidative enzymes) according to methods detailed in German et al. (2012). The enzyme classes assayed consisted of hydrolytic cellulose and starch degradation (β-glucosidase, cellobiohydrolase, and α-glucosidase; or BG, CBH, and AG, respectively), hydrolytic hemicellulose degradation (β-xylidosidase; or BX), hydrolytic chitin-degradation (N-acetylglucosaminidase; or NAG), peptide degradation (leucine-aminopeptidase; or LAP), and oxidative degradation (peroxidase and phenol oxidase; or PER and PPO, respectively). Negative potential activities were converted to zero values for statistical analyses.

**Bacterial cell density**

Methods for estimating bacterial cell density were identical to those used in Allison et al. (2013). In brief, ground litter was suspended in a phosphate-buffered, 1% glutaraldehyde solution on the day of sample collection to fix bacterial cells for storage. Within two weeks, 0.1 M tetrasodium pyrophosphate was added to each sample, and samples were sonicated to dislodge bacterial cells. Filtered extracts of sonicated litter were stained with 1× SYBR Green (Life Technologies, Grand Island, New York, USA) and then analyzed with an Accuri flow cytometer (BD Biosciences, San Jose, California, USA) to determine cell counts from fluorescing bacterial cells.

**Fungal hyphal length**

Methods for measuring fungal hyphal length were identical to those used in Allison et al. (2013). In brief, ground litter was suspended in 0.395% (mass per volume) sodium hexametaphosphate and vigorously stirred before being vacuum-filtered and stained with acid fuchsin. Two filters were made for each litter sample and affixed to a glass slide. Hyphae were counted with a Nikon Eclipse E400 microscope (Nikon Instruments, Melville, New York, USA) at 100× magnification using the grid-intercept method (Newman 1966, Giovanetti and Mosse 1980) and 50 grids per filter. Hyphal counts were converted to estimates of hyphal length in m/g of dry litter using a modified procedure of Sylvia (1992).

**Litter chemistry**

Oven-dried litter was sent to Cumberland Valley Analytical Services for near-IR spectroscopy, whereby reflectance of near-infrared wavelengths of light from each sample are matched to a verified database of spectra for plant materials with known chemical composition as determined by wet chemistry (Shepherd et al. 2005). Relative amounts of the following organic compounds were determined as proportions of total dried litter mass: lignin, cellulose (acid detergent fiber minus lignin) hemicellulose (neutral detergent fiber minus acid detergent fiber), ash, and non-ash dry mass (1 minus ash fraction). The proportion of total litter mass attributable to different C compounds will be referred to as concentration in the text. The concentration of non-ash dry mass was multiplied by the recovered dry mass at each time point to determine mass loss from the organic portion of litter. The same calculation was used to determine mass loss for each carbon compound (lignin, cellulose, and hemicellulose). The total mass or mass lost from each carbon compound will be referred to as content in the text.

**Statistical methods**

Effects of UV treatment, litter type, and sampling date on non-ash dry mass, litter chemistry, litter moisture, and bacterial cell counts were analyzed using mixed-model ANOVA with the identity of each pair of
split plots as a random factor. We originally compared this simple model with a more complex model whereby plot identity was a random factor within which UV, litter type, and time were nested, but Akaike’s information criterion (AIC) comparison showed no significant differences between the two models. The simpler model had a lower AICc (Akaike’s information criterion corrected for sample sizes; 51.7 vs. 60.3), AIC (42.6 vs. 47.5), BIC (Bayesian information criterion; 85.0 vs. 97.0), and log-likelihood (~3.3 vs. ~2.7), allowing us to employ it with a high degree of confidence. Tukey contrasts were used to determine the effect of UV within litter types at each time point.

