Summer sunlight impacts carbon turnover in a spatially heterogeneous Patagonian woodland

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Abstract

Purpose We evaluated the importance of dry season (summer) sunlight on carbon (C) turnover in a Mediterranean-type climate ecosystem in the context of spatially heterogeneous distribution of vegetation.

Methods We manipulated summer sunlight exposure of litter and soil at the ecosystem scale in a natural Patagonian woodland over two years and evaluated its effect on C turnover in litter and surface soil. We measured decomposition of standing dead litter of dominant grass and shrub species, changes in labile C pools in soil microsites with and without plant litter, and potential enzyme activity of litter and both soil microsites, evaluating seasonal and legacy effects of summer sunlight exposure.

Results Summer sunlight exposure significantly increased standing litter decomposition for both shrub and grass litter ($p < 0.05$). Additionally, summer sunlight significantly increased labile carbohydrate availability (saccharification) and potential microbial enzymatic activity of grass (but not shrub) litter. Interestingly, summer sunlight exposure also had effects on soil, reducing by 50% labile organic C while stimulating potential extracellular enzyme activity in both soil microsites, with and without plant litter.

Conclusion Summer sunlight accelerates C loss from standing litter and soil consistently across patches of heterogeneously distributed vegetation. In addition, sunlight exposure demonstrated carryover effects on the acceleration of grass litter decay in the following rainy season, when sunlight increased decomposition five times more than in the dry season. These results suggest that summer sunlight is an important and lasting control of C turnover at the ecosystem scale even in seasonally and spatially heterogeneous ecosystems.

Keywords Litter decomposition · Mediterranean-type climate · Photodegradation · Soil C cycling · Semi-arid ecosystems · Standing dead litter

Introduction

Biogeochemistry in semiarid ecosystems is regulated, in addition to climate and edaphic factors, by the heterogeneous distribution of vegetation (Charley and West 1975; Schlesinger et al. 1996). Vegetated patches, composed of shrubs and grasses (also trees or cacti), buffer harsh environmental conditions,
resulting in microsites of high soil organic matter (SOM) and nutrient availability that act as hotspots for soil microbial activity (Gonzalez-Polo and Austin 2009; Schaeffer and Evans 2005). In addition, plant litter in vegetated patches often remains as standing dead material, attached to the original plant for long periods of time before falling to the ground (Frouz et al. 2011; Pan et al. 2015; Wang et al. 2017a), particularly in systems with low fire frequency (Bennett et al. 2003; Kitzberger et al. 1997). In contrast, non-vegetated patches have much lower aboveground input of plant organic matter and are vulnerable to nutrient and organic matter loss due to wind and water erosion, resulting in patches with low carbon (C) and nutrient availability (Bertiller et al. 2004). In addition, we can also distinguish heterogeneity within vegetated patches, due to differences in C quality represented in plant life forms, and in non-vegetated patches, among bare soil microsites. This particular spatial distribution of vegetation defines the spatial heterogeneity that characterizes semiarid ecosystems (Austin et al. 2004; Charley and West 1975; Schlesinger et al. 1996).

Semi-arid ecosystems are characterized by low cloud cover, abundant incident solar radiation and discontinuous vegetation cover dispersed in a matrix of bare soil (Austin 2011; Noy-Meir 1973). Under these conditions, biological processes are often limited by the harsh environmental conditions of low soil moisture availability, high surface temperature and irradiance, and heterogeneous plant canopy cover (Austin 2011). At the same time, aboveground litter decomposition is often faster than would be expected (Austin 2011; Berenstecher et al. 2021) based on climatic parameters and litter quality that are traditionally used to predict litter mass loss (Aerts 1997; Meentemeyer 1978; Melillo et al. 1982). Instead, alternative drivers accelerate decomposition in aridlands, such as rainfall pulses and non-precipitation sources of moisture (Austin et al. 2004; Dirks et al. 2010), soil-litter mixing (Barnes et al. 2012; Hewins et al. 2013; Throop and Archer 2009), and exposure to solar radiation (e.g. Austin and Vivanco 2006; Brandt et al. 2007; Berenstecher et al. 2020). Therefore, an integrated understanding of the controls on C turnover in semiarid ecosystems is incomplete if these alternative drivers are not considered.

In particular, exposure to sunlight has been identified as an important control of C loss in semiarid ecosystems. In some semiarid ecosystems, more than half of C loss during decomposition of plant litter placed on the surface of bare soil occurs due to sunlight exposure (Austin and Vivanco 2006; Berenstecher et al. 2020). Sunlight accelerates litter decay by two pathways. On the one hand, solar radiation causes photochemical mineralization of organic matter in plant litter, due to exposure to ultraviolet (UV) and blue-green wavelengths (Austin and Vivanco 2006; Brandt et al. 2009; Lee et al. 2012; Schade and Crutzen 1999), an abiotic process known as photodegradation. On the other hand, the photochemical reactions associated with sunlight exposure can alter litter in ways that accelerate biotic decomposition (Austin et al. 2016; Baker et al. 2015; Berenstecher et al. 2020; Day et al. 2018, 2022; Gallo et al. 2009; Méndez et al. 2019), a process named photofacilitation or photopriming. One of the principal mechanisms that have been identified to explain photofacilitation is that lignin in litter exposed to sunlight is degraded, which increases microbial access to labile carbohydrates (Austin et al. 2016; Méndez et al. 2019). In line with this, some studies have shown an increase in extracellular microbial enzymes and the amount of carbohydrates released by microbial enzymatic processing of cellulose in photodegraded litter (Austin et al. 2016; Berenstecher et al. 2020; Méndez et al. 2019, 2022).

