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Journal
Ecosystems, 17(1)

ISSN
1432-9840

Authors
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Publication Date
2014

DOI
10.1007/s10021-013-9712-x

Effects of UV exposure and litter position on decomposition in a California grassland

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Running Title: UV and Litter Position Effects on Decomposition

Author Contributions: YL and JK designed the study; YL conducted the field study and lab analyses with contributions from JK; YL and JK analyzed the data and wrote the paper.

Abstract

The importance of photodegradation in surface litter decomposition has recently been recognized in arid and semi-arid terrestrial ecosystems, yet its importance in decomposing dense litter and the mechanisms through which it acts remain unclear. We investigated how ultraviolet (UV) radiation exposure and litter position affected decomposition processes in a California annual grassland. In a split-plot design, we exposed *Bromus diandrus* litter to two levels of UV radiation (UV pass and UV block) at two aboveground locations (at the top, suspended above the litter layer, and at the bottom of the litter layer) for one year. We found that UV radiation increased the litter decay constant by 23% at the top location over one year, consistent with the occurrence of photodegradation. Surprisingly, UV radiation also increased the litter decay constant by 30% at the bottom location over one year. We speculate that photodegradation indirectly increased microbial decomposition through priming effects. Overall, litter in the top location had a 29% higher decay constant than litter in the bottom location. In terms of litter chemistry, exposure to UV radiation increased loss of hemicellulose by 26%, but not loss of lignin. Litter in the bottom location exhibited greater loss of the cell soluble fraction and greater nitrogen immobilization, but lower loss of hemicellulose than litter in the top location. Our results demonstrate that litter position significantly regulates the contribution of photodegradation to overall decomposition, both through direct (top location) and indirect (bottom location) effects. Therefore, better quantification of both direct and indirect effects of photodegradation can greatly improve understanding of biogeochemical cycling in grasslands.

Keywords

Photodegradation, decomposition, UV-A, UV-B, invasive species, hemicellulose, cellulose, lignin, litterbag, drylands

Introduction

Litter decomposition is a crucial process in terrestrial ecosystems because it regulates the turnover and fate of carbon, soil fertility, and eventually plant growth and productivity (Berg and McClaugherty 2008). Litter decomposition is usually considered as a biotic process that is influenced by environmental variables, such as temperature, water availability, and litter chemical quality (Melillo et al. 1982; Nagy and Macauley 1982; Aerts 1997). These environmental and litter quality variables have long been used to model litter decomposition rates in terrestrial ecosystems; however, such models usually underestimate mass loss in arid and semi-arid ecosystems (Meentemeyer 1978; Moorhead et al. 1999; Adair et al. 2008). In recent years, more and more studies have recognized the importance of abiotic decomposition processes in these ecosystems (Throop and Archer 2007; Austin 2011; King et al. 2012; Hewins et al. 2013).

Exposure to sunlight or artificial radiation sources can increase surface litter mass loss by up to 60% through an abiotic process, photodegradation (Gehrke et al. 1995; Austin and Vivanco 2006; Gallo et al. 2006; Brandt et al. 2007). Photodegradation is the process by which ultraviolet (UV; 280-400 nm) and photosynthetically active radiation (PAR; 400-700 nm) oxidize organic matter. Even though UV radiation only accounts for a small proportion of incoming solar radiation, its high-energy photons can effectively induce photochemical mineralization of organic matter (Brandt et al. 2009). While PAR is thought to be less effective in photodegradation than UV radiation on a per-photon basis, it can still significantly contribute to litter mass loss, especially in the wavelength range of 400 to 500 nm (Brandt et al. 2009; Austin and Ballaré 2010). On the other hand, exposure to UV radiation may also inhibit microbial activities, consequently leading to slower litter mass loss (Johnson 2003; Smith et al. 2010).

Evidence of photodegradation has changed our current understanding of the controls on litter decomposition processes in arid and semi-arid ecosystems. For instance, the nitrogen (N) immobilization and mineralization patterns observed during microbial decomposition may not be apparent in photodegradation (Brandt et al. 2007; Smith et al. 2010). Photodegradation can preferentially decompose lignin, a recalcitrant substrate in microbial decomposition (Day et al. 2007; Henry et al. 2008; Austin and Ballaré 2010). The occurrence of photodegradation also highlights the role of litter position. Most previous studies have found that litter suspended above ground decomposed slower than litter placed on the soil surface (Deshmukh 1985; Christensen 1986; Holland and Coleman 1987; Thurow 1989; Dukes and Field 2000). It was thought that the proximity of litter to the soil surface influenced litter decomposition mostly through affecting microbial activity. However, litter position can also change the relative contribution of photodegradation to decomposition processes. Photodegradation can be significant at the surface of a litter layer where solar exposure is high; yet, it can be negligible relative to microbial decomposition near the soil surface where the litter is shaded. Therefore, the relative balance between photodegradation and microbial decomposition is expected to change significantly between positions within a litter layer. Very few studies have considered the importance of litter position (but see Holland and Coleman 1987; Dukes and Field 2000); yet it may be critical for understanding litter dynamics in communities where both microbial processes and photodegradation can affect litter decomposition.

The objective of this study was to examine how the contribution of photodegradation to overall litter decomposition changes with different positions within a litter layer. We designed a 1-year litter decomposition experiment in a model semi-arid grassland in California, an ecosystem where photodegradation could be significant given the long, hot, and sunny Mediterranean summers. We manipulated UV radiation using specially designed screens and decomposed litter at the top and bottom of the litter layer. We tested the following hypotheses: 1) photodegradation would increase litter mass loss at the top of the litter layer, as the top location is under strong solar radiation exposure; 2) the relative contribution of photodegradation to overall decomposition would be negligible at the bottom of the litter layer, because the bottom location is heavily shaded by the litter layer; and 3) lignin loss would be faster at positions where photodegradation was significant, as lignin would be preferentially decomposed through photodegradation.