Because litter moisture content was found to be significantly affected by UV treatment (Appendix A: Fig. A1, Table A1) and is known to be a strong control on decomposition processes in Mediterranean ecosystems, the model was run for all variables as an ANCOVA with litter moisture content as the covariate. Data were checked for normality using the Shapiro-Wilk test, and nonnormal data were log-transformed or square-root transformed to improve normality. Original mass across both UV treatments, with an average of 23.2% mass loss by June 2013. High-lignin litter lost most mass across both UV treatments, with an average of 23.2% mass loss by June 2013 under UV-pass, but exhibited negligible mass loss in UV-block samples, but otherwise lost negligible mass. Low-lignin litter lost an average of 11.0% of original mass across both UV treatments over the same time period. There was no significant interaction between litter type and UV treatment. High-lignin litter lost 16.2% of original mass by June 2013 under UV-pass, but exhibited negligible (≤1%) mass loss under UV-block. Low-lignin samples showed a similar pattern (29.0% mass loss in UV-pass samples vs. 17.4% mass loss in UV-block samples), but post hoc tests within dates were only marginally significant (Fig. 1). Mass loss was not significantly affected by UV treatment after the first dry season (July 2012–September 2012), for either high-lignin or low-

### RESULTS

**Litter mass loss and moisture content**

Litter mass loss was affected by both litter type ($P < 0.001, F_{1,72} = 112.1$) and by UV treatment ($P < 0.001, F_{1,72} = 60.9$; Table 1, Fig. 1). Low-lignin litter lost the most mass across both UV treatments, with an average of 23.2% mass loss by June 2013. High-lignin litter lost an average of 11.0% of original mass across both UV treatments over the same time period. There was no significant interaction between litter type and UV treatment. High-lignin litter lost 16.2% of original mass by June 2013 under UV-pass, but exhibited negligible (≤1%) mass loss under UV-block. Low-lignin samples showed a similar pattern (29.0% mass loss in UV-pass samples vs. 17.4% mass loss in UV-block samples), but post hoc tests within dates were only marginally significant (Fig. 1). Mass loss was not significantly affected by UV treatment after the first dry season (July 2012–September 2012), for either high-lignin or low-

### Table 1. P values from ANCOVA for each dependent variable with respect to UV treatment, litter type, time of sampling, and all possible interactions with litter moisture content as a covariate.

<table>
<thead>
<tr>
<th>Variable</th>
<th>H2O</th>
<th>UV</th>
<th>Litter</th>
<th>Time</th>
<th>UV:Litter</th>
<th>UV:T</th>
<th>Lit:T</th>
<th>UV:Litter:T</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-ash dry mass</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.084</td>
<td>0.370</td>
<td>0.750</td>
<td>0.946</td>
</tr>
<tr>
<td>Lignin (g)</td>
<td>&lt;0.001</td>
<td>0.090</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.016</td>
<td>0.064</td>
<td>&lt;0.001</td>
<td>0.346</td>
</tr>
<tr>
<td>Cellulose (g)</td>
<td>&lt;0.001</td>
<td>0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.006</td>
<td>0.061</td>
<td>&lt;0.001</td>
<td>0.872</td>
</tr>
<tr>
<td>Hemicellulose (g)</td>
<td>0.068</td>
<td>&lt;0.001</td>
<td>0.963</td>
<td>&lt;0.001</td>
<td>0.300</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.016</td>
</tr>
<tr>
<td>Bacterial cells</td>
<td>0.522</td>
<td>0.151</td>
<td>0.223</td>
<td>&lt;0.001</td>
<td>0.533</td>
<td>0.297</td>
<td>0.042</td>
<td>0.508</td>
</tr>
<tr>
<td>Fungal hyphae</td>
<td>0.609</td>
<td>0.024</td>
<td>0.004</td>
<td>&lt;0.001</td>
<td>0.115</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.017</td>
</tr>
<tr>
<td>BG activity</td>
<td>0.884</td>
<td>0.444</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.132</td>
<td>0.212</td>
<td>&lt;0.001</td>
<td>0.217</td>
</tr>
<tr>
<td>CBH activity</td>
<td>0.143</td>
<td>0.406</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.107</td>
<td>0.026</td>
<td>0.002</td>
<td>0.030</td>
</tr>
<tr>
<td>AG activity</td>
<td>0.036</td>
<td>0.070</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.072</td>
<td>0.340</td>
<td>0.252</td>
<td>0.281</td>
</tr>
<tr>
<td>BX activity</td>
<td>&lt;0.001</td>
<td>0.230</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.194</td>
<td>&lt;0.001</td>
<td>0.008</td>
<td>0.113</td>
</tr>
<tr>
<td>PPO activity</td>
<td>0.021</td>
<td>0.822</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.918</td>
<td>&lt;0.001</td>
<td>0.059</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>PER activity</td>
<td>0.935</td>
<td>0.233</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.733</td>
<td>0.415</td>
<td>0.001</td>
<td>0.041</td>
</tr>
<tr>
<td>NAG activity</td>
<td>&lt;0.001</td>
<td>0.085</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.028</td>
<td>0.061</td>
<td>0.042</td>
<td>0.170</td>
</tr>
<tr>
<td>LAP activity</td>
<td>&lt;0.001</td>
<td>0.017</td>
<td>0.109</td>
<td>&lt;0.001</td>
<td>0.001</td>
<td>0.008</td>
<td>0.020</td>
<td>0.343</td>
</tr>
<tr>
<td>Ndf, Ddf</td>
<td>1, 72</td>
<td>1, 72</td>
<td>1, 72</td>
<td>3, 72</td>
<td>1, 72</td>
<td>3, 72</td>
<td>3, 72</td>
<td>3, 72</td>
</tr>
</tbody>
</table>