There is evidence suggesting that photofacilitation occurs at the daily (Gliksman et al. 2016; Lin et al. 2018) and seasonal scale (Berenstecher et al. 2020; Gliksman et al. 2018) for surface soil litter. However, it is unclear if sunlight effects are equally important for other key C pools, like standing dead litter of different life forms or soil C. In addition, the contribution of sunlight to leaf litter decomposition, either by photodegradation, photofacilitation, or both varies significantly among plant species (Austin et al. 2016; Pan et al. 2015; Wang et al. 2015). While traits like lignin, nitrogen (N) content or lignin/N ratio are some of the better predictors of decomposition when litter decay is primarily driven by biotic degradation (Cornwell et al. 2008; Hättenschwiler et al. 2011; Melillo et al. 1982), specific leaf area (SLA, Liu et al. 2018) and lignin for photochemical reactions (Austin and Ballaré 2010) become important when plant litter is exposed to sunlight. Thus, there is still much to be understood regarding how litter quality determines C turnover in semiarid ecosystems.
Mediterranean-type climate ecosystems are characterized by two contrasting seasons, a hot, dry summer and a cool, wet winter season (Cowling et al. 2005; Seager et al. 2019). The asynchrony of rainfall and temperature has negative effects on biological activity (Baldrian et al. 2013). In a previous study in a Mediterranean-type climate woodland in Patagonia, we showed that climate seasonality was relevant in determining the differential controls of biota and sunlight controlling C losses from surface litter, and the predominance of solar radiation as a control on litter decomposition at an annual scale (Berenstecher et al. 2020). Sunlight acceleration of litter decomposition has been reported in many other Mediterranean-type climate ecosystems (Almagro et al. 2015, 2017; Austin and Vivanco 2006; Baker et al. 2015; Gliksman et al. 2018; Henry et al. 2008; Méndez et al. 2019), although its seasonal variation has been rarely considered and may be important in our understanding and predictions of C dynamics in aridland ecosystems.

Empirical models of C loss from arid and semiarid ecosystems improve when they take into account the effects of photodegradation on litter decomposition (Adair et al. 2017). Still, we have little understanding of how the complexity of semiarid ecosystems, in terms of spatial heterogeneity of vegetation and precipitation seasonality, contributes to the importance of sunlight effects for C cycling at the ecosystem scale. For example, a major proportion of aboveground litter in many semiarid ecosystems is in standing dead position, which can be exposed to higher doses of solar radiation than litter laying on the soil surface that can be buried by soil particles, or shaded by vegetative cover (Austin 2011; Frouz et al. 2011; Wang et al. 2017a). At the same time, surface SOM in non-vegetated patches can be exposed directly to sunlight or may be influenced indirectly by sunlight when covered by plant litter. Adding to this complexity, sunlight has different roles for decomposition in dry and wet seasons (Berenstecher et al. 2020). Taken together, sunlight could play a key role controlling C loss from different C pools, although only a few studies have evaluated sunlight effects on standing litter (Almagro et al. 2015, 2017; Angst et al. 2017; Liu et al. 2015), and even fewer on soil C (Foereid et al. 2018; Mayer et al. 2012; Méndez et al. 2019; Rutledge et al. 2010).

The major aim of this study is to assess the role of summer sunlight on litter and soil C turnover on an annual scale in a Mediterranean-type climate woodland in Patagonia, Argentina. We hypothesized that summer sunlight would accelerate C loss from standing litter and soil due to direct exposure during summer itself, and also in the following wet winter season due to carryover effects of summer exposure on litter and SOM chemistry. In addition, we hypothesized that the response to sunlight would differ between standing litter and soil due to their differences in the amount and quality of organic matter, and its degree of exposure to sunlight. Thus, the heterogeneous distribution of vegetation, with vegetated and non-vegetated patches, would modulate the effect of sunlight on carbon turnover in this semiarid ecosystem. In order to incorporate spatial heterogeneity of vegetation in our design, we manipulated sunlight interception of litter at the ecosystem scale (in 1 m² plots) during the dry summer season for two years. We evaluated summer sunlight effects on standing litter of dominant grass and shrubs, and on bare and litter-covered soil surfaces seasonally over two years.

**Materials and methods**

**Study site**

Our study was conducted in the Meliquina Valley (40° 26´S 71° 13´W), 40 km south from San Martín de los Andes, in the Neuquén province, Argentina (Hess and Austin 2014; Araujo and Austin 2015; Berenstecher et al. 2017, 2020). This woodland is characterized by a spatially heterogeneous distribution of trees, shrubs, and grasses in a matrix of bare soil, which generates conditions of C pools exposed to different environmental conditions over the year (Araujo and Austin 2020). Moreover, solar irradiance varies seasonally, with maximum irradiance during the dry summer season with clear skies, and minimum in the wet winter, when cloudy and rainy days prevail. Due to the asynchrony between temperatures and rainfall, and the marked water deficit that occurs during the summer, this ecosystem is classified as semi-arid in spite of the relatively high mean annual precipitation (Paruelo et al. 1998; Berenstecher et al. 2020). As such, this study site turned out to be particularly interesting to study the importance of seasonality and spatial heterogeneity modulating controls on C turnover.
The study site is located at an elevation of 906 m and corresponds to a semi-arid ecosystem with Mediterranean-type climate. Average annual temperature is 8.9 °C, with minimum average of -0.9 °C in winter and maximum average of 23 °C in summer (AIC). Average annual rainfall is 1100 mm, where more than 70% occurs during autumn and winter with long dry periods in summer. As such, two different seasons can be distinguished: a dry summer season, from December to April, and a wet winter season, from May to November. During the two years of the experiment, the precipitation was 983 mm (2014–2015) and 685 mm (2015–2016), of which 95% and 80% occurred in the wet winter season in the first and second years, respectively [Autoridad Interjurisdiccional de las Cuencas (AIC), 2014, 2015, 2016, Fig. S1]. Soil are Molisols derived from volcanic ash modified by transport and mixing with river sands and silts (Etchevehere and Dimitri 1972). The site corresponds to the transition between the Andean-Patagonian forest and the gramineous-shrub steppe. Natural vegetation is a semi-arid woodland of Nothofagus antarctica (G. Forst.) Oerst, in some cases associated with Schinus patagonicus, with a shrub–grass understory dominated by Mulinum spinosum Pers. and perennial grasses of Pappostipa spp. (Trin. & Rupr.) (Hess and Austin 2014, 2017; Araujo and Austin 2015). 28% of the soil is uncovered, as non-vegetated patches, while 10% is covered by grasses, 29%, by shrubs, and 33%, by detritus, and scattered individual trees (Araujo 2014). We installed the experiment in an area of shrub-grass steppe.

