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Effects of UV photodegradation on subsequent microbial decomposition of *Bromus diandrus* litter

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Abstract

Aims

Photodegradation acts as a direct contributor to litter decomposition in arid and semi-arid ecosystems. However, its indirect effects are unclear. Does photodegradation *condition* litter for subsequent microbial decomposition?

Methods

We conditioned litter of *Bromus diandrus* with ambient or reduced ultraviolet (UV) radiation and three periods of exposure (summer, summer-winter, and one year) in a California annual grassland. We then investigated how field UV exposure affected subsequent microbial decomposition of litter using a controlled laboratory incubation.

Results

Surprisingly, microbial decomposition was decreased by UV radiation when the exposure occurred during summer but was unaffected by UV treatment for exposure longer than summer. Litter lignin concentrations did not explain these results, as they were not affected by UV radiation for any of the exposure periods. However, for the summer period exposure, UV radiation was associated with decreased litter N concentration, which corresponded with lowered subsequent microbial activity.

Conclusions

Our results suggest a new mechanism through which photodegradation interacts with litter microbial decomposition: photodegradation may decrease microbial decomposition through inhibition of microbial N immobilization. Our results imply that solar radiation can interact with litter N cycling dynamics to influence litter decomposition processes.

Keywords

photo-oxidation, photo-mineralization, dryland, grass, invasive species, drought

Introduction

In arid and semi-arid ecosystems, photodegradation has been recently identified as a key process in ecosystem carbon (C) cycling (King et al. 2012; Song et al. 2013, and references therein). Photodegradation refers to the process through which solar radiation decomposes organic matter. Multiple field experiments have demonstrated that ultraviolet (UV) radiation and visible radiation increase litter mass loss via photodegradation (Austin and Vivanco 2006; Barnes et al. 2011; Brandt et al. 2010; Day et al. 2007; Gallo et al. 2006; Liu et al. 2014). A meta-analysis showed that increased exposure to solar radiation enhanced litter mass loss by 23% on average (King et al. 2012). Despite the increasing interest in understanding the role of photodegradation in ecosystem C cycling, it remains relatively unclear exactly *how* photodegradation induces litter mass loss.

Photodegradation can *directly* contribute to litter mass loss through photochemical mineralization. Laboratory-based studies found that exposure to radiation can induce trace gas emissions (CO_2, CO, and CH_4) from plant litter (Brandt et al. 2009; Lee et al. 2012; McLeod et al. 2008; Schade et al. 1999). Rutledge et al. (2010) suggested that photodegradation accounted for almost 60% of CO_2 flux from a California grassland during summer. Photodegradation can also *indirectly* affect litter decomposition by influencing litter chemical composition. Lignin has been found to be preferentially degraded by photodegradation, as lignin strongly absorbs UV and visible radiation (Austin and Ballaré 2010; Day et al. 2007; Henry et al. 2008). Consequently, photodegradation is thought to improve the biodegradability of litter, since lignin often degrades slower than other compounds in litter (Aerts 1997; Meentemeyer 1978). Adding another level of complexity, solar radiation, especially UV radiation, also suppresses

56 microbial activity, as it is known to damage microbial nucleic acids (Hughes et al. 2003;
57 Sinha and Häder 2002). Several studies have found that UV exposure decreases litter
58 nitrogen (N) immobilization (Brandt et al. 2010; Smith et al. 2010), a microbial process
59 through which N is transferred from the environment to litter. There is a significant gap
60 in understanding the relative importance of the direct and indirect contributions of
61 photodegradation, as few studies have attempted to separate and quantify them.
62 Arid ecosystems characterized by distinct dry and wet periods present an
63 opportunity to separate the direct and indirect contributions of photodegradation to litter
64 mass loss. Radiation exposure during the dry season can "condition" litter for microbial
65 decomposition in the following wet season (Foereid et al. 2010). If photodegradation
66 preferentially degrades lignin in the dry season, it might relieve the inhibitory effect of
67 lignin on subsequent microbial decomposition in the wet season. This conditioning effect
68 of photodegradation can have significant implications at ecosystem scales. For example,
69 severe drought might increase the importance of photodegradation and the loss of lignin
70 during the dry season. If these changes made up for a drought-induced decrease in
71 microbial decomposition, then drought would not suppress decomposition in arid
72 ecosystems. However, mixed results have been reported about the conditioning effect of
73 photodegradation (Brandt et al. 2010; Foereid et al. 2010; Henry et al. 2008; Lambie et al.
74 2014; Wang et al. 2015). For example, several studies have found that prior exposure of
75 litter to UV radiation facilitates microbial decomposition (Foereid et al. 2010; Henry et al.
76 2008; Wang et al. 2015). Brandt et al. (2009) and Lambie et al. (2014), on the other hand,
77 reported negligible or even negative effects of UV radiation exposure on subsequent
78 microbial decomposition. The UV exposure in most of the above studies was achieved

using UV lamps in the laboratory or greenhouse. Few studies to date have examined whether field UV exposure will facilitate microbial decomposition, particularly as litter experiences distinct dry and wet seasons (except Henry et al. 2008).

The objective of this study was to examine how field UV radiation exposure affected subsequent microbial decomposition of litter of an abundant grass in California, *Bromus diandrus*. Litter was exposed in the field to two levels of UV radiation (ambient vs. reduced) for different periods: summer, summer-winter, or one year. Then the litter was incubated with microbial inoculum for a period of 25 days under laboratory conditions to evaluate its biodegradability. We asked the following questions: 1) does intensive UV exposure during a Mediterranean summer increase subsequent microbial decomposition by increasing loss of persistent substrates, such as lignin? and 2) does the conditioning effect of UV exposure differ among exposure periods?