Methods

Study Site

This study was conducted at the University of California's Sedgwick Reserve in Santa Ynez, California, USA (43°42'N, 120°2'W). The Reserve is located approximately 50 km from the Pacific coast and features a Mediterranean climate with hot, dry summers and cool, wet winters. Mean annual precipitation is 380 mm, and mean annual temperature is 16.8°C. Soils range from Xerorthents to Haploxerolls with a texture of silty clay loam (Gessler et al. 2000). With the elimination of livestock grazing in 1995, *Bromus diandrus*, a Eurasian annual grass species, quickly came to dominate some of the formerly grazed grasslands, particularly those on untilled soils. The specific site for this experiment is located in relatively flat terrain. A litter layer between 5 and 15 cm in height persists above the soil surface and is mainly made of *B. diandrus* litter. Scattered oaks (*Quercus lobata* and *Q. agrifolia*) occur within the grassland matrix, but our specific study site is not shaded by oaks. We monitored UV radiation with a broadband UV radiometer (CUV5, Kipp & Zonen, Bohemia, New York, USA) at a meteorological station less than 20 m away from the study site. During the one-year experiment from August 2011 to August 2012, the site received approximately 320 MJ m^{-2} of UV radiation.

Experimental Design

To manipulate UV radiation (280-400 nm) received by the litter layer, ten pairs of steel frames of 75 cm * 150 cm * 25 cm (l * w * h) with plastics louvers that either block or transmit UV radiation were placed over the litter layer, as described in detail by Brandt et al. (2010). In short, two types of plastic materials were used because of their distinct optical properties: UV-transparent acrylic (UV pass, which transmits 90% of UV-A and UV-B radiation, Solacryl SUVT, Spartech Polycast, Stamford, Connecticut, USA) and UV-absorbing polycarbonate (UV block, which blocks 90% of UV-A and UV-B radiation, Lexan XL, GE, Pittsfield, Massachusetts, USA). Both materials pass greater than 85% of PAR. Compared to these specifications, the transmission properties of both materials are attenuated by atmospherically-deposited dust, abrasion, and degradation of the material over time in the field. Therefore, we periodically wiped the materials with a dampened cloth and measured their transmission properties as described below. The frame design allows penetration of rainfall and avoids excessive heating. Frames were placed over a relatively homogeneous area of *B. diandrus* litter.

To examine the impacts of litter position on decomposition, litterbags of 20 cm * 20 cm (l * w) containing *B. diandrus* litter were placed under each frame in late August

2011 either (1) suspended above the litter layer, 5 cm below the screen, and supported from below by a stainless steel mesh (> 95% light transmission for the steel mesh; hereafter, top location), or (2) on the soil surface underneath the litter layer (hereafter, bottom location). All litterbags were placed at least 10 cm from the edges of the frames to avoid edge effects. Litterbags were made with 1.5-mm aluminum mesh, which allows high penetration of solar radiation (> 70%). Its small mesh size helps to keep small litter parts inside the litterbags. Litter used here was collected in July 2011 and then air-dried, cut into pieces that fit the mesh bags, and mixed. A total of 160 litterbags were deployed to achieve 4 harvests in one year and 10 replicates for each combination of UV and position factors in each harvest. During the growing season, green grasses under the screens were periodically cut to avoid shading the litterbags at the top location.

To ensure that the UV treatments were effective, we checked the transmission of UV-A, UV-B, and PAR through the screens at various times of day (including solar noon and up to 3 hours before and after noon) monthly from August 2011 to January 2012. We measured UV radiation under and outside of the screens using a radiometer with separate sensors for UV-A and UV-B (UV-X, UV Products, Upland, California, USA). The spectral response curve of the UV-A sensor ranged from 300 to 400 nm with a peak at 365 nm. The spectral response curve of the UV-B sensor ranged from 260 to 370 nm with a peak at 310 nm. We also measured PAR using a sensor calibrated to natural sunlight (Apogee Instruments, Logan, Utah, USA).

To evaluate impacts of UV radiation and position treatments on microclimate of the litter layer, we sealed temperature sensors (n = 3 for each combination of UV and litter position; DS1921 iButton, Maxim Integrated, San Jose, California, USA) in small aluminum mesh bags of 5 cm * 5 cm (l * w) with litter and placed the bags at either top or bottom locations from August 2011 to January 2012. These sensors were programmed to record temperature every two hours. We replaced the temperature sensors with relative humidity (RH) sensors (n = 2-3 for each combination of UV and litter position; DS1923 iButton, Maxim Integrated, San Jose, California, USA) from January to July 2012.

Litterbag Collection

Litterbags were collected at 3, 6, 9, and 12 months after deployment (late November 2011, early March 2012, early June 2012, and early September 2012). Visible soil, green plants, and arthropods were separated from the litter. Litter was then oven-dried at 55°C for 2 days before weighing. Litter was ground using a Wiley mill with U.S. standard #40 mesh, and a subsample was ashed at 600°C for 4 hours to calculate ash-free dry mass.

Chemical Analysis

We analyzed for litter composition, including the cell soluble fraction (including soluble carbohydrates, proteins, and lipids; hereafter, cell solubles), hemicellulose, cellulose, and lignin, using a sequential extraction technique (Van Soest 1963). Subsamples were subjected to neutral fiber detergent, acid fiber detergent, and sulfuric acid digestions using an ANKOM fiber analyzer (ANKOM Technology, Macedon, New York, USA). After the sulfuric acid digestion, samples were ashed (4 hours at 600°C) to correct for any mineral particles in the lignin fraction. It has been recognized that the lignin fraction includes not only lignin and lignin-like aromatic components, but also other recalcitrant components including cutin, suberin, and waxes (Von Lützow et al. 2007; Yanni et al. 2011). We refer to this fraction as lignin to be consistent with many previous studies using this technique in studying litter decomposition (e.g. Hobbie 2000; Melillo et al. 1982). Chemical characteristics of the initial litter material are given in Table 1. A subsample of litter was then ground to powder using a roller mill and weighed into tin capsules for analysis of carbon (C) and N concentrations using an elemental analyzer (Fisons NA1500, Fisons Instruments, Beverly, Massachusetts, USA).