Experimental design

We conducted a field experiment where we manipulated sunlight in 1 m² plots during the dry summer season (Fig. 1a). We delimited ten plots distributed in pairs in five blocks and assigned sunlight treatments randomly to each plot of the pair. We used plastic filters to achieve two different sunlight conditions: (1) reduced summer sunlight (SS-), with a filter that attenuates all wavelengths below 550 nm (UV-B, UV-A, and part of the visible spectrum, Rosco E-Color 135 Deep Golden Amber, Austin and Ballaré 2010), and (2) full summer sunlight (SS+), with a filter that transmits 95% of solar radiation (agroethylene, 80 μm thick, Agropol). Filter transmittances were measured with a UV–VIS spectrophotometer (Shimadzu Scientific Instruments, Fig. S2). Filters were held above the ground using aluminum poles with east–west orientation to ensure that all receive solar radiation at the same angle and approximately 50 cm from the ground over 1.2×1.2 m plots. We selected plots that were similar in terms of vegetation cover and floristic composition, so that each plot had bare soil (non-vegetated patches) and plants of Pappostipa spp., the dominant grass genus at the site (vegetated patches). To simulate a standing dead shrub in the plot, we concentrated plant litter of M. spinosum into a ball (20 cm diameter) and placed it on bare soil (+litter). Thus, there were two microsites in non-vegetated patches of each plot: without (-litter) and with shrub litter (+litter).

We placed the filters at the beginning of the dry summer (December 2014, 2015) and withdrew them at the beginning of the wet winter (May 2015, 2016) for two consecutive years (Fig. 1b). We defined the beginning and the end of the dry and wet seasons (May and December) using records of rainfall in the area for the last 18 years (AIC). We removed the filters at the end of the dry summer season, when solar irradiance began to decrease and rainfall increased, to allow water to enter the plots. Therefore, during wet winter season all plots were exposed to full sunlight. In this way, we evaluated the effect of dry summer sunlight without blocking rainfall in the wet winter season, when water availability is key regulating biological processes (Berenstecher et al. 2020).

Under the filters, we installed a decomposition experiment to estimate standing dead litter decomposition and the importance of sunlight exposure in this process. Pappostipa spp. and M. spinosum, the grass and shrub dominant species, are characterized by having a large proportion of their dead biomass standing, attached to the original plant. To simulate that natural standing dead position, we placed four litterbags of each species in each plot (n=5) suspended in the air hanging from an iron pole (Fig. 1c). We designed specific litterbags for each plant species to capture the natural conditions of the standing dead position and uniform exposure to sunlight. Because of this, the shape and size, as well as the mass inside them, differed between grass and shrub litterbags (1.50 g of Pappostipa spp. or 1.00 g of M. spinosum litter, Fig. 1c). Litterbags were constructed with a combination of 5 mm mesh on the more exposed side (upper and pointing north-facing side), that allowed sunlight...
Fig. 1 Sunlight manipulation during the dry summer season of two consecutive years impacts carbon turnover. **a** Photo of solar attenuation filters in the field resulted in two sunlight treatments: reduced summer sunlight (SS-, orange filter that attenuated wavelengths < 550 nm, Rosco E-Color 135 Deep Golden Amber) and full summer sunlight (SS+, transparent filter that transmits 95% of solar radiation, agroethylene 80 μm thick, Agropol). **b** Graphical representation depicting the experimental design of the study. Orange and gray lines represent the sunlight treatments: reduced (SS-, orange) and full (SS+, gray) sunlight. We suspended the attenuation filters during the dry seasons (solid line) and removed them during the wet winters (dotted line). We incorporated the spatial heterogeneity of vegetation in the experimental design by hanging litterbags of grasses and shrub, and artificially generating two different soil microsites in each plot: without (-litter) and with shrub litter (+litter). Green and brown arrows indicate litterbag collection and soil sampling, respectively. Photo of **c** suspended litterbags containing *Pappostipa* spp. and *Mulinum spinosum* litter simulating a natural standing dead position. During the dry seasons, litterbags were under the filters and during wet seasons were exposed to ambient conditions of temperature and precipitation.
exposure, and 2 mm mesh in the bottom side, that avoided litter loss not due to decomposition. We had collected litter at the study site during the fall (May 2014) when plant litter was recently senesced. We collected tussocks of *Pappostipa* spp. and branches of *M. spinosum* with clippers. All collected material was dried at room temperature. In the laboratory, yellow (recently senescent) material was separated from the green and gray material that was discarded. We selected only entire and undamaged leaves in order to homogenize initial litter conditions. This litter represented the youngest cohort of dead plant material, which allowed to assess decomposition from the first stages of senescence. In this Patagonian woodland, we previously demonstrated that the dry summer is the season when sunlight dominates litter decomposition (Berenstecher et al. 2020). Thus, in order to evaluate summer sunlight at the ecosystem scale and its legacy in the following wet season we started the experiment at the beginning of the dry season in December 2014.