Materials and methods

Litter collection and UV treatments

Litter samples of *B. diandrus* were collected from the University of California's Sedgwick Reserve in Santa Ynez, California, USA (43°42'N, 120°2'W; 25 km north of Santa Barbara). A detailed description of the site can be found in Lin and King (2014). Briefly, the site is dominated by European annual grasses, particularly *B. diandrus*, and it experiences a Mediterranean climate of distinct wet and dry seasons with average annual precipitation of 380 mm, mostly occurring between November and April. Annual grasses typically fully senesce by late April. Senesced litter lying across the ground surface forms a litter layer of 5 cm to 15 cm thickness, the surface of which is exposed to intensive solar

radiation during the dry season from May to September. To manipulate UV radiation (280-400 nm) received by litter samples, 20 pairs of steel frames (l × w × h: 75 × 150 × 25 cm) were constructed with plastic louvers that either block or pass UV radiation. A subset of the screens were used in Lin and King (2014), which reported the technical details of these screens, including dimensions, placement, optical properties, and effects on air temperature and relative humidity. In short, the "UV block" screens eliminated 93 and 85% of UV-A (315-400 nm) and UV-B (280-315 nm) radiation, respectively, whereas the "UV pass" screens transmitted 80 and 79% of UV-A and UV-B radiation, respectively. Screens allowed penetration of rainfall and controlled for heating by having a louvered design. There was no difference between UV block and UV pass screens in their effects on photosynthetically active radiation (PAR), air temperature, or relative humidity.

Litter samples were under either UV block or UV pass treatments in the field for three periods (summer, summer-winter, and one year) (Table 1). For litter that received UV treatments in summer, 10 pairs of UV block and UV pass screens were placed over areas dominated by litter of *B. diandrus* in mid August, 2011. During the set-up of the screens, some standing litter was pushed over by hand so that it would fit underneath the screens. In late October 2011, litter was removed from under the screens resulting in UV treatment that lasted for 2.5 months. Only litter at the very top of the thatch layer and constantly exposed to solar radiation was collected for this study. The other two sets of litter were obtained from the experiment reported in Lin and King (2014). In short, *B. diandrus* litter was sealed in 20 × 20 cm aluminum bags of 1.5-mm mesh size and suspended at 5 cm beneath the louvers of 10 pairs of UV pass and UV block screens and

above the thatch layer in the field in mid August, 2011. The bags were supported from below by a stainless steel screen. The UV screens were not the same ones used for treating litter during summer, but they were identical in design. Litter samples (n = 10) were collected both in early March 2012 and early September 2012 to achieve UV radiation exposure periods of summer-winter and one year, respectively. These three sets of litter all originated from the 2010-2011 growing season at the same field site. Even though that aluminum mesh bags were not used for samples exposed during summer, we believe the use of mesh bags was not a confounding factor to the exposure period. The aluminum mesh material transmits greater than 70% of UV radiation, and its mesh size is big enough for microbial decomposers to colonize the litter inside the mesh.

We monitored UV radiation at 1.7 m above the soil surface with a broadband UV radiometer (CUV5, Kipp & Zonen) at a meteorological station adjacent to the site. After considering light transmission of screens and aluminum mesh, as well as length of exposure, we estimated the amount of UV radiation received by each treatment during field exposure (Table 1).

Sample processing and chemical analysis

After collection of the litter from the field site, green plants, visible soil, and arthropods were removed from the litter. Litter was then oven-dried at 55°C for 2 days. Four out of ten replicates were randomly taken from each combination of UV treatment and exposure duration for chemical analysis and measurement of biodegradability. These samples were ground using a Wiley mill with U.S. standard #20 mesh.

We analyzed litter carbon fractions, including the cell solubles fraction (which includes soluble carbohydrates, proteins, and lipids; hereafter, cell solubles),

148 hemicellulose, cellulose, and lignin, using a sequential extraction technique (Van Soest
149 1963). Subsamples were treated with neutral fiber detergent, acid fiber detergent, and
150 sulfuric acid digestions using an ANKOM fiber analyzer (Type 2000, ANKOM
151 Technology). We refer to the fraction left after sulfuric acid digestion as 'lignin' so that
152 our results can be compared with many previous studies that have adopted the same
153 method in examining litter decomposition and photodegradation (Austin and Vivanco
154 2006; Brandt et al. 2010; Rozema et al. 1997). We recognize that this lignin fraction also
155 includes cutin, suberin, and waxes (von Lützow et al. 2007). For litter C and N
156 concentrations, subsamples were ground to powder using a roller mill and analyzed using
157 an elemental analyzer (Fisons NA1500, Fisons Instruments) with acetanilide standards.
158 Each sample was analyzed in duplicate, and the average value was used. For extraction, a
159 100 mg subsample was soaked in 50 ml deionized water at 4°C for 24 hours. Extracts
160 were filtered through glass fiber filter paper (Type A/E, Pall Corporation) and analyzed
161 for water extractable C (WEC) and N (WEN) using a total organic C/total N (TOC/TN)
162 analyzer (Series V, Shimadzu Corporation). Potassium hydrogen phthalate and potassium
163 nitrate were used to prepare the standards for WEC and WEN, respectively. WEC and
164 WEN were calculated as the average of three measurements. All litter chemical
165 characteristics were reported on a dry litter mass basis.
166 *Litter biodegradability*
167 Litter biodegradability was evaluated by measuring microbial respiration in a 25-day
168 laboratory incubation experiment on subsamples of the coarsely ground litter (n = 4,
169 #20 mesh). Subsamples (250 mg each) were first placed into 50-mL plastic beakers.
170 Microbial inoculum was added to introduce a uniform community of decomposers to all