Data Analysis

Statistical analyses were conducted using R software (2.10.1). For each litterbag harvest, percent dry mass remaining, litter N concentration, litter N content (% of initial), and carbon fractions were analyzed using a split-plot ANOVA with UV as the main-plot factor and position as the sub-plot factor. Before the ANOVA, data were checked for the normality and equality of variance, and no transformation was needed. Differences among treatments were compared using Ryan-Einot-Gabriel-Welsch procedure (hereafter, Ryan procedure), which controls for family-wise error rate (Zar 1999). To calculate decay constants (k), mass loss data were fitted to a negative exponential model: $X(t) = 100\ e^{-kt}$, and a linear model: $X(t) = -kt + c$, where X is the percent mass remaining in the litterbag, t is the time, and k is the decay constant (year^{-1}). Decay constants were calculated for all combinations of treatments and replicates (2 UV * 2 position * 10 replicates). We compared the fitness of the two models using the second-order correction of Akaike's information criterion (AICc; Burnham and Anderson 2002). When the difference between the two AICc values was greater than 3, the model with the lower AICc was considered a better fit. Relationships between carbon fractions and percent dry mass remaining were evaluated with Pearson's correlations.

Results

UV Radiation and Microclimate

The UV block treatments were successful in altering radiation received, and the two litter positions differed dramatically in their exposure to radiation. On average, UV block treatments eliminated 93% and 85% of UV-A and UV-B radiation, respectively, while UV pass transmitted about 80% and 79% of UV-A and UV-B radiation, respectively. Transmission of PAR was 83% and 87% for UV block and pass treatments, respectively. On average, the bottom location received 3%, 3%, and 5% of UV-A, UV-B, and PAR received at the top location, respectively. At the top location, litter inside litterbags received approximately 180 MJ m^{-2} and 22.4 MJ m^{-2} UV radiation (UV-A + UV-B) in UV pass and block treatments over the one-year experiment, respectively. At the bottom location, both UV treatments received less than 5 MJ m^{-2} UV radiation over one year.

From August 2011 to January 2012, UV treatments did not affect daily mean, maximum, or minimum temperature (data not shown). Even though there was no difference in daily mean temperature between the two locations, daily maximum temperature was 9.0°C higher in the top location (t-test: $P = 0.008$), and daily minimum temperature was 5.2°C lower in top location (t-test: $P = 0.004$, Table 2). No UV-position interaction was found on daily mean, maximum, or minimum temperature (data not shown).

The relative humidity (RH) was affected by position (Table 2) but not by either UV or UV-position interaction (data not shown). During the wet season from January to April 2012, daily mean and minimum RH at the bottom location were 29.3% (t-test: $P = 0.001$) and 44.5% (t-test: $P = 0.008$) higher than those at the top location, respectively (Table 2). There was no difference in daily maximum RH between the two locations in the wet season. During the dry season from May to July 2012, daily maximum RH was 18.5% higher (t-test: $P = 0.008$) at the top than at the bottom location. Daily minimum RH was 13.4% lower (t-test: $P = 0.017$) at the top than at the bottom location. No difference in daily mean RH was found between the two locations during the dry season (Table 2).

Mass Loss

Mass loss was not steady across the harvests: mass loss occurred most quickly before the first harvest and between the second and third harvests, which corresponded to the fall season (28% of the total rainfall over the experiment) and the spring-early summer season (46% of the total rainfall), respectively (Figure 1). Both UV treatment and position affected the fraction of litter mass remaining at all harvests, and there was no significant interaction between UV treatment and position at any harvest. Across all harvests, the UV pass treatment increased litter mass loss by 30% compared to the UV block treatment, and being in the top location increased litter mass loss by 39% compared to the bottom location. In the bottom location, UV exposure increased mass loss at the first three harvests but not at the final harvest.

Differences in AICc values between linear and negative exponential models were smaller than 3 in all combinations of treatments and replicates, suggesting that the two models fit the mass remaining data equally well. Overall, negative exponential models had reasonable fits (median of $R^2 = 0.784$, 5% percentile of $R^2 = 0.400$, 95% percentile of $R^2 = 0.971$). Decay constants from negative exponential models are presented here, as the negative exponential model is more widely used in decomposition studies. The decay constant was higher with UV exposure (UV pass, split-plot ANOVA: $P = 0.002$, Figure

2), such that UV exposure increased the litter decay constant by 23% and 30% at the top (Ryan procedure: $P < 0.05$) and the bottom locations (Ryan procedure: $P < 0.05$), respectively. Litter in the top location also had a 29% higher decay constant than litter in the bottom location (split-plot ANOVA: $P = 0.002$, Figure 2).

Carbon Fraction Loss and Nitrogen Dynamics

After one year, the fractions of cell solubles, hemicellulose, cellulose, and lignin each responded differently to UV and position treatments. No significant loss of cell solubles was found at the top location; however, there was an average 8% loss of cell solubles at the bottom location (Figure 3a). The fraction of cell solubles remaining was affected by both position (split-plot ANOVA: $P = 0.034$) and the interaction between UV treatment and position ($P = 0.033$) so that, under UV block, percent cell solubles remaining tended to be higher in the top compared to the bottom location (Ryan procedure: $P = 0.09$). Loss of hemicellulose was 26% greater in UV pass than in UV block (split-plot ANOVA: $P < 0.001$), and it was 83% greater in the top than in the bottom location ($P < 0.001$, Figure 3b). Higher exposure to UV radiation (UV pass) increased the loss of cellulose by 11% compared to UV block (split-plot ANOVA: $P = 0.037$, Figure 3c). There was a trend that the top location had more cellulose remaining (split-plot ANOVA: $P = 0.065$). The bottom location had 47% higher lignin content than the top location (split-plot ANOVA: $P < 0.001$, Figure 3d) after one year; in fact, litter lignin content at the bottom location was 30% greater than in the original litter (t-test: $P < 0.001$). There was no UV effect on the percent lignin remaining (split-plot ANOVA: $P = 0.420$).