**Litterbag collection and soil sampling**

In May (end of the dry summer season) and December (end of the wet winter season) of two consecutive years, we collected one litterbag of each species of each plot (Fig. 1b). Also, in May and December of the second year of the experiment, we took soil samples (0–5 cm) in two microsites (-litter and +litter) of each plot. This depth (0–5 cm) allowed us to evaluate possible effects on soil mediated by the effects of sunlight on litter quality and litter leachates, because most of the aboveground litter C remains in the 0–5 cm mineral soil layer (Cotrufo et al. 2015). We kept litterbags and soil samples refrigerated until processing in the laboratory at the Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura (IFEVACONICET), Faculty of Agronomy, Buenos Aires. On the same sampling dates, we measured solar irradiance (PAR, UV-B and UV-A) under the filters at noon and temperature at the ground surface and at depth (0–10 cm) (Table S1). Solar radiation was measured with a radiometer (Skye SpectroSence2+), soil surface temperature with an infrared thermometer (Fluke 63 IR Thermometer), and soil temperature at 10 cm with a digital thermometer (9841 model, Taylor Precision Products, Illinois, USA).

**Litterbag and soil processing**

Once in the laboratory, we determined ash-free dry mass loss and potential β-glucosidase activity in litter from each collection date, and saccharification in litter of the second and third litterbag collection. β-glucosidase is an extracellular microbial enzyme involved in the degradation of labile C (hydrolyzes cellobiose into glucose) and can be used as an indicator of the microbial demand for C (Sinsabaugh et al. 1999, 2008). The saccharification assay measures the potential amount of C compounds accessible to commercial microbial cellulase enzyme and informs about litter quality (Miller 1959; Selig et al. 2008; Austin et al. 2016; Méndez et al. 2019). Together, β-glucosidase activity and saccharification allow us to evaluate the mechanisms involved in the acceleration of biotic decomposition due to exposure to sunlight (photofacilitation).

We opened litterbags, removed foreign debris (soil, volcanic ashes, plant material of other species, etc.) from the litter, and weighed it. We kept a 100 mg subsample of fresh litter to determine potential activity of the microbial enzyme 1–4-β-glucosidase (see details of the assay in the following section). We dried the remaining litter in a 60 °C oven for 48 h to determine water content and calculate dry mass loss. Then, we ground the litter and placed a 200 mg subsample in a muffle furnace at 500 °C for 4 h to estimate ash-free dry mass (Harmon et al. 1999). We also determined water content and ash-free dry mass of the initial litter in three subsamples of each species to calculate dry mass loss (see *Calculation and statistical analyses*). A 50 mg subsample of dry and ground litter of the second and third litterbag collection was used to determine saccharification.

We processed soil samples to determine gravimetric water content, organic matter, potential soil respiration, microbial biomass, extracellular organic carbon and potential extracellular enzyme activity (β-glucosidase, phenol-oxidase and phosphatase). Extracellular organic carbon (EOC) represents the most labile fraction of SOM. EOC is used as a measure of available C to microorganisms and is closely related to their activity and growth (Hofman and Dušek 2003). β-glucosidase and phenol-oxidase are involved in the degradation of labile and recalcitrant C, respectively, and phosphatase is involved in phosphorus mineralization (Sinsabaugh et al. 2009).
Methods to measure potential respiration, microbial biomass, EOC, and potential extracellular enzyme activity have been adapted in our laboratory to the study site (Gonzalez-Polo and Austin 2009; Méndez et al. 2019). We determined the gravimetric water content sieving soil using a 2-mm sieve, and placed 10 g of soil in an oven at 105 °C for 48 h. For determination of SOM content, we ground a 400 mg subsample and combusted it in a muffle furnace at 450 °C for 4 h (Harmon et al. 1999).

Laboratory analyses

We determined potential litter activity of the enzyme 1–4-β-glucosidase mixing 100 mg of fresh litter with 7.5 ml of 50 mM sodium acetate buffer (pH 5.5) and shaking for 2 min in an orbital shaker (Sinsabaugh et al. 1999). We used 1 ml of the litter homogenate to incubate with 1 ml of 10 mM substrate (4-Nitrophenyl b-D glucopyranoside, N7006, Sigma-Aldrich) in constant agitation for 2 h at ambient temperature (24 °C). Sample controls consist of 1 ml of the homogenate with 1 ml buffer and substrate controls contained 1 ml buffer and 1 ml of substrate. At the end of the incubation, we added 0.2 ml NaOH (1 N) for color development and measured absorbance at 410 nm with SP1105 spectrophotometer (Spectronic Instruments, VWR, Boston, MA, USA). We measured saccharification by the analysis of the activity of a cellulase enzyme (from Trichoderma spp. C1794, Sigma-Aldrich), which degrades accessible cellulose (Dubois et al. 1956; Ghose 1987; Chen and Dixon 2007; Austin et al. 2016). 50 mg of ground litter were incubated with 50 U/ml enzyme in 10 ml of pH 5.5 acetate buffer 50 mM and 0.2 ml of toluene. Samples were incubated at 50 °C in constant agitation for 72 h. The product (glucose) was quantified using the dinitrosalicylic acid method (Breuil and Saddler 1985), and absorbance was measured at 575 nm.