171 of the litter samples and to offset potential effects of UV exposure on the microbial
172 community on the litter itself. To make the microbial inoculum, soil from the field site
173 was mixed with water at 1:3.5 (soil:water, mass:volume ratio) and extracted at 50 rpm on
174 a bench shaker for 2 hr. After shaking, the extract was filtered through Whatman 40 filter
175 paper to remove soil particles and then used as microbial inoculum. For each plastic
176 beaker, 250 μL of microbial inoculum was added with 2 mL deionized water to fully soak
177 the litter sample. The TOC measurements revealed that there was approximately 20 μg C
178 in the inoculum for each plastic beaker, which represents less than 0.3% of total CO_2-C
179 produced during the incubation. The 50-mL beakers were then placed into 473 mL glass
180 jars, sealed, and incubated at 20°C in the dark. Microbial respiration was estimated by
181 measuring CO_2 production during the incubation. For each glass jar, a 1 mL headspace
182 sample was obtained through a butyl stopper in the lid using a needle and syringe, and its
183 CO_2 concentration was measured using an infrared gas analyzer (IRGA, LI-COR 820, LI-
184 COR Corporation) every one or two days. The IRGA was calibrated at each measurement
185 time point using four CO_2 standards ranging from 500 to 25,000 ppm (Scott Specialty
186 Gases, Plumsteadville, PA). The CO_2 concentration was converted to grams CO_2-C using
187 the ideal gas law. All glass jars were vented when any single headspace CO_2
188 concentration exceeded 2%. Average microbial respiration rate between two
189 measurements was calculated as the increase of CO_2-C in each glass jar between the two
190 time points per hour incubated per dry mass of litter. Cumulative microbial respiration
191 (CMR) for the 25-day incubation period was calculated as the sum of CO_2-C production
192 in each glass jar per dry mass of litter and was used to represent litter biodegradability.
193

194 *Statistical analysis*

195 Preliminary two-way analysis of variance (ANOVA) found significant interaction effects
196 between UV treatment and exposure period on most of the studied variables, suggesting
197 that the effects of UV treatment should be examined for each exposure period separately.
198 Therefore, we conducted Student's t-test to compare differences in litter carbon fractions,
199 C and N concentrations, WEC, WEN, and CMR between the UV block and UV pass
200 treatments for each period of UV treatment separately. Before applying the t-test, samples
201 were checked for equality of variances using Levene's test. If equal variances could not
202 be assumed between two treatments, the degrees of freedom of the t-statistic were
203 adjusted using the Welch-Satterthwaite method. Pearson correlation was used to examine
204 the relationship between litter chemical characteristics and CMR. All statistical analyses
205 were carried out in SPSS (Version 20, IBM Corporation).

206

207 **Results**

208 *Litter chemical quality*

209 For litter exposed to UV treatments during summer, litter N concentration was lower in
210 the UV pass than in the UV block treatment ($n = 4$, $P = 0.013$, Table 2). Its C
211 concentration was higher under UV pass than under UV block ($n = 4$, $P = 0.021$). Litter
212 WEN also tended to be lower under UV pass compared to UV block ($n = 4$, $P = 0.066$).
213 Litter lignin concentration and other measured chemical characteristics were not affected
214 by the summer UV treatments. For litter exposed to UV treatments over summer-winter,
215 UV pass did not affect litter lignin concentration ($n = 4$, $P = 0.139$) or other measured
216 chemical characteristics. After one year of UV treatments, litter hemicellulose

concentration was lower under UV pass compared to UV block (n = 4, P = 0.009). This decrease in hemicellulose corresponded to a trend of higher cell solubles under UV pass than under UV block (n = 4, P = 0.082). No other litter chemical characteristics, including lignin concentration, were affected by one year of UV treatments.

Litter biodegradability

For litter exposed to UV treatments during summer, the UV block treatment increased its biodegradability (represented by cumulative microbial respiration (CMR)) by 28% during the 25-day incubation period compared to UV-exposed litter (Fig. 1, n = 4, P = 0.046). The positive effect of blocking UV radiation on litter biodegradability was most pronounced at the peak of microbial activity (Fig. 2, 2nd day since the start of the incubation) when the microbial respiration rate associated with litter from the UV block treatment was 35% higher than that associated with litter from the UV pass treatment (374.7±26.8 μg C g^{-1} litter hr^{-1} vs. 279.5±25.2 μg C g^{-1} litter hr^{-1}; n = 4, P = 0.041). The litter from the UV block treatment also showed consistently higher microbial respiration rates during the second half of the incubation. Exposure to UV radiation treatments did not affect litter biodegradability when the exposure occurred over summer-winter (Fig. 1, n = 4, P = 0.972) or one year (n = 4, P = 0.367), and microbial respiration for those exposure durations was not affected by UV treatments at any time point throughout the incubation (data not shown).