There was a weak negative correlation between litter mass loss and hemicellulose concentration at the bottom location for all samples taken from the four harvests (Figure 4a, $r = -0.285$, $P = 0.011$). This negative correlation became much stronger at the top location ($r = -0.762$, $P < 0.001$). Unlike hemicellulose, cell solubles had a positive correlation with litter mass loss, and the correlation was much stronger at the top ($r = 0.682$, $P < 0.001$) than at the bottom location ($r = 0.270$, $P = 0.017$, Figure 4b).

After one year, both UV pass (split-plot ANOVA, $P = 0.041$) and being at the top location ($P = 0.012$) decreased percent litter N remaining (Figure 5a). In fact, litter in all treatments exhibited N immobilization (higher N content than the initial amount) except at the top location under UV pass. However, N concentration was not affected by UV, position, or their interaction after one year (Figure 5b).

Discussion

Litter Decomposition Rates

Our results support the hypothesis that photodegradation can significantly contribute to litter decomposition (Fig.1 and Fig. 2). In a meta-analysis, King et al. (2012) found that the mass loss of litter exposed to ambient solar radiation was on average 32% faster than that exposed to reduced solar radiation, similar to the 30% enhancement of litter mass loss by UV exposure found in this study. Our results suggest that photodegradation is an important driver of the C cycling in Mediterranean grasslands. Similarly, Henry et al. (2008) found that mass loss was much faster in litter exposed to sunlight compared to shaded litter in a California grassland, and Rutledge et al. (2010) found that photodegradation can contribute as much as 60% of CO_2 emission in summer in a California grassland.

Contrary to our hypothesis, UV exposure not only consistently increased litter mass loss at the top location, but also enhanced litter decay in several harvests at the bottom location (Fig. 1 and Fig. 2). Since very limited UV radiation and PAR penetrated the litter layer, this UV effect at the bottom location is unlikely a result of direct organic matter mineralization by photodegradation. The UV treatment also did not affect temperature or relative humidity at the bottom location. Previous studies found that photodegradation can indirectly contribute to decomposition processes by enhancing the solubility of litter organic matter, consequently leading to increased leaching (Gallo et al. 2006; Feng et al. 2011). We also found that in the top location the concentration of cell solubles, a group of labile C compounds, increased as mass loss increased (Fig. 4). This result suggests that photodegraded C compounds, e.g. some cell solubles, accumulated in the litter layer and could be relocated to the bottom of the litter layer through leaching. We speculate that this leachate increased litter decomposition rates near the soil surface through priming effects (reviewed by Kuzyakov et al. 2000). This mechanism, if proven, would mean that effects of photodegradation in dryland ecosystems are not limited to increasing litter mass loss. This proposed mechanism suggests that solar radiation not only directly contributes to litter decomposition through photochemical mineralization, but also indirectly increases decomposition rates through interactions with microbial processes. Further studies are needed to examine this indirect effect of radiation exposure on litter decomposition in order to better understand its role in C cycling.

Unlike many previous studies (Christensen 1986; Holland and Coleman 1987; Dukes and Field 2000), faster litter decomposition occurred away from soil than at the soil surface in this study (Fig. 1 and Fig. 2), suggesting other decomposition processes could be at least as important as microbial decomposition in this study. During this one-year experiment, the total rainfall (290 mm) was much lower than the average annual precipitation (380 mm). Microbial decomposition rates may have been suppressed during the experiment because of the limited rainfall, consequently increasing the relative contribution of other decomposition processes to the overall litter mass loss. At the top location, PAR very likely contributed to decomposition through photodegradation (Brandt et al. 2009). Besides photodegradation, other abiotic processes also likely contributed to litter mass loss in this study. Wind abrasion might have contributed to litter mass loss at the top location (Anderson 1973; Austin 2011). Soil-litter mixing has been found to be an important process in litter decomposition in dryland ecosystems (Throop and Archer 2007; Hewins et al. 2013). Across the four harvests in this study, a weak relationship between the ash content and litter mass loss was observed at the bottom location ($R^2 = 0.145$, $P < 0.001$, data not shown), but no relationship between the two was observed at the top location ($R^2 = 0.01$, $P = 0.501$, data not shown). These results suggest that soil-litter mixing contributed to litter decay at the bottom location where litter directly contacted the soil. Our results further highlight the importance of abiotic processes (not limited to photodegradation) in decomposition in grassland ecosystems, especially under drought conditions.

Seasonal patterns in mass loss were related to seasonal changes in radiation, temperature, and precipitation. Among four litterbag collection time points, the slowest mass loss was found from November 2011 to March 2012 (Fig. 1). This period had the lowest solar intensity and temperature among all four sampling periods. Both photodegradation and microbial decomposition were likely to be limited, contributing to the low mass loss. During this period, bottom locations did not show net mass loss (Fig. 1). This phenomenon is not uncommon in litter decomposition studies, especially in the early stages of decomposition (e.g. Quideau et al. 2005; Brandt et al. 2010). The slight increase in remaining mass could be related to microbial growth on the decomposing litter. Variation among litterbags might also contribute to this pattern. Differences in mass loss between UV block and pass at the top location tended to become bigger from June to September 2012 (Fig. 1), which was likely driven by UV photodegradation. The overall decay, however, was slowed down in this dry period (Fig. 1), suggesting limited contribution by microbial decomposition to overall litter decay during this period.

Carbon Fractions

Contrary to our hypothesis, loss of lignin was not increased by UV exposure. This result adds to the current discussion about the role of lignin during photodegradation. Lignin is believed to be the only substrate in the plant cell wall that has strong absorption in both UV and short-wavelength PAR ranges (George et al. 2005). Therefore, lignin is usually assumed to be the photo-reactive compound in photodegradation. Some studies have shown that photodegradation could preferentially decompose lignin over other carbon fractions (Day et al. 2007; Henry et al. 2008; Austin and Ballaré 2010); however, this phenomenon was not found in other studies (Gehrke et al. 1995; Brandt et al. 2007; Brandt et al. 2010). The above studies used three different methods to measure lignin, including the Klason method, the acetyl bromide soluble method, and the acid detergent method. It has been documented that lignin concentrations vary greatly depending on the method employed (Hatfield et al. 1994; Hatfield and Fukushima 2005). Our study used the acid detergent method, which usually results in lower lignin concentration than other methods (Hatfield and Fukushima 2005). *Bromus* species also tend to have lower lignin concentrations (2-5%) than many other grass and woody species when comparing across species using the acid detergent method (Van Soest 1965; Jung et al. 1999; McLauchlan et al. 2006). It is possible that the relatively low lignin concentration made it difficult to observe changes induced by photodegradation.

