



Short-term facilitation of microbial litter decomposition by ultraviolet radiation



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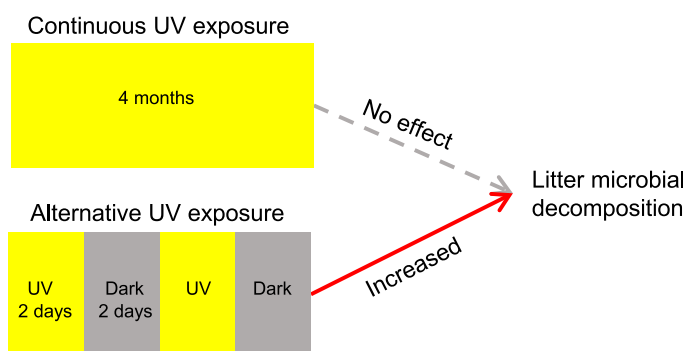
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HIGHLIGHTS

- Four months of continuous UV exposure increased mass loss by 3–4%.
- Four months of continuous UV exposure did not affect litter degradability.
- Abiotic photodegradation had limited effects on lignin chemistry.
- Microbial decomposition explained UV-induced lignin changes seen in the field.
- UV exposure facilitated microbial decomposition of litter on a timescale of days.

GRAPHICAL ABSTRACT



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ABSTRACT

Solar radiation plays an important role in carbon cycling by increasing the decomposition rates of plant litter and soil organic matter (i.e. photodegradation). Previous work suggests that exposure to radiation can facilitate microbial decomposition of litter by altering litter chemistry and consequently litter degradability (i.e. photopriming). However, it remains unclear to what extent photopriming contributes to litter decomposition processes and on what timescale photopriming operates. We conducted laboratory experiments to compare the effects of UV photopriming at two temporal scales (months versus days). In one experiment, we found that four months of UV exposure induced a significant but small (3–4%) mass loss in two of three litter species commonly found in California oak savanna; however, UV exposure did not alter litter degradability as measured by microbial respiration in an incubation experiment. We also found that UV exposure had limited effects on lignin and other cell wall structures, but one month of microbial decomposition (in absence of UV exposure) significantly reduced lignin β -aryl ether inter-unit linkages and acetylated xylans. These results indicate that abiotic photodegradation alone was ineffective at breaking down lignin. In another experiment, litter of a common grass was exposed to either alternating UV radiation and dark conditions or constant darkness for 128 days. We found that the alternating UV exposure increased litter CO_2 production in both dark and UV phases over that observed in constant darkness. This led to a 35% greater release of CO_2 from the alternating UV exposure treatment between days 65 and 128 of the experiment. These results demonstrate that alternating UV exposure with dark conditions is key to enabling photopriming on a timescale of days. Overall, we identify short-term

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photopriming as a novel mechanism behind photodegradation. Our results also challenge the conventional hypothesis that abiotic processes are primarily responsible for degrading lignin during photodegradation.

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1. Introduction

There are large uncertainties in current predictions of how the terrestrial carbon (C) cycle will respond to future climatic changes (Smith et al., 2013; Carvalhais et al., 2014; Smith et al., 2016). A major source of uncertainty is the difficulty in quantifying ecosystem C fluxes and attributing their variations among abiotic and biotic controls (Lombardozzi et al., 2015; Wieder et al., 2015). Litter decomposition is the central ecosystem process that transfers C from a transient pool in vegetation to a stabilized pool in soil (Berg and McClaugherty, 2008). Conventional theories of litter decomposition focus on understanding the environmental and chemical controls of biotic decomposition (Melillo et al., 1982; Coûteaux et al., 1995). Empirical models developed based on these theories are successful overall, but they systematically underestimate litter decomposition rates in many arid and semi-arid environments (Schaefer et al., 1985; Parton et al., 2007; Adair et al., 2008). This knowledge gap has sparked a new and growing field of research on photodegradation (Austin and Vivanco, 2006; King et al., 2012; Song et al., 2013; Liu et al., 2014; Barnes et al., 2015). Here, the term “photodegradation” refers to the combination of abiotic and biotic effects of solar radiation on decomposition processes.

Abiotic photodegradation refers to the photochemical and/or thermal mineralization of organic matter upon exposure to solar radiation, including ultraviolet (UV; 280–400 nm) and photosynthetically active radiation (PAR; 400–700 nm) (Brandt et al., 2009; Lee et al., 2012; Whelan and Rhew, 2014). Laboratory studies have linked abiotic photodegradation processes to the breakdown of litter and soil organic matter and emissions of CO₂, CO, CH₄, and volatile organic compounds (Schade et al., 1999; Leff and Fierer, 2008; Brandt et al., 2009). These abiotic emissions of trace gases are typically small in magnitude (reviewed by King et al., 2012), making it difficult to directly measure them in the field (van Asperen et al., 2015). The litter mass loss induced by abiotic photodegradation is also generally small (reviewed by Song et al., 2013; Wang et al., 2015) compared to the results from field studies showing that exposure to solar radiation increased mass loss by 25% to 60% (Austin and Vivanco, 2006; Brandt et al., 2010; Huang et al., 2017).