For litter in the summer UV treatments, its biodegradability was strongly positively correlated with litter N concentration (Fig. 3a, n = 8, r = 0.928, P < 0.001). When UV treatments lasted over summer-winter, the correlation between

biodegradability and N concentration was marginally significant (Fig. 3b, $n = 8$, $r = 0.669$, $P = 0.070$). When UV treatments lasted for one year, the correlation between biodegradability and N concentration was no longer significant (Fig. 3c, $n = 8$, $r = 0.575$, $P = 0.136$). Similarly, correlations between litter biodegradability and WEN were significant when UV treatments occurred over summer (data not shown, $n = 8$, $r = 0.938$, $P < 0.001$) and summer-winter ($n = 8$, $r = 0.858$, $P = 0.006$), but not significant for litter exposed to one year of UV treatments ($n = 8$, $r = 0.341$, $P = 0.408$). In fact, none of the measured litter chemical characteristics had a significant correlation with litter biodegradability for litter exposed to one year of UV treatments.

Discussion

Contrary to our hypotheses, we did not find positive effects of UV exposure on litter biodegradability for any of the exposure periods (Fig. 1). Lignin concentration was also not affected by up to one year of UV treatments (Table 2). In this study, we used *B. diandrus*, a common invasive species found in California grasslands. This species has lower lignin concentrations (2-5%) than many other grasses or woody species (Jung et al. 1999; McLauchlan et al. 2006; Van Soest 1963). Thus, it could be difficult to detect changes in lignin concentration induced by photodegradation. However, UV treatments had limited effects on all of the other litter chemical characteristics as well, suggesting that UV exposure did not improve litter biodegradability through breakdown of recalcitrant substrates.

Surprisingly, we found that exposure to UV treatments during summer *decreased* litter biodegradability (Fig. 1 and 2). This result is consistent with a laboratory study in

263 which Lambie et al. (2014) found that exposure to UV radiation decreased subsequent
264 microbial respiration from pine (*Pinus radiata*) and mānuka (*Leptospermum scoparium*)
265 litter. However, the results of Lambie et al. (2014) did not demonstrate the mechanism
266 behind this negative conditioning effect of UV radiation. Photodegradation could increase
267 litter mass loss and decrease the quality and biodegradability of the remaining litter.
268 Exposure to UV radiation did increase litter mass loss when exposure occurred over
269 summer-winter and one year (Lin and King 2014). Litter mass loss was not measured
270 during summer only, but the same UV exposure effect was likely. However, if UV
271 exposure decreased litter biodegradability mainly through reducing litter quality, then a
272 negative effect of UV exposure on biodegradability would have been found in all
273 exposure durations, and this effect would have been strongest in litter with the longest
274 UV exposure (one year). Instead, UV exposure only decreased litter biodegradability in
275 summer, the shortest UV exposure. We found a strong positive relationship between litter
276 biodegradability and N concentration only when UV treatments occurred during summer
277 (Fig. 3), suggesting that the early stage of litter decay is limited by N availability in our
278 incubation. This N limitation to short-term microbial respiration has been commonly
279 observed (e.g. Allen and Schlesinger 2004; Vance and Chapin 2001). Given the strong
280 correlation between biodegradability and N concentration, we speculate that the UV-
281 induced decrease in litter N concentration (Table 2) led to lower biodegradability in the
282 UV pass treatment.

283 Several studies have reported reduced N immobilization on photodegraded litter
284 (Brandt et al. 2010; Lin and King 2014; Smith et al. 2010; Song et al. 2011). It is likely
285 that UV exposure over summer decreased litter N concentration through suppression of

286 microbial N immobilization. This inhibitory effect of UV on N immobilization was
287 temporary, as litter N concentration was no longer different between UV treatments for
288 litter exposed during summer-winter and one year (Table 2, Lin and King 2014). Litter N
289 immobilization presumably occurs during early stages of decomposition (e.g. the first
290 summer after *B. diandrus* senesces), when litter N cannot meet the N requirements of
291 microbial decomposers. The UV effect on N immobilization should be much stronger in
292 summer than in winter, as high moisture availability and low UV intensity in winter favor
293 microbial activity (Johnson 2003; Xiang et al. 2008). Therefore, favorable environmental
294 conditions during the wet season likely mask the difference in N immobilization induced
295 by UV during summer.

296 Our results suggest a new mechanism through which photodegradation affects
297 litter mass loss: alteration of biodegradability through changes in microbial N
298 immobilization patterns (Fig. 4). This mechanism can potentially explain the negative
299 conditioning effect of UV on litter mass loss found in Lambie et al. (2014). Given that
300 photodegradation can both positively and negatively affect litter mass loss, it is critical to
301 understand the controls of these mechanisms. Our study indicates that the relative
302 importance of different photodegradation pathways (Fig. 4) is affected by seasonal
303 patterns of environmental factors, such as solar radiation and moisture. As discussed
304 above, the negative effect of UV on litter biodegradability is likely to occur during early
305 stages of litter decomposition when N immobilization is necessary and during summer
306 when environmental conditions favor photodegradation. The cumulative dose of radiation
307 could also regulate the balance among photodegradation pathways (Foereid et al. 2010);
308 however, the strong seasonal variation in solar radiation (Table 1) limits our ability to

separate its effect. Future studies are needed to specifically characterize the mechanistic controls of different mass loss pathways during photodegradation.