We measured potential soil respiration as carbon dioxide (CO2) production in closed incubation jars with NaOH solution traps for 12 days (Robertson et al. 1999). We weighed 30 g of fresh soil in 0.5 l glass jars (diameter 8 cm) with 0.3 M NaOH traps. We added distilled water to obtain 60% of field water-holding capacity and incubated the soils at 23 °C for a total of 12 days. Vials were replaced and analyzed at 4, 8, and 12 days. Empty jars with NaOH traps were also included as part of the incubation for controls. Carbonates in NaOH traps were determined through double end point titration with 0.1 M HCl.

We determined soil microbial biomass C and EOC by the chloroform fumigation-extraction method (Vance et al. 1987). We fumigated 40 g of fresh soil with chloroform for 24 h, and extracted labile C by shaking the samples with 0.5 M K2SO4 solution for 1 h and filtering. We determined total microbial biomass C by digestion with K2S2O8 and then titrated double end point method using 0.025 M HCl with a titrator. We calculated microbial biomass values as the difference between fumigated and unfumigated extractable C concentrations corrected for extraction efficiency, using a standard k constant of 0.45 (Jenkinson et al. 2004). EOC was determined as the unfumigated extractable C concentration corrected for extraction efficiency. For potential soil extracellular enzyme activity determination, we sieved soil samples through a 2 mm mesh and mixed 5 g of soil with 25 ml of distilled water and agitated for 2 min. We transfer 1 ml aliquot to incubation tubes and combined with 1 ml of 5 mM substrate prepared with acetate buffer. We used the same substrate as for litter for β-glucosidase, 3,4-dihydroxy-L-phenylalanine (D9628, Sigma-Aldrich) for phenol-oxidase, and 4-nitrophenyl phosphate (N2765, Sigma-Aldrich) for phosphatase. Incubation and measurements of supernatant were identical to litter (described above), with the exception that for phenol-oxidase we did not add NaOH and absorbance was read at 460 nm.

Calculation and statistical analyses

We calculated the decomposition rate (k) for each sunlight treatment and litter species using a simple exponential model by regressing the log of the fraction of mass remaining against time: ln (Mt/M0) = -kt, where M0 is initial ash-free dry mass and Mt is ash-free dry mass at the time t, and decomposition rate k is the slope (Swift et al. 1979). We analyzed data using the analysis of variance (ANOVA) of one or two factors. Mass remaining and saccharification were analyzed with ANOVAs of one factor: sunlight. Decomposition rate and litter β-glucosidase potential activity were analyzed with two-way ANOVAs in a split plot design, with sunlight and litter type for decomposition rate, and sunlight and time for β-glucosidase potential activity. Sunlight was applied at the level of the main plot and litter species or time.
were applied at subplot level. Litterbags were considered different experimental units. Soil variables were analyzed with two-way ANOVA in a split plot design: sunlight and microsite, where sunlight was applied at the level of the main plot and microsite was applied at subplot level. When interactions were significant, we made posteriori comparisons with the Tukey test. We transformed data in cases where the assumptions of homogeneity of variances were not met. We performed data analyses using Infostat version 2009 (National University of Córdoba, Statistics and Design, Córdoba, Argentina Di Rienzo et al. 2003).

**Results**

Decomposition rates of standing dead plant material were significantly higher when litter was exposed to full sunlight (SS+) during the dry summer seasons for both plant species ($p<0.0001$, Fig. 2a). Decomposition rates ($k$) were 39% and 19% higher under full (SS+) than reduced summer sunlight (SS-), for the grass (*Pappostipa* spp.) and the shrub (*M. spinosum*), respectively. Plant species also had a significant effect on decomposition rate ($p<0.0001$). Shrub decomposition rate was approximately twice that of grass. Litter mass loss of standing litter was faster when it was exposed to summer sunlight, although the timing of this effect differed between plant species. For *Pappostipa* spp. litter, a marginally significant ($p=0.06$) effect of summer sunlight was observed from the first harvest at the end of the dry season (Fig. 2b). This effect was larger at the end of the wet season, after one year ($p=0.003$), with 110% higher organic matter loss of standing litter under full (SS+) than reduced summer sunlight (SS-). In contrast, summer sunlight effects on *M. spinosum* litter were observed later, after one year and a half of incubation, at the end of the second dry season ($p=0.001$, Fig. 2c), when organic matter loss was 112% higher under total (SS+) than reduced sunlight (SS-).

Summer sunlight effects on litter β-glucosidase activity and saccharification differed between plant species (Fig. 3). Potential β-glucosidase activity in *Pappostipa* spp. litter was higher when it was exposed to full sunlight (SS+) in the dry season ($p=0.026$) over the two years of the experiment (SS x T $p=0.78$, Fig. 3a). Furthermore, saccharification was 56% higher in *Pappostipa* spp. litter under full sunlight (SS+) but only at the end of the second dry season ($p=0.0047$). In contrast, summer sunlight did not have effects on *M. spinosum* litter β-glucosidase activity and saccharification.
Fig. 3. β-glucosidase potential enzyme activity (lines), and saccharification (bars) of a Pappostipa spp. and b Mulinum spinosum standing litter for a two-year field experiment under reduced (SS-, gray symbols and bars) and full summer sunlight (SS+, white symbols and bars). Gray lines on the x-axis shows seasons over time: dry season (solid line) and wet season (dotted line). Note that left y-axis scale differs among species. Means ± SE are shown (n = 3–5). Statistical results are for significant differences for a one-way (for saccharification) or two-way (for β-glucosidase activity) ANOVA: * p < 0.05, ** p < 0.01, **** p < 0.0001.

(Fig. 3b). In addition, β-glucosidase in M. spinosum litter activity was almost an order of magnitude higher than that of Pappostipa spp. since the second sampling date.