Our study did find that UV photodegradation increased the breakdown of the hemicellulose fraction by 26% (Fig. 3b), which is consistent with previous studies (Rozema et al. 1997; Brandt et al. 2010). We also found that UV photodegradation increased the loss of cellulose by 11% (Fig. 3c). It is possible that the responses of hemicellulose and cellulose to photodegradation are more prominent when the lignin concentration is low. Even though only one species was examined here, it is reasonable to expect that photodegradation can influence carbon fractions other than lignin in other species as well. In many grass species, hemicellulose and cellulose are more abundant than lignin. Photodegradation would have a significant contribution to overall decomposition if it preferentially degraded hemicellulose or cellulose. More studies are needed to better understand the mechanisms behind changes in carbon fractions due to photodegradation.

The two litter locations showed distinct patterns in changes of carbon fractions (Fig. 4), suggesting that the relative balance between abiotic and biotic decomposition processes was different at the two locations. At the top location, photodegradation via UV and PAR likely preferentially decomposed hemicellulose into more labile forms, such as cell solubles, resulting in a negative relationship between hemicellulose and mass loss and a positive relationship between cell solubles and mass loss. Even though we did not directly measure microbial activity in this study, the carbon fraction data strongly support the idea that microbial activity dominated decomposition processes at the bottom location: the depletion of labile cell solubles at the bottom location was likely the result of microbial consumption; and the accumulated lignin fraction at the bottom location was likely comprised of lignin-like microbial by-products, such as partially humified compounds (Coŭteaux et al. 1995).

Such distinct decomposition processes between the two litter positions stem from differences in physical factors, including radiation, relative humidity, and temperature. High radiation (UV and/or PAR) and high temperature during daylight hours resulted in significant photodegradation at the top location, consistent with results of Lee et al. (2012) who showed both thermal and photochemical degradation and greater release of photochemical gaseous C under higher temperature (Lee et al. 2012). The higher relative humidity in the wet season (29% higher) and narrower temperature range (10~45 °C) likely helped to maintain microbial activity at the bottom location relative to the top location. These physical factors can be critical when incorporating abiotic processes into decomposition models in grassland ecosystems.

N Dynamics

We found that UV exposure decreased N immobilization at the top location (Fig. 5a). Meanwhile, N immobilization was greater at the bottom location, which provides further evidence that microbial activity dominated litter decomposition at the bottom location. It is possible that UV exposure reduced microbial activity by damaging microbial nucleic acids and inhibiting fungal colonization and growth (Johnson 2003; Pancotto et al. 2003;

Hughes et al. 2003). Brandt et al. (2007) found that N immobilization was positively correlated with initial C:N of litter under UV block treatment, but not under UV pass treatment, suggesting that photodegradation weakened N immobilization. Smith et al. (2010) also found that increased UV-B radiation reduced litter N immobilization, especially when the soil microbial community was not suppressed. Together with these previous studies, our results suggest that exposure to solar radiation not only can increase litter decomposition through photodegradation, but also can negatively affect microbial processes. Indeed Smith et al. (2010) reported negative impacts of UV exposure on overall decomposition rates. For the exposed litter in this study, the positive contribution of photodegradation to decomposition overshadowed the possible negative effects of radiation on microbial decomposition, especially because microbial activity was likely to be low during the study period. In a more mesic environment where microbial decomposition contributes more to overall decomposition, one would be more likely to observe negative effects of radiation exposure on N dynamics and overall decomposition (e.g. Smith et al. 2010).

Conclusion

Our results show that photodegradation increased litter mass loss by 30% overall. This influence of photodegradation on litter decay depended on litter position such that litter exposed at the top of the litter layer showed a significant UV radiation effect via photochemical mineralization, while the heavily shaded litter at the bottom of the litter layer also showed a UV radiation effect which we interpret as an indirect contribution by photodegradation. This potential indirect effect indicates that photodegradation can greatly contribute to the overall decomposition through interaction with microbial processes. Our data suggest that litter position regulates the balance between photodegradation and microbial decomposition through effects on physical factors, including radiation exposure, temperature, and moisture. Our study also highlights the importance of abiotic decomposition processes, including photodegradation and litter-soil mixing, in dryland ecosystems. Our study calls for more thorough examination of litter chemical composition and its relationship with photodegradation in order to accurately predict the degree of photodegradation. The results indicate that both the direct and indirect effects of photodegradation should be examined to better understand, quantify, and model decomposition processes in grassland ecosystems.

Acknowledgements

We thank Dad Roux-Michollet, Keri Opalk, Kenneth Marchus, Matt Mass, Viviane Vincent, Molly Zimmerman, and Heather Christian for their assistance in the field and lab. We thank Oliver Chadwick and Carla D'Antonio for their valuable comments on the experimental design and on this manuscript. We thank Kate McCurdy, Eric Massey, and the University of California's Sedgwick Reserve for providing the study site, field facilities, and technical support. This work was supported by the National Science Foundation under DEB-0935984.

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Figure Captions (please see published article for figures - files could not be entered here)

Figure 1. Fraction ash-free dry mass remaining (%) over time in *B. diandrus* litter affected by ultraviolet radiation (UV pass or UV block) and position (top or bottom). Means and standard errors shown (n = 10).

Figure 2. Litter decay constant (k, y^{-1}) from a single exponential decay model for *B. diandrus* litter affected by ultraviolet radiation (UV pass or UV block) and position (top or bottom). Means and standard errors shown (n = 10). Different letters indicate significant difference (Ryan procedure, $\alpha = 0.05$).