Furthermore, there are several alternative mechanisms behind the conditioning effect of photodegradation that require further examination. For example, even though this experiment did not find positive effects of UV radiation exposure on subsequent microbial decomposition of litter, microbial decomposers on our litter samples might have already consumed the labile substrates released by photodegradation before the samples were collected from field. In other words, the conditioning effects of UV radiation on biodegradability might operate at a much shorter time scale than that measured in this experiment. Specifically, during summer in California grasslands, photodegradation likely dominates litter decomposition during daylight hours and may condition organic matter for microbial decomposition at night. Another alternative mechanism is that exposure to UV radiation may also induce physical fragmentation of litter and increase its biodegradability. We ground our litter samples prior to the incubation study; therefore, our results did not evaluate the impacts of UV exposure on litter physical characteristics.

In arid and semi-arid ecosystems, it has been suggested that C and N dynamics during decomposition are decoupled, as observations have shown that litter decomposition does not depend on litter C:N ratio, and N immobilization is not observed regardless of initial litter N content (Parton et al. 2007; Vanderbilt et al. 2008). Several abiotic processes have been proposed to explain this decoupling of C and N dynamics, such as photodegradation and soil-litter mixing (Brandt et al. 2010; Hewins et al. 2013; Throop and Archer 2007). Our results, however, suggest that C and N dynamics during

litter decomposition can be coupled by photodegradation, as photodegradation likely decreased microbial decomposition by altering N immobilization. Similarly, a combination of photodegradation and N addition was shown to decrease the overall decomposition rate of *Pinus massoniana* litter (Song et al. 2014b). Song et al. (2014a) also found that the interaction between photodegradation and N addition induced faster litter mass loss than the sum of their individual effects. Photodegradation appears to either positively or negatively affect litter decomposition through interaction with litter N dynamics. More work is needed to fully understand the mechanisms behind these seemingly contradictory results. Nevertheless, impacts of photodegradation on the interaction between C and N dynamics during litter decomposition are much more complex than a single "decoupling" effect.

In summary, our study shows that up to one year of conditioning with UV radiation does not facilitate microbial decomposition of *B. diandrus* litter. In fact, UV exposure decreased the subsequent microbial respiration rate when the exposure occurred during summer and had no significant effects when exposure was longer. We suggest that UV radiation suppressed N immobilization and consequently limited subsequent microbial decomposition of litter. Together with previous studies (Foereid et al. 2010; Lambie et al. 2014), our results imply that photodegradation may influence subsequent microbial decomposition through altering microbial activity and/or affecting litter chemical composition. Instead of decoupling C and N dynamics, photodegradation may affect litter C loss by interacting with litter N turnover. Further studies are required to closely examine the nature and controls of these mechanisms to better understand photodegradation, as well as its contribution to decomposition processes in general.

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References

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79: 439-449

Allen AS, Schlesinger WH (2004) Nutrient limitations to soil microbial biomass and activity in loblolly pine forests. Soil Biol Biochem 36: 581-589

Austin AT, Ballaré CL (2010) Dual role of lignin in plant litter decomposition in terrestrial ecosystems. Proc Natl Acad Sci USA 107: 2-6

Austin AT, Vivanco L (2006) Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442: 555-558

Barnes PW, Throop HL, Hewins DB, Abbene ML, Archer SR (2011) Soil coverage reduces photodegradation and promotes the development of soil-microbial films on dryland leaf litter. Ecosystems 15: 311-321

Brandt LA, Bohnet C, King JY (2009) Photochemically induced carbon dioxide production as a mechanism for carbon loss from plant litter in arid ecosystems. J Geophys Res-Biogeo 114: G02004

Brandt LA, King JY, Hobbie SE, Milchunas DG, Sinsabaugh RL (2010) The role of photodegradation in surface litter decomposition across a grassland ecosystem precipitation gradient. Ecosystems 13: 765-781

Day TA, Zhang ET, Ruhland CT (2007) Exposure to solar UV-B radiation accelerates mass and lignin loss of *Larrea tridentata* litter in the Sonoran Desert. Plant Ecol 193: 185-194

Foereid B, Bellarby J, Meier-Augenstein W, Kemp H (2010) Does light exposure make plant litter more degradable? Plant Soil 333: 275-285

Gallo ME, Sinsabaugh RL, Cabaniss S (2006) The role of ultraviolet radiation in litter decomposition in arid ecosystems. Appl Soil Ecol 34: 82-91

Henry HAL, Brizgys K, Field CB (2008) Litter decomposition in a California annual grassland: interactions between photodegradation and litter layer thickness. Ecosystems 11: 545-554