Potential activity of microbial enzymes in surface soil was significantly higher when soil was exposed to full summer sunlight (Fig. 4). At the end of the dry summer, potential enzymatic activity was 33–45%
greater in soil exposed to full summer sunlight (SS+) for the three enzymes evaluated, β-glucosidase ($p=0.026$, Fig. 4a), phosphatase ($p=0.032$, Fig. 4e), and phenol-oxidase (Fig. 4c). Although in the latter, the sunlight effect depended on microsite (SS x M $p=0.035$). Soil phosphatase potential activity was also higher in the full summer sunlight (SS+) at the end of the wet winter ($p=0.003$, Fig. 4f). Potential enzyme activity in the soil also varied by microsite. The microsite without litter addition (-litter) had significantly lower soil enzymatic activity than soil with litter (+litter) for most of the studied enzymes at the end of dry summer and wet winter, except for phosphatase activity that was significant only at the end of the dry summer ($p=0.005$, Fig. 4e).

Summer sunlight also had effects on soil extracellular organic C but did not modify significantly soil microbial biomass or potential respiration (Fig. 5). Soil extracellular organic C was 50% lower in soil exposed to full (SS+) than reduced (SS-) summer sunlight at the end of the dry summer in both microsites ($p=0.011$) and was higher in microsites without (litter-) than in microsites with litter (litter+) addition ($p=0.036$, Fig. 5a). These levels of soil EOC decreased to a third at the end of the wet winter season (Fig. 5a, b), while soil microbial biomass increased 65% at the end of the wet winter in both microsites (Fig. 5c, d). There were no significant differences between sunlight treatments in potential soil respiration at the end of the dry summer season ($p=0.327$, Fig. 5e).
Discussion

In this study, we evaluated the role of summer sunlight on litter and soil C turnover at an annual scale in a spatially heterogeneous Mediterranean-type climate woodland in Patagonia, Argentina. We originally hypothesized that summer sunlight would accelerate C loss from standing litter and soil due to direct exposure during summer itself, and in the following wet winter season due to carryover effects of summer exposure on litter and SOM chemistry. Additionally, we hypothesized that the response to sunlight would differ between standing litter and soil due to the differences between these pools. Our results support these hypotheses in that summer sunlight exposure significantly increased standing litter decomposition for both shrub and grass litter, reduced soil labile organic C, and increased soil potential extracellular enzyme activity. However, in contrast with the original hypotheses, the legacy effects during the wet winter season were only seen in grass litter, and not in shrub and soil C pools. In addition, summer sunlight effects on soil were similar in both microsites, with and without plant litter, while differences between soil microsites became more evident during the wet winter. Taken together, our results demonstrate that summer sunlight is an important and lasting control of C turnover in this semiarid Patagonian woodland, and that the heterogeneous distribution of vegetation modulates these observed sunlight effects.

Dry summer sunlight and its legacies on standing litter decay of shrubs and grasses

Summer sunlight exposure accelerated decomposition of plant litter and an appreciable part of C from standing litter was lost due to summer sunlight exposure for both grass (Pappostipa spp.) and shrub (M. spinosum) litter (Fig. 2). Standing litter decomposition in our study was similar to values reported in other Mediterranean ecosystems (Almagro et al. 2015, 2017; Lin and King 2014) but slower than those shown in other ecosystems that do not have an extended dry summer season (Deshmukh 1985; Erdenebileg et al. 2018; Liu et al. 2015; Wang et al. 2017a), suggesting that precipitation seasonality could also be an important modulator of standing litter decay (Berenstecher et al. 2020). The importance of the standing dead position on litter decomposition is beginning to be appreciated beyond aquatic macrophyte vegetation (e.g., Kuehn et al. 2004; Newell et al. 1989) and these studies in general demonstrate rates of organic mass loss from litter that can be similar or greater than rates of litter decay on the soil surface (Liu et al. 2015; Wang et al. 2017a), or somewhat lower (Almagro et al. 2015, 2017; Deshmukh 1985). Our results for standing litter decomposition were on par with litter decomposition on the soil surface demonstrated in other studies in the same site (Araujo and Austin 2015; Berenstecher et al. 2020; Méndez et al. 2019). This suggests that C loss from standing litter is important, due to a significant proportion of the aboveground biomass may remain as standing dead for long periods of time (Araujo and Austin 2020).

Summer sunlight significantly increased decay by 39% and 19% in grass and shrub litter, respectively. Interestingly, rates of decay are similar to that found in other studies that evaluated sunlight effects on standing dead decomposition throughout the entire year (Almagro et al. 2015, 2017; Erdenebileg et al. 2018; Henry et al. 2008; Lin and King 2014). Additionally, these values are higher than those reported in a meta-analysis, where on average UV increased decomposition rate by 11% (Wang et al. 2015). This comparison may be somewhat imbalanced, however, since the vast majority of the reported studies only evaluated the effects of UV radiation. In addition, our findings are in the upper limit of the estimations based on soil surface litter decay for dryland modeling, where photodegradation increased litter decay between 6–15% per year (Adair et al. 2017). This suggests that maximum solar radiation exposure may occur in standing rather than surface litter, thereby influencing in situ photodegradation (Pan et al. 2015). In our experiment, we placed litterbags imitating as much as possible a standing dead position, in vertical position and at the same height as extant vegetation and standing litter (Fig. 1c). We believed this to simulated realistic conditions of standing litter, although not directly attached to the plant meristems. These results demonstrate the importance of position that modulates the effect of sunlight accelerating C release from litter in semiarid ecosystems (Austin 2011; Pan et al. 2015; Berenstecher et al. 2021).