**Notes:** Significant P values ($P < 0.05$) are in bold. Ndf and Ddf are the degrees of freedom for the numerator and denominator of F, respectively. BG is β-glucosidase, CBH is cellobiohydrolase, AG is α-glucosidase, BX is β-xyllosidase, PPO is phenol oxidase, PER is peroxidase, NAG is N-acetylglucosaminidase, and LAP is leucine-aminopeptidase. Abbreviations are lit, litter; T, time.
increase in lignin content over time (Tables 1 and 2) is significantly lower by 0.67 percentage points in low-lignin samples (L–) compared to high-lignin litter (L+). Lignin content was significantly affected by litter type (P < 0.001, F_{1,72} = 137.9) and UV treatment (P < 0.001, F_{1,72} = 74.5). There was a significant interaction between UV treatment and litter type on cellulose content because UV had a stronger effect on cellulose content in high-lignin litter than in low-lignin litter (Tukey P = 0.017 for UV effect in low-lignin litter, P < 0.001 in high-lignin litter; Appendix B: Fig. B1). Litter hemicellulose content was not significantly affected by litter type, but was significantly affected by UV treatment (P < 0.001, F_{1,72} = 25.5; Table 1). Both litter types had reduced cellulose and hemicellulose content under UV-pass compared to UV-block (Table 2).

**Bacterial cell counts**

Neither litter type nor UV treatment had a significant effect on bacterial cell counts (Table 1; Appendix A: Fig. 2A). Bacterial abundance across and within all treatments was significantly higher on 4 June 2013 when compared to all other time points (Tukey P < 0.001).

**Fungal hyphal length**

In contrast to bacterial abundance, fungal hyphal length was significantly affected by both UV treatment (P = 0.024, F_{1,72} = 5.3) and litter type (P = 0.004, F_{1,72} = 8.7; Table 1, Fig. 2B). The UV-pass treatment did not, in