392 Hewins D, Archer S, Okin G, McCulley R, Throop H (2013) Soil–litter mixing accelerates
393 decomposition in a Chihuahuan desert grassland. Ecosystems 16: 183-195
394 Hughes KA, Lawley B, Newsham KK (2003) Solar UV-B radiation inhibits the growth of
395 Antarctic terrestrial fungi. Appl Environ Microbiol 69: 1488-1491
396 Johnson D (2003) Response of terrestrial microorganisms to ultraviolet-B radiation in ecosystems.
397 Res Microbiol 154: 315-320
398 Jung H-JG, Varel VH, Weimer PJ, Ralph J (1999) Accuracy of Klason lignin and acid detergent
399 lignin methods as assessed by bomb calorimetry. J Agric Food Chem 47: 2005-2008
400 King JY, Brandt LA, Adair EC (2012) Shedding light on plant litter decomposition: advances,
401 implications and new directions in understanding the role of photodegradation.
402 Biogeochemistry 111: 57-81
403 Lambie SM, Kirschbaum MUF, Dando J (2014) No photodegradation of litter and humus
404 exposed to UV-B radiation under laboratory conditions: No effect of leaf senescence or
405 drying temperature. Soil Biol Biochem 69: 46-53
406 Lee H, Rahn T, Throop H (2012) An accounting of C-based trace gas release during abiotic plant
407 litter degradation. Global Change Biol 18: 1185-1195
408 Lin Y, King J (2014) Effects of UV exposure and litter position on decomposition in a California
409 grassland. Ecosystems 17: 158-168
410 Liu S, Hu R, Cai G, Lin S, Zhao J, Li Y (2014) The role of UV-B radiation and precipitation on
411 straw decomposition and topsoil C turnover. Soil Biol Biochem 77: 197-202
412 McLauchlan KK, Hobbie SE, Post WM (2006) Conversion from agriculture to grassland builds
413 soil organic matter on decadal timescales. Ecol Appl 16: 143-153
414 McLeod AR, Fry SC, Loake GJ, Messenger DJ, Reay DS, Smith KA, Yun B-W (2008)
415 Ultraviolet radiation drives methane emissions from terrestrial plant pectins. New Phytol
416 180: 124-132
417 Meentemeyer V (1978) Macroclimate and lignin control of litter decomposition rates. Ecology 59:
418 465-472
419 Parton W, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS, King JY, Adair EC,
420 Brandt LA, Hart SC, Fasth B (2007) Global-scale similarities in nitrogen release patterns
421 during long-term decomposition. Science 315: 361-364
422 Rozema J, Tosserams M, Nelissen HJM, van Heerwaarden L, Broekman RA, Flierman N (1997)
423 Stratospheric ozone reduction and ecosystem processes: enhanced UV-B radiation affects
424 chemical quality and decomposition of leaves of the dune grassland species
425 *Calamagrostis*. Plant Ecol 128: 285-294
426 Rutledge S, Campbell DI, Baldocchi D, Schipper LA (2010) Photodegradation leads to increased
427 carbon dioxide losses from terrestrial organic matter. Global Change Biol 16: 3065-3074
428 Schade GW, Hofmann R-M, Crutzen PJ (1999) CO emissions from degrading plant matter.
429 Tellus (B Chem Phys Meteorol) 51: 889-908
430 Sinha RP, Häder D-P (2002) UV-induced DNA damage and repair: a review. Photochem
431 Photobiol Sci 1: 225-236
432 Smith WK, Gao W, Steltzer H, Wallenstein MD, Tree R (2010) Moisture availability influences
433 the effect of ultraviolet-B radiation on leaf litter decomposition. Global Change Biol 16:
434 484-495
435 Song X, Jiang H, Zhang H, Peng C, Yu S (2011) Elevated UV-B radiation did not affect
436 decomposition rates of needles of two coniferous species in subtropical China. Eur J Soil
437 Biol 47: 343-348
438 Song X, Jiang H, Zhang Z, Zhou G, Zhang S, Peng C (2014a) Interactive effects of elevated UV-
439 B radiation and N deposition on decomposition of Moso bamboo litter. Soil Biol
440 Biochem 69: 11-16

441 Song X, Peng C, Jiang H, Zhu Q, Wang W (2013) Direct and indirect effects of UV-B exposure
442 on litter decomposition: a meta-analysis. PloS One 8: e68858, DOI:
443 68810.61371/journal.pone.0068858
444 Song X, Zhang H, Jiang H, Peng C (2014b) Combination of nitrogen deposition and ultraviolet-B
445 radiation decreased litter decomposition in subtropical China. Plant Soil 380: 349-359
446 Throop HL, Archer SR (2007) Interrelationships among shrub encroachment, land management,
447 and litter decomposition in a semidesert grassland. Ecol Appl 17: 1809-1823
448 Van Soest PJ (1963) Use of detergents in the analyses of fibrous feeds. A rapid method for the
449 determination of fiber and lignin. J Assoc Off Ana Chem 46: 829-835
450 Vance ED, Chapin FS (2001) Substrate limitations to microbial activity in taiga forest floors. Soil
451 Biol Biochem 33: 173-188
452 Vanderbilt KL, White CS, Hopkins O, Craig JA (2008) Aboveground decomposition in arid
453 environments: Results of a long-term study in central New Mexico. J Arid Environ 72:
454 696-709
455 von Lützow M, Kögel-Knabner I, Ekschmitt K, Flessa H, Guggenberger G, Matzner E,
456 Marschner B (2007) SOM fractionation methods: Relevance to functional pools and to
457 stabilization mechanisms. Soil Biol Biochem 39: 2183-2207
458 Wang J, Liu L, Wang X, Chen Y (2015) The interaction between abiotic photodegradation and
459 microbial decomposition under ultraviolet radiation. Global Change Biol 21: 2095-2104
460 Xiang S-R, Doyle A, Holden PA, Schimel JP (2008) Drying and rewetting effects on C and N
461 mineralization and microbial activity in surface and subsurface California grassland soils.
462 Soil Biol Biochem 40: 2281-2289

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465 Table 1. *Bromus diandrus* litter samples and their field UV exposure characteristics.

Litter Exposure	Duration of UV Treatment (months)	UV Treatment Period		Estimated UV Radiation Received by Litter During Treatments (MJ/m^2)	
		Start	End	UV block	UV pass
summer	2.5	Aug. 2011	Oct. 2011	6.1	48.6
summer-winter	6	Aug. 2011	Mar. 2012	8.3	66.1
one year	12	Aug. 2011	Sep. 2012	22.8	182.6

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468 Table 2. Effects of UV treatments on chemical characteristics of *Bromus diandrus* litter.