Figure 3. Effects of ultraviolet radiation (UV pass or UV block) and position (top or bottom) on (a) cell solubles remaining (% of initial), (b) hemicellulose remaining (% of initial), (c) cellulose remaining (% of initial), and (d) lignin remaining (% of initial) of *B. diandrus* litter after one year. Means and standard errors shown ($n \geq 9$). Different letters indicate significant difference (Ryan procedure, $\alpha = 0.05$).

Figure 4. (a) Relationships between ash-free dry mass loss (%) of *B. diandrus* litter and hemicellulose (%) at bottom (black circle, solid line, Pearson's correlation coefficient r = -0.285, P = 0.011) and at top (gray circle, dashed line, r = -0.762, P < 0.001) location for samples taken from the four harvests; (b) relationships between ash-free dry mass loss (%) of *B. diandrus* litter and cell solubles (%) at bottom (black circle, solid line, r = 0.270, P

= 0.017) and at top (gray circle, dashed line, r = 0.682, P < 0.001) location for samples taken from the four harvests.

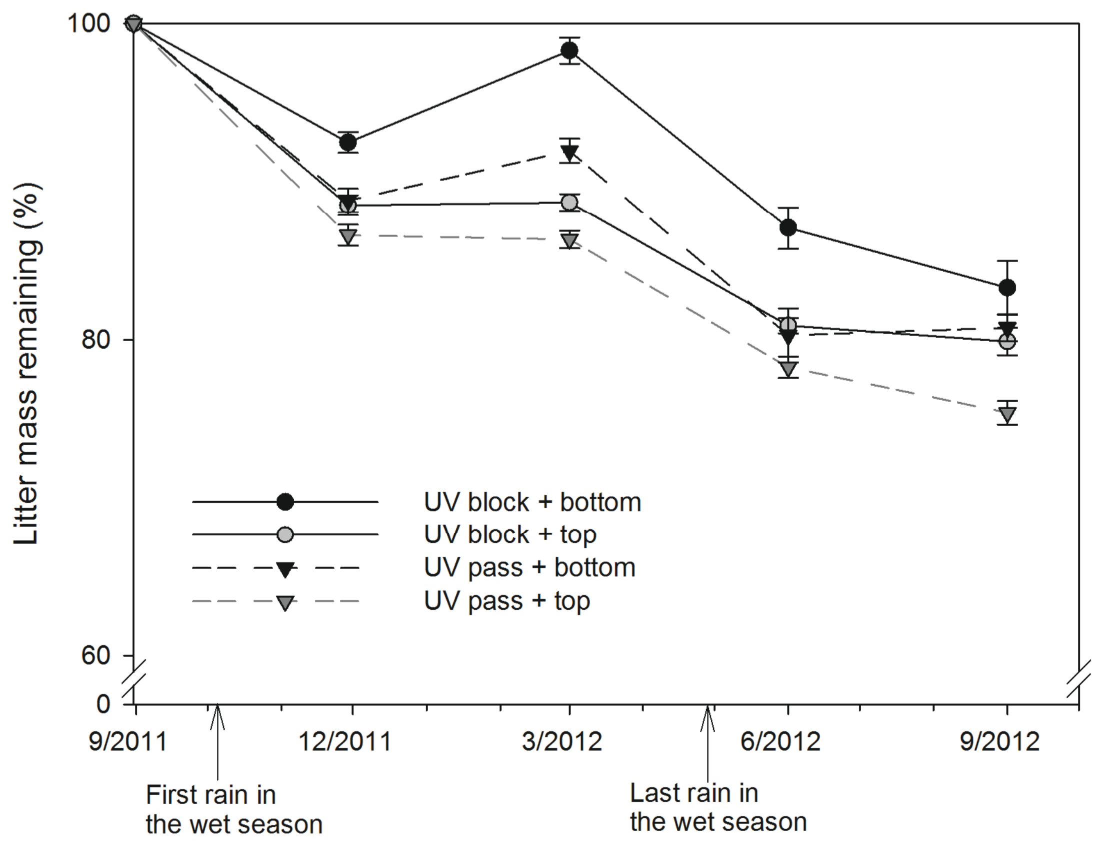
Figure 5. Effects of ultraviolet radiation (UV pass or UV block) and position (top or bottom) on (a) litter N remaining (% of initial) and (b) litter N concentration (%) of *B. diandrus* litter after one year. Means and standard errors shown. Different letters indicate significant difference (Ryan procedure, $\alpha = 0.05$).

Table 1. Initial chemistry of *B. diandrus* litter. Means and standard errors shown (n = 10).

Initial Chemistry	*B. diandrus*
% Carbon	41.25 (0.12)
% Nitrogen	0.48 (0.02)
% Cell Solubles	25.46 (0.62)
% Hemicellulose	31.65 (0.27)
% Cellulose	39.69 (0.45)
% Lignin	3.19 (0.15)
C:N	85.97 (2.71)
Lignin:N	6.66 (0.39)

Table 2. Impacts of litter position and UV treatment on temperature and relative humidity. Mean and standard errors are shown (n = 4-6). Different letters indicate significant difference.

Litter position or UV treatment	Temperature (°C, August 2011 to January 2012)			Relative humidity (%, January to April 2012)			Relative humidity (%, May to July 2012)		
	Daily mean	Daily maximum	Daily minimum	Daily mean	Daily maximum	Daily minimum	Daily mean	Daily maximum	Daily minimum
Top	15.1 (0.7)a	35.4 (0.6)a	3.8 (0.1)a	69.9 (0.2)a	99.7 (0.3)a	23.3 (0.6)a	60.8 (0.3)a	98.9 (2.6)a	15.9 (3.5)a
Bottom	14.7 (0.2)a	26.4 (2.7)b	9.0 (0.4)b	98.9 (2.6)b	103.2 (1.7)a	67.8 (4.0)b	57.9 (3.8)a	80.4 (4.5)b	29.3 (2.9)b
UV block	14.9 (0.6)a	31.2 (2.8)a	6.2 (1.1)a	82.0 (8.8)a	102.4 (1.8)a	47.3 (17.4)a	59.4 (1.7)a	89.8 (5.8)a	22.9 (4.6)a
UV pass	14.8 (0.2)a	31.2 (2.7)a	6.2 (1.3)a	79.3 (6.8)a	100.4 (0.8)a	43.8 (14.1)a	59.1 (1.6)a	87.7 (6.8)a	23.6 (5.2)a



