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Climate change may reduce litter decomposition while enhancing the contribution of photodegradation in dry perennial Mediterranean grasslands

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ABSTRACT

Understanding how the interactions between solar UV radiation and climate will affect leaf litter decomposition is fundamental to predict how soil and ecosystem biogeochemical cycles will respond to ongoing climate change. We carried out a manipulative experiment to investigate how UV radiation and its interaction with increased temperature (3 °C on average) and a ~35% reduction in precipitation affect the decomposition of "standing" and "on the ground" litter of *Stipa tenacissima*, a dominant species in semiarid Mediterranean grasslands. UV radiation was manipulated using specially designed screens that either passed or blocked 90% of the UV radiation. All climate change manipulation treatments decreased litter decomposition compared to the control treatment. In particular, litter decay rates were reduced by a 34%, 43% and 62% in the rainfall reduction (RE), warming (W), and the combination of warming and rainfall reduction (WRE) treatments, respectively, compared to the control treatment. Across climate manipulation treatments, higher decay rates were observed in litter exposed to UV radiation than in litter non-exposed to UV radiation, and in litter placed on the ground than in standing litter. However, significant interactions were found between climate manipulation and UV exposure or position treatments. In the control and RE treatments, litter on the ground decomposed 25% faster than standing litter. In the W and WRE treatments, litter decomposition rates increased by 29% when exposed to UV radiation despite lower overall decay rates were observed in these treatments. Overall, lignin losses were paralleled by increases in soluble cell materials, particularly when litter was exposed to UV radiation. Our results indicate that predicted climate change scenarios will likely reduce leaf litter decomposition rates, while enhancing the relative contribution of photodegradation to overall litter decomposition in dry perennial Mediterranean grasslands.

1. Introduction

Plant litter decomposition plays an important role in the formation of soil organic matter, the mineralisation of organic nutrients, and the carbon balance of terrestrial ecosystems (Berg and McClaugherty, 2008). As a result of a growing concern about climate change, and the increasingly recognized importance of the role of soil organic matter as a sink for atmospheric CO_2, much effort is being devoted to improving our understanding of the factors driving litter decomposition dynamics and subsequent soil C storage in terrestrial ecosystems (Zhang et al., 2008; García-Palacios et al., 2013). Extensive research has focused on predicting litter decay rates based on climate, litter quality and soil biotic

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interactions (e.g., Couteaux et al., 1995; Aerts, 1997). However, models based on climatic drivers consistently underestimate decay rates in arid and semiarid ecosystems (Whitford et al., 1981; Parton et al., 2007), suggesting that factors other than temperature and water availability may act as drivers of surface litter decomposition in these water-limited ecosystems (Throop and Archer, 2009; King et al., 2012; Barnes et al., 2015). A growing body of literature is showing that solar ultraviolet (UV; 280–400 nm) and high-energy visible radiation (400–550 nm) can be important drivers of leaf litter decomposition in arid and semiarid ecosystems (Austin and Vivanco, 2006; Brandt et al., 2007, 2009; Day et al., 2007; Gallo et al., 2009; Austin and Ballaré, 2010; Rutledge et al., 2010). Photodegradation is a process by which solar radiation breaks down directly organic matter components, releasing CO_2 and thus promoting a direct loss of carbon from ecosystems to the atmosphere without being incorporated into the soil organic matter pool (Austin and Vivanco, 2006). Although results differ among litter types, site-specific characteristics and experimental conditions, a recent meta-analysis has shown that litter exposed to solar radiation speeds up decomposition by 32% (King et al., 2012). However, the magnitude and proposed mechanisms for this mass loss remain unclear (Song et al., 2013; Wang et al., 2015). Besides facilitating microbial decomposition through breakdown of large organic compounds into more easily degradable ones (Foereid et al., 2010), photodegradation enhances the solubility of litter leading to increased leaching losses of dissolved organic carbon (Gallo et al., 2006), while promoting direct photochemical mineralisation of litter releasing CO_2 (Brandt et al., 2009; Lee et al., 2012). On the other hand, exposure to solar radiation may directly affect microbial populations by inhibiting microbial activity slowing down litter decomposition rates (Verhoef et al., 2000; Johnson, 2003; Pancotto et al., 2003; Smith et al., 2010) or changing the composition of microbial communities and the chemical characteristics of litter (Anesio et al., 1999; Schade et al., 1999; Smith et al., 2010). Thus, photodegradation is a complex process in which several mechanisms may counterbalance each other so its role on surface litter decomposition remains unclear. Moreover, the interaction between UV radiation and water availability or temperature is not yet fully understood and different responses have been found among studies. Photodegradation generally increases with increasing litter moisture content (Schade et al., 1999; Smith et al., 2010) and air temperature (Lee et al., 2012). However, some studies have observed that UV exposure increases decomposition rates by 25% under dry conditions in high C:N litter, but had no effects under wet conditions (Brandt et al., 2007). Nevertheless, and to the best of our knowledge, the interactive effect of high temperature and decreased water availability on litter decomposition rates by UV radiation has not been evaluated so far.