The acceleration of decomposition of standing dead litter due to sunlight exposure occurred directly, due to the photochemical mineralization of litter organic matter, and through carryover effects
in the subsequent wet season, as we hypothesized. During the first year, sunlight increased grass litter decay by 112%, although only 18% of this increase occurred in the dry season and 94% in the wet season, when sunlight was not manipulated. Additionally, dry summer sunlight increased the amount of accessible labile carbohydrates and enzyme activity in grass litter (Fig. 3a), suggesting that summer photodegradation enhanced subsequent biotic degradation due to the increase of plant litter carbohydrates for microbial enzymes (Austin et al. 2016). Alternately, labile carbohydrates could also be lost through litter leaching when the wet season starts (Berenstecher et al. 2020; Day et al. 2022). These results imply that a considerable fraction of litter C is lost from the ecosystem to the atmosphere, directly and indirectly, due to sunlight exposure before the litter reaches the soil surface, and without incorporation into SOM pools (Austin and Vivanco 2006; Méndez et al. 2019; Berenstecher et al. 2020).

Summer sunlight had differential carryover effects on standing dead litter decay in grass and shrubs, suggesting an important context for the interaction of litter quality and sunlight exposure. For grass litter, effects of sunlight exposure were evident in the subsequent wet season (Fig. 2b), while summer sunlight effects on shrub standing litter decay were clear only after the second dry summer season (Fig. 2c). This is consistent with the assertion that the impact of sunlight exposure accelerating litter decay may be greater in more advanced stages of decomposition (Adair et al. 2017; Day et al. 2015; Liu et al. 2015). This may be due to the fact that over time many of the most soluble and labile compounds have been lost from the litter (Coutéaux et al. 1998), and the impact of lignin degradation due to sunlight exposure becomes more important (Day et al. 2018). In contrast, sunlight had no discernible effects on available carbohydrates in shrub litter, which was consistent with another study for the same litter type decomposing on the soil surface (Berenstecher et al. 2020). These results highlight the importance of species identity modulating sunlight effect on litter C turnover in semiarid ecosystems. Pappostipa spp. has higher specific leaf area and less total polyphenols and sunscreens compounds than M. spinosum (Austin et al. 2016), which suggests that more surface exposed and less protection from sunlight could explain the greater response of the grass to sunlight exposure. However, the complexity of litter quality, morphology and position of dominant life forms clearly deserves more attention when assessing the impact of solar radiation on C turnover in semi-arid ecosystems.

Manipulating sunlight as we did in field conditions presents some limitations that are important to consider. The filters we used to generate different levels of sunlight, common to many photodegradation studies (e.g. Austin and Vivanco 2006; Berenstecher et al. 2020; Brandt et al. 2010; Day et al. 2015, 2018), may modify rain interception, dew, and temperature, all of which could directly alter environmental conditions or interact with the effects of sunlight exposure. Our design is advantageous in that the way these methodological artefacts only occurred during the dry season, when biota plays a relatively minor role in decomposition (Berenstecher et al. 2020), compared to other experimental approaches that may maintain filters throughout rainy and dry seasons. However, we acknowledge that, even during the dry season, small amounts of rain could have been excluded by the filters, although this reduction is equal in both light treatments. It is also clear that reducing incident solar radiation inevitably implies a decrease in temperature (Table S1), which could have affected carbon turnover in the experiment in two ways: through changes in thermal degradation (abiotic degradation induced by high temperatures) of organic matter, and/or accelerating (or reducing) biotic decomposition, which could presumably interfere with the quantification of the indirect effects of sunlight on C turnover. However, thermal emission from direct degradation appeared to represent a very minor pathway of C loss from litter in this range of temperature (Day et al. 2019) and temperature does not alter saccharification or lignin in sunlight-exposed litter (Mendez et al. 2022). Taken together, this suggests that temperature differences between light treatments may not contribute to large differences in observed C losses. Nevertheless, due to the experimental challenges that the manipulative experiments of photodegradation implies, future studies should be focused on understanding how these possible artefacts and potential interactions could affect the measured effects of sunlight on C turnover in terrestrial ecosystems.
Dry summer sunlight effects on surface soil C pools in a Patagonian woodland

The intrinsic spatial heterogeneity of vegetation in this site (Araujo and Austin 2020; Hess and Austin 2014, 2017), and semi-arid ecosystems in general (Austin et al. 2004; Schlesinger et al. 1996), where soil C and nutrients is distributed unevenly in vegetated and non-vegetated patches, present additional challenges for evaluating the impact of summer sunlight on C turnover of soil surface pools. In addition to the spatial discontinuity in this woodland ecosystem, soil has much less organic matter susceptible to being photodegraded (<4% on average for this site, Table 1) than litter (>90% for grass and shrub litter, Berenstecher et al. 2020). At the same time, a proportion of the SOM is found at depth, where light is unlikely to penetrate. In addition, SOM is usually protected from decomposition by mechanisms such as aggregate occlusion and organo-mineral bonds (Dungait et al. 2012; Six et al. 2002) that could also protect it from degradation due to exposure to sunlight. While previous studies have shown increased C release due to direct solar radiation exposure in peatlands (Foereid et al. 2018; Rutledge et al. 2010), a consistent pattern has not emerged in semi-arid ecosystems, with sunlight exposure having no effect (Wang et al. 2015) or a negative impact on labile soil C pools (Méndez et al. 2019).