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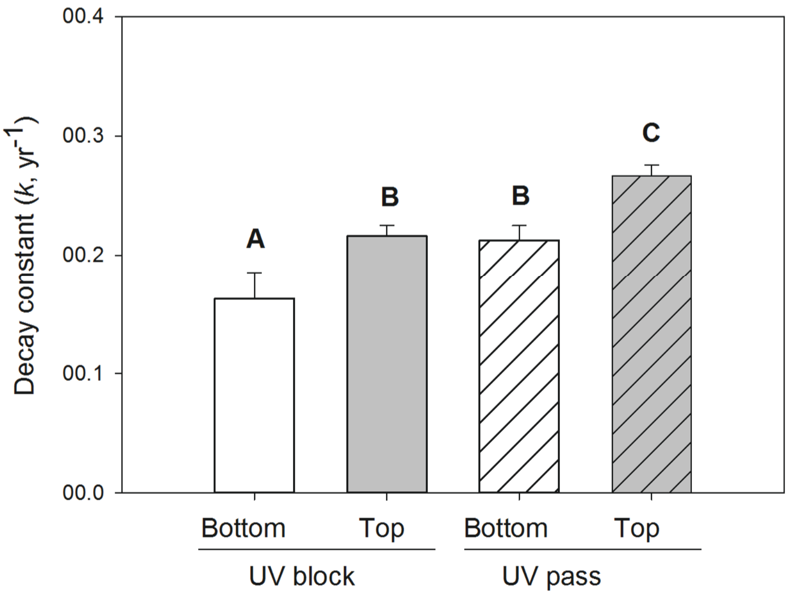

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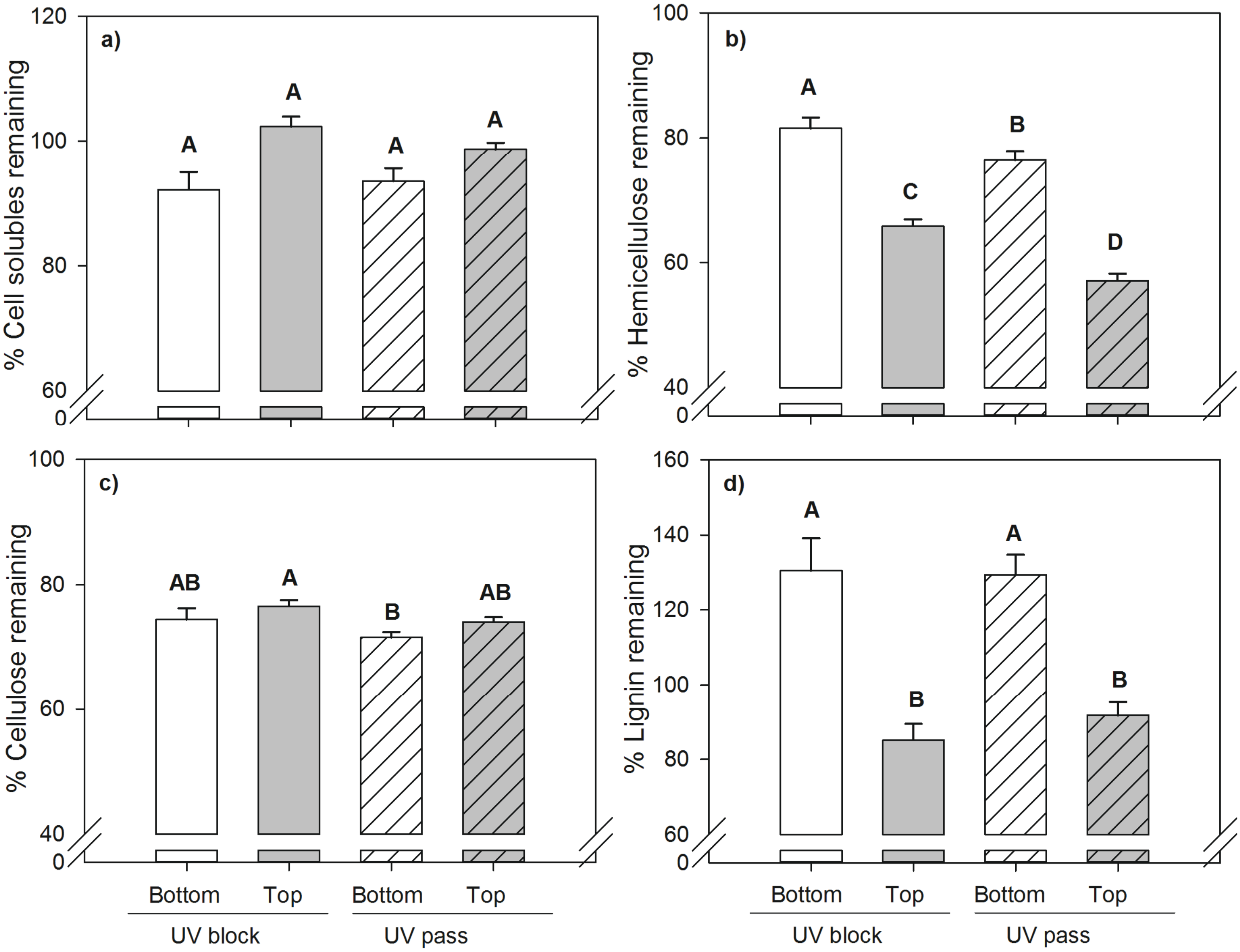