Period of UV treatment	Summer		Summer-winter		One year	
UV Treatment	Block	Pass	Block	Pass	Block	Pass
Litter chemical characteristics						
Carbon (%)	**41.0 (0.3)**	**42.1 (0.3)**	41.0 (0.2)	41.1 (0.1)	39.5 (0.2)	39.5 (0.3)
Nitrogen (%)	**0.69 (0.03)**	**0.54 (0.01)**	0.59 (0.03)	0.59 (0.04)	0.65 (0.02)	0.64 (0.02)
Cell solubles (%)	27.8 (0.6)	28.6 (0.6)	28.4 (1.1)	27.7 (0.9)	32.1 (0.6)	33.6 (0.4)
Hemicellulose (%)	28.5 (0.9)	28.6 (0.2)	29.1 (0.9)	29.7 (0.3)	**26.3 (0.4)**	**24.2 (0.4)**
Cellulose (%)	38.4 (0.4)	39.7 (0.6)	37.6 (0.3)	38.7 (0.8)	38.3 (0.1)	38.4 (0.3)
Lignin (%)	3.7 (0.3)	3.2 (0.2)	4.9 (0.5)	3.9 (0.1)	3.3 (0.4)	3.8 (0.2)
Water extractable carbon (WEC, mg g^{-1} litter)	26.3 (1.3)	26.2 (2.3)	25.6 (1.3)	25.4 (1.3)	24.2 (0.9)	26.3 (1.4)
Water extractable nitrogen (WEN, mg g^{-1} litter)	1.5 (0.1)	1.2 (0.1)	1.6 (0.1)	1.5 (0.2)	1.3 (0.1)	1.3 (0.1)

469

470 Means and standard errors are shown ($n = 4$). Means that significantly differ from each

471 other (within period; $\alpha \leq 0.05$) are indicated in bold. See Methods for description of "cell

472 solubles" fraction.

473

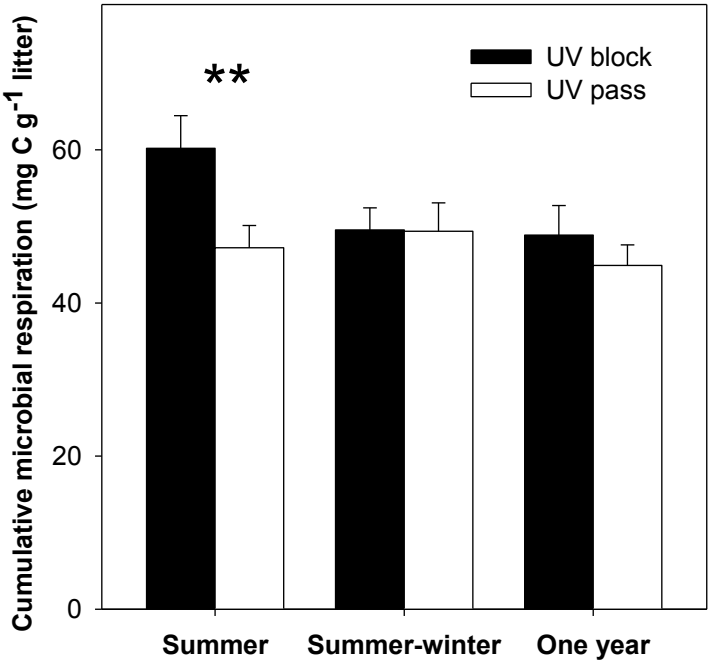
Figure Captions:

Fig. 1. Effects of UV manipulation and exposure periods (summer, summer-winter, and one year) on subsequent cumulative microbial respiration from *Bromus diandrus* litter measured in a laboratory incubation. Mean and standard errors are shown ($n = 4$). $^{**}P < 0.05$.

Fig. 2. Subsequent microbial respiration rate from *Bromus diandrus* litter as a function of time for litter exposed during summer. Mean and standard errors are shown ($n = 4$). $^{*}P < 0.1$ and $^{**}P < 0.05$.

Fig. 3. Relationship between litter N concentration and cumulative microbial respiration when the treatments were applied during a) summer, b) summer-winter, and c) one year. *r*, Pearson correlation coefficient.

Fig. 4. Conceptual model of solar radiation effects on litter mass loss. Rectangles indicate litter decomposition pathways. Ellipses indicate factors that affect litter decomposition. Radiation induces photochemical mineralization that increases litter mass loss. Radiation also affects litter microbial decomposition through either suppressing microbial activity or altering litter chemistry. This study suggests that radiation-induced changes in microbial activity (e.g. reduced N immobilization) can influence litter chemistry (dashed arrow), which further affects litter mass loss.