**Carbon fractions**

High-lignin litter began the study with 13.05% ± 0.08% lignin by mass and low-lignin litter began the study with 7.38% ± 0.06%. Lignin content was significantly affected by litter type (P < 0.001, F_{1,72} = 371.9), but UV treatment had only a marginally significant effect (P = 0.090, F_{1,72} = 2.96). The significant increase in lignin content over time (Tables 1 and 2) is likely due to the deposition over time of particulate matter containing organic compounds, either microbial byproducts or plant detritus, that have a lignin-like near-IR signal. Litter cellulose content was significantly affected by litter type (P < 0.001, F_{1,72} = 13.1; Appendix A: Table A1, Fig. A1). Litter moisture content ranged from 7% to 14% of litter mass (Appendix A: Fig. A1). UV-block significantly reduced litter moisture content by 0.47 percentage points (P = 0.04, F_{1,73} = 4.4), and moisture content was significantly lower by 0.67 percentage points in low-lignin litter compared to high-lignin litter (P < 0.001, F_{1,73} = 13.1; Appendix A: Table A1, Fig. A1). Litter moisture also varied significantly over time with the lowest values in January 2013 (P < 0.001, F_{1,73} = 94.3).

**Table 2.** Pearson coefficients and P values for the correlation (Corr.) between C fraction concentration and potential enzyme activity of the enzyme class that degrades that fraction.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>BG (cellulose)</th>
<th>CBH (cellulose)</th>
<th>BX (hemicellulose)</th>
<th>PER (lignin)</th>
<th>PPO (lignin)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L–, UV–</td>
<td>0.475 0.011</td>
<td>0.423 0.025</td>
<td>0.243 0.213</td>
<td>0.690 &lt;0.001</td>
<td>0.551 0.002</td>
</tr>
<tr>
<td>L+, UV+</td>
<td>0.043 0.823</td>
<td>0.096 0.612</td>
<td>0.096 0.612</td>
<td>0.333 0.083</td>
<td>0.517 0.005</td>
</tr>
<tr>
<td>L+, UV–</td>
<td>0.017 0.927</td>
<td>0.023 0.233</td>
<td>0.198 0.293</td>
<td>-0.510 0.004</td>
<td>-0.484 0.007</td>
</tr>
<tr>
<td>L–, UV+</td>
<td>0.018 0.925</td>
<td>0.224 0.233</td>
<td>0.092 0.628</td>
<td>0.146 0.440</td>
<td>0.236 0.210</td>
</tr>
</tbody>
</table>

*Note: Bold text indicates significant correlations between enzyme activity and carbon fraction concentration.*
treatments are in gray. Error bars represent mean ± SE. UV-pass treatments are shown in black and UV-block are shown with dashed lines and high-lignin samples with solid lines. Length of fungal hyphae in m/g dry litter. Low-lignin samples had no discernible effect on fungal hyphal length in high-lignin litter. We did find a significant three-way interaction between UV treatment, litter type, and sampling date (P = 0.017, F3,72 = 3.6), likely because fungal hyphal length in the wet season compared to UV-block samples (25.0 ± 1.7 [mean ± SE] m/g hyphae in low-lignin litter under UV-pass vs. 15.4 ± 1.8 m/g under UV-block in January 2013; Tukey P < 0.001). In contrast, UV-block samples did not attain peak fungal abundance until the end of the wet season.

**Potential extracellular enzyme activities**

Potential extracellular enzyme activities varied with time, litter type, and occasionally by UV treatment (Table 1). In general, potential enzyme activities were lower in high-lignin litter compared to low-lignin litter, and lower during the dry season compared to the wet season (Fig. 3). The main effect of UV treatment was only significant for potential leucine aminopeptidase activity (P = 0.017, F1,72 = 6.0). There were significant interactions with UV for the four enzymes depicted in Fig. 3, in addition to peroxidase (trends similar to phenol oxidase) and N-acetylglucosaminidase (trends similar to leucine aminopeptidase). Leucine aminopeptidase exhibited significantly higher (Tukey P < 0.001) potential activity under UV-pass compared to UV-block across all time points in high-lignin litter only (Fig. 3D). UV-block had marginally significant negative effects on potential activity of α-glucosidase (P = 0.070, F1,72 = 3.4) and N-acetylglucosaminidase (P = 0.085, F1,72 = 3.0).