Alterations in vegetation cover driven by global change drivers, such as land use intensification or climate change, will accelerate degradation of senescent plant material through increased UV radiation exposure, stimulating the CO_2 release and mineralisation of nutrients, and thus limiting soil carbon sequestration and reducing soil fertility in drylands (Sala et al., 2000; Bornman et al., 2014; Williamson et al., 2014). It has been suggested that the Mediterranean region is highly sensitive to global climate change (Sala et al., 2000; Schröter et al., 2005). Recent global and regional models predict a 1.4–5.8 °C warming and 25–30% lower soil water availability over the next three decades in Mediterranean ecosystems as a result of lower rainfall and changes in rain distribution (Giorgi and Lionello, 2008; IPCC, 2013), which may alter litter decomposition dynamics and pathways, and hence soil C storage. Under this scenario, photodegradation could become increasingly more important in semiarid Mediterranean grasslands with sparse vegetation since more dead plant material might be exposed to solar radiation. Expected reductions in rainfall will result in reduced soil microbial activity, while potentially increased UV radiation resulting from reduced cloud cover will accelerate photo-oxidation of significant amounts of standing senescent plant material (Pancotto et al., 2003; Austin and Vivanco, 2006; Brandt et al., 2009; Throop and Archer, 2009). Therefore, understanding how climate change will impact litter decomposition is fundamental to accurately forecast the ecological consequences of ongoing global environmental change.

Despite the recent interest in the role of photodegradation as a driver of litter decomposition, it is uncertain how the process of photodegradation will be affected by climatic change. We carried out a multi-factorial 15-month field litter decomposition experiment designed to understand the role of UV-photodegradation on litter decomposition and its interaction with climate change and litter position. The main purpose of this study is to investigate how climate change will influence the impact (magnitude and direction) of UV radiation on litter decomposition of *Stipa tenacissima*, a dominant species in semiarid Mediterranean perennial grasslands (Le Houérou, 2001). Specifically, the objectives of this study were to: (i) assess the effect of increased temperature, decreased precipitation, and their interaction, on leaf litter decomposition dynamics of *Stipa*, (ii) quantify the contribution of photodegradation to overall leaf-litter decomposition, and (iii) evaluate how the position of the litter (standing *vs.* on the ground) affects these rates. We tested the following hypotheses: (i) expected increases in temperature and reductions in rainfall inputs will diminish overall litter decomposition because decomposition processes are highly dependent on soil moisture and dew events in semiarid Mediterranean areas (Dirks et al., 2010), which can be lessened by these climatic changes (Maphangwa et al., 2012; Maestre et al., 2013); (ii) photodegradation is an important mechanism of leaf litter decomposition in semiarid Mediterranean perennial grasslands, and thus, even during the dry season, important leaf litter decomposition will take place; (iii) the contribution of photodegradation will increase with warming and rainfall reduction, as microbial activity will be suppressed under less suitable environmental conditions (Brandt et al., 2010; Smith et al., 2010); and (iv) changes in the initial chemistry of plant material exposed to UV radiation are expected since photodegradation promotes the preferential degradation of lignin with respect to other relatively less recalcitrant carbon fractions (Pancotto et al., 2005; Austin and Ballaré, 2010) and the solubility of litter (Gallo et al., 2006; Foereid et al., 2010).

For the purposes of this study, and following previous research (Brandt et al., 2010; Barnes et al., 2015), we defined the net effect of photodegradation as the balance between positive direct (e.g., photo-lysis, photo-oxidation, fragmentation, thermal degradation, photo-dissolution) and indirect (e.g., changes in litter chemistry that facilitate leaching, fragmentation, or microbial decomposition) effects minus indirect negative (e.g., microbial photo-inhibition) effects. Thus, litter decomposition may be enhanced, lessened or unaffected by UV radiation exposure.

2. Material and methods

2.1. Soil and litter collection

Standing senescent leaf-litter from *Stipa* and soil were collected in a semiarid Mediterranean perennial grassland from Sorbas (Almería, SE Spain) dominated by this species (37° 05′ N, 2° 04′ W; 397 m a. s. l.). The soil from this site is derived from gypsum, has a pH value *ca.* 7, and is classified as a Gypsiric Leptosols (IUSS Working Group WRB, 2006). Recently senescent leaves of *Stipa* were collected on May 20th 2012, and were air-dried in paper bags