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498 Fig. 1

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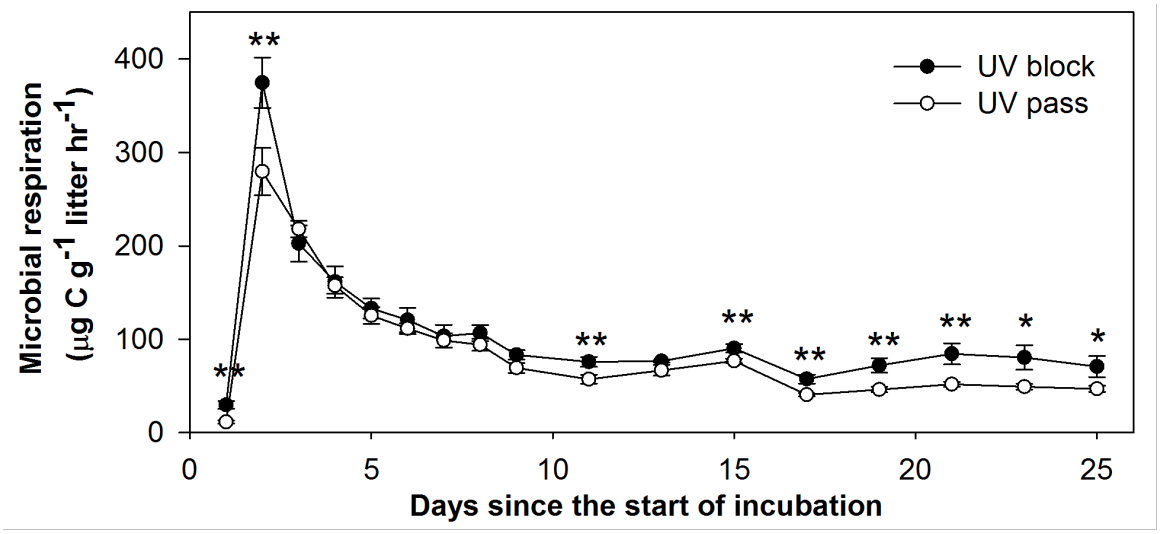

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502 Fig. 2

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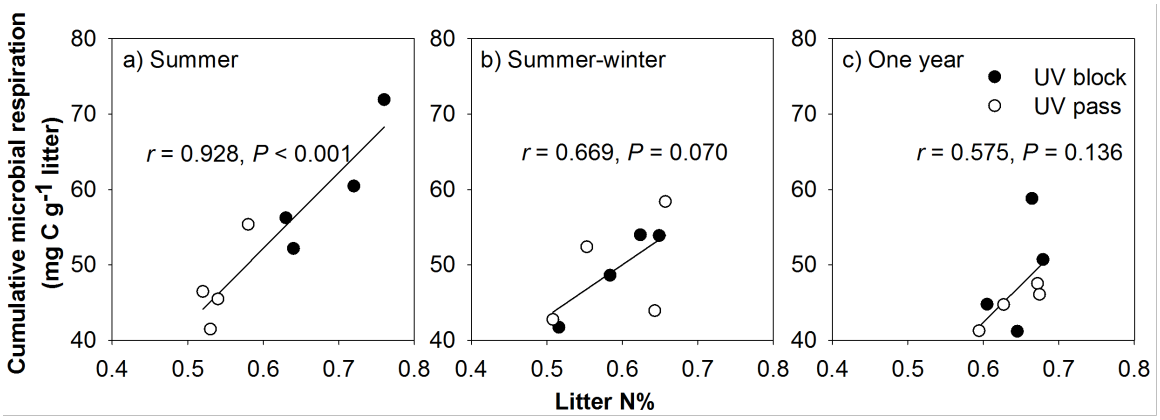

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505 Fig. 3

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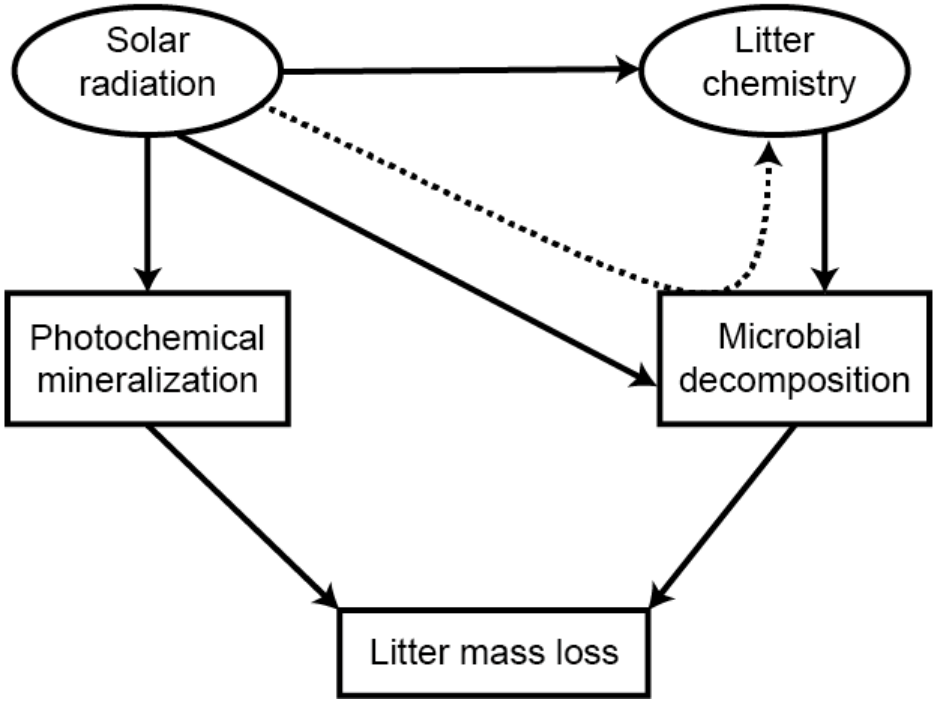

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508 Fig. 4

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