Potential activities of β-glucosidase and cellobiohydrolase were significantly positively correlated with percent mass of cellulose in low-lignin litter, but only under UV-pass. Potential activities of peroxidase and phenol oxidase were significantly positively correlated with percent mass of lignin in both litter types under UV-pass, but, with the exception of phenol oxidase in low-lignin litter, not under UV-block (Table 3). Potential activities of three enzymes were significantly positively correlated with the rate of change in the content of their target carbon compounds, but only in litter under UV-pass. β-xylosidase was positively correlated with the rate of change in hemicellulose content in low-lignin litter, and phenol oxidase was positively correlated with the rate of change in lignin content in high-lignin litter. Peroxidase activity was positively correlated with the change in lignin content in both litter types (Table 4).

**Discussion**

Our first hypothesis was that UV-block would reduce mass loss in both high- and low-lignin litter. Our results supported this hypothesis: reducing UV transmittance by 68% in the UV-block treatment significantly reduced mass loss in high-lignin litter and reduced mass loss to a marginally significant extent in low-lignin litter (Fig. 1). This effect was significant even after accounting for a slight but significant negative effect of UV-block on litter moisture. Several previous studies have shown that attenuating solar radiation through shading can reduce litter mass loss in arid (Gallo et al. 2009) and semiarid (Henry et al. 2008) ecosystems. A number of studies have also found, as we did, that reducing UV can reduce litter mass loss rates in semiarid ecosystems. Austin and Vivanco (2006), Day et al. (2007), Brandt et al. (2007, 2010), and Lin and King (2014) all found that blocking UV reduced litter mass loss in the field anywhere from 3% over 5 months (Day et al. 2007) to 33% over 18 months (Austin and Vivanco 2006). Taken together, these results confirm that UV can increase litter mass loss in dryland ecosystems.

Contrary to our second and third hypotheses, our study indicates that UV photodegradation does not result in enhanced mass loss from the lignin fraction, nor does it inhibit microbial decomposition. Instead, UV photodegradation appears to facilitate microbial decomposition by increasing the efficiency of extracellular enzymes produced by microbial communities. Lignin...
mass loss in our litter was not affected by UV treatment, with UV-blocking instead reducing the loss of litter cellulose and hemicellulose (Tables 1 and 2). In addition, the net effect of UV-pass on litter microbial communities does not appear to be inhibitory; we found no effect of UV treatment on bacterial abundance (Fig. 2A), a potentially positive effect of UV-pass on fungal abundance (Fig. 2B), and no consistent effect of UV treatment on potential extracellular enzyme activity. Instead, we found that litter-degrading extracellular enzymes may be more effective under UV-pass. We found correlations between potential enzyme activity and both substrate availability and substrate degradation in litter under UV-pass and no such correlations under UV-block. Our results indicate that the functioning of Mediterranean grassland microbial communities may be dependent on ambient UV.

Though most studies of photodegradation have hypothesized that UV acts directly upon the lignin fraction in litter, it should be noted that these studies have not established a direct link between UV exposure and lignin degradation. Although lab studies suggest that lignin-like model compounds are photochemically active and absorb light in the ultraviolet range (Lanzalunga and Bietti 2000, Austin and Vivanco 2006), it is unclear to what extent photodegradation affects the physical and chemical structure of lignin. Kirschbaum et al. (2011) exposed grass litter and pine needles to UV equivalent to midday levels continuously for 60 days and found no direct effect of UV on either litter mass loss or concentration of lignin. Over the course of 10 weeks in the laboratory, Brandt et al. (2009) tested the effects of UV exposure on five different litter types with initial lignin concentrations varying from