We found significant effects of summer sunlight on soil labile C in microsites with and without plant litter addition. Sunlight exposure increased soil potential enzyme activity (Fig. 4a, c, e) and decreased soil labile C (Fig. 5a) in both microsites. This mirrors the acceleration of C turnover observed in peatlands (Foereid et al. 2018; Rutledge et al. 2010) but there is almost no evidence of this acceleration on soil labile C in semiarid ecosystems. In fact, some studies suggest the opposite, that microbial activity may be stimulated under conditions of sunlight attenuation (Méndez et al. 2019). Rutledge et al. (2010) estimated, using eddy covariance, that photodegradation contributed almost 60% of the dry season CO₂ flux from a seasonally dry grassland in California, but the source of this flux remains unresolved, and likely involves both litter and soil C release. Soil labile C could be lost directly due to photochemical mineralization of SOM. In addition, photodegraded SOM could also be more easily degraded by microorganisms, similar to the observed increase in labile carbohydrates in sun-exposed litter (Austin and Ballaré 2010; Austin et al. 2016; Berenstecher et al. 2020; Méndez et al. 2019) or litter dissolved organic C, as other studies have found (Day et al. 2018; Wang et al. 2017b). Sunlight effects on the most labile fraction of soil C and soil enzyme activity suggest that summer sunlight can influence C turnover in soil surface directly and indirectly in this ecosystem, supporting our hypothesis of sunlight effects on SOM.

It is well documented that a large pulse of CO₂ often results from the first rainfall after the dry summer in many Mediterranean-type climate ecosystems (e.g. Almagro et al. 2009; Austin et al. 2004; Barnard et al. 2020; López-Ballesteros et al. 2016; Placella et al. 2012), although the mechanism behind these pulses is still a matter of debate. It is reasonable to postulate that during the dry summer season, labile carbohydrates could accumulate in the soil due to

| Table 1 Soil characteristics during the second year of the experiment under reduced (SS-) and full (SS+) summer sunlight, in two microsites: without (-litter) and with Malinum spinosum (shrub) litter (+litter), at two sampling dates (at the end of the dry summer and wet winter season). Water content (%. g H₂O/g dry soil) and organic matter (%. g organic matter/g dry soil) in surface soil (0–5 cm; means ± SE, n = 5). Different letters indicate significant differences between microsite and seasonal transition | -litter | + litter |
|---|---|---|
| **End of dry summer** | | |
| water content (%) | 29.0 ± 1.3b | 28.0 ± 0.4b |
| organic matter (%) | 2.49 ± 0.49 | 3.03 ± 0.25 |
| **End of wet winter** | | |
| water content (%) | 2.56 ± 0.46 | 3.24 ± 0.34 |
| organic matter (%) | 4.21 ± 0.3 | 4.84 ± 0.44 |
sunlight exposure, but microbial access and activity would be limited by low soil moisture. Soil microorganisms could respond rapidly to first water pulse, when the wet season begins, with a rapid mineralization of this labile C (Austin et al. 2004; Barnard et al. 2020; Placella et al. 2012). This pattern is consistent with the fortuitous timing of our experiment. We sampled soil two days after removing the filters at the end of the summer season, when there had been a substantial precipitation event in this two-day window (reflected in the soil water content, Table 1). This event could have triggered a burst of microbial activity (Austin et al. 2004; Tang and Baldocchi 2005; Xu and Baldocchi 2004) and leached labile C compounds from surface soil and litter, since the latter are greater in photodegraded litter (Day et al. 2022). In line with this, we found more labile organic C at the end of the dry summer than at the end of the wet winter (Fig. 5a, b), while microbial biomass showed the reverse pattern (Fig. 5c, d). This suggests that microorganisms could respire this labile C, but only when sufficient soil water was available. Taken together, this evidence provides suggestive insight as to the possible mechanism behind the pulsed nature of soil respiration at the beginning of the rainy season.

Carryover effects of summer sunlight on soil were not observed in the wet winter season, suggesting that response to sunlight differs between standing litter and soil, as we hypothesized. Probably, soil processes occur on different time scales, typically slower and with smaller windows of peaks of microbial activity, than litter. In addition, differences between soil microsites with and without plant litter became more evident during the wet winter, hinting that sunlight effects on soil C pools could be counteracted by the presence of vegetation patches. In this context, spatial heterogeneity emerges as a key component of the ecosystem controlling both sunlight exposure and substrate availability for biotic activity in vegetated patches (Gonzalez-Polo and Austin 2009).

Conclusions

We found that exposure to sunlight only during dry summer season had effects on ecosystem-scale C turnover not only in the summer season but over the entire year in this Mediterranean-type climate ecosystem. The acceleration of standing litter decomposition of both grasses and shrubs due to sunlight exposure, implies that a substantial fraction of litter C is lost before reaches soil (Austin and Vivanco 2006; Berenstecher et al. 2020). In addition, the carryover effects of summer sunlight in altering grass litter quality accelerated C turnover in the following wet season, when abundant water favors decomposer organism activity and other physical processes that together determine C turnover (Berenstecher et al. 2020). Surprisingly, this acceleration on grass litter decomposition due to carryover effects was five times greater than sunlight effects during the dry summer season. Our results reinforce the idea that sunlight has a prominent role in C turnover in this Mediterranean-type climate ecosystem (Berenstecher et al. 2020; Méndez et al. 2019), where the asynchrony between rainfall and temperature limits microbial activity during a large part of the year (Almagro et al. 2015, 2017; Berenstecher et al. 2020; Gliksman et al. 2016, 2018; Henry et al. 2008; Rutledge et al. 2010). Future studies should focus on understanding sunlight impacts on C turnover in semiarid ecosystems where rainfall and high temperatures coincide. Our study also provides a new dimension to the role of sunlight on the acceleration of C turnover showing its spatial and temporal range in this Patagonian woodland, highlighting the importance of spatial and temporal heterogeneity modulating how sunlight exposure affects C pools in semiarid ecosystems.

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Authors’ contributions P.B. and A.T.A. conceived the study. All authors performed field experiments. P.B. performed laboratory analyses and analyzed data. All authors interpreted results. P.B. led the writing of the manuscript. All authors commented on and edited versions of the manuscript.

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Data availability  The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

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