Photodegradation can also contribute to litter mass loss by facilitating microbial decomposition, a process known as photopriming (Barnes et al., 2015). Photopriming has often been included as a key component of photodegradation (e.g., Day et al., 2007; Gallo et al., 2009). More recent studies have begun to isolate and quantify the specific contribution of photopriming to litter decomposition (Foereid et al., 2010; Lin et al., 2015b; Wang et al., 2015; Yanni et al., 2015; Austin et al., 2016). It is hypothesized that photopriming is enabled via abiotic photodegradation of lignin, a main component of the plant cell wall that usually impedes microbial decomposition (King et al., 2012; Baker and Allison, 2015). Degradation of lignin allows microbial decomposers to access other litter substrates, thus increasing microbial litter decomposition. Many studies support this mechanism and report radiation-induced decreases in litter lignin content and increases in litter degradability during microbial decomposition (Henry et al., 2008; Austin and Ballaré, 2010; Frouz et al., 2011; Wang et al., 2015; Austin et al., 2016). However, it is unclear whether the loss of lignin was caused solely by abiotic photodegradation or a combination of abiotic photodegradation and photopriming of microbial decomposition. In addition, a large number of studies did not find facilitation effects of radiation exposure on litter degradability, further questioning the prevalence of photopriming (Brandt et al., 2009; Kirschbaum et al., 2011; Lambie et al., 2014; Lin et al., 2015b).

Identifying the underlying mechanisms of photopriming would help to resolve the above contradicting results of photopriming research. Past photopriming studies usually separated radiation treatment and the assessment of litter degradability into two consecutive phases. The first phase, radiation treatment, typically lasted for several months to a year and was often implemented under field or greenhouse conditions (Henry et al., 2008; Lin et al., 2015b; Wang et al., 2015; Austin et al., 2016). The second phase, assessment of litter degradability, was generally conducted without radiation manipulation under controlled field or laboratory conditions (Brandt et al., 2009; Lambie et al., 2014; Yanni et al., 2015; Austin et al., 2016). However, under natural conditions, litter experiences abiotic photodegradation and microbial decomposition simultaneously on a daily basis. Gliksman et al. (2016) recently demonstrated that daytime photodegradation primed litter microbial decomposition at night in a Mediterranean ecosystem, suggesting photopriming can occur at a diel scale. Therefore, photopriming might have occurred but was undetected during the first phase of a two-phase experiment. The two-phase design is thus likely to underestimate or misrepresent the contribution of photopriming to litter decomposition in the field. A comparison of the photopriming effects at different temporal scales (e.g. seasonal vs. daily) is currently lacking and would improve our understanding of the role of photopriming in litter decomposition processes.

Unlike the studies mentioned above, a number of other studies did not find preferential breakdown of lignin by photodegradation (Brandt et al., 2007; Lin and King, 2014; Baker and Allison, 2015), highlighting the lack of understanding of the underlying chemical mechanism behind photodegradation. Most previous studies relied on proximate analyses that sequentially extracted litter with solvents and assumed the acid-unhydrolyzable residues to be lignin. This assumption is strongly challenged in the field of decomposition science (Sluiter et al., 2010; Preston and Trofymow, 2015), which has led to several recent studies that examined changes in lignin chemical composition during photodegradation (Feng et al., 2011; Frouz et al., 2011). For instance, using two-dimensional nuclear magnetic resonance (2D NMR) spectroscopic techniques, we found that field UV radiation exposure degraded lignin β-aryl ether units and hemicelluloses (Lin et al., 2015a). In the current literature, however, there is no consistent pattern to describe how photodegradation alters lignin chemistry. It is also unclear whether abiotic photodegradation and microbial decomposition target similar lignin structures.

Here we present results from two controlled laboratory experiments that examine the mechanisms of photopriming at two different temporal scales. In the first experiment (*two-phase photopriming*), we exposed three types of litter to UV radiation for four months in the laboratory and evaluated the effects of abiotic photodegradation induced by UV radiation (hereafter, abiotic UV photodegradation) on litter mass loss and litter degradability. We also compared the effects of abiotic UV photodegradation and microbial decomposition on litter cell wall chemistry using 2D NMR techniques. In the second experiment (*short-term photopriming*), a grass litter was exposed to either alternating UV radiation and dark conditions or kept continuously in darkness in order to assess photopriming on a daily temporal scale. We hypothesized that 1) an extended period of UV exposure would stimulate litter mass loss due to abiotic photodegradation and increase litter biodegradability as a result of UV-induced lignin degradation; 2) abiotic UV photodegradation would be more effective in altering lignin chemistry compared to microbial decomposition; and 3) microbial decomposition of litter would be enhanced under an alternating light regime compared to continuous darkness as a result of short-term photopriming.

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