Table 3. Carbon fraction content across all treatments presented as grams of dry litter mass at the beginning of the study and in June 2013.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Lignin (g)</th>
<th>Cellulose (g)</th>
<th>Hemicellulose (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Initial</td>
<td>June 2013</td>
<td>Initial</td>
</tr>
<tr>
<td>L–, UV–</td>
<td>0.139 ± 0.001</td>
<td>0.167 ± 0.011</td>
<td>0.738 ± 0.006</td>
</tr>
<tr>
<td>L–, UV+</td>
<td>0.139 ± 0.001</td>
<td>0.181 ± 0.015</td>
<td>0.738 ± 0.006</td>
</tr>
<tr>
<td>L+, UV–</td>
<td>0.244 ± 0.001</td>
<td>0.230 ± 0.013</td>
<td>0.827 ± 0.003</td>
</tr>
<tr>
<td>L+, UV+</td>
<td>0.244 ± 0.001</td>
<td>0.263 ± 0.023</td>
<td>0.827 ± 0.003</td>
</tr>
</tbody>
</table>

Notes: Bold values indicate when means under UV-block were significantly different (P < 0.05, Tukey test) from means of the same litter type under UV-pass. Low-lignin samples are L–, and high-lignin samples are L+. UV block samples are UV–, and UV pass samples are UV+. 

Fig. 3. Potential extracellular enzyme activities in nanomoles of substrate per hour per gram of dry litter for four representative enzymes: (A) cellobiohydrolase (CBH); (B) β-xylosidase (BX); (C) phenol oxidase (PPO); and (D) leucine-aminopeptidase (LAP).
photoexcitation of the lignin litter. Cellulose can be cleaved through direct photolysis of cellulose and hemicellulose, but our results showed a significant, strong effect of UV treatment on litter cellulose and hemicellulose, which was not significantly affected by UV treatment. Instead, our results showed a significant, strong effect of UV treatment on litter lignin, which was significantly affected by UV treatment. This effect was greater than direct photolysis, reactive intermediates resulting from indirect photolysis of nonlignin compounds, such as cellulose and hemicellulose, could be a significant mechanism through which UV affects litter decomposition. It is likely that the effects of UV on mass loss could also result from degradation of the lignocellulose matrix without significantly affecting lignin mass loss. Brandt et al. (2007, 2010) also found no effect of UV treatment on the concentration of lignin in litter, but a significant, if small, negative effect of UV on the combined cellulose and hemicellulose concentration in their 2007 study and a highly significant effect of UV on hemicellulose concentration in their 2010 study. Our results also fall in line with a study by Lin and King (2014), where attenuated UV reduced losses of hemicellulose content by 29% without having a significant effect on lignin content. Likewise, Gallo et al. (2009) found that cottonwood litter mass loss was partially driven by photomineralization of cellulose. In addition to the aforementioned mechanisms of direct and indirect photolysis of cellulose and hemicellulose, it is likely that the effects of UV on mass loss could also result from degradation of the lignocellulose matrix without significantly affecting lignin mass loss. UV breakdown of lignin shielding other C compounds could make previously occluded cellulose, hemicellulose, and soluble C available to microbial decomposers, facilitating enhanced microbial decomposition of litter (Gallo et al. 2006). Based on NMR analyses of litter that had been photodegraded in the field during their 2014 study, Lin et al. (Y. Lin, J. King, S. Karlen, and J. Ralph, unpublished manuscript) found that UV degraded interunit ether linkages of lignin polymers without causing lignin mass loss, suggesting a mechanism whereby UV could weaken the lignocellulose matrix. Our results are also consistent with this potential mechanism, as cellulose mass loss was more affected by UV treatment in high-lignin litter than it was in low-lignin litter. In contrast to our original hypothesis, we found little evidence for inhibition of microbial activity by UV. | Table 4. Pearson coefficients and P values for the correlation (Corr.) between potential enzyme activity and the change (Δ) in the carbon content attributable to the compound degraded by that enzyme class. |

<table>
<thead>
<tr>
<th>Treatment</th>
<th>ΔHemicellulose (BX at t – 1)</th>
<th>ΔLignin (PER at t – 1)</th>
<th>ΔLignin (PPO at t – 1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L–, UV+</td>
<td>–0.452</td>
<td>0.163</td>
<td>0.040</td>
</tr>
<tr>
<td>L–, UV–</td>
<td>–0.058</td>
<td>0.799</td>
<td>-0.058</td>
</tr>
<tr>
<td>L+, UV+</td>
<td>–0.227</td>
<td>0.287</td>
<td>-0.497</td>
</tr>
<tr>
<td>L+, UV–</td>
<td>–0.028</td>
<td>0.896</td>
<td>–0.167</td>
</tr>
</tbody>
</table>