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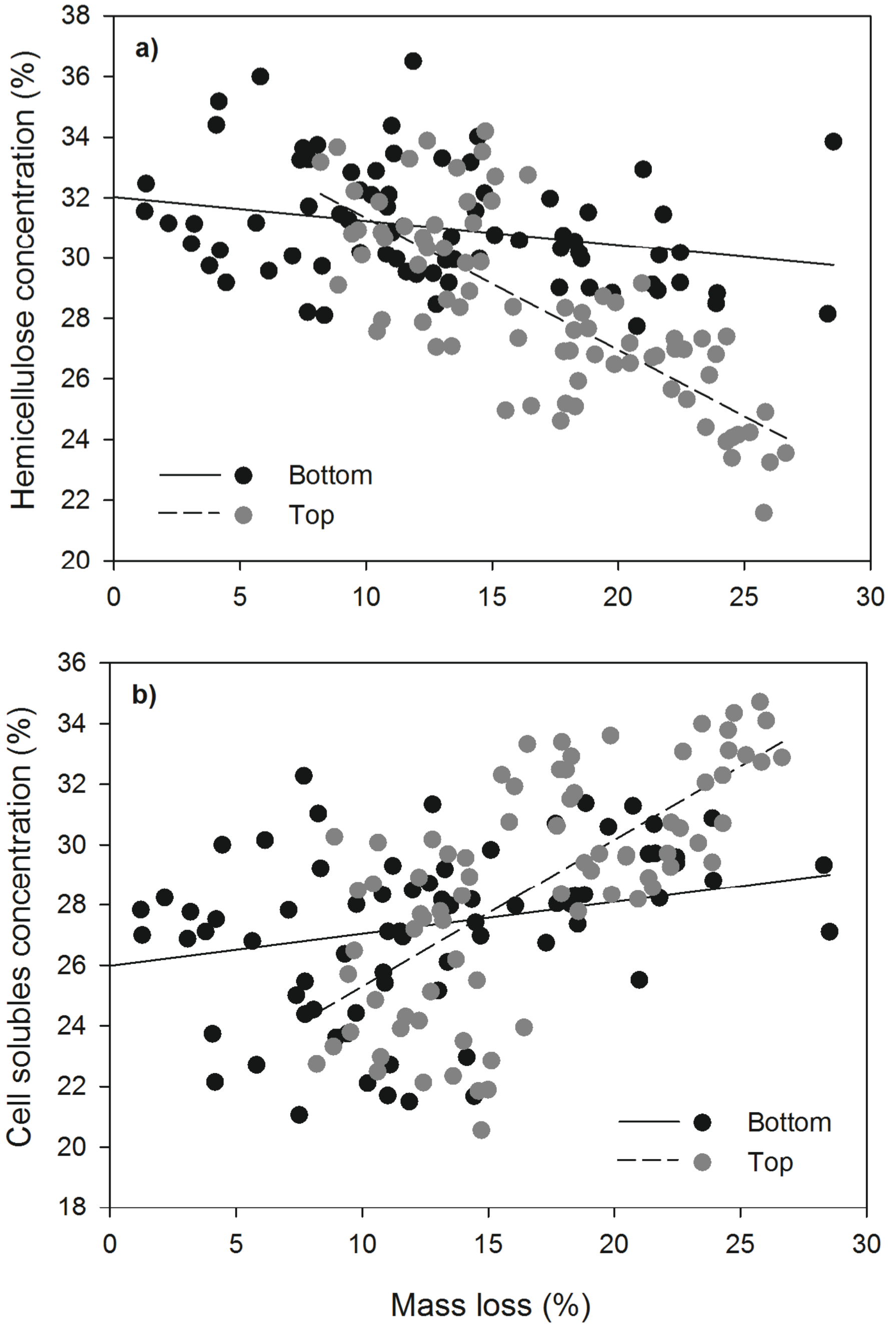

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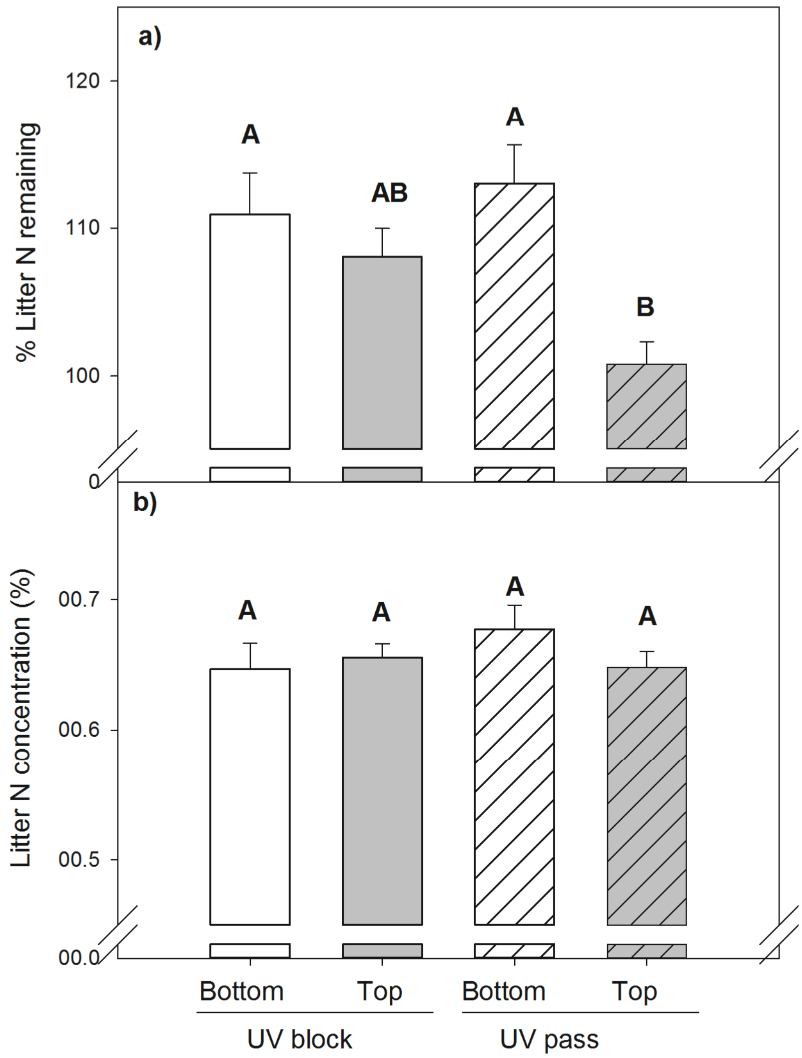

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