Note: R² values for the linear regression of change in C content as a function of potential enzyme activity are shown for significant correlations and indicated by bold text. The change in carbon extracellular enzyme activity at the earlier time point (e.g., BX at t – 1).
Bacterial and fungal abundances did not increase in litter under UV-block. Instead, UV-block treatment negatively affected fungal abundance during the wet season in our low-lignin litter. In addition, potential activities of six of eight extracellular enzymes were not affected by UV treatment, indicating that ambient UV does not generally inhibit extracellular enzyme activity (Table 1, Fig. 3). These results are somewhat surprising given the known detrimental effects of UV on microbial DNA (Rohwer and Azam 2000) and microbial community growth (Hughes et al. 2003). However, UV might promote microbial decomposition through biochemical interactions. We observed significant correlations between potential enzyme activities and the concentrations of their target carbon fractions, but almost exclusively under UV-pass (Table 3). We also only found significant correlations between the mass loss of a carbon fraction and its associated enzyme activity at the previous time point under UV-pass, and mainly for oxidative enzymes that target more complex organic compounds (Table 4).

In other words, investment in enzymes targeting the most complex compounds in litter only had a significant effect on the mass change of those compounds when litter was exposed to ambient levels of UV. This result falls in line with previous findings by Gallo et al. (2009) and Brandt et al. (2010) that the amount of potential enzymatic activity required to degrade a litter cohort is greater when UV is blocked.

There have been several other studies, in addition to our own, that indicate that facilitation of microbial decomposition by photodegradation may occur when microbial communities are allowed to interact with photodegraded litter. Foereid et al. (2010) found that litter exposed to light for 289 days had much higher rates of CO₂ efflux in lab incubations when compared to litter that had only been exposed to radiation treatment for 43 days. Henry et al. (2008) found that wet season decomposition was significantly greater when litter had been exposed to ambient radiation during the preceding summer dry period. Similarly, Lin and King (2014) found that shaded litter exposed to attenuated UV exhibited carbon fraction dynamics similar to shaded litter exposed to ambient UV, but with significantly slower litter mass loss rates, indicating that decomposition of shaded litter in contact with the microbial community may be facilitated by UV photodegradation and the resulting release of soluble C in the surface litter layer. The results of our study suggest a mechanism that could explain UV facilitation of litter decomposition in these studies. Photodegradation of cellulose, hemicellulose, or the lignocellulose matrix might allow extracellular enzymes to break down their substrates more effectively.

**Conclusions**

Our study shows that UV photodegradation has a positive effect on both litter decomposition rates and microbial decomposer activity. UV-blocking reduces litter mass loss, but does not have a significant direct effect on litter lignin content. Instead, UV-blocking significantly reduces the degradation of cellulose and hemicellulose, potentially by limiting the direct or indirect photolysis of cellulose or the lignocellulose matrix that would otherwise occur under ambient UV. UV-blocking does not appear to increase bacterial or fungal abundance, and may in fact be detrimental for microbial decomposition, as extracellular enzymes produced by the microbial decomposer community were more effective at degrading their target substrates under ambient UV. These results indicate that UV photodegradation is an important driver of litter decomposition through its effects on non lignin compounds and facilitation of microbial activity. These mechanisms of litter decomposition will likely become more important in the American Southwest if this region experiences a more arid climate in the future.

**Acknowledgments**

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**SUPPLEMENTAL MATERIAL**

**Ecological Archives**

Appendices A and B are available online: [http://dx.doi.org/10.1890/14-1482.1.sm](http://dx.doi.org/10.1890/14-1482.